

**Fox Sparrow (*Passerella iliaca schistacea*):
A Technical Conservation Assessment**

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

April 14, 2004

Aran S. Johnson and Stanley H. Anderson
University of Wyoming
Wyoming Cooperative Fish and Wildlife Research Unit
Box 3166, University Station
Laramie, WY 82070

Johnson, A.S. and S.H. Anderson. (2004, April 14). Fox Sparrow (*Passerella iliaca schistacea*): a technical conservation assessment. [Online]. USDA Forest Service, Rocky Mountain Region. Available: <http://www.fs.fed.us/r2/projects/scp/assessments/foxsparrow.pdf> [date of access].

AUTHORS' BIOGRAPHIES

Aran S. Johnson is a wildlife biologist for the Southern Ute Indian Tribe in Ignacio, Colorado. He received his B.S. in 1995 at the University of Wisconsin at Green Bay and his M.S. in 2001 at the University of Wyoming. His master's project investigated logging effects on riparian and upland songbird species. Aran has written conservation assessments for the Black Hills National Forest on several raptor species.

Stanley H. Anderson is the leader of the Wyoming Cooperative Fish and Wildlife Research Unit. He received his Ph.D. from Oregon State University in 1970 and his B.S. from the University of Redlands in 1961. During his career at Kenyon College, Oak Ridge National Laboratories, Patuxent Research Center and the Wyoming Cooperative Fish and Wildlife Research Unit he has worked extensively on wildlife habitat, publishing as author or co-author more than 230 scientific articles. Stan has done extensive work on raptors throughout the United States, South America, and Australia. He has worked with nearly 100 graduate students at the Coop and presented courses in ornithology and wildlife management. Throughout his career he has served on many national and international wildlife committees working toward the protection of declining species.

SUMMARY OF KEY COMPONENTS FOR CONSERVATION OF *PASSERELLA ILIACA SCHISTACEA*

Four distinct groups of the fox sparrow (*Passerella iliaca*) are recognized by the American Ornithological Union. This assessment focuses on the slate-colored fox sparrow (*P. i. schistacea*) group within Region 2 of the USDA Forest Service. All fox sparrow groups appear stable across their prospective ranges. Within Region 2 the fox sparrow is tied to mid- to high-elevation riparian habitats. The threats within Region 2 include degradation or destruction of riparian habitats. Several conservation groups and national forests within Region 2 recognize that the loss of riparian habitat through dewatering for agriculture and disturbance by livestock grazing and recreational activities in riparian areas is a concern for several riparian songbird species, including the fox sparrow. Management and conservation elements should focus on maintaining healthy riparian habitats.

TABLE OF CONTENTS

AUTHORS' BIOGRAPHIES	2
SUMMARY OF KEY COMPONENTS FOR CONSERVATION OF <i>PASSERELLA ILLACA SCHISTACEA</i>	3
LIST OF TABLES AND FIGURES	6
INTRODUCTION	7
Goal	7
Scope	7
Treatment of Uncertainty	7
Publication of Assessment on the World Wide Web	8
Peer Review	8
MANAGEMENT STATUS AND NATURAL HISTORY	8
Management Status	8
Existing Regulatory Mechanisms, Management Plans and Conservation Strategies	8
Biology and Ecology.....	9
Description and classification.....	9
Distribution and abundance.....	10
Population trends.....	10
Activity patterns and movements.....	10
Circadian.....	10
Broad scale movement patterns.....	10
Habitat characteristics	12
Breeding habitat.....	12
Stopover habitat.....	12
Winter habitat	12
Food habits	13
Breeding biology	13
Phenology	13
Breeding behavior	13
Brood information	14
Parental care of the young	14
Nestling dispersal	14
Nest parasitism	14
Demography	14
Population size	14
Population density	14
Life history	14
Community ecology	16
Predators	16
Competitors	16
Parasites and disease.....	16
Symbiotic and mutualistic interactions	16
CONSERVATION.....	16
Threats.....	16
Conservation Status of the Fox Sparrow in Region 2.....	18
Management of the species in Region 2	19
Implications and potential conservation elements	19
Tools and practices	20
Species and Population Inventory	20
Population management approaches.	21
Information Needs.....	21
REFERENCES	22
APPENDIX A.....	25
Matrix Model Assessment of the Fox Sparrow.....	25

Life cycle model	25
Sensitivity analysis	26
Elasticity analysis	27
Other demographic parameters	28
Stochastic model	28
Potential refinements of the models	30
References	31

EDITOR: Greg Hayward, USDA Forest Service, Rocky Mountain Region

LIST OF TABLES AND FIGURES

Tables:

Table 1. North American Breeding Bird Survey Data (1966-2000) for the fox sparrow.....	10
Table 2. Audubon Christmas Bird Count data (1959-1988) for fox sparrows.....	11
Table A1. Parameter values for the component terms (P_i and m_i) that make up the vital rates in the projection matrices for the fox sparrow.	26
Table A2. Stable age distribution (right eigenvector) for the high- and low-ratio cases.	28
Table A3. Reproductive values (left eigenvector) for the high- and low-ratio cases.....	28
Table A4. Summary of four variants of stochastic projections for the fox sparrow with $N_0 = 10,000$ individuals.....	29

Figures:

Figure 1. North American Breeding Bird Survey and Christmas Bird Count distribution and density maps for the fox sparrow in North America.	15
Figure 2. Envirogram depicting ecological relationships of the fox sparrow in Region 2.	17
Figure A1. Life cycle graph for the fox sparrow.....	25
Figure A2a. Symbolic values for the projection matrix of vital rates, \mathbf{A} (with cells a_{ij}) corresponding to the fox sparrow life cycle graph of Figure A1.	26
Figure A2b. Numeric values for the high-ratio case of the matrix whose symbolic values are given in Figure A2a.	26
Figure A3a. Sensitivity matrix, \mathbf{S} , for the high-ratio case.....	27
Figure A3b. Sensitivity matrix, \mathbf{S} , for the low-ratio case.....	27
Figure A4a. Elasticity matrix, \mathbf{E} , for the high ratio case.....	28
Figure A4a. Elasticity matrix, \mathbf{E} , for the low ratio case.....	28

INTRODUCTION

This assessment is one of many being produced to support the Species Conservation Project for the Rocky Mountain Region (Region 2) of the USDA Forest Service (USFS). The slate-colored fox sparrow (*Passerella iliaca schistacea*) is the focus of an assessment because it is considered a Management Indicator Species (MIS) on the Rio Grande National Forest. As a barometer for species viability at the forest level, a MIS serves two functions: 1) to estimate the effects of planning alternatives on fish and wildlife populations (36 CFR 219.19 (a)(1)); and 2) to monitor the effects of management activities on species via changes in population trends (36 CFR 219.19 (a)(6)).

This assessment addresses the biology of the slate-colored fox sparrow throughout Region 2. This introduction defines the goal of the assessment, outlines its scope, and describes the process used in its production.

Goal

Species conservation assessments produced as part of the Species Conservation Project are designed to provide forest managers, research biologists, and the general public with a thorough discussion of the biology, ecology, conservation status, and management of certain species, based on available 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. In our assessment we do not develop specific management recommendations for the fox sparrow, but we do try to provide ecological background upon which its management can be based. We also focus on the consequences of changes in the environment that result from management (i.e., management implications). Furthermore, we cite management recommendations proposed elsewhere and, when management recommendations have been implemented, we report the results of the implementation.

Scope

This assessment examines the biology, ecology, conservation status, and management of the slate-colored fox sparrow with specific reference to the geographic and ecological characteristics of the USFS Rocky Mountain Region. Although a majority of the literature on fox sparrows originates from

field investigations outside the region, we place that literature in the ecological and social context of the central Rockies. Similarly, we address the reproductive behavior, population dynamics, and other characteristics of fox sparrows in the context of their current environment rather than historical conditions. We considered the evolutionary environment of the species when conducting the synthesis, but we placed it in a present-day context.

In producing this assessment, we reviewed refereed literature, non-refereed publications, research reports, and data accumulated by resource management agencies. Not all publications on fox sparrows are referenced in this assessment, nor was all published material considered equally reliable. Our assessment emphasizes refereed literature because this is the accepted standard in science. However, we chose to use some non-refereed literature in the assessment when information was unavailable elsewhere; these references were regarded with greater skepticism, and all information was treated with appropriate uncertainty. Unpublished data (e.g. Natural Heritage Program records) were especially important in estimating geographic distribution. We believe that these data require special consideration because of the variety of persons and methods used to in collection.

Treatment of Uncertainty

Science represents a rigorous, systematic approach to obtaining knowledge. Competing ideas regarding how the world works are measured against observations. However, because our descriptions of the world are always incomplete and our observations are limited, science focuses on approaches for dealing with uncertainty. A commonly accepted approach to science is based on a progression of critical experiments to develop strong inference (Platt 1964). However, it is difficult to conduct experiments that produce clean results in the ecological sciences. Often, observations, inference, good thinking, and models must be relied on to guide our understanding of ecological relations.

Confronting uncertainty then is not without problems. In this assessment, we note the strength of evidence for particular ideas, and we describe alternative explanations where appropriate. While well-executed experiments represent a strong approach to developing knowledge, alternative approaches such as modeling, critical assessment of observations, and limited inference are also accepted as sound approaches to understanding features of biology.

Publication of Assessment on the World Wide Web

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

Peer Review

Assessments developed for the Species Conservation Process 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

Across its range the fox sparrow is considered common, secure, and abundant (NatureServe 2001, Weckstein et al. 2003). Within Region 2, South Dakota has no status for the fox sparrow because it only occurs irregularly as a transient or migrant (NatureServe 2001). In Nebraska the fox sparrow is considered an uncommon spring and fall migrant in the east and rare in the west. Generally, individuals seen in the east are red fox sparrows (*Passerella iliaca iliaca*), while those seen in the far west are usually slate-colored fox sparrows (*P. i. schistacea*; Sharpe et al. 2001). In Kansas the red fox sparrow (*P. i. iliaca*) is a common transient and an uncommon winter resident in the eastern part of the state, and the slate-colored fox sparrow is a casual winter resident in the west (Thompson and Ely 1992). Wyoming considers the fox sparrow common (Luce et al. 1999). The slate-colored fox sparrow, once considered rare in Colorado, is considered more common now (Kingery 1998).

Existing Regulatory Mechanisms, Management Plans and Conservation Strategies

We found no conservation measures implemented specifically for fox sparrows. Within Region 2 only

the Rio Grande National Forest thoroughly evaluated the fox sparrow as a MIS. No specific measures have been implemented for the conservation of this sparrow on the forest. The Colorado Partners in Flight suggests several measures to protect fox sparrows and other high-elevation riparian songbird species, including eliminating activities that degrade riparian habitats such as timber harvest, dewatering streams, and livestock grazing. However, fox sparrows are protected by several laws that broadly apply to many wildlife species including the Migratory Bird Treaty Act of 1918, the National Forest Management Act of 1976, and the Neotropical Bird Conservation Act of 2000.

The Migratory Bird Treaty Act of 1918 established a federal prohibition, unless permitted by regulations, to “pursue, hunt, take, capture, kill, attempt to take, capture or kill, possess, offer for sale, sell, offer to purchase, purchase, deliver for shipment, ship, cause to be shipped, deliver for transportation, transport, cause to be transported, carry, or cause to be carried by any means whatever, receive for shipment, transportation or carriage, or export, at any time, or in any manner, any migratory bird, included in the terms of this Convention . . . for the protection of migratory birds . . . or any part, nest, or egg of any such bird.” (16 U.S.C. 703; <http://laws.fws.gov/lawsdigest/migtrea.html>). Additionally, treaties formed as a result of the Migratory Bird Treaty Act of 1918 obligate the federal government to take measures to protect identified ecosystems of special importance to migratory birds against pollution, detrimental alterations, and other environmental degradations.

The National Forest Management Act of 1976 stipulates that Forests must “provide for multiple use and sustained yield of the products and services obtained there from in accordance with the Multiple-Use, Sustained-Yield Act of 1960, and in particular, include coordination of outdoor recreation, range, timber, watershed, wildlife and fish, and wilderness management” (<http://www.fs.fed.us/forum/nepa/nfmalaw.html>).

The Neotropical Bird Conservation Act of 2000 provides grants to countries in Latin America and the Caribbean, and to the United States for the conservation of neotropical migratory birds that winter south of the United States-Mexico border and summer in North America (<http://laws.fws.gov/lawsdigest/neotrop.html>). The law encourages habitat protection, education, research, monitoring, and capacity building to provide for the long-term protection of neotropical migratory birds (<http://laws.fws.gov/lawsdigest/neotrop.html>).

Loosely related to conservation strategies, several monitoring programs are used to collect information on population trends of many bird species, including the fox sparrow. These programs include the North American Breeding Bird Survey (BBS), the Monitoring of Avian Productivity and Survivorship (MAPS) Program, and the Rocky Mountain Bird Observatory's Monitoring Colorado's Birds Program.

The BBS is a large-scale survey of North American birds (<http://www.mbr-pwrc.usgs.gov/bbs/intro00.html>). It is a roadside survey, primarily covering the continental United States and southern Canada, although survey routes have recently been initiated in Alaska and northern Mexico (<http://www.mbr-pwrc.usgs.gov/bbs/intro00.html>). The BBS was started in 1966, and over 3,500 routes are surveyed in June by experienced birders (<http://www.mbr-pwrc.usgs.gov/bbs/intro00.html>). The primary objective of the BBS has been the estimation of population change for songbirds (<http://www.mbr-pwrc.usgs.gov/bbs/intro00.html>). However, the data have many potential uses, and investigators have used the data to address a variety of research and management objectives (<http://www.mbr-pwrc.usgs.gov/bbs/intro00.html>).

MAPS was created by The Institute for Bird Populations in 1989 to assess and monitor the vital rates and population dynamics of over 120 species of North American landbirds in order to provide critical conservation and management information on their populations (<http://www.birdpop.org/maps.htm>). The MAPS Program uses constant-effort mist netting and banding through a continent-wide network of monitoring stations staffed by both professional biologists and highly trained volunteers (<http://www.birdpop.org/maps.htm>). MAPS is organized around research and management goals as well as monitoring goals. MAPS data are used to describe temporal and spatial patterns in the vital rates of target species, and relationships between these patterns and (1) ecological characteristics and population trends of the target species, (2) station-specific and broad scale habitat characteristics, and (3) spatially explicit weather variables (<http://www.birdpop.org/maps.htm>). Information from these patterns and relationships is then used: (1) to identify the causes of population declines, (2) to formulate management actions and conservation strategies that would reverse declines and maintain healthy populations, and (3) to evaluate the effectiveness of management actions and conservation strategies (<http://www.birdpop.org/maps.htm>).

The Monitoring Colorado's Birds project focuses on obtaining count-based data for all breeding-bird species in the state on a randomly allocated and habitat-stratified basis. Leukering et al. (2000) summarizes the methods and future objectives for this project. Three methods are used (transects, colony counts, and censuses) to obtain population data for Colorado's breeding-bird species, with transects being the primary method. Transects (15 point counts in each transect) are performed in 30 randomly selected stands in each of the 14 habitats monitored. Standard distance-sampling techniques are used during all transect surveys, and density estimates of bird species are derived using program DISTANCE (Thomas et al. 1998). The program was recently expanded to include Wyoming and the Black Hills National Forest in Region 2.

Biology and Ecology

Description and classification

The fox sparrow is the largest of the sparrows and averages 15 to 18 cm in length and weighs 30 to 47 grams. Sexes are similar in appearance with heavily streaked breasts and grayish-brown plumage above. Blotching on the breast merges into a central spot. The tail and flight feathers have a reddish tint. The bill is light gray, and the legs are light (Wassink 1991, Fisher 1997). Song sparrows, which have a similar chest spot but are much smaller, are often mistaken for fox sparrows. Hermit thrushes are also confused with fox sparrows, but they are distinguished by a slimmer bill and less heavily streaked underparts and back (Farrand 1988).

The fox sparrow has been the focus of extended studies to determine speciation. Early in the nineteenth century four species of fox sparrow were recognized, based on plumage and bill size (Zink and Kessen 1999). In 1886 however, the first edition of the American Ornithologists' Union (AOU) recognized only one species of fox sparrow but acknowledged four groups within that species. By 1957 the AOU recognized 18 separate subspecies within those groups. Most recently, DNA testing has supported the separation of the four groups: the red fox sparrow (*Passerella iliaca iliaca*), the sooty fox sparrow (*P. i. unalaschensis*), the slate-colored fox sparrow (*P. i. schistacea*), and the thick-billed fox sparrow (*P. i. megarhyncha*) (Rising 1996, Zink 1996, Zink and Kessen 1999, Garrett et al. 2000, Weckstein et al. 2003). However, hybridization is known to occur, and scientists are reluctant to further divide the groups into separate species (Zink and Kessen 1999).

Distribution and abundance

The *Passerella iliaca iliaca* group breeds from Newfoundland across Canada to northwest Alaska and south to northern British Columbia and central Alberta. The *P. i. unalaschcensis* group breeds from the Alaska Peninsula through south British Columbia and east into Alberta. The *P. i. schistacea* group is found in central British Columbia and southwest Alberta to east-central Colorado north to north-central and eastern Oregon and west to east-central California and central Nevada. The *P. i. megarhyncha* group breeds in central and southern Oregon to southern California (Zink and Kessen 1999). Within each group there is geographic variation in plumage coloration and body size. Hybridization is limited between all pairs of groups except *megarhyncha* and *schistacea* for which mitochondrial DNA evidence suggests a narrow contact zone along the interface of the Great Basin and Sierra Nevada/Cascade Mountains (NatureServe 2001).

Discontinuities in distribution throughout Region 2 are attributed to habitat requirements. The slate-colored fox sparrow is generally restricted to montane shrub-willow thickets along riparian zones, beaver ponds, overgrown clear-cuts, the edges of meadows and avalanche slopes (Dobkin 1994, Fisher 1997, Kingery 1998, Luce et al. 1999, Weckstein et al. 2003). Within Region 2, Colorado and Wyoming provide the largest amount of suitable fox sparrow breeding habitat. Kansas, Nebraska, and South Dakota are dominated by agricultural landscapes that do not provide the extensive riparian habitats are required for breeding. Thus, distribution of fox sparrows within Region 2 is generally limited to montane areas within western and central Colorado and western Wyoming (Johnsgard 1986, Price et al. 1995).

Based on Breeding Bird Survey data from Region 2, Price et al. (1995) suggested the densest breeding populations of fox sparrows occur in west-central Colorado and northwest Wyoming with 1 to 10 birds recorded per route. South Dakota, Nebraska, and Kansas normally show no breeding populations (Thompson and Ely 1992, NatureServe 2001, Sharpe et al. 2001).

Population trends

Little is known of fox sparrow natural history, in part because of the bird's shyness and its propensity for almost impenetrable habitat (Threlfall and Blacquiere 1982, Burns and Hackett 1993, Kingery 1998, Weckstein et al. 2003). Population trends are not clear, and there is a great deal of uncertainty in the data regarding this species. Although the BBS provides population trends for the fox sparrow, only 22 percent of the reports have even moderate precision (Sauer et al. 2001). Data for individual states within Region 2 have various deficiencies including: regional abundances of less than 0.1 birds per route, samples based on less than five routes for the long term, and results so imprecise that a 5 percent per year change would not be detected over the long term (Sauer et al. 2001). Data for the western BBS region, the United States as a whole, and survey-wide have adequate sample sizes; however, *P*-values are insignificant and 95 percent confidence intervals all overlap 0, suggesting a stable population (**Table 1**).

Christmas Bird Count (CBC) data provide no better evidence of trend for areas within Region 2 (**Table 2**). Fox sparrows do not normally winter within the Rocky Mountain region, except at the lowest and warmest elevations, so this lack of trend information could be expected. **Table 2** presents winter count data from the western U.S. Birds counted in Arizona, California, and New Mexico likely represent breeding birds (*P. i. schistacea*) from Region 2 (Swarth 1920, Weckstein et al. 2003).

Activity patterns and movements

Circadian

Information regarding daily movement of fox sparrows was not found.

Broad scale movement patterns

Fox sparrow migration is illustrated by several examples. Birds in eastern North America from as far

Table 1. North American Breeding Bird Survey Data (1966-2000) for the fox sparrow (from Sauer et al. 2001).

	Trend	P-value	N	95% C.I.	Relative Abundance
Western BBS	-0.1	0.87	181	-1.8 – 1.58	1.58
U.S.	1.0	0.11	146	-0.2 – 2.2	1.53
CO	8.6	0.07	19	0.0 – 17.1	0.67
WY	0.8	0.90	5	-10.6 – 12.2	0.13

Table 2. Audubon Christmas Bird Count data (1959-1988) for fox sparrows (from Sauer et al. 1996).

	Trend	N	95% C.I.	Relative Abundance
Survey-wide	-0.2	1358	-1.4 - 1.0	0.94
CA	1.3	125	-0.4 - 3.0	2.33
AZ	-0.5	26	-1.4 - 0.4	0.15
CO	-0.4	16	-1.7 - 0.9	0.18
NM	0.2	14	-1.2 - 1.6	0.15
KA	0.2	29	-1.0 - 1.4	0.19

north as northeastern Manitoba and Labrador tend to winter in the southeastern United States. Fox sparrows on the west coast exhibit “leap-frog” migration (Bell 1997); sparrows that breed farthest north winter farthest south, while birds that breed at intermediate longitudes winter closer to their breeding range and the most central group is essentially a resident population.

There is some discrepancy in whether the fox sparrow is a neotropical migratory songbird or a short-distance migrant (Dobkin 1994, Kingery 1998, Luce et al. 1999, J. Weckstein personal communication 2003). Some subspecies of fox sparrows migrate as far south as Baja and Sonora, Mexico; however, the classic examples of neotropical migrant songbirds are those that migrate to Central and South America. The bulk of wintering fox sparrows occur in the southeastern United States and along the California coast. Here, we consider the fox sparrow a short distance migrant, recognizing that some migrate long distances within North America. The slate-colored fox sparrow that breeds within Region 2 likely migrates to Arizona, New Mexico, and southern California.

Very little information has been published on the migration of the slate-colored fox sparrow (Garrett et al. 2000, Weckstein et al. 2003). As a rule they generally migrate earlier than the red fox sparrow group, with fall migrants arriving on wintering grounds as early as August, and spring migrants arriving on breeding grounds as early as late March (Weckstein et al. 2003). The slate-colored fox sparrows include Arizona and New Mexico in their winter range. Thus, birds migrating to Colorado and Wyoming to breed may include birds from these areas (Swarth 1920, American Ornithologists’ Union. 1957). Garrett et al. (2000) supported this by suggesting that slate-colored fox sparrows migrate southwesterly and that, although rare in southern Arizona, they are common in the Hualapai Mountains (in the northwest corner of the state) in the winter. The fox sparrow may be a resident in some areas of Colorado

and a regular breeder west of the Continental Divide, but it migrates to Montana in early April and Idaho in March (Johnsgaard 1986, Kingery 1998). No arrival dates were found for fox sparrows in Wyoming.

Bird atlases from Kansas, Nebraska, and South Dakota classify their fox sparrows as migratory and identify them as red fox sparrows. The South Dakota Ornithologists’ Union (1991) suggests that the average arrival of migrant fox sparrows occurs between the last three weeks in April and the first week of May, with early dates occurring mid-March. Although not suggested by other authors, we believe that birds in far western South Dakota may be slate-colored fox sparrows, while eastern birds are red fox sparrows. Likewise, Nebraska may show a similar pattern in the subspecies that migrate through that state. The red fox sparrow is found in eastern Nebraska from March through early April (Bruner et al. 1904), while in western Nebraska the slate-colored fox sparrow is dominant. Sharpe et al. (2001) suggested that Nebraska is primarily populated by red fox sparrows, and only one specimen of slate-colored fox sparrow was collected in Keith County. Kansas’ fox sparrows are identified as red fox sparrows, and Thompson and Ely (1992) suggested that all birds seen are probably migrants of the eastern race. Migrants are seen in Kansas mid-March to early May.

Sex and age differences in dispersal capabilities and patterns. Not reported for fox sparrows.

Regional differences in migration and other broadscale movement patterns. Migration patterns for slate-colored fox sparrows within Region 2 can range from year-round residents to those that show altitudinal migrations or are fully migratory (Cramp and Perrins 1994, Weckstein et al. 2003). We speculate that fox sparrows breeding south and west in Region 2 may migrate attitudinally, while those breeding further north may migrate out of the region in the fall.

Habitat characteristics

Breeding habitat

Information on habitat selection for fox sparrows is limited. Most studies on the natural history for this species were done in the late nineteenth and early twentieth centuries, and they did not quantify habitat characteristics. More recent observations suggest that fox sparrows in the Great Basin nest in “impenetrable riparian thickets” (Weckstein et al. 2003). Vegetation associated with nesting includes alder (*Alnus* spp.), water birch (*Betula occidentalis*), willows (*Salix* spp.), currants and gooseberries (*Ribes* spp.), and rose (*Rosa* spp.) (Weckstein et al. 2003). It has been suggested that fox sparrows do not select habitat based on microhabitat variables; rather they select habitat on a broader scale, i.e., shrub cover or thick ground cover near riparian zones (Burns and Hackett 1993). Early studies briefly described slate-colored fox sparrow nest sites as located in thick shrub cover such as willow thickets, wild rose bushes, and occasionally in tall rye grass, “but always close to water” (Bent 1968).

Slate-colored fox sparrows were described as breeding in “willows and rose thickets along the streams in the more open country, but is generally most abundant close to the foot-hills of the mountains” (Bendire 1889). Similarly in Montana, this subspecies was described as using the thickest and most impenetrable willow stands in the valley (Saunders 1911 in Linsdale 1928). In Nevada they were most common on rocky slopes covered with chinquapin (*Castanopsis sempervirens*) and quaking aspen (*Populus tremuloides*) thickets, interspersed with mountain mahogany (*Cercocarpus* spp.) and limber pine (*Pinus flexilis*) and were often found in association with white-crowned sparrows (*Zonotrichia leucophrys*) and MacGillivray’s warbler (*Oporonis tolmiei*) near springs in mountain meadows (Taylor 1912 in Linsdale 1928).

Because little has been published regarding fox sparrow habitat selection, particularly the *Passerella iliaca schistacea* group, we present information from studies of other subspecies as examples of habitat use. These examples demonstrate the range of habitats used but also imply some common elements. Fox sparrows are described as nesting a few inches to six feet above the ground, but they also nest directly on the ground. Breeding habitat in Newfoundland is much different than that found in Region 2. Active nests in Newfoundland were in conifer trees and on the ground beneath alders (Threlfall and Blacquiere 1982). Nests constructed earlier in the breeding season were built

significantly higher than nests constructed later in the season (Threlfall and Blacquiere 1982). Fox sparrow habitat in Oregon was described as brushy areas and occasionally in fireweed (*Erechtites arguta*) areas, but nests were never located in forested areas (Hagar 1960). More contemporary studies have only described fox sparrow habitat in the simplest terms. In the Yukon Territory, fox sparrows used dense willow and alder thickets at lake edges with stands of white spruce (*Picea glauca*) and sitka spruce (*Picea sitchensis*) nearby (Webster 1975).

Nest sites in California were not found under coniferous trees (Burns and Hackett 1993). Of 23 nests, 59 percent were found in or under mountain whitethorn (*Ceanothus cordulatus*), 18 percent were in or under greenleaf manzanitas (*Arctostaphylos patula*), 15 percent were in or under bush chinquapin (*Castanopsis sempervirens*), 4 percent were under Sierra gooseberry (*Ribes roezlii*), and 4 percent were in willows (*Salix* spp.). Vegetation immediately surrounding the nest (0.5 m radius) was similar to vegetation further from the nest (4.0 m radius). Burns and Hackett (1993) suggested that fox sparrows were not selecting particular plant species for nest sites; rather they were showing a general preference for dense shrubby vegetation that may aid in concealment from predators.

Breeding habitat has not been quantified in the Rocky Mountain region. However, from the above descriptions we can speculate that fox sparrows will use similar habitats in Region 2, i.e., shrub thickets. Mid- to high-elevation riparian habitats are believed to be particularly important (Kingery 1998) where alder, willow, and aspen are most similar to riparian habitats described elsewhere. Wet meadow habitats and associated willows should also be important, as well as treeline shrub communities, avalanche slopes, and early successional clear cuts or blowdowns.

Stopover habitat

Desert oases provide stopover habitat in California, and fox sparrows migrating through Colorado use wooded riparian areas (Andrews and Righter 1992, Garrett et al. 2000, Weckstein et al. 2003). We could not find additional information describing stopover habitats.

Winter habitat

Winter habitat within Region 2 has not been described because most birds migrate from the Rocky Mountain region. Outside of Region 2, the slate-colored

fox sparrow is most abundant during the winter in chaparral habitat (Weckstein et al. 2003).

Food habits

During migration, fox sparrow diets are likely varied (Weckstein et al. 2003). A bird collected in Wisconsin had consumed fifty chinch bugs (*Lygaeidae*), and another had eaten large quantities of *Panicum crusgalli* seeds. A Canadian study examined the stomachs from three specimens and found they contained both insects and vegetation (Linsdale 1928). The insects included weevils (*Aphodius*), Elaterid larvae, lepidoptera larvae, millipedes (*Diplopoda*), and spiders (*Arachnida*). Vegetation included the seeds of *Lithospermum*, *Panicum*, *Phleum pratense*, *Polygonum*, and *Rumex* (Linsdale 1928). Breaking the diet down into percentages of plant and insect matter showed a division of 14 percent insect and 86 percent plant (Linsdale 1928).

Terres (1980) described fox sparrows as essentially vegetarian, feeding primarily on *Polygonum*, blueberries, elderberries, grapes, and other wild fruit. Insects consumed included beetles, crane flies, chinch bugs, spiders, millipedes, and minute shellfish. Fox sparrows also frequent bird feeders for wild birdseed and breadcrumbs, but no specifics were given regarding whether the feeding habits described were during breeding, migration, or wintering periods (Terres 1980). We believe that in Region 2, fox sparrows consume many of the same foods that are mentioned in the literature from other geographic regions. For example, during the breeding season they likely consume beetles and weevils (*Coleoptera*), fly larvae (*Diptera*), caterpillars (*Diplopoda*), ants and bees (*Hymenoptera*), scale insects (*Hemiptera*), spiders, millipedes, the seeds and fruit of sedges (*Carex* spp.) raspberries and blackberries (*Rubus* spp.), cinquefoil (*Potentilla* spp.), and serviceberry (*Amelanchier* spp.) (Linsdale 1928, Grinnell et al. 1930, Weckstein et al. 2003). During migration they likely concentrate on arthropods and seeds and the fruits from the previous season (Weckstein et al. 2003). From the information we reviewed we believe fox sparrows concentrate on invertebrates during the breeding and nesting seasons and switch to a more vegetarian diet when invertebrates are not available.

Breeding biology

Phenology

As noted above, there is little published information on fox sparrow arrival times to areas within Region 2. However, Johnsgard (1986) noted that fox sparrows migrate to Montana in early April and to Idaho in March, and Kingery (1998) found regular breeders in Colorado west of the Continental Divide where territorial behavior was recorded as early as 7 May. Males and females usually arrive on their breeding grounds at the same time and establish pair bonds within a week (Weckstein et al. 2003). Both sexes sing, although the female sings less frequently (Weckstein et al. 2003). Nest construction begins at the end of May and incubation lasts from 12 to 14 days. Both sexes incubate eggs (Bendire 1889). Hatching probably begins mid- to late June, and the young fledge mid-July to early August (Kingery 1998).

In Colorado, territorial behavior can begin in early April, and fledgling-associated activity ranges from mid-June to August, which suggests double brooding (Kingery 1998). No arrival dates were reported for fox sparrows in Wyoming (Cerovski et al. 2001). In northern Utah, fox sparrows arrive on breeding grounds and establish territories between late March and mid-May (Martin 1980). By early June, the birds are paired, have constructed nests, and are laying and incubating eggs (Martin 1980).

In developing monitoring strategies, breeding birds should be monitored beginning immediately after arrival until pair formation ceases. Colorado populations and populations in other northern Rocky Mountains states (USFS Region 1) appear to arrive at similar times, so similar monitoring dates would be appropriate. Birds can migrate through Kansas, Nebraska, and South Dakota between early April and mid-May, and monitoring dates should be adjusted accordingly if monitoring of migrants is a goal (Bruner et al. 1904, South Dakota Ornithologists' Union 1991).

Breeding behavior

Territory fidelity was recorded in one population of red fox sparrows in Newfoundland. Researchers

found that 12 of 51 birds (23 percent) returned to a particular island in consecutive years (Threlfall and Blacquiere 1982). Nine of those birds were recaptured in mist nets located in the same place each year, and the other 3 were recaptured within 50 m of their original banding location (Threlfall and Blacquiere 1982). As with all studies of this type, survival of birds that failed to return is not certain. Fidelity has not been reported for slate-colored fox sparrows.

Brood information

Fox sparrows typically have one brood per season. However, slate-colored fox sparrows are thought to occasionally have a second brood late in the season (Weckstein et al. 2003). Typically a nest will contain two to five eggs (Weckstein et al. 2003).

Parental care of the young

Young fox sparrows are fed almost exclusively by the female. However, the male occasionally feeds young or passes food to the female who then feeds the young (Bent 1968, Weckstein et al. 2003). Feeding occurs at two to five minute intervals (Linsdale 1928). While nestlings are fed primarily animal matter, there is one report of a female feeding nestlings plant material (Linsdale 1928 referenced in Weckstein et al. 2003).

Nestling dispersal

Nestlings fledge at 9 to 10.5 days post hatching (Ryan 1974, Blacquiere 1979, Weckstein et al. 2003). Most young hop from the nest and continue hopping, as opposed to the traditional pattern of young birds flying out of the nest (Blacquiere 1979). Our literature review did not identify information on how long the adults remain with the young. Based on the behavior of other sparrows, parental care could last several weeks to several months (Weckstein et al. 2003).

Nest parasitism

Parasitism by brown-headed cowbirds (*Molothrus ater*) has been recorded in several geographic locations. Most notably, parasitism of slate-colored fox sparrows was considered common in south central Montana in the early 1900s (Bent 1968). Additionally parasitism of fox sparrows was reported in Saskatchewan, Canada; the Wasatch Range of Utah; Oregon; Washington; and Mono County, California (Bent 1968). More contemporary studies of cowbird parasitism on fox sparrows were not available. We believe that parasitism is not a serious issue for fox sparrows because of

their inherently secretive nature and their propensity for nesting in very thick habitats away from primary cowbird habitat.

Demography

Population size

We found no information regarding fox sparrow population size.

Population density

We found only imprecise estimates of fox sparrow densities from published accounts, such as the BBS (**Figure 1**). Fox sparrows within Region 2 are generally recorded in densities ranging between one and 10 birds per route surveyed. However, a more focused study within Jackson Hole, Wyoming recorded fox sparrow abundance at two birds per 4.5 ha (Salt 1957).

Life history

Information on age at first breeding, survivorship, and nesting and fledging success was unavailable; however, we assume that like most other sparrows and Passerines in general, fox sparrows will breed at one year of age. Fox sparrow clutch size ranges from three to five eggs, with four the most common number (Bendire 1889, Fisher 1997, Weckstein et al. 2003). Incubation lasts 12 to 14 days (Bendire 1889, Rising 1996, NatureServe 2001). Nest success appears to be high (approximately 60 percent); however, this is based on only one study in Alaska (Rogers 1994).

In Newfoundland, red fox sparrow territory sizes were variable between sites (Threlfall and Blacquiere 1982). One area had territories approximately 1 ha in size, while another supported birds with territory sizes of approximately 0.25 ha. Because slate-colored fox sparrow territory size has not been described, we can only hypothesize that these numbers may apply to birds in Region 2.

Conditions on breeding grounds rather than on wintering grounds are thought to most affect neotropical migrant songbirds (DeSante 1990, Chase et al. 1997). The opposite may be true for short-distance migrants. Snow-pack on breeding grounds may dictate nest height, and late snow-falls during the breeding season may cause nest abandonment (Threlfall and Blacquiere 1982). Severe weather on wintering grounds may have significant effects on populations of short-distance migrant songbirds (Sauer et al. 1996). For example,

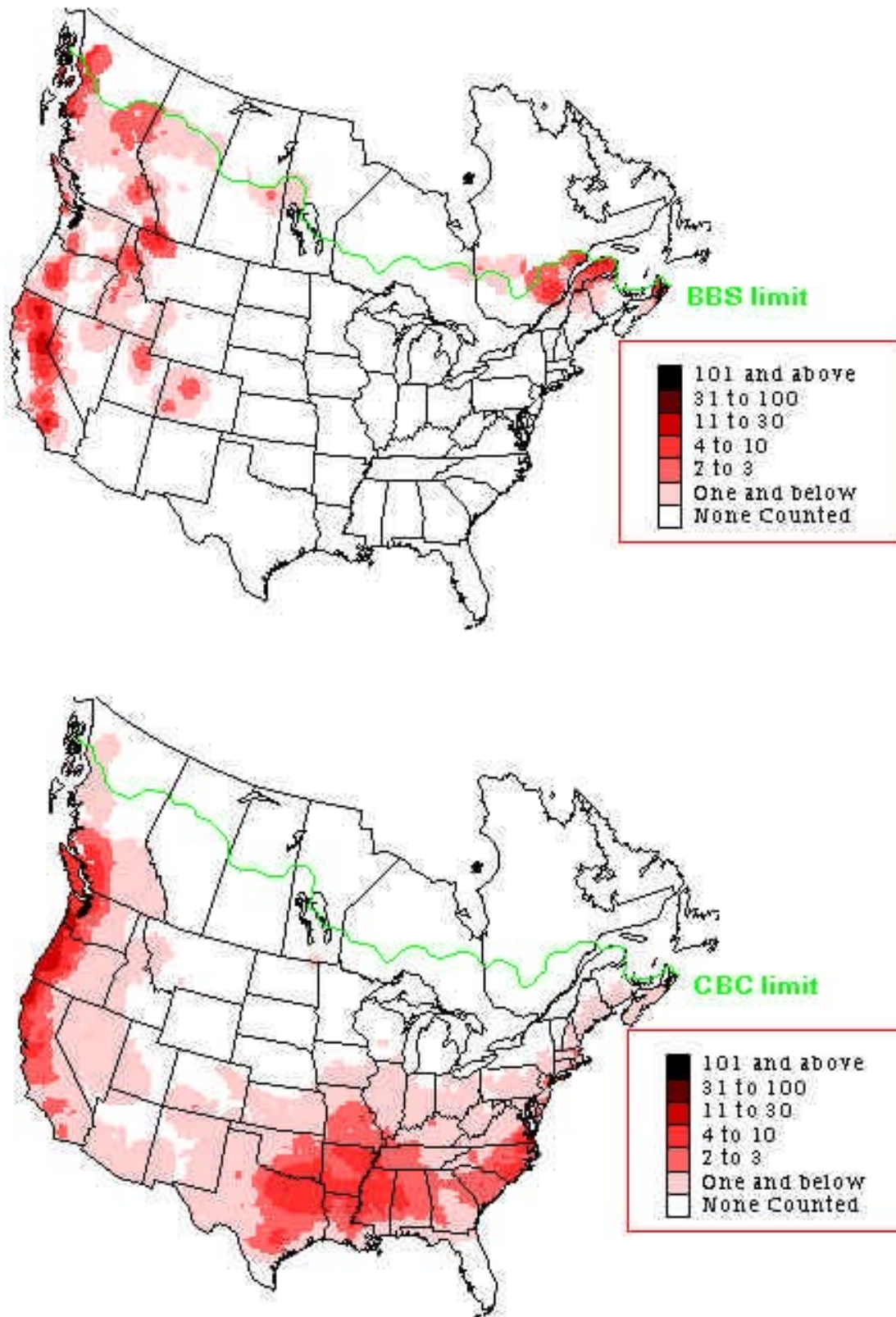


Figure 1. North American Breeding Bird Survey (top) and Christmas Bird Count distribution and density maps for the fox sparrow in North America (Sauer et al. 2001 and Sauer et al. 1996, respectively).

the winter of 1976-1977 was particularly severe in the eastern United States and “was the only large scale environmental event that can be shown to have had a major direct association with bird populations and we conclude that the pattern of population change...may well be a consequence of these severe winters” (Sauer et al. 1996). Relating to fox sparrows, Bent (1968) remarked that inclement weather during migration or on wintering grounds was perhaps their greatest threat. Severe storms in the southeastern United States have resulted in die-offs of thousands of fox sparrows (Bent 1968). **Appendix A** summarizes the results of demographic analysis of a life-cycle graph for fox sparrow. Unfortunately, our lack of understanding of fox sparrow demography significantly limits the specificity of the analysis, which required numerous assumptions regarding vital rates for the species. Therefore, the model should be considered the starting place for building a more useful analysis once more specific information on vital rates for fox sparrow in Region 2 becomes available.

Community ecology

Predators

Direct predation and nest predation on fox sparrows are not well reported in the literature. There are reports of nests being destroyed by sheep grazing in shrubby areas, and by Steller’s jays (*Cyanocitta stelleri*; Bent 1968). As mentioned above, weather can also cause adult mortality and desertion of nests.

Though unreported, we believe that Accipiter hawks, small mammals, snakes, and meso-predators (e.g., raccoons [*Procyon lotor*], weasels [*Mustela* spp.], and opossums [*Didelphis virginianus*]) will prey on fox sparrow adults, young, and eggs. Because fox sparrows generally nest in very thick cover, their vulnerability to predators is likely reduced. Again, it is not reported, but we infer that any activity that reduces cover of nest stands or increases visibility of adults coming and going from nests would increase nest predation rates. Such activities may include livestock grazing and recreational activities within riparian areas (Aitchison 1977, McCormick 1980, Knopf et al. 1988, Kingery 1991, Ohmart 1994, Rottenborn 1999).

Competitors

Potential competitors for food reported in the literature include the northern waterthrush (*Seiurus noveboracensis*), the white-throated sparrow (*Zonotrichia albicollis*), and the dark-eyed junco (*Junco*

hyemalis) (Blacchiere 1979). Interspecific interactions with the slate-colored fox sparrow in Region 2 could include other species of riparian songbirds such as Lincoln’s sparrows, white-crowned sparrows, and Wilson’s warblers, which use habitats similar to the fox sparrow. The Lincoln’s sparrow and Wilson’s warbler along with fox sparrow were considered by the Rio Grande National Forest as possible group of Management Indicator Species due to their similar breeding habitat associations. Additionally they all nest on or near the ground in thick cover and feed on similar prey species. Therefore, we believe there may be some degree of competition for nest sites and food items.

Parasites and disease

Fox sparrows host at least 20 genera of parasites, including 12 internal (Haematozoan and Helminth) and 8 arthropod ectoparasites (Jewer and Threlfall 1978). The Haematozoans include *Haemoproteus fringillae* and *Haemoproteus orizivora* and the Helminths include five genera of Tremetoda (*Conspicuun*, *Brachylecithum*, *Zonorchis*, *Tanaisia*, and *Shistosomid*), two genera of Cestoda (*Paricterotaenia* and *Aploparaksis*), and three genera of Nematoda (*Syngamus*, *Capillaria*, and *Porrocaecum*). The ectoparasites carried by fox sparrows include four genera of Pthiraptera (*Philopterus*, *Myrsidea*, *Ricinus*, and *Brueelia*), one genus of Siphonaptera (*Ceratophyllus*), and three genera of Acarina (*Haemaphysalis*, *Proctophyllodes*, and *Analges*) (Jewer and Threlfall 1978, Weckstein et al. 2003).

Symbiotic and mutualistic interactions

No symbiotic or mutualistic interactions have been reported for the fox sparrow. See **Figure 2** for an Envirogram depicting complex ecological interactions (Andrewartha and Birch 1984).

CONSERVATION

Threats

The largest threats to the western races of fox sparrow include any activities that degrade the structure and quality of riparian shrub communities. These activities include dewatering for municipal or agricultural uses, livestock and wild ungulate grazing, burning, and recreation (Ammon and Gilbert 1999, Colorado Partners in Flight 2000).

The loss of riparian habitat is of historical significance across the western United States. An

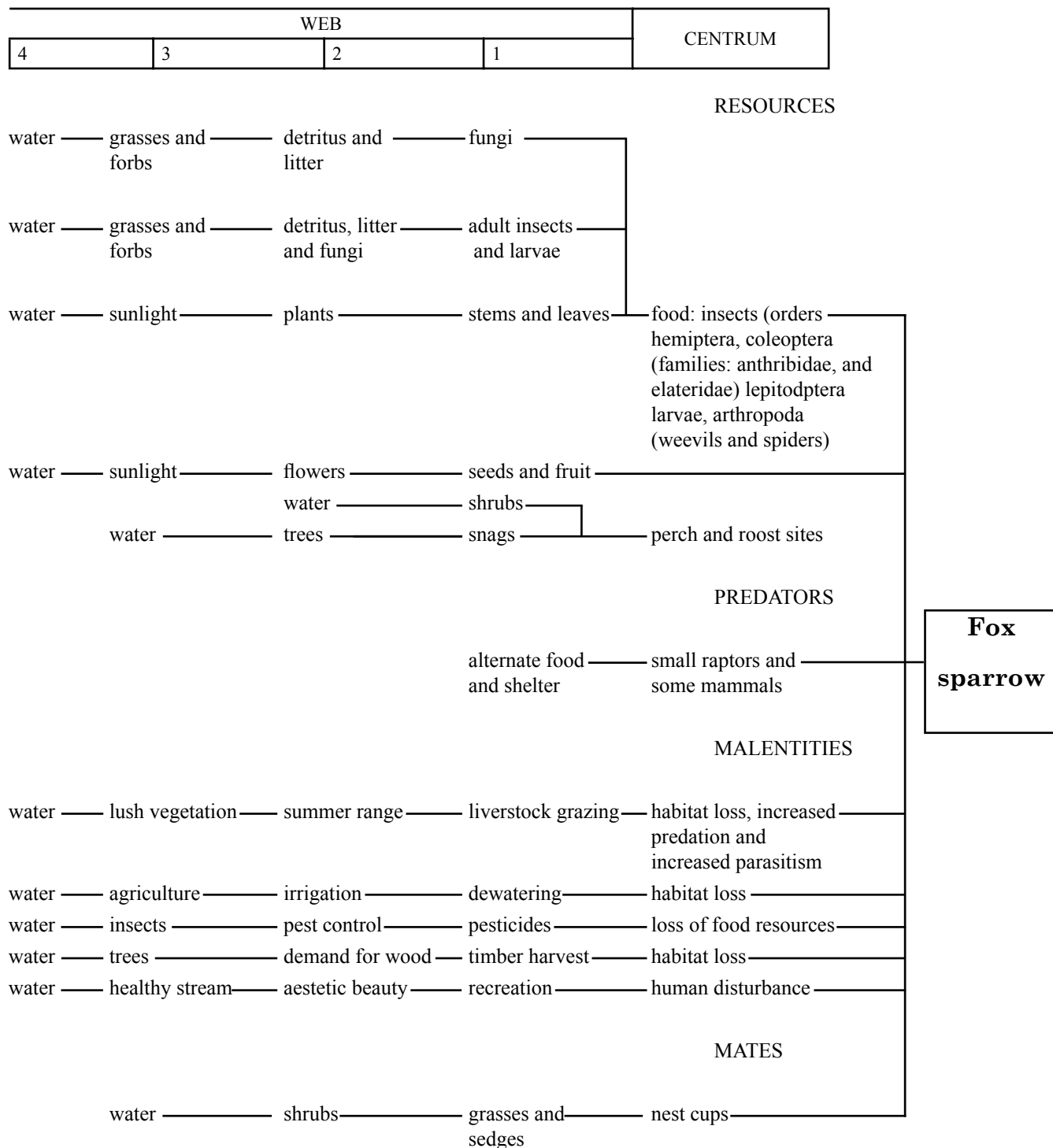


Figure 2. Envirogram depicting ecological relationships of the fox sparrow in Region 2.

example of the loss of riparian habitat is from the lower Colorado River, which is important to fox sparrows as a migration stopover and winter habitat (Rosenberg et al. 1991). Based on historic descriptions, the authors estimated that there were approximately 2000 ha of riparian cottonwood (*Populus fremontii*) forests along

the lower Colorado River in the 1600s. This was reduced to a few scattered groves of about 1100 ha in the 1970s, of which only 200 ha were pure cottonwood. Reasons for the decline varied but included conversion to agriculture crops, grazing, urban development, and disease (Ohmart et al. 1977).

Within Region 2, fox sparrows appear to favor mid- to high elevation riparian zones (Kingery 1998). Higher elevation, montane riparian habitats may be less affected by human disturbances than lower elevation riparian habitats for several reasons. First, agricultural activities and the conversion of riparian habitats are concentrated in lower, more accessible elevations. Second, dewatering rarely affects high elevation riparian zones because water diversions occur primarily at lower elevations. However, livestock grazing on public lands represents one of the most serious threats to high elevation, montane riparian vegetation and can contribute significantly to habitat degradation (Carothers 1977, Knopf and Cannon 1982, Bock et al. 1992, Ammon and Stacey 1997, Toolen 1998).

Fox sparrows rely on thick ground- and shrub cover for nesting, and grazing can negatively affect these attributes. Within riparian communities in northern Colorado, Knopf and Cannon (1982) found that livestock alter the size, shape, volume, and quantity of live and dead stems of riparian vegetation. Livestock also alter the spacing of plants and the width of riparian corridors. Unfortunately, willow communities recover slowly from grazing impacts, even after the complete removal of cattle (Knopf and Cannon 1982). Apart from habitat alteration, livestock grazing also poses a direct threat to ground nests through trampling (Bent 1968).

Avian nest success on grazed and ungrazed riparian sites has been studied in northwest Nevada (Ammon and Stacey 1997). Grazing was shown to decrease willow abundance and decrease overall vegetation diversity. Real and artificial nests had higher predation rates on grazed versus ungrazed sites, suggesting that grazing was not only affecting available nesting substrate, but also was influencing bird populations by increasing predation on nests (Ammon and Stacey 1997).

Like many attributes of the fox sparrow, nest site characteristics have not been examined. We found no studies that discuss slate-colored fox sparrow nesting or that quantified nesting habitat preferences for any of the subspecies, except the thick-billed fox sparrow. Burns and Hackett (1993) found that this subspecies preferred thick cover in California; of 23 nests found, 40 percent were completely concealed, 32 percent were 25 percent visible, 12 percent were 50 percent visible, and 16 percent were completely visible without moving branches. In addition to nesting in the thickest shrub cover available, fox sparrows forage in the same microhabitat (Weckstein et al. 2003). Currently there are no published guidelines for cover thresholds needed to accommodate fox sparrows.

Recreational activities, such as fishing, rafting, picnicking, bird watching, and hiking, may also be detrimental to wildlife that rely on montane riparian habitats. Along the Snake River in Grand Teton National Park, 77 species of songbirds were observed using riparian habitat; however 88 percent of these species decreased in abundance when humans were present (Buhler 1998). Similarly, Aitchison (1977) reported that breeding bird density and diversity decreased at campgrounds located in riparian woodlands in Arizona. When the campgrounds were closed, songbird density and diversity were similar to adjacent natural areas (Aitchison 1977).

The effect of human encroachment specifically on fox sparrows has not been addressed in the literature. However, we can make some inferences. Since fox sparrows prefer nearly impenetrable riparian habitat for breeding and foraging, interactions between people and fox sparrows may be limited. Additionally, in areas where trails or campgrounds border the thickest riparian habitats, fox sparrows can avoid detection and may not perceive people as a threat. We believe that recreation is unlikely to be a major threat to fox sparrows in Region 2 except in cases where developed recreation or other activities change riparian vegetation structure.

In addition to human induced threats, natural disturbances may impact populations of fox sparrows or the quality and availability of their habitat. Wildfire may be an important threat to higher elevation riparian habitats within Region 2. While we were unable to locate information on fire effects in montane riparian habitats, studies from lower elevations may be applicable. In particular, shifts in plant species composition may be the largest threat posed by wildfire in riparian habitats. Busch (1995) found that saltcedar (*Tamarix* spp.) and arrowweed (*Tessaria sericea*) dominated post-fire riparian communities, replacing riparian forests formerly dominated by cottonwood and willow and more valuable to fox sparrows.

Conservation Status of the Fox Sparrow in Region 2

To review, the continent-wide status of the fox sparrow is considered secure and widespread (NatureServe 2001). Among Region 2 states, Wyoming and Colorado both rank the fox sparrow as being secure with many breeding and non-breeding records. South Dakota, Nebraska, and Kansas do not have breeding populations but do list it as a common migrant.

Within Colorado, the Rio Grande National Forest is considering the fox sparrow as a possible MIS. Rationale for inclusion of this species as a MIS included “Riparian species tied to different structural elements susceptible to grazing and other activities within riparian areas; monitored as a group due to close habitat associations with willow communities at various elevations” (Rio Grande National Forest 2001 online: <http://www.fs.fed.us/r2/riogrande/planning/planreversal.htm>). The slate-colored fox sparrow is associated with mid- to high-elevation riparian habitats within its breeding range in Region 2 (Kingery 1998). Therefore, we believe widespread impacts to riparian habitats could have the greatest detrimental effects on fox sparrow populations within Region 2. Misguided forest or stream management practices and water development could limit breeding habitat within the region, which would have population-wide effects for fox sparrows. These practices include activities such as ill-planned timber harvest regimes that reduce shrub cover along riparian areas or change hydrologic conditions in a way that reduces riparian shrub cover. For example, if forests are harvested near riparian shrub communities, the loss of trees may cause changes in hydrologic regimes and micro-climates that will reduce riparian vegetation width, breadth, and abundance. Similarly, thinning riparian shrub communities to improve habitat for other wildlife species or to increase recreational access to water sources will undoubtedly have negative impacts on fox sparrows. Dewatering for irrigation also impacts riparian habitat. For example, some rivers in southwest Region 2 are dry during summer months due to irrigation. Spring runoff may promote bank storage, but reduction in water during the summer, fall, and winter months has serious effects on native riparian vegetation and promotes infestation of phreatophytic exotic plants that are not as suitable for fox sparrows. Livestock grazing in riparian corridors can denude shrubs close to the ground and trample associated vegetation.

Information on population status for the fox sparrow in Region 2 is lacking, and we cannot speculate on whether distribution or abundance of the fox sparrow is changing. Several studies suggest that slate-colored fox sparrows are tied to riparian habitats in Region 2. However, habitat selection and preferences have not been studied, so we find it difficult to comment on the habitat use of the subspecies that occurs in Region 2. We believe that there is a range of habitat attributes that influence fox sparrow selection of breeding and nesting sites. Additionally, disturbances such as those mentioned above likely have a threshold effect on fox sparrows. Limited grazing or dewatering may not

affect the species’ presence or abundance. However, if a threshold of disturbance or habitat loss is reached such that nesting and foraging cover are significantly reduced, fox sparrows may be eliminated. Specific habitat selection studies are needed to understand what thresholds exist for the species.

Habitat preference for slate-colored fox sparrows suggests that it is vulnerable to habitat alterations. It is important that managers understand that this subspecies is tied to riparian shrub habitats, although the other three subspecies of fox sparrows are considered more generalist in habitat use.

Management of the species in Region 2

Implications and potential conservation elements

In addition to riparian habitats, some attention should be directed toward subalpine shrub habitats. Again, we are handicapped by a lack of information on habitat use by fox sparrows. Within Region 2, along mid- to high-elevation riparian zones, we predict that a variety of willow species as well as alder make up the shrub community most attractive to fox sparrows. Additionally, mountain mahogany (*Cercocarpus* spp.) shrub communities that adjoin riparian zones may serve as fox sparrow habitat. We believe that short-statured willow communities commonly found in wet meadow areas do not provide ideal habitat for fox sparrows. Conservation of shrub communities is essential in conjunction with conservation of riparian communities. When management activities are implemented in areas of riparian and shrub communities, we feel that a buffer of at least 50 m of shrub cover is advantageous for fox sparrows. We also believe that moderate amounts of grazing or burning are acceptable as long as the entire patch is not affected. Creating a mosaic of thick shrubs interspersed with thinner areas should be ideal for fox sparrows, while burning or grazing an entire shrub community is likely detrimental to the species.

In addition to setting standards for maintaining riparian health, the Rio Grande National Forest has also provided guidelines for maintaining wildlife on the forest, including two that apply to fox sparrows: 1) “In areas where tall dense cover is desired for ground-nesting birds, residual cover needs to be carried over from previous growing seasons, since some species begin nesting in April and May before spring growth.,” and 2) “Some bird species prefer to nest in undisturbed cover. In areas where these birds are a primary consideration, manage livestock grazing to

avoid adverse impacts on nesting habitat". Although the Rio Grande National Forest standards are general, we believe they represent practical approaches to achieving or maintaining suitable riparian songbird habitat within Region 2.

Tools and practices

Species and Population Inventory

Specific guidelines for monitoring fox sparrows are not available. However, in reviewing inventory and monitoring schemes, the Rocky Mountain Bird Observatory's (RMBO) *Monitoring Colorado's Birds* (MCB) program stood out as a comprehensive monitoring plan that is being implemented on a Region-wide scale, although it is not currently used to monitor fox sparrows. The MCB format has already been applied to the Wyoming Partners in Flight-Wyoming Bird Conservation Plan renamed as *Monitoring Wyoming's Birds* (MWB). The RMBO-MCB method obtains count-based data for breeding bird species within specified areas (i.e., states) on a randomly allocated and habitat-stratified basis (Leukering et al. 2001). For example, using this plan RMBO has used point transects to survey for Wilson's warblers in high elevation riparian areas of Colorado. Colorado GAP data were used to randomly select 60 publicly-owned stands within each of 12 habitat types, including high elevation riparian. Thirty of these stands were randomly selected from the 60 for establishing transects. Fifteen sample locations or point counts were then established in each of the 30 randomly selected stands. The locations consisted of 15 five-minute point counts spaced at 250 m intervals along a transect. At each point, the radial distance to each bird was recorded. Additionally, while walking the transects between counts, surveyors recorded perpendicular distances to birds previously identified as having low population densities. The surveyors noted weather conditions, determined if the point was within 100 m of a road, and recorded the specific habitat and seral stage for each of two predominant habitats around each point. Finally, the observers recorded the two most common understory types and the percentage that each occupied of a 50m-radius circle centered on the point. Although the RMBO has not established monitoring protocols specifically for fox sparrows, they do record reports from birders across the state to monitor populations and record the sparrow when it is located on transects (Leukering et al. 2001).

Bird surveys in riparian areas often include fox sparrows, and many of these have been performed recently within Region 2 through various graduate

student projects and agency monitoring activities. These data are usually collected by transect, point counts, or spot mapping. A compilation of these studies would provide useful information on fox sparrows; however, it would be a time intensive task and analyzing data collected using different methods, in different years, and in different geographic areas would be a challenge. A detailed description of various monitoring and survey methods for landbirds can be found in Ralph et al. (1995) and would be an excellent starting point for anyone designing survey protocols for fox sparrows or other passerine birds.

Habitat inventory. Population and habitat management recommendations specific to the fox sparrow are not available. However, we did find habitat management techniques that are specific to riparian obligates. The Wyoming Partners in Flight Wyoming Bird Conservation Plan (Cerovski et al. 2001) suggests useful guidelines for riparian habitat management including techniques like grazing, timber harvesting, wildlife management, and engineering practices that can be used to improve riparian areas. In higher elevation riparian habitats of Region 2, grazing and forestry practices will be more immediate threats than agricultural activities. Although fox sparrows are not mentioned specifically in grazing studies, we can infer that they are negatively impacted. Fox sparrows nest on or near the ground. Livestock grazing in riparian bottoms generally causes compaction of soils and removal of plant material, both which indirectly reduce water infiltration and reduce vegetation density. Also livestock along streams can reduce riparian vegetation through channel widening, channel aggrading, or lowering the water table (Bock et al. 1992, Knight 1994). Finally, livestock grazing in fox sparrow nesting habitat may directly impact nests by trampling. Fencing riparian corridors and reducing grazing or employing different grazing strategies can all be used to reduce detrimental effects.

While fox sparrows and other riparian songbirds have evolved with wild ungulate grazers, differences in stocking rates and in duration and timing of use are vastly different between livestock and native ungulates. Domestic livestock are often confined on riparian habitats, or they seek out riparian areas within grazing allotments or pastures. Season-long use is especially detrimental to riparian areas and should be avoided.

Agricultural practices can affect riparian habitats in several ways. Dewatering affects riparian habitats at lower elevations that rely on runoff throughout the growing season. Irrigation removes water from streams,

changing channel morphology and reducing riparian vegetation. However, irrigation canals, irrigation, and return flows can create riparian habitat in areas where it otherwise would not be found. These habitats often resemble riparian corridors and can provide tremendous wildlife habitat. Unfortunately, water issues throughout the western United States are politically charged and little consideration is given to wildlife. Water rights are tied to specific land parcels and are often passed down through generations of landowners. Presently, land and associated water rights are being sold across the western United States to satisfy the growing needs of urban areas, regardless of whether wildlife habitat is being lost. Shifts from agricultural to urban uses of water will undoubtedly impact riparian obligates like fox sparrows that rely on habitat created from return flows and irrigation. Other impacts of agriculture may be less obvious. For example, pesticide and herbicide use can degrade both habitat quality and quantity.

Forestry practices have been mitigated over the past several decades to reduce impacts to riparian habitats. Both the USFS and the Bureau of Land Management have initiated measures to protect habitat around riparian areas (Kreuper 1992). Such measures include buffer zones and management of activities within those zones according to variables such as soil type, slope of surrounding terrain, and dominant vegetation.

Population management approaches.

Other than broad habitat protection, we found no management approaches that specifically target fox sparrows.

Information Needs

Information needs for the fox sparrow are broad and varied. As with most songbird species, there are large gaps in our knowledge of its life history characteristics, including habitat selection during wintering, migration and breeding periods. Additionally there are gaps in our knowledge of what effects various habitat manipulations might have on fox sparrows, including upland habitat and riparian habitat management, or lack thereof. Like many passerine birds, the fox sparrow's secretive nature contributes to this lack of knowledge. The information that seems particularly lacking for fox sparrows

includes a better understanding of migration routes, habitat use during migration, microhabitat selection on wintering and breeding grounds, and the effect that different management activities have on the species. More information is needed regarding the geographical differences in the breeding biology and habitat needs of fox sparrows, as these differ in across the species' range. We believe that fox sparrows prefer deciduous riparian shrub lands in the western United States, but that is conjecture based on a few incomplete studies.

Migration patterns are also not well documented for fox sparrows, especially in the Rocky Mountain region. This is important because of implications to populations on wintering grounds. Populations found on the extreme West Coast of North America have been well studied, and their leap-frog migrations are well documented. Eastern populations are known to migrate to the southeastern United States, but migration patterns for fox sparrows in the Rocky Mountains are not well-defined.

The impact of vegetation manipulation, whether upland or riparian, is especially unreported with respect to songbirds. The information most lacking concerns threshold limits beyond which impacts to populations may occur. Microhabitat selection information is important in this regard because it could help identify thresholds. For example, if habitat preferences (e.g., shrub cover, foliage volume) were known for fox sparrows, then grazing levels could be adjusted to maintain those goals. Or, if recreational activities such as camping, fishing, and hiking are shown to reduce the effectiveness of riparian vegetation to levels beyond what fox sparrows select, then actions could be taken to mitigate these losses.

Methods are available to monitor fox sparrow population trends within Region 2 and are used in Region-wide monitoring programs such as Monitoring Colorado Birds. North American Breeding Bird Survey methods are sound for nation-wide trends of many species. However, throughout the western United States route coverage is a problem, as these surveys are conducted on roads and many mid- and high-elevation riparian habitats are far from roads. Ultimately the *MCB* monitoring program may be a better method for obtaining a more accurate picture of fox sparrow population numbers and trends within Region 2.

REFERENCES

- Aitchison, S.W. 1977. Some effects of a campground on breeding birds in Arizona. Pages 175-182 in R.R. Johnson, and D.A. Jones, technical coordinators. Importance, preservation and management of riparian habitat: A symposium. USDA Forest Service General Technical Report RM-43.
- Ammon, E.M. and W.M. Gilbert. 1999. Wilson's warbler (*Wilsonia pusilla*). In A. Poole and F. Gill, editors. The Birds of North America, No. 478. The Birds of North America, Inc., Philadelphia, PA.
- Ammon, E.M. and P.B. Stacey. 1997. Avian nest success in relation to past grazing regimes in a montane riparian system. *Condor* 99:7-13.
- Andrewartha, H.G. and L.C. Birch. 1984. The ecological web: more on the distribution and abundance of animals. University of Chicago Press, Chicago, IL.
- Bell, C.P. 1997. Leap-frog migration in the fox sparrow: minimizing the cost of spring migration. *Condor* 99:470-477.
- Bendire, C.E. 1889. Notes on the general habits, nests and, eggs of the genus *Passerella*. *Auk* 6:107-116.
- Bent, O.L. 1968. *Passerella iliaca* (Merrem) Fox sparrow. Pages 1392-1434 in O.L. Austin Jr., editor. Life histories of North American Cardinals, Grosbeaks, Buntings, Towhees, Finches, Sparrows, and Allies. U.S. Natural Museum Bulletin 237.
- Blacquiere, J.R. 1979. Some aspects of the breeding biology and vocalizations of the fox sparrow (*Passerella iliaca* Merrem) in Newfoundland. Masters thesis. Memorial University of Newfoundland, St. Johns, Newfoundland, Canada.
- Bruner, L., R.H. Wolcott, and M.H. Swenk. 1904. A preliminary review of the birds of Nebraska with synopses. Kloop and Bartlett Co, Omaha, NE.
- Buhler, M.L. 1998. Avian habitat ecology within the riparian corridor along the Snake River in Grand Teton National Park, Wyoming. Master's Thesis. University of Wyoming, Laramie, WY.
- Burns, K.J., and J. Hackett. 1993. Nest and nest-site characteristics of a western population of fox sparrow (*Passerella iliaca*). *Southwestern Naturalist* 38:277-279.
- Busch, D.E. 1995. Effects of fire on southwestern riparian plant community structure. *Southwestern Naturalist* 40: 259-267.
- Carothers, S.W. 1977. Importance, preservation, and management of riparian habitats: An Overview. Pages 2-4 in R.R. Johnson and D.A. Jones, technical coordinators. Importance, preservation and management of riparian habitat: A symposium. USDA Forest Service General Technical Report RM-43.
- Chase, M.K., N. Nur, and G.R. Geupel. 1997. Survival, productivity, and abundance in a Wilson's warbler population. *Auk* 114:354-366.
- Cerovski, A., M. Gorges, T. Byer, K. Duffy, and D. Felley, editors. 2001. Wyoming Bird Conservation Plan, Version 1.0. Wyoming Partners in Flight. Wyoming Game and Fish Department, Lander, WY.
- Colorado Partners in Flight. 2000. Partners in Flight land bird conservation plan: Colorado. Colorado Partners in Flight, Estes Park, CO.
- Cramp, S. and C.M. Perrins, editors. 1994. Handbook of the birds of Europe, the Middle East and North Africa: the birds of the western palearctic. Vol. IV. Oxford Press, Oxford, UK.
- DeSante, D.F. 1990. The role of recruitment in the dynamics of a Sierran subalpine bird community. *The American Naturalist* 136:429-445.
- Dobkin, D.S. 1994. Conservation and management of neotropical migrant landbirds in the northern Rockies and Great Plains. University of Idaho Press, Moscow, ID.
- Fisher, C.C. 1997. Birds of the Rocky Mountains. Lone Pine Publishing, Edmonton, Canada.

- Garrett, K.L., J.L. Dunn, and R. Righter. 2000. Call notes and winter distribution in the fox sparrow complex. *Birding* 32:412-417.
- Grinnell, J., J. Dixon, and J.M. Linsdale. 1930. Vertebrate natural history of a section of northern California through the Lassen Peak region. *University of California Publication of Zoology* 35:1-594.
- Hagar, D.C. 1960. The interrelationships of logging, birds, and timber regeneration in the Douglas-fir region of northwestern California. *Ecology* 41:116-125.
- Jewer, D.D. and W. Threlfall. 1978. Parasites of the fox sparrow (*Passerella iliaca*) and northern waterthrush (*Seiurus noveboracensis*) in Newfoundland, Canada. *Proceedings Of the Helminthological Society of Washington* 45: 270-272.
- Johnsgard, P.A. 1986. *Birds of the Rocky Mountains*. Colorado Associated University Press, Boulder, CO.
- Kingery, H. 1991. Riparian value to birds. Pages 7-15 in D. Roth, C. Bridges, and C. Zimmerman, editors. *Riparian: What does it mean to me?* Proceedings of the third annual convention of the Colorado Riparian Association, Pueblo, CO.
- Kingery, H.E., editor. 1998. *Colorado breeding bird atlas*. Colorado Bird Atlas Partnership and Colorado Division of Wildlife.
- Knight, D.L. 1994. *Mountains and plains, the ecology of Wyoming landscapes*. Yale University Press, New Haven, CT.
- Knopf, F.L. and R.W. Cannon. 1982. Structural resilience of a willow riparian community to changes in grazing practices. Pages 198-207 in J.M. Peek and P.D. Dalke, editors. *Wildlife-livestock relationships symposium: Proceedings 10*. University of Idaho Forestry, Wildlife and Range Experiment Station, Moscow, ID.
- Knopf, F.L., R.R. Johnson, T. Rich, F.B. Samson, and R.C. Szaro. 1988. Conservation of riparian ecosystems in the United States. *Wilson Bulletin* 100:272-284.
- Linsdale, J.M. 1928. Variations in the fox sparrow (*Passerella iliaca*) with reference to natural history and osteology. *University of California Publication of Zoology* 30:251-392.
- Luce, B., A. Cerovski, B. Oakleaf, J. Priday, and L. Vanfleet. 1999. *Atlas of birds, mammals, reptiles and amphibians in Wyoming*. Wyoming Game and Fish Department, Lander, WY.
- Leukering, T., D. Faulkner, R. Levad, and A. Panjabi. 2001. *Monitoring Colorado's Birds: The year 2000 final report*. Unpublished document, Rocky Mountain Bird Observatory, Brighton, CO. 21 pp.
- Martin, D.J. 1980. Response by male fox sparrows to broadcast of particular conspecific songs. *Wilson Bulletin*. 92: 21-32.
- McCormick, J.F. 1980. *Riparian ecosystems: A preliminary assessment of their importance, status, and needs*. Eastern Energy and Land Use Team, National Water Resources Analysis Group, U.S. Fish and Wildlife Service, Kearneysville, WV.
- NatureServe. 2001. An online encyclopedia of life [web application]. Version 1.6. Arlington, Virginia, USA: NatureServe. Available: <http://www.natureserve.org/explorer/>.
- Ohmart, R.D. 1994. The effects of human-induced changes on the avifauna of western riparian habitats. *Studies in Avian Biology* 15:273-285.
- Ohmart, R.D., W.O. Deason, and C. Burke. 1977. A riparian case history: The Colorado River, Pages 35-47 in R.R. Johnson, and D.A. Jones, technical coordinators. *Importance, preservation and management of riparian habitat: A symposium*. USDA Forest Service General Technical Report RM-43.
- Platt, J.R. 1964. Strong inference. *Science* 146:347-353.
- Price, J., S. Droege, and A. Price. 1995. *The summer atlas of North American birds*. Harcourt Brace and Company, Pubs. Academic Press.

- Ralph, C.J., J.R. Sauer, and S. Droege, editors. 1995. Monitoring bird populations by point counts. USDA Forest Service General Technical Report PSW-GTR-149. USDA Forest Service, Pacific Southwest Research Station, Albany, CA. 187 pp.
- Rising, J.D. 1996. A guide to the identification and natural history of the sparrows of the United States and Canada. Academic Press, London, UK.
- Rosenberg, K.V., R.D. Ohmart, W.C. Hunter, and B.W. Anderson. 1991. Birds of the Lower Colorado River Valley. The University of Arizona Press, Tucson, AZ.
- Rottenborn, S.C. 1999. Predicting the impacts of urbanization on riparian bird communities. *Biological Conservation* 88:289-299.
- Ryan, A.G. 1974. An incubation period and a nestling period for the fox sparrow. *The Canadian Field-Naturalist* 88: 230-231.
- Salt, G.W. 1957. Observations on fox, Lincoln, and song sparrows at Jackson Hole, Wyoming. *Auk* 65:373-383.
- Sauer, J.R., G.W. Pendleton, and B.G. Peterjohn. 1996. Evaluating causes of population change in North American insectivorous songbirds. *Conservation Biology* 10:465-478.
- Sauer, J.R., S. Schwartz, and B. Hoover. 1996. The Christmas Bird Count Home Page. Version 95.1. Patuxent Wildlife Research Center, Laurel, MD.
- Sauer, J.R., J.E. Hines, and J. Fallon. 2001. The North American Breeding Bird Survey, Results and Analysis 1966 - 2000. Version 2001.2, *USGS Patuxent Wildlife Research Center*, Laurel, MD.
- Sharpe, R.S., W.R. Silcock, and J.G. Jorgensen. 2001. Birds of Nebraska, their distribution and temporal occurrence. University of Nebraska Press, Lincoln, NE. 520 pp.
- South Dakota Ornithologists' Union. 1991. The birds of South Dakota, 2nd edition. South Dakota Ornithologists' Union, Aberdeen, SD.
- Swarth, H. 1920. Revision of the avian genus *Passerella* with special reference to the distribution and migration of the races in California. *University of California Publication of Zoology* 21:75-224.
- Terres, J.K. 1980. The Audubon Society encyclopedia of North American Birds. Alfred A. Knopf, New York, NY.
- Thompson, M.C. and C. Ely. 1992. Birds in Kansas vol. 2. University of Kansas Museum of natural History, Lawrence, KS.
- Threlfall, W. and J.R. Blacquiere. 1982. Breeding biology of the fox sparrow in Newfoundland. *Journal of Field Ornithology* 53:235-239.
- Wassink, J. 1991. Birds of the central Rockies. Mountain Press Publishing Co., Missoula, MT.
- Webster, J.D. 1975. The fox sparrow in southwestern Yukon and adjacent areas. *Condor* 77:215-216.
- Weckstein, J.D., D.E. Kroodsma, and R.C. Faucett. 2003. Fox sparrow (*Passerella iliaca*). In A. Poole and F. Gill, editors. *The Birds of North America*, No. 715. The Birds of North America, Inc., Philadelphia, PA.
- Zink, R.M. 1996. Comparative phylogeography in North American birds. *Evolution* 50:308-317.
- Zink, R.M. and A.E. Kessen. 1999. Species limits in the fox sparrow. *Birding* 31:508-517.

APPENDIX A

Matrix Model Assessment of the Fox Sparrow

Life cycle model

Due to the similarities of life history characteristics and a dearth of demography data, we pooled the data available for Lincoln’s sparrows (*Melospiza lincolni*), fox sparrows (*Passerella iliaca*), and Wilson’s warblers (*Wilsonia pusilla*) to construct a life cycle model. The studies of Speirs and Speirs (1968), Ammon (1995), Ammon (1999), and Weckstein et al. (2003) provided the basis for formulating a life cycle graph for the fox sparrow that comprised two stages (censused at the egg stage and “adults”), and assigned a lower clutch size to yearlings. Survival rates for “adults” came from Ammon (1995) and Ammon (1999). Because no estimate for first-year survival was available, and even the data for “adult” survival were sparse, first-year and “adult” survival (P_{21}) were assigned values that yielded a population growth rate (λ) of 1.0. This “missing element” method (McDonald and Caswell 1993) is justified by the fact that, over the long term, λ must be near 1 or the population will go extinct or

grow unreasonably large. We bracketed what we felt were reasonable ranges of values by having a high adult to first year-survival ratio case ($P_{22} = 0.59$, $P_{21} = 0.18$) and a low adult to first-year survival case ($P_{22} = 0.5$, $P_{21} = 0.225$). From the resulting life cycle graph (**Figure A1**), we produced a matrix population analysis with a post-breeding census (McDonald and Caswell 1993, Caswell 2000). The model has two kinds of input terms: P_i describing survival rates and m_i describing fertilities (**Table A1**). **Figure A2a** shows the symbolic terms in the projection matrices corresponding to the life cycle graphs. **Figure A2b** gives the corresponding numeric values for the low-ratio as well as the high-ratio case. The model assumes female demographic dominance so that, for example, fertilities are given as female offspring per female; thus, the egg number used was half the total clutch, assuming a 1:1 sex ratio. The population growth rate, λ , was 1.003 for the high ratio case and 1.006 for the low ratio case, based on the estimated vital rates used for the matrix. Although these rates suggest stationary populations, the λ value (~ 1.0) 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.

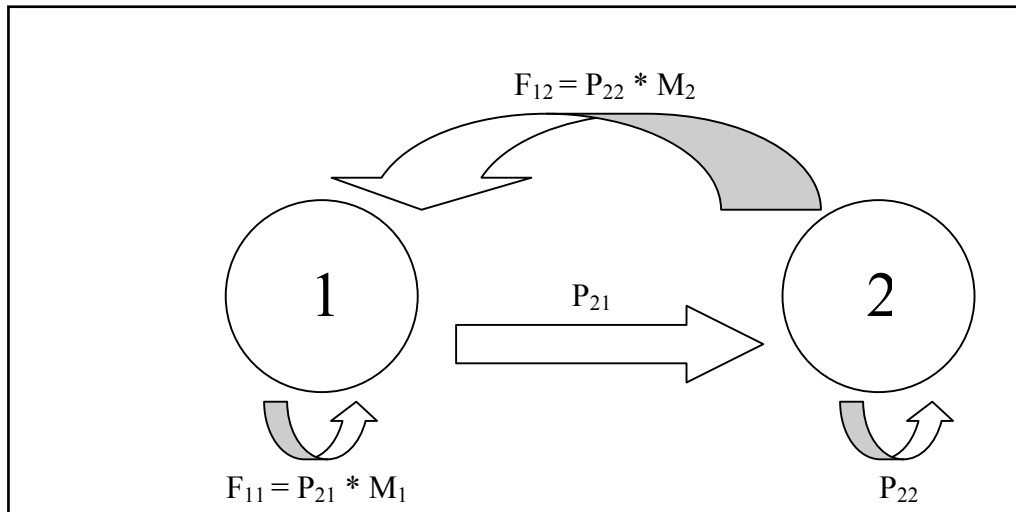


Figure A1. Life cycle graph for the fox sparrow. The numbered circles (nodes) represent the two stages. The arrows (arcs) connecting the nodes represent the vital rates — transitions between age-classes such as survival (P_{ji}) or fertility (the arcs pointing back toward the first node). Note that reproduction begins in the first year.

Table A1. Parameter values for the component terms (P_i and m_i) that make up the vital rates in the projection matrices for the fox sparrow. Bracketed values are for the low-ratio case.

Parameter	Numeric value	Interpretation
m_1	2	Number of female eggs produced by a first-year female
m_2	2.5	Number of female eggs produced by an “adult” female
P_{21}	0.18 (0.225)	First-year survival rate (low-ratio case in brackets)
P_{22}	0.59 (0.5)	“Adult” survival rate (low-ratio case in brackets)

	1	2	
1	F_{11}	F_{12}	A
2	P_{21}	P_{12}	

Figure A2a. Symbolic values for the projection matrix of vital rates, **A** (with cells a_{ij}) corresponding to the fox sparrow life cycle graph of **Figure A1**. Meanings of the component terms and their numeric values are given in **Table A1**.

	1	2
1	0.36	1.475
2	0.18	0.59

Figure A2b. Numeric values for the high-ratio case of the matrix whose symbolic values are given in **Figure A2a**. The high-ratio case assumes a relatively wide disparity between “adult” survival ($P_{22} = 0.59$) and first-year survival ($P_{21} = 0.18$).

	1	2
1	0.45	1.25
2	0.225	0.5

Figure A2c. Numeric values for the low-ratio case of the matrix whose symbolic values are given in **Figure A2a**. The low-ratio case assumes a smaller disparity between “adult” survival ($P_{22} = 0.5$) and first-year survival ($P_{21} = 0.225$).

Sensitivity analysis

A useful indication of the state of the population comes from the sensitivity and elasticity analyses. *Sensitivity* is the effect on λ of an absolute change in the vital rates (a_{ij} , the arcs in the life cycle graph [**Figure A1**] and the cells in the matrix, **A** [**Figure A2**]). Sensitivity analysis provides several kinds of useful information (see Caswell 1989, p.118-119). First, sensitivities show “how important” a given vital rate is to λ or fitness. For example, one can use sensitivities to assess the relative importance of survival (P_i) and reproductive (F_i) transitions. Second, sensitivities can be used to evaluate the effects of inaccurate estimation of vital rates from field studies. Inaccuracy will usually be due to a paucity of data, but it could also result from the use

of inappropriate estimation techniques or other errors of analysis. In order to improve the accuracy of the models, researchers should concentrate additional effort on transitions with large sensitivities. Third, sensitivities can quantify the effects of environmental perturbations, wherever those can be linked to effects on stage-specific survival or fertility rates. Fourth, managers can concentrate on the most important transitions. For example, they can assess which stages or vital rates are most critical to increasing λ of endangered species or the “weak links” in the life cycle of a pest. **Figure A3** shows the “possible sensitivities only” matrix for this analysis (one can calculate sensitivities for non-existent transitions, but these are usually either meaningless or biologically impossible — for example, the sensitivity of λ to moving from Age-class 3 to Age-class 2).

	1	2	S
1	0.391	0.17	
2	1.397	0.609	

Figure A3a. Sensitivity matrix, **S**, for the high-ratio case. The three transitions to which the λ of the fox sparrow is most sensitive are highlighted: first-year survival (Cell $s_{21} = 1.397$, 54 percent of the total), second-year survival ($s_{32} = 0.609$), and first-year fertility ($s_{11} = 0.391$).

	1	2	S
1	0.476	0.212	
2	1.177	0.524	

Figure A3b. Sensitivity matrix, **S**, for the low-ratio case. The three transitions to which the λ of the fox sparrow is most sensitive are highlighted: first-year survival (Cell $s_{21} = 1.177$, 49 percent of the total), second-year survival ($s_{32} = 0.524$), and first-year fertility ($s_{11} = 0.476$).

In general, changes that affect one type of age-class or stage will also affect all similar age-classes or stages. For example, any factor that changes the annual survival rate of Age-class 3 females is very likely to cause similar changes in the survival rates of other “adult” reproductive females (those in Age-classes 4 and 5). Therefore, it is usually appropriate to assess the summed sensitivities for similar sets of transitions (vital rates). For the high-ratio case, the result is that the summed sensitivity of λ to changes in survival is of overriding importance. Fox sparrows show much greater sensitivity (78 percent of total) to changes in survival, with first-year survival alone accounting for 54 percent of the total. The major conclusion from the sensitivity analysis is that first-year (egg to yearling) survival is very important to population viability. The low-ratio case is similar but places a slightly less emphasis on survival (71 percent of total).

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, a 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, a 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.

The elasticities have the useful property of summing to 1.0. The difference between sensitivity and elasticity conclusions results from the weighting of the elasticities by the value of the original arc coefficients (the a_{ij} cells of the projection matrix). Management conclusions will depend on whether changes in vital rates are likely to be absolute (guided by sensitivities) or proportional (guided by elasticities). By using elasticities, one can further assess key life history transitions and stages as well as the relative importance of reproduction (F_i) and survival (P_i) for a given species.

Elasticities for the fox sparrow are shown in **Figure A4**. For the high-ratio case, λ is most elastic to changes in “adult” survival ($e_{22} = 35.8$ percent of total elasticity on arc P_{22} , the self-loop arc from the second node back to the second node in Figure A1). Next most elastic are first-year survival and “adult” reproduction ($e_{12} = e_{21} = 25.1$ percent of total elasticity). Least important is reproduction by first-year birds (14 percent of total elasticity). The sensitivities and elasticities for the fox sparrow differ in emphasizing first-year survival for the sensitivities and “adult” survival for the elasticities. The summed survival elasticities account for 60.9 percent of the total (compared to 39.1 percent for the summed reproductive elasticities). Thus, survival rates are the data elements that warrant careful monitoring in order to refine the matrix demographic analysis. For the low-ratio case, the elasticities of λ to changes in first-year survival, “adult” survival and “adult” fertility are all almost equal. The summed survival (52.4 percent) and fertility (47.6 percent) elasticities are more similar than for the high-ratio case.

	1	2
1	0.140	0.251
2	0.251	0.358

E

Figure A4a. Elasticity matrix, **E**, for the high ratio case. The three transitions to which the λ of the fox sparrow is most sensitive are highlighted: adult survival (Cell $e_{22} = 0.36$, or 36 percent of the total), and then slightly lower equivalent values (both 25 percent) for first-year survival (e_{21}) and adult fertility (e_{12}).

	1	2
1	0.213	0.263
2	0.263	0.26

E

Figure A4b. Elasticity matrix, **E**, for the low ratio case. No values are highlighted because they are nearly equivalent (all ~25 percent).

Other demographic parameters

The *stable age distribution* (SAD; **Table A2**) describes the proportion of each age-class in a population at demographic equilibrium. Under a deterministic model, any unchanging matrix will converge on a population structure that follows the stable age distribution, regardless of whether the population is declining, stationary or increasing. Under most conditions, populations not at equilibrium will converge to the SAD within 20 to 100 census intervals. For the fox sparrow at the time of the post-breeding annual census (just after the end of the breeding season), eggs represent 69.6 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, egg) stage. The reproductive value of the

first stage is always 1.0. An “adult” female individual in Stage 2 is “worth” 3.57 eggs (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 “adult” females are important stages in the life cycle. The cohort generation time for this species is 2.6 years (SD = 1.9 years).

Stochastic model

We conducted a stochastic matrix analysis for the fox sparrow. We incorporated stochasticity in several ways (**Table A4**), by varying different combinations of vital rates, by varying the amount of stochastic fluctuation and by varying the “base matrix” (the high or low adult-first-year survival ratio cases of **Figure A2**). We varied the amount of fluctuation by changing

Table A2. Stable age distribution (right eigenvector) for the high- and low-ratio cases. At the census, slightly more than two-thirds of the individuals in the population should be eggs.

Stage	Description	High-ratio	Low-ratio
1	Eggs (to yearling)	0.696	0.692
2	“Adult” females	0.304	0.308

Table A3. Reproductive values (left eigenvector) for the high- and low-ratio cases. Reproductive values can be thought of as describing the “value” of a stage as a seed for population growth relative to that of the first (newborn or, in this case, egg) stage. The reproductive value of the first age class is always 1.0.

Stage	Description	Reproductive values (high-ratio case)	Reproductive values (low-ratio case)
1	Eggs/first-year females	1.00	1.00
2	“Adult” females	3.57	2.47

Table A4. Summary of four variants of stochastic projections for the fox sparrow with $N_0 = 10,000$ individuals.

	Variant 1	Variant 2	Variant 3	Variant 4
Input factors:				
Affected cells	P_{21} and P_{22}	F_{11} and F_{12}	P_{21} and P_{22}	P_{21} and P_{22}
Base matrix	High-ratio	High-ratio	High-ratio	Low-ratio
S.D. of random normal distribution	1/4	1/4	1/8	1/4
Output values:				
Deterministic λ	1.003	1.003	1.003	1.006
# Extinctions / 100 trials	38	1	0	0
Mean extinction time	1,325	1,894	Not Applicable (N/A)	Not Applicable (N/A)
# Declines / # survived pop	49/62	36/99	12/100	23/100
Mean ending population size	531,192	372,964	1.8×10^6	1.9×10^9
Standard deviation	3.6×10^6	1.1×10^6	9.2×10^6	1.6×10^{10}
Median ending population size	350	30,247	127,067	171,913
Log λ_s	-0.00441	0.00026	0.00128	0.00149
λ_s	0.9956	1.0003	1.0013	1.0015
% reduction in λ	0.73	0.27	0.17	0.44

the standard deviation of the truncated random normal distribution from which the stochastic vital rates were selected. The high variability variant used a standard deviation of one quarter of the “mean” (with this “mean” set at the value of the original matrix entry [vital rate], a_{ij} under the deterministic analysis). The low variability variant used a standard deviation of one eighth of the mean. Under Variant 1 we subjected both reproductive arcs (F_{21} and F_{22}) to stochastic fluctuations with high variability (SD one quarter of mean) using the high ratio base matrix. Under Variant 2 we varied both survival arcs (P_{21} and P_{22}) with high variability (SD one quarter of mean), using the high ratio base matrix. Under Variant 3 we again varied survival but reduced the stochastic variability to one eighth of the mean, again using the high ratio matrix. Variant 4 analyzed the low ratio matrix with other parameters as in Variant 2. Each run consisted of 2,000 census intervals (years) beginning with a population size of 10,000 distributed according to the Stable Age Distribution (SAD under the deterministic model. Beginning at the SAD 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 Equation 14.61 of Caswell (2000), after discarding the first 1,000 cycles in order to further avoid transient dynamics. We also calculated the number of runs that resulted in a population decline greater than 5 percent of the starting size.

The stochastic model (**Table A4**) produced two major results. First, high variability on survival under the high-ratio case had the greatest detrimental effect. For

example, 38 of 100 runs led to extinctions with highly variable survival under Variant 1. The next greatest effect came from varying the fertility rates of all age classes using the high-ratio base matrix — 1 extinction and 37 declines. Low variability on survival eliminated extinctions using the high-ratio matrix and led to only 12 declines. Finally, even under high variability for survival the low ratio base matrix showed no extinctions and a modest 23 declines. The difference in the effects of which arc was most important is predictable largely from the elasticities. The single highest elasticity of λ was to “adult” survival under the high ratio case ($e_{22} = 0.36$). This detrimental effect of variability occurs despite the fact that the average vital rates remain the same as under the deterministic model — that is, the mean random selection should equal the deterministic matrix value. Why should stochasticity have a depressive effect even when the mean effect is neutral? This apparent paradox is due to the lognormal distribution of stochastic ending population sizes (Caswell 2000). The lognormal distribution has the property that the mean exceeds the median, which exceeds the mode. Any particular realization will therefore be most likely to end at a population size considerably lower than the initial population size. Second, the magnitude of stochastic fluctuation has a discernible effect on population dynamics (compare Variant 1 to Variant 3 in **Table A4**). These results indicate that populations of the fox sparrow are vulnerable to stochastic fluctuations in survival (due, for example, to annual climatic change or to human disturbance), especially when the magnitude of fluctuations is high. Pfister (1998) showed that for a wide range of empirical life histories, high sensitivity or

elasticity was negatively correlated with high rates of temporal variation. That is, most species appear to have responded to strong selection by having low variability for sensitive or elastic transitions in their life cycles. For the fox sparrow, with stochasticity having the greatest impact on survival, the life history may not allow the kind of adjustment of risk load that may be possible in other species. Variable survival, especially in the first year, is likely to be the rule rather than the exception.

Potential refinements of the models

Clearly, the better the data on survival rates, the more accurate the resulting analysis. The most important “missing elements” in the life history for the fox sparrow are for survival rates, which emerges as the vital rates to which λ is both most sensitive and 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 variations in vital rates. Using observed correlations would improve on our “uncorrelated” assumption, by incorporating forces that we did not consider. Those forces may drive greater positive or negative correlation among life history traits. Other potential refinements include incorporating density-dependent effects. At present, the data appear insufficient to assess reasonable functions governing density dependence.

Summary of major conclusions from the matrix projection models:

- ❖ Survival accounts for 78 percent of the total “possible” sensitivity in the high-ratio case
- ❖ Survival (P_{21} and P_{22}) account for 60.9 percent of the total elasticity, compared to the 39.1 percent accounted for by the fertilities under the high-ratio case. The relative importance of survival and fertility (52 percent vs. 47 percent) is more even in the low-ratio case. Nevertheless, in both cases proportional changes in first-year and “adult” survival will have a major impact on population dynamics.
- ❖ The reproductive value of “adult” females is moderately high (they are “worth” 3.6 eggs in the high ratio case and 2.5 eggs in the low-ratio case). Their reproductive value makes them possible buffers against the detrimental effects of variable conditions.
- ❖ Stochastic simulations echoed the elasticity analyses in emphasizing the importance of variation in survival to population dynamics, especially in the high-ratio case. In comparison to life histories of other vertebrates, fox sparrows appear slightly less vulnerable to environmental stochasticity (because of the buffering effect of a reservoir of “adult” females). Management should emphasize the collection of improved demographic data, particularly for first-year survival.

References

- Ammon, E.M. 1995. Lincoln's sparrow (*Melospiza lincolnii*). In A. Poole and F. Gill, editors. The Birds of North America, No. 191. The Academy of Natural Sciences. Philadelphia, PA; The American Ornithologists' Union, Washington, D.C.
- Ammon, E.M. 1999. Wilson's warbler (*Wilsonia pusilla*). In A. Poole and F. Gill, editors. The Birds of North America, No. 478. The Academy of Natural Sciences. Philadelphia, PA; The American Ornithologists' Union, Washington, D.C.
- Caswell, H. 2000. Matrix Population Models: Construction, Analysis, and Interpretation, Second Edition. Sinauer Associates, Sunderland, MA.
- McDonald, D.B. and H. Caswell. 1993. Matrix methods for avian demography. *Current Ornithology* 10:139-185.
- Pfister, C.A. 1998. Patterns of variance in stage-structured populations: Evolutionary predictions and ecological implications. *Proceedings of the National Academy of Sciences* 95:213-218.
- Speirs, J.M. and D.H. Speirs. 1968. *Melospiza lincolnii lincolnii* (Audubon) – Lincoln's Sparrow. Pages 1434-1467 in O.L. Austin, Jr., editor. Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. U. S. National Museum Bulletin 237, Part 3, Washington, D.C.
- Weckstein, J.D., D.E. Kroodsma, and R.C. Faucett. 2003. Fox sparrow (*Passerella iliaca*). In A. Poole and F. Gill, editors. The Birds of North America, No. 715. The Academy of Natural Sciences. Philadelphia, PA; The American Ornithologists' Union, Washington, D.C.
- Williams, G.C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. *American Naturalist* 100:687-690.

The U.S. Department of Agriculture (USDA) prohibits discrimination in all its programs and activities on the basis of race, color, national origin, age, disability, and where applicable, sex, marital status, familial status, parental status, religion, sexual orientation, genetic information, political beliefs, reprisal, or because all or part of an individual's income is derived from any public assistance program. (Not all prohibited bases apply to all programs.) Persons with disabilities who require alternative means for communication of program information (Braille, large print, audiotape, etc.) should contact USDA's TARGET Center at (202) 720-2600 (voice and TDD). To file a complaint of discrimination, write to USDA, Director, Office of Civil Rights, 1400 Independence Avenue, S.W., Washington, DC 20250-9410, or call (800) 795-3272 (voice) or (202) 720-6382 (TDD). USDA is an equal opportunity provider and employer.