Wilson's Warbler (*Wilsonia pusilla pileolata*): A Technical Conservation Assessment

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COVER PHOTO CREDIT

Wilson's warbler (*Wilsonia pusilla pileolata*). © Don DesJardin, photographer. Used with his permission.

SUMMARY OF KEY COMPONENTS FOR CONSERVATION OF THE WILSON'S WARBLER

Wilson's warbler (*Wilsonia pusilla pileolata*) populations are reported to be stable to declining range-wide, and appear to be stable to increasing within U.S. Forest Service, Rocky Mountain Region. Loss of riparian habitats through dewatering, livestock grazing, and development and disturbance by recreation in riparian areas are the primary threats to Wilson's warblers. Neotropical migrant songbirds, such as the Wilson's warbler, represent a unique challenge for identifying threats and potential impacts to populations. In general, it is difficult to monitor songbird populations, and this is exacerbated in large portions of U.S. Forest Service, Rocky Mountain Region due to isolated mountainous habitat. Consequently, the population status of Wilson's warblers is difficult to determine for this assessment. However, if impacts and future threats to important habitat areas are identified and mitigated, we believe positive responses for species such as the Wilson's warbler will result within this region.

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INTRODUCTION

This assessment is one of many produced to support the Species Conservation Project for the U.S. Forest Service (USFS), Rocky Mountain Region. The Wilson's warbler (*Wilsonia pusilla pileolata*) is being assessed because it is a Management Indicator Species (MIS) on multiple forests in the region. A MIS serves as a barometer for species viability at the Forest level and has 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 Wilson's warbler throughout its range in the Rocky Mountain Region (Region 2). The broad nature of the assessment leads to constraints on the specificity of information for particular locales. Furthermore, available information from field studies limited inferences that could be made regarding local situations. This introduction defines the goal of the assessment, outlines its scope, and describes the process used in its production.

Goal

The Wilson's warbler conservation assessment is produced as part of the Species Conservation Project and is designed to provide forest managers, research biologists, and the general public with a thorough review of the biology, ecology, conservation status, and management of the Wilson's warbler based on available scientific knowledge. This assessment is limited to critical summaries of scientific knowledge and includes a discussion of broad implications of that knowledge and information needs. The assessment does not define specific management recommendations but provides the ecological background upon which management can be based. However, the assessment does focus on the consequences of changes in the environment that result from management (i.e., management implications) and their potential impacts to the species. Furthermore, we cite management recommendations proposed elsewhere and, when management recommendations have been implemented, we examine the success of the implementation.

Scope

The Wilson's warbler assessment examines the biology, ecology, conservation status, and management of this species with specific reference to the geographic and ecological characteristics of Region 2. Although a majority of the literature on the species originates from field investigations outside the region, we attempt to keep the literature in the ecological and social context of the central Rocky Mountains. In this assessment we focus on reproductive behavior, population dynamics, habitat associations, and other characteristics of Wilson's warblers under current environmental conditions, rather than under historical conditions.

In producing this assessment, we reviewed refereed literature, non-refereed publications, research reports, and data accumulated by resource management agencies. Not all publications on Wilson's warblers are referenced in this assessment, nor was all published material considered equally reliable. The assessment emphasizes refereed literature; however, we chose to use some non-refereed literature in the assessment when information was unavailable elsewhere. Unpublished data (e.g. Natural Heritage Program records) were especially important in estimating geographic distribution of the species. We believe that these data require special consideration because of the diversity of persons and methods used in its 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, interpretation of evidence is open to debate. 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 critical experiments in the ecological sciences, and often observations, inference, good thinking, and models must be relied on to guide the understanding of ecological relations. In this assessment, the strength of evidence for particular ideas is noted, and alternative explanations are described when appropriate. While well-executed experiments represent the strongest

approach to developing knowledge, alternative methods (modeling, critical assessment of observations, and inference) are accepted approaches to understanding features of biology.

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.

Publication of Assessment on the World Wide Web

To facilitate the use of species assessments in the Species Conservation Project, all assessments are being published on the 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 assessment, which will be accomplished based on 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 increase the rigor of the assessment.

MANAGEMENT STATUS AND NATURAL HISTORY

Management Status

Based on Breeding Bird Survey (BBS) trends from 1978-1988, the Wilson's warbler appears to be maintaining a stable population across its range (NatureServe 2001). Within Region 2, Wilson's warblers are essentially absent as a breeding species within South Dakota, Kansas, and Nebraska due to a lack of suitable habitat (Goodrich 1945, South Dakota Ornithologists'

Union 1991, Sharpe et al. 2001). Colorado and Wyoming both consider Wilson's warblers common during the breeding season (Johnsgard 1986, Toolen 1998, Cerovski et al. 2001). The Natural Heritage Program's global rank for Wilson's warbler is G5. The Natural Heritage Program's state rank in Wyoming is S5B and S5N; Colorado is S4B and SZN. Wilson's warblers have been proposed as a MIS on the Arapahoe-Roosevelt, Rio Grande, and Pike-San Isabel National Forests.

Existing Regulatory Mechanisms, Management Plans and Conservation Strategies

Within Region 2, only Colorado Partners in Flight has a special designation for Wilson's warbler: a Priority Species within high elevation riparian habitats in physiographic area 62 that occur in central Colorado, with small extensions into southern Wyoming and northern New Mexico. The Colorado Partners in Flight suggests several measures to protect Wilson's warbler and other high elevation riparian songbird species, including eliminating activities that degrade riparian habitats such as timber harvest, dewatering streams, and livestock grazing.

We did not find any other existing legal mechanisms, management plans, or conservation strategies specifically for the Wilson's warbler. However, Wilson's warblers are protected by several laws that broadly apply to many wildlife species including the Migratory Bird Treaty Act of 1918, National Forest Management Act of 1976, and the Neotropical Migratory 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 the USFS must " provide for multiple use and sustained yield of the products and services obtained therefrom 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" (http://www.fs.fed.us/forum/nepa/nfmalaw.html).

The Neotropical Migratory 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 U. S border and summer in North America. The law encourages habitat protection, education, researching, 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 Wilson's warbler. These programs include the North American Breeding Bird Survey (BBS), Monitoring of Avian Productivity and Survivorship (MAPS) Program, and Monitoring Colorado's Birds.

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 by means of an index (http://www.mbr-pwrc.usgs.gov/bbs/intro00.html). Since the BBS is based on a series of yearly counts, rather than a census, it is an index. This index can only provide an indicator of trend. Results may be influenced by year-to-year changes in observers, weather, and changes in habitat. However, the data are considered useful, and investigators have used the data to address a variety of research and management objectives including understanding of broad-scale population trends (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 the 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 are then used to identify the causes of population declines, to formulate management actions and conservation strategies to reverse declines and maintain healthy populations, and 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) summarized the methods and future objectives for this project. Three methods are used (transects, colony counts, and censusing) to obtain population data for Colorado's breeding-bird species, with transects being the primary method. Transects (15 point counts per 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).

Biology and Ecology

Systematics, distribution and abundance

The Wilson's warbler is a small wood warbler. Body length ranges from 10 to 12 cm and weight ranges between 5.4 to 10.5 gm (Ammon and Gilbert 1999). Males in breeding plumage are olive-green above and bright yellow below and distinguishable by a round glossy, dark cap on the top of the head. The eye is black and topped by a yellow streak. The body shows no streaking, no wing bars or tail bars. Females may show traces of a black cap, but most show plain olive-green on the crown (Terres 1980, Farrand 1988). Breeding males are unlikely to be confused with any other species.

Females and immature birds, however, may be confused with other warblers that are predominantly yellow and olive, such as immature hooded, orange-crowned and yellow warblers (Ammon and Gilbert 1999).

Although three subspecies of Wilson's warbler are recognized, this assessment generally covers aspects of the biology and ecology of *Wilsonia pusilla pileolata*. In comparison to the other subspecies, *W. p. pileolata* is the largest and tends to be brighter green above and brighter yellow below.

Breeding distribution

Global distribution of the Wilson's warbler is limited to the Americas. Based on BBS data, Price et al. (1995) mapped the densest breeding populations of Wilson's warbler along coastal northern California, Oregon and, Washington. Northern Colorado, west central Wyoming, and western Montana also appear to support relatively high populations. East of the Mississippi River, northern New England, and Quebec, Canada support the highest breeding densities.

Within Region 2, habitat suitable for Wilson's warbler breeding occurs locally and is not extensive. The mountains of north central Colorado support the greatest abundance of Wilson's warblers. Both Wyoming and Colorado have broadly dispersed populations due to the distribution of high elevation riparian habitats in those states. The remaining states in Region 2 (South Dakota, Nebraska, and Kansas) do not support breeding populations; Wilson's warblers are considered transients, only using these states on their way to breeding areas further north (Bruner et al. 1904, Goodrich 1945, Johnsgard 1997, Sharpe et al. 2001).

Discontinuities in distribution throughout Region 2 are attributed to habitat requirements. Wilson's warblers are generally restricted to montane shrub-willow thickets along riparian zones, beaver ponds, overgrown clear-cuts and the edges of meadows (Finch 1989, Dobkin 1994, Toolen 1998, Ammon and Gilbert 1999, Cerovski et al. 2001).

Migratory distribution

The migratory nature of the Wilson's warbler causes obvious seasonal fluctuations in abundance within Region 2. Within montane riparian areas of Colorado and Wyoming where breeding population densities are greatest, abundance peaks between late April and late May, with egg-laying occurring in June and July (Terres 1980, Johnsgard 1986). Nebraska, Kansas and South Dakota normally see migrating birds earlier in the spring and later in the fall, as Wilson's warblers are traveling between breeding and wintering areas.

Population trends

Ammon and Gilbert (1999) provide a thorough list of Wilson's warbler population trends across several regions of the United States and Canada. These trends were derived from the BBS. Two time periods were reviewed, 1966 to 1979 and 1980 to 1996. Between 1966 and 1979 northeastern populations of Wilson's warbler exhibited increasing trends from +12.4 to +15.7 percent (+12.4 percent, [$p = 0.01$, n = 59), +15.7 percent ($p = <0.01$, n =16)], while northwestern populations were exhibiting decreasing trends from -9.5 to -14.4 percent [-9.5 percent ($p = 0.04$, n =39), -14.4 percent ($p = 0.02$, n = 14)]. Increasing trends were reported between 1980 and 1996 in the northern Rocky Mountains (+9.2 percent, ($p = 0.06$, n = 14)).

Survey-wide results for 1980 to 2000 suggested declining trends in Wilson's warbler populations of 2.02 percent per year ($P = <0.01$, n = 434). The United States also showed a declining trend from 1980 to 2000 of 2.17 percent per year ($P = <0.01$, n = 287), and the western BBS Region showed a declining trend of 1.51 percent per year ($P = 0.01$, n = 367). These results suggest either fluctuations in abundance or variation in detection, since the addition of four years data resulted in major changes in the perceived trend.

Within Region 2, Colorado is the only state with reliable BBS trend results, and from 1980 to 2000 Wilson's warbler populations are thought to have declined 6.8 percent per year ($P = 0.08$, n = 37). Wyoming is the only other state within Region 2 with BBS data for Wilson's warblers, but the data are insufficient to calculate reliable trends due to inadequate numbers of survey routes and lack of statistical power necessary for a thorough analysis (Sauer et al. 2001). **Table 1** summarizes relevant BBS data between 1966 and 2000.

Activity pattern and movement

Broadscale movement patterns

Sexual differences in Wilson's warbler migrations are well documented in the literature. Spring migration patterns indicate that in 18 species of wood warblers examined, including Wilson's warbler (*Wilsonia pusilla pusilla*), males arrived earlier than females in spring (Otahal 1995, Stewart 1973, Chase et al. 1997, Yong et al. 1998). Migration to Colorado and Wyoming begins

Table 1. North American Breeding Bird Survey data (1966 to 2000) presented for Wilson's warbler (from Sauer et al. 2001).

	Trend	*P*-value	N	95% CI	Relative Abundance[a]
Western U.S.	-1.1%	0.03	398	-2.0 - 0.1	2.49
CO	-5.1%	0.10	41	-11.1 - 0.9	1.31
WY	12.7%	0.35	13	-13.0 - 38.3	0.52

[a]reported as average numbers seen per survey.

in late April and continues until late May, with montane populations arriving in late May (Raley and Anderson 1990, Toolen 1998, Ammon and Gilbert 1999). Egg laying and brooding dates vary with elevation but occur between early June and early July (Raley and Anderson 1990, Johnsgard 1986, Toolen 1998). Within Region 2 where Wilson's warblers are migrating to more northern breeding areas, arrival dates vary, depending on weather. Wilson's warblers in South Dakota arrive between early April and late May. More contemporary reports by Johnsgard (1997) suggest that the majority of Wilson's warbler migrations through Nebraska occur in the middle of May.

Because Region 2 covers a wide geographic range, fall migration begins at different times depending on longitude and elevation of breeding areas. In Wyoming and Colorado, migration dates vary between early July and mid-November (Johnsgard 1986, Ammon and Gilbert 1999). Discrepancy between dates is attributed either to elevation or annual weather variation. Throughout its range, peak fall migration for Wilson's warbler is in early September, and this is most likely true within Region 2. Between mid-July and September adults and young-of-year birds are probably "wandering" as described by Stewart (1973). Within Region 2 fall migration has a similar wide distribution of dates, ranging between early August and late October (South Dakota Ornithologists' Union 1991). One Nebraska report describes Wilson's warblers migrating through in early September (Bruner et al. 1904). They are reported as an "occasional migrant" in Kansas, with no dates reported (Goodrich 1945).

Daily activity patterns are not well reported in the literature. We can infer that Wilson's warblers generally remain within their territories during the breeding season. However, some birds have been observed as far away as 300 m from their normally defended territory boundaries, possibly due to boundary disputes (Stewart 1973). Males sing from various perch sites within their territory and feed within the same area. No patterns of daily movement have been described for the Wilson's warbler.

Sex and age differences in dispersal capabilities and patterns. Not reported for Wilson's warbler.

Regional differences in migration and other broadscale movement patterns. Few regional differences in migration were found regarding Wilson's warbler. See Discussion above regarding differences in migration dates across states within Region 2.

Habitat

Breeding habitat

Throughout their range, Wilson's warblers use mesic shrub communities for breeding habitat. The edges of beaver ponds and lakes, riparian zones, fens, bogs and overgrown clear-cuts appear to provide the optimal habitat for this species (Stewart et al. 1977, Toolen 1998, Ammon and Gilbert 1999). Western montane populations also occur into alpine zones (Finch 1989, Colorado Partners in Flight 2000).

In southeastern Wyoming, Wilson's warblers select habitat with less than 10 trees per 100 m^2, dense shrub cover less than 2.0 m high, greater than 70 percent willow cover, and dense shrub foliage (Finch 1989). Of 20 breeding bird species found along riparian stream gradients in Wyoming, Wilson's warblers exhibited the narrowest range of habitat use and were found to be "zone dependent", or more abundant in certain elevation zones within the high elevation subalpine shrub habitats of southeast Wyoming (Finch 1989). Additionally, Wilson's warblers breed at mid to high elevations within Colorado and Wyoming, ranging from 2500 to 3000 m (Finch 1985, Johnson 2001). Other habitat associations reported for Wilson's warbler in southeastern Wyoming include little use of lodgepole pine habitat, and increased use of areas with increasing grass cover and understory foliage (Johnson 2001).

Along the Snake River in northwestern Wyoming, Wilson's warblers occupied sites that were dominated by whiplash willow (*Salix lasiandra*) and planeleaf

willow (*Salix planifolia*) (Buhler 1998). In this same area, singing occurred at an average height of 2.8 m in planeleaf willow that was 4.5 m tall with an average diameter at breast height (DBH) of 5.0 cm. In comparing use to random plots, Buhler (1998) found that singing occurred in areas with greater deciduous shrub cover, greater vertical foliage cover from 0 to 3 m, and greater numbers of quaking aspen (*Populus tremuloides*) trees with DBH of 3 to 23 cm.

Using a protocol developed by the Rocky Mountain Bird Observatory, Leukering et al. (2001) detected Wilson's warblers in six habitat types, although high elevation riparian and alpine tundra accounted for 65 percent and 12 percent of detections, respectively. Other occupied habitats included cottonwood, willow, Russian olive, and mixed shrub.

Nesting and foraging habitat

Wilson's warbler nests may occur on or near the ground within willow thickets or wet meadow settings. In Colorado, nests were observed both in the middle of wet meadows and near forest edges with no observed preference for either habitat (Ammon and Gilbert 1999). Vegetation characteristics of nest sites in the Rocky Mountains (*n* = 75 nests) included willow 80 percent, grasses 41 percent, shrubby cinquefoil 9 percent, and alder 5 percent (Ammon 1995). Nests were found in moist meadows 91 percent, stream banks 6 percent, and willow thickets 3 percent of the time with 87 percent of nests located on the ground and the remainder in willow stems (Ammon 1995). Wilson's warbler nests in California were described as occurring in such thick cover that ground predators may have found it difficult to penetrate (Stewart 1973). Nests usually consist of interwoven leaves, twigs and small branches (Ammon and Gilbert 1999) and the inside cup may be matted with animal hair, moss and leaves (Stewart 1973). Bent (1953) described ground nests as sunken into the ground and covered by overhanging moss, willows, or grasses (Bent 1953). Wilson's warblers may also nest in loose colonies (Terres 1980).

Microhabitat data regarding foraging substrates are not well documented. However, two studies in northwestern Wyoming suggest that Wilson's warbler forage heavily in whiplash willow with an average DBH of 2.5 cm (Hutto 1981, Buhler 1998). In willows less than 4 m tall, Wilson's warblers foraged near the top of the shrub (Buhler 1998). In willows less than 2 m tall, foraging occurred at lower levels between 0.6 and 1.2 m (Hutto 1981). When Buhler (1998) compared used plots to random plots he found that Wilson's warblers foraged in areas with a greater density of deciduous shrub cover and greater vertical foliage cover between 0 and 3 m.

Discussions of Wilson's warblers and their response to landscape features and habitat juxtaposition are rare. In southeastern Wyoming, the adjacent habitat, including clear-cuts, sage flats, wet meadows, and lodgepole pine forests, did not appear to be important in determining the presence of Wilson's warblers (Johnson 2001). As a macrohabitat variable, the presence of riparian vegetation, including both tall and short species of willows, appeared to be the most important predictor for the presence of Wilson's warblers (Johnson 2001). Habitat use within montane landscapes of the greater Rocky Mountain Region and specifically within Region 2 is assumed to be similar, that is, Wilson's warblers that inhabit mountainous regions of Montana and Idaho presumably select similar habitats to those warblers in Wyoming and Colorado.

Migratory habitat

Habitat use for Wilson's warblers migrating through Nebraska, South Dakota, and Kansas has not been reported. However, inference can be drawn from other studies such as those conducted in the southwest United States. Wilson's warblers migrating in New Mexico were most often captured in willow-dominated habitats during spring migration (Yong et al. 1998). Conversely, during fall migration capture rates were highest in salt cedar and lowest in willow habitats (Yong et al. 1998). Therefore, we predict that during migration in Nebraska, South Dakota, and Kansas stopover habitat will be primarily willow corridors in the spring and may be more variable in the fall.

Between subspecies, it is suggested that *Wilsonia pusilla pileolata* and *W. p. pusilla* select and use similar habitats (Ammon and Gilbert 1999). However, Pacific Coast populations of *W. p. chyrseola* may use a wider variety of mesic and xeric shrub habitats, including *Rhododendron* spp. thickets and stands of conifer and deciduous saplings. Unlike the other subspecies, *W. p. chyrseola* is commonly found in the shrub understory of forests, including riparian woodlands and broadleaf evergreen and mixed coastal forests (Ammon and Gilbert 1999).

Winter habitat

Wilson's warblers winter from southern California coasts, southward through Baja California, southern Sonora, southern Texas, and south through Mexico and Central America to northern Panama. They

are generally found in scattered forests and sometimes riparian shrub land where they consume a broader array of foods than on breeding grounds, including substantial amounts of nectar. See Ammon and Gilbert (1999) for details on winter habitat use.

Food habits

During a two-year study in southeastern Wyoming, Raley and Anderson (1990) identified 53 families of arthropods in diet samples from Wilson's warblers. The top ten foods in order of preference were beetles (*Coleoptera*), mayflies (*Ephemeroptera*), stoneflies (*Plecoptera*), true flies (*Diptera*), wasps (*Hymenoptera*), bugs (*Hemiptera*), caddis flies and moths (*Trichoptera – Lepidoptera*), spiders (*Araneae*), leafhoppers (*Homoptera*), and larvae. Prey in the 1 to 3 mm size class were underrepresented in diet samples, suggesting selectivity. The prey most preferred tended to be non-cryptic and patchy in distribution. Analysis of biomass however, showed that larvae comprised 30 percent, *Diptera* 24 percent, *Hymenoptera* 23 percent, *Lepidoptera* 17 percent, *Homoptera* 16 percent, *Coleoptera* 9 percent, and *Hemiptera* 5 percent of the diet (Raley and Anderson 1990, Ammon and Gilbert 1999).

Breeding biology

Phenology

See discussion above in *broadscale movement patterns*. The spring migration to the lowlands of Colorado begins in late April and continues into late May with montane populations generally arriving in late May (Ammon and Gilbert 1999). Peak egg laying usually occurs between 1 June and 3 July (Johnsgard 1986). In northern Colorado, the first arrival of males during a three-year study occurred on 21 May, 23 May, and 19 May, and pair bonding occurred the first two weeks of June (J. Ruth, personal communication 2002). The first eggs were found on 12 or 13 June with incubation continuing until 26 June (J. Ruth, personal communication 2002). Wyoming birds arrived in mid to late May, with egg laying proceeding from early June through early July (Johnsgard 1986, AJ personal observation).

Breeding behavior

Site fidelity in Wilson's warbler has been recorded in two subspecies, *Wilsonia pusilla chryseola* and *W. p. pileolata*. In the Sierra Nevada Mountains, 9 of 20 males (45 percent) and 8 of 18 females (44 percent) returned to the same breeding territories as the year before (Stewart et al. 1977). No data are given for return

to specific breeding territories in Colorado. However, an overall return rate of 30 to 31 percent was recorded for central Colorado (Ammon and Gilbert 1999).

Alternate nests and double brooding is not reported for Wilson's warbler. In northern Colorado and the Sierra Nevada Mountains re-nesting did not occur after nest predation (Stewart et al. 1977, Ammon and Gilbert 1999).

Brood information

All clutch size data reported here are taken from Ammon and Gilbert (1999). Clutch size varies geographically, normally ranging between 3 and 5 eggs. Clutches furthest east and west (coastal) tend to be smaller than interior clutches. Alaskan breeders have the largest clutches 5.3 ± 0.2 SE (range 4 to 7, $n = 14$), while clutches in the Rocky Mountains are smaller, 4.4 ± 0.1 SE (range 3 to 6, $n = 73$). The smallest clutches were found in Pacific coast *Wilsonia pusilla chryseola* populations, 3.9 ± 0.03 SE (range 2 to 5, $n = 279$). Two-egg clutches are typical of birds nesting late in the season.

Parental care of young

Eggs and nestlings are brooded by females exclusively. However, both sexes aid in feeding the young (Stewart et al. 1977, Ammon and Gilbert 1999). Males can average over 17 visits per hour while the female can average over 40 visits per hour (Stewart 1973). During a normal 14-hour day the adults may make over 800 feeding trips to the nest, with the male accounting for up to a quarter of the visits (Stewart 1973).

Nestling dispersal

Fledging occurs 9 to 11 days post hatching, and the young will remain in their parent's territory for approximately 32 days (Stewart 1973). Feeding by the parents may continue for up to 25 days post fledging (Ammon and Gilbert 1999).

Brood parasitism

Although literature addressing cowbird parasitism of Wilson's warblers was not found, there is some descriptive information from California. By observing nests, Stewart et al. (1977) reported that cowbirds parasitized Wilson's warbler nests but with limited success. On several occasions, young warblers were found in the nest with a single cowbird chick. It appeared that the parent birds were able to raise all

chicks to fledging. On at least one occasion, it appeared that the warblers recognized the cowbird chick as alien and refused to feed it after it left the nest.

Demography

Life history

Within the Rocky Mountains, the breeding distribution of Wilson's warbler follows the Rocky Mountain Range from northern New Mexico to northern Montana and Idaho (Price et al. 1995). Though suitable habitat is patchy across this range, there is no information regarding the spatial relationship among disjunct groups in Region 2. Information regarding source-sink populations also is not available. Additionally, we found no information regarding genetic characteristics and concerns of isolated populations. Given the native patchy distribution of the species, demographic problems associated with isolation would not be expected.

Wilson's warblers can breed at the end of their first year. However, males do not appear to successfully establish territories until their second year (Ammon and Gilbert 1999), because older males precede younger males during the spring migration (Stewart 1973). Older males also may defend larger territories and may practice polygyny more than younger males (Stewart et al. 1977). Adult abundance and the number of adults captured for the first time have been positively correlated with the previous year's productivity. Annual adult survival for summer residents was estimated at 50.3 percent (Chase et al. 1997).

Territories are reported to be elastic in size and shape across years and may or may not be used in subsequent years after establishment (Ammon and Gilbert 1999). In northern Colorado, the average territory was 0.18 ha ± 0.02 SE (range 0.06 to 0.39, $n = 24$; Ammon and Gilbert 1999). Another northern Colorado study found an average territory size of 0.31 ha ± 0.02 SE, and territories often shared common boundaries with other conspecifics (Eckhardt 1979). These data illustrate plastic territory size, suggesting that territoriality plays a role in population regulation on breeding grounds.

Nest success is reported to be lower in Pacific lowland populations (15 to 33 percent) than in montane populations (>70 percent). However, in some years high elevation sites may be unusable due to snowpack persisting through the breeding season (DeSante 1990). Fledging and nesting success varied annually in northern and central Colorado (Eckhardt 1979, Ammon and Gilbert 1999). Between 1987 and 1989 Wilson's warblers in northern Colorado had an average of 83 percent fledging success (reported as percent of eggs laid, $n = 113$) and 96 percent nesting success (reported as percent of nests with eggs, $n = 25$), while between 1990 and 1991 fledging success was only 38 percent and nesting success was 46 percent (Ammon and Gilbert 1999). From 1992 to 1994 nesting success was between 55 and 93 percent in Colorado (Ammon and Gilbert 1999).

At 32 days old, fledglings appeared to be securing their own food and soon thereafter left their parent's territory (Stewart 1973). Reports on where the young go after leaving parental territories are rare. In montane populations in northern Colorado, fledglings may migrate vertically to lower elevations before leaving for the fall migration (J. Ruth, Personal communication 2002).

"Adult wandering" occurs after breeding, when territoriality is waning (Stewart 1973). A California study documented an influx of unbanded adults into a study area with marked birds (Stewart 1973). All unmarked birds were in late stages of breeding condition with brood patches or cloacal protuberances and had low subcutaneous fat levels. A breakdown in territories allows for unrestricted searching for food among the population, which aids in the preparation for molt and migration (Stewart 1973).

The conditions on breeding grounds rather than those on wintering grounds are thought to have the greatest effect on Wilson's warbler populations (DeSante 1990). At breeding sites within the Sierra Nevada Mountains, El Niño southern oscillations caused unusually heavy snowpack that did not melt until late July or early August (DeSante 1990). Consequently, Wilson's warblers did not breed in the study area during those years and did not return until four years later (DeSante 1990). Adult abundance and productivity may not be related to adult winter survival—rather they may be related to the previous year's productivity. Also, adult abundance and productivity have little influence on winter survival, suggesting density-independent mortality on wintering grounds (Chase et al. 1997).

Demographic analysis of Wilson's warbler is difficult because of the paucity of field data on demographic rates (**Appendix A**). However, some hypotheses regarding demography are possible, if we assume warbler life history can be inferred from information on several passerines that occur in similar environments: Lincoln's sparrows (*Melospiza lincolnii*),

fox sparrow (*Passerella iliaca*), and Wilson's warbler (*Wilsonia pusilla*). Analysis of a simple life cycle diagram and the associated matrix model demonstrates that population growth in Wilson's warbler is more sensitive to changes in survival than reproduction (**Appendix A**). Further analysis of the life cycle supports the contention that variation in reproduction threatens the warbler less than variation in survival – the reproductive value of an adult warbler corresponds to somewhere between 2.5 and 3.6 eggs, and a stochastic analysis demonstrates that high variation in adult survival leads to relatively high probability of population extinction. These conclusions depend critically on the assumptions of the model outlined in **Appendix A**.

Community ecology

Predators

In 32 neotropical migrant species studied, including Wilson's warblers, nest predation was the primary source of nesting mortality, and nest predation influenced habitat selection and demography (Martin 1992). This study also showed that the greatest nest success, lowest predation rates, and lowest brood parasitism rates were in birds that nest close to or on the ground, such as Wilson's warblers. In California, Wilson's warblers had 60 percent nest success (fledged at least one young) with 35 percent nest predation, mainly by weasels (*Mustela* spp.; Stewart 1973, Stewart et al. 1977). Stewart's (1973) prediction that Wilson's warbler nests occur in such thick cover that ground predators may find it difficult to find them was supported with these low predation rates. Indeed, Martin (1992) suggested that, on the level of the nest site and nest patch, concealed nests in complex habitats have less chance of being predated. However, nest predation rates are variable from year to year. In central Colorado between 1992 and 1994 predation rates were 32 percent (*n* = 38), 28 percent (*n* = 35) and 7 percent (*n* = 15; Ammon 1997). Local site conditions may influence predation rates. Nearly 100 percent predation occurred near human settlement, compared to <20 percent in undisturbed sites within the same region (Ammon 1995, Ammon and Gilbert 1999).

Actual predators of Wilson's warblers likely vary among regions. Near human settlement the main predator is likely the domestic cat (*Felis domestica*). However, a variety of nocturnal predators are attracted to human disturbances including raccoons (*Procyon lotor*) and skunks (*Mephitis* sp.). Other predators reported for the Wilson's warbler include *Accipiter* hawks, corvids, and snakes (Ammon and Gilbert 1999).

Competitors

Negative impacts of interspecific competition are not well documented for Wilson's warbler. A study in northern Colorado and southern Wyoming suggested that yellow warblers nest in large, high volume shrubs, while Wilson's warblers nest under small, low volume shrubs (Ruth and Stanley 2002). Additionally Wilson's warblers tend to be found at sites higher in elevation than most yellow warblers (Ruth and Stanley 2002).

Resource partitioning between Wilson's warbler and Lincoln's sparrow has been investigated in southern Wyoming (Raley and Anderson 1990). Although competition was not directly addressed, the foraging strategies of the two species suggested a lack of competition. Arthropods that were preferred by warblers were noncryptic and patchy in distribution, while sparrows preferred more cryptic, uniformly distributed prey. Wilson's warblers were active searchers that gleaned arthropods from foliage, but they also took prey while hovering and would sally for insects. Lincoln's sparrows, on the other hand, demonstrated a much slower foraging mode, suggesting a more thorough search and an ability to catch more cryptic prey (Raley and Anderson 1990).

Parasites and disease

All disease and parasite information reported here is from Ammon and Gilbert (1999). Northeastern populations of *Wilsonia pusilla pusilla* are known to be infected with the blood parasites *Leucocytozoon* spp. and *Haemoproteus* spp., and combinations of blood parasites also may occur, e.g., *Leucocytozoon fringillinarum*, *L. dubreuili* and *L. majoris*. Macroscopic body parasites were thought to be rare on Wilson's warblers in Colorado because none were found during a five-year study. However an Alaskan study found *W. p. pileolata* fledglings infected with larvae of *Protocalliphora hurido hurido* (Diptera: calliphoridae). Other parasites are likely to occur as suggested by infections of co-occurring birds, but none are reported for the Wilson's warbler. Likewise, the effects of diseases and parasites on survivorship are unknown.

Symbiotic and mutualistic interactions. No symbiotic or mutualistic interactions have been reported for the Wilson's warbler. See **Figure 1** for an Envirogram depicting complex ecological interactions (Andrewartha and Birch 1984).

WEB				CENTRUM
4	3	2	1	

RESOURCES

annual precipitation

water availability

water withdrawal

herbivory

foliage volume

annual precipitation

water availability

water withdrawal

plant species

herbivory — diversity

food:

annual precipitation

seeds and insects

time since fire

fire suppression

water availability

WILSON'S WARBLER

annual precipitation

water availability

water withdrawal

herbivory

foliage volume

annual precipitation

water availability

water withdrawal

plant species

herbivory — diversity

cover and roost

annual precipitation

sites

time since fire

fire suppression

water availability

MATES

See above for
'cover and roost sites' ———— nest sites

herbivory

alternative prey

predators

weather ———— females

disturbance

Figure 1. Envirogram representing the web of linkages between Wilson's warblers and the ecosystem in which they occur.

Figure 1. (Concluded).

WEB				CENTRUM
4	3	2	1	

MALENTITIES

water and soil ——— vegetation ——————— herbivory ——————— alteration of habitat structure ———

recreation in willow communities ——

water and soil —— vegetation ——————— herbivory ——————— alteration of vegetation structure ——————— predation (short-tailed weasels and voles) ——————

inclement weather ———

drought ————————

water withdrawal ——— decreased water availability ———————

eradication of beaver ——

WILSON'S WARBLER

—habitat loss ———

invasion of conifers fire suppression ——————— into meadows ——————

urbanization —————

dredge mining —————

shortening of the photoperiod ——— migration ——————— loss of migratory stopover habitat ——————— reduced food availability ———————

shortening of the photoperiod ——— migration ——————— ingestion of pesticides ———————

CONSERVATION

Threats

Western riparian areas have been called some of the most threatened habitats in North America (Terborgh 1989). Within the western states, riparian corridors and deciduous woodlands are limited to narrow zones along rivers and streams. However, development is often concentrated in these narrow habitats, and many desert riparian habitats have been destroyed by flood control and irrigation projects. It is estimated that 90 percent of the original extent of desert riparian habitat has already been lost (Terborgh 1989). Neotropical migrants, such as Wilson's warblers, are dependent on riparian habitats. Therefore, their populations may be vulnerable to disturbance (Terborgh 1989).

The largest threats to Wilson's warblers include activities that degrade the structure and quality of willow shrub riparian systems. These activities may include dewatering for municipal or agricultural uses, browsing by native herbivores, livestock grazing, habitat conversion, and recreation (Ammon and Gilbert 1999, Colorado Partners in Flight 2000). Additionally, other activities may alter the hydrology of wetland habitats such as beaver management, road and culvert placement, and changes in adjacent upland vegetation (e.g., timber harvest, development).

In areas where beavers are abundant, the ponds created by beaver dams create willow habitats that are suitable to a variety of riparian-obligate species. Removing beaver from an area may have serious implications to associated riparian habitats (McKinstry et al. 2001). The loss of beaver ponds leads to lowered water tables and will ultimately reduce the area of associated riparian vegetation.

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, water diversions occur primarily at lower elevations, so dewatering does not affect high elevation riparian zones to a large extent. 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). 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. Willow communities recover slowly from grazing impacts even after total removal of cattle (Knopf and Cannon 1982).

Research on avian nest success on grazed and ungrazed riparian sites in northwest Nevada suggested that grazing decreases ground vegetation, but it also decreases willow abundance and overall vegetational diversity (Ammon and Stacey 1997). Real and artificial nests had higher predation rates on grazed versus ungrazed sites. This suggests that grazing may not only affect available nesting substrate, but may also influence bird populations by increasing nest predation (Ammon and Stacey 1997). An Idaho study demonstrated little differences in breeding bird densities between grazed and ungrazed riparian sites, but total bird biomass, bird species richness, and bird species diversity were higher on ungrazed sites (Medin and Clary 1990). Of particular importance to this assessment was the finding that neotropical migrant songbirds were found in significantly higher densities on ungrazed sites (Medin and Clary 1990). The studies noted above illustrate some aspects of the negative impact that livestock grazing can have on riparian vegetation. These impacts will affect Wilson's warblers by decreasing suitable nesting substrate and potentially increasing predation and parasitism rates.

In addition to livestock grazing, recreational activities including 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, Atchinson (1977) working in Arizona reported that breeding bird density and diversity decreased at campgrounds located in riparian woodlands. When the campgrounds were closed, songbird density and diversity were similar to adjacent natural areas (Atchinson 1977). In central Colorado, Wilson's warblers deserted nests more often in areas subjected to heavy recreational traffic (Ammon and Gilbert 1999). Nests appeared to be most sensitive during the incubation period, and premature departure of young was attributed to human visitation of nests. Conversely, Wilson's warblers exhibited no desertions from nests <1 m from recreational trails in California (Ammon and Gilbert 1999). A Wyoming study suggested that song occurrence and singing consistency in subalpine birds

were more affected by occasional human disturbance than by frequent disturbance (Ammon and Gilbert 1999). In areas where human intrusion is common and frequent, birds may be able to differentiate people as non-predators; while in less disturbed areas, birds may view people as potential predators.

The aesthetic beauty of riparian habitats may contribute to human use. Like many species of wildlife, people may be most attracted to healthy riparian systems (Hoover et al. 1985). Thus, as human populations continue to grow, more people will seek out pristine riparian habitats, and riparian systems as a whole will continue to be affected (Krueper 1992).

In addition to human induced threats, natural disturbances may impact habitat quality and availability, and subsequently populations of Wilson's warbler. Wildfire may be a relevant threat to higher elevation riparian habitats. However, we were unable to locate specific information on fire effects in montane riparian habitats.

The single largest factor limiting populations of neotropical migrants in the western United States is habitat degradation and loss (Terborgh 1989, Finch 1991, Dobkin 1994, Ammon and Gilbert 1999). As discussed above, factors on breeding grounds appear to play a larger role in abundance than factors on wintering grounds (Chase et al. 1997). The majority of neotropical migrants that breed in the western United States do so in riparian deciduous habitats. Because these habitats are restricted in distribution, population numbers of neotropical migrants in the west may be smaller than their eastern counterparts, making them more vulnerable to habitat destruction and disturbance (Terborgh 1989, Finch 1991). Disturbances that are believed to limit Wilson's warbler abundance include heavy livestock grazing, heavy browsing by native herbivores, pesticide use, and heavy recreational use of riparian habitats (Ammon and Gilbert 1999). Although some of the examples of habitat degradation were taken from areas outside of Region 2, we believe that activities detrimental to riparian areas will negatively affect the distribution and viability of Wilson's warblers.

Conservation Status of Wilson's Warbler in Region 2

To review, the range-wide status of Wilson's warbler is unknown but appears to be declining. Within Colorado, Partners in Flight considers the Wilson's warbler a Priority Species because of its dependence on riparian habitat. Additionally, populations of neotropical migrants in the western United States may be more vulnerable to disturbances than birds in large eastern deciduous forests because western riparian habitats tend to be smaller and more restricted (Terborgh 1989).

Organizations within Colorado, such as Colorado Partners in Flight and the Rocky Mountain Bird Observatory, believe that habitat is limiting for Wilson's warblers. Although the Wilson's warbler is closely associated with riparian willow communities, it does show some flexibility in habitat use. Throughout its range the Wilson's warbler exploits habitats ranging from early successional clear-cuts, shrub willow carrs and wet meadows, and aspen and cottonwood riparian forests. However, Wilson's warblers are intimately tied to riparian habitats within their breeding range in Region 2. Due to the Wilson's warbler's reliance on healthy riparian habitats it is believed that breeding habitat within Region 2, rather than wintering habitat, has the greatest affect on their population (DeSante 1990, Chase et al. 1997). Recent literature suggests that western riparian habitats have been reduced by as much as 90 percent and livestock grazing, development of recreation facilities, dewatering, and timber harvest have further degraded riparian habitats within national forests of Region 2. Any impacts that are detrimental to riparian cover will likely be detrimental to Wilson's warblers that breed in those areas. Thus, conservation of riparian habitats, which are considered isolated and highly threatened across the western United States, is necessary for population viability (Terborgh 1989).

Management of the Species in Region 2

Implications and potential conservation elements

Historically, some management activities have had negative impacts on riparian habitats in the western United States. As riparian habitats are degraded within Region 2, either by land management activities or natural events, Wilson's warblers will decrease in abundance at local and regional scales. Cause and effect relationships between land management and Wilson's warbler should be straightforward: degradation of riparian habitat will lead to decreased populations of this species. More specifically, riparian plant species composition, density, height, vigor, and the extent of the shrub component are important to many riparian bird species, including Wilson's warblers. Ultimately, it is the condition of the hydrologic regime that will influence the long-term quantity and quality of riparian habitats.

Specific parameters defining optimal Wilson's warbler habitat are difficult to describe and are likely to be region-specific. However, approaches to managing habitats that are suitable to Wilson's warblers should focus on restoration and conservation of riparian habitats within the region. Colorado Partners in Flight recognizes the Wilson's warbler as a vulnerable species and suggests reducing or eliminating any activities that degrade the structure and quality of willow shrub riparian systems to help perpetuate their populations. Colorado Partners in Flight also suggests restricting timber cutting within 30 m of riparian areas, and locating roads, trails, and campgrounds outside of riparian habitats. They also suggest that dewatering should be limited in areas where it could degrade dense, extensive willow carrs. Finally, they recommend tightly controlling or eliminating livestock grazing in high elevation riparian areas.

Tools and practices

Species inventory

In our review of inventory and monitoring schemes, the Rocky Mountain Bird Observatory's *Monitoring Colorado's Birds* program stood out as a comprehensive monitoring plan that could be implemented on a region-wide scale. This plan used point transects to survey for Wilson's warbler in high elevation riparian areas of Colorado. Colorado GAP data are used to randomly select 60 publicly owned stands within each of twelve habitat types, including high elevation riparian. Thirty of these stands are randomly selected from the 60 for establishing transects. Transects are then established in each of the 30 randomly selected stands. The transects consist of 15 five-minute point counts spaced at 250 m intervals along the line. At each point the radial distance to each bird is recorded. The surveyors note weather conditions, determine if the point is within 100 m of a road, and record the specific habitat and seral stage for each of two predominant habitats. Finally, the observers record the two most common understory types and the percentage that each occupy of a 50 m-radius circle centered on the point. Surveys are usually conducted in the spring and early summer in the early morning prior to 1000h. The time of day may vary with latitude. In northern New Mexico and southern Colorado, birds begin appearing in April. In northern parts of the breeding range, they do not establish themselves until May, suggesting that surveys must be conducted later in the year.

Habitat management and population monitoring

Population and habitat management approaches specific to Wilson's warbler are not available. However, techniques regarding managing riparian habitats are applicable to Wilson's warblers. The Wyoming Partners in Flight Wyoming Bird Conservation Plan (Cerovski et al. 2001) suggests guidelines for riparian habitat management. In higher elevation riparian habitats of Region 2, grazing and forestry practices are greater threats than crop agriculture. Bock et al. (1992) noted that Wilson's warblers usually respond negatively to grazing. This observation focused on the fact that Wilson's warblers usually nest on or near the ground. Cattle grazing in riparian bottoms generally causes compaction of soils and removal of plant material, both of which indirectly reduce water infiltration and reduce vegetation density. Also, grazing can reduce riparian vegetation through channel widening, channel aggrading, and by lowering the water table leading to reduced riparian shrub land habitat (Bock et al. 1992).

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. Other impacts of agriculture may be less obvious such as pesticides and contaminants.

Forestry practices have recently been mitigated in attempts to lessen the impacts to riparian habitats. Both the U. S. Forest Service and the U. S. Bureau of Land Management have initiated measures to protect riparian habitats (Kreuper 1992). Such measures include riparian buffer zones and management of activities within those zones depending on such variables as soil type, slope of the surrounding terrain, and the vegetation present. Manipulation of adjacent habitats can have significant effects on hydrologic systems that feed riparian habitats. For example, removing adjacent forests may increase water temperatures and increase evaporation by decreasing shade (Kreuper 1992). By disturbing adjacent communities, invasive, hydrophilic plant species may colonize the area, which will have detrimental effects on native riparian plant and animal communities. Additionally, opening the canopy by removing adjacent

forest and shrub communities can increase exposure to wind, which increases evaporation and may reduce water yields. Whether these methods are effective or appropriate for Wilson's warblers requires investigation. However, mitigation techniques are continuing to be developed, and protection of riparian habitats remains a high priority for land management agencies.

Information Needs

We believe that the continental distribution of Wilson's warbler is understood in sufficient detail to formulate regional conservation strategies. However, based on the relative isolation of many high elevation riparian habitats throughout the mountainous regions of Colorado and Wyoming, distribution at smaller scales is not well known. We assume that Wilson's warblers inhabit many of these areas, but lacking survey data we are uncertain. Extrapolation of information from representative sites such as those studied in central and southeastern Wyoming is useful, but these studies do not give an idea of population numbers.

The response of Wilson's warblers to broad-scale habitat changes is not as well understood as its response to fine-scale changes. Research generally focuses on fine-scale disturbances or stand-scale habitat alterations, rather than on broad-scale impacts. Based on Johnson's (1980) four orders of habitat selection, the first-order selection of habitat affects each additional order.

Therefore, broad-scale (first-order) habitat changes will ultimately have implications on selection down to fourth-order selections (food items) within a home range. A better understanding of responses to alterations in broad-scale habitat should help managers understand responses to fine-scale changes.

We also believe that the natural history and demography of the Wilson's warbler is sufficiently understood to evaluate the effects of management and changes in natural disturbance patterns. Likewise, annual, seasonal, and daily movements are also sufficiently understood to evaluate the influence of habitat changes on their population. However, the nature of neotropical migrant songbirds makes it difficult to predict the effects of changes to stopover habitats, other than in general terms. Many studies have shown that migrants such as Wilson's warblers show fidelity to wintering grounds as well as breeding grounds, but stopover sites may not be used year to year.

Methods are available to reliably monitor trends in Wilson's warbler populations within Region 2 including the North American BBS. However, route coverage is a problem throughout the western United States. Breeding Bird Surveys are conducted on roads and most high elevation riparian habitats are not close to roads. Ultimately, a monitoring program that adequately samples isolated areas needs to be developed in order to get an accurate estimate of population numbers and trends.

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Matrix Model Assessment of Wilson's Warbler

Life cycle model

Due to similarities of life history characteristics and a lack of demography data, we pooled the data available for Lincoln's sparrows (*Melospiza lincolnii*), fox sparrows (*Passerella iliaca*), and Wilson's warblers (*Wilsonia pusilla*) together to construct a life cycle model. The studies of Speirs and Speirs (1968), Ammon (1995), Ammon and Gilbert (1999), and Weckstein et al. (2003) provided the basis for formulating a life cycle graph for Wilson's warbler 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 and Gilbert (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 and high-ratio cases. 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 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.

Sensitivity analysis

A useful indication of the state of the population comes from the sensitivity and elasticity analyses. *Sensitivity* is the effect on population growth rate (λ) of an *absolute* change in the vital rates (a_{ij}, the arcs in the life cycle graph [**Figure A1**] and the cells in the matrix, A [**Figure A2**]). Sensitivity analysis provides several kinds of useful information (Caswell 1989:118-119). First, sensitivities show "how important" a given vital rate is to population growth rate (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 paucity
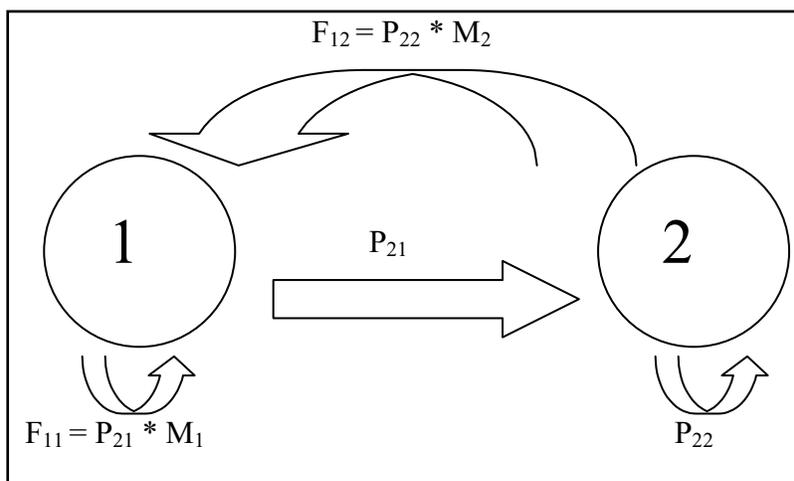

$$F_{12} = P_{22} * M_2$$

1

$$P_{21}$$

2

$$F_{11} = P_{21} * M_1$$

$$P_{22}$$

Figure A1. Life cycle graph for Wilson's warbler. 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 Wilson's warbler. 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)
P_{22}	0.59 (0.5)	"Adult" survival rate (low-ratio case)

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

	1	2
1	F_{11}	F_{12}
2	P_{21}	P_{22}

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	0.36	1.475
2	0.18	0.59

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 ($P_{21} = 0.225$).

	1	2
1	0.45	1.25
2	0.225	0.5

of data, but could also result from use of inappropriate estimation techniques or other errors of analysis. In order to improve the accuracy of the models, researchers should concentrate additional effort on transitions with large sensitivities. Third, sensitivities can quantify the effects of environmental perturbations, wherever those can be linked to effects on stage-specific survival or fertility rates. Fourth, managers can concentrate on the most important transitions. For example, they can assess which stages or vital rates are most critical to increasing the population growth (λ) of endangered species or

the "weak links" in the life cycle of a pest. **Figure A3** shows the "possible sensitivities only" 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).

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. Wilson's warblers 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 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 Wilson's warbler 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 Wilson's warbler 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.

Other demographic parameters

The *stable age distribution* (SAD, **Table A2**) describes the proportion of each age-class in a population

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

	1	2
1	0.391	0.17
2	1.397	0.609

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

	1	2
1	0.476	0.212
2	1.177	0.524

at demographic equilibrium. Under a deterministic model, any unchanging matrix will converge on a population structure that follows the SAD, 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 Wilson's warbler 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 Wilson's warbler. 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 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 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* λs, 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

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

	1	2
1	0.140	0.251
2	0.251	0.358

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

	1	2
1	0.213	0.263
2	0.263	0.26

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	High-ratio	Low-ratio
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 Lincoln's 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	N/A	N/A
# Declines / # survived population	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	1.6×10^6
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

— 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 Wilson's warbler 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 Wilson's warbler, 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 Wilson's warbler 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 variation in vital rates. Using observed correlations would improve on our "uncorrelated" assumption, by incorporating forces that we did not consider. Those forces may drive greater positive or negative correlation among life history traits. Other potential refinements include incorporating density-dependent effects. At present, the data appear insufficient to assess reasonable functions governing density dependence.

Summary of major conclusions from matrix projection models

❖ Survival accounts for 78 percent of the total "possible" sensitivity in the high-ratio case ($P_{22} = 0.59$ vs. $P_{21} = 0.18$). Any absolute changes in survival rates will have major impacts on population dynamics. Survival accounts for slightly less (71 percent) of the total when first-year ($P_{21} = 0.23$) and "adult" ($P_{22} = 0.5$) survival are more similar. In both cases, however, survival is considerably more important than is fertility.

❖ Survival (P_{21} and P_{22}) accounts 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 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, Wilson's warblers 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.

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