Point Blue Conservation Science

Foothills to Summit

Conservation Objectives for Birds in California's Sierra Meadows

May 2022

Yellow Warbler (Credit: Michael Mahoney/Point Blue)
Cover photo: Childs Meadow (Credit: Michael Mahoney/Point Blue)

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Prepared by

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Abstract

Meadow restoration and conservation have been a priority in the Sierra Nevada and southern Cascades of California for more than a decade, due to their ecological importance, rarity on the landscape, and highly degraded condition. To support collaborative efforts to conserve and restore these meadows, we integrated these meadows into the Central Valley Joint Venture's conservation framework for the first time, adapting a general framework and a transparent, science-based approach to developing conservation objectives. We defined four planning regions, assessed the extent of meadow habitat available in each region, and for each of 10 focal bird species, we used recent bird survey data to estimate regional average breeding densities and population sizes. We estimated that 90% of the regional populations are *small* (<10,000) or *very small* (<1,000), and may be vulnerable to extirpation, and that Willow Flycatcher (*Empidonax traillii*), a California endangered species, is *steeply declining*. For each focal species in each region, we defined long-term (100-year) breeding density objectives and corresponding population size objectives that are intended to be feasible to achieve with extensive efforts to restore and enhance habitat quality in existing meadows, and we defined a long-term habitat quantity objective of no net loss of existing meadows. To provide a means by which progress toward the long-term conservation objectives can be measured, we also defined short-term (10-year) objectives that represent 10% of the improvement in breeding density and population size needed to reach the long-term objectives. We expect that protecting and restoring meadows to reach the conservation objectives defined here will improve the long-term viability and resilience of these focal species while also helping to restore the multiple benefits meadows provide to birds, other wildlife, and human communities within, nearby, and downstream of these rare and ecologically important meadows.

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INTRODUCTION

Wet meadows are a rare but important component of the Sierra Nevada and southern Cascades in California (hereafter, Sierra meadows), and their conservation value far outweighs the 2% land cover of the ecosystem they represent (Drew et al. 2016). Sierra meadows provide diverse ecological services when healthy, including flood attenuation, sediment filtration, groundwater storage, improved water quality, extended late season baseflows, and carbon sequestration (DeLaney 1995, Woltemade 2000, Hammersmark et al. 2008, Reed et al. 2021). However, more than 50% of these meadows are in a degraded state (Hunsaker et al. 2015) reducing their ability to provide these services. Sierra meadows are also biodiversity hotspots that provide important habitat for numerous fish and wildlife species, including several rare and declining species with special conservation status such as the state endangered Willow Flycatcher (Kattelmann and Embury 1996). Most of the avifauna in the Sierra and southern Cascades use meadows at some point in their annual cycle (Siegel & DeSante 1999). As the result of their ecological importance, rarity on the landscape, and degraded condition, numerous private (e.g., Sierra Nevada Meadow Restoration Business Plan, NFWF 2010; Sierra Meadows Partnership, Drew et al. 2016), state (e.g., California State Water Action Plan), and federal (e.g., USDA Forest Service Region 5 Ecological Restoration Leadership Intent) initiatives are underway to increase the pace, scale, and efficacy of meadow restoration efforts and improve their management to enhance their ecological services.

To support these meadow conservation efforts, we applied conservation planning approaches developed through the Central Valley Joint Venture (CVJV) to derive conservation objectives for breeding birds. The CVJV has established a general framework for setting population size objectives for breeding birds (Dybala et al. 2017a), and applied this framework to develop transparent, science-based objectives for the extent of habitat enhancement and restoration needed to support robust, self-sustaining, and resilient breeding bird populations across ecosystems (e.g., Dybala et al. 2017b, DiGaudio et al. 2017, Strum et al. 2017). These objectives were then combined in a comprehensive, integrated conservation strategy in their Implementation Plan (CVJV 2020). However, this conservation strategy is largely focused on the floor of the Central Valley, the CVJV's "primary focus area" (Figure 1). Here, we describe our process for setting long-term (100-year) and short-term (10-year) conservation objectives for landbirds breeding in meadows in the Sierra Nevada and southern Cascades, as part of the CVJV's secondary focus area. Specifically, we evaluate the current status for each of 10 focal species populations in each of four planning regions and then define long-term (100-year) and short-term (10-year) breeding density objectives and corresponding population size objectives. Our approach integrates wet meadows into the CVJV's conservation framework for the first time, and provides a transparent, repeatable decision-making process for setting conservation objectives.

METHODS

Study Area

The Sierra Nevada and southern Cascade Mountains of California occur across 10 national forests or management units, 3 national parks, and vast amounts of other public and private lands that encompass approximately 17 million hectares (42 million acres). The climate is Mediterranean, with most of the precipitation occurring from November to March, falling primarily as snow at the higher elevations and rain elsewhere, with total precipitation generally increasing with elevation. The study area consists predominantly of Sierra mixed-conifer and true-fir cover types, with smaller

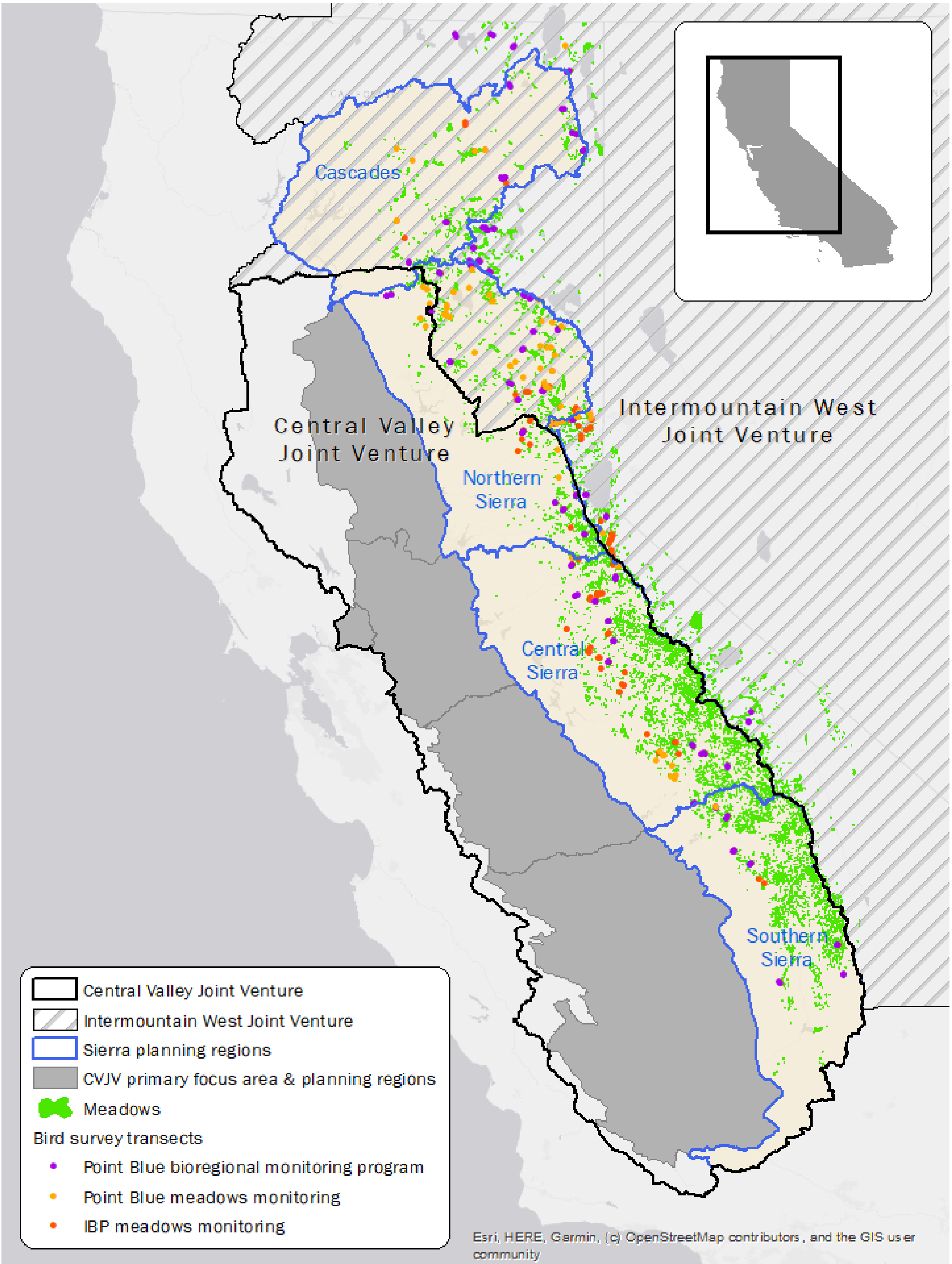

Figure 1. Sierra meadows planning regions, shown with the boundaries of the Central Valley and Intermountain West Joint Venture perimeters, and planning regions within the CVJV's primary focus area. Also shown are the extent of Sierra meadows included in the Meadows Layer and the approximate centroids of bird survey transects (groups of multiple survey locations) included in these analyses, both of which extend beyond the planning region boundaries.

amounts of montane chaparral and hardwood-dominated habitat. Meadows within this region make a small proportion of the total area, under 120,000 hectares (300,000 acres), but have a disproportionate influence on ecosystem health and function (Drew et al. 2016).

To assess the status of breeding birds in meadows across this region, we defined four conservation planning regions following a similar approach to that used by the CVJV to define planning regions in the CVJV's primary focus area on the Central Valley floor (Figure 1). Planning regions are bounded primarily by the CVJV secondary focus area, extending from the Central Valley floor up to the crest of the Sierra Nevada, and divided along HUC8 watershed boundaries (http://datagateway.nrcs.usda.gov). To define the Southern Sierra and Northern Sierra planning regions, we aligned the borders with the watershed boundaries for the Tulare and Sacramento planning regions, respectively, and combined the area east of the Yolo-Delta and San Joaquin planning regions into a single Central Sierra planning region. However, to derive cohesive planning units that better reflect ecological boundaries, hydrology, and meadow conservation and planning, we added an additional Cascades planning region extending north into the southern Cascades range and extended the boundary of the Northern Sierra planning region eastward. These two planning regions overlap the Intermountain West Joint Venture but represent entire watersheds that flow westward toward the Central Valley and are included within regional management planning and coordination efforts such as the Sierra Meadows Partnership (https://www.sierrameadows.org).

Meadow Habitat and Focal Species

The Sierra Nevada Multi-source Meadow Polygons Compilation v.2 (hereafter, Meadows Layer) represents the most thorough accounting of meadow habitat in the region (UC Davis 2017). In version 2, polygon boundaries were updated using high-resolution (1m) NAIP imagery, and methods to delineate meadow boundaries relied on hydrology, soil maps, vegetation cover, topography, geology, and transportation maps. We intersected the Meadows Layer with our planning region boundaries to estimate the regional extent of meadow habitat and important characteristics associated with each meadow polygon that may influence the breeding densities of meadow bird species. These characteristics included total area, mean and maximum size of the individual meadow polygons, total count of meadow polygons, mean elevation, and the mean proportion of the area of each polygon in the "interior" zone, which we defined as the area more than 20m from any polygon boundary; we defined the area within 20m of the boundary as meadow "edge" (Table 1).

Because birds are recognized as good indicators of ecosystem condition (Carignan and Villard 2002; Ortega-Alvarez and Lindig-Cisneros 2012), we selected a suite of 10 focal species that we assumed would collectively be a good indicator of the health of the network of meadows in each region (Table 2). We based this list on 14 focal species identified by Campos et al. (2014), but we excluded Wilson's Phalarope and Swainson's Thrush (for which we had inadequate sample size for fitting models), White-crowned Sparrow (found at very high elevations and poorly represented in our survey data), and Black-headed Grosbeak (more closely associated with riparian forest than open meadow habitat; see Table 2 for scientific names). These 10 focal species collectively represent a range of life histories and vegetation associations within meadows. All except Lincoln's Sparrow breed in other habitats in the Sierra and southern Cascades, including montane riparian, aspen, conifer-hardwood forest, and mesic montane chaparral. Individuals from these other habitats are almost certainly part of the same populations and these non-meadow habitats may support a substantial portion of their populations. However, almost all these species reach their greatest densities in meadows (Point Blue, unpublished data) and the meadow portion of their populations may be more resilient to habitat alteration as a result of climate and fire. As such, meadows likely have a disproportionately high importance for the long-term resilience of these populations.

Table 1. Total area of meadows by planning region, ha (ac), shown with statistics about the size, count, elevation, and proportion considered interior (>20m from boundary). Statistics exclude meadow polygons smaller than 0.61 ha (1.5 ac) and those located at very high or low elevations (see Methods).

Planning Region	Total area, ha (ac)	Mean size, ha (ac)	Max size, ha (ac)	Meadow count	Mean elevation (m)	Mean proportion interior
Cascades	15,441.3 (38,156.2)	31.8 (78.6)	1,648.0 (4,072)	486	1,690.9	0.44
Northern Sierra	21,767.8 (53,789.5)	9.8 (24.2)	2,094.9 (5,177)	2,227	1,884.7	0.32
Central Sierra	16,972.5 (41,940.0)	3.3 (8.2)	141.9 (350.6)	5,168	2,433.0	0.23
Southern Sierra	14,312.3 (35,366.5)	4.6 (11.4)	1,862.7 (4,603)	3,140	2,659.6	0.22
Total	68,494.0 (169,252.4)	6.2 (15.3)	2,094.9 (5,177)	11,021	2,354.0	0.25

Breeding Densities, Population Sizes, and Trends

For each of the focal species, we developed models relating their breeding densities to metrics describing meadow characteristics and condition. To represent the wide range of meadow conditions across all four planning regions, we assembled bird survey data from three monitoring programs that all used a similar point count survey protocol. Point counts are a standardized method for surveying bird populations, in which highly trained observers record all individuals of all species detected by sight or sound and the estimated distance to each within a 5-minute observation period, during morning hours and favorable weather conditions (Ralph et al. 1995). Surveys were conducted between mid-May and early July, during the peak of the breeding season. We first included survey records from a Point Blue bioregional monitoring program (Roberts et al. 2011), which comprised 36% of the 21,319 total detections of our focal species in the compiled dataset. This survey program consisted of a spatially balanced random sample across the entire region (n=536 survey points grouped into 126 transects) and included survey points distributed across all four planning regions during 2010-2017, 2019, and 2021. Most transects were surveyed repeatedly during that time frame, with an average of 7.0 years surveyed per transect, and a total of 1357 survey visits. The second monitoring program was developed by Point Blue to target meadows that were either the focus of restoration efforts or other management importance (e.g., Willow Flycatcher habitat; Burnett and Campos 2015). This program provided the majority of survey points (n=697 points grouped into 71 transects) and accounted for 58% of all bird detections, but survey points were concentrated in the Northern Sierra planning region (largely in the Lassen and Plumas National Forest area), with only a few locations in the other regions. Surveys were conducted during 2010-2021, with an average of 3.8 years surveyed per transect, and a total of 491 survey visits. Finally, we included data from a meadows monitoring program managed by the Institute for Bird Populations (IBP), which contributed the smallest portion of bird detections (6%) but included locations in National Parks that were not covered by the other programs. Survey points from this program (n=721 points grouped into 81 transects) were spread across all four planning regions, and in some cases overlapped with the Point Blue meadows monitoring project (i.e., some of the same locations were included in both projects but surveyed in different years; Campos et al. 2020). Surveys were conducted during 2010-2012, with an average of 1.4 years surveyed per transect, and a total of 214 survey visits.

Table 2. Focal species life history traits, specific vegetation associations, and conservation status.

Species common name (Latin name, 4-letter code)	Migratory status	Nest substrate	Meadow habitat and vegetation associations	Conservation status
Lincoln's Sparrow (*Melospiza lincolnii*; LISP)	Short-distance Migrant	Ground	Dense herbaceous vegetation, scattered shrubs, higher elevations	Ranked among the most vulnerable to the impacts of climate change in California[3]
Song Sparrow (*Melospiza melodia*; SOSP)	Resident/Short Distance Migrant	Shrub/Herbaceous	Standing water, tall herbaceous vegetation, some willow thickets	
Yellow Warbler (*Setophaga petechia*; YEWA)	Neotropical Migrant	Shrub	Dense willow thickets, meadow interiors	California Bird Species of Special Concern[2]
MacGillivray's Warbler (*Geothlypis tolmiei*; MGWA)	Neotropical Migrant	Shrub	Dense shrubs, meadow margins, Willow/alder/dogwood/spirea	
Calliope Hummingbird (*Selasphorus calliope*; CAHU)	Neotropical Migrant	Tree	Willow thickets, nectar producing forbs and shrubs	Partners in Flight Yellow Watch List; long-term planning in Sierra Nevada BCR needed to maintain population[1]
Warbling Vireo (*Vireo gilvus*; WAVI)	Neotropical Migrant	Tree/Shrub	Riparian hardwood tree/shrubs, meadow edges	Species of regional concern in the Sierra Nevada BCR due to moderate population declines and threats; management actions needed[1]
Wilson's Warbler (*Cardellina pusilla*; WIWA)	Neotropical Migrant	Ground	Willow/alder thickets, meadow edges, dense understory	Common bird in steep decline; long-term planning in Sierra Nevada BCR needed to maintain population[1]
Wilson's Snipe (*Gallinago delicata*; WISN)	Short-distance Migrant	Ground	Saturated soils, dense herbaceous understory, meadow interiors	
Red-breasted Sapsucker (*Sphyrapicus ruber*; RBSA)	Short-distance Migrant	Tree, 1° cavity	Riparian deciduous trees and shrubs, snags	
Willow Flycatcher (*Empidonax traillii*; WIFL)	Neotropical Migrant	Shrub	Willow & alder thickets, standing water, large meadow interiors	California endangered species[4]; Southwestern subspecies (*E. t. extimus*) is a federal endangered species and ranked among most vulnerable to the impacts of climate change in California[3]

[1]Partners in Flight 2021; [2]Shuford and Gardali 2008; [3]Gardali et al. 2012; [4]CDFW 2022

We evaluated the locations of the survey points from all three monitoring programs relative to our planning region boundaries and the meadow polygons in the Meadow Layer. Most survey points fell within our planning region boundaries (91%), but also included points east of the Sierra Nevada crest which we removed prior to the analyses described below. In addition, most survey points from the Point Blue and IBP meadows monitoring programs were located in meadow interiors (59% for each) and a smaller proportion in meadow edges (11% for Point Blue, 14% for IBP). Some of the remaining survey points fell just outside meadow polygons (within 50m), a zone we defined as meadow "fringe" (6% for Point Blue, 5% for IBP), with the remainder located 50-500m (average = 95m) outside any meadow polygon in the Meadow Layer, a zone we defined as meadow "exterior" (24% for Point Blue, 22% for IBP). In contrast, the Point Blue bioregional monitoring program included, by design, a broader definition of meadow habitats that did not restrict based on shrub cover or in some cases conifer encroachment, with survey points more evenly distributed among meadow interior, edge, and fringe zones (22%, 22%, and 14%, respectively) and a larger proportion within the exterior zone (42%). Although these "exterior" points were not located within meadow polygons as defined in the Meadow Layer, all of these points had been ground-truthed as occurring within 50m of a meadow when they were selected as a bird survey location. The mismatch between these points and the Meadows Layer polygons likely reflects a difference in how meadows are delineated, with the Meadows Layer prioritizing open areas dominated by herbaceous vegetation. Nevertheless, to bolster sample size and help fit models, we included in our analyses data from bird survey points located in all four zones (interior, edge, fringe, and exterior), and included zone as a predictor in our modeling to account for potential variation in breeding densities among zones.

From the combined survey dataset, which spanned 2010-2021, we restricted our analyses to detections of focal species within 50m of the observer. We fit distance-sampling occupancy models for each focal species using the R package *UBMS* (Kellner et al. 2021) to model breeding density as a function of several predictors, while accounting for variation in detection probability as a function of distance from the observer. Specifically, we used the "stan_distsamp" function to fit the Royle et al. (2004) hierarchical distance sampling model, assuming detection probability follows a half-normal function and incorporating three distance bins: 0-20, 21-35, and 36-50 meters. All detections in the survey data included an estimated distance to each individual, except IBP surveys which recorded distance as solely within or beyond 50m; for these data, we coded all detections as occurring at 25m. We also included two detection covariates: monitoring survey project ID, to help account for variation among different observers and field methods, and ladder fuel density in 2020, derived from California Forest Observatory maps (CFO 2020), which represents the amount of surface and understory vegetation and may affect detection probability for many species.

We modeled breeding density (number of individuals per hectare) as a function of several covariates representing spatial and temporal variation in the characteristics and condition of meadows across all four planning regions. These included fixed effects of meadow area and meadow catchment area, each square-root transformed to reduce the influence of a few very large area values, and meadow slope to account for influences related to hydrogeomorphology; each of these values was taken from those reported in the Meadows Layer. For points located exterior to meadow polygons, we applied the values from the nearest polygon. We included year as a continuous covariate (plus quadratic term) to account for potential trends over time across the 11 years of our surveys. To represent variation in vegetation structure among meadows, we included meadow zone (i.e., interior, edge, fringe, or exterior, as described above) to account for small-scale spatial habitat effects, as well as ladder fuel density (described above) and canopy bulk density, which reflects the mass of leaves and small branches in the canopy (also derived from CFO 2020). The CFO metrics were acquired from 2020 imagery and were considered static over time. However, to account for variation in environmental conditions, we also included annual values for the mean June daily maximum temperature (plus quadratic term) and climatic water deficit (CWD), a metric that reflects drought stress in vegetation, both derived from the Basin Characterization Model dataset, 2010-2020 (BCM, Flint and Flint 2014). We also included annual values for the Normalized Difference Water Index (NDWI), an index that reflects moisture content in leaves and is derived from summer (June-August) Landsat imagery (Gao 1996, Roberts et al. 2019). Annual values were matched to the dates each point was visited, except that because BCM data were not available for 2021, so we applied the 2020 estimates to 2021 survey data as well. The NDWI, CWD, and temperature covariates help account for highly variable climatic conditions during the years over which bird survey data were collected, including a historic drought during 2013–2017. In addition, temperature is strongly correlated with elevation ($R>0.9$), and effectively accounts for elevational variation in bird population distributions. All continuous covariates were standardized to mean = 0.0 and standard deviation = 1.0. A few covariates had a small number of extreme outlier values associated with a point count location, which may represent errors in the covariates and may overly influence model results. Rather than exclude these covariates or point count locations, we replaced the outliers with less extreme values, a process also known as Winsorizing (Dixon 1960). Specifically, we replaced outlier values for ladder fuel density (maximum 31%, truncated <1% of data to 20%), canopy bulk density (maximum 11.1 kg/m^3, truncated <1% of data to 6 kg/m^3), and slope (maximum 217%, truncated <1% of data to 30%). We evaluated the multicollinearity of these variables using the "vif" function in the R package *car* (Fox and Weisberg 2019) and verified that there was no strong collinearity (all vif < 2.0) among these variables that would influence model fitting.

In addition to these fixed effects, we incorporated two random effects to account for additional variation among meadows and imbalances in sample sizes. One of the advantages of using the *UBMS* package over the popular occupancy and abundance modeling package *unmarked* (Fiske and Chandler 2011) is that it provides the additional capability of including random effects in fitted models. Random effects included: planning region ID, to account for geographic differences among regions including the latitudinal gradient; and vegetation majority type (i.e., riparian, hardwood/shrub, conifer, or other) as classified in the Meadows Layer, to account for additional variation in below-ground hydrology and vegetation class.

For each species, we fit the full model to the survey data and generated posterior samples for each model parameter from across 3 chains of 500-1100 iterations, using a larger number of iterations when necessary to ensure model convergence using the Gelman-Rubin diagnostic (Gelman and Rubin 1992; $\hat{r}$ ~1.0). We then used the fitted models to estimate the population sizes for each focal species in each planning region, deriving all of the same covariates for each meadow polygon. For covariates that varied annually (NDWI, CWD, temperature, year), we used covariates from the year 2020, a dry but moderate temperature year. In assessing the full range of these metrics across all meadow polygons, we found that, despite the large bird survey sample size of 1,954 point count locations ranging from 831 to 2,508 meters in elevation and spread across nearly the entire latitudinal range of the Sierra Nevada bioregion, our bird surveys did not sample the full range of environmental conditions represented by the meadows polygons. Thus, to avoid projecting species densities for meadows with environmental conditions that fell outside the range of values used to fit the models, which can result in highly uncertain and unrealistic densities, we limited our projections to only the range of meadow conditions that closely resembles our bird sampling universe. Specifically, we again truncated extreme values for some covariates using the same maximum truncated values as described above: ladder fuel density from a maximum in the Meadows

Layer of 40.7% to 20.0%, canopy bulk density from a maximum of 11.2 kg/m^3 to 6.0 kg/m^3, and slope from a maximum of 66.9% to 30.0%. We also truncated additional covariates to the maximum measured values at bird survey points, including NDWI from a maximum of 0.92329 to 0.91848, CWD from a maximum of 197.71 to 179.96, and meadow patch area from a maximum of 17,392 to 5,177 acres.

To further limit our projections to meadows that resemble our bird sampling universe, we also excluded from our projections very small meadow polygons (< 0.61 ha, 1.5 acres), as well as meadows located at very high and low elevations. Although the small meadows may contribute habitat for some focal species, our bird surveys did not adequately sample small meadows, and because meadow size is an important predictor of breeding density for many species (described further below), including these small meadows would greatly increase uncertainty in the population size estimates. We implemented elevation restrictions by excluding only the most extreme values for June daily maximum temperatures to match the range of values found at our bird survey locations (14.43–31.62°C). Specifically, we excluded meadow patches with temperatures exceeding 31℃ (measured primarily at very low elevation sites), and temperatures less than 14.5°C (measured primarily at very high elevation sites). In both cases, the excluded meadows were primarily from the Central and Southern Sierra planning regions (Figure 1). These restrictions resulted in the removal of 22 meadows in the Cascades planning region (10.8 ha, 26.7 acres), 334 in the Northern Sierra (161.1 ha, 398.1 acres), 1852 meadows in the Central Sierra (906.6 ha, 2240.2 acres), and 1296 meadows in the Southern Sierra (639.4 ha, 1579.9 acres).

We then used the fitted models to project the breeding densities of each focal species in each of the remaining meadow polygons, with separate projections for the interior and edge meadow zones; to ensure population size estimates reflected only the meadow area itself, as mapped in the Meadows Layer, we excluded any projections for the fringe and exterior zones. We then estimated the total number of individuals per meadow polygon by multiplying projected density by the area of each zone and summing over both zones. With these estimates of total abundance per meadow polygon, we then summed across all polygons in each planning region to generate regional population size estimates for each focal species. We then estimated the overall regional average density by dividing the total regional population size by the total area of the meadow polygons included in each region.

To evaluate long-term population trends for each focal species, we compiled trend estimates for the Sierra Nevada Bird Conservation Region (BCR-15) from Breeding Bird Survey data, 1968–2019 (Sauer et al. 2020). We also evaluated whether the year covariate in our density models was significant, where we considered the covariate significant if the coefficient value (mean of the posterior distribution) +/- 2 standard deviations did not include 0.0. Evaluating the relationships between breeding densities and other covariates were not central to the goals of this analysis, but we describe general patterns across species, and provide model covariate and model fit values in the Supplementary Materials (Table S1).

For Willow Flycatcher, a California endangered species, we supplemented these analyses with the most recent, comprehensive evaluations of their population size and trend available (Loffland et al. 2014), which reported estimates of the current (in 2014) number of breeding territories throughout the study area but grouped into different geographic units than our planning regions. Where more recent information was known to any of the authors, we updated numbers from Loffland et al. (2014) to include these more recent estimates. We attempted to compile or segregate their estimates as needed to match our planning regions, and then, assuming each breeding territory consists of two breeding adults, we doubled their estimates to generate estimates of the total population size in each region. To estimate the current average breeding density in each region, we divided the total population size estimates by the total area of meadows included in each region. As a proxy for the long-term trend in population size, we also adopted the Loffland et al. (2014) estimates of the trend in the number of sites with breeding detections from 2000 to 2013.

Current Population Status

Using the focal species as indicators of the state of Sierra Nevada meadows, we evaluated the status (population size and trend) of the focal species' populations within each planning region. We applied a population status framework derived from general principles of conservation and population biology (Dybala et al. 2017a), and previously applied to develop conservation objectives for other taxonomic groups by the Central Valley Joint Venture, including breeding populations of riparian landbirds, shorebirds, and grassland-oak savannah birds (Dybala et al. 2017b, Strum et al. 2017, DiGaudio et al. 2017). The framework is structured as a hierarchy of four population size and status categories that mark expected milestones in the process of becoming a genetically robust, self-sustaining, and resilient wildlife population (*very small*, *small*, *viable*, and *large*), along with population size thresholds representing the general orders of magnitude at which most vertebrate wildlife populations are expected to reach each population status (Table 3; Dybala et al. 2017a). The framework also provides two modifiers to indicate populations that are *steeply declining*, and thus at high risk of extirpation regardless of population size, or *resilient*, which are more capable of recovering from an environmental catastrophe in one part of the range if they have more than one self-sustaining sub-population.

Although the birds in each of the Sierra Nevada planning regions are not likely to be isolated biological populations, achieving the goal of resilient focal species populations requires the population status of each region to be evaluated independently. Therefore, we applied the framework to each regional focal species population, and we considered each focal species to be *resilient* in the Sierra Nevada if it had at least two regional meadow populations that were *viable* (> 10,000) or *large* (> 50,000; Table 3). We then collectively evaluated the populations within each region as an indicator of the state of meadow ecosystems in each region.

Table 3. Population status framework. Reproduced from Dybala et al. (2017a).

Population status	Description	Proposed thresholds
Very small	Expected to be well below minimum viable population size (MVP), and at increased risk of inbreeding depression in the short term.	< 1,000
Small	May be below MVP and vulnerable to extirpation through environmental and demographic stochasticity and long-term loss of genetic diversity.	< 10,000
Viable	Expected to meet or exceed MVP, reducing vulnerability to environmental and demographic stochasticity and preserving genetic diversity.	> 10,000
Large	Expected to be well above MVP, minimizing vulnerability to environmental and demographic stochasticity, preserving genetic diversity, and improving ability to maintain key ecological interactions and functions.	> 50,000
Additional modifiers		**Criteria**
Steeply declining	Increased risk of extinction or extirpation until the causes of the decline are addressed, no matter the population size.	> 30% decline in 10 years (observed or projected)
Resilient	Multiple viable or large populations to hedge against environmental catastrophes.	Viable populations (> 10,000) in more than one region

Conservation Objectives

As with other Central Valley Joint Venture conservation objectives (e.g., Dybala et al. 2017b), we assumed that the population sizes of many focal species are primarily limited by the quantity and/or quality of meadow habitat in the Sierra Nevada. We also assumed the spatial extent of meadows is largely fixed and determined by geography. Thus, unlike other CVJV conservation objectives, instead of an emphasis on restoring additional acres of meadow habitat, conservation and restoration efforts in Sierra Nevada meadows focus on improving the quality of existing meadow habitat. Because over 50% of Sierra Nevada meadows are considered degraded (Hunsaker et al. 2015), we assumed the current average breeding densities (individuals / ha) of the focal species in each region are lower than they otherwise could be in high quality habitat, and that enhancing meadow habitat quality should result in increasing breeding densities (Campos et al. 2020), thereby increasing the overall size of focal species populations. Therefore, we defined a long-term habitat quantity objective of no net loss of existing meadow extent and developed long-term (100-year) density and population size objectives for each focal species in each planning region.

In support of the long-term goal of genetically robust, self-sustaining, and resilient populations of each of the focal species in the Sierra Nevada, our initial approach to setting long-term population objectives was to aim for multiple stable or increasing regional populations of each focal species that are at least *viable* and preferably *large* (Table 3, following Dybala et al., 2017b). To first examine whether *viable* or *large* population sizes are reasonable objectives for each focal species in each planning region, we estimated the average breeding density that would be required, given the total area of meadows in each planning region. We then compared this estimate to the range of density estimates projected from our models for each individual meadow polygon in each region. For most species, the average breeding densities required to reach a *viable* or *large* population size well exceeded this range of density estimates or were exceeded only by a small number of outliers (Figure S1). Therefore, we adopted a different approach, first defining density objectives within the range of projected estimates, and thus assumed to be feasible, and then defining population objectives based on these densities.

Excluding Willow Flycatcher (treated separately, below), we defined long-term density objectives for each focal species within each region as the larger of either (1) the 75th percentile of the projected density estimates for each meadow polygon in each region, or (2) the mean of the projected density estimates that exceeded the overall regional average density. We initially selected the 75th percentile following the approach of Dybala et al. (2017b), to reflect a density objective that is above the median and reflects densities that can be reached in relatively high-quality habitat. However, for some regional populations, the overall weighted average density was higher than the 75th percentile, due to both the variation in meadow size and the influence of meadow size on breeding density. For example, if a few large meadows with relatively high densities are greatly outnumbered by small meadows with relatively low densities, the meadow with a density equal to the 75th percentile may be one of the small, low-density meadows, even if the weighted average density is higher. Thus, we included the second criteria as an alternate means of selecting a long-term density objective that is higher than the current regional average density but still within the range of density estimates projected from our models. Where the resulting density objective was very close (within 0.1 birds/ha) to the density required to reach the threshold for a *viable* population size, we rounded the density objective up to meet this threshold. We then defined long-term population size objectives as the population size that would result from achieving the long-term density objectives. To provide milestones against which progress toward the long-term objectives can be measured, we also estimated short-term (10-year) population size and density objectives as 10% of the improvement from current density and population size estimates required to meet the long-term objectives.

For Willow Flycatcher, we instead based our objectives on existing conservation objectives that were defined in terms of the number of breeding territories per HUC8 watershed based on an unpublished draft conservation plan being developed for the species in California (H. Loffland unpublished data). We adopted these objectives as our short-term (10-year) population size objective, refined to include only the watersheds within each of our 4 planning regions, and doubled to convert the number of breeding territories to a total population size. We then defined long-term population size objectives as 10x the improvement from current population size estimates required to meet the short-term objective. Finally, we calculated the corresponding short-term and long-term breeding density objectives as the population size objective divided by the total area of meadows in each region.

RESULTS

Meadow Habitat and Focal Species

Across the four planning regions, we estimated a current total of 68,494 ha (169,252 ac) of meadows after excluding polygons that were either outside of planning region boundaries (n=1759 meadow polygons, 33,257.6 ha total area, average elevation = 2,340.0 m), smaller than 0.61 ha (1.5 ac), or at very high or low elevations, defined as having a monthly average high temperature in June 2020 of >31 or <14.5°C (Table 1). The remaining meadow habitat area was distributed relatively evenly across the four planning regions, although the average size and elevation of meadows differ substantially. In the northern planning regions (Cascades and Northern Sierra), meadows tend to be larger, less numerous, and occur at lower elevations, while in the southern planning regions (Central Sierra and Southern Sierra), meadows tend to be smaller, more numerous, and occur at higher elevations. As a result of their smaller size on average, the meadows in the Central Sierra and Southern Sierra planning regions also tend to have a smaller proportion of their area in the interior zone, more than 20 meters from any polygon boundary.

We found that each focal species was associated with a unique combination of model covariates, but that some general patterns across all focal species were evident (Table S1). For example, associations with specific meadow zones were strong across most of the focal species. Song Sparrow, Yellow Warbler, Lincoln’s Sparrow, Wilson’s Snipe, Calliope Hummingbird, and Willow Flycatcher were all expected to have higher breeding densities in meadow interiors relative to edge, fringe, or exterior zones, whereas Warbling Vireo and Wilson’s Warbler preferred edge, fringe, and exterior zones over meadow interiors. Red-breasted Sapsucker was unique in preferring fringe only, and MacGillivray’s Warbler had no association with any of the meadow zones. Most species also had a positive association with the June monthly average maximum temperature, indicating a preference for warmer, lower elevation meadows. The exceptions to this pattern were found in Lincoln’s Sparrow and Wilson’s Warbler, which preferred cooler, higher elevation meadows, and Wilson’s Snipe and Willow Flycatcher, for which we found no strong relationship. Most species were also positively associated with one or more of the vegetation indices, including NDWI, ladder fuel density, and canopy bulk density, indicating that meadow focal species densities increased with woody vegetation cover and/or vegetation productivity. The exception to this pattern was Wilson’s Snipe, which were more associated with wet, open, and sparsely vegetated locations.

Relationships with many of the other covariates were mixed or important to only a few species. Climatic water deficit, the variable we used as a proxy for drought conditions, had a strong relationship with only three species: Yellow Warbler and Wilson's Snipe densities had negative relationships with CWD, indicating a preference for wetter climate conditions, and Wilson's Warbler had a positive relationship. Eight out of the ten focal species were associated with one or both of meadow catchment area and meadow patch area, but the direction of associations was very mixed, including often different directions for catchment and patch area. Five of the ten species had strong associations with the planning regions, indicating a geographical distribution pattern that we expect is generally consistent with a latitudinal driven pattern. The vegetation majority variable from the Meadows Layer was only important for two species, Lincoln's Sparrow and Wilson's Snipe.

Breeding Densities, Population Sizes, and Trends

Extrapolating regional average density estimates (Table 4A) across the meadow area in each region, breeding size population estimates ranged from 45,551 (95% CI: 34,111–61,405) for Lincoln's Sparrow in the Central Sierra region to as low as 20 (0–91) for Wilson's Snipe in the Southern Sierra region (Table 5A). Our model-predicted regional estimates for Willow Flycatcher were 580 (170–1,390), 440 (190–890), 0 (0–20), and 20 (0–60), from north to south, respectively. However, because of the timing of this species' migration through the Sierra, which is far later than any of the other meadow birds we evaluated here, and the relatively large number of migrants compared to local breeders, the number of detections during point count surveys conducted in late May through June may be strongly influenced by migrants breeding farther north of our study area. Thus, we considered our model-based estimates of the regional Willow Flycatcher population sizes as likely to be overestimates of the true local breeding population sizes, and we instead adopted estimates from the most recent, comprehensive assessment of Willow Flycatcher available (Loffland et al. 2014). After aligning their estimates to our planning regions, we estimated from north to south, respectively, a total of 30, 110, 2 and 8 breeding territories, for a total population size of 60, 220, 4, and 16 birds (shown rounded to the nearest 10 birds in Table 5A).

Based on trend estimates from Breeding Bird Survey data in the Sierra Nevada Bird Conservation Region (BCR-15), none of these 10 focal species have a significant, long-term increasing population trend over the period 1968–2019, and only Wilson's Warbler had a significant declining trend (Table S2; Sauer et al. 2020). However, the long-term average rate of decline was not sufficient to meet the criteria for a *steeply declining* population (>30% decline over 10 years). In comparison, based on the coefficient for the year variable in our own models of breeding density, most species had a negative coefficient, indicating a declining trend over the 12 years of surveys included in our data set (2010–2021). However, only four species had significant negative trends, including Yellow Warbler, Red-breasted Sapsucker, Warbling Vireo, and MacGillivray's Warbler, but not Wilson's Warbler, and none of these declines were sufficient to meet the criteria for a *steeply declining* population. In addition, we identified a significant positive year coefficient for Lincoln's Sparrow, indicating the potential for an increasing trend for this species.

Neither the Breeding Bird Survey nor our own models identified a significant trend for Willow Flycatcher. Relying instead on the estimated 33% decline in the number of breeding sites with Willow Flycatcher detected over 13 years, 2000–2013 (Loffland et al. 2014) and supporting data of localized declines at multi-year study sites (Mathewson et al. 2012, Loffland et al. 2022), we assumed the long-term Willow Flycatcher population trend met the criteria for a *steeply declining* population.

Table 4. Regional breeding density estimates (individuals / ha) and density objectives. Current density estimates are derived from hierarchical distance sampling models, except for Willow Flycatcher (WIFL) estimates, which are derived from Loffland et al. (2014) population size estimates.

Species	Cascades	Northern Sierra	Central Sierra	Southern Sierra
(A) Current estimates of breeding density (individuals / ha)				
LISP	0.119 (0.085–0.163)	0.712 (0.546–0.925)	2.684 (2.010–3.618)	1.517 (1.118–2.059)
SOSP	0.457 (0.368–0.558)	1.312 (1.147–1.490)	0.374 (0.308–0.448)	0.124 (0.083–0.174)
YEWA	0.124 (0.092–0.161)	0.297 (0.249–0.349)	0.101 (0.078–0.129)	0.085 (0.057–0.120)
MGWA	0.042 (0.026–0.066)	0.172 (0.112–0.252)	0.151 (0.090–0.216)	0.078 (0.043–0.118)
CAHU	0.066 (0.031–0.120)	0.270 (0.162–0.423)	0.045 (0.020– 0.084)	0.026 (0.005–0.067)
WAVI	0.059 (0.043–0.079)	0.241 (0.194–0.294)	0.160 (0.125–0.203)	0.058 (0.041–0.080)
WIWA	0.012 (0.007–0.020)	0.286 (0.180–0.487)	0.128 (0.076–0.235)	0.053 (0.029–0.105)
WISN	0.069 (0.024–0.159)	0.030 (0.015–0.057)	0.003 (0.001–0.008)	0.001 (0.000–0.006)
RBSA	0.029 (0.016–0.048)	0.028 (0.017–0.045)	0.022 (0.013–0.039)	0.015 (0.005–0.030)
WIFL	0.004	0.010	0.000	0.001
(B) Short-term (10-year) density objectives (individuals / ha)				
LISP	0.204	0.949	2.876	1.741
SOSP	0.479	1.357	0.395	0.129
YEWA	0.133	0.313	0.107	0.090
MGWA	0.052	0.201	0.167	0.089
CAHU	0.070	0.289	0.048	0.027
WAVI	0.074	0.283	0.172	0.066
WIWA	0.016	0.354	0.138	0.060
WISN	0.073	0.032	0.003	0.002
RBSA	0.034	0.031	0.024	0.016
WIFL	0.029	0.028	0.015	0.010
(C) Long-term (100-year) density objectives (individuals / ha)				
LISP	0.967	3.084	4.607	3.753
SOSP	0.678	1.764	0.589	0.172
YEWA	0.211	0.459	0.164	0.132
MGWA	0.145	0.459	0.306	0.185
CAHU	0.113	0.459	0.078	0.042
WAVI	0.207	0.664	0.283	0.134
WIWA	0.052	0.965	0.226	0.123
WISN	0.107	0.050	0.006	0.003
RBSA	0.075	0.062	0.040	0.030
WIFL	0.256	0.185	0.147	0.092

Table 5. Regional population size estimates and population size objectives. All estimates are rounded to the nearest 10 individuals. Current estimates are derived from hierarchical distance sampling models, except for Willow Flycatcher (WIFL) estimates, which are derived from Loffland et al. (2014).

Species	Cascades	Northern Sierra	Central Sierra	Southern Sierra
(A) Current estimated population size				
LISP	1,840 (1,320–2,510)	15,500 (11,890–20,130)	45,550 (34,110–61,410)	21,710 (16,000–29,470)
SOSP	7,050 (5,680–8,620)	28,550 (24,960–32,440)	6,340 (5,220–7,610)	1,780 (1,190–2,490)
YEWA	1,920 (1,420–2,480)	6,460 (5,420–7,600)	1,710 (1,330–2,180)	1,220 (820–1,710)
MGWA	650 (410–1,020)	3,750 (2,430–5,480)	2,560 (1,540–3,670)	1,120 (620–1,680)
CAHU	1,010 (480–1,860)	5,880 (3,520–9,210)	760 (340–1,430)	370 (80–960)
WAVI	920 (660–1,220)	5,250 (4,239–6,400)	2,720 (2,120–3,450)	840 (590–1,150)
WIWA	180 (110–320)	6,230 (3,930–10,600)	2,170 (1,290–3,980)	760 (410–1,500)
WISN	1,070 (370–2,460)	650 (320–1,240)	50 (10–130)	20 (0–90)
RBSA	450 (250–750)	600 (370–970)	380 (220–660)	210 (80–430)
WIFL	60	220	0	20
(B) Short-term (10-year) population size objectives				
LISP	3,150	20,660	48,820	24,910
SOSP	7,390	29,530	6,710	1,850
YEWA	2,050	6,820	1,820	1,280
MGWA	810	4,370	2,830	1,270
CAHU	1,080	6,290	820	390
WAVI	1,140	6,170	2,930	940
WIWA	240	7,710	2,340	860
WISN	1,130	700	50	20
RBSA	520	680	410	240
WIFL	450	600	250	150
(C) Long-term (100-year) population size objectives				
LISP	14,940	67,120	78,200	53,710
SOSP	10,470	38,390	10,000	2,470
YEWA	3,250	10,000	2,790	1,880
MGWA	2,230	10,000	5,200	2,650
CAHU	1,740	10,000	1,320	600
WAVI	3,190	14,460	4,800	1,920
WIWA	800	21,010	3,830	1,760
WISN	1,660	1,080	100	40
RBSA	1,150	1,350	680	430
WIFL	3,960	4,020	2,500	1,320

Current Population Status

Fitting these population size and trend estimates into the population status framework (Table 3), we estimated that zero regional populations are currently *large* (>50,000 individuals) and only four are currently *viable* (>10,000), while 90% (36 of 40) are *small* or *very small* (Figure 2A). Lincoln's Sparrow was the only focal species we considered *resilient*, with more than one *viable* regional population, and we considered Willow Flycatcher to be *steeply declining*. Examining focal species status collectively by region, we estimated meadows in the Northern Sierra planning region to be in the best condition overall, supporting the most *viable* populations and the fewest *very small* populations.

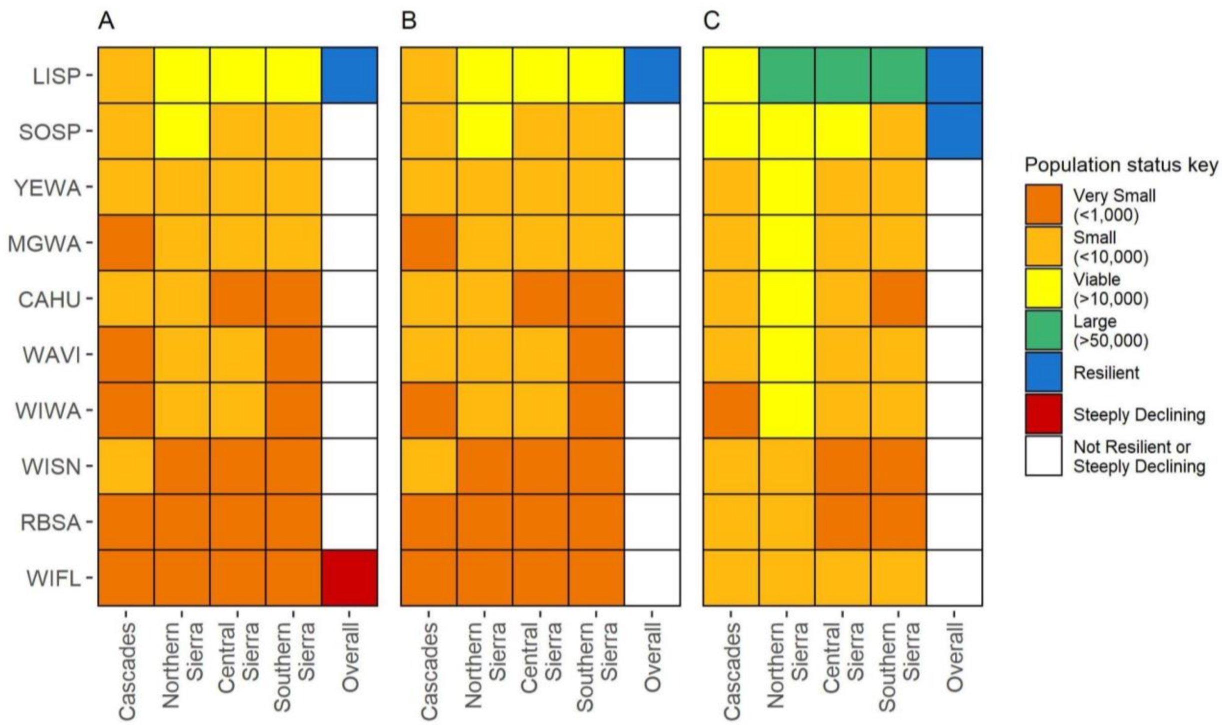

Figure 2. Regional population status for each focal species. (A) Current population status. (B) Projected population status if short-term (10-year) density objectives are met. (C) Projected population status if long-term (100-year) density objectives are met. (See Table 3 for details.)

Conservation Objectives

Excluding Willow Flycatcher, the long-term (100-year) objectives for breeding densities in Sierra meadows generally represent only modest increases over the current regional averages for each focal species (Table 4C). By limiting the long-term density objectives to fall within the range of objectives currently projected for meadows in each region, we sought to ensure the density objectives were feasible, but they may underestimate the densities that can be achieved in high quality habitat. The corresponding long-term population size objectives therefore also represent modest increases over the current regional population sizes (Table 5C) and may underestimate the population sizes that can be achieved over the long-term. As milestones for achieving the long-term objectives within a 100-year time frame, we set short-term (10-year) density objectives for each region equal to 10% of the improvement required to reach the long-term density objectives (Tables 4B, 5C).

For Willow Flycatcher, we applied territory objectives for HUC8 watersheds that are being developed as part of a conservation plan for this species for California (H. Loffland, unpublished data) to define short-term population size objectives for Willow Flycatcher as: 450 breeding adults for the Cascades planning region (including the McCloud, Upper Pit, Lower Pit, Battle Creek, Lost, and Sacramento Headwaters watersheds); 600 for the Northern Sierra planning region (including the North Fork and Middle Fork Feather, East Branch North Fork Feather, Upper Yuba, Big Chico Creek-Sacramento River, Thomes Creek-Sacramento River, Butte Creek, and North and South Fork American watersheds); 250 for the Central Sierra planning region (including the Upper Tuolumne, Upper Stanislaus, Upper Mokelumne, Upper Merced, and Upper San Joaquin watersheds); and 150 for the Southern Sierra planning region (including the Upper King, Upper Kern, and South Fork Kern watersheds; Table 5B). Extrapolating the rate of change required to reach these short-term objectives over 10 years, we then defined long-term (100-year) population size objectives as 3,960 for the Cascades planning region, 4,020 for the Northern Sierra, 2,500 for the Central Sierra, and 1,320 for the Southern Sierra.

Assuming no further losses or degradation of currently existing meadow extent, and meadow restoration and enhancement improves average regional breeding densities to meet the short-term density and population objectives, we anticipate the transition of 1 *very small* regional population to *small* within 10 years (Warbling Vireo in the Cascades planning region; Figure 2B). With further restoration and enhancement to meet the long-term density and population objectives, we anticipate the transition of another 11 *very small* populations to *small*, 8 *small* populations to *viable*, and 3 *viable* populations to *large*, for an increase in the proportion of regional populations that are at least *viable* from 0.1 (4/40) to 0.3 (12/40) and increase from 1 to 2 focal species considered *resilient* (Figure 2C).

DISCUSSION

Birds have been identified as excellent indicators of ecosystem condition in many landscapes, and the Central Valley Joint Venture has defined population size and density objectives for focal bird species to help estimate the magnitude of conservation effort required to achieve long-term conservation goals and track progress toward achieving these goals (CVJV 2020, Dybala et al. 2017b, Strum et al. 2017, DiGaudio et al. 2017). Here, for the first time, we have extended this approach to Sierra meadows, where birds have been identified as a priority target as part of the multi-benefit approach to meadow restoration and conservation. We have established conservation planning regions, defined a set of focal species that are associated with a wide range of meadow characteristics across those regions, and we have adapted the same general framework (Dybala et al. 2017a) used for other ecosystems and taxa in a transparent, science-based process to develop regional population and density objectives for each focal species.

In this application of the framework, our conservation objectives were constrained by the assumptions that no new meadow area could be added to any of the planning regions and that, for the long-term density objectives to be feasible, they must fall within the range of densities currently projected for Sierra meadows. Consequently, our objectives were driven primarily by this range of current density estimates rather than the desired long-term population status, resulting in more modest projected outcomes (Figure 2C) than those developed for other taxa (Dybala et al. 2017b, Strum et al. 2017, DiGaudio et al. 2017). Thus, our application of the framework primarily provides insights into our current assessment of the long-term population status that may be feasible to achieve, whereas the framework was initially intended to help define long-term population objectives of an appropriate order of magnitude for achieving long-term population status goals (Dybala et al. 2017a). However, we emphasize that our assumptions in this assessment may be overly conservative; there are several limitations in the available data, described further below, that suggest we are currently underestimating the population size and status of most focal species. While the conservation objectives defined here represent the current best available science, we recommend that these objectives be revised as new information becomes available, just as is recommended for all of the other conservation objectives that have been established by the CVJV (CVJV 2020).

We anticipate that protecting, restoring, and managing Sierra meadows will increase the average breeding densities and population sizes of these focal species, reflecting progress toward a network of Sierra meadows capable of supporting a diverse, self-sustaining, and resilient bird community. Simultaneously, we expect these efforts will also restore and preserve the multiple ecological benefits healthy meadows afford, including well beyond the meadow boundaries to downstream water users in the Central Valley. For example, these may include increased water storage capacity, attenuated peak flows, increased base flows, and improved water quality (DeLaney 1995, Woltemade 2000, Hammersmark et al. 2008), all of which can benefit fish, wildlife, and human communities downstream and in and around these meadows. Meadow restoration and conservation have been a priority in the Sierra Nevada and southern Cascades of California for more than a decade with federal, state, tribal, and private entities collaborating to increase the pace and scale of restoration and conservation of these important areas (Drew et al. 2016). By establishing these conservation objectives for birds, we aim to support these collaborative efforts and provide a means by which progress toward long-term conservation goals can be measured.

Strategies for Restoring & Protecting Sierra Meadows

To enhance the rate and magnitude of bird population increases, efforts to restore meadows for multiple benefits should intentionally incorporate these conservation objectives into their project objectives and incorporate the specific needs of individual bird species into their restoration designs (Campos et al. 2014, Gardali et al. 2021). Habitat associations are well known for each of these species and can be used as an aid in prioritizing meadows for restoration and guiding restoration design elements (Campos et al. 2014). Without attention to these specific elements, improvements in local breeding density and abundance may be slow or negligible: a recent evaluation of the response of birds to meadow restoration found only 5 of the 10 species we developed targets for here had a significantly increasing trend at restored meadows, even up to 18 years after restoration (Campos et al. 2020). To increase the benefits of meadow restoration for focal species, they recommended: active planting of dense clumps of riparian deciduous shrubs (e.g., willows), protection of those shrubs from herbivory, and prioritizing restoration sites based on proximity to established stable or increasing populations. This last recommendation may be especially important for those species with very small populations that are patchily distributed such as Willow Flycatcher (Loffland et al. 2014, Loffland et al. 2022).

Willow Flycatcher have received considerable conservation attention since their listing as endangered under the California Endangered Species Act in 1988, including a draft conservation strategy being developed to aid their recovery. We relied heavily on previous efforts to quantify the population of this now very rare, endangered bird (Loffland et al. 2014). Unfortunately, the most recent assessment of their population found precipitous declines in the number of sites occupied by this species including near extirpation from the central and southern Sierra planning regions. At this rate of decline, a redoubling of efforts may be required to save this species from extinction in the Sierra and southern Cascades in the next 20 years. Loffland et al. (2014), and a unpublished draft Conservation Plan (Schofield et al. in review), outlined detailed measures to save this species from extinction in the region, including active restoration of meadows within the known dispersal distance of currently occupied breeding sites to a very wet condition, with dense stringers of willow covering at least 20% of the meadow area, and limiting livestock grazing in occupied sites and historically occupied sites. Another recent report found a strong relationship between Willow Flycatcher occupancy and beaver activity (Campos et al. 2019). Restoration actions that encourage the occupancy of beavers, including potentially re-introducing them into meadows and/or watersheds where they have been extirpated is likely to result in habitat modifications preferred by this imperiled species. In addition, more resources are needed to increase surveillance of this endangered species to track progress towards its recovery and adaptively manage meadows to recover their populations.

We assumed no net loss of meadow habitat in setting our conservation objectives. However, many meadows in our study area are privately owned and at risk of conversion to a land use that could result in reductions in breeding densities and population sizes, easily eroding population gains from restoration actions. Thus, land conservation is an important component of maintaining the current extent of meadow habitat. In addition, it is our experience that land acquisitions and easements often lead to restorative actions in these meadows, which may further contribute to achieving these conservation objectives. Land conservation should not be overlooked as an important strategy for meeting meadow conservation goals.

Monitoring Progress

Making progress toward the population and density objectives for these species will inform the need for course corrections and guide adaptive management of conservation and restoration efforts, require region-wide monitoring to track progress towards the objectives, and help understand how climate change (including drought and wildfire) is interacting with conservation efforts to affect meadow condition and population sizes. For example, climate warming may be impacting the suitability of high elevation meadows for some species and the extent of meadow habitat that is available to them during the breeding season. In addition, because the total area and average size of meadows differs substantially among the four planning regions, along with landscape position, topography, elevation, and other ecological conditions, management and restoration strategies may need to be tailored to address differing environmental stressors and anthropogenic influences in each region. Thus, continuation of existing broad scale monitoring of meadows across the study area (e.g., Roberts et al. 2011) will be essential to meeting this need, as well as increased coverage of the highest elevation meadows, which are not adequately sampled now. Although very high elevation meadows may be covered by snowpack during most breeding seasons, during drier years, they may contribute substantially to the breeding habitat available for some species and may become increasingly suitable breeding habitat for more species with warming temperatures and more frequent drought conditions under climate change.

In addition to region-wide monitoring, effectiveness monitoring of individual projects can quantify the magnitude and rates of change in species densities and abundances, whether they are on track to meet the short-term and long-term density objectives within 10 and 100 years, respectively, and estimate the contribution of individual projects toward meeting the population objectives. These data can also be used to evaluate and compare the efficacy of meadow restoration and management approaches between sites, contributing to the development of improved recommendations for restoration design and strategies for effective management. Finally, these data would help refine long-term density and population size objectives. Our density objectives represent hypotheses for densities that can be achieved in high-quality habitat, but they are based on the range of densities projected for individual meadows from our analyses. If we have not yet conducted surveys within areas that are truly optimal habitat, then we may have not yet observed the full range of densities that are possible, and the density and corresponding population size objectives may be set too low. Alternatively, if the density objectives prove to be unreasonably high for some species, such as due to future impacts of climate change, the density and population objectives may need to be revised downward.

Research Needs

Our estimates of population size and density represent our interpretation of the best available data, collected throughout all four planning regions at meadows with a wide range of physical characteristics and conditions. However, for several reasons, we assumed that our population size estimates are underestimates of the true population sizes. Where information was lacking or highly uncertain, we chose to err on the side of underestimating population sizes. Here, we identify several limitations with the available data, and highlight research needs that would improve these estimates and help refine these conservation objectives.

First, the Meadows Layer we relied on throughout these analyses has made it possible to assess the distribution of this uncommon but important habitat type, and to evaluate numerous ecological and management questions surrounding meadow habitat and species. However, a mismatch between the methods used to delineate meadow polygons and the methods used to select bird survey points highlighted variation in the ways meadows are defined for different purposes. In particular, areas within meadows that feature dense woody vegetation such as willows and alders may be excluded from the Meadows Layer even while they provide important habitat to many meadow-associated bird species. Although we were able to estimate species densities in the fringe and exterior zones outside of the polygons in the Meadows Layer, the total additional area of meadow habitat available to birds but excluded by the meadow polygons was highly uncertain, and we did not incorporate these areas in our population size estimates. Thus, the total extent of meadow habitat available to birds in each planning region is likely to be higher than is currently represented by the Meadows Layer, contributing to an underestimate of the current population size and status of the focal species and an underestimate of the population sizes that can be supported by Sierra meadows in the long-term. In addition, some of the bird survey points may currently be located in areas that were once open meadows but have since become encroached by conifers. Although we assumed there was little capacity to add to the current extent of meadow habitat throughout the study area, it is possible that some conifer-encroached areas could be restored to open meadow once again. However, without a thorough evaluation of the extent of these areas, it was difficult to assess their potential for contributing to population size objectives. Instead, we assumed they would not contribute, and therefore we may have further underestimated the population sizes that can be supported in the long-term.

Second, our population sizes are likely to be underestimated because we had to remove some polygons within the Meadows Layer that were not well represented in our field samples, including very small meadows (<1.5 acres), and very high and low elevation meadows. For example, Lincoln's Sparrow had an affinity with high elevation meadows, such that excluding these meadows from our calculations is likely to have reduced our estimates of breeding population size. Similarly, there were several species for which breeding densities were expected to be higher in smaller meadow polygons, including Song Sparrow, Yellow Warbler, Warbling Vireo, and Lincoln's Sparrow, such that excluding the smallest meadows from our analysis may have contributed to an underestimate of their population sizes. However, the total area of these very small meadows is relatively small (<5,000 acres) and unlikely to be a large source of error in our population size estimates. In addition, the related covariate meadow catchment area is likely to be a more informative indicator of true meadow size than the area of individual meadow polygons because the Meadows Layer frequently subdivided contiguous meadows into several discrete polygons. Indeed, the focal species associations with catchment area better reflected our field experience, the results of prior analyses, and our understanding of these species' life histories.

Third, the protocols used to survey birds throughout the study area did not include identification of the sex of each individual detected, but during the breeding season, it is likely that a majority of detections were from territorial males that are more likely to be singing, calling, or visible in the field than females on nests. Although the detectability of females is likely to vary by species, we recognize that our density estimates are likely to primarily represent the density of males and under-represent females. Therefore, while we assume our density and population size estimates are highly correlated with true population density and size, we recognize they may be underestimated. We included in our analyses all detections of all individuals for each of these focal species, but an alternative approach that could be used in future analyses would be to include only detections of singing males, as an indicator of the density of active breeding territories.

Finally, we also recognize that these focal species are not strictly limited to breeding in meadows and that their biological population boundaries may not be aligned with our planning region boundaries. For example, several of the focal species exhibited a preference for meadow edge or fringe zones (which tend to have more shrub cover and are in closer proximity to conifer tree cover) over meadow interiors (which are often wetter and contain less woody vegetation), including Warbling Vireo, Wilson's Warbler, and Red-breasted Sapsucker. In addition, while these species are expected to reach their greatest breeding densities in and around meadows, several are also likely to use other vegetation types (e.g., montane riparian, mesic montane chaparral), supplementing our estimates of their population size in meadows by an unknown amount. While there is also likely to be some connectivity and movement between our planning regions and beyond (e.g., east of the Sierra Nevada crest), further contributing to gene flow and population sizes by an unknown amount, a recent study identified apparently separate populations of Swainson's Thrush with distinct migration routes despite breeding as close as 60 miles apart in the Sierra (Humple et al. 2020), supporting the idea that the study area may support multiple biologically-distinct breeding populations. Thus, we restricted our population size estimates to meadows themselves, and defined conservation objectives designed to improve the capacity of Sierra meadows within each planning region to support diverse, self-sustaining, and resilient populations.

CONCLUSIONS

While meadows have only a small footprint within the Sierra, when they are intact and properly functioning, they can support high densities of meadow birds as well as provide multiple benefits to other wildlife species and human communities within, nearby, and downstream. Meadow degradation has likely resulted in substantial declines of most meadow bird species, and we found that most focal species currently have *small* or *very small* regional populations within meadows and that Willow Flycatcher, a California endangered species, is *steeply declining.* While meadows may represent only a portion of these species' populations in the Sierra, for most, their densities are greatest in meadows and meadows are likely to provide important refugia for these species in a warmer, drier future. Thus, increasing meadow habitat quality for these species is likely to be critical to the long-term persistence of these species, even if the meadows in each planning region may not be able to support viable populations on their own. Protecting and restoring meadows to reach the conservation objectives defined here will help restore meadow health, benefits to human communities, and improve the long-term viability and resilience of these species in the face of accelerating environmental change.

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SUPPLEMENTARY MATERIAL

Table S1. Results of hierarchical distance sampling model fitting for each focal species. Values listed are the mean of posterior distributions for each covariate, shown with standard deviations (in parentheses). Statistically significant coefficients are shown in bold, assessed as whether the mean +/- 2 standard deviations includes 0.0.

	LISP	SOSP	YEWA	MGWA	CAHU	WAVI	WIWA	WISN	RBSA	WIFL
intercept	-1.38 (0.513)	-0.53 (0.584)	-1.28 (0.62)	-2.093 (0.369)	-2.616 (0.738)	-2.025 (0.45)	-2.748 (0.579)	-4.573 (0.931)	-3.254 (0.317)	-5.578 (1.243)
zone: edge	**-0.282 (0.057)**	**-0.326 (0.047)**	**-0.215 (0.059)**	0.006 (0.067)	**-0.543 (0.167)**	**0.243 (0.06)**	**0.292 (0.072)**	**-0.68 (0.296)**	-0.21 (0.166)	-0.076 (0.238)
zone: fringe	**-0.295 (0.077)**	**-0.553 (0.047)**	**-0.323 (0.061)**	-0.025 (0.08)	**-0.861 (0.192)**	**0.317 (0.071)**	**0.237 (0.087)**	**-1.302 (0.487)**	**0.327 (0.145)**	-0.301 (0.282)
zone: exterior	**-0.281 (0.092)**	**-0.442 (0.045)**	**-0.232 (0.058)**	-0.039 (0.068)	**-0.89 (0.161)**	**0.363 (0.067)**	**0.239 (0.075)**	-2.875 (0.602)	-0.096 (0.13)	**-1.042 (0.356)**
June monthly avg max temp	**-0.652 (0.042)**	**0.246 (0.021)**	**0.328 (0.026)**	**0.354 (0.039)**	**0.343 (0.067)**	**0.06 (0.03)**	**-0.182 (0.037)**	0.123 (0.105)	**0.24 (0.047)**	0.254 (0.128)
June monthly avg max temp^2	**-0.28 (0.025)**	**-0.054 (0.011)**	**-0.069 (0.014)**	**-0.097 (0.02)**	0.021 (0.033)	**-0.103 (0.016)**	**-0.047 (0.02)**	-0.073 (0.058)	-0.001 (0.022)	**-0.183 (0.071)**
slope	-0.003 (0.027)	-0.184 (0.017)	**-0.146 (0.02)**	**0.271 (0.022)**	0.093 (0.052)	**0.057 (0.02)**	**0.1 (0.022)**	**-0.456 (0.132)**	**0.225 (0.048)**	-0.211 (0.111)
climatic water deficit (CWD)	0.062 (0.035)	-0.028 (0.014)	**-0.094 (0.016)**	-0.041 (0.029)	-0.094 (0.059)	0.045 (0.025)	0.105 (0.027)	-0.156 (0.077)	0.081 (0.044)	-0.172 (0.091)
NDWI	**0.352 (0.027)**	**0.173 (0.014)**	**0.186 (0.017)**	**0.288 (0.028)**	0.076 (0.055)	**0.417 (0.024)**	**0.359 (0.024)**	**0.465 (0.079)**	**0.317 (0.052)**	**0.564 (0.1)**
ladder fuel	-0.058 (0.056)	**0.095 (0.029)**	**0.201 (0.029)**	0.287 (0.191)	-0.055 (0.099)	**0.091 (0.028)**	**0.395 (0.132)**	**-1.464 (0.231)**	**0.295 (0.062)**	-0.04 (0.137)
canopy bulk density	0.003 (0.028)	**0.135 (0.017)**	**0.225 (0.02)**	**0.32 (0.027)**	**0.514 (0.047)**	**0.181 (0.021)**	**0.236 (0.02)**	-0.114 (0.151)	**0.34 (0.046)**	0.079 (0.108)
year	**0.168 (0.032)**	-0.009 (0.016)	**-0.285 (0.021)**	**-0.081 (0.03)**	0.077 (0.066)	**-0.075 (0.026)**	0.039 (0.032)	-0.041 (0.091)	**-0.278 (0.058)**	-0.23 (0.101)
year^2	**-0.143 (0.026)**	**0.037 (0.015)**	**0.046 (0.022)**	**0.186 (0.028)**	-0.052 (0.058)	**0.126 (0.023)**	-0.014 (0.035)	**0.142 (0.082)**	-0.04 (0.051)	0.082 (0.097)
meadow catchment area	**-0.953 (0.08)**	**0.297 (0.019)**	**0.46 (0.022)**	**-0.363 (0.051)**	**-0.424 (0.102)**	**-0.193 (0.043)**	**-0.228 (0.042)**	0.11 (0.111)	-0.082 (0.08)	**0.259 (0.11)**
meadow polygon area	**-0.339 (0.08)**	**-0.311 (0.017)**	**-0.258 (0.022)**	**0.115 (0.042)**	**0.356 (0.061)**	**-0.093 (0.042)**	**0.126 (0.052)**	-0.005 (0.076)	-0.006 (0.083)	0.089 (0.092)
planning region (random effect)	0.483 (0.291)	**1.056 (0.459)**	0.777 (0.401)	0.478 (0.283)	**1.147 (0.553)**	**0.763 (0.381)**	**1.086 (0.484)**	1.315 (0.747)	0.539 (0.292)	**2.099 (0.917)**
vegetation type (random effect)	**0.73 (0.379)**	0.458 (0.291)	0.653 (0.353)	0.423 (0.243)	0.386 (0.25)	0.477 (0.415)	0.378 (0.325)	**0.965 (0.465)**	0.602 (0.448)	1.134 (0.626)

Table S2. Breeding Bird Survey population trend estimates (1968-2019) for the Sierra Nevada Bird Conservation Region (BCR-15). Trends are shown as both the annual growth rate (AGR; % with 95% CI) extracted from Sauer et al. (2020), and the corresponding cumulative change over 10 years, calculated as: $((1 + AGR/100)^{10} - 1) * 100$. Statistically significant trends are shown in bold, assessed as confidence intervals not overlapping zero.

	Annual growth rate (%), 1968 – 2019	**Cumulative change over 10 years (%)**
LISP	0.55 (-1.65 – 2.92)	5.6 (-15.3 – 33.3)
SOSP	0.72 (-0.22 – 1.86)	7.4 (-2.2 – 20.2)
YEWA	-0.53 (-1.71 – 0.73)	-5.2 (-15.8 – 7.5)
MGWA	0.71 (-0.45 – 1.90)	7.3 (-4.4 – 20.7)
CAHU	0.71 (-1.25 – 2.92)	7.3 (-11.8 – 33.4)
WAVI	0.02 (-0.97 – 1.09)	0.2 (-9.3 – 11.5)
WIWA	-2.05 (-3.80 – -0.16)	-18.7 (-32.1 – -1.6)
WISN	-1.38 (-3.69 – 0.88)	-13.0 (-31.3 – 9.2)
RBSA	-1.09 (-2.59 – 0.40)	-10.4 (-23.1 – 4.1)
WIFL*	-1.28 (-3.70 – 0.71)	-12.1 (-31.4 – 7.3)

*Combined trend with Alder Flycatcher

Figure S1. For each focal species and region, comparison of the range of density estimates predicted across all meadows (box and whiskers), the current regional average density estimate (blue point and error bar), the average densities required to reach *large* (green horizontal line) or *viable* (gold horizontal line) population sizes, and the long-term density objective (red star) as listed in Table 4C.