Grasshopper Sparrow (*Ammodramus savannarum*): A Technical Conservation Assessment

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

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The grasshopper sparrow (*Ammodramus savannarum*). ©Kent Nickell. Used with permission.

Summary of Key Components for Conservation of Grasshopper Sparrow

The grasshopper sparrow (*Ammodramus savannarum*) is considered globally "secure" by the Natural Heritage Program because of its wide distribution across North America. However, according to the Breeding Bird Survey, grasshopper sparrow populations have declined by over 60 percent during the past 25 years. The U.S. Fish and Wildlife Service lists the grasshopper sparrow as a species of special concern, and the Florida subspecies is listed as federally endangered. Within the states of USDA Forest Service Region 2, which represent the core of this species' breeding range, grasshopper sparrow populations have also exhibited long-term declines. Declines in Colorado and South Dakota have outpaced national trends. In Colorado and Wyoming, the species is considered "vulnerable" by the S/B Natural Heritage Program. The grasshopper sparrow is listed as a priority bird species in the Colorado and Wyoming Partners in Flight bird conservation plans.

Within Region 2, the greatest threats to grasshopper sparrows are habitat loss, habitat fragmentation, and habitat degradation from grazing and current fire regimes. Habitat loss occurs mostly through urban development and conversion of grasslands to croplands. Grasshopper sparrows are sensitive to habitat fragmentation because they prefer large grassland patches and avoid smaller patches with low area to edge ratios. Although fire and grazing are obligatory disturbance processes necessary for the maintenance of grassland ecosystems and their avifauna, current regimes fail to replicate the natural dynamics under which grassland bird species and their habitats evolved. Their mismanagement often has a negative impact on the quality and availability of grasshopper sparrow habitats.

Conservation in Region 2 should focus on maintaining a heterogeneous grassland landscape that replicates conditions historically created by climate, native-species grazing, and fire. Because grassland types and their dominant disturbance processes vary across Region 2, a simple set of strategic guidelines for grasshopper sparrow management will not work As an overriding strategy, management of native and agricultural grasslands should attempt to mimic the natural disturbance regime (Samson and Knopf 1994). While found in most grassland types, grasshopper sparrows require large patches of grasslands of intermediate height and cover. The creation and maintenance of this habitat condition is best accomplished by managing multiple large patches of grassland habitat in a variety of successional stages through different or rotating management schemes (e.g., fire, grazing, mowing). This ensures that some habitat patches will always be in an intermediate seral stage, favored by grasshopper sparrows.

Besides a renewed emphasis on appropriate habitat management, successful conservation efforts for grasshopper sparrows and other grassland birds will require new and innovative strategies. Less than 7 percent of the grasslands within the states of Region 2 are in federal ownership, and management of these lands alone is unlikely to ensure the long-term population viability of this species. There is a critical need to develop partnerships between private landowners, conservation organizations, and state and federal agencies that are actively involved in the conservation of prairie lands important to birds. Federal grasslands can play a significant role by demonstrating appropriate management for the maintenance and restoration of the biotic integrity of these lands.

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Introduction

This assessment is one of many being produced to support the Species Conservation Project for the Rocky Mountain Region (Region 2), USDA Forest Service (USFS). The grasshopper sparrow (*Ammodramus savannarum*) is the focus of an assessment because it has been identified as a sensitive species in Region 2 (**Figure 1**). Within the National Forest System, a sensitive species is a plant or animal whose population viability has been identified as a concern by a regional forester because of significant current or predicted downward trends in abundance or habitat capability that would reduce its distribution (FSM 2670.5 (19)). Because a sensitive species may require special management, knowledge of its biology and ecology is critical. This assessment addresses the biology, ecology and conservation of the grasshopper sparrow throughout its range in Region 2. This introduction defines the goal of the assessment, outlines its scope, and describes the process used in its production.

Goal

Species assessments produced as part of the Species Conservation Project are designed to provide managers, biologists, government agencies, and the public with a thorough discussion of the biology, ecology, conservation, and management of select species based on current scientific knowledge. The assessment goals limit the scope of the work to critical summaries of scientific knowledge, discussion of broad implications of that knowledge, and outlines of information needs. This assessment does not seek to develop prescriptive management recommendations. Rather, it provides the ecological background upon which management must be based and focuses on the consequences of changes in the environment that result from management (i.e., management implications). This assessment does cite management recommendations proposed elsewhere, however, and when management recommendations have been implemented, I describe the results of the implementation.

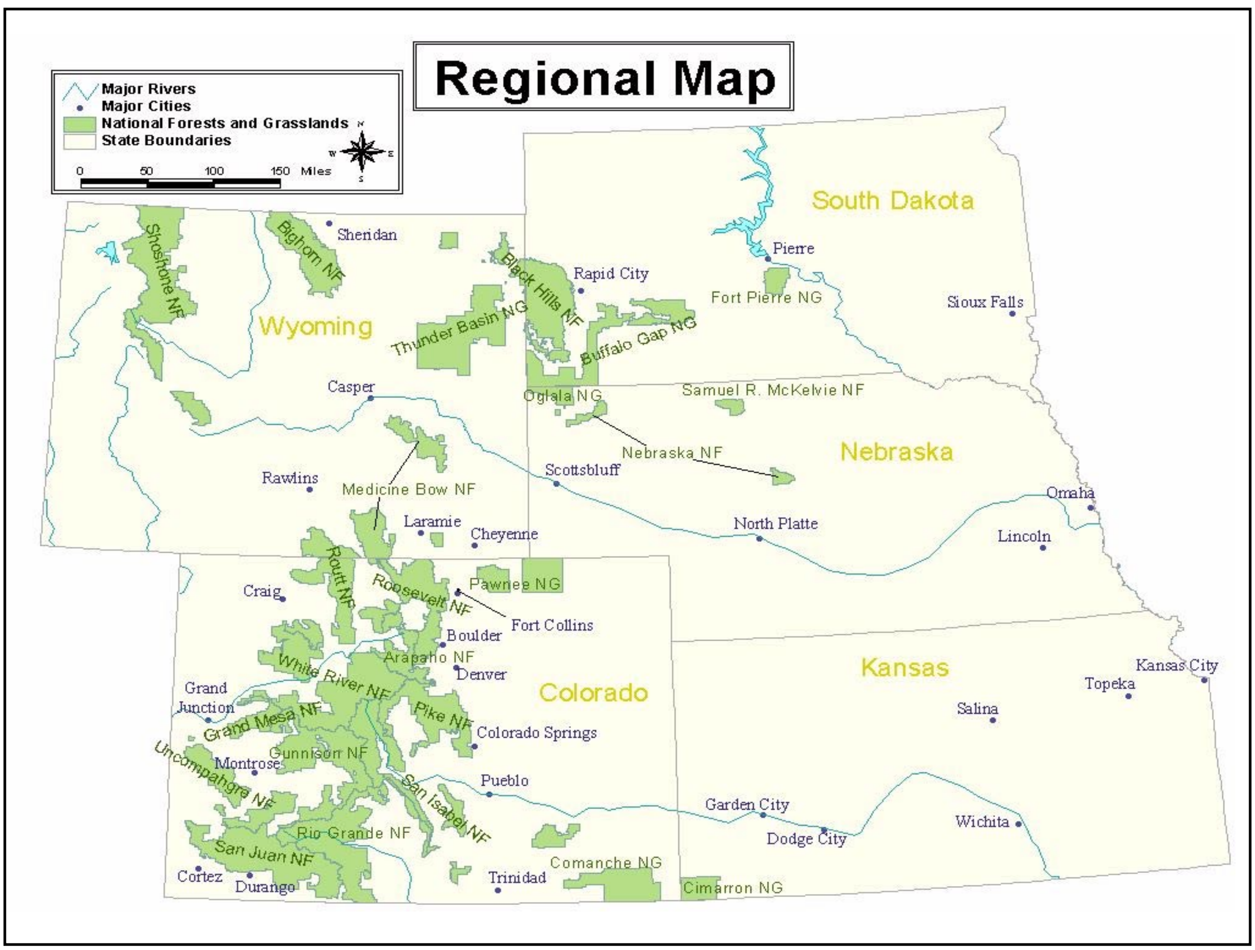

Figure 1. Regional map of USDA Forest Service, Region 2. National grasslands and forests are shaded green.

Scope

The grasshopper sparrow assessment examines the biology, ecology, conservation, and management of this species with specific reference to the geographic and ecological characteristics of the USFS Rocky Mountain Region. Although some of the literature on the species originates from field investigation outside the region, this document works to place that literature in the ecological and social context of the central Rockies. Similarly, this assessment is concerned with reproductive behavior, population dynamics, and other characteristics of the grasshopper sparrow in the context of the current environment rather than under historical conditions. The evolutionary environment of the species is considered in conducting the syntheses, but placed in a current context.

In producing the assessment, I reviewed refereed literature, non-refereed publications, research reports, and data accumulated by resource management agencies. Not all publications on grasshopper sparrows are referenced in the assessment, nor are all published materials considered equally reliable. The assessment emphasizes refereed literature because this is the accepted standard in science. Non-refereed publications or reports were used when published information was not available, but these were regarded with greater skepticism.

Treatment of Uncertainty

Science represents a rigorous, systematic approach to obtaining knowledge. Competing ideas regarding how the world works are measured against observations. However, because our descriptions of the world are always incomplete and observations limited, science focuses on approaches for dealing with uncertainty. Sorting among alternatives may be accomplished using a variety of scientific tools (experiments, modeling, logical inference). In this assessment, the strength of evidence for particular ideas is noted and alternative explanations described when appropriate. While well-executed experiments represent a strong approach to developing knowledge, alternative approaches such as modeling, critical assessment of observations, and inference are accepted as sound approaches to understanding and used in synthesis for this assessment.

Publication of Assessment on the World Wide Web

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

Peer Review

Assessments developed for the Species Conservation Project have been peer reviewed prior to 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 two grasshopper sparrow subspecies found in Region 2, *A. s. perpallidus* and *A. s. pratensis*, are not listed under the U.S. Endangered Species Act. However, the Florida subspecies, *A. s. floridanus*, is federally Endangered (Federal Register 1986), and *A. s. perpallidus* is listed as Endangered in British Columbia, Canada (Cannings 1991). USFS Region 2 includes the grasshopper sparrow in its revised sensitive species list, effective December 1, 2003. Of the states within Region 2 (Colorado, Kansas, Nebraska, South Dakota, and Wyoming), only one has a special designation for the grasshopper sparrow; in Wyoming, the species is designated as a species of special concern (Fertig and Beauvais 1999). The grasshopper sparrow is designated by the U.S. Fish and Wildlife Service as a Bird of Conservation Concern (nationally, in Region 6, and in the following Bird Conservation Regions [BCR]: Prairie Pothole [BCR 11], Badlands and Prairies [BCR 17], and Eastern Tallgrass Prairie [BCR22]) (U.S. Fish and Wildlife Service 2002).

The Natural Heritage Program's global rank for grasshopper sparrow is G5 (secure) (NatureServe Explorer 2003). Within the states of Region 2, Heritage ranks vary from S3 to S4 during the breeding season, indicating the species is considered vulnerable to apparently secure (**Table 1**, NatureServe Explorer 2003). During the non-breeding season, either no rank or a rank of SZN is given, indicating that the species is not abundant enough to warrant conservation concern (**Table 1**). The grasshopper sparrow is considered a priority bird species in the Partners in Flight (PIF) Wyoming Bird Conservation Plan (Cerovski et al. 2001) and the Colorado Land Bird Conservation Plan (Colorado Partners in Flight 2000) for the Central Shortgrass Prairie Physiographic Area; PIF Bird Conservation Plans for South Dakota, Nebraska, and Kansas have not been completed.

Table 1. Status of the grasshopper sparrow in states within USDA Forest Service Region 2 based on the Natural Heritage Program rankings (NatureServe Explorer 2001).

State	Natural Heritage Rank
Wyoming	S3B and SZN
South Dakota	S4B and SZN
Nebraska	S4
Kansas	S4B
Colorado	S3S4B and SZN

S3	Vulnerable - Either because rare and uncommon, or found only in a restricted range (even if abundant at some locations).
S4	Apparently Secure - Uncommon but not rare, and usually widespread, although the species may be quite rare in parts of its range, especially at the periphery.
B	Breeding population.
N	Non-breeding population.
Z	Taxa that is not significant concern in a state during the non-breeding season.

Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies

No regulatory mechanisms or laws specifically target protection of the grasshopper sparrow. However, several laws exist that provide protection to a broad array of wildlife species, including the grasshopper sparrow.

The Migratory Bird Treaty Act of 1918 establishes a federal prohibition, unless permitted by regulations, to "pursue, hunt, take, capture, kill, attempt to take, possess, offer for sale, sell, offer to purchase, purchase, export, at any time, or in any manner, any migratory bird, including any part, nest, or egg of any such bird." (16 U.S.C. 703). The National Environmental Policy Act of 1969 requires agencies to specify environmentally preferable alternatives in land use management planning. Under the National Forest Management Act of 1976, the USFS is required to sustain habitats that support healthy populations of all native and desired non-native plant and animal species on national forests and grasslands. Additional laws with which USFS management plans must be in compliance are the Endangered Species, Clean Water, Clean Air, Mineral Leasing, Federal Onshore Oil and Gas Leasing Reform, and Mining and Minerals Policy acts; all are potentially relevant to grasshopper sparrow conservation.

Although existing laws appear adequate to protect grasshopper sparrow breeding habitat on federal lands in Region 2, protection solely of these lands is unlikely to result in conservation of this species. The amount of federally protected grassland habitats is small relative to the overall area of grasslands in Region 2 and virtually nonexistent for eastern grasslands. The history of grasslands in the United States suggests that conservation will depend not only on protection of federal lands, but also on conservation efforts by private landowners, state wildlife agencies, and private conservation groups.

PIF, an international coalition dedicated to "keeping common birds common" and "reversing the downward trends of declining species", has coordinated the development of Landbird Conservation Plans for each state and/or physiographic region (modified from original strata devised by the Breeding Bird Survey; Robbins et al. 1986). These Bird Conservation Plans form the foundation of PIF's long-term strategy for bird conservation by identifying priority species and habitats, establishing biological objectives, and identifying actions to achieve objectives. Although priorities and biological objectives are identified at the physiographic area level, implementation of PIF objectives is meant to take place at multiple scales, including individual states, federal agency regions, joint ventures, and BCRs.

In Region 2, two states (Colorado and Wyoming) have completed PIF Landbird Conservation Plans, and both have identified the grasshopper sparrow as a priority species in the Central Shortgrass Prairie Physiographic Region. The Colorado Plan suggests key management actions that 1) provide a landscape mosaic of grassland parcels of different structural stages; 2) provide suitable habitat in patches large enough (>12 ha) to accommodate breeding birds; 3) graze lightly or not at all in areas of short, sparse grasses; 4) burn parcels in rotation; and 5) delay mowing until nesting is complete (Colorado Partners in Flight 2000). The Wyoming plan does not provide a list of key management strategies specifically for grasshopper sparrows. Instead, it provides an overall discussion of best management practices for native shortgrass prairie (Cerovski et al. 2001).

The Rocky Mountain Bird Observatory has developed a conservation program, "Prairie Partners", for grassland habitats and the birds that depend on them in the Great Plains region. As part of that program, they created a Best Management Practices manual for grassland birds (including the grasshopper sparrow) of the Comanche National Grassland in Colorado (Gillihan 1999). This document recommends that habitat for grasshopper sparrows should be managed in patches greater than 8 ha, and it suggests that optimal breeding habitat should include a mix of short to tall grasses (up to 30 cm), with tall forbs or scattered shrubs (<35 percent cover), and up to 35 percent bare ground. There is no information on whether federal or state agencies or private landowners have implemented these management practices.

In general, grassland bird conservation has been a relatively recent phenomenon, and comprehensive approaches to stem the long-term declines in grassland birds are only beginning to be discussed and implemented (Herkert and Knopf 1998). However, given the extensive loss and degradation of grassland habits and the fact that most are in private ownership, it is clear that successful conservation efforts will largely depend upon the creation of a broad range of partnerships among private landowners, federal and state wildlife agencies, and private conservation groups.

Biology and Ecology

Systematics and species description

The grasshopper sparrow is in the Order: Passeriformes, Family: Emberizidae. Twelve grasshopper sparrow subspecies are recognized based on plumage and morphometric analyses. However, evidence for differentiation among several subspecies is weak (Paynter and Storer 1970, Olson 1980). Four subspecies breed in North America. Two are highly migratory: *A. s. pratensis* in the eastern United States west to Michigan and Wisconsin and south to eastern Oklahoma and northeast Texas, and *A. s. perpallidus* in the western United States. *A. s. ammolegus* is a partial migrant that breeds in southeast Arizona and southwest New Mexico to northern Sonora, Mexico. The fourth, *A. s. floridanus*, is a resident of central Florida. Four grasshopper sparrow subspecies found in the in the Caribbean are presumed resident and nonmigratory: *A. s. borinquensis* (Puerto Rico), *A. s. intricatus* (lowland savannas of Hispanola), *A. s. savannarum* (Jamaica), and *A. s. caribaeus* (Curacao and Bonaire Islands). Four resident subspecies are found in Central and South American: *A. s. bimaculatus*, *A. s. cracens*, *A. s. beatriceae*, and *A. s. caucae* (Vickery 1996).

The grasshopper sparrow is a small (11 to 13 cm long), flat-headed grassland sparrow. Unlike other *Ammodramus* sparrows, the buff-cream breast of this species is unmarked to faintly streaked. The crown is blackish with narrow, buff streaks and a white-buff median crown stripe. It has a pale buff face with a complete eye-ring and a dark spot on rear auriculars. The grasshopper sparrow has a gray nape with fine reddish brown streaks that blend into an intricate pattern of chestnut-rust, black, and gray streaks on its back. The tail is short and rounded, with the rectrices pointed and with a bare shaft at the tip. Sexes are monomorphic. Juveniles (May through September) have a band of streaks across their breasts. There is only slight color variation among subspecies, but Florida birds (*A. s. floridanus*) are recognizably blacker on their backs and more whitish on their breasts (Vickery 1996, Sibley 2000).

Grasshopper sparrows are one of the few North American sparrows with two completely different songs: Primary Song and Sustained Song (Vickery 1996). The Primary Song is a short, staccato, high-pitched initial note followed by a long, dry, insect-like trill (Smith 1959). It appears to be mostly territorial, is sung by unpaired males, and is often alternated with wing-flutter displays (Vickery 1996). The Sustained Song is more musical with a sustained (5 to 15 s) series of short, buzzy notes. It appears to be connected to attracting mates and maintaining pair bonds through the breeding season (Smith 1959). Only males sing this song, from fixed perches or in flight. A third vocalization, the Trill, is sung by both sexes and is used to maintain pair bonds and to announce presence around a nest (Walkinshaw 1940, Smith 1959).

Distribution and abundance

The grasshopper sparrow has a widespread distribution throughout most of the Americas, but it often breeds locally and is considered rare to uncommon in much of its range (Vickery 1996). Except for *A. s. pratensis* and *A. s. perpallidus*, which overlap in the eastern Great Plains (extent unknown), all subspecies are allopatric during the breeding season (Phillips et al. 1978, Vickery 1996).

The breeding range of grasshopper sparrows extends north to the southernmost portions of Alberta, Saskatchewan, and Manitoba, all but northeastern Minnesota, the lower Upper Peninsula of Michigan, southeastern Ontario, southern Quebec, western Vermont, southeastern New Hampshire, and extreme southern Maine. It breeds south to the upper coastal plains of the Carolinas, central portions of Georgia, Alabama, and Mississippi, northern Louisiana, and all but the southeastern and southernmost parts of Texas, and it breeds west to extreme northeastern Arizona, central Colorado and Wyoming, and western Montana. In Florida, the grasshopper sparrow is a resident and breeds in the central interior, north of Lake Okeechobee (Stevenson and Anderson 1994). In western North America, grasshopper sparrows breed in southern British Columbia, eastern Washington and Oregon, central Idaho, northeastern Nevada, northern Utah, southwestern Wyoming, north-central Nevada, along the California coast, the western edge of the Sierra Nevada, and in northwestern Baja California (where they are resident) (Vickery 1996). Breeding range is poorly known in Mexico and Central America (Howell and Webb 1995), but resident populations occur along the Atlantic slope of Mexico, in the central plateau region of Zacarecas, Mexico, in central Belize, Costa Rica (Stiles and Skutch 1989), Panama (Ridgely and Gwynne 1989), western Columbia (Hilty and Brown 1986), Jamaica (Downer and Sutton 1990), Hispanola (Stockton de Dod 1978), and Puerto Rico (Raffaelle 1989).

Even though the grasshopper sparrow maintains a widespread breeding range, populations have declined substantially, and several populations on the fringe of its range are endangered. In the United States, numbers of grasshopper sparrows (primarily *A. s. pratensis* and *A. s. perpallidus*) have declined 69 percent since the late 1960's, concomitant with the loss of native prairies and their conversion to croplands (Herkert 1994a). In coastal Massachusetts and much of New England, *A. s. pratensis* has been reduced to remnant populations (<400 pairs; Jones and Vickery 1995). The Florida subspecies, formerly widespread in central Florida, is now limited to four counties north of Lake Okeechobee (Delany et al. 1985). In contrast, *A. s. pratensis* has increased in South Carolina in recent years (McNair and Post 1993). The statuses of the Caribbean and Central and South American subspecies are not well documented.

Breeding density varies considerably across North America, but according to the North American Breeding Bird Survey (BBS) the highest numbers of grasshopper sparrows occur on the grasslands of North and South Dakota, Nebraska, Colorado, and Kansas (**Figure 2**; Sauer et al. 2003). In Wisconsin, density averaged 0.75 territories/ha (Wiens 1969), while in North Dakota density was 0.24 to 0.25 territories/ha in native and lightly grazed prairie (Renken and Dinsmore 1987). In Florida, territory density (± SD) was highest on plots that were recently burned (0.41 ± 0.14), but it decreased by half over the following 30 months. However, grasshopper sparrow density should not be considered a good indicator of habitat quality or potential breeding success (Van Horne 1983, Vickery et al. 1992a). During the non-breeding season, northern limits of this species' range are poorly known because of its secretive nature and low abundance. Grasshopper sparrows winter north across the southeastern United States, west through Texas, southern Arizona, and southern California (**Figure 3**; Sauer et al. 1996, Vickery 1996). The species winters south to southern Baja California and Chiapas, Mexico, southern Guatemala, northern El Salvador, and southwestern Honduras, the Valle Central of Costa Rica, the Gulf coast, southern Florida, north Bahama Island, and Cuba. It has also been observed locally in the Yucatan Peninsula (Vickery 1996).

Regional distribution and abundance

In Colorado, grasshopper sparrows nest throughout the eastern plains, with highest concentrations in the northeastern counties of Phillips, Sedgewick, Logan, and northern Yuma and Washington; along the Arkansas River in Kiowa, Prowers, and Bent counties, and on the Comanche National Grassland in southeastern Colorado (Kuenning 1998, Colorado Partners in Flight 2000). Sparrow distribution and abundance decreases westward to the mountains as grasslands become scarce. In suitable habitat, grasshopper sparrows breed throughout Kansas, South Dakota (except for the Black Hills where breeding is sporadic), and Nebraska (irregular in extreme west) (Johnsgard

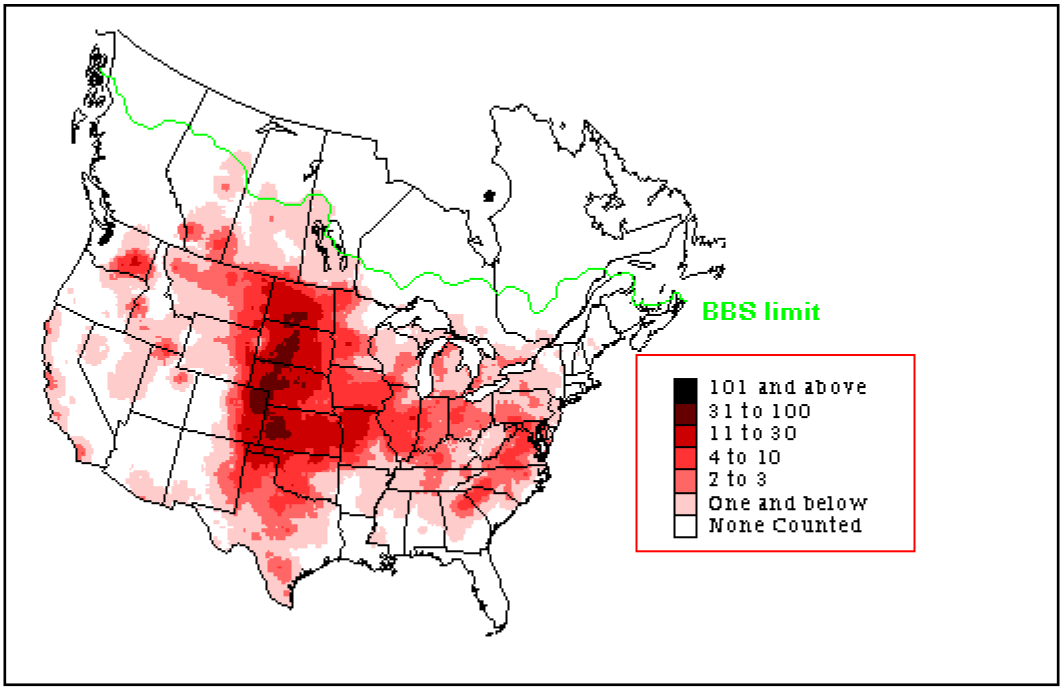

Figure 2. Relative breeding season abundance (average number of birds per route) of grasshopper sparrows, based on Breeding Bird Survey data from 1982 to 1996 (Sauer et al. 2003).

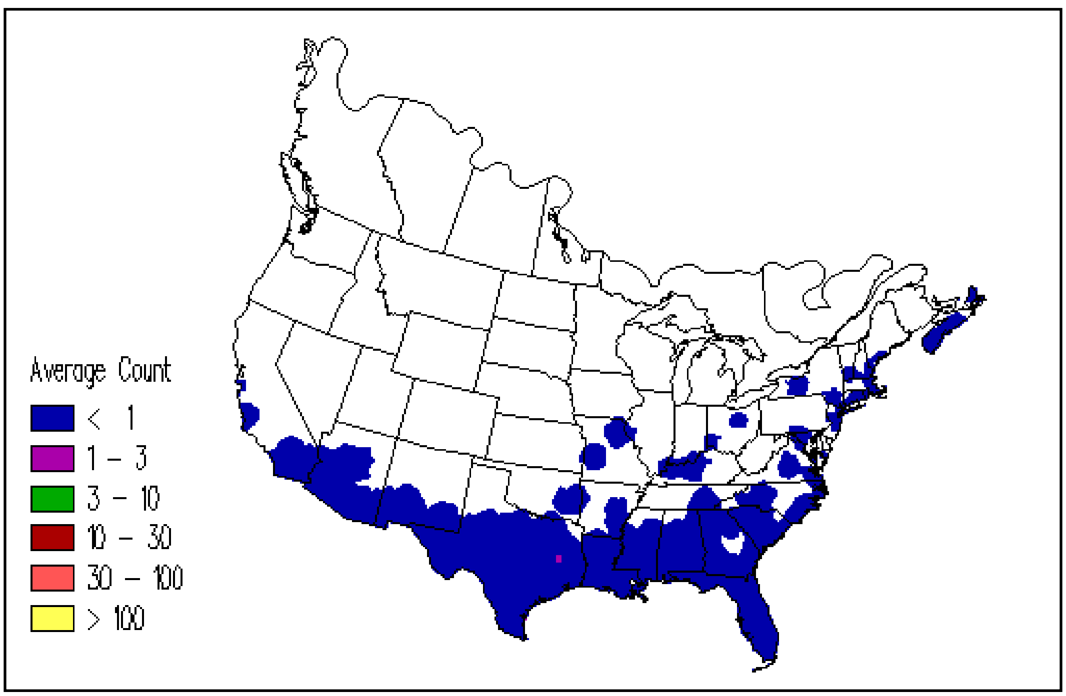

Figure 3. Winter season distribution and relative abundance of grasshopper sparrows based on Christmas Bird Counts from 1982 to 1996 (Sauer et al. 1996).

1979). According to the South Dakota Breeding Bird Atlas (Peterson 1995), grasshopper sparrows are considered common and widespread (**Figure 4**). In Wyoming, they breed in suitable habitat, mostly in eastern shortgrass prairies (Fertig and Beauvais 1999). The predicted occurrence of grasshopper sparrows based on Wyoming Gap Analysis is shown in **Figure 5**.

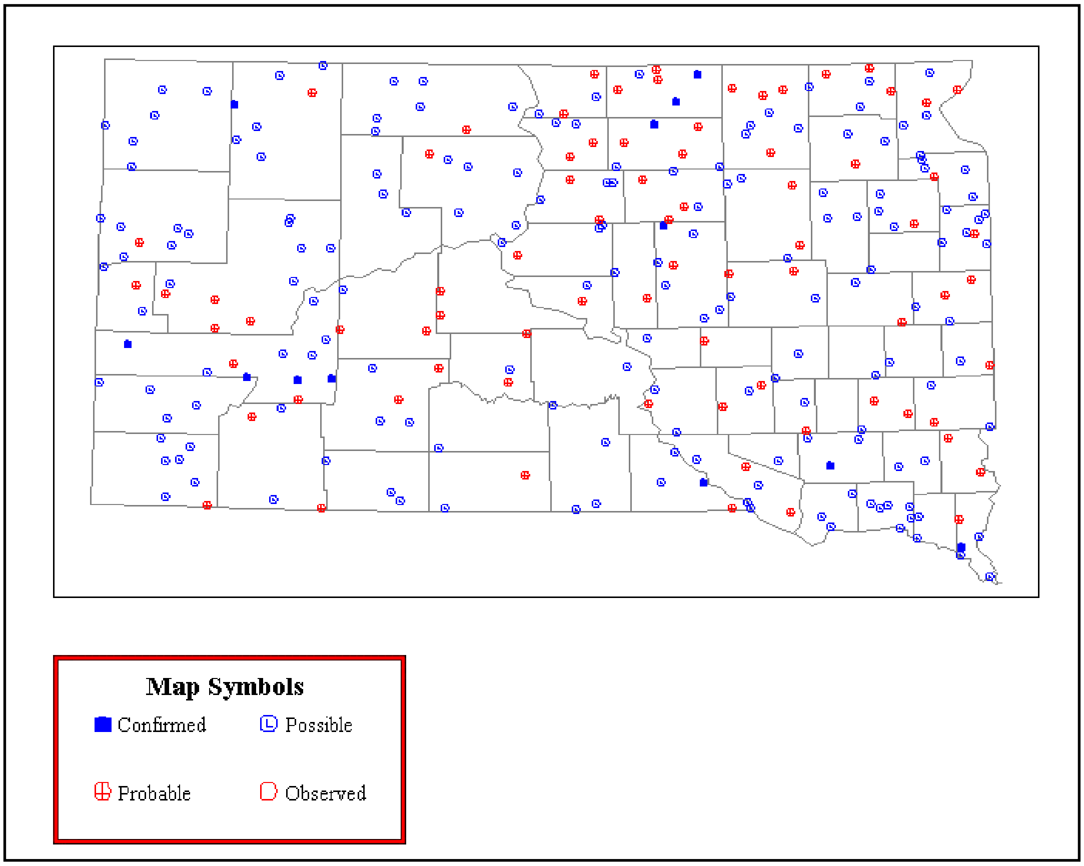

Figure 4. Map of South Dakota Breeding Bird Atlas grasshopper sparrow detections (Peterson 1995).

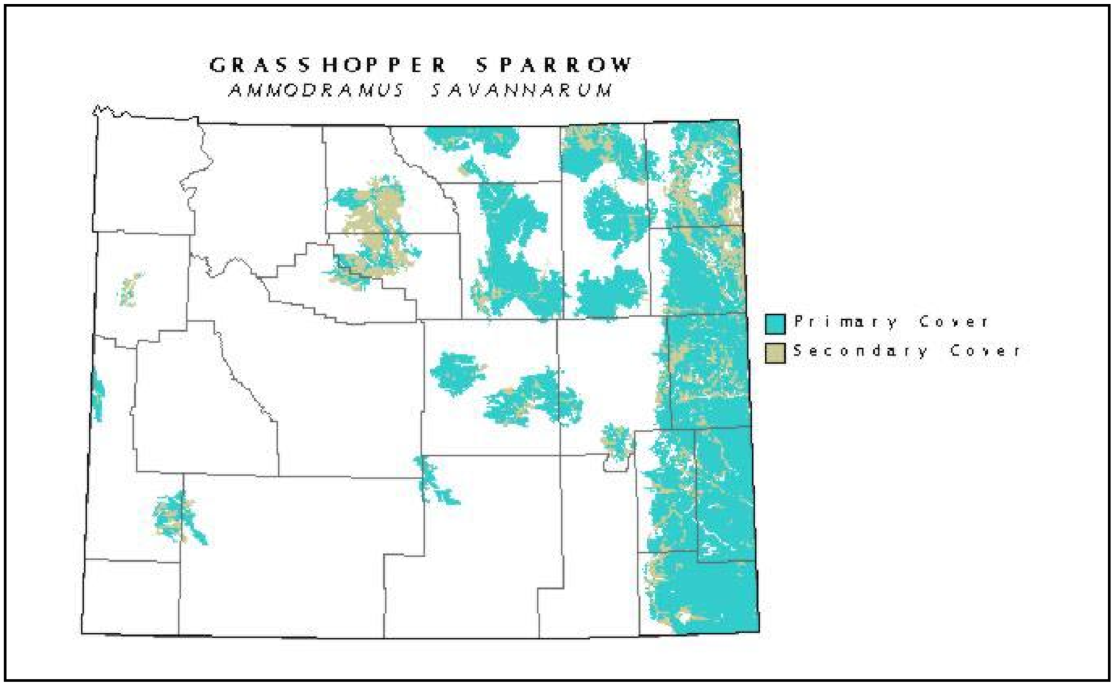

Figure 5. Map of predicted occurrences for the grasshopper sparrow in Wyoming based on GAP Analysis (Fertig and Beauvais 1999).

Few studies have attempted to estimate density of grasshopper sparrows in USFS Region 2. In Conservation Reserve Program (CRP) fields in eastern Montana, North and South Dakota, and western Minnesota, grasshopper sparrow abundance averaged 0.21 males/ha compared to 0.005 males/ha in active cropland (Johnson and Schwartz 1993). In Nebraska CRP fields seeded to native tallgrass species, grasshopper sparrow density was 0.77 territories/ha (Delisle and Savidge 1997).

Regional discontinuities in distribution and abundance

Although this species inhabits a wide variety of grassland types, their specific vegetation structural requirements often result in a localized and patchy distribution. Populations may be geographically isolated, but there is no information on movement between populations or the genetic and demographic consequences of this pattern. Outside of Region 2, a disjunct population occurs in central Nevada, and the federally endangered Florida subspecies is completely isolated. Certainly, *A. s. pratensis* and *A. s. perpallidus* populations at the periphery of their breeding distributions are more likely to become isolated due to habitat loss and fragmentation.

Population trend

There has been no effort to enumerate population size or to evaluate the population trend of this species range-wide. The most significant long-term effort to assess broad scale patterns and population trends in birds, including the grasshopper sparrow, is the BBS, conducted annually in Canada and the United States since 1966. The BBS produces an index of relative abundance rather than a measure of absolute abundance or density estimate for breeding bird populations. Data analyses assume that fluctuations of abundance indices are representative of the population as a whole. However, these data should be viewed with caution. Large sample sizes are needed to average local variations and to reduce the effects of sampling error (variation in counts attributable to both sampling technique and real variation in trends) (Sauer et al. 2003). Consequently, local trends, if based on few surveys, are difficult to interpret and can be quite different from larger-scale BBS trends (Peterjohn and Sauer 1999). Credibility measures have been incorporated for BBS data (Sauer et al. 2003). Only data in the highest reliability category are presented here.

According to the BBS (Reference Period 1966 to 2002), grasshopper sparrow populations declined significantly ($P < 0.01$) at a rate of 3.8 percent per year in the United States; this translates to a cumulative population decline of 60 percent (Sauer et al. 2003). Similarly, results for the Central Region of the BBS indicate a decline of 3.1 percent per year ($P < 0.01$). Within Region 6 of the U.S. Fish and Wildlife Service (Montana, North and South Dakota, Wyoming, Nebraska, Utah, Colorado, and Kansas), there is also a significant ($P < 0.01$) decline of 2.9 percent per year (**Table 2**). In Physiographic Area 36 (Central Shortgrass Prairie) BBS data indicate an annual decline of 2.6 percent (1966 to 1996; $P = 0.09$; $n = 54$ routes) (Colorado Partners in Flight 2000). Of the 16 states with reliable data, nine (56 percent) have a significant decreasing trend; no state or physiographic region indicates a significant increasing trend (Sauer et al. 2003).

The National Audubon Society's Christmas Bird Count (CBC) represents another long-term data set to assess the status and trends of bird populations albeit in the non-breeding season. Like the BBS, there are serious limitations in the CBC's ability to investigate population trends, and more research is needed in developing analysis methods (Sauer et al. 1996). Currently, population trend data from CBC data need to be viewed with caution. For grasshopper sparrows,

Table 2. Breeding Bird Survey trend data for grasshopper sparrow, 1966-2002 (From Sauer et al. 2003).

	1966-2002			1966-1979			1980-2002		
	Trend	***P***	***N***	**Trend**	***P***	***N***	**Trend**	***P***	***N***
United States	-3.8	0.00	1459	-4.4	0.00	814	-3.1	0.00	1306
Central Region	-3.1	0.00	569	-2.2	0.01	283	-2.8	0.00	543
U.S. Fish and Wildlife Service Region 6	-2.9	0.00	318	-3.1	0.00	139	-2.8	0.00	304
Colorado	-2.7	0.12	46	-1.4	0.74	9	-6.3	0.00	45
Nebraska	-1.4	0.55	44	-3.8	0.36	26	-2.2	0.51	43
South Dakota	-4.4	0.00	43	-5.8	0.00	30	-4.0	0.02	38

CBC data indicates a relatively low, but even abundance across the southern portion of the United States (**Figure 3**). CBC data (1959 to 1988) indicate a survey-wide trend of -0.1 percent per year in the United States (n = 286 survey circles; Sauer et al. 1996).

Regional

Much like the population trends observed throughout its range, grasshopper sparrows are declining through most of the Rocky Mountain Region of the USFS (**Figure 6**). Specific BBS statewide trends are described below.

Colorado. According to the BBS, grasshopper sparrow populations declined at a non-significant rate of 2.7 percent per over the period from 1966 to 2002 (**Table 2**). However, more recently (1980 to 2002), BBS data indicate a steeper and more significant decline of 6.3 percent per year ($P < 0.01$). The average number of grasshopper sparrows detected per route ($n = 46$) in Colorado from 1966 to 2002 was 11. The grasshopper sparrow was present on 70.98 percent (SE = 1.88) of the BBS routes in Central Shortgrass Prairie in Colorado between 1988 and 1997, and average abundance equaled 21.05 (SE = 1.31) individuals per route (Colorado Partners in Flight 2000).

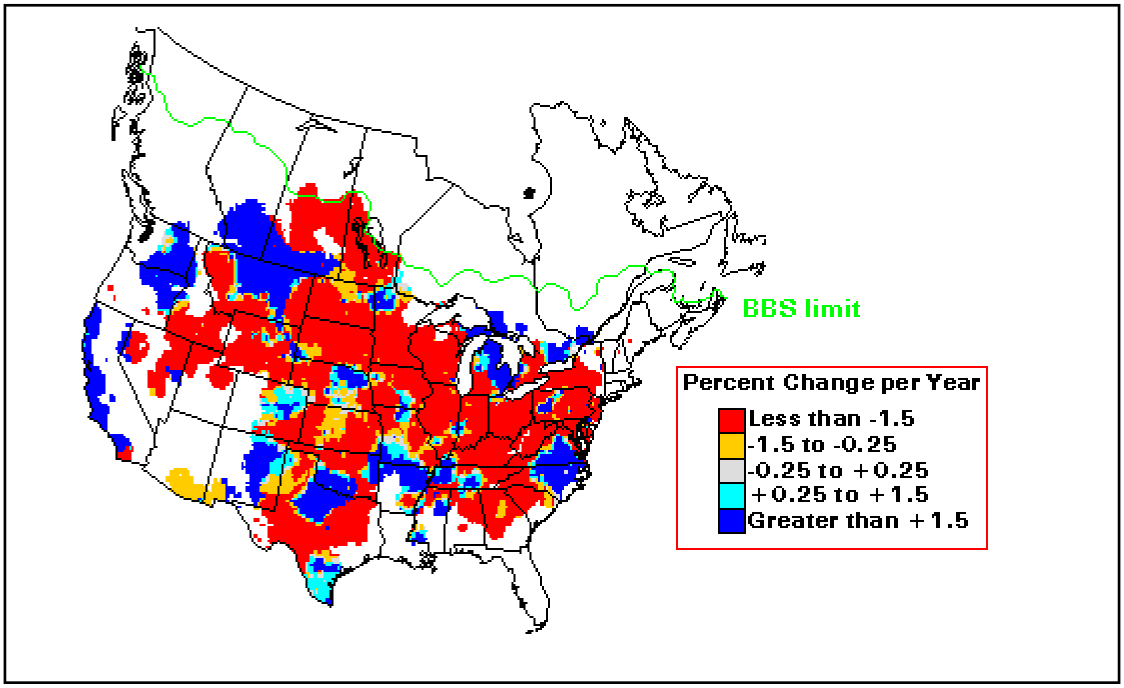

Figure 6. Grasshopper sparrow trends (average percent population change per year) based on Breeding Bird data from 1966 to 1996 (Sauer et al. 2003).

Nebraska. In Nebraska, trend estimates do not indicate significant declines (**Table 2**). The average number of grasshopper sparrows per route in Nebraska between 1966 and 2002 was 19.14 (n = 44), almost twice that of routes in Colorado.

South Dakota. Grasshopper sparrows declined significantly ($P < 0.01$) during the period from 1966 to 2002 in South Dakota. Populations decreased 4.4 percent per year (**Table 2**). The average number of grasshopper sparrows per route was 21.38 ($n = 43$).

Wyoming and Kansas. BBS data for Wyoming and Kansas are not sufficient to estimate trends.

Activity pattern and movements

No formal daily (circadian) time budgets have been reported for grasshopper sparrows (Vickery 1996). Diurnal time budgets in Wisconsin indicated that grasshopper sparrows (presumably males) spent 63.8 percent of their time singing, 19.3 percent foraging, 10.2 percent perching, 4.4 percent flying, 1.4 percent preening, and 0.9 percent in aggression and display (Wiens 1969). In aviary trials, grasshopper sparrows spent 53 percent of their time searching for prey, 10 percent handling prey, and 37 percent in nonforaging activities (Joern 1988).

Only *A. s. pratensis* and *A. s. perpallidus*, both of which are found in the Rocky Mountain Region, are highly migratory. Given their widespread distribution, it is not surprising that there is substantial variation in the timing of grasshopper sparrow migration. Southern populations tend to arrive on breeding grounds earlier than northern populations (Vickery 1996). In Colorado, and most likely adjacent states in Region 2, grasshopper sparrows arrive on their breeding grounds in early to mid-May (Kuenning 1998).

In general, information on sex and age differences in migration patterns is lacking. Males appear to arrive on the breeding grounds before females in Colorado (Kuenning 1998) and in other parts of their range (Vickery 1996). The arrival of many males in June to establish territories suggests that individuals in their first breeding season either migrate later than older birds or delay breeding (Wiens 1969).

Like spring migration, departure from the breeding ground is variable and likely depends on latitude and weather conditions. In general, fall migration appears to be more protracted that spring migration. In Region 2, birds likely begin moving south from late August through September (Vickery 1996). Migration pathways and linkages between breeding and non-breeding populations are unknown. Grasshopper sparrows migrate nocturnally, usually in small numbers or individually. However, they often join mixed-species flocks containing other sparrow species (Vickery 1996). Guidance mechanisms during migration are unknown, but they are probably similar to those of savannah sparrows (*Passerculus sandwichensis*), which include stellar, magnetic, and solar compasses (Able and Able 1990a, b).

Habitat

The grasshopper sparrow is found in a broad array of open grassland types, but it is notably area-sensitive, preferring large grassland patches greater than 8 ha in size (Samson 1980, Herkert 1994b, Vickery et al. 1994, Helzer 1996). Minimum area requirements vary over the species' range. In Maine, Vickery et al. (1994) estimated that the individual area requirement for the grasshopper sparrow approached 100 ha, while in Illinois, fragments >30 ha were required (Herkert 1994b). In Nebraska, grasshopper sparrows were found in fragments larger than 8 ha (Helzer 1996).

Grasshopper sparrows may select larger patches so that they can nest in interior sites and avoid edge habitats, where they suffer higher predation and parasitism rates (Johnson and Temple 1990, Bock et al. 1999). Grasshopper sparrows were more abundant and had higher productivity, presumably due to lower predation, on large fragments >100 m from a forest edge (Johnson and Temple 1986). These patterns were also supported by studies from states in Region 2. In Colorado, Bock et al. (1999) found grasshopper sparrows significantly more abundant on plots >200 m from the interface between suburban development and upland or lowland habitat. In Nebraska CPR fields, only one of 31 territories was located within 50 m of an edge (Delisle and Savidge 1997). However, rates of parasitism by cowbirds in Kansas tallgrass prairie did not differ between edges (within 100 m) and interior sites (Jensen 1999).

Within open grasslands of suitable patch size, grasshopper sparrows prefer grasslands habitats of intermediate height (~30 cm) with clumped vegetation interspersed with patchy bare ground, and sparse shrub cover (Bent 1968, Vickery 1996, Dechant et al. 2001). Grasslands across the grasshopper sparrow's breeding range vary in physiognomy and plant composition; this is mostly due to differences in soil and climate conditions and local disturbance regimes. Because of this variation, grasshopper sparrows often favor different vegetation components, depending on the specific grassland ecosystem in which they occur. For example, in arid grasslands of the West and Southwest, they occupy lusher areas with small amounts (<35 percent) of shrub or tall forbs. In the East and Midwest, they occupy grasslands on drier sites with sparser vegetation. Besides native prairie, grasshopper sparrows breeding habitat also includes pasture, hayland, CRP fields, airports, and reclaimed surface mines (Whitmore 1980, Vickery 1996, Dechant et al. 2001). They occasionally breed in croplands, such as corn and oats, but at a severely reduced density than in grassland habitats (Basore et al. 1986, Best et al. 1997, McMaster and Davis 1998).

In Region 2, grasshopper sparrows are found in Wyoming in mixed- and northern shortgrass prairies and open sagebrush grasslands (Cerovski et al. 2001). In Colorado, they almost exclusively prefer prairie grasslands that contain some degree of shrubs or tall plants (e.g., rabbitbrush or saltbush) (Kuenning 1998). In South Dakota, Nebraska, and Kansas they are primarily associated with mixed-grass prairies, but they can also be found in short-grass and tall-grass prairies, sage prairie, and disturbed grassland habitats such as stubble fields, hayfields and cropland (Johnsgard 1979).

In contrast to their broad-scale habitat choices, at the local scale, grasshopper sparrows have very specific structural vegetation requirements. Due to the difficulty in finding nests, only a few nest-site habitat studies have been conducted. However, numerous studies across many states and provinces have investigated the habitat characteristics associated with territories and/or species presence. Habitat associations identified in many of these studies are summarized and tabled in the comprehensive document by Dechant et al. (2001; available electronically at http://www.npwrc.usgs.gov/resource/literatr/grasbird/grasshop/grasshop.htm), and I encourage users of this assessment to browse that document. In **Table 3** I have summarized the most important characteristics based on studies in Region 2.

Table 3. Mean habitat characteristics associated with grasshopper sparrows in or adjacent to USDA Forest Service Region 2.

Source	Location	Habitat	Grass height	Grass Cover (percent)	Bare ground (percent)
Bock and Webb (1984)	AZ	Semi-desert shortgrass	30 cm	72	23
Gillihan (1999)	CO	Shortgrass	—	76	10
Jensen (1999)	KS	Tallgrass	33 cm	53	16
Renken and Dinsmore (1987)	ND	Mixed-grass	40 cm	62	19
Kantrud and Kogolski (1982)	CO, NE, WY, ND, SD	Mixed- and shortgrass	28 cm	—	—
Wiens (1970)	CO	Shortgrass	—	87	12

Grasshopper sparrows avoid habitats where vegetation is less than 10 cm (Wiens 1973) and appear to prefer grass heights of ~30 cm and mean grass cover values of >50 percent (**Table 3**). Grasshopper sparrows require some areas of bare ground for foraging, but it is unclear how much is desirable; most empirical studies suggest a range of 2 to 34 percent. Grasshopper sparrows require some taller vegetation, such as tall grasses, forbs, or scattered shrubs, to use as singing perches during territory establishment and for defense. However, they avoid habitats where shrub cover exceeds 35 percent (Smith 1968, Bock and Webb 1984). Scattered trees provide acceptable habitat and are used as song perches (Johnsgard 1979).

Few grasshopper sparrows winter in the Rocky Mountain Region, and empirical studies of habitat association during migration are lacking. During migration, however, they likely use a variety of grassland habitats similar to those used in the breeding season (Vickery 1996).

Habitat loss

The current distribution of suitable habitat available to grasshopper sparrows is a fraction of its historic extent (Vickery 1996). Loss of native prairies and grasslands, for agricultural and urban development, has been pervasive throughout North America. Initially, conversion of native prairie and grassland to hayfields and pastures partially subsidized the loss of native habitat. However, the conversion of hayfields and pastures to cropland has greatly affected this species' long-term decline (Vickery 1996).

No grassland types in North America have escaped the extensive loss and degradation of habitat. Tallgrass prairies, which historically extended from the central Great Plains to the Midwest, have been reduced by 88 to 99 percent, exceeding the losses found in any other major ecosystem type in North America (Samson and Knopf 1994, Vickery et al. 2000). Ninety-nine percent of the Palouse Prairie grasslands of eastern Washington, Oregon, and Idaho have been converted to agriculture. The loss of shortgrass prairie to agriculture (especially to winter wheat on marginally arable lands) is significant; in Saskatchewan, for example, over 85 percent of the original prairie has been lost. In the southwestern Great Plains, nearly 32 percent of the shortgrass prairie region (including 31 percent in Colorado, 78 percent in Kansas, 65 percent in Nebraska, and 12 percent in Wyoming) has been converted to cropland (Knopf and Rupert 1999). In other mixed- and tallgrass prairies of Region 2, conversion to agriculture is probably higher because these less arid areas are better able to support agriculture without extensive irrigation.

At first glance, the degree of habitat loss in Region 2 may appear to be less than in other areas, but figures of direct loss are misleading. Areas that have not disappeared due to urban development or agriculture have been degraded due to grazing and fire suppression.

Grazing management strategies favor uniformly grazed rangelands and remove the natural heterogeneous landscape favorable to grassland birds (Vickery et al. 2000). Grazing and fire suppression also cause habitat degradation by changing plant height, vigor, and in some cases, community composition (Colorado Partners in Flight 2000).

Food habits

The grasshopper sparrow forages almost exclusively on bare ground. During the breeding season, insects, mostly grasshoppers (Orthoptera), comprise the majority (>60 percent) of their diet, with seeds taken secondarily (Vickery 1996). In Oklahoma mixed prairie, grasshopper sparrow diet consisted of Orthoptera (36 percent), Lepidoptera larva (20 percent), Coleoptera (18 percent), seeds (14 percent), Hemiptera (9 percent), and Araenida (4 percent) (Wiens 1973). In South Dakota tallgrass prairie, diet consisted of seeds (31 percent), Orthoptera (30 percent), Lepidoptera larva (16 percent), Coleoptera (10 percent), Hemiptera (9 percent), Homoptera (6 percent), Araenida (3 percent), Hymenoptera (2 percent), and Hemiptera (1 percent) (Wiens 1973). In the winter, sparrows switch to a seed-dominated diet (Martin et al. 1951). Stomach content analysis of *A. s. pratensis* (n = 35) identified seeds in the following order of abundance: bristlegrass (*Setaria* spp.), sheepsorrel (*Rumex* spp.), oats (*Avena* spp.), and smartweed (*Polygonum* spp.). For *A. s. perpallidus* (excluding California; n = 60), the order of abundance is as follows: bristlegrass, ragweed (*Ambrosia* spp.), panicgrass (*Panicum* spp.), wood sorrel (*Oxalis* spp.), sunflower (*Helianthus* spp.), and sedge (*Carex* spp.) (Martin et al. 1951).

Breeding biology

Phenology and nesting

The start of the grasshopper sparrow breeding season varies according to subspecies and locality, with resident species and southern populations breeding slightly earlier than migrants and northern populations. For migratory subspecies, pair formation occurs on the breeding grounds as soon as females arrive, which is usually 3 to 5 days after males arrive (Vickery 1996).

Specific nest-site selection behavior has not been described for the grasshopper sparrow, and because of their secretive behavior and cryptic nests, few studies of their breeding ecology have been conducted (Vickery 1996). For the migratory subspecies, nest-building probably begins immediately after pair formation, while the resident subspecies in Florida begins nest-building approximately four weeks after the start of territorial singing (Vickery 1996). In Region 2, nest initiation by *A. s. pratensis* and *A. s. perpallidus* usually begins in May and lasts about 90 days, but it may be extended in years of favorable weather (Vickery 1996). The female alone builds the cup nest, which is domed with overhanging grasses and has a side entrance. Construction usually takes two to three days.

There is little information on breeding-site fidelity among years. Several studies in areas outside of Region 2 have observed that between 20 and 50 percent of breeding adults, typically those that were successful, returned in proximity to their breeding site (Crossman 1989, Collier 1994, Vickery 1996). However, none of 85 banded adults and juveniles returned to a mixed-grass prairie in the Nebraska Sandhills over a three-year period (Kaspari and O'Leary 1988).

Clutch size, incubation, and parental care

McNair (1987) examined museum egg data slips and found an average rangewide clutch size of 4.30 ± 0.69 (SD; range 3 to 6; n = 438); egg data slips that noted less than three eggs were excluded because they were thought to be for incomplete clutches. These results are similar to those found in field studies. In West Virginia, mean annual clutch size ranged from 4.1 to 4.5 over a three year period (n = 44; Wray et al. 1982), and in Michigan, mean clutch size was 4.4 (range 4 to 5; n = 7; Walkinshaw 1940). Clutch size declines with clutch initiation date, suggesting that females lay fewer eggs in nests after their initial attempt (McNair 1986).

Only the female incubates the eggs, and incubation likely commences with the laying of the penultimate egg (Vickery 1996). The incubation period lasts 11 to 13 days for *A. s. pratensis*, *A. s. perpallidus*, and *A. s. floridanus* (Vickery 1996). Nestlings are brooded and fed by both adults. Non-parental attendants, juveniles unrelated to the parents and adults from neighboring territories whose nests had been recently depredated, assisted with food delivery at 17 percent (n = 23) of nests in Nebraska (Kaspari and O'Leary 1988). When non-parental attendants arrived with food, parents moved away from the nest; however, they vigorously chased away unrelated birds that did not bring food. Parental males made significantly fewer feeding trips ($P < 0.05$) to nests with non-parental attendants (Kaspari and O'Leary 1988). The nestling period is relatively short. In Michigan and Pennsylvania, nestlings generally left the nest at eight or nine days (Walkinshaw 1940, Smith 1963); in Nebraska, nestlings departed between six and eight days (Kaspari and O'Leary 1988). Young do not fly when leaving nest, but run through the vegetation. Both male and female provide postfledging care; the duration of this care is unknown. The female probably only provides four to 19 days of postfledging care before attempting a second brood (Vickery 1996).

Typically, grasshopper sparrows can complete at least two broods annually, even in northern parts of their range. Nests are not reused (Vickery 1996). Kuenning (1998) suggested that Colorado Breeding Bird Atlas data indicated the sparrow does not engage in second nesting. In contrast, double brooding in Nebraska was common (Kaspari and O'Leary 1988). Confusion regarding second broods may be due, in part, to late-arriving birds in June, which are thought to be first year breeders (Smith 1963, Wiens 1969, Santner 1992). These individuals likely produce only one brood per season. Grasshopper sparrows will renest quickly after failure and may renest as many as three to four times during the breeding season. The young of the first brood have usually dispersed from natal territories by the time parents are feeding nestlings of the second brood, but it is not known if this dispersal is independent or promoted by parents (Vickery 1996). In Florida, fledglings are known to gather in loose flocks with no parental care three to four weeks after fledging (Vickery 1996).

Demography

Genetic issues

No studies that examine genetic diversity among and within subspecies and populations have been conducted. With a widespread, mostly contiguous distribution throughout North America, it is unlikely that grasshopper sparrow subspecies, *A. s. pratensis* and *A. s. perpallidus*, and their populations in the Rocky Mountain Region suffer from genetic issues related to small populations. However, the continued loss and fragmentation of grassland habitats may have genetic consequences in the future, particularly at the outermost limits of their range. Habit loss and fragmentation isolate and create smaller populations; this, in turn, increases the likelihood of local extinctions, decreases the probability of colonization, and genetically isolates populations. This then leads to increased probabilities of inbreeding and genetic drift and a lowering of genetic diversity. Fragmentation can potentially turn continuous populations into "metapopulations of semi-independent demes" that gradually disappear (Risser 1996).

Life history characteristics

As noted previously, few breeding studies of this species have been conducted, resulting in a paucity of demographic data. The age of first breeding by grasshopper sparrows is presumed to be the first spring after hatching and annually thereafter (Vickery 1996). Information on age-related variation in reproductive success is unavailable. However, first-year breeders likely produce fewer young, given their late arrival on the breeding grounds (Wiens 1969). Nesting success (probability of producing at least one fledgling per nest) is quite variable and is largely determined by predation pressure (Vickery 1996). In areas outside of Region 2 (i.e., Florida, Illinois, Iowa, and Maine), nesting success varied from 16 to 50 percent (Vickery et al. 1992b, Vickery 1996). In southeast Nebraska, the only published study from Region 2, nesting success was reported as 52 percent (Delisle and Savidge 1996). The only measure of annual productivity (fledglings per year) comes from Iowa where grasshopper sparrows nesting in grassed strips in agricultural land produced 0.8 fledglings per year (Vickery 1996).

Like most landbirds, adequate information on lifespan and survivorship is missing. In Florida, a banding study of 48 males from a resident population indicated an annual survival rate of 0.60 with a mean longevity of 2.9 years (Delany et al. 1993). Several authors have reported annual return rates (i.e., apparent survival) for migratory populations, but these are unreliable estimates of annual survival because they do not consider the probability that a bird was alive but not resighted due to variation in site fidelity and observer effort. One would expect that survival in migratory populations should be lower than resident populations, due to the high cost of migration.

Life cycle diagram and model development (prepared with David B. McDonald). We created a life cycle graph and constructed a two-stage matrix population model for the grasshopper sparrow. When substantial data are available for a species, demographic modeling can be used to predict population growth rates (λ) under various environmental, demographic, and genetic conditions, providing a measure of the stability (e.g., population viability) of the wildlife population being modeled. However, in cases where data are limited, such as for the grasshopper sparrow, λ cannot and should not be estimated. Yet, modeling exercises (e.g., sensitivity and elasticity analyses) can provide valuable information regarding certain aspects of the population biology of the species of interest. For example, these analyses can improve 1) our understanding of how important specific vital rates are to λ, 2) our ability to identify those vital rates that are the most important for researchers to focus their efforts, and 3) our ability to quantify the effects of environmental perturbations, wherever those can be linked to effects on stage-specific survival or fertility rates.

In this section, we present a summary of our model results, and we direct readers to **Appendix A** for the complete methodological considerations and technical analyses. The matrix population analysis was produced with a post-breeding census for a birth-pulse population with a one-year census interval (McDonald and Caswell 1993, Caswell 2001).

Our first exercise was to conduct a sensitivity analysis. Sensitivity is the effect on population growth rate (λ) of an absolute change in the vital rates (i.e., survival and fertility). The vital rate to which λ was most sensitive for the grasshopper sparrow was adult (i.e., >1 year old) survival (33 percent of total). Nearly as important was first-year survival (29.5 percent of total). Thus, our major conclusion from the sensitivity analysis is that survival rates are most important to population viability.

Next, we conducted the elasticity analysis. Elasticities are useful in resolving a problem of scale that can affect conclusions drawn from the sensitivity analysis. Interpreting sensitivities can be somewhat misleading because survival rates and reproductive rates are measured on different scales. The elasticities have the useful property of summing to 1.0. Elasticity analyses for grasshopper sparrow indicate that population growth rate (λ) was most elastic to changes in adult survival (e_{22} = 39 percent of total elasticity). Next most elastic were first-year survival and adult reproduction ($e_{21} = e_{12}$ = 26.1 percent of total elasticity). Reproduction by first-year birds was relatively unimportant (e_{11} = 8.8 percent of total elasticity). The sensitivities and elasticities for the grasshopper sparrow were generally consistent in emphasizing survival transitions. Thus, survival rates, particularly for adults, appear to be the data elements that warrant careful monitoring in order to refine the matrix demographic analysis.

Finally, we constructed a stochastic model to simulate the effect of environmental variation on population growth rate (λ). The stochastic model produced two major results. First, high levels of stochastic fluctuations affecting survival had the greatest detrimental effects, and second, varying adult survival had the greatest detrimental effects. These results indicate that populations of grasshopper sparrow are vulnerable to stochastic fluctuations in survival (due, for example, to annual climatic change or to human disturbance) when the magnitude of fluctuations is high. Pfister (1998) showed that for a wide range of empirical life histories, high sensitivity or elasticity was negatively correlated with high rates of temporal variation. That is, most species appear to have responded to strong selection by having low variability for sensitive transitions in their life cycles. Grasshopper sparrows, however, may have little flexibility in reducing variability in first-year survival, which has a relatively high elasticity. Variable early survival, and probably fertility, is likely to be the rule rather than the exception.

Clearly, improved data on survival rates and age-specific fertilities are needed in order to increase confidence in this demographic analysis. The most important "missing data elements" in the life history of grasshopper sparrows are for survival transitions, which emerge as vital rates to which population growth rate (λ) is most sensitive as well as most elastic. Data from natural populations on the range of variability in the vital rates would allow more realistic functions to model stochastic fluctuations.

Summary of major conclusions from matrix projection model:

❖ Survival accounts for 65 percent of the total "possible" sensitivity, fairly equally distributed between first-year and "adult" survival. Any absolute changes in survival rates will have major impacts on population dynamics.

❖ "Adult" (e_{22} = 39 percent) and first-year (e_{21} = 26 percent) survival account for 65 percent of the total elasticity. Proportional changes in survival rates will have major impacts on population dynamics.

❖ Stochastic simulations echoed the elasticity analyses in emphasizing the importance of survival and rates to population dynamics.

❖ Reformulation of a matrix analysis when improved data are available might substantially change some of the values, but it would be unlikely to radically revise the major emphases presented here.

Home range and territory size

There is no information on grasshopper sparrow home ranges during the breeding or non-breeding season. However, defended territories of grasshopper sparrows are exclusive and aggressively defended by males against conspecific males. Territories are delineated by singing at conspicuous song-perches, flight displays, and agonistic interactions. After chasing an intruding male from its territory, males generally sing and flick wings. Territory defense is less vigorous after the young fledge, and young often move into adjacent territories (Smith 1968). The average territory size for grasshopper sparrows is small (<2 ha), but it can be quite variable depending on the habitat (Dechant et al. 2001). No studies in Region 2 have determined territory size, but estimates from other parts of their range include: 0.8 ha in Pennsylvania (*n* = 22; Smith 1968), 0.85 ha (*n* = 73) in Wisconsin (Wiens 1969), and 1.8 ± 0.96 ha (SD; *n* = 30) in Florida (Delany et al. 1993. During the breeding season, territory size decreases, primarily in response to late-arriving males establishing new territories (Wiens 1969).

Source/sink, demographically linked populations

There have been no studies of source-sink dynamics in this species, and there is a dearth of information on the effects of landscape outside of breeding patches. However, this issue may be critically important as it relates to source-sink dynamics and the maintenance of grasshopper sparrow populations. If grasshopper sparrows select larger patches, then, in times of low regional abundance, small patches will be less likely to attract breeding birds the following year, resulting in a greater probability of periodic local extinctions. Larger patches are less likely to suffer local extinctions because they support greater numbers of birds, which improves their chance of survival from one year to the next based on probability alone. Moreover, if larger patches provide higher nesting success than smaller ones, they should have a higher return rate of previous year's nesters and be more attractive to juveniles and other adults (Helzer and Jelinski 1999).

Factors limiting population growth

There is little doubt that the extensive loss of native grassland through urban and agricultural development and habitat degradation from grazing and fire suppression have been the primary factors in this species' long-term population decline (Saab et al. 1995, Vickery 1996). Under stable habitat conditions, however, there is little information on factors that influence reproduction and survival and that might play a proximate role in regulating populations.

During the breeding season, food availability and interspecific competition do not appear to affect grasshopper sparrow populations (Wiens and Rotenberry 1979, 1981). Predation appears to severely reduce this species' reproductive rates, yet reproduction likely varies temporally and spatially and long-term effects are unknown (Vickery 1996). The lack of information from the wintering grounds on winter mortality also hampers our ability to understand population regulation in this species.

Community ecology

Predators and competitors

The primary avian predator of the grasshopper sparrow is the loggerhead shrike (*Lanius ludovicianus*), based upon frequent observations of impaled adults and juveniles (Leppla and Gordon 1978, Stewart 1990). Raptors are likely infrequent predators (Vickery 1996). Some mammals and snakes are likely predators, taking adults and juveniles on the ground.

Nest predation is probably the primary cause of nest failure. Documented nest predators include: striped skunk (*Mephitis aurantia*), raccoon (*Procyon lotor*), weasels (*Mustela* spp.), ground squirrels (*Citellus* spp.), foxes (*Vulpes* spp.), cats (*Felis silvestrus*), feral pigs (*Sus scrofa*), crows (*Corvus* spp.), snakes (*Coluber constrictor*, *Elaphe* spp., *Thamnophis sirtalis*, *Lampropeltis* spp., and *Sistrurus miliarus*), and probably armadillos (*Dasypus novemcinctus*) (Smith 1968, Vickery 1996). Many predators appear to find nests incidentally to other foraging activities (Vickery et al. 1992c). In Maine, nest predation rates for grasshopper sparrows were positively correlated with skunk invertebrate foraging (Vickery et al. 1992c).

Nest predation rates for grasshopper sparrows decreased farther from woodland edge habitats and were lower in large (130 to 486 ha) than small (16 to 32 ha) grassland fragments. In a study in eastern Washington shrubsteppe habitats, predation rates for artificial nests and real nests were greater in fragmented than in continuous landscapes; this was attributed to increased predation by corvids (Vander Haegen et al. 2002). This type of pattern could also be expected in grassland habitats, where fragmentation and tree plantings have extended the range of nest predators such as crows and raccoons.

There is no evidence of direct competition between grasshopper sparrows and any other species. Savannah sparrows frequently occupy similar habitat as grasshopper sparrows and may dominate aggressive interactions with them (Wiens 1969). However, no interspecific interactions were observed in Maine, even though countersinging between the two species regularly occurred (Vickery 1996). Similarly, in overlapping territories in Pennsylvania, no agonistic behavior between the two species was observed (Piehler 1987). Grasshopper sparrows are occasionally displaced from singing posts by meadowlarks (*Sturnella* spp.) and bobolinks (*Dolichonyx oryzivorous*) (Vickery et al. 1994).

Parasites and disease

A nasal mite (*Ptilonyssus sairae*) was reported from a grasshopper sparrow in Texas (Spicer 1977). In a Florida population, a low incidence of Gulf Coast tick (*Amblyomaq maculatum*) and bird tick (*Haemaphysalis chordeillis*) was reported (Vickery 1996). In no instances has a disease or parasite been indicted to have a population level effect in this species.

Envirogram

An envirogram is a tool to depict the proximal and ultimate causes/components that affect a species' chance to survive and reproduce. Within the envirogram model, the environment comprises everything that might influence a species' chance to survive and reproduce. The environment consists of the "centrum" and the "web". Only those things that are the proximate causes of changes in the physiology or behavior of the animal are placed in the "centrum". These are recognized as directly-acting components of the environment. Everything else acts indirectly, through an intermediary or a chain of intermediaries that ultimately influences the activity of one or other of the components in the "centrum". All of these indirectly acting components are placed in the "web" (Andrewartha and Birch 1984).

Within the "centrum", the directly acting components are classified into four subdivisions according to the response of the animal to the component and the consequent reaction of the component to the animal. The four subdivisions are "mates", "resources", "predators", and "malentities". The names "resources" and "mates" refer to well-understood colloquial meanings. "Malentities" are components that directly affect the animal, causing a decrease in life expectancy or fecundity, but the consequent component activity decreases or does not change. "Predators" also cause a decrease in life expectancy or fecundity in the animal, but, unlike "malentities", the consequent component activity increases.

An envirogram consists of a dendogram whose branches trace pathways from distal causes in the web to proximate causes in the centrum. **Figure 7** show the envirogram for the grasshopper sparrow.

CONSERVATION

Threats

The largest vegetative province in North America, native grasslands are among the most endangered ecosystems in North America because of extensive loss and degradation over the last 200 years (Samson and Knopf 1994, Noss et al. 1995). Grasslands have been reduced in size due to agricultural and urban development, and altered grazing and fire regimes have degraded most intact remnants. Not surprisingly, grassland birds have experienced steeper, more consistent declines than any other guild in North America over the last 25 years (Vickery et al. 2000).

In Region 2, three primary grassland types occur in a west-to-east continuum in response to precipitation, elevation, and soil. Arid grasslands of short-stature grasses dominate western regions and are referred to as "shortgrass prairie". Taller grass species dominate mesic locations in eastern areas of Region 2; these areas are referred to as "tallgrass prairie". The semiarid "mixed-grass prairie" occupies the transitional section between the shortgrass and tallgrass prairies of Region 2 (Bragg and Steuter 1996, Steinauer and Collins 1996, Weaver et al. 1996). Grazing by native herbivores was historically the primary ecological force on western shortgrass habitats, whereas fire became more prominent in eastern tallgrass habitats (Vickery et al. 2000). The heterogeneous grassland landscape was dynamic, with specific habitat conditions shifting ephemerally in response to plant succession and disturbance agents. This variation was critical to the maintenance of the grassland avifauna because it insured that the specific habitat requirements for each uniquely adapted species were available.

Today, the greatest threats to the grassland avifauna in Region 2, including the grasshopper sparrow, continue to be habitat loss, habitat fragmentation, and habitat degradation from grazing and fire regimes that often fail to replicate the natural dynamics under which these species and their habitats evolved (Samson and Knopf 1994, Vickery et al. 2000). Specific threats to grasshopper sparrow habitat and its populations are

Web 4	Web 3	Web 2	Web 1	CENTRUM
				RESOURCES
		water/weather	vegetation	food: insects
		water/weather	vegetation	food: seeds
		winter precipitation	vegetation	food
soil type	water/weather	fire	vegetation	food: cover
topography	water/weather	vegetation	microhabitat	cover
human	grazing	water/weather	vegetation	food: cover
	humans	habitat conversion	vegetation	food: cover
				MALENTITIES
humans	grazing	water/weather	vegetation	fecundity, densities
humans	grazing	soil; vegetation	disturbance	fecundity, densities
humans	grassland eradication	fragmentation	vegetation	fecundity, densities
humans	oil/gas development	fragmentation	disturbance	fecundity, densities
	humans	agriculture	fragmentation/habitat loss	fecundity, densities
water/weather	vegetation	food: cover	winter distribution	winter survival
	water/weather	vegetation	microclimate	nest phenology
	water/weather	vegetation	habitat selection	distribution
	humans	agriculture	fragmentation/habitat loss	population decline
	humans	prescribed fire	vegetation	fecundity, densities
	humans	pesticides	food: cover	fecundity, densities
		humans	pesticides	densities, mortality
		humans	grazing	nest mortality
				PREDATORS/COMPETITORS
	humans	agriculture	fragmentation	nest predator abundance
		humans	grazing	brown-headed cowbird abundance

Grasshopper Sparrow

Figure 7. Envirogram of the grasshopper sparrow envirogram. Resources (red text), malentities centrum (blue text) and predators/competitors (green text).

described below. The lack of data on grasshopper sparrow demographics, minimum area requirements for sustainable populations, or meta-population dynamics limits our ability to directly assess threats in terms of population viability. Thus, most of the threats are described in reference to their effect on individuals and habitat quality and availability; when appropriate, population effects are discussed. Because this species is rarely observed in Region 2 during the non-breeding season, threats during migration and on their wintering areas are not presented here. Note that what may be a threat to the grasshopper sparrow may be an important component to another grassland bird.

Urban development and conversion of grasslands to cropland are significant threats to the long-term persistence of grasshopper sparrow populations in Region 2. Both threats eliminate habitat directly, as grasshopper sparrows are unable to exploit either urban areas or cropland. Urbanization may be a more important threat because its impacts are permanent, while cropland, if taken out of production, has the potential to be restored to grassland habitat. Rapid population growth and accompanying land development are of particular concern within the Front Range Corridor of Colorado, where shortgrass prairie habitats are disappearing in the counties of Denver, Boulder, Jefferson, Arapahoe, Larimer, and Douglas as population densities have increased to 1,180 people per km^2, compared to the 0.4 to 6.6 people per km^2 found outside of the corridor (Colorado Partners in Flight 2000). The rapid loss of habitat in this area has likely contributed to the considerable grasshopper sparrow population declines in Colorado over the last 25 years, the largest declines observed in any state in Region 2. As human populations continue to increase and as urban areas expand further into the prairie ecosystem of Region 2, loss of grassland habitat, particularly around population centers, will continue to be a significant threat to grasshopper sparrow populations.

The conversion of native prairie and agricultural grasslands to crop production is a more imminent threat to grasshopper sparrows on the mesic grasslands of Region 2, where soils, climate, and precipitation make row crops more economically viable (Steinauer and Collins 1996). Less than 4 percent of the presettlement area of tallgrass prairie remains in North America, the majority of which lies within Region 2 (Samson and Knopf 1994). South Dakota, Nebraska, and Kansas, the only states in Region 2 with sizeable areas of tallgrass, had 15, 2, and 17 percent of their tallgrass habitats remaining in the early 1990's, respectively (Samson and Knopf 1994); undoubtedly, those values have declined further over the last decade. Large tracts of tallgrass prairie remain in the Flint Hills of eastern Kansas and on glacial moraines of northeastern South Dakota because these areas have poor topography or soils for farming. Relative to tallgrass prairies, the loss of short- and mixed-grass habitats to commercial agriculture in central and western Region 2 is not as pervasive because the arid conditions there are less suitable for farming (Weaver et al. 1996). However, conversion to cropland is still extensive. For example, in the southern mixed-grass prairie (Kansas, Oklahoma) dominated by the bluestem-grama grass association, less than 10 percent of grasslands remain (Bragg and Steuter 1996). In northeastern Wyoming, 60 percent of the region's shortgrass prairie has been converted to cropland (Cerovski 2001). Future technological advances, such as the development of improved irrigation systems or the creation of engineered seed sources capable of growing in arid environments, could open up grassland habitats that are currently economically unviable for agriculture and pose a future threat to grasshopper sparrow habitats and their populations.

Fire and grazing are obligatory disturbance processes necessary for the maintenance of grassland ecosystems and their avifauna in Region 2. Yet, when management of these processes fails to reflect their natural patterns, they often have negative impacts on the quality and availability of grasshopper sparrow habitats. Both fire and grazing act similarly in that they remove standing vegetation and litter and increase nutrient cycling (Bragg and Steuter 1996). However, their effects vary with respect to grassland type, season, intensity, frequency, local climate, and their interaction with each other (Bragg and Steuter 1996, Steinauer and Collins 1996, Weaver et al. 1996). Because grasshopper sparrows require intermediate amounts of grass cover, they tend to benefit from frequent disturbance factors in the lusher, more productive grassland communities in eastern parts of Region 2, where grasses are taller, denser, and recover more quickly after disturbance. In the arid, short-stature grassland communities of Region 2, frequent disturbances negatively affect sparrow habitat.

Fire suppression in eastern tallgrass habitats of Region 2 has a negative effect on grasshopper sparrow habitat quality (Vickery et al. 2000). Without fire, the percentage of woody and forb plant species increases, and grasses increase in height and density; these are habitat attributes that grasshopper sparrows avoid. Fire was a dominant and frequent disturbance factor in tallgrass habitats prior to Euro-American settlement, with an average fire interval of two to five years (Steinauer and Collins 1996). Most natural fires were ignited by lightning and occurred in mid- to late summer, coinciding with the end of the grasshopper sparrow's breeding season (Steinauer and Collins 1996). Grasshopper sparrows readily occupy recently burned (<2 years) Kansas tallgrass habitats (Zimmerman 1993, Jensen 1999). However, when a fire occurs in a drought year sparrow abundance may initially be reduced because grasses take longer to recover (Zimmerman 1992). In general, grasshopper sparrows will avoid spring-burned areas in the summer immediately following a burn (Huber and Steuter 1984, Johnson 1997), and fire is detrimental during the breeding season.

Fire suppression in tallgrass habitats has also increased the number and size of wooded forest patches, particularly along river corridors. This action, along with tree planting on the Great Plains to control soil erosion, has allowed many eastern forest animal species, including grasshopper sparrow nest predators, such as American crows and raccoons, to extend their range (Knopf 1986, Samson and Knopf 1994, Cerovski et al. 2001). Although data are lacking to determine the population level consequences of this threat, this factor likely has had, and will continue to have, a serious impact on local populations. Grasshopper sparrows appear to have extremely low fecundity, and their status as ground-nesters increases their vulnerability to predation.

There is less known about the ecological role of fire in mixed- and shortgrass prairie communities of Region 2, although historically it was probably less frequent than on tallgrass prairies (Weaver et al. 1996). Grasshopper sparrows tend to inhabit later seral stages in mixed- and shortgrass habitats because grasses are shorter in stature than in tallgrass habitats. In these habitats frequent ignition, as opposed to fire suppression, is an important threat as grasses recover slowly, requiring two to three years with normal precipitation (Wright and Bailey 1980). Consequently, fires in arid habitats initially depress the abundance of grasshopper sparrows, often taking greater than three years post-fire before abundance increases (Bock and Webb 1984, Forde et al. 1984, Bock and Bock 1987, Johnson 1997). When fires occur during periods of drought, vegetation will likely take longer to recover. There is little information on the effects of long-term fire suppression (>five years) to grasshopper sparrow habitats. However, in some locations, long-term fire suppression may be detrimental. For example in mixed-prairie, grasshopper sparrow densities decreased the year after a burn and then increased until year 5, when density declined again (Johnson 1997).

Overgrazing in mixed- and shortgrass prairies is a serious threat to grasshopper sparrow habitats. On public lands of western North America, including National Forest System lands in Region 2, grazing by cattle is the most widespread economic use (Saab et al. 1995, Senner and Ladd 1996). Prior to Euro-American settlement, the mixed- and shortgrass communities evolved under grazing regimes where large ungulates wandered widely and prairie dogs colonies expanded, contracted, and moved in response to climatic and ungulate grazing influences. The result was an ephemeral landscape mosaic with some areas grazed intensively while others were not grazed at all; this provided birds with a variety of successional stages and conditions from which to choose (Knopf 1996). In these habitats, grasshopper sparrows utilize ungrazed or sparsely grazed habitats.

Most grazing causes the vegetation to become too short and too open for grasshopper sparrow use (Bock and Webb 1984, Bock et al. 1993). Studies in shortgrass and most mixed-grass habitats of Region 2 have indicated that grasshopper sparrows decline or disappear in grazed habitats (Wiens 1970, Kantrud and Kogolski 1982, Saab et al. 1995). However, one study in North Dakota mixed-grass prairies found little effect on grasshopper sparrow when grazing was restricted to light to moderate levels (Kantrud 1981). Currently, most grazing management practices favor uniformly grazed rangelands (Vickery et al. 2000), and this practice has likely played a strong role in the decline of grasshopper sparrow populations in the states of Region 2.

Although grazing was not very important historically in tallgrass communities, its use as a management tool can often mimic the effects of fire. Indeed, grasshopper sparrows have benefited from low to moderate grazing in tallgrass habitats prior to or after the breeding season, although heavy grazing is apparently detrimental (Saab et al. 1995). Like fire though, grazing during the breeding season (May through July) negatively affects grasshopper sparrows, as cattle trample nests and reduce vegetation height, thus preventing birds from renesting.

On tallgrass and some mixed-grass habitats in Region 2, mowing is another management activity that can degrade grasshopper sparrow habitat. Mowing during the breeding season has the direct negative effect of destroying nests and prohibiting birds from renesting in the area. It may also decrease adult survival because adults are forced to disperse to new areas with which they are unfamiliar. However, depending on the location and timing, mowing can be tolerated and may benefit grasshopper sparrows if it is performed after the breeding season. In Nebraska tallgrass habitats that were mowed three out of four years, grasshopper sparrows maintained consistent populations, and in North Dakota hayfields, there was no difference in grasshopper sparrow abundance in the year after mowing between non-mowed and mowed portions of fields (Horn and Koford 2000).

Grasshopper sparrows are area-sensitive species, and fragmentation of grassland habitats poses a significant threat to their populations. Grasshopper sparrows prefer larger grassland patches and avoid smaller patches, with minimum area requirements ranging from 8 to 12 ha in Nebraska to 100 ha in Maine (Samson 1980, Herkert 1994b, Vickery et al. 1994, Helzer 1996). They are also more likely to utilize patches with larger core areas and less edge (i.e., circular patches) (Helzer and Jelinski 1999). There is no information on how the distribution of patches and patch size and configuration influence population viability. Certainly, as grassland patches become smaller they will support fewer individuals and populations. Moreover, as fragmentation isolates populations and reduces population size, the likelihood of a local extirpation increases and the probability of recolonization after extirpation decreases. Fragmentation is not an issue restricted to private lands. Fragmentation on some public lands is severe. For example, Thunder Basin National Grassland in Wyoming contains 338 grassland fragments less that 2.6 km^2 (Senner and Ladd 1996). Not only does this negatively impact grassland bird populations, but it also decreases the USDA Forest Service's ability to manage effectively for species conservation and to provide an effective demonstration site for private landholders (Senner and Ladd 1996). Fragmentation is also a threat to grasshopper sparrows because it reduces the demographic potential within a habitat patch, potentially contributing to decreasing local population trends. Within a grassland patch, grasshopper sparrows are more successful and have higher productivity on interior territories than in edge habitats. This is, in part, due to lower predation and parasitism rates in interior sites (Johnson and Temple 1986, Bock et al. 1999). Nest predation rates were higher on small (16 to 32 ha) than large (130 to 486 ha) grassland fragments in Minnesota tallgrass prairie (Johnson and Temple 1990). In addition, brood parasitism by brown-headed cowbirds (*Molothrus ater*) decreased farther from woody edges (Johnson and Temple 1990).

Conservation Status of the Species in Region 2

Sufficient evidence exists to suggest that the grasshopper sparrow should be considered a species of high conservation concern in USFS Region 2. Although the grasshopper sparrow has a wide distribution across North America, range-wide populations have declined by more than 60 percent since the mid 1960's (Sauer et al. 2003). In Region 2, which represents the core of this species' range, BBS data indicate that the species has suffered long-term population declines. Since 1980, population declines in the states of Colorado and South Dakota (-6.3 and –4.0 percent per year, respectively) have substantially outpaced national trends (Sauer et al. 2003). Unfortunately, population trend data are lacking in the states of Wyoming and Kansas, and these information gaps represent uncertainty in the ability to assess the conservation status of this species. However, there is little reason to believe that declines in those states are less severe than in other parts of Region 2, because the factors (e.g., habitat loss, fragmentation, unnatural land management practices) attributed to the specie's decline are equally pervasive. Finally, the fact that this species' status is "endangered" in areas where it was previously abundant (i.e., northeastern United States, Florida, and British Columbia) also clearly demonstrates this species' vulnerability to human activities.

The grasshopper sparrow's narrow habitat requirements make it vulnerable to land use and habitat management practices in Region 2. Studies from Region 2 and elsewhere suggest that habitats vary in their ability to support this species in response to land use changes and habitat management. However, support for these patterns is mostly based on comparative studies of abundance and not on demographics. Thus, linkages between habitat variability (due to habitat management) and population viability are poorly understood. Habitat patch size is clearly an important factor in habitat suitability for grasshopper sparrow. Many studies have documented grasshopper sparrow's avoidance of small patches of grassland (<10 ha), even when vegetation composition and structure appear suitable (Sampson 1980, Herkert 1994b, Vickery et al. 1994, Helzer 1996). However, it is unclear how patch size and patch distribution interact to affect local grasshopper sparrow populations.

Habitat also varies in its capacity to support grasshopper sparrows in relation to the time since the last disturbance factor or land management activity that mimics the disturbance process. Because of this species' preference for intermediate grass heights and cover, disturbance processes may initially create less suitable habitats for grasshopper sparrows before habitat quality improves through plant succession. Similarly, high quality patches will become less suitable as succession occurs and disturbance is again needed to create high quality habitats. This disturbance-mediated feedback loop is why the presence of multiple habitat patches in different successional stages is so important for the management of this species. The time required for habitats to circle through this feedback loop is much shorter on the lusher, more productive tallgrass prairies. Disturbance factors there may be necessary every two to three years; while on shortgrass, habitats disturbance may only be desired every five to seven years.

The grasshopper sparrow's nesting ecology also may contribute to this species' vulnerability. Ground-nesters, like the grasshopper sparrow, have especially low reproduction rates. This aspect of its life history may reduce its ability to recover from local population declines due to habitat change and environmental variation, and may increase the probability of local population extirpations.

Overall, the likelihood of extirpation within Region 2 is low because of the species' widespread distribution. However, considering the long-term declines in Region 2, downward trend in habitat capability, the history of this species in other regions, its specific habitat requirements, and ecological characteristics, this species should elicit a high level of conservation concern. Without active land management aimed at maintaining populations of grasshopper sparrows, local extirpations will likely occur with increasing frequency.

Potential Management of the Species in Region 2

Implications and potential conservation elements

In Region 2, long-term declines in grasshopper sparrow populations indicate that existing landscape conditions and management activities are having a profound negative effect on this species. These impacts are not restricted to grasshopper sparrows, as most of the grassland avifauna is also exhibiting long-term population declines. Prior to Euro-American settlement, large expanses of prairie habitat were shaped by the ecological forces of fire, grazing, and climate, resulting in a shifting landscape mosaic where grassland birds had access to patches of vegetation in a variety of successional stages and conditions (Vickery et al. 2000). Today, the cumulative effects of habitat loss, fragmentation, and land management practices that fail to replicate natural disturbance processes have severely altered the grasslands of Region 2 and significantly impacted its biotic integrity.

Conservation of the grasshopper sparrow in Region 2 will require a renewed emphasis on creating the necessary landscape matrix and habitat conditions needed to support this species. Because grasslands and their dominant disturbance processes vary across Region 2, a simple set of strategic guidelines for grasshopper sparrow management will not work. In general, though, management of native and agricultural grasslands should attempt to mimic the natural disturbance regime (Samson and Knopf 1994). Grasshopper sparrows require large patches (>12 ha) of grasslands of intermediate height and ground cover. The creation and maintenance of this habitat condition are best accomplished by managing multiple large patches of grasslands in a variety of successional stages through different or rotating management schemes. This ensures that some habitat patches will always be in an intermediate seral stage favored by grasshopper sparrows. As grassland patches age to late seral stages, they become unsuitable for grasshopper sparrows, and management actions should be implemented to return them to early seral stages; the process can then be repeated again. In eastern tallgrass habitats, disturbance would be implemented more frequently, while in arid, shortgrass habitats disturbance should be limited.

However, given the small size of many prairie remnants and the large scale and complexity of disturbance processes required, this approach may not always be feasible (Steinauer and Collins 1996). Steinauer and Collins (1996) recommend a flexible, regional scheme to replicate a heterogeneous grassland landscape that would benefit grasshopper sparrows. Their framework incorporates management approaches based not only on the size and use of the local reserve, but also on the management of nearby reserves and adjacent land use. For example, grazing may not be an important management approach in an area surrounded by grazed prairie. Strategies that encompass public and private lands will be the most successful in replicating the natural heterogeneous landscape of grasslands

Besides a paradigm shift in habitat management, the successful conservation of the grasshopper sparrow and other grassland birds will require new and innovative strategies that go beyond basic habitat management. Although national grasslands support all of the major grassland associations found within Region 2, they represent less than 7 percent of all Region 2 grasslands. The remainder are mostly in private and limited state ownership. Thus, management of Federal lands alone for species conservation is unlikely to ensure the long-term population viability of this species. There is a significant need to develop partnerships between landowners and state and federal managers that are actively involved in the conservation of prairie lands important to birds. Federal grasslands must play a role in demonstrating the appropriate management activities that maintain the biotic integrity of the lands they manage (Senner and Land 1996). Undoubtedly, there must also be a more conservative use of resources in the agricultural community (Bragg and Steuter 1996). This may be accomplished through incentive-based programs for landowners to conduct agricultural practices in a manner beneficial to wildlife, but with a reasonable economic cost. Finally, a greater effort is needed to educate the public on the conservation value of healthy, intact grasslands.

An example of a program attempting to create multi-stakeholder partnerships interested in grassland conservation is the Rocky Mountain Bird Observatory's (RMBO) large-scale grassland conservation plan, "Prairie Partners: Conserving Great Plains Birds and Their Habitats." With over 70 percent of the Great Plains privately owned, RMBO's focus is on building a coalition of landowners and land managers who are actively involved in the conservation of prairie lands important to birds. They accomplish this goal by: 1) working with interested landowners and other federal, state, and private partners to design projects that enhance bird habitat on private lands; 2) providing technical assistance to landowners and land managers on how to incorporate birds into their management strategies; 3) conducting outreach to increase awareness and understanding of prairie birds and their habitat requirements; and 4) monitoring prairie birds and their habitats. There is no information on the effectiveness of this program.

Tools and practices

Species inventory and monitoring

The practice of inventory and monitoring of bird populations has received much discussion over the last two decades. This is due, in part, because birds are excellent indicators of ecosystem health and monitoring programs can been used to gain insight into avian-habitat relationships and the effects of physical and biological factors (e.g., climate, human disturbance, environmental contaminants) in many habitats. For birds, an "inventory" is a term applied to methods that determine presence, relative abundance, and/or distribution of a species, while "monitoring" is applied to methods that determine population trends or measure the health of populations over space or time (Hunter 2000). In general, most techniques used between these two approaches are identical.

An important factor in developing inventory and monitoring methods is to ensure standardized approaches to reduce bias. Without standardization, it is difficult to determine a species' status over space and time within and among habitats, between management units, or within ecoregions. By using standardized inventory and monitoring protocols and analyses, researchers and managers can also benefit from the existence of nationally standardized programs and protocols that aid in repeatability and interpretation of results (e.g., Ralph et al. 1995, Martin et al. 1997).

A variety of techniques have been used to count landbirds. Counting techniques can be divided into two groups: (1) methods that use counts of bird detections as an index to relative abundance and (2) empirical modeling techniques that estimate bird density (Rosenstock et al. 2002). In the first group of techniques, known as index counts, bird detections are tallied during one or more surveys of points, transects, or defined areas (Bibby et al. 1992, Ralph et al. 1995). Index counts have been extensively used in bird studies in multiple habitats and geographic regions, including BBS surveys (Martin and Geupel 1993, Ralph et al. 1995, Hutto and Young 1999). The second group of techniques was developed with the recognition that some birds are missed during sampling. These techniques use similar field procedures but have an analytic component that models variation in species' detectability and estimates species density. Examples of these techniques include variable-distance transects (e.g., Emlen 1977), variable circular-plots (Reynolds et al. 1980), distance sampling (e.g., Buckland et al. 1993, Rosenstock et al. 2002), the double-observer method (Nichols et al. 2000), and the double sampling method (Bart and Earnst 2002)

Index counts are the most widely used method for avian monitoring studies (Rosenstock et al. 2002). The primary assumption of this methodology is that the number of individuals detected represents a constant proportion of *actual* numbers present across space and time. For example, if the true number of birds increases by 25 percent during successive samples, then observed counts are assumed to increase by the same percentage.

Similarly, counts in different areas and at different times are assumed to represent similar proportions (Thompson 2002). This assumption, however, has been questioned (Burnham 1981, Nichols et al. 2000). Specifically, this method has been criticized for not taking into consideration issues of detectability, which can vary as a result of many factors.

Bird detectability can vary in relation to at least three factors, causing bias of avian counts. First, an observer's ability to detect and correctly identify birds varies among and within individuals as a function of training, age, experience, motivation, hearing acuity, eyesight, physical health, and fatigue level (Rosenstock et al. 2002). Second, environmental variables including weather, light intensity, topography, and vegetation characteristics affect bird behavior and observer efficiency and ultimately detectability (Anderson and Ohmart 1977, Dawson 1981, Verner 1985). The third factor affecting detectability is behavioral and physical attributes of individuals and species that make them more or less conspicuous to human observers. These include body size, plumage coloration, characteristics of vocalizations (loudness, rate, sonic frequency), flight behavior, physiological status, flock size, density, age, and sex (Rosenstock et al. 2002). To address potential bias associated with index counts, standardized sampling protocols have been developed, particularly with respect to time of day, season, and weather (e.g., Ralph et al. 1995). In addition, the issue of observer bias is minimized through training, and habitat bias can be minimized by collecting data from within a fixed-radius (Hutto and Young 2002). However, even with protocols that reduce the influence of some confounding factors, the validity of the assumption of constant detectability is likely not met in many studies (see Nichols et al. 2000, Thompson 2002, Rosenstock et al. 2002).

Methods that take into consideration issues of detectability include the double-observer method, double sampling, and distance sampling, and these have gained increasing support. With double-observer sampling, two observers count at each point. One observer, the "primary", counts all birds that he/she sees or hears, while a "secondary" observer records the birds detected by the primary observer, but also notes any birds not detected by the primary observer. The two observers alternate roles between points. Detection rates can then be calculated for species or species groups and are combined with the number of birds detected to adjust observed counts. This approach assumes that each observer's counts are independent, and Nichols et al. (2000) discuss ways to meet this assumption. This approach does not work well for rare species or species with low detectability. It also is labor intensive, requiring two people to conduct counts.

Double sampling is an approach where index counts (incomplete counts) are conducted within a random sample of sampling units, and then more intense counts (complete counts; e.g., territory mapping or nest-searching) within a random subsample of these selected units is performed. Results from the subsample are applied as a correction factor to the unadjusted counts, typically in the form of a ratio estimator (Bart and Earnst 2000). The critical assumption of this methodology is that all individuals are counted within the subsample of units.

Finally, in distance sampling, methods are nearly identical to point counts, except that for each bird heard or seen during the count, its horizontal distance from the observer is estimated. In line transect sampling, the observer records either the perpendicular distance to each bird heard or seen on the transect or the sighting angle and distance. Data are analyzed using Program DISTANCE (Laake et al.1994), a program that requires a significant time investment to understand and run. A minimum of 60 to 80 detections is required to develop a robust detection function and estimate density for individual species. Key assumptions of this method are: (1) birds at, or near, the point or line are detected, (2) birds do not move in response to the observer prior to detection, and (3) distances are accurately estimated. Of these, the first two are most problematic for avian counts. Rosenstock et al. (2002) discuss approaches to help meet these assumptions. Hutto and Young (2002) discuss the consequences of these violations.

Overall, there is still work to be completed on validating any of these counting methods and the consequences of violating key assumptions (Thompson 2002). In most cases, the same field methods are used whether one incorporates detection probability estimates or not. For now, the decision on what type of method to use should be based on the goals that one hopes to achieve. For some cases, unadjusted point counts may be suitable. For example, species richness estimation methods work fine with unadjusted counts when assessing ecological integrity of a refuge or other land management unit with respect to a local region (Nichols et al. 1998). However, for most other goals such as monitoring over space and time, there is general agreement that counting techniques need to account for and to measure detectability between observers, habitat, years, etc. Consequently, any inventory or monitoring program developed in Region 2 should incorporate detectability into its sampling design.

The most reasonable strategy for a grasshopper sparrow monitoring program may be as a component of a community-wide monitoring effort for grassland birds. This approach maximizes the efficiency of data collection and results in monitoring information for many species. Given the patchy distribution and shifting mosaic of grassland conditions in response to plant succession, disturbance processes, or management activities, monitoring should occur at the broadest scales possible. This ensures that local population fluctuations resulting from habitat succession or management activities are not misidentified as population declines. Likewise, monitoring at large temporal scales will be critical for understanding local trends in grasshopper sparrow populations. Because of the relatively flat and open nature of grassland habitats, line transects may be the preferred methodology. Line transects are efficient because data are collected continuously and distance sampling methodologies can be employed. Sampling sites can be established in a variety of ways, depending on the resources available. Sites can be placed systematically or randomly across the landscape. Sampling can also be stratified (e.g., the area is stratified by habitat and random points are selected within each habitat type).

Monitoring programs, however, only signify if a species population level has increased, decreased, or remained stable. Demographic studies (e.g., productivity, survivorship) are needed to provide explanations for changes in abundance. Demographic techniques such as nest-searching, color banding, and mist-netting are the standard methods to collect this information. Data from demographic monitoring permit biologists to construct demographic models that assess population viability, determine correlates to habit and other ecological factors (e.g., weather), identify management priorities, and evaluate the effectiveness of management actions. Moreover, habitat- and landscape-specific data on vital rates provide a clear index of habitat and landscape quality and can identify population sources and sinks (Fancy and Sauer 2000).

Thus, an integrated approach of demographics and population trend monitoring of grasshopper sparrows is suggested for determining causes of population changes and for identifying and testing management actions and conservation strategies that may reverse population declines. Comprehensive monitoring programs should contain both counting and demographic components (Marzluff et al. 2000).

Habitat inventory and monitoring

Habitat inventory and monitoring should be conducted concomitant to grasshopper sparrow monitoring and demographic studies. Identifying relationships among grasshopper sparrow abundance, trends, and vital rates with habitat characteristics is critical for determining causes of population changes and for identifying, as well as testing, management actions and conservation strategies (Fancy and Sauer 2000). Hutto and Young (1999) found that within only a few years, and long before they ever calculated a species population trend, habitat data revealed potential issues of management concern for many species.

Vegetation should be characterized at multiple spatial scales, including the site-, patch-, and landscape-level. Site- and patch- vegetation variables measured should include structural characteristics of the vegetation at different layers, as well as tree and shrub species composition; characteristics that may be important to grasshopper sparrows are described previously in the Habitat section. Specific techniques for sampling avian habitats and analysis can be found in Young and Hutto (2002) and BBIRD protocols (a national program for monitoring breeding productivity and habitat conditions for nongame birds using standardized sampling protocols; Martin et al. 1997). Digital photographs should be taken at each vegetation sampling point to improve the habitat relationship database for grasshopper sparrows throughout Region 2 (see Hutto and Young 1999). GIS techniques should be used to identify landscape-level characteristics such as patch size, distance to other habitat patches, amount of edge, and amount, type, and distribution of other patches that are important to grasshopper sparrow populations.

Management approaches

Within Region 2, few management recommendations have been developed specifically for grasshopper sparrows. Dechant et al. (2001) provide recommendation for this species at a range-wide scale. Most recommendations are based on information gained from studies investigating the relationship between grasshopper sparrow abundance and habitat management. As noted previously, there is a lack of data on the demographic consequences of habitat choice by grasshopper sparrows. This is problematic as density has been shown to be a poor indicator of grasshopper sparrow nesting success (Vickery et al.

1992a). Consequently, information on the effectiveness of specific habitat management approaches or their impacts on population viability is lacking.

The Rocky Mountain Bird Observatory developed a best management practices for grassland birds, including grasshopper sparrows for the Comanche National Grassland, which lies in the shortgrass prairie physiographic region (Gillihan 1999). They recommend that grasshopper sparrow populations are best served by managing for their desired habitat conditions using the tools (fire, grazing, haying) that best simulate the site's natural disturbance factors. However, in relation to grazing they acknowledge that given the annual variation and differences in precipitation, temperature, soil conditions, and plant species composition, blanket grazing prescriptions to achieve desired habitat goals are of little use to land managers. Instead, mangers need to identify goals (i.e., the desired habitat conditions for priority species) and adjust local management regimes accordingly (Gillihan 1999). This same argument can be used for the other primary management techniques available to land managers, fire and haying, and can be applied to other grassland types within Region 2.

Most bird conservation plans, such as PIF State Plans, provide habitat management recommendations for the overall grassland avifauna as opposed to individual species. Given our current understanding of avian-habitat relationships in the grassland community, this appears to be the most appropriate strategy. These community approaches to conservation encourage the use of the primary management tools available to land managers in Region 2: grazing, fire, and mowing, in a manner consistent with the natural disturbance patterns under which these avian species evolved. The following section summarizes the suggestions/approaches, relevant to Region 2, reported in PIF State Bird Conservation Plans (Colorado Partners in Flight 2000, Cerovski 2001) and other scientific reports (Gillihan 1999, Vickery et al. 2000, Dechant et al. 2001) to achieve the desired conditions for healthy grassland ecosystems and grasshopper sparrow populations. Many of these approaches fall into major categories such as grazing, fire, and agriculture; however, some are general enough to cross categories.

General

1. The most important conservation approach for grasshopper sparrows is to maintain suitable grassland parcels that are large enough (>30 ha) to support breeding populations of grasshopper sparrows. Ideally, plots should be larger than 100 ha; if plots smaller than 30 ha are the only option, they should be as numerous as possible and no farther apart than 1.6 km.

2. Public land mangers and private landowners should provide a landscape mosaic of grassland parcels of different structural stages to provide grasshopper sparrows with options for establishing breeding grounds in any given year.

3. Landowners, land managers, and private organizations should develop conservation partnerships particularly to combine core areas (e.g., national grasslands) with buffer areas, such as ranches, where some areas of natural vegetation can be maintained.

4. Regardless of management treatment, disturbing nesting habitat during the breeding season, approximately mid-May to early August, should be avoided.

5. Environmental conditions (e.g., moist vs. drought years) need to be considered when implementing management activities.

6. If pest control is necessary, follow the principles of Integrated Pest Management to determine the best course of action. The use of pesticides for insect and grasshopper control can greatly reduce the food base for many bird species. Moreover, pesticides can cause lethal effects, particularly when nestlings are fed tainted insects. Sublethal effects of pesticide intake may include decreased survival and reproduction.

Grazing

1. In shortgrass habitats, livestock practices that allow large acreages of grasslands to go to climax successional stages will benefit grasshopper sparrows.

2. On a landscape level, use livestock grazing and prescribed fire to produce a mosaic of patches.

3. Grazing treatments could be conducted in early spring, prior to the arrival of grasshopper sparrows, or in the fall after the breeding season. However, untreated areas

should be left nearby to provide refuge for fledglings or late or re-nesting individuals.

4. The current practice of deferring grazing in some pastures for haying should be modified to manage for a “nesting refuge”. Nesting refuges can produce more young birds per acre than rotational grazing. Refuges should be a contiguous area up to 1/3 of the total pasture area and located away from trees, buildings, and crop fields to minimize disturbance and to reduce the potential for predation and cowbird nest parasitism. If appropriate, some areas may be grazed lightly before the start of the breeding season (approximately May 15^{th}).

Fire

1. Grassland parcels should be burned in rotation so that some unburned habitat is always available.

2. Depending on the management objectives, burns should be conducted prior to mid-May or after 1 August; burns should not be conducted during the breeding season.

Agriculture

1. For hayfields, spring mowing should be delayed as long as possible (preferably until nesting ends), and nighttime mowing should be avoided. Late maturing legumes could be grown, to allow for delayed cuttings.

2. Conversion of grasslands to agriculture should be avoided, especially in areas too dry to farm without irrigation.

3. For landowners that farm and ranch, intensive rotational grazing should be used; this converts row crop and alfalfa acreage to pasture and has the potential to provide significant high quality habitat for grassland birds.

Information Needs

Demographic studies of grasshopper sparrows and other grassland birds are the greatest research need on the breeding grounds (Herkert and Knopf 1998). Without information on fecundity of females and adult and juvenile survivorship and dispersal patterns, it is impossible to understand and to predict the effects of different management options and conservation actions on source-sink dynamics (Vickery 1996, Herkert and Knopf 1998). Because the grasshopper sparrow is an area-dependent species, studies that improve our knowledge of how landscape context influence grasshopper sparrow’s sensitivity to habitat fragmentation and nest predation and parasitism rates are also needed. These studies will provide information that can guide conservation planners in determining how large grassland conservation areas should be, how they should be spatially arranged, and into what type of landscapes they should be placed (Herkert and Knopf 1998).

To date, most studies that have examined the relationship between grassland management and abundance of grasshopper sparrows and other grassland birds have been short-term, limiting a manger’s ability to predict how short-term effects interact to create long-term responses under different management regimes. Long-term studies that monitor avian response to different management frequencies, intensities, and combination of management practices are needed. Using an adaptive management approach will allow for refinement in management decisions and additional research questions (Herkert and Knopf 1998). In addition, patterns of grasshopper sparrow abundance need to be understood in the context of precipitation patterns and their effect on management activities. Both fire and grazing are important management activities affected by precipitation patterns (Zimmerman 1992); however, this pattern has not been given much attention (Herkert and Knopf 1998).

As with many grassland species, information about the winter ecology of grasshopper sparrows is lacking, and there is a need for detailed research on nearly all aspects of this topic. A better understanding of this species’ winter distribution, habitat use, and survivorship is needed (Vickery 1996). Additionally, studies on the effect of food limitation on the wintering grounds need to be conducted. There is evidence that some wintering sparrow populations in southern Arizona can be food limited, particularly in years of low seed production (Herkert and Knopf 1998).

Research priorities in Region 2

The Colorado PIF Bird Conservation Plan (2000) outlines six research priorities for the central shortgrass prairie: (1) the relationships among precipitation, habitat condition, and population distribution at the landscape level; (2) the effects of prescribed burning on bird populations; (3) the effects of different grazing regimes; (4) the identification of key migratory stopover and wintering areas; (5) the effects of prairie dog hunting and sport hunting on bird populations; and (6) patch-size effects and area sensitivity of shortgrass prairie birds. Additionally, the impacts of new construction for gas and oil exploration, wind-power development, and water-well drilling need to be investigated.

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Appendix A

Matrix Model Development for the Grasshopper Sparrow

Life cycle graph and model development

We formulated a life cycle graph for grasshopper sparrows that comprised two stages (censused at the fledgling stage and "adults"). The scanty data on survival (Shriver et al. 1996) suggested an "adult" survival rate of 60 percent. We further assumed lower survival in the first year, a value for which we solved by assuming population growth (λ) was 1.002. This "missing element" method (McDonald and Caswell 1993) is justified by the fact that, over the long term, λ must be near 1 or the species will go extinct or grow unreasonably large. In addition we assumed that first-year reproduction was half that of "adult" birds (**Table A1**), based on evidence that first-year birds produce only one brood, whereas "adult" birds regularly produce two broods per season (Wiens 1969). The fertility estimate for "adult" birds was based on the suggestion of two broods per season, a clutch size of 4.3 (McNair 1987), 52 percent nest success (Delisle and Savidge 1996), and an assumption that "success" meant fledging half the eggs per clutch. The model assumes female demographic dominance so that, for example, fertilities are given as female offspring per female; thus, the fledgling number used was half the total annual production of fledglings, assuming a 1:1 sex ratio. From the resulting life cycle graphs (**Figure A1**), we produced a matrix population analysis with a post-breeding census for a birth-pulse population with a one year census interval (McDonald and Caswell 1993, Caswell 2001). The models had two kinds of input terms: P_i describing survival rates, and m_i describing number of female fledglings per female (**Table A1**). **Figure A2** shows the symbolic and numeric values for the matrix corresponding to the life cycle graph of **Figure A1**. Note also that the fertility terms (F_{ij}) in the top row of the matrix include both a term for fledgling production (m_i) and a term for the survival of the mother (P_i) from the census (just **after** the breeding season) to the next birth pulse almost a year later. The population growth rate was 1.002, based on the estimated vital rates used for the matrix. Although this suggests a stationary population, the value was used as an assumption for deriving a vital rate, and should not be interpreted as an indication of the general well-being of the population. Other parts of the analysis provide a better guide for assessment.

Sensitivity analysis

A useful indication of the state of the population comes from the sensitivity and elasticity analyses. **Sensitivity** is the effect on population growth rate (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 use sensitivities to assess the relative importance of survival (P_{ij}) and fertility (F_{ij}) 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 transitions with large sensitivities. Third, sensitivities can quantify the effects of environmental perturbations, wherever those can be linked to effects on stage-specific survival or fertility rates. Fourth, managers can concentrate on the most important transitions. For example, they can assess which stages or vital rates are most critical to increasing the population growth (λ) of endangered species or the "weak links" in the life cycle of a pest. **Figure A3** shows the "possible sensitivities only" matrices for this analysis (one can calculate sensitivities for non-existent transitions, but these are usually either meaningless or biologically impossible — for example, the biologically impossible sensitivity of λ to the transition from Stage 2 "adult" back to being a Stage 1 first-year bird).

Table A1. Parameter values for the component terms (P_i and m_i) that make up the vital rates in the projection matrix for Grasshopper Sparrow.

Parameter	Numeric value	Interpretation
m_1	0.559	Number of female fledglings produced by a first-year female
m_a	1.18	Number of female fledglings produced by an "adult" female
P_{21}	0.45	First-year survival rate
P_a	0.6	Survival rate of "adults"

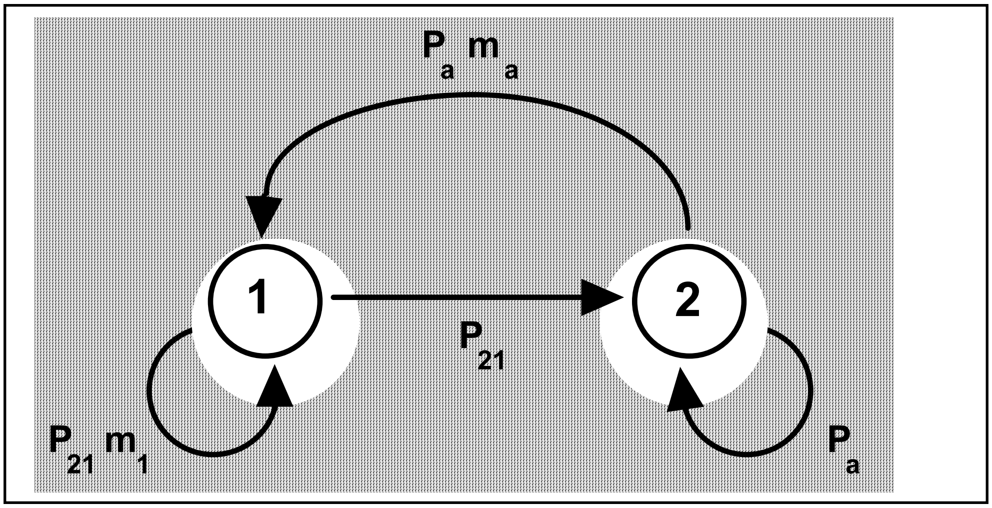

Figure A1. Life cycle graph for the grasshopper sparrow. The numbered circles ("nodes") represent the two stages (first-year birds and "adults"). The arrows ("arcs") connecting the nodes represent the vital rates — transitions between stages, such as survival (P_{ji}) or fertility (F_{ij}), the arcs pointing back toward the first node). Note that the two fertility arcs contain both a term for offspring production (m_i) and a term for the survival of the mother (P_{ij}).

(A)

	1	2
1	$P_{21}m_1$	$P_a m_a$
2	P_{21}	P_a

(B)

	1	2
1	0.252	0.671
2	0.45	0.6

Figure A2. Symbolic and numeric values for grasshopper sparrow matrix corresponding to the life cycle graph of **Figure A1**. (A) Symbolic values for the projection matrix of vital rates, **A** (with cells a_{ij}). Meanings of the component terms and their numeric values are given in **Table A1**. (B) Numeric values for the projection matrix,

	1	2
1	0.349	0.39
2	0.582	0.651

Figure A3. Possible sensitivities only matrix, $\mathbf{S_p}$ for the grasshopper sparrow matrix (blank cells correspond to zeros in the original matrix, **A**). The population growth (λ) of grasshopper sparrows is most sensitive to changes in "adult" survival (Cell s_{22} = 0.651), closely followed by first-year survival (Cell s_{21} = 0.582).

The summed sensitivity of λ to changes in survival (62.5 percent of total sensitivity accounted for by survival transitions) was greater than the summed sensitivity to fertility changes (37.5 percent of total). The single transition to which λ was most sensitive was "adult" survival (33 percent of total). Nearly as important was first-year survival (29.5 percent of total). The major conclusion from the sensitivity analysis is that survival rates are most important to population viability.

Elasticity analysis

Elasticities are useful in resolving a problem of scale that can affect conclusions drawn from the sensitivities. Interpreting sensitivities can be somewhat misleading because survival rates and reproductive rates are measured on different scales. For instance, an absolute change of 0.5 in survival may be a large alteration (e.g., a change from a survival rate of 90 percent to 40 percent). On the other hand, an absolute change of 0.5 in fertility may be a very small proportional alteration (e.g., a change from a clutch of 3,000 eggs to 2,999.5 eggs). Elasticities are the sensitivities of λ to **proportional** changes in the vital rates (a_{ij}) and thus partly avoid the problem of differences in units of measurement (for example, we might reasonably equate changes in survival rates or fertilities of 1 percent). The elasticities have the useful property of summing to 1.0. The difference between sensitivity and elasticity conclusions results from the weighting of the elasticities by the value of the original arc coefficients (the a_{ij} cells of the projection matrix). Management conclusions will depend on whether changes in vital rates are likely to be absolute (guided by sensitivities) or proportional (guided by elasticities). By using elasticities, one can further assess key life history transitions and stages as well as the relative importance of reproduction (F_{ij}) and survival (P_{ij}) 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 grasshopper sparrow are shown in **Figure A4**. λ was most elastic to changes in "adult" survival (e_{22} = 39 percent of total elasticity). Next most elastic were first-year survival and "adult" reproduction ($e_{21} = e_{12}$ = 26.1 percent of total elasticity). Reproduction by first-year birds was relatively unimportant (e_{11} = 8.8 percent of total elasticity). The sensitivities and elasticities for grasshopper sparrow were generally consistent in emphasizing survival transitions. Thus, survival rates, particularly for "adults", are the data elements that warrant careful monitoring in order to refine the matrix demographic analysis.

	1	2
1	0.349	0.39
2	0.582	0.651

Figure A4. Elasticity matrix, **E** (remainder of matrix consists of zeros) for the grasshopper sparrow matrix. The population growth (λ) of grasshopper sparrows is most elastic to changes in "adult" survival (e_{22} = 0.39), followed by first-year fertility and survival ($e_{12} = e_{21}$ = 0.261).

Other demographic parameters

The **stable stage distribution** (SSD, **Table A2**) describes the proportion of each stage or age-class in a population at demographic equilibrium. Under a deterministic model, any unchanging matrix will converge on a population structure that follows the stable age distribution, regardless of whether the population is declining, stationary or increasing. Under most conditions, populations not at equilibrium will converge to the SSD within 20 to 100 census intervals. For grasshopper sparrow at the time of the post-breeding annual census (just after the end of the breeding season), fledglings represent 47 percent of the population, and "adult" birds represent the remaining 53 percent of the population. **Reproductive values** (**Table A3**) can be thought of as describing the value of a stage as a seed for population growth relative to that of the first (newborn or, in this case, fledgling) stage (Caswell 2001). The reproductive value 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, 1.0. An "adult" female is worth 1.7 fledglings. The cohort generation time for this species was 2.9 years (SD = 2.0 years). Note that this corresponds well with the average 2.9-year lifespan found by Shriver et al. (1996).

Table A2. Stable age distribution (right eigenvector). At the census, 47 percent of the individuals in the population should be fledglings. The rest will be older "adult" females in their second year or older.

Stage	Description	Proportion	Mean age (± SD) Variant 1
1	Fledglings (to yearling)	0.47	0 ± 0
2	"Adult" females	0.53	2.5 ± 1.9

Table A3. Reproductive values (left eigenvector). Reproductive values can be thought of as describing the "value" of an age class as a seed for population growth relative to that of the first (newborn or, in this case, egg) age class. The reproductive value of the first age class is always 1.0. The peak reproductive value (second-year females) is highlighted.

Stage	Description	Reproductive value
1	Fledglings/first-year females	1
2	"Adult" females	1.7

Stochastic model

We conducted a stochastic matrix analysis for grasshopper sparrow. We incorporated stochasticity in several ways (**Table A4**), by varying different combinations of vital rates, and by varying the amount of stochastic fluctuation. We varied the amount of fluctuation by changing the standard deviation of the truncated random normal distribution from which the stochastic vital rates were selected. To model high levels of stochastic fluctuation we used a standard deviation (SD) of one quarter of the "mean" (with this "mean" set at the value of the original matrix entry [vital rate], a_{ij} under the deterministic analysis). Under Case 1 we subjected the fertility arcs (F_{11} and F_{12}) to high levels of stochastic fluctuations (SD one quarter of mean). Under Case 2 we varied the survival arcs (P_{21} and P_{22}) with high levels of stochasticity (SD one quarter of mean). Under Case 3 we varied only "adult" survival (P_{22}), again with high levels of stochastic fluctuation. Case 4 varied the two survival transitions, like Case 2, but with only half the stochastic fluctuations (SD one eighth of mean). Each run consisted of 2,000 census intervals (years) beginning with a population size of 10,000 distributed according to the Stable Stage Distribution (SSD) of the deterministic model. Beginning at the SSD helps avoid the effects of transient, non-equilibrium dynamics. The overall simulation consisted of 100 runs (each with 2,000 cycles). We calculated the stochastic growth rate, $log\lambda_S$, according to Eqn. 14.61 of Caswell (2001), after discarding the first 1,000 cycles in order to further avoid transient dynamics.

Table A4. Results of four cases of different stochastic projections for Grasshopper Sparrow. Stochastic fluctuations have the greatest effect when acting on survival transitions with high stochasticity (Cases 2 and 3).

	Case 1	Case 2	Case 3	Case 4
Input factors:				
Affected cells	All the F_{ij}	All the P_{ij}	P_{22} ("adult" survival)	All the P_{ij}
S.D. of random normal distribution	1/4	1/4	1/4	1/8
Output values:				
Deterministic λ	1.002	1.002	1.002	1.002
# Extinctions/100 trials	0	69	32	0
Mean extinction time	N.a.	1,215	1,432	N.a.
# Declines/# surviving populations	62/100	28/31	60/68	33/100
Mean ending population size	331,119	38,430	28,918	417,411
S.D.	$2.1X10^6$	182,078	107,938	$1.4X10^6$
Median ending size	4,022	116	249	28,643
Log λ_s	-0.0002	-0.007	-0.003	0.0006
λ_s	0.9998	0.993	0.9968	1.0006
percent reduction in λ	0.23	0.91	0.54	0.15

The stochastic model (**Table A4**) produced two major results. First, high levels of stochastic fluctuations affecting survival had the greatest detrimental effects. Low level stochastic fluctuations (Case 4, SD of one eighth) resulted in no extinctions and 48 declines. High fluctuations in fertility transitions resulted in no extinctions and only 33 declines. Second, varying "adult" survival had the greatest detrimental effects. In Case 3, where only "adult" survival was affected, modeled populations resulted in 32 extinctions and an additional 60 declines, much more of an impact than varying both fertilities (0 extinctions, 62 declines). The difference in the effects of which arc was most important is predictable largely from the elasticities. λ was most elastic to changes in the first-year transitions. This detrimental effect of stochasticity occurs despite the fact that the average vital rates remain the same as under the deterministic model — the random selections are from a symmetrical distribution. This apparent paradox is due to the lognormal distribution of stochastic ending population sizes (Caswell 2001). The lognormal distribution has the property that the mean exceeds the median, which exceeds the mode. Any particular realization will therefore be most likely to end at a population size considerably lower than the initial population size. These results indicate that populations of grasshopper sparrow are vulnerable to stochastic fluctuations in survival (due, for example, to annual climatic change or to human disturbance) when the magnitude of fluctuations is high. Pfister (1998) showed that for a wide range of empirical life histories, high sensitivity or elasticity was negatively correlated with high rates of temporal variation. That is, most species appear to have responded to strong selection by having low variability for sensitive transitions in their life cycles. Grasshopper sparrow, however, may have little flexibility in reducing variability in first-year survival, which has a relatively high elasticity. Variable early survival, and probably fertility, is likely to be the rule rather than the exception.

Potential refinements of the models

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

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