Lark Bunting (*Calamospiza melanocorys*): A Technical Conservation Assessment

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COVER PHOTO CREDIT

Lark buntings (*Calamospiza melanocorys*), Pawnee National Grassland, May 2004. Photograph by Doug Backlund. Used with permission.

Summary of Key Components for Conservation of the Lark Bunting

The Global and U.S. National Heritage Programs give the lark bunting (*Calamospiza melanocorys*) a conservation ranking of G5 and N5 respectively, which indicates that the species is widespread and secure. The Canadian National Heritage Program designates the lark bunting as N4, which indicates the species is uncommon but apparently secure with some cause for concern over the longterm (NatureServe 2005). The lark bunting is a Management Indicator Species on the Pawnee National Grassland, which is managed by the Rocky Mountain Region (Region 2) of the USDA Forest Service (USFS). A recent study suggests that lark bunting populations on the Pawnee National Grassland may be declining (Yackel Adams et al. in revision), but the supporting data are not conclusive. Our matrix model suggests that survival of adult lark buntings has the greatest impact on population growth; adult survival rate data are needed in the Pawnee and other areas of its range to validate these estimations.

Within Region 2, the greatest threats to lark buntings include habitat loss and habitat fragmentation due to conversion of native grassland to cropland, urbanization, and oil and gas extraction. The World Wildlife Fund classifies most breeding habitats of lark buntings as critical or endangered, with conversion to cropland being the major cause of habitat loss. While lark buntings will nest in some agricultural fields, activities such as plowing, tilling, discing, mowing, and use of pesticides can be very harmful during the nesting period. Human population growth, particularly along the Front Range of Colorado, will likely put increasing demands on lark bunting habitat over the next several decades as grassland is converted to a suburban environment. Current and future increases in oil and gas extraction will continue to fragment and degrade lark bunting habitat in Wyoming and Colorado, and the impacts of these activities will need to be assessed.

Heavy grazing by cattle in shortgrass prairie can be detrimental to lark buntings as it reduces the cover required for nesting. Conversely, the lack of grazing in some taller grasses limits the number of lark buntings found in that habitat. Management of grasslands involving moderate grazing and prescribed fire to maintain the mosaic habitat typical of native prairie prior to European settlement would benefit the lark bunting as well as other grassland species. Protection of large tracts of land from agricultural development would help to limit habitat fragmentation and potentially lessen the impacts of nest predation and brood parasitism on lark buntings. Most lark bunting habitat is privately owned, a fact that is unlikely to change in the future. Therefore, landowner incentive programs (e.g., Conservation Reserve Program) and partnerships among conservation organizations, government agencies, and landowners will be needed to increase and preserve lark bunting habitat in the future.

On the wintering grounds of the lark bunting, outside of Region 2, potential threats include habitat loss due to urbanization and cropland conversion and habitat degradation in the form of woody species encroachment onto playas. Playas are important areas for feeding and roosting in much of this species' winter range. Little research has examined lark bunting wintering ecology and the threats specific to its conservation. Study of the impacts of habitat modifications on wintering grounds should be a priority for this species.

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INTRODUCTION

This species assessment is one of many being produced to support the Species Conservation Project for the Rocky Mountain Region (Region 2) of the USDA Forest Service (USFS). Region 2 includes 17 national forests and seven national grasslands throughout Colorado, Kansas, Nebraska, South Dakota, and Wyoming. The lark bunting is the focus of an assessment because it is considered a Management Indicator Species (MIS) on the Pawnee National Grassland in north-central Colorado. As a barometer for species viability at the forest level, a MIS serves two functions: 1) to estimate the effects of planning alternatives on fish and wildlife populations (36 CFR 219.19 (a)(1); and 2) to monitor the effects of management activities on species via changes in population trends (36 CFR 219.19 (a)(6)).

This assessment addresses the lark bunting's biology, conservation threats, and management status as it pertains to its range in Region 2. The broad nature of the assessment leads to some constraints on the specificity of the information in some locales. This introduction defines the goal of the assessment, outlines its scope, and describes the process used in its production.

Goal

In response to the National Forest Management Act of 1976, the Species Conservation Project aims to conserve the plant and animal species and the ecosystems in the national forests and grasslands. These species conservation assessments are designed to provide forest and grassland managers, research biologists, and the public with a thorough discussion of the biology, ecology, conservation status, and management of species based on available scientific information. The assessment goals limit the scope of the document to critical summaries of scientific knowledge, discussion of broad implications of that knowledge, and outlines of information needs. In this assessment, we do not develop specific management recommendations for the lark bunting. Rather we provide the ecological background upon which its management can be based and discuss the consequences of changes in the environment that result from management (i.e., management implications). We also review management recommendations proposed elsewhere and the results of those recommendations that have been implemented.

Scope

In this assessment we review the biology, ecology, conservation status, and management of the lark bunting with specific reference to the geographic and ecological characteristics of Region 2. Although some of the referenced literature originates from investigations outside the region, we place that literature into the ecological and social context of the Great Plains of Region 2. Furthermore, we focus on the reproductive behavior and population dynamics under the current environment rather than historical conditions. We consider the evolutionary environment of lark buntings in our assessment but in a current context.

This assessment was developed from refereed literature, non-refereed publications, research reports, data accumulated by resource management agencies, and personal communications with experts. Due to the goals and limited scope of our assessment, not all publications on lark buntings were referenced nor were all published materials considered equally reliable. In this assessment, as in most scientific works, refereed literature is emphasized, and non-refereed publications and reports are regarded with greater skepticism. Unpublished data (e.g., Breeding Bird Survey, Christmas Bird Count) were important in estimating the geographic distribution of this species. These data required special attention due to the diversity of persons and methods used in their collection.

Treatment of Uncertainty

Science represents a rigorous, systematic approach to obtain 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, strong inference, as described by Platt suggests that experiments will produce clean results (Hillborn and Mangel 1997), as may be observed in certain physical sciences. The geologist T. C. Chamberlain (1897) suggested an alternative approach to science where multiple competing hypotheses are confronted with observations and data. Sorting among alternatives may be accomplished using a variety of scientific tools (e.g., experiments, modeling, logical inference). As in geology, it is difficult to conduct critical experiments in ecology, and so ecologists must rely on observations, inference, critical thinking, and models to guide their understanding of the world (Hillborn and Mangel 1997). Confronting uncertainty, then, is not prescriptive. In this assessment, we note the strength of evidence for particular ideas and describe alternative explanations where appropriate.

Publication of Assessment on the World Wide Web

To facilitate use of species assessments in the Species Conservation Project, they are being published on the Region 2 World Wide Web site. The placement of documents on the Web makes them available to agency biologists and the public more rapidly than publishing them as reports. More important, Web publication facilitates the revision of assessments, which will be accomplished based on guidelines established by Region 2.

Peer Review

Assessments developed for the Species Conservation Project have been peer reviewed before release on the Web. This report was reviewed through a process administered by the Society for Conservation Biology, employing 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

The USFS does not list the lark bunting as a sensitive species, nor is it proposed to be listed on the Region 2 list of sensitive species. However, this species is currently identified as a Management Indicator Species on the Pawnee National Grassland. The Global and U.S. National Heritage Programs give the lark bunting a rank of G5 and N5 respectively, which indicates that the species is widespread, abundant, and secure. The Canadian National Heritage Program ranks the lark bunting as N4, which indicates the species is uncommon but not rare, and apparentaly secure. However, there is cause for concern over the longterm due to population declines or other factors (NatureServe 2005). For individual states in Region 2, the lark bunting is given a rank of S5 in Kansas, Nebraska, and South Dakota and S4 in Colorado and Wyoming (NatureServe 2005).

The lark bunting is listed on the U.S. Fish and Wildlife's Birds of Management Concern in the United States (U.S. Fish and Wildlife Service 2002).

Partners in Flight (PIF) aims to conserve the land birds of the western hemisphere through a consortium of non-governmental agencies, state and federal agencies, and industry groups. By focusing attention on species when they are common, PIF hopes to prevent significant declines. Lark buntings are designated as a Stewardship Species by PIF. These are species that have a high percentage of their global population in a single biome (e.g. Prairie). In most regions of North America where they occur, lark buntings are designated by PIF as a species requiring management attention (Northern Rockies, Prairie Potholes, Badlands and Praries, and Shortgrass Prairies). In the Central Mixed Grass Praries they are designated as a species of immediate management concern (Rich et al. 2004).

Lark buntings are listed as a priority species by Colorado PIF, which indicates species most in need of conservation (Colorado PIF 2000). Wyoming PIF designates lark buntings as a Level II Status species, which is a species that is not known to be exhibiting significant population declines but is a priority for monitoring (Nicholoff 2003). The remaining Region 2 states do not have individual PIF plans.

Existing Management and Conservation Strategies

This assessment does not seek to review all federal and state codes, regulations, or management plans regarding the lark bunting. Instead, it reviews significant management recommendations for the species. The Prairie Pothole Joint Venture, a part of the North American Waterfowl Management Plan, synthesized reports on the effects of management practices on grassland birds. The goal of these reports is to stabilize or increase the populations of declining birds and wetland-associated birds in the Prairie Pothole region. Dechant et al. (2003) used the habitat requirements, area requirements, brood parasitism frequencies, and the responses to management to make eight management recommendations for lark buntings:

- ensure that large grassland areas are available during the breeding season
- exercise caution when monitoring nests because mammalian predators may follow human scent to the nests

- avoid burning the nesting habitat if it eliminates all of the brush cover, particularly in shrubsteppe habitats

- delay the mowing of hayfields until after the breeding season to prevent nest destruction

- avoid heavy summer grazing in shortgrass habitats as it reduces nesting cover

- allow heavy grazing of taller grasses (>30 cm) to provide the shorter grassland habitats that lark buntings prefer for nesting

- avoid discing during the breeding season as it destroys nests and implement no-tillage or minimum tillage practices instead of fall cultivation to maintain nesting cover

- use rapidly degrading, low toxicity chemicals in very low application rates for pest management and avoid overgrazing, which makes the habitat more susceptible to pest outbreaks.

In addition to the above recommendations, Wyoming PIF also recommends changes in grazing practices in areas where brown-headed cowbird (*Molothrus ater*) parasitism occurs. They recommend alternating livestock use within 6.5 km of songbird nesting areas between years to give local songbird populations the chance to nest without high parasitism pressure. They also recommend that prescribed burns be conducted in the fall and that they be kept small so that some nesting cover is retained at all times (Nicholoff 2003). Colorado PIF (2000) makes two recommendations for lark bunting management and conservation. The first is that grazing should be light in the summer or heavy in the winter to maintain vegetation height for nesting and successful foraging of lark buntings. Furthermore, shrubs, cacti and other taller vegetation should be retained for nest shading. Secondly, given the importance of grasshoppers and other invertebrates to lark buntings during the breeding season, a system of integrated pest management should be implemented to maintain prey populations.

It is not known how effective these strategies are in management of lark buntings. Due to large fluctuations in local populations, evaluating management practices is difficult, and monitoring is not effective at fine spatial scales. Examination of these recommendations will be discussed in the sections related to potential management of the lark bunting in Region 2.

Biology and Ecology

Systematics and species description

The lark bunting, a passerine endemic to North American grasslands, is the only species within the genus *Calamospiza*. It is a large, stocky sparrow (length: 14-18 cm; Rising 1996) with a short tail and a relatively large, blue-grey bill (Byers et al. 1995). Lark buntings are sexually dimorphic in plumage. Adult females have a gray-brown crown, nape, and upper-parts streaked with black. A buffy supercilium extends from the bill to ear coverts and a pale submoustachial is bordered in dark brown. The female's wings are dark brown with broad, pale buffy edges that form a wing patch. Adult males have two age-related body plumages. In the summer, the male's body plumage is black with white tips on the undertail-coverts and narrow white fringes on upper-tail coverts, back, and scapulars. The wings are black with large, white wing patches. In the winter, the male resembles the female except that the wing patches are brighter buff, the head and back are rustier, and the abdomen feathers are black beneath the light edgings (Baumgarten 1968, Rising 1996). Juveniles resemble the female but are overall more buffy and scaly in appearance (Byers et al. 1995). During the breeding season, males range in mass from 36.1 to 41.3 g, and females range in mass from 35.3 to 39.4 g (Baldwin and Boyd 1973). Lark buntings are often described as gregarious during migration and on their wintering grounds (Shane 2000). During breeding, males have a repertoire of one to a few complex songs that are delivered from perches and with distinctive aerial flights (Stillwell and Stillwell 1955, Ervin 1981).

Distribution

The lark bunting is one of only six passerines endemic to the Great Plains of North America (Mengel 1970). They can be found on grasslands from the southern parts of central Canada through the Great Plains of the central United States and into northern Mexico (**Figure 1**, **Figure 2**).

Breeding range

Shane (2000) recently provided a detailed description of the breeding range for the lark bunting. Here we summarize his description providing updated references where appropriate. The northern expanse of the breeding range extends from southeastern Alberta, southwestern and extreme southeastern Saskatchewan, and extreme southwestern Manitoba. The range extends south through Montana (east of the Rocky

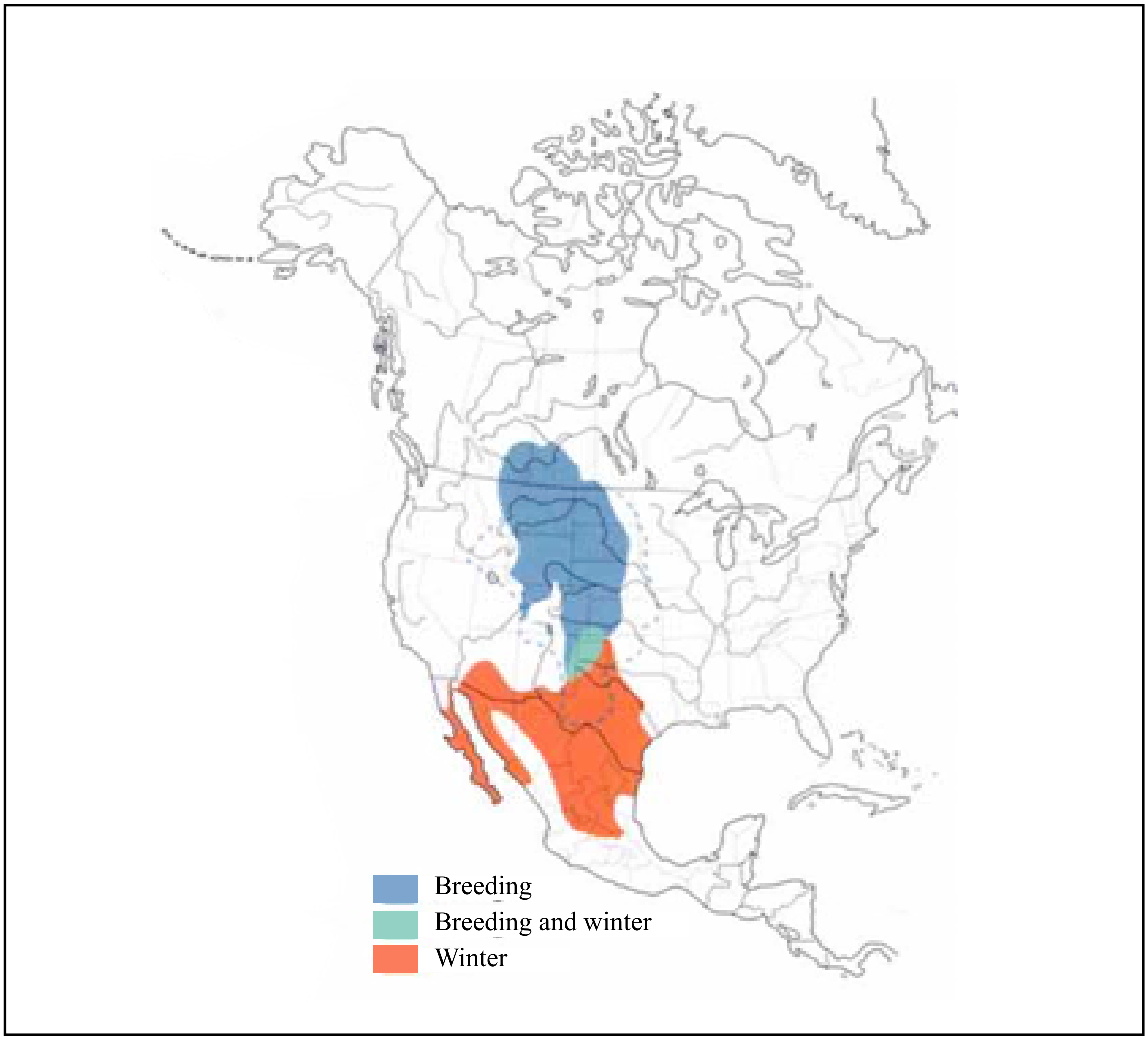

Figure 1. Distribution of the lark bunting (Shane 2000) Retrieved with permission from The Birds of North American Online database: http://bna.birds.cornell.edu/BNA/account/Lark_Bunting/.

Mountains; Lenard et al. 2003), all except some far western parts of Wyoming (**Figure 3**; Dorn and Dorn 1999), all of the western portions of North Dakota and South Dakota (**Figure 4**), western and central Nebraska (Mollhoff 2001), portions of Colorado (**Figure 5**), and western Kansas (Busby and Zimmerman 2001). The southern end of the normal breeding range includes the eastern plains of New Mexico to the Oklahoma Panhandle (Shane 2004) and the northern portion of the Texas Panhandle (Seyffert 2001, Lockwood and Freeman 2004).

Breeding populations have also occurred periodically outside this range in southwestern Minnesota, western Iowa, northwestern Missouri, eastern Kansas, and north-central Oklahoma. In addition, breeding has occurred in west-central and southwestern Texas (Lockwood and Freeman 2004) to northwestern New Mexico. To the west of their normal breeding range, lark buntings have bred in northern Utah, south-central and southeastern Idaho, and southern California (see Shane 2000 and references therein).

Non-breeding range

The current normal wintering grounds for lark buntings (see Shane 2000 and references therein for details) include the areas from extreme southeastern Colorado and extreme southwestern Kansas south through western Oklahoma and the Texas Panhandle (see also Seyffert 2001) south through central Texas to the lower gulf coast and the Rio Grande, southern New Mexico and Arizona and into Mexico. In Mexico, the winter range includes eastern and southern Baja California, the high plains of northern Mexico, and as far south as Hidalgo.

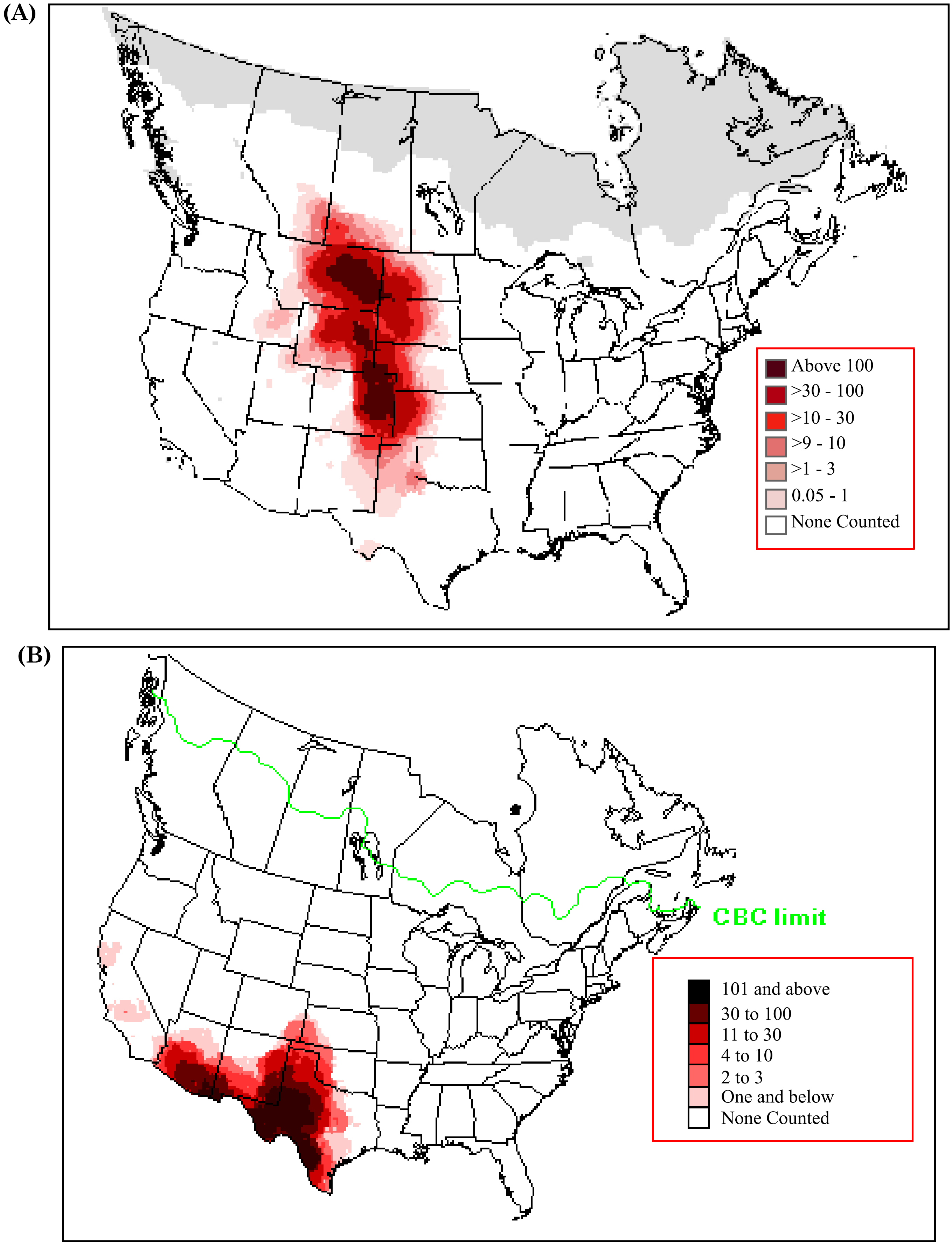

Figure 2. (A) Lark bunting breeding distribution based on Breeding Bird Survey (BBS) data from 1994 to 2003 (Sauer et al. 2004). The average count given predicts the average number of birds that could be observed along roadsides in approximately 2.5 hr. Gray shading indicates areas beyond BBS limit. (B) Relative winter abundance of lark buntings within the United States from Christmas Bird Count data from 1966 to 1989. Numbers of birds per 100 party hours are averaged over the time period for each survey circle (Sauer et al. 1996).

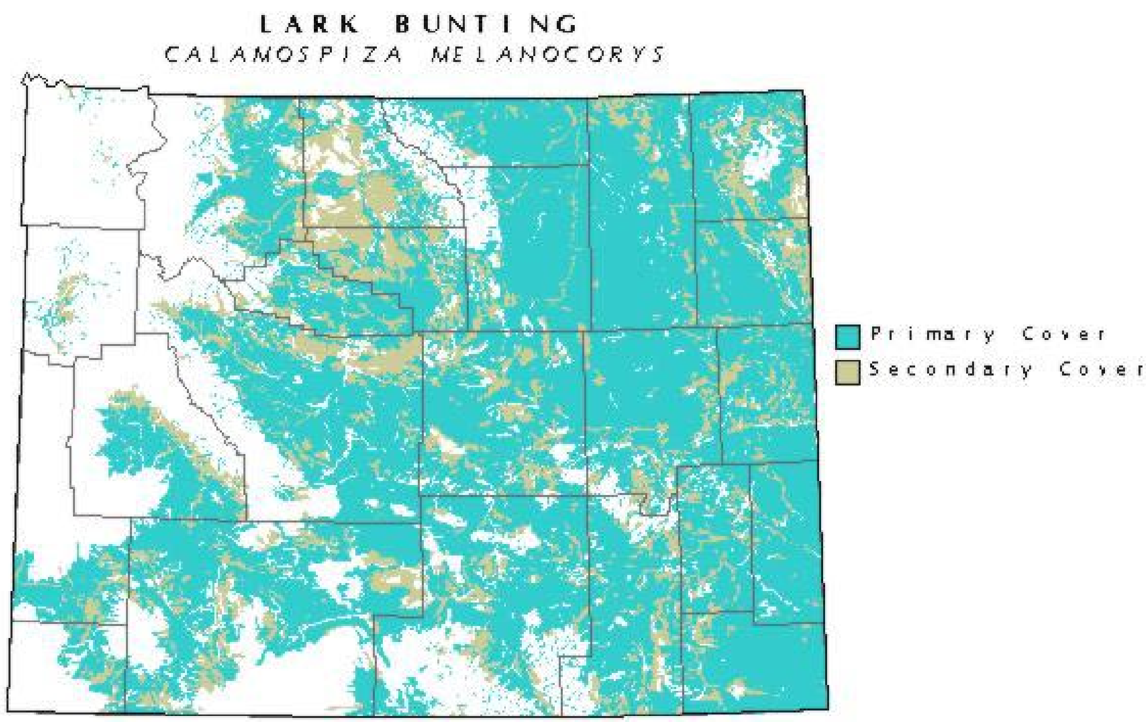

Figure 3. Potential distribution of lark buntings in Wyoming as determined by habitat associations using Wyoming GAP analysis. Primary cover refers to the predicted presence of lark buntings based on land cover occupying the largest proportion of habitat polygons. Secondary cover refers to the species predicted presence based on the land cover occupying the second largest proportion of the polygon area. Source: http://www.sdvc.uwyo.edu/wbn/gap.html.

Historic range

Historical reports indicate that lark buntings periodically nested in western Minnesota (Roberts 1936, Baumgarten 1968). However, Minnesota, Iowa, and Missouri are within the current range of infrequent extralimital breeding for lark buntings, and there is no evidence that these areas were historically part of their regular range although several authors make this reference. Current reports list lark buntings as casual summer residents of Minnesota, with the last reported breeding taking place in 1964 in Rock and Pipestone counties (Janssen 1987).

In the mid-twentieth century, lark bunting wintering grounds extended only as far north as north-central Texas (Shane and Seltman 1995). However, the lark bunting began making rare appearances in the Texas Panhandle (Oberholser 1974). Between 1961 and 1993, lark buntings were recorded by the Friona, Texas Christmas Bird Count (CBC; 11 of 12 counts from 1961 to 1973), the Amarillo, Texas CBC (8 of 18 counts from 1975 to 1993), and the Buffalo Lake National Wildlife Refuge, Texas CBC (12 of 17 counts from 1977 to 1993). The Arnett, Oklahoma CBC first reported lark buntings in 1975 (8 of 18 counts from 1975 to 1993; Shane and Seltman 1995).

Since the mid-1970's, lark buntings have established wintering populations in both Colorado and Kansas. Reports of single wintering lark buntings in Colorado occurred in December 1901, January 1977, February 1977, January 1980, January 1981, November 1989 until January 1990, and January 1993 (reviewed by Shane and Seltman 1995). Regular migration into eastern Colorado and Kansas begins in May, so the flock of 30 lark buntings observed in Larimer County, Colorado on 28 March 1977 (Andrews 1978) may be classified as the first record of a wintering flock. On February 16, 1993, a flock of 250 lark buntings was

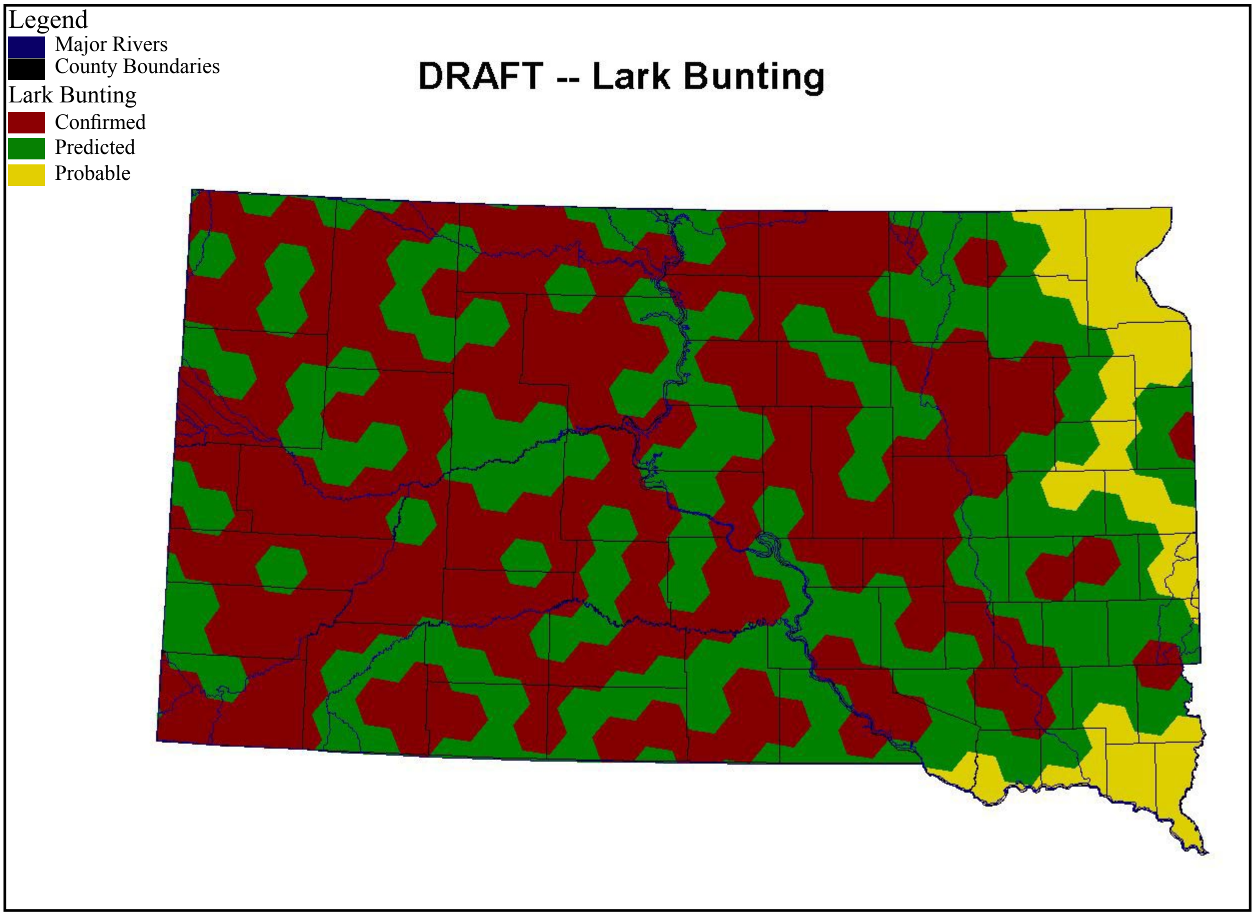

Figure 4. Potential distribution of lark buntings in South Dakota as determined by habitat associations using South Dakota GAP analysis. Map shows hexagons, each representing a 635 square km area. Source: http://wfs.sdstate.edu/sdgap/birds/lark%20bunting.htm.

observed in Baca County, Colorado (Prather 1993). Lark buntings began using Kansas as a fairly regular wintering ground by 1976 when CBC participants of Morton County observed 209 lark buntings with buffy wing patches characteristic of immatures in four separate locations (Shane and Seltman 1995).

Abundance and population trends

The only long-term population data of lark buntings over a broad scale come from the Breeding Bird Survey (BBS) and CBCs. The BBS is a cooperative program of the United States and Canadian Wildlife Services in which roadside counts (performed by experienced volunteers) are conducted along a 24.5 mile route with 50 equally spaced recording stations each surveyed for 3 minutes (Robbins et al. 1986). Based on BBS data, the densest breeding populations of lark buntings in Region 2 occur in eastern Colorado and eastern Wyoming, with averages of over 100 birds per route (**Figure 2a**). The next highest densities on BBS routes occur in western South Dakota, Nebraska, and Kansas and in central Wyoming, with averages of 30 to 100 birds per route.

Population trends of lark buntings are not well documented. Most available data are from unpublished BBS analysis. Throughout their breeding range, lark buntings are increasing in some areas while decreasing in others (**Figure 6**). BBS data from 1966 to 2003 show a survey-wide decline of 1.3 percent per year ($P = 0.01$) for lark buntings (**Table 1**; Sauer et al. 2004). Within Region 2, the population trend appears stable or downward. The point estimate for the population trend over the 37 year period suggests a decline of 1.7 percent per year from 1966 to 2003 ($P = 0.69$), but the 95 percent confidence interval on the estimated trend ranges from -9.9 to 6.6 percent per year (Sauer et al. 2004). Between 1966 and 2003, population declines are evident in all states within Region 2, with significant declines occurring in Colorado and South Dakota (**Table 1**; Sauer et al. 2004). The BBS has created

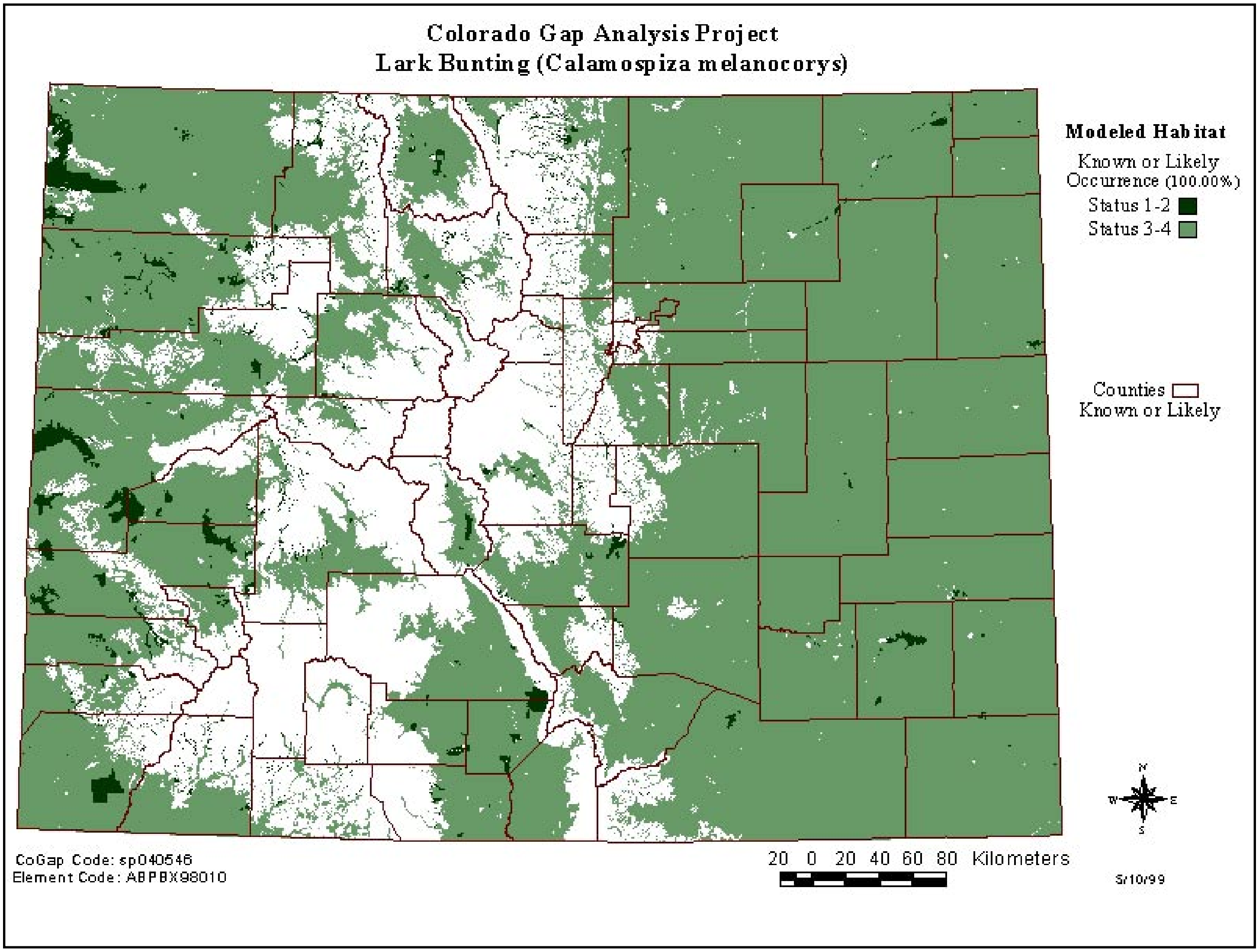

Figure 5. Potential distribution of lark buntings in Colorado as determined by habitat associations using Colorado GAP analysis. Status 1 or 2 refers to land with the highest and most permanent level of maintenance for biodiversity. Lands ranked 3 or 4 have lower levels of management or unknown management practices. Most private lands were assigned to category 3 or 4 depending on information available on their intended long-term management. Source: http://ndis1.nrel.colostate.edu/cogap/birds3/sp040546.html.

three levels of credibility estimates for its trend data to reflect different levels of potential deficiencies with data (e.g., small sample sizes, missing data) that should be considered when interpreting results. For the lark bunting, individual state trend data within Region 2 are at the highest of the three credibility levels. This indicates at least moderate precision with an adequate number of routes (i.e., sample size greater than 14) and moderate abundance on routes (i.e., greater than 1 bird per route on average). Trend data for Region 2 as a whole are less reliable due to the inconsistency in trend data over time (**Table 1**).

The biological significance of BBS trends for lark buntings must be viewed with caution (Shane 1996, Peterjohn and Sauer 1999). Due to fluctuations in precipitation and food availability, lark buntings make nomadic, short-term movements that may obscure or accentuate the trends documented by the BBS (Stewart 1975, Andrews and Righter 1992, Peterjohn and Sauer 1999). Because local populations increase in one location while decreasing in other areas, Shane (1996) suggests that clear evidence of population trends may require several decades. Furthermore, localized fluctuations may not explain nation-wide declines

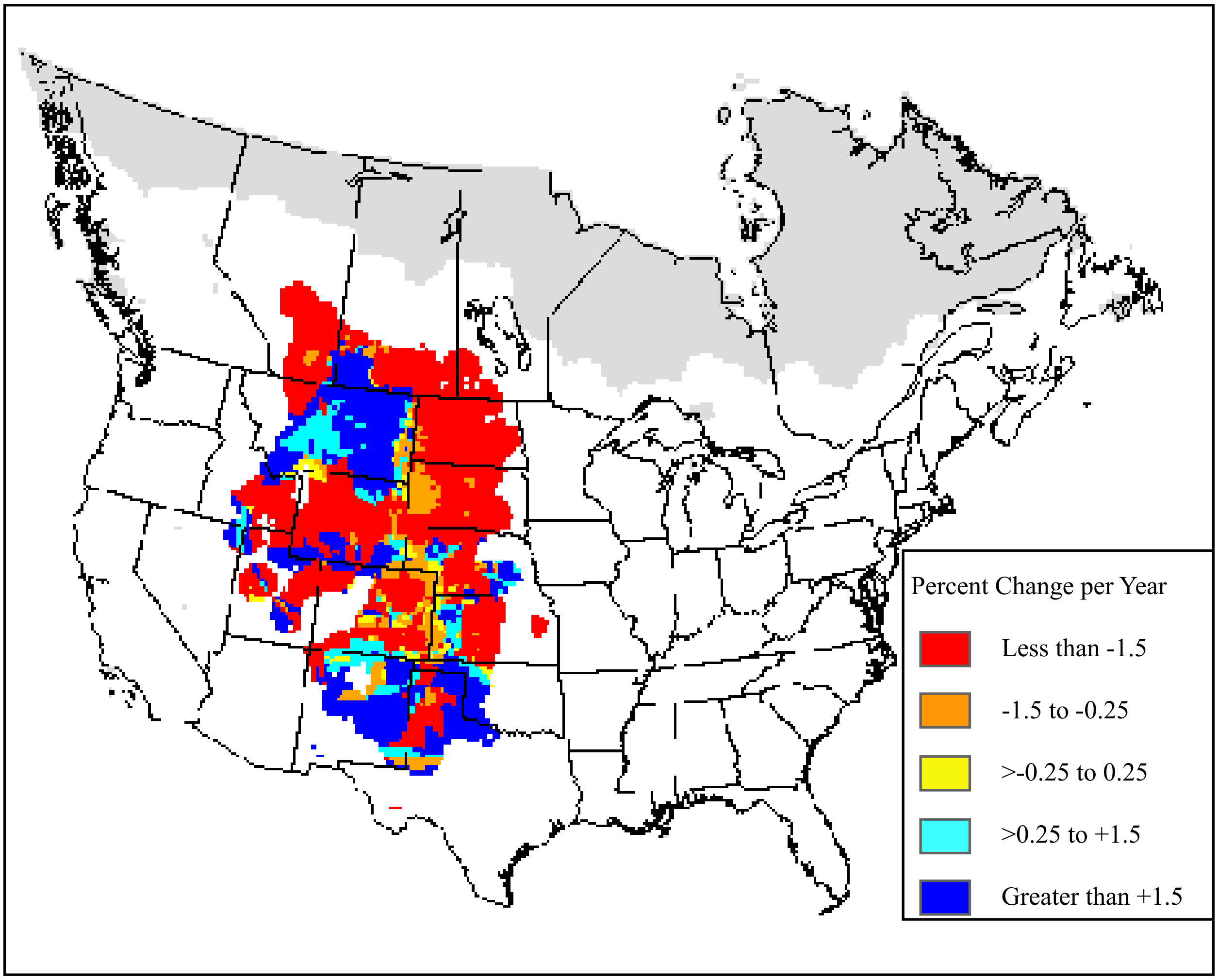

Figure 6. Population trends of lark buntings from 1966 to 2003 based on Breeding Bird Survey data (Sauer et al. 2004). Areas of population increase are blue; areas of decline are red. Trends were estimated as a yearly change, using the Link and Sauer (1994) procedure.

(**Table 1**). In recent years, the population of lark buntings has stabilized or increased in some regions of their breeding range but declined in others (**Figure 6**). It is not clear if observed increases are the beginning of recovery for grassland birds (and lark buntings) or if they are merely in response to favorable weather conditions or other short-term conditions (Peterjohn and Sauer 1999). In addition to the above-stated problems, BBS data date back only to 1966. Thus, if populations undergo fluctuations over several decades, a longer time-series may be necessary to elucidate actual declines. For example, based on anecdotal observations by early ornithologists, lark buntings may not have been much more common 100 years ago than they are today. In fact, the famous naturalist, Tom Say, made the trip up the Platte River in June to the foothills of Colorado then down the Arkansas River in late July and early August of 1820 on the Stephen Long Expedition. Say collected many type specimens on that trip, but he completely missed the lark bunting (James 1823). The species was not officially discovered until 17 years later, in 1837, by J.K. Townsend in the same area of Nebraska that Say had traversed (Baumgarten 1968). Allen (1874) describes a trip from Hays, Kansas to Wyoming in 1871 where he observes "a number of pairs are found in the same vicinity, while again not an individual may be met with for many miles…I met with several colonies not far from Fort Hays in June and July, and later at Cheyenne, Laramie, and in South Park…". On the same route in 1969 or 1970, one would have almost never been out of view of a lark bunting (Shane personal observation).

CBCs from 1959 to 1988 show a decline of 3.7 percent per year ($P < 0.01$) for lark buntings (Knopf 1996). CBC surveys count early winter (approximately December 14 to January 5) birds at feeders and along

Table 1. Estimated lark bunting population trend (percent change per year) in Region 2 states, Region 2, and survey wide from Breeding Bird Survey data from 1966 to 2003 (Sauer et al. 2004). Significant changes are indicated in bold.

	Trend	P-value	N	95% C.I.	Relative Abundance
Colorado	**-2.5**	**<0.01**	**50**	**- 3.6 to -1.4**	**76.66**
Kansas	-3.1	0.18	23	- 7.4 to 1.3	36.28
Nebraska	-2.2	0.26	34	- 5.9 to 1.6	19.51
South Dakota	**-3.4**	**0.02**	**38**	**- 6.0 to - 0.7**	**69.63**
Wyoming	-1.3	0.35	79	- 4.1 to 1.4	52.76
Region 2	-1.7	0.69	28	- 9.9 to 6.6	1.85
Survey wide	**-1.3**	**0.01**	**367**	**- 2.2 to - 0.3**	**33.64**

routes traveled by foot or vehicle at a resolution of 24 km diameter circles. They are conducted by volunteers associated with Audubon Societies across the western hemisphere. Some biologists are skeptical of CBC reports due to wide variance in the methodologies used to count birds. Also, bird movements associated with the use of feeders and shifts in distribution may confound the results of CBC trends. Nevertheless, over a broad scale CBC data can be used to determine regions of highest winter densities. Highest winter densities of lark buntings from the period between 1966 and 1989 occurred in southwestern Texas (**Figure 2b**).

Local population trends vary based on a variety of reports. Some studies have shown year-to-year fluctuations in local populations (e.g., Wiens et al. 1972, Winter et al. 2003) whereas others have reported longer term declines (e.g., Johnson and Igl 1995). In one study of shortgrass prairie habitat in Boulder County, Colorado, lark bunting populations declined from abundant in 1909 and 1913, to common in 1937, and finally to non-existent in 1986 though 1996 (Jones and Bock 2002). The authors state in reference to the lark bunting that "No grassland bird has declined more drastically in Boulder County over the past century." They speculate that urban habitat fragmentation and changing land use practices may be to blame. Abundance data through 1937 came from published checklists while later estimates were from fixed-distance transect counts and point counts.

Activity patterns and movement

Daily and seasonal activity

The activity of male lark buntings during daylight hours in South Dakota consisted primarily of singing (27 percent of time) and foraging (21 percent) with less time devoted to flight (16 percent) or nest maintenance (11 percent); males spent only 1 percent of their time engaged in territorial defense (Pleszczynska 1977). The actual times that male lark buntings forage are distributed equally throughout the day (Creighton and Baldwin 1974). Males are on the nest with eggs more than females in the mid-day hours (Rice 1965). Female daily activity during the breeding season was dominated by foraging (25 percent of time), flight (22 percent), and nesting activities (17 percent; Pleszczynska 1977).

In Colorado, peak song-flight activity occurs during the last three weeks of May and the first three weeks of June. Most song-flights occur during the first four hours after sunrise, with a lull in the afternoon until song begins again just before sunset (Ervin 1981). Therefore, census programs that rely on observing or hearing the species would be most effective during late May and early June and during the hours near sunrise and sunset.

Movement patterns

During March and April, males begin their diurnal migration from the wintering grounds in Texas, Arizona, and the high plateau of northern Mexico to the high plains of central North America. Migrating with somewhat irregular movements, flocks forage on the ground and rest in trees (Baumgarten 1968). Evidence from the 1994-1996 North American Migration Count reveals that the most heavily used route of migration is along the 102nd meridian from Midland County, Texas to Perkins County, South Dakota (Shane 1998). During migration, lark buntings feed primarily on weed seeds, wheat, insects, and arachnids (Knowlton 1947).

Males arrive on Region 2 breeding grounds from mid-April through May (Shane 2000, Seyffert 2001). The first flocks are predominantly male (Creigton 1971). Upon arrival males forage in small groups and periodically perform communal flight displays (Taylor and Ashe 1976) before dispersing within two weeks into suitable nesting habitats (Johnsgard 2001). In Colorado, females begin to arrive five days after males appear (Creighton 1971).

As lark buntings leave breeding grounds in Colorado, they gather in flocks along roadside ditches before migrating to wintering areas (Giezentanner 1970). During roadside counts that were conducted from July 1968 through December 1969, migrating lark buntings were last observed in mid- to late September in north-central Colorado (Giezentanner and Ryder 1969, Creighton 1971).

Lark buntings are gregarious during the wintering season, living a nomadic lifestyle and congregating in areas where food is abundant (Shane 2000). They forage in very large flocks (hundreds per flock) in northern Mexico moving as cohesive units (Baird et al. 1874).

Dispersal

Of the many studies of lark buntings in the literature, there are only four reports of banded birds returning to a study area; all were in Colorado (reviewed in Shane 2000). Furthermore, little information is available on initial dispersal from natal site. One radio-tracking study reported that juveniles may move up to 800 m from the nest within the first 21 days of fledging (Yackel Adams et al. 2001). If time allows for renesting, female buntings frequently disperse (>10 km) from the initial nest site (Yackel Adams et al. in revision).

Habitat

Breeding

The broad-scale breeding habitats of lark buntings are the grasslands and shrub-steppe of the North American Great Plains and some agricultural areas. The most commonly selected habitat for nesting is shortgrass prairies/pastures. Lark buntings also nest in mixed-grass prairie, retired croplands (Stewart 1975, Johnson and Schwartz 1993b), tallgrass areas with weedy edges and scattered shrubs (Johnsgard 1980), croplands, haylands, wheat fields, sand-sage grasslands, shrubsteppe, semidesert shrubsteppe, wet meadows, seeded pastures (Faanes and Lingle 1995), and mountain meadows (Bailey and Neiedrach 1965) (**Table 2**).

Nesting habitats and nest site selection: Since migrating flocks of males arrive first in the breeding range, male lark buntings select the breeding area. The actual nest site is chosen by the female, who visits possible sites as the male follows (Creighton 1971, Johnson 1981). Nesting habitat preference is a compromise between the sexes in which nest sites are selected to provide increased visibility of the nest surroundings for the female and concealment for the darker male (Baldwin et al. 1969, Johnson 1981).

Lark buntings nest within a shallow depression in the ground under the cover of shrubs, grass bunches, and other vegetation. During the breeding season, they are more frequently found in habitats with less woody vegetation than in areas with more woody vegetation (**Table 3**; Wiens 1973). In Weld County, Colorado, buntings were found in vegetation with mean height of 7.1 cm and cover consisting of short grasses (65.6 percent), mid-grasses (4.7 percent), sedges (7.8 percent), forbs (7.2 percent), cacti (2.1 percent), shrubs (2.1 percent), bare ground (9.7 percent), and rocks (0.7 percent) (Creighton and Baldwin 1974).

In the Pawnee National Grassland (Weld County, Colorado), nests were most often associated with *Aristida longiseta* (red triple-awn grass), *Atriplex canescens* (four-winged saltbush), *Erigonum effusum* (eriogonum), and *Chrysothamnus nauseosus* (rabbitbrush) (**Table 4**). In western Kansas, lark buntings nested beneath *Kochia scoparia* (summer cypress; 30.0%), *Artemisia filofolia* (sandhill sage; 26.6%), *A. longiseta* (10.0%), and *Helianthus* spp. (sunflowers; 10.0%) (Shane 2000). Wilson (1976) found that in west-central Kansas, lark buntings nested under vegetation that allowed clear visibility in at least two directions. In milo stubblefields, nests were located beneath the milo and *Conyza canadensis* (marestail). In the native grasslands, nests were at the base of *Scutellaria resinosa* (resinous skullcap), *Gutierrezia sarothrae* (broom snakeweed), *Tetraneuris stenophylla* (stemless tetraneuris), and *Cirsium ochracentrum* (yellowspine thistle).

Nesting habitats – outside normal breeding range: In areas outside their typical breeding range (i.e., northeastern Utah), lark buntings spent 86 percent of their time in open, low-growing desert shrub (mean height 6 to 30 cm); this habitat comprised only 37.3 percent of the study area that included large areas of grasslands. Most nests were located at ecotones between *Sarcobatus vermiculatus* (greasewood) and grassland communities (Johnson 1981). In Saskatchewan, lark bunting ground nests were situated in various types of vegetation (primarily

Table 2. Review of breeding habitats used by lark buntings. Habitat classification is given as categorized in primary literature source (modified from Dechant et al. 2003).

Habitat	**Location**	**Reference**
Agricultural field	Atchinson County, MO	Easterla 1970
Agricultural field	Deuel, Garden, and Keith counties, NE	Faanes and Lingle 1995
Cold desert shrub community	Uinta County, UT	Johnson 1981
Conservation Reserve Program (CRP), restored grasslands (Great Plains Roughlands)	Butte County, SD Fallon County, MT Hettinger County, ND	Johnson and Igl 2001
CRP, restored grasslands (Native and tame grasses)	Butte County, SD Fallon County, MT Hettinger County, ND	Johnson and Swartz 1993b
Hayfields	Shawnee County, KS	Rice 1965
Hayland	Saskatchewan	Maher 1974
Midgrass prairie	Riley County, KS	Cody 1968
Mixed grass hayland	Regina, SK	Smith and Smith 1966
Mixed grass hayland (undisturbed)	Hughes County, SD	Pleszczynska 1978
Mixed prairie grassland	Richland County, MT	Hickey et al. 1979
Mixed prairie	Adams County, CO	Fairbanks et al. 1977
Native grasslands	Northern Great Plains (portions of MT, ND, SD, NE, WY, CO)	Kantrud and Kologiski 1982
Native mixed grass (some mixed-grass hayland)	North Dakota	Kantrud 1981
Sage grasslands	Montana	A.R. Dood in Kantrud and Kologiski 1982
Sagebrush foothills	Rosebud County, MT	Hickey et al. 1979
Sagebrush foothills	Natrona, WY	Hickey et al. 1979
Sandhill prairie	Niobrara Valley Preserve, NE	Griebel et al. 1998
Seeded grassland	Adams County, CO	Fairbanks et al. 1977
Shortgrass pasture	Harper and Beaver counties, OK	Dunn 1986
Shortgrass plains	Colorado	Cody 1968
Shortgrass prairie	Pawnee National Grassland, CO	Wiens 1973, With and Webb 1993
Shrubsteppe	Bighorn County, MT	Bock and Bock 1987
Upland Prairie	Platte River Valley, NE	Faanes and Lingle 1995
Weedy Field	Adams County, CO	Fairbanks et al. 1977

Symphoricarpos occidentalis [western snowberry]; Smith and Smith 1966) while in Missouri, lark buntings nested in a field planted with rows of *Dactylis glomerata* (orchardgrass; Easterla 1970).

Nest placement: Studies of nest placement show that nests are oriented to optimize the radiative cover of the vegetation. For example, most nests in Colorado were oriented so that the protective vegetation was located to the west and/or north of the nest to provide protection from the sun and to a lesser extent the prevailing winds (Creighton 1971, With and Webb 1993). In western Kansas, lark bunting nest orientation differed among vegetation types in such a way to maximize shade during the hottest parts of the day but to also take advantage of morning sun and cooling winds (Shane 1972, Shane 1974). Adequate nest shading is important for nesting success (Pleszczynska 1978) and may help to keep the male cool during incubation (With and Webb 1993).

Minimum habitat area: Some species require a specified amount of contiguous habitat before occupying the habitat. However, there is no research to date that

Table 3. Microhabitat structure of study plots occupied (N = 80) and not occupied (N = 20) by lark buntings in heavily winter-grazed study plots, Weld County, Colorado. Sampling took place in mid June 1969 (modified from Wiens 1973).

	Percentage of cover[1]						Density[2]			Litter	
Area	Grass	Forb	Woody	Cactus	Bare ground	Rock	Forb	Woody	Cactus	Depth (cm)[3]	Coverage[4]
Occupied	82	6	2	1	16	0	361	48	137	0.29	24
Unoccupied	85	5	15	0	10	0	545	194	39	0.50	35

[1]Frequency that each type of cover was at a sampling point. Categories were not mutually exclusive.

[2]Individuals per m^2

[3]Mean litter depth in a 3-cm radius around sampling point

[4]Visual estimate of percent of ground covered by litter in a 3 cm radius around point

Table 4. Vegetation associated with lark bunting nests in Weld County, Colorado, in 1968 and 1969. Baldwin et al. (1969) reported on vegetation associated with 37 nests in 1968, and Creighton (1971) reported on 43 nests in 1969.

Plant Type	Plant Species	% of nests associated (Baldwin et al. 1969)	Average vegetation height in inches (Baldwin et al. 1969)	% of nests associated (Creighton 1971)
Browse	*Atriplex canescens*	45.9	8.9	4.7
	Erigonum effusum	16.2	8.7	4.7
	Chrysothamnus nauseosus	10.8	8.3	23.2
	Opuntia polyacantha	2.7	4	✹✹
Grass	*Aristida longiseta*	13.5	7.4	62.7
	Bouteloua gracilis	2.7	2.7	✹✹
Annual forb	*Melilotus officinalis*	5.4	10.0	✹✹
	Psoralea tenuiflora	2.7	10.0	✹✹
	Salvia reflexa	✹✹	✹✹	4.7

✹✹No nests reported to be associated with vegetation type.

defines the minimum habitat area for lark buntings. Finch et al. (1987) found that male lark bunting territories ranged from 0.2 to 0.75 ha and estimated (very conservatively) that the minimum habitat area is probably greater than 0.75 ha. In a broad-scale survey of Conservation Reserve Program (CRP) lands in the northern Great Plains, Johnson and Igl (2001) were unable to detect a pattern of area sensitivity in the lark bunting. However, the species occurred in only a few of the counties surveyed, and these tended to be counties with larger grassland fragments. Habitat areas greater than or equal to 10 km^2 may be necessary to attract lark buntings (Shane 2000).

Winter habitat

Most of the winter range of the lark bunting falls outside of Region 2. Lark buntings winter in southwestern Kansas where they forage in sorghum stubble, ditches, and cattle feed lots (Shane and Seltman 1995). In Texas, lark buntings inhabit flat, semiarid country where they wander on plains, open fields, and in brushland (Oberholser 1974). In the Midland, Texas area, very large flocks of lark buntings were previously found in the numerous milo fields of the region (F. Williams personal communication 1995).

In New Mexico, the lark bunting is often found in the maize and hegari fields (Ligon 1961), in small playas fringed with stands of *Hilaria mutica* (tobosa), *Panicum obtusum* (vine mesquite grass), and *Prosopis glandulosa* (tall mesquite), and in areas of *Yucca elata* (palmillo) and *Bouteloua eripoda* (black grama) grassland (Raitt and Pimm 1977). They are abundant to common winter residents in brushless, weedy, or barren looking parts of the lower Sonoran Zone of southeastern Arizona but scarcer and irregular westward (Phillips et al. 1964). Habitat utilized in the Lower Colorado River Valley of Arizona is primarily agricultural fields and occasionally sparse riparian woodland or desert flats (Rosenberg et al. 1991). In southern California, winter flocks feed quietly upon the ground in the open, whether along a river bottom or over the baldest desert (Dawson 1923) and rarely in overgrazed pastures (Wilbur et al. 1971).

In Durango, Mexico, lark buntings occur most often in playas, which are dry in winter. Large flocks are also found around small Chihuahuan desert towns that are often surrounded by milo fields (J. Nocedal personal communication 1995, Shane 2000). In northwestern Chihuahua, lark buntings are abundant on the large prairie-dog (*Cynomys ludovicianus*) towns (Manzano-Fischer et al. 1999). Lark buntings tend to concentrate along roadsides in northern Chihuahua and Durango, Mexico (Leukering in Shane 2000) and are the most abundant species found on the Ejido San Pedro CBC in northern Chihuahua. The region is dominated by semidesert grasslands, mesquite woodlands, foothill oak-savannah and riparian woodlands (Dieni et al. 2003). Kennerly (in Baird et al. 1874) reported large flocks of lark buntings in the river valley early in the morning in Sonora and at Epsia while on the Mexican Boundary Survey. During most of the day, they were found on the hillsides among the bushes. More recently in Sonora, Mexico, lark buntings were observed in agriculture fields consuming waste grain, weed seeds, and grain spilled along roads (Russell and Monson 1998).

Foraging habitat

Lark buntings forage on the ground in leaf litter, the loose top layer of soil, and in vegetatively barren spots with nearby ant colonies (Baldwin 1973). In Saskatchewan and Colorado, lark buntings spent 100 percent of their time foraging in vegetation under 8 cm in height (Cody 1968). Buntings spend a large portion of their time feeding in one locale followed by rapid movements from one place to another, which suggests that they distinguish between patches in the habitat. Since tall grass restricts rapid running, this type of habitat may not be compatible with lark bunting foraging behavior (Cody 1968).

While female lark buntings are fertile, males are more likely to feed on their territories in order to effectively guard their mates. However, adults gather food for nestlings off their territory. Pleszczynska (1977, 1978) states that since most food for nestlings is obtained outside the territory, food available inside the territory is not a characteristic of importance to females in selecting a mate (but see Creighton 1971). Abundance of nesting cover is likely to be more important in choosing territories (Pleszczynska 1977, 1978).

Roosting habitat

No data are available that describes the roosting habitat of lark buntings.

Food habits

Diet

In the summer, when lark buntings are on breeding grounds that lie within Region 2, their diet consists of insects, grains, and some leafy matter (Martin et al. 1951, Baldwin et al. 1969). Visual estimates of digestive tract remains revealed that both animal (62 percent) and plant (38 percent) items constituted the diet of 101 lark buntings from May through July in Colorado (Baldwin 1973). Lark buntings consumed animal food from 56 different families (**Table 5**). The seeds of grasses (57.2 percent of total seed food by dry weight), forbs (40.1 percent), and shrubs (1.3 percent) made up 95 percent of the plant items recovered from lark bunting digestive tracts (Baldwin 1973). Prominent seeds eaten by lark buntings are *Triticum aestivum* (wheat), *Buchloe dactyloides* (buffalograss), *Helianthus annus* (annual sunflower), and *Carex* spp. (sedge) (Baldwin et al. 1969). Stomach contents of lark bunting collected in Nephi, Utah revealed a mix of insects and weed seeds similar to other locales (Knowlton 1947). Zimmerman (1996) hypothesized that the ingestion of insects satisfies the water requirement of the lark bunting, which is highly adapted to arid grassland conditions.

Nestlings are fed a diet that is exclusively insects (Creighton and Baldwin 1974). In Colorado, grasshoppers (mean length 13 mm) constituted 84 percent of the prey fed to nestlings (Baldwin et al. 1969). As the juveniles begin to forage for themselves, they take more seeds. The mean percent of animal prey items taken by juveniles decreases by 10 percent every two weeks as the proportion of plant food items increases correspondingly. In Colorado, the juveniles consume animal and plant foods in the same proportions as adults by the end of August (n = 40; Baldwin and Boyd 1973).

In the winter, lark buntings feed on small seeds, grain, and insects (Ligon 1961). During migration, their diet consists of weed seeds, wheat, few insects (beetles and ants), arachnids, and leaves (Knowlton 1947).

Table 5. Arthropod components of lark bunting diet in Colorado. Percent of biomass dry weight recovered from digestive tract anterior to intestine (Baldwin 1973).

Arthropod Type	Rank	% of total animal food
Grasshoppers	1	36.4
1 family		
Ground-dwelling beetles	2	34.6
7 families		
Ants	3	9
1 family		
Bees and wasps	4	4.3
10 families		
Leaf and flower beetles	5	3.8
9 families		
Flies	6	2.6
9 families		
Bugs and hoppers	7	2
14 families		
Caterpillars and moths	8	0.5
3 families		
Spiders	9	0.5
2 families		
Unidentified	—	6.1

Diet selection

A comparison of dietary composition to food availability showed that during May lark buntings in Colorado selected grasshoppers (Acrididae) and seeds of *Lithospermum*, *Amaranthus*, and *Buchloe* and avoided ants (Formicidae), scarab beetles (Scarabaeidae), and seeds of *Helianthus* and *Avena* (Baldwin 1973). The degree of diet flexibility is not known, but lark buntings eat both insects and seeds in the summer months (**Table 6**, **Table 7**; Baldwin 1973).

Foraging behavior

Lark buntings capture prey primarily by stalking it on the ground (58.4 percent), sometimes with erratic movements; hawking (37.8 percent) and gleaning (3.8 percent) are used less often (Baldwin and Creighton 1972, Shane 2000). In general, lark buntings spend a large portion of their time foraging in one place then run to the next foraging area, with females foraging in a direct path and males foraging in one place and moving forward more slowly. Females also use hawking strategies in prey capture more than males (Cody 1968, Baldwin et al. 1969). Phillips et al. (1964) describe winter foraging behavior as a 'bounce' in which lark buntings hop as they forage the brushless, weedy, and barren-looking areas.

Breeding biology

Phenology

Lark buntings arrive in Region 2 in mid-April and throughout May (Shane 2000). Due to the large fluctuations in annual local abundances, breeding site fidelity is not suspected. The first flocks to arrive are predominantly male; the males disperse rapidly upon arrival. Females begin to arrive five to nine days after males first appear (Creighton 1971, Wilson 1976). Nesting can be delayed up to two weeks due to cool, wet weather (Huntley in Shane 2000). Once females arrive, courtship begins with male aerial song-flight displays. In these displays described as primary flight song, the male flies up several meters and sings as he glides (Ervin 1981).

Mating system

Lark buntings engage in a highly variable mating system that may depend on the sex ratio of the population. Shane (2000) classifies the lark bunting as predominantly monogamous, but other studies find that polygyny occurs if males are able to attract a second mate (Pleszczynska and Hansell 1980). In addition, polyandry may also occur rarely (Verner and Willson 1969). In Utah, two of nine nests had two males feeding

Table 6. Occurrence of arthropods in lark bunting diet from May 1 through July 9 in Colorado. Values are percentage of total animal food by dry weight biomass (Baldwin 1973).

Arthropod Family	May 1 - 14	May 15 - 28	May 29 - June 11	June 12 - 25	June 26 - July 9
Acrididae	36	47	51	16	29
Curculionidae	30	23	26	20	12
Formicidae	16	9	1	15	12
Scarabaeidae	8	2	2	9	3
Tenebrionidae	1	<1	2	3	10
Carabidae	3	7	1	4	3
Meloidae	—	4	2	2	2
Ichneumonidae	2	—	<1	5	4
Cerambycidae	—	—	2	5	—
Anthomyiidae	—	—	—	6	—
Sphecidae	—	<1	1	2	3
Chrysomelidae	<1	<1	1	2	2
Calliphoridae	—	—	—	—	4
Cicadellidae	<1	<1	<1	1	1
Other families	2	4	9	10	25

Table 7. Occurrence of seeds in lark bunting diet from May 1 to July 9 in Colorado. Values are the percent of dry weight biomass of total seed food recovered from 101 lark bunting digestive tracts (Baldwin 1973).

Seeds Genus (Family)	May 1 - 14	May 15 - 28	May 29 - June 11	June 12 - 25	June 26 - July 9
Avena (Graminaceae)	19	27	48	13	2
Oryzopis (Graminaceae)	1	1	6	8	56
Polygonum (Polygonaceae)	17	6	7	25	3
Buchloe (Graminaceae)	27	28	11	3	1
Helianthus (Compositae)	16	9	1	10	5
Lithospermum (Boraginaceae)	8	6	1	9	14
Tradescantia (Commelinaceae)	<1	<1	—	13	1
Aristida (Graminaceae)	—	6	9	2	2
Triticum (Graminaceae)	—	—	7	7	—
Amaranthus (Amaranthaceae)	7	1	1	<1	5
Salsola (Chenopodiaceae)	—	7	1	3	—
Verbena (Verbenaceae)	2	1	2	3	—
Scirpus (Cyperaceae)	2	2	2	1	1
Mamillaria (Cactaceae)	—	—	4	—	—
All other genera	—	5	—	2	10

at the nest in a population that had a 3:1 male to female ratio (Johnson 1981).

Nest-building, egg laying, and clutch size

Egg laying begins 2 to 3 days after nest completion (Creighton 1971). Eggs are laid in the early morning (before 0530 MST in Colorado; Creighton 1971). In Kansas, clutch size ranged from two to six eggs (mean = 4.8; **Table 8**), and means differed only slightly among habitats: alfalfa (5.0), grassland (4.5), and stubble (4.9). Six of the seven, six-egg clutches were in stubble (Wilson 1976). In Colorado, mean clutch sizes ranged from 3.9 to 4.62 (**Table 8**).

Parental care

Once the first egg is laid, both parents attend the nest. Often, the second parent arrives at the nest before the attending adult leaves, or the nest is left

Table 8. Clutch size and reproductive success for lark buntings from four different areas within their range.

Location	Year	Nests observed	Mean clutch size	Eggs hatched per nest	Percent hatched	Young fledged per nest	Percent fledged	Source
Regina, Saskatchewan	1965	7	4.9	2.29	47.1	1.57	32.4	Smith and Smith 1966
Ellis County, Kansas	1976	78	4.8	1.13	26.3	0.74	17.3	Wilson 1976
Pawnee National Grassland, Colorado	1970	31	3.9	2.4	60	1.6	42	Strong 1971
Pawnee National Grassland, Colorado	1971	37	4	3.1	76	2.3	56	Strong 1971
Pawnee National Grassland, Colorado	2001-2003	66	4.62	3.77	Not available	1.33	40.9	Yackel Adams et al. In revision
Uintah County, Utah	1980	9	4.4	2.67	60	1.67	37.5	Johnson 1981

unattended for only short periods. The female stays on the nest at night and until >1 hr after sunrise (Huntley 1997). Incubation begins with the penultimate egg (Pleszczynska 1977) and lasts 11.7 days in Colorado (n = 90 nests; Creighton and Baldwin 1974). Both parents incubate eggs, with the female spending more time incubating than the male (Shane 2000).

The blue eggshells are promptly removed from the nest by both parents after the 28 hr hatching period. After hatching, males become more attentive to the nest (Creighton 1971). Both adults feed the nestlings and continue to feed the young after they leave the nest (**Table 9**; Baldwin et al. 1969, Shane 2000). Brood division occurred on the first day of fledging in one study (n = 6 nests); this may be a strategy to increase foraging efficiency under conditions of reduced food availability (Yackel Adams et al. 2001).

Movements and requirements of young

Young lark buntings typically fledge 8 to 9 days after hatching (Baldwin et al. 1969) unable to fly (Shane 2000). Fledglings start to make short flights by fledgling day 6 (Yackel Adams et al. 2001). Young fledglings remain concealed in the vegetation near the nest while parents continue to feed them a diet exclusively of insects. As juveniles begin to forage for themselves, they begin to take more seeds (Baldwin and Boyd 1973).

Dispersal of young

The age at independence is between 20 and 28 days post fledge (Yakel Adams et al. 2001). Radio-tracking studies determined that fledglings stay with parents for at least 21 days after leaving the nest, and they may travel as far as 1600 m from the nest but typically 800 m (Yackel Adams et al. 2001, Yackel Adams et al. 2006). Immatures flock together and stay on breeding grounds longer than adults before migrating (Shane 2000).

Demography

Genetic characteristics

Hybridization is not reported in lark buntings, and there are no data pertaining to genetic problems with this species.

Life history characteristics

One-year-old male lark buntings (identified by first alternate plumage) were observed mating and providing parental care (Huntley in Shane 2000). Despite the occurrence of polygyny in some high-density areas, not all adult males breed in each year (see Mating system). Pleszczynska (1978) found no statistical differences among bachelors, monogamists, and bigamists with respect to body size, surface area

Table 9. Feeding rates (deliveries per offspring per hr) to one-day and nine-day old nestlings in South Dakota (Pleszczynska 1977) and to twelve-day old fledglings in western Kansas (Shane 2000).

Parent	1-day old	9-dayold	12-day old
Female	1.2	2.2	1.11
Male	0.85	1.95	1.00

of white wing patch, or time spent singing. Vegetation cover was associated with the mating status of males ($r = 0.85$, $P <0.01$). Bigamist males had territories with the lowest illuminance (most vegetative cover), which provided protection from solar radiation. Likewise, the number of young fledged per nest was highly correlated to shading provided by vegetative cover at the nest ($P <0.01$; Pleszczynska 1978). Major factors responsible for nestling mortality include predation, heavy precipitation, and extreme temperatures (Pleszczynska 1978).

Lark buntings typically breed once per year. Yackel Adams et al. (in revision) found that 30 percent of females on their Colorado study site produced second broods. Nesting success (measured as fledging at least one young) ranged from 17.3 to 56 percent among five studies involving four different sites (**Table 8**). At present, there are not enough data to determine lifetime reproductive success.

Little information is available regarding longevity and variables affecting survival of lark buntings. According to U.S. Bird Banding Laboratory data, the longest period between banding and recovery was three years for a male who was initially banded a year after hatching (Klimkiewicz and Futcher 1987). Due to their nomadic nature, lark buntings are a difficult species in which to accurately assess return rates. An overall estimate for survival rates for ground-nesting passerine species from grassland-shrub habitat is 0.55 (Martin 1995). Other estimates for small passerines range from 0.4 to 0.6 (Ricklefs 1973, Møller and Cuervo 2003). Using seven seed-eating passerines for which survival rate data were available, we estimated lark bunting survival rate from a linear regression of mass on survival rate. This yielded an estimated survival rate of 0.4924 for lark buntings (**Appendix A**).

The life cycle diagram we constructed (**Figure A1**) and the associated analysis suggests that lark bunting populations may be relatively robust to environmental fluctuations. According to our model, there was a tendency for adult survival values to have the most impact on population growth. Yackel Adams et al. (in revision) recently estimated that an adult survival rate of 70 to 76 percent was needed to sustain the Pawnee National Grassland population. Clearly, survival rate data are needed for lark buntings in order to refine our analyses.

Densities

Breeding densities ranged from 0.02 to 1.65 individuals per ha in plots where lark buntings were found in middle and western North America (Rotenberry and Wiens 1980). At the western limits of the breeding range in northeastern Utah, densities were 0.62 per ha in 1979 and 0.64 per ha in 1980, for a 3:1 male-biased population (Johnson 1981). The mean breeding densities vary by habitat in the Platte River Valley of Nebraska: wheat stubble fields, 0.23 pairs per ha; upland prairie, 0.16 pairs per ha; alfalfa, 0.03 pairs per ha; and wet meadows, 0.01 pairs per ha (Faanes and Lingle 1995). In the Pawnee National Grassland in 1969, nests were found to be as close as 10.7 m from each other with a density of 1.83 nests per ha (Baldwin et al. 1969).

Limits to breeding and survival

Few studies have specifically addressed potential limiting factors in lark buntings. **Figure 7** summarizes the environmental factors that directly (centrum) or indirectly (web) influence lark bunting populations based on the sources described in this document (see Andrewartha and Birch 1984). In general, the availability of food and nesting cover are major limiting factors for lark buntings. Indirectly associated with these necessary resources are the natural phenomena such as weather (i.e., adequate rainfall impacts food supply, fire, soil requirements) and human activities such as agricultural practices (i.e., planting crops, clearing land, burning, and applying insecticides and herbicides). Shortgrass prairie habitat is particularly susceptible to climatic conditions, and resource levels are more directly affected by rainfall than in other grassland habitats (Wiens 1973).

During the winter, food availability is the most likely factor that limits lark bunting populations, as suggested by the species' nomadic lifestyle (Shane 2000). Large flocks are often associated with agriculture fields of sorghum. Winter survival is tied to availability

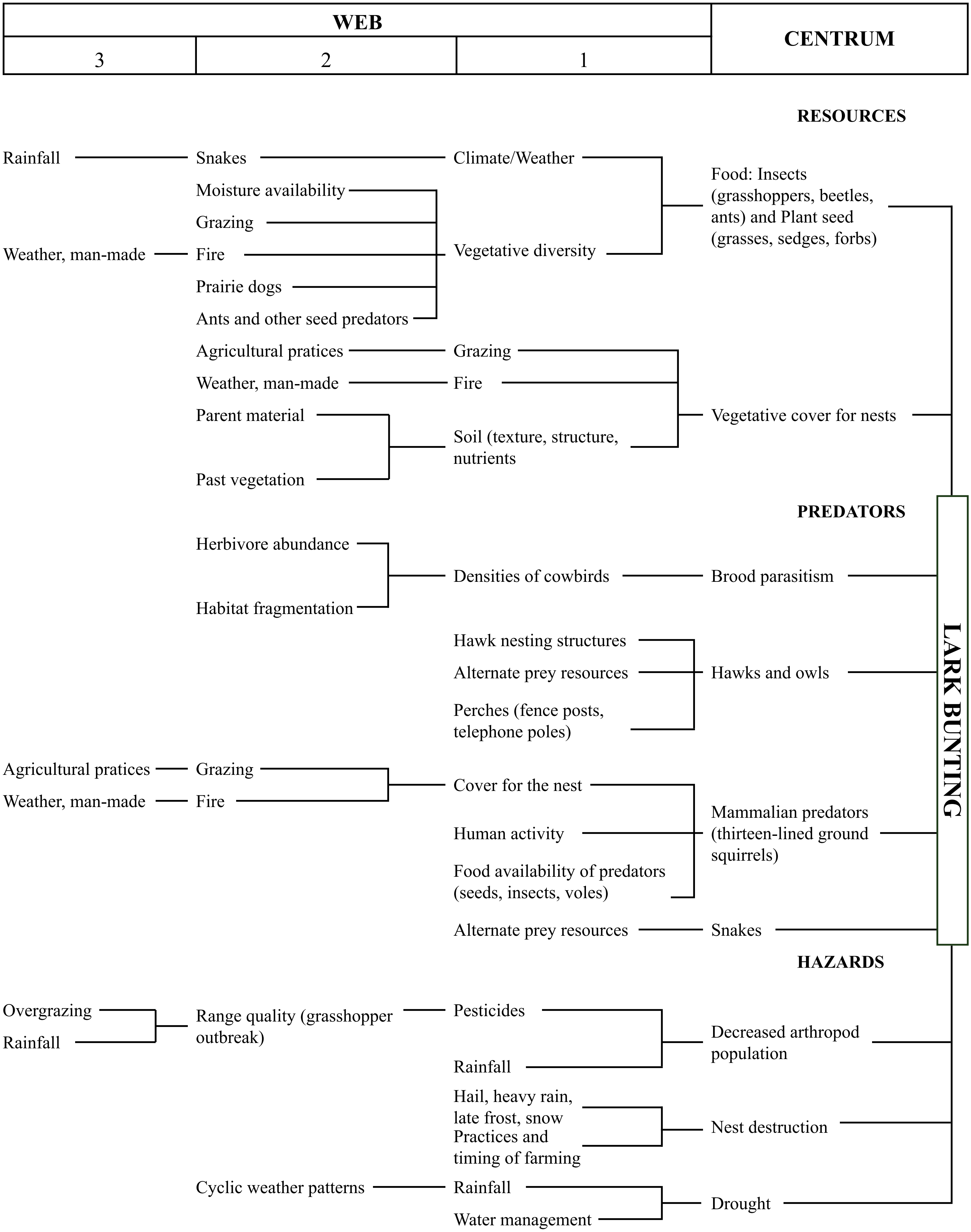

Figure 7. Enivorgram representing the resources, predators, and hazards that interact directly (centrum) and indirectly (web) with lark buntings.

of both natural and anthropogenic seed sources, the presence of which is largely affected by rainfall. Ground foraging seedeaters like the lark bunting are highly susceptible to drought conditions, and local populations fluctuate accordingly (Bock and Bock 1999).

Summer food sources of lark buntings include insects and seeds. Grasshoppers are an important food source for adults and nestlings at this time of year, and nest initiation is closely tied to grasshopper abundance (Creighton and Baldwin 1974). Population fluctuations of lark buntings in the breeding season may represent the species tracking optimal insect resources (Wiens 1973, Winter et al. 2003).

Nest sites with appropriate cover to protect from solar radiation may be another limiting factor to nesting success (With and Webb 1993). Lark bunting nests are always situated under cover of overhanging vegetation in the form of shrubs or bunch grasses (Creighton and Baldwin 1974), and shaded nests have greater fledging success (Pleszczynska 1978). Males defending territories with less shade are less likely to attract mates (Pleszczynska 1978). Ideal nesting conditions occur in habitats with 10 to 30 percent canopy cover of vegetation taller than the dominant grass stratum and less than 15 percent bare ground (reviewed in Finch et al. 1987). Some bare ground is necessary for nesting and foraging, but too much is undesirable due to reduced shade cover.

No studies have specifically examined minimum habitat area requirements in the lark bunting, but fragment size is likely a limiting factor as it is for other grassland birds (Johnson and Igl 2001). Small fragments may be avoided due to their isolation or their potential for edge effects, which may lead to high incidences of brood parasitism and nest predation (Wiens 1995). Three grassland sparrow species in Saskatchewan were found to have minimum area requirements ranging from 25 to 134 ha, but it is important to note that variation among different study sites can be considerable due to differences in species abundance and habitat characteristics (Davis 2004).

Community ecology

Predators

In Region 2 the main predators on adult lark buntings include hawks and owls (**Figure 7**). Specific species of predators differ spatially across the lark bunting's range. In South Dakota, reported predators include burrowing owls (*Athene cunicularia*; MacCracken et al. 1985) and ferruginous hawks (*Buteo regalis*; Blair and Schitoskey 1982). In Colorado, lark buntings form a significant portion of Swainson's hawk (*Buteo swainsoni*) diets. Other predators in Colorado include ferruginous hawks, great horned owls (*Bubo virginianus*; Olendorff 1973), burrowing owls, and barn owls (*Tyto alba*; Marti 1974). In Wyoming, prairie falcons (*Falco mexicanus*) are frequent predators on adult lark buntings (Squires et al. 1989). Other potential predators on adults include loggerhead shrikes (*Lanius ludovicianus*; Easterla 1970), northern harriers (*Circus cyaneus*), merlins (*Falco cyaneus*), and American kestrels (*Falco sparverius*; Lima 1990) and domestic cats (*Felis domesticus*; R. Harold personal communication in Shane 2000).

The major nest predators in Region 2 are thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*) and snakes (Baldwin et al. 1969, Pleszczynska 1977, Shane 2000). Reported snake predators include western plains garter snakes (*Thamnophis radix*), blue racers (*Coluber constrictor*), bull snakes (*Pituophis melanoleus*), and coachwhip (*Masticophis flagellum*). Avian nest predators include long-billed curlews (*Numenius americanius*), upland sandpipers (*Bartramia longicauda*), and western meadowlarks (*Sturnella neglecta*) (Pleszczynska 1977). Coyotes (*Canis latrans*), swift fox (*Vulpes velox*), long-tailed weasels (*Mustela frenata*), badgers (*Taxidea taxus*), and striped skunks (*Mephitis mephitis*) may also prey on nestlings (Woolfolk 1945, Yackel Adams et al. in revision). Note that mammalian predators may follow human scent trails to nests (Baldwin et al. 1969, but see Skagen et al. 1999).

Competitors

No significant impacts of interspecific competition have been reported for lark buntings. Potential competitors include horned larks (*Eremophila alpestris*), McCown's longspurs (*Rhychophanes mccownii*), chestnut-collared longspurs (*Calcarius ornatus*), and western meadowlarks. In Colorado, Cody (1968) found that the territories and habitat variables of lark buntings, horned larks, western meadowlarks, and McCown's longspurs overlapped, which suggests that these species do not horizontally partition the area (**Table 10**). However, these species may reduce interspecific competition by differences in their foraging behaviors. In a Colorado study plot, lark buntings and McCown's longspurs fed at the same average speed, but lark buntings spent more time stationary (Cody 1968). When lark buntings and western meadowlarks share the same habitat, they differ

Table 10. Characteristics (mean ± standard deviation) of three habitat features for grassland bird species in Colorado (from Cody 1968).

Species	Height[1]	Vertical density[2]	Horizontal density[3]
Lark bunting	10.36 ± 4.57	1.00 ± 0.38	3.38 ± 1.46
Horned lark	10.67 ± 4.27	0.93 ± 0.36	3.39 ± 1.48
Western meadowlark	10.67 ± 3.96	1.01 ± 0.38	3.40 ± 1.49
McCown's longspur	10.06 ± 3.96	1.04 ± 0.37	3.18 ± 1.35

[1]height of vegetation (cm) above the ground above which the number of contacts of vegetation with a metal rod moved horizontally through the sampling area dropped below one per 61 cm.

[2]number of leaves or stems contacting a 91 cm vertical rod.

[3]the number of vegetation contacts made with a 91 cm metal rod as it is moved horizontally through the sampling area at a height of 5 cm.

in the size of insects consumed (Giezentanner 1970). Furthermore, Creighton and Baldwin (1974) suggest that competition is reduced between lark buntings, horned larks, McCown's longspurs, and chestnut-collared longspurs through temporal segregation of nesting cycles and use of different prey capture tactics. According to Wiens (1977), competition for food may not occur in most years in the variable environment of the prairie but instead represent an important interaction only in harsh years (such as drought) when food resources are scarce.

Parasites and diseases

There are few studies of ectoparasites or endoparasites of lark buntings. Nasal mites (*Ptilonyssus morofskyi*) were collected from two adult females in northern Texas (Spicer 1978). A study of avian hematozoa revealed that lark buntings were infected with *Haemoproteus* (2 of 15 birds), *Trypanosoma* (1 of 15), and microfilariae (1 of 15; Greiner et al. 1975). Impacts of these parasites on lark buntings are not known.

Brood parasitism

The impact of brood parasitism by brown-headed cowbirds on lark buntings is not well studied. Reported incidences of cowbird parasitism on lark bunting nests range from 0 to 100 percent (**Table 11**). Friedmann (1963) reported lark buntings to be infrequent hosts, but more recent studies have indicated high parasitism frequencies in some populations (**Table 11**). In small, fragmented grasslands of southwestern Manitoba, 100 percent of observed nests (n = 7) were parasitized (Davis and Sealy 2000), and in cropland habitat in North Dakota parasitism occurred in 61 percent of the nests (n = 23; Koford et al. 2000). Multiple parasitism has also been reported in several studies (**Table 11**). One study reported lark buntings as ejectors of cowbird eggs (Hill 1976), but further experimental tests have not supported this classification (Sealy 1999). Only one study has reported lark buntings successfully rearing cowbird young to fledging (Sealy 1999).

As with other hosts, the potential impact of cowbirds on lark buntings will tend to vary among habitats. Cowbirds have the most potential to impact lark buntings in fragmented habitats with high cowbird densities (Johnson and Temple 1990). High cowbird densities can result in higher incidences of multiple parasitism and consequently very low fledging success of host young (Trine 2000). Proximity to woodland edges and numerous perches (e.g., fence posts, woody vegetation) allows cowbirds to monitor host activity and find host nests (Clotfelter 1998). Cowbirds prefer to forage in short vegetation, particularly areas grazed by large mammals, as well as agricultural fields, livestock corrals, and mowed lawns (Mayfield 1965), and they will commute up to 15 km between feeding and breeding areas (Curson et al. 2000). High densities of cowbirds in the northern Great Plains (including Colorado, Nebraska, South Dakota, and Wyoming) were found in moderately grazed native grasslands (Kantrud and Kologiski 1982). Cowbirds are highly adaptable to foraging on different anthropogenic food sources, but they prefer to associate with large grazing ungulates, usually cattle. Cowbird abundance and host parasitism frequency are highest in areas close to cowbird foraging areas (Goguen and Mathews 1999).

Cowbirds and their hosts share a long coexistence on the Great Plains, and thus hosts have had more time than their forest-nesting counterparts to evolve defenses against cowbird parasitism such as nest desertion or egg ejection (Mayfield 1965). According to BBS data, cowbird numbers in Region 2 and across the United States and Canada have declined between 1966 and 2004. Of the Region 2 states, only South Dakota has shown a significant increase in cowbird

Table 11. Incidence and fate of lark bunting nests parasitized by brown-headed cowbirds.

Location of study	Rate of parasitism	Response	Source
Central Kansas	16 of 77 (20.8%) nests	8 of 16 nests deserted 3 of 16 nests destroyed by predators 4 of 16 nests destroyed by human activity 1 cowbird egg and 1 bunting egg disappeared, but 2 remaining buntings fledged	Wilson 1976
Central Kansas	22 of 142 (15.5%) nests	5 of 22 eggs ejected from nests 7 of 13 nests destroyed by predators 5 of 13 nests deserted while only 3 of 49 non-parasitized nests were deserted 1 or 13 nests had cowbird offspring raised to 5 days	Hill 1976
Southwestern Manitoba	6 of 6 (100%) nests	Unknown	Davis and Sealy 2000
Colorado	Artificially parasitized	3 cowbird eggs accepted and nestlings fed until experiment terminated	Huntley 1997
Southwestern Saskatchewan	12 of 22 (54%) nests	0 of 22 nests deserted	Sealy 1999
		12 of 12 naturally parasitized nests accepted egg(s); one nest had 2 cowbird eggs embedded in nest material	
Southwestern Saskatchewan	Artificially parasitized	4 of 5 artificial eggs accepted when it was added during laying or incubation; fifth cowbird egg was missing 24hrs after placement, but nest was naturally parasitized 3 days later and egg was accepted	Sealy 1999
Western Kansas	0 of 30 (0%) nests	Unknown	Shane 2000
North Dakota	23 of 38 (61%) nests	Unknown	Koford et al. 2000

numbers from the period of 1966 to 2004. The highest cowbird densities in Region 2 occur in South Dakota and Kansas (Sauer et al. 2004), and it may be these areas where lark buntings are most likely to face threats from cowbird parasitism.

Conservation

Threats

In this section we consider three major categories of threats to lark buntings in the context of habitat. These include habitat loss, habitat fragmentation, and habitat degradation. Within each of these we discuss specific threats related to the particular category. We then consider a separate category of threats to buntings on the wintering grounds. Although the wintering grounds occur outside of Region 2, knowledge of the potential threats to buntings in these areas is essential for proper management of the species. Unfortunately, the ecology and status of lark buntings on their wintering grounds has received little research attention and thus is a topic with the least information available.

Habitat loss

Habitat loss represents the biggest threat to wildlife conservation, and the grasslands of North America are no exception. According to Knopf (1994), grassland species as a whole have experienced more widespread and significant declines than any other ecological guild in North America due largely to habitat loss and degradation.

Grassland ecosystems in North America are varied due to differences in soil type, rainfall, disturbance, elevation, geology, and geography (Vickery et al. 1999). Grassland and shrubland ecosystems of Region 2 that are used by lark buntings during the breeding season include (from west to east): the shrubsteppe, shortgrass prairie, and mixed-grass prairie (**Figure 8**, **Table 12**). The shrubsteppe is found in large portions of Wyoming and in western and central Colorado. It is dominated by sagebrush, greasewood, saltbush, and rabbitbrush and has a variable grass component (Nicholoff 2003). The shortgrass prairie is found in much of eastern Colorado, western Kansas, southwestern Nebraska, and southeastern Wyoming. It

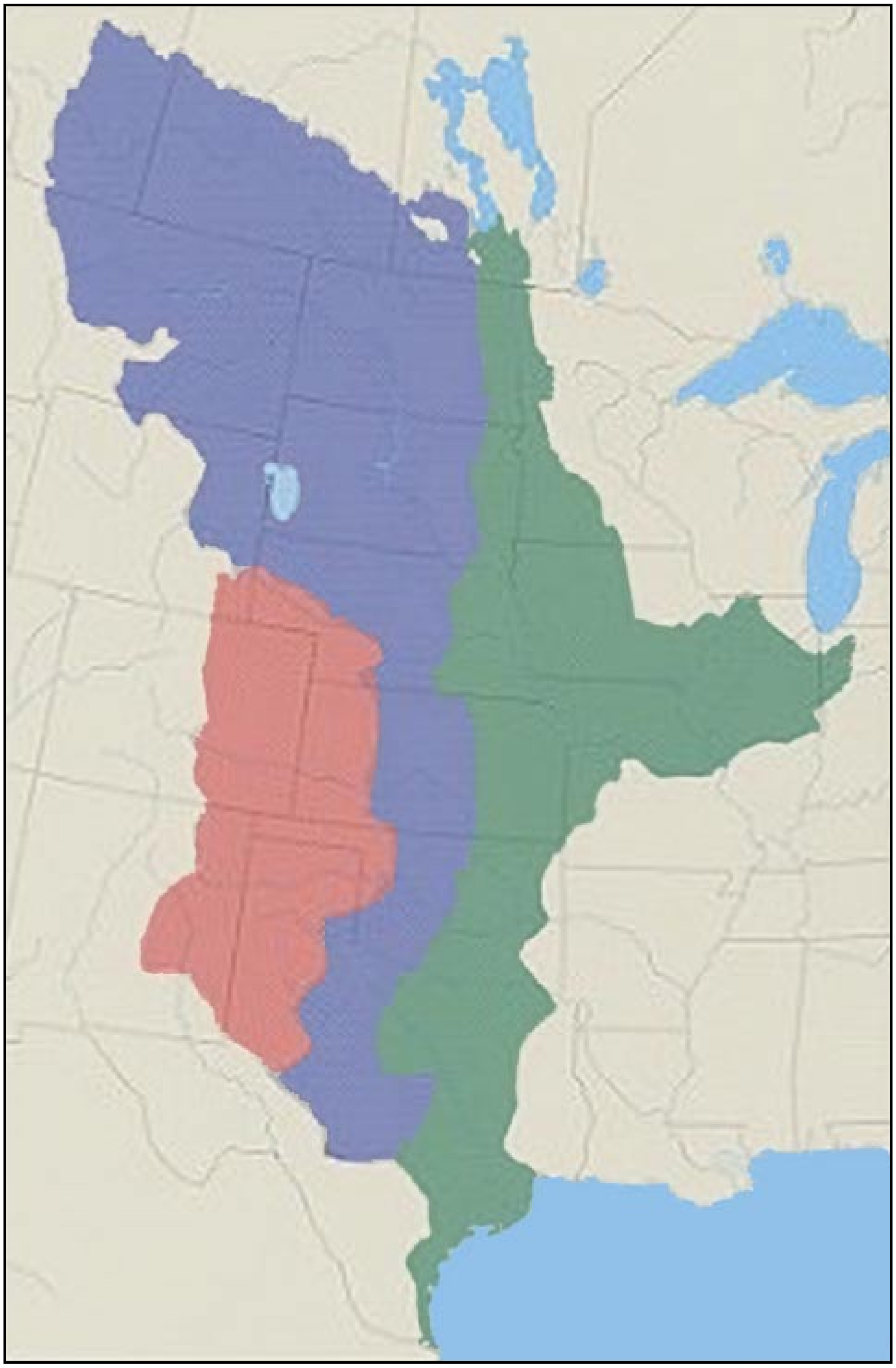

Figure 8. Extent of historical (pre-European) tallgrass, mixed-grass, and shortgrass prairies on the North American Great Plains. URL: http://biology.usgs.gov/s+t/SNT/noframe/gr139.htm.

Table 12. Summary of ecoregions within USDA Forest Service Region 2 used by lark buntings, including World Wildlife Fund Status, degree of habitat fragmentation, and major threats to the habitats (from Ricketts et al. 1999).

Ecoregion	World Wildlife Fund status	Degree of fragmentation	Major threats to habitat
Northern Mixed Grasslands	Critical/Endangered	Very High	Conversion to cropland
Central and Southern Mixed Grasslands	Critical/Endangered	Moderate to High	Conversion to cropland, overgrazing, and fire suppression
Northern Short Grasslands	Critical/Endangered	Low	Conversion of rangeland to cropland
Western Short Grasslands	Critical/Endangered	Moderate, some large areas intact	Conversion to cropland
Nebraska Sandhills Mixed Grasslands	Relatively Stable/Intact	Low	Localized overgrazing, conversion to cropland
Colorado Plateau Shrublands	Relatively Stable/Intact	Moderate to High	Overgrazing, mining
Wyoming Basin Shrub Steppe	Vulnerable	Low	Overgrazing, fire suppression, oil and gas exploration, mining

consists of low-growing grasses in a semi-arid climate (Weaver et al. 1996, Colorado Partners in Flight 2000). Mixed-grass prairie represents the transition between shortgrass and tallgrass prairies and is found in all but the far eastern part of South Dakota, northwestern Wyoming, and central Nebraska, and Kansas (**Figure 8**). The mixed-grass prairie is characterized by warm season grasses of the shortgrass prairie to the west and cool and warm-season grasses, which grow much taller, to the east. Mixed-grass prairie is essentially an ecotone and thus contains more plant species than other prairie types (Bragg and Steuter 1996). In the shortgrass and mixed-grass prairies of Region 2, conversion to agriculture is a problem, but unlike tallgrass prairie habitats, relatively large expanses of these habitats still remain (Askins 2000).

Prior to European settlement, the grasslands of Region 2 were a mosaic of habitat patches in different stages of recovery from the effects of grazing and fire, where different species found their ideal habitats. Lark buntings are one of nine avian species, and six passerines, endemic to the grasslands of the central Great Plains (Mengel 1970, Knopf 1996). They evolved along side bison (*Bison bison*) and have adapted to the mosaic landscape created by a combination of grazing by large native ungulates, prairie dog towns, and periodic fire (Nicholoff 2003).

Loss of grassland habitat in Region 2 is due largely to conversion of grasslands to cropland and urbanization. Until recently the shortgrass prairie was considered too dry to farm without irrigation, and thus the overall proportion of cropland was not high. However, new machinery and genetically modified crops are resulting in a shift from traditional grazing to monoculture grain farming in the northern Great Plains (Higgins et al. 2002), and the conversion of native grassland to cropland has the potential to impact lark bunting populations. Lark buntings occur at higher densities in CRP land than cropland (Johnson and Swartz 1993a). Johnson and Igl (1995) estimated that the recultivation of the CRP land to cropland could cause a 17 percent population decline of lark buntings in North Dakota.

Croplands are not entirely unusable habitat for lark buntings. Lark buntings will use wheat and alfalfa as well as stubble fields for nesting (Wilson 1976, Busby and Zimmerman 2001). For example, the clumped arrangement of wheat stubble provides vegetative cover required for nesting. However, nesting success may be lower in cropland than grassland depending on the type and the timing of farming practices (Wilson 1976, Faanes and Lingle 1995). In wheat fallow systems, where surface tillage is used for spring weed control, nests will be destroyed (Higgins 1975, 1977). Mulch tillage, a method of subsurface tilling that leaves the stubble intact, is less destructive to nests (Rodgers 1983). In this method, blades pass under the soil surface to cut roots but generally leave nests intact except for those directly crushed by tractors or implement wheels. However, this practice is being replaced in some areas in favor of heavy pesticide use to control weeds (see below; Rodgers 2002). Furthermore, a shift toward shorter, semi-dwarf wheat varieties could be problematic for the lark bunting by reducing nesting cover. Semi-dwarf wheat varieties accounted for over 75 percent of the wheat crop on the Colorado High Plains by 1989, which is up from less than 2 percent in 1978 (Snyder 1991). A reduction in wheat stubble height has been attributed to low winter survival for ring-necked pheasants (*Phasianus colchicus*) in Kansas (Rodgers 2002). Whether short stubble heights would also impact lark buntings needs to be investigated.

Urbanization may be a more significant threat to lark bunting habitat due to its permanence. While cropland can be restored to grassland habitat if taken out of production, urbanization leads to permanent loss of habitat (Colorado Partners in Flight 2000). Colorado has undergone rapid population growth and land development, particularly along the Front Range, including Denver, Boulder, Jefferson, Arapahoe, Larimer, and Douglas counties. The human population of the Front Range Metropolitan area increased by 31 percent between 1990 and 2000 compared with the national population, which increased by 13 percent. Furthermore, the human population in this region is projected to increase an additional 63 percent by 2030 (SpatialNews 2005). Such growth has resulted and will continue to result in significant alterations in the Front Range landscape and is coincident with declines in lark buntings in some local populations (Jones and Bock 2002).

Habitat fragmentation

Habitat fragmentation is the result of separating large, contiguous areas of habitat into smaller isolated patches. The dominant effects of fragmentation are increased "edge effects" and the creation of isolated patches of habitat. As the habitat becomes fragmented, the patches have a greater edge to interior ratio. Species nesting near edges may experience increased levels of nest predation and brood parasitism, and these smaller fragments may be avoided altogether by some species (Brittingham and Temple 1983, Herkert et al. 1996, Davis and Sealy 2000, Johnson and Igl 2001). Some grassland bird species have shown a preference to nesting in interior areas of fragments rather than in areas adjacent to treelines (O'Leary and Nyberg 2000).

Little is known about the specific effects of fragmentation on grassland birds, and even less is known about its effects on lark bunting populations. Johnson and Igl (2001) investigated the effects of area requirements of 15 grassland bird species in shortgrass prairies in Montana, North Dakota, South Dakota, and western Minnesota. Lark buntings were only detected in three of nine counties, and fragment size tended to be larger in those three counties. Additional studies in states where lark buntings are more likely to occur might prove more useful. Other studies of grassland birds have found that some species are more sensitive to fragment size than others (Davis 2004). Species that require areas much larger than their home range, and that tend to be absent from small patches, are referred to as "area sensitive". It is currently not known if the lark bunting is an area sensitive species.

Elevated rates of cowbird parasitism have been well documented for fragmented forest habitats (e.g., Robinson et al. 1995), but fewer studies have examined cowbird parasitism in fragmented grasslands. Proximity to woodland edges and numerous perches (i.e., fence posts, woody vegetation) allows cowbirds to monitor host activity in grasslands and to find host nests. Host species that nest in smaller fragments, with greater ratios of edge to interior habitat, should suffer greater parasitism frequencies, but surprisingly few studies have examined this phenomenon in grassland birds (but see Johnson and Temple 1990, Davis and Sealy 2000, Winter et al. 2000). Herkert et al. (2003) found no relationship between grassland fragment size and cowbird parasitism on four species in an extensive study involving 39 prairie fragments in five states (Illinois, Kansas, Missouri, North Dakota, and Oklahoma). Instead, their findings suggested that parasitism frequencies were related more to cowbird densities in a given area. However, the researchers found significantly higher nest predation in smaller fragments than larger (>1000 ha) ones.

The level of habitat fragmentation in areas used by lark bunting varies across Region 2 (**Table 12**). The most fragmented habitats include the mixed grasslands. The Northern Mixed Grasslands are the most disturbed among all grassland ecoregions, with only a few patches remaining and none with protected status within the United States. The Central and Southern Mixed Grasslands are also highly fragmented, with virtually no protection for the remaining remnant habitats, which include the Platte River Valley and Rainwater Basins in Nebraska and the Central Kansas wetlands, Red Hills and Smokey Hills River Breaks in Kansas (Ricketts et al. 1999).

Habitat degradation

Under the category of habitat degradation, we consider factors that potentially alter the habitat of lark buntings, making it less desirable for breeding. These include the use of pesticides, grazing, fire/

fire suppression, natural resource extraction, and human activity.

Pesticides

Direct effects of pesticides on birds include illness or death from exposure to the pesticide. In a Wyoming shortgrass prairie, experimental application of diazinon for grasshopper control resulted in declines in numbers and observed mortality of lark buntings and three other species within days of the application (McEwen et al. 1972) presumably from ingesting poisoned prey. Diazinon has been banned recently from residential use due to its toxicity to vertebrates (e.g., Anderson 1985), but agricultural use is still permitted (www.epa.gov). In a 1994 report based on a survey of Wyoming farmers, diazinon was used to treat less than 1 percent of cattle and was applied to less than 1 percent of corn crops (Ferrell et al. 1994), so its usage appears to be declining.

Pesticide use can indirectly affect birds in several ways. Application of insecticides reduces arthropod abundance thereby reducing food available for adults and young during the breeding season. Herbicide use depletes weed species that produce seeds consumed by birds as well as their arthropod prey (Taylor and O'Halloran 2002, Boatman et al. 2004). Herbicide use can also reduce nesting cover (Johnson et al. 2004).

Correlations between increased use of pesticides and declines in grassland birds have been suggested (Bellar and Maccarone 2002), but few experiments have been conducted. Long-term investigations in a variety of environmental settings are needed to understand potential indirect effects. 2,4-D is a commonly used herbicide by livestock growers and farmers in the Great Plains (Ferrell et al. 1994). A single treatment of 2,4-D and picloram in tallgrass prairie habitat was found to reduce species richness and abundance of forbs but not arthropod richness or abundance (Fuhlendorf et al. 2002). Insecticide treatment (e.g., malathion, sevin-4 oil, and carbaryl bait) for grasshopper control on western rangelands (including Colorado, Wyoming) did not cause a significant change in grassland bird densities (with the exception of western meadowlarks) within 21 days of application. This finding demonstrates a lack of acute effects but does not assess long-term consequences on breeding. As grasshoppers are a primary food source for lark buntings, effects on nesting success should also be examined.

Grazing

Lark buntings traditionally used habitat grazed by bison and other large native herbivores, which have now largely been replaced by cattle. Therefore, some grazing is essential to maintaining lark bunting breeding habitat, particularly in taller grassland settings. The effects of grazing on lark bunting nesting densities depend on the type of grassland and the timing and intensity of the grazing. Lark buntings respond negatively to heavy grazing in shorter grasslands, but they respond positively to light to moderate grazing in taller grasslands (Bock et al. 1993).

Rand (1948), Finzel (1964), and Giezentanner (1970) found that heavy grazing in shortgrass areas correlated to lower numbers of lark buntings. In the Pawnee National Grassland, the densities of lark buntings were lowest in areas where heavy summer grazing of shortgrass vegetation occurred (**Table 13**; Giezentanner 1970). On the other hand, Kantrud and Kologiski (1982) found that heavy grazing in lands dominated by typic ustolls soils resulted in optimum-breeding habitat for lark buntings in some areas of the Great Plains. Additionally, aridic borolls and borollic aridisols with moderate to heavy grazing (mean resulting heights of vegetation = 13 to 25 cm) had higher population densities while warm,

Table 13. Breeding density of lark buntings in association with grazing intensity, season, and vegetation characteristics at Pawnee National Grassland, Colorado in 1969 (from Giezentanner 1970).

	Grazing Intensity/Season	**Vegetation Characteristics**	**Number of pairs breeding on 8-ha plot**
Plot 1	Heavy/Summer	Shortgrass, prickly pear	1
Plot 2	Light/Summer	Short-moderate grass, prickly pear	5.8
Plot 3	Heavy/Winter	Shortgrass, occasional brush	3.9
Plot 4	Moderate/Summer	Short-moderate grass, little brush	3
Plot 5	Moderate/Winter	Short-moderate grass, frequent brush	3.9
Plot 6	Light/Winter	Moderate grass, much brush	3

[1] Lark buntings did forage on this plot.

dry soils with increased grazing intensity supported populations in lower densities (Kantrud and Kologiski 1982). This suggests that the heavy grazing of the tallgrass plots results in shorter and more preferable vegetation heights.

Fuhlendorf and Engle (2001) suggest that traditional rotational grazing, where cattle are rotated among pastures throughout the summer, promotes maximum use of forage but favors a homogenous habitat. They suggest that in mesic grasslands a combination of prescribed fire followed by moderate grazing in focal areas favors a more heterogeneous landscape favorable for grassland birds.

A potential problem associated with grazing is the use of manmade stock tanks to water livestock. Birds and small mammals can fall in and drown while attempting to drink (Chilgren 1979). Ramps can be constructed to allow escape from stock tanks and troughs (Nicholoff 2003).

Fire

Fire is a natural and important disturbance in grassland ecosystems. However, the historical role of fire varies among these ecosystems (reviewed in Wright and Bailey 1982). Fire can be detrimental to grassland birds during the nesting season, but suppression of fire leads to woody species encroachment in some environments and build up of leaf litter that can make habitats less attractive to grassland bird species (Madden et al. 1999, Askins 2000). The effectiveness of fire in maintaining of lark bunting habitat will depend on the type of grassland ecosystem, the level of grazing in the particular area, the current climatic conditions, and the timing of the burn.

Few studies have examined the impacts of fire on shortgrass and mixed-grass prairies. Historically, fires in these ecosystems were less common than in tallgrass prairies. In general, Wright and Bailey (1982) reported that most shortgrass prairies are harmed by fire during dry years. When fire occurs in dry years, both shortgrass and mixed-grass prairie grasses take three growing seasons to recover whereas recovery time is less during wetter years.

Little information is available about the effects of fire on lark buntings in these habitats, but studies show positive relationships between fire frequency and abundance and richness of grassland bird species in some mixed-grass habitats (Madden et al. 1999). Moderate-intensity, patchy burns leave a mosaic of successional stages that can be beneficial to a variety of grassland birds (Petersen and Best 1987). Thus fire every 5 to 10 years can be beneficial in short and mixed-grass prairies. Over the short term (2 to 3 years), fire may eliminate nesting cover such as sagebrush (*Artemisia* spp.) plants, and lark buntings may therefore avoid the burned habitat (Bock and Bock 1987).

Natural resource extraction

In Region 2 the biggest threat dealing with energy development is in the form of oil and gas wells, which directly alter and threaten shrubsteppe habitats in Wyoming and Colorado. Associated with these wells are networks of roads, pipelines, and powerline transmission corridors that directly destroy habitat, fragment habitats, and provide perches for avian nest predators (**Figure 9**; Knick et al. 2003). According to Debevoise and Rawlins (1996), 6000 to 11,000 new oil and gas wells could be drilled in southwestern Wyoming by 2015, with each new well occupying 5 acres of land. The impacts of this activity on lark buntings and other shrubsteppe species are yet to be assessed.

Human activity

The effects of other human activities on lark bunting populations have not been studied. With human population expansion within the Great Plains and consequently increased recreational use of lark bunting habitat, new pressures may be introduced. Some potential threats associated with human encroachment include predation by domestic cats (R. Harold personal communication in Shane 2000), nest destruction by grazing horses (Smith and Smith 1966), damage to habitat or nests by off road vehicles (Nicholoff 2003), and vehicle collisions (Baumgarten 1968). Tree plantings in grassland areas alter the community and provide nesting sites for non-grassland birds such as American crows (*Corvus brachyrhyncos*) and blue jays (*Cyanocitta cristata*), which are known nest predators (Berkey et al. 1993, Nicholoff 2003). Trees and power lines also provide perch sites for brood parasitic brown-headed cowbirds (see Clotfleter 1998) and raptors that may prey on adults (e.g., Steenhof et al. 1993).

Threats on the wintering grounds

Loss and degradation of winter habitat may be responsible for declines in some grassland bird species (see Herkert et al. 1996). Major lark bunting wintering areas include the Sonoran and Chihuahuan deserts in the southern United States and Mexico, where they spend much of their time in dry playas, feeding on

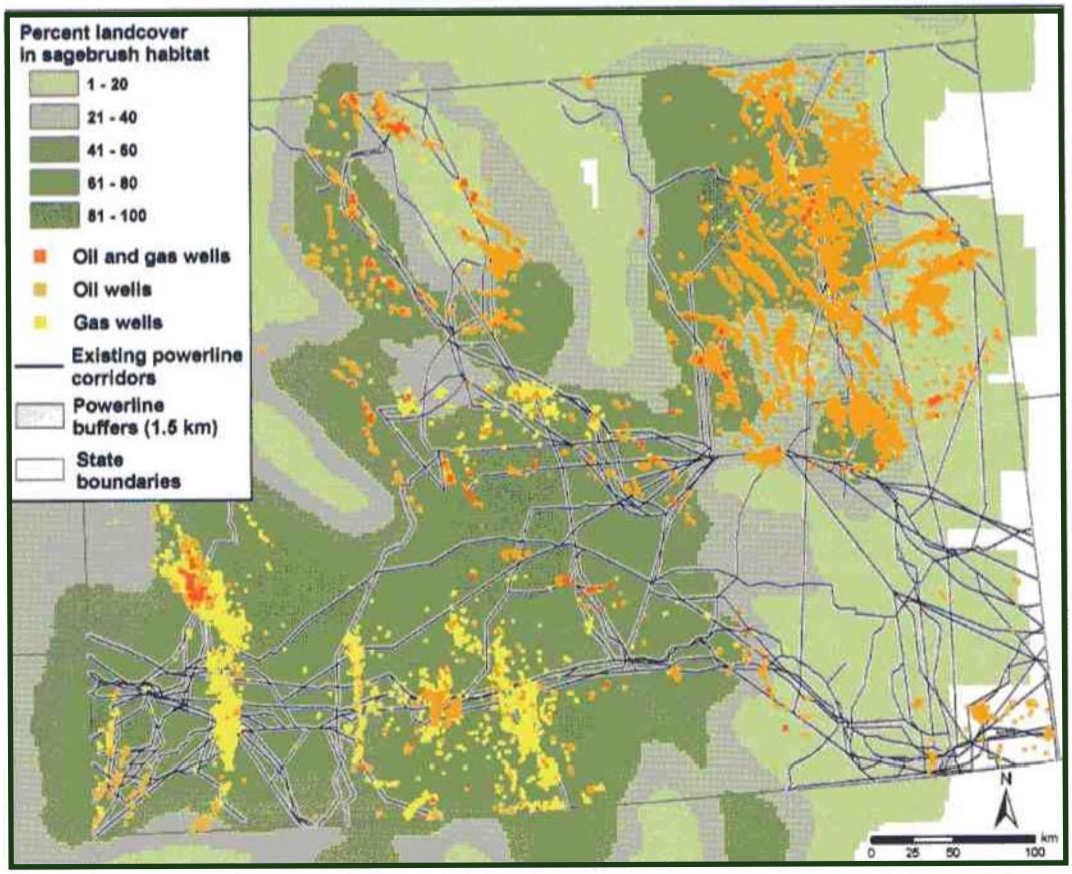

Figure 9. Oil and gas development in Wyoming relative to sagebrush distribution. Powerlines include a 1.5 km buffer due to potential for increased risk of predation by raptors and corvids in these areas. From Knick et al. 2003. © The Cooper Ornithological Society. Used with permission.

seeds from annual plants and roosting in large numbers. Very little research has explored the specific threats to lark buntings on their wintering grounds. Woody species encroachment in playas is a potential threat to lark buntings as they prefer more open areas for foraging (Lima 1990, Shane personal observation). Urbanization is resulting in habitat loss as large cities such as Phoenix, Tucson, Las Cruces, and El Paso grow. Large flocks of buntings may be found in agricultural fields during the winter and in migration. Broad-scale spraying for grasshoppers (Shane personal observation) on public and private land in late summer could impact migrating birds by depleting food supplies. In northern Mexico, sorghum fields near villages have been used by large numbers of lark buntings (Shane 1996). As human populations increase in this region and in proximity to bunting concentrations during winter, lark buntings may be viewed as pests and control actions proposed.

Conservation Status of the Lark Bunting in Region 2

Shortgrass prairie, mixed-grass prairie, and shrubsteppe habitats are the predominant habitats used for nesting and foraging by lark buntings in the breeding season (Dechant et al. 2003). Much of this habitat is endangered due to conversion to cropland, urbanization, overgrazing, and natural resource extraction. Lark buntings can nest and raise offspring in agricultural and hay fields if adequate vegetative cover is available and direct mortality from farm equipment is avoided (Wilson 1976, Shane 1996). However, these agricultural environments are not ideal for maintaining productive breeding populations.

Global and National populations of lark buntings are considered secure (NatureServe 2005). However in

Region 2, lark buntings are listed as either a species requiring management attention or a species of immediate management concern (Colorado PIF 200, Nicholoff 2003, Rich et al. 2004). Although populations are globally secure, most agencies agree that the lark bunting should be monitored closely.

Shane (1996) analyzed lark bunting population abundance using five different approaches to conclude that populations fluctuate at particular locales but that the lark bunting population is not in peril. However, due to the lack of information regarding population fluctuations and the confirmed decline of many other grassland bird species, this species should be monitored to ensure that it is not overlooked should the population become unstable.

Potential Management of the Lark Bunting in Region 2

As discussed above, the major threats to lark bunting populations include habitat loss, habitat fragmentation, and habitat degradation. In this section we begin with a summary of existing management plans and recommendations for the lark bunting. We follow with a discussion of the implications of various management techniques and our conclusions regarding their value in the conservation of the lark bunting. We conclude with a brief discussion of the methodologies most appropriate for monitoring lark bunting populations.

Management approaches

There have been few studies that report comprehensive management recommendations specific to the lark bunting. Dechant et al. (2003) provide a comprehensive list of management recommendations specific for the lark bunting across its breeding range. Wyoming Partners in Flight provides detailed recommendations for management of lark bunting habitats within the state as well as recommendations specific to the lark bunting (Nicholoff 2003). Colorado Partners in Flight (2000) make some management recommendations for lark buntings within the Central Shortgrass Prairie Physiographic Area. Below we combine and summarize the recommendations of these studies.

General habitat

1. Provide contiguous areas of grassland habitat since small fragments are avoided by lark buntings.
2. Retain shrubs, cacti, and other tall vegetation (10 to 30 percent of total vegetative cover) to provide shade for nests.

Grazing

1. Avoid heavy summer grazing in lark bunting nesting areas to retain vegetation for nesting cover. This is particularly true in shortgrass habitats; grazing can be beneficial to lark buntings in taller grass habitats.
2. Avoid long-term grazing in shortgrass prairie habitat. Use rotational-grazing over the short term to create patchy habitats that are desirable for lark buntings and other grassland species.
3. In areas where cowbird parasitism occurs, rotate livestock in alternate years during the breeding season. This will rest areas from high cowbird concentration and allow birds to breed without experiencing high parasitism frequencies.

Burning

1. Perform prescribed burns in the fall to avoid destruction of lark bunting nesting habitat. Burns should be small or patchy so some nesting cover is left for the following spring.

Agriculture

1. Avoid or minimize the use of insecticides in lark bunting nesting habitat until after the breeding season to ensure adequate food for adults and young. Use integrated pest management practices to minimize insecticide exposure.
2. Delay mowing of hayfields as much as possible (mid-July) if lark buntings are nesting in the field. Avoid night mowing.
3. Minimize field operations that destroy nests (e.g., discing). Utilize subsurface tillage methods.
4. Leave crop residue in agricultural fields where lark buntings nest to provide cover for nest sites and insect prey.

Implications and potential conservation elements

Most of the habitats used by lark buntings are classified as critical or endangered by the World Wildlife Fund with conversion to cropland being the major cause of habitat loss (Ricketts et al. 1999). Urban sprawl resulting from growing human populations, particularly in the Front Range of Colorado, will likely put increasing demands on lark bunting habitat over the next several decades. Future increases in oil and gas extraction will continue to fragment and degrade habitats in Wyoming and Colorado (Knick et al. 2003). Only a paucity of shrubsteppe habitat is protected with most being in private ownership (Knick et al. 2003). New oil and gas exploration leases in the shrubsteppe habitats require careful review of environmental impacts and development of suitable mitigation measures (Ricketts et al. 1999).

Management of grasslands involving a combination of moderate grazing and prescribed fire to maintain the mosaic habitat typical of native prairie prior to European settlement would be beneficial to numerous grassland species including the lark bunting (see Fuhlendorf and Engle 2001). Frequent burns (2 to 3 years) eliminate nesting cover. Partial burns allow patches of nesting cover to be retained. In short and mixed grass prairies, burns every 5 to 10 years result in a mosaic of successional stages that can be beneficial to a variety of grassland birds (Petersen and Best 1987).

Preserving large tracts of land and reducing habitat fragmentation would lessen risks of brood parasitism and nest predation on lark buntings. As much of the lark bunting habitat is privately owned, landowner incentives such as the CRP and partnerships with conservation agencies have the potential to increase lark bunting habitat. CRP lands are considered beneficial to lark bunting populations (Johnson and Schwartz 1993a, Johnson and Igl 1995; but see Shane 1996). However, in tallgrass areas or regions where CRP supports tall vegetation, some management of the vegetation to promote patchiness and reduce plant height would benefit lark bunting. Furthermore, incentives and education programs that help landowners to minimize insecticide use through integrated pest management practices would benefit lark buntings during the nesting season.

Tools and practices

Methods for monitoring bird populations are divided into two categories: 1) index counts that use counts or bird detections on maps as an index to relative abundance and 2) empirical modeling techniques that take into account variation in species detectability when estimating bird density (Rosenstock et al. 2002). Traditionally, researchers monitoring populations of birds have relied on index counts (e.g., BBS, CBC) despite admitted problems with variability in observer skill level and in bird detectability due to differences in species, habitats, and distances from observers (Diefenbach et al. 2003). More recent monitoring studies employ "distance sampling" to address these problems (Buckland et al. 2001). In distance sampling, direct estimates of density may be made without confounding effects of variation in detectability. Field methods of distance sampling are similar to index sampling. Rather than accounting for all individuals within a set distance, the observer estimates the perpendicular distance of the bird from a line transect or estimates the distance of the bird at an angle from a point. There are three critical assumptions in distance sampling: 1) all birds occurring on the transect (or at the point for point sampling) are detected; 2) birds are detected by the observer before they make evasive movements; and 3) distances are accurately estimated by the observer. A free computer program called DISTANCE (Thomas et al. 1998; available at http://www.ruwpa.st-and.ac.uk/distance/) is used to analyze data and calculate density estimates. Distance sampling is a strong approach to use for estimating lark bunting abundance on plots.

Long-term population monitoring of lark buntings may be problematic due to fluctuations in local populations that occur from year to year (Dechant et al. 2003). Thus a broad-scale monitoring program at the landscape level is likely to be more accurate in assessing year-to-year variation in the population. This approach would involve a coordinated monitoring program across all of the states in Region 2.

Line transects that incorporate distance sampling would be the most appropriate method for estimating the abundance of individual lark bunting populations (e.g., Diefenbach et al. 2003). Demographic studies should be included with population monitoring. Banding individuals to determine survivorship and nest success data will be important in determining causes of lark bunting declines in different regions, but only through a large banding program, coordinated across states, will estimates of survival be possible.

Information Needs

Lark buntings have a large range through the United States, Mexico, and Canada, but many of the scientific studies on lark bunting ecology and behavior have occurred in Weld County, Colorado (Baldwin et al. 1969, Giezentanner and Ryder 1969, Giezentanner 1970, Creighton 1971, Baldwin and Creighton 1972, Baldwin and Boyd 1973, Wiens 1973, Wunder 1979, Rotenberry and Wiens 1980, With and Webb 1993, Yackel Adams et al. 2006). Therefore, much of the information on lark buntings comes from populations occupying the same habitat, which may lead to a distorted view of bunting ecology across its broad breeding range. Research in diverse landscapes is needed to fully understand the biology, ecology, and management of this species.

Local fluctuations in lark bunting populations are documented (Shane 1996, Peterjohn and Sauer 1999). However, the reason for such local fluctuations across breeding seasons is not fully understood. Long-term studies are needed to determine the causes of these fluctuations.

Little demographic work has been conducted on the lark bunting since the 1970s (but see Yackel Adams et al. 2006, Yackel Adams et al. in revision), and most of those studies were done in Weld County, Colorado. Information on survival rates and lifetime reproductive success are needed from all major lark bunting breeding habitats.

The types and characteristics of plants used as vegetative cover for nests are well described. However, the relationships between habitat suitability and management actions (e.g., grazing, prescribed burns, pesticides) and natural disturbances (e.g., drought, wildfire) are not well studied. Other information needs pertaining to breeding habitat are the relationship between patch size and nest success and rates of brown-headed cowbird parasitism (Dechant et al. 2003). More information is needed on the effects of fragmentation on breeding success and population source/sink dynamics. The growing threat to shrubsteppe habitats from increased oil and gas extraction (Debevoise and Rawlins 1996) and the direct impacts of these activities on the lark bunting need study.

Studies of grassland birds during migration and on their wintering grounds should be a priority for future research. Habitat use, particularly the relative importance of agriculture fields versus natural habitats, and the potential pest status of lark buntings are areas of research that need investigation. Impacts of habitat loss, fragmentation, and degradation on the wintering grounds are needed. Areas in northern Mexico represent a large portion of the lark bunting’s winter range, but little study of the species has occurred there.

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APPENDIX A

Matrix Model Assessment of Lark Buntings

(Prepared by David B. McDonald)

Life cycle graph and model development

Matrix demographic models facilitate assessment of critical transitions in the life history of a species. A key first step is to create a *life cycle graph*, from which we compute a projection matrix amenable to quantitative analysis using computer software (Caswell 2001). We constructed a stage-classified life cycle graph for lark buntings that had two stages (**Figure A1**), first-year and "adult". From the life cycle graph, we conducted a matrix population analysis assuming a birth-pulse population with a one-year census interval and a post-breeding census (Cochran and Ellner 1992, McDonald and Caswell 1993, Caswell 2001). Note that the breeding pulse comes at the end of each one-year census interval. Individuals counted as fledglings are therefore able to breed as "yearlings" just before they are censused again in the second stage (almost a year later).

Because of the nature of the data, we conducted two distinct analyses. One took the available demographic data (vital rates) at "face value" while the other used various adjustments in order to arrive at a projection matrix with a population growth rate (λ) close to 1.0. The demographic term for a population that is neither growing in size nor shrinking is a "stationary" population. For the "face value" model we used the following criteria in order to estimate the vital rates.

- The number of fledgling females per female was based on a weighted average of fledglings in data from Saskatchewan, Kansas, two sites in Colorado, and one in Utah (**Table A1**).

- First-year survival was decremented from the "adult" survival rate by using the average from data for six bird species spanning a range of body sizes around that of the lark bunting (**Table A2**). The decrement factor used was 0.9031.

- Adult survival rate was estimated at 0.492, based on a regression for survival rates of granivorous open-country birds spanning a range of body sizes (14.5 to 82 g) around the body size (37.6 g) of the lark bunting (**Table A3**). The body weight data came from Møller and Cuervo (2003). The linear regression equation for annual survival (P_a) was P_a = 0.0017 g + 0.4285, where g is body weight in grams.

The criteria for vital rate estimation under the stationary model were:

- The number of fledgling females per female was based on the data in **Table A1**, omitting the low values observed in Kansas.

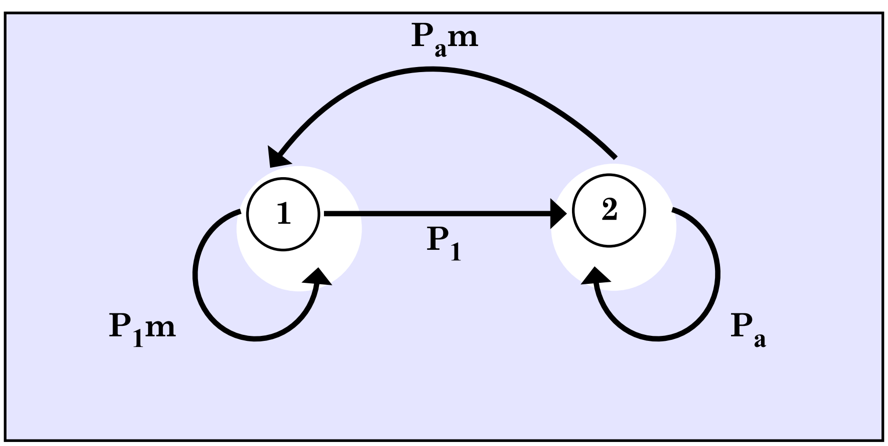

Figure A1. Life cycle graph for lark bunting, consisting of circles (*nodes*), describing stages in the life cycle and *arcs*, describing the *vital rates* (transitions between stages). Node 1 denotes first-year females, while Node 2 denotes "adult" females. The horizontal arc describes the first-year survival rate. The arcs, pointing back to Node 1 describe fertility (e.g., $P_a * m$). The self-loop on Node 2 denotes the annual survival rate of "adult" females. Each of the arcs corresponds to a cell in the matrix of **Figure A2**.

Table A1. Weighted average for number of fledglings from studies at four lark bunting study sites. The values of *m* in **Table A3** are half the values calculated here, because they are female-only.

Location	Number of nests	Number fledged	Source
Saskatchewan	7	1.57	Smith and Smith 1966
Kansas	78	0.74	Wilson 1976
Colorado (1)	31	1.6	Strong 1971
Colorado (2)	37	2.3	Strong 1971
Utah	9	1.67	Johnson 1981
Weighted average		1.348	
Weighted average (excluding KS)		1.913	

Table A2. Ratio of first-year to "adult" survival rates from Siriwardena et al. (1999).

Common name	Scientific name	Survival ratio
Bullfinch	*Pyrrhula pyrrhula*	0.8049
Chaffinch	*Fringilla coelebs*	0.9661
Goldfinch	*Carduelis carduelis*	0.9
Greenfinch	*Carduelis chloris*	0.9302
Linnet	*Carduelis cannabina*	0.9211
House sparrow	*Passer domesticus*	0.8964

Table A3. Survival data for seven species of open-country birds, used to estimate the "adult" survival rate of lark buntings, based on their body mass. The data are from Møller and Cuervo (2003). Survival rate for lark bunting was fitted from its body mass (37.6 g) using the linear fit to these data, as described in the text.

Common name	Scientific name	Weight (g)	Survival rate
Corn bunting	*Emberiza calandra*	48	0.48
Chaffinch	*Fringilla coelebs*	21.4	0.489
Blue grosbeak	*Guiraca caerulea*	27.5	0.376
Savannah sparrow	*Passerculus sandwichensis*	17.4	0.485
Lazuli bunting	*Passerina cyanea*	15.5	0.462
Indigo bunting	*Passerina amoena*	14.5	0.49
Western meadowlark	*Sturnella neglecta*	82	0.594

- ❖ First-year survival was decremented as described above.
- ❖ Adult survival rate was estimated at 0.54, within the range for the estimates for the comparator species in **Table A2** and **Table A3**.

Because the models assume female demographic dominance, the fledgling number used was half the published values, assuming a 1:1 sex ratio. We assumed reproduction beginning the year after hatch (i.e., at the end of Stage 1).

The models had two kinds of input terms: P_{ij} describing survival rates, and m_i describing fertilities (**Table A4** and **Table A5**). **Figure A2a** shows the symbolic terms in the projection matrix corresponding to the life cycle graph. **Figure A2b** and **Figure A2c** give the corresponding numeric values for the "face value" and stationary models. Note also that the fertility terms (F_i) in the top row of the matrix include a term for offspring production (m_i) as well as 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 "face value" model yielded λ of 0.792, which would represent a drastic population decline. The λ under the stationary model was 1.007. This should, of course, not be taken to indicate stationary population dynamics because the near-1 value of λ was used as

Table A4. Vital rates for lark bunting, used as inputs for projection matrix entries of **Figure A1** and **Figure A2** for the "face value" model.

Vital rate (fertility or survival)	Numerical value	Description
m	0.674	Number of female fledglings produced by a female
P_1	0.445	Survival of first-year females
P_a	0.492	Survival of "adult" females

Table A5. Vital rates for lark bunting, used as inputs for projection matrix entries of Figures A1 and A2 for the stationary population model.

Vital rate (fertility or survival)	Numerical value	Description
m	0.957	Number of female fledglings produced by a female
P_1	0.488	Survival of first-year females
P_a	0.54	Survival of "adult" females

$$\begin{array}{c|cc} \textbf{Stage} & 1 & 2 \\ \hline 1 & P_1{*}m & P_a{*}m \\ 2 & P_1 & P_a \end{array}$$

Figure A2a. Symbolic values for the cells of the projection matrix. Each cell corresponds to one of the arcs in the life cycle graph. The top row is fertility, with compound terms describing survival of the mother (P_i) and fledgling production (m). The matrix differs from a strictly age-classified (Leslie) matrix because of the entry in the bottom right, corresponding to the self-loop on the second ("adult") node in the life cycle graph.

$$\begin{array}{c|cc} \textbf{Stage} & 1 & 2 \\ \hline 1 & 0.30 & 0.332 \\ 2 & 0.445 & 0.492 \end{array}$$

Figure A2b. Numeric values for the "face value" projection matrix.

$$\begin{array}{c|cc} \textbf{Stage} & 1 & 2 \\ \hline 1 & 0.467 & 0.517 \\ 2 & 0.488 & 0.54 \end{array}$$

Figure A2c. Numeric values for the stationary projection matrix.

Figure A2. The input matrix of vital rates, corresponding to the lark bunting life cycle graph (**Figure A1**). A2a) Symbolic values. A2b) Numeric values for the "face value" model ($\lambda = 0.79$). A2c) Numeric values for the stationary model ($\lambda = 1.007$).

a target toward which to adjust the estimated "adult" survival rate and was subject to the many assumptions used to derive all the transitions. The value of λ should, therefore, not be interpreted as an indication of the general well-being or stability of the population. Much more detailed and long term data would be required to have any confidence in the estimation of λ. The two models do, however, provide a basis for assessing the relative vulnerability of portions of the life cycle, when considering the management of lark buntings.

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 A1**] and the cells in the matrix, **A** [**Figure A2**]). 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 population growth rate (λ), which Caswell (2001, pp. 280-298) has shown to be a useful integrative measure of overall fitness. One can therefore use sensitivities to assess the relative importance of the 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 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 accurate estimation of transitions with large sensitivities. Third, sensitivities can quantify the effects of environmental perturbations, wherever those can be linked to effects on age-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 endangered species or the "weak links" in the life cycle of a pest.

Figure A3 shows the sensitivity matrices for the two models. In this analysis, the sensitivity of λ to changes in the vital rates was fairly even across all four transitions, especially in the stationary model. Overall, changes in survival rates would have slightly more impact on population dynamics than would changes in fertility rates.

Elasticity analysis

Elasticities are the sensitivities of λ to proportional changes in the vital rates (a_{ij}). 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 vital rates (the a_{ij} arc coefficients on the graph or 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 the lark bunting are shown in **Figure A4**. Under either model, the λ of lark buntings was most elastic to changes in "adult" survival, followed by first-year survival and "adult" reproduction", with first-year reproduction having the lowest value. Overall, survival transitions accounted for approximately 53.6 percent of the total elasticity of λ to changes in the vital rates under the stationary model and 62.2 percent of the total under the "face value" model. Survival rates are therefore the demographic parameters that warrant most careful monitoring in order to refine the matrix demographic analysis. They are also the most challenging to collect and least available. Caswell (2001) suggested that when elasticities and sensitivities are relatively evenly apportioned across the transitions in the life history, populations should be relatively robust to environmental fluctuations. It seems likely that lark buntings are, in this respect, fairly robust to environmental variability.

Other demographic parameters

The **stable stage distribution** (SSD; **Table A6**) describes the proportion of each stage in a population at demographic equilibrium. Under a deterministic model, any unchanging matrix will converge on a population structure that follows the stable stage distribution,

a)

Stage	1	2
1	0.378	0.561
2	0.419	0.622

b)

Stage	1	2
1	0.464	0.485
2	0.513	0.536

Figure A3. Possible sensitivities only matrix, $\mathbf{S_p}$ (remainder of matrix is zeros). a) "Face value" model with l = 0.79. b) Stationary population model, with l = 1.007. The λ of the lark bunting is almost equally sensitive to changes in any of the vital rates.

a)

Stage	1	2
1	0.378	0.561
2	0.419	0.622

b)

Stage	1	2
1	0.464	0.485
2	0.513	0.536

Figure A4. Elasticity matrix, **E** (remainder of matrix is zeros). a) "Face value" model. b) Stationary model. The λ of the lark bunting is most elastic to changes in "adult" survival (Cell e_{22}), followed by first-year survival and "adult" reproduction, followed by first-year reproduction. The evenness of the elasticities, especially under the stationary model, suggests that lark buntings should be relatively resistant to detrimental effects of variability.

Table A6. Stable Stage Distribution (SSD, right eigenvector). At the time of the census, just after the breeding season, the population is almost evenly divided between recent fledglings and "adult" birds under the stationary model.

Stage	Description	"Face value" SSD	Stationary SSD
1	First-year females	0.403	0.489
2	"Adult" females	0.597	0.511

regardless of whether the population is declining, stationary or increasing. Under most conditions, populations not at equilibrium will converge to the SSD within 20 to 100 census intervals. For lark buntings at the time of the post-breeding annual census, fledglings should represent 48.9 percent of the population and "adults" the remaining 51.1 percent. **Reproductive values** (Table A7) 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, egg) stage (Caswell 2001). 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 reproductive value of the first stage is, by definition, always 1.0. For lark buntings, an "adult" female (age of first breeding) is "worth" approximately 1.1 fledglings. The cohort generation time for lark buntings is 2.2 years (SD = 1.6 years).

Potential refinements of the models

Clearly, data on survival from Region 2 would increase the relevance and accuracy of the analysis. The present analysis should be considered as at best only an approximate guide to the forces acting on the demography of lark buntings in Region 2. Data from natural populations on the range of variability in the vital rates would allow modeling 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 variations in vital rates. Using observed correlations would incorporate 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

Table A7. Reproductive values for females. Reproductive values can be thought of as describing the "value" of a stage as a seed for population growth, relative to that of the first (fledgling) stage, which is always defined to have the value 1. Values were equivalent under the two variant models.

Stage	Description	"Face value" SSD
1	First-year females	1.0
2	"Adult" females	1.1

insufficient to assess reasonable functions governing density dependence.

Summary of major conclusions from matrix projection models

- The major purpose of the matrix model is to assess critical stages in the life history (e.g., juvenile vs. adult survival, fertility vs. survival) rather than to make (often unwarranted) predictions about population growth rates, population viability, or time to extinction. Because the data are scanty, the model also provides preliminary guidance on which vital rates should be the focus of any future monitoring efforts.

- Each of the transitions in the life cycle graph contributes relatively equally to the sensitivity and elasticity transitions. Such evenness of the values and similarity of the sensitivity and elasticity values is not true for many life histories.

- Survival accounts for slightly more than 50 percent of the total elasticity under both models. Proportional changes in survival will have the largest impacts on population dynamics.

- The evenness of the elasticities suggests that lark bunting population dynamics may be relatively robust to environmental variability. Nevertheless, their ability to respond to such variability, by moving over vast areas, presents other challenges for managers and should not be a basis for complacency.

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