Ecological Applications, 25(1), 2015, pp. 39–51

Documenting stewardship responsibilities across the annual cycle for birds on U.S. public lands

Frank A. La Sorte,[1,3] Daniel Fink,[1] Wesley M. Hochachka,[1] Jocelyn L. Aycrigg,[2] Kenneth V. Rosenberg,[1] Amanda D. Rodewald,[1] Nicholas E. Bruns,[1] Andrew Farnsworth,[1] Brian L. Sullivan,[1] Chris Wood,[1] and Steve Kelling[1]

[1]*Cornell Laboratory of Ornithology, Cornell University, Ithaca, New York 14850 USA*
[2]*National Gap Analysis Program, Department of Fish and Wildlife Sciences, University of Idaho, Moscow, Idaho 83844 USA*

Abstract. In the face of global environmental change, the importance of protected areas in biological management and conservation is expected to grow. Birds have played an important role as biological indicators of the effectiveness of protected areas, but with little consideration given to where species occur outside the breeding season. We estimated weekly probability of occurrence for 308 bird species throughout the year within protected areas in the western contiguous USA using eBird occurrence data for the combined period 2004 to 2011. We classified species based on their annual patterns of occurrence on lands having intermediate conservation mandates (GAP status 2 and 3) administered by the Bureau of Land Management (BLM) and the United States Forest Service (USFS). We identified species having consistent annual association with one agency, and species whose associations across the annual cycle switched between agencies. BLM and USFS GAP status 2 and 3 lands contained low to moderate proportions of species occurrences, with proportions highest for species that occurred year-round or only during the summer. We identified two groups of species whose annual movements resulted in changes in stewardship responsibilities: (1) year-round species that occurred on USFS lands during the breeding season and BLM lands during the nonbreeding season; and (2) summer species that occurred on USFS lands during the breeding season and BLM lands during spring and autumn migration. Species that switched agencies had broad distributions, bred on high-elevation USFS lands, were not more likely to be identified as species of special management concern, and migrated short (year-round species) to long distances (summer species). Our findings suggest cooperative efforts that address the requirements of short-distance migratory species on GAP status 2 lands ($n = 20$ species) and GAP status 3 lands ($n = 24$) and long-distance migratory species on GAP status 2 lands ($n = 9$) would likely benefit their populations. Such efforts may prove especially relevant for species whose seasonal movements result in associations with different environments containing contrasting global change processes and management mandates.

Key words: birds; BLM; citizen science; cooperation; eBird; GAP status; North America; protected areas; seasonal migration; USFS.

Introduction

Protected areas serve as a cornerstone of conservation and management and continue to play critical roles in maintaining biological diversity and ecosystem services worldwide (Chape et al. 2008). The current global terrestrial protected-area coverage is ~13%, with an international goal of increasing the coverage to 17% by 2020 (Butchart et al. 2012). As human populations grow, and the drivers of global change such as land-use/land-cover change (Meyer and Turner 1992), climate change (Karl and Trenberth 2003), and species introductions (Vitousek et al. 1997) persist, protected areas are expected to grow in importance. Because establishing new protected areas can be challenging (Fairfax et al. 2005) and the long-term integrity of designated protected areas is not always certain (Mascia and Pailler 2011), many agencies and organizations are reevaluating management of existing protected areas as an alternative to land acquisition. Such an adaptive management strategy has the potential, if properly informed, to improve the effectiveness of existing protected areas, especially within the context of global environmental change where responsiveness and flexibility are likely to be key elements of successful long-term conservation efforts (Pressey et al. 2007, Hole et al. 2009, Bagchi et al. 2013).

Birds have long been used as indicators of ecological condition and biodiversity status within and outside of protected areas (Rodrigues et al. 2004, Pereira and Cooper 2006, Butchart et al. 2010), in part due to the availability of large amounts of high-quality data, and birds have played an important role in the development

Manuscript received 11 April 2014; accepted 23 May 2014. Corresponding Editor: R. L. Knight.
[3] E-mail: fal42@cornell.edu

of adaptive and cooperative management strategies among agencies and organizations. However, current assessments of conservation needs of birds are often constrained to the breeding season, a period of time when data are typically easier to acquire (Faaborg et al. 2010*a*). Yet the breeding season represents only a small proportion of the annual cycle of birds, especially for migratory species that may spend only a few weeks on the breeding grounds. Thus, to assess stewardship responsibilities for birds in a more comprehensive fashion, complete annual cycles (i.e., breeding, non-breeding, and migration) must be considered.

Another challenge facing stewardship organizations is that conservation responsibilities often transcend ownership and/or administrative jurisdictions of a single organization. Multiple organizations usually share responsibility for managing contiguous ecosystems, and often these organizations have disparate or even competing interests (Albers et al. 2008). The need for cooperation across organizations is particularly relevant for migratory bird species, which in North America display a broad range of migratory behaviors (Faaborg et al. 2010*b*).

The large stewardship role of federal agencies on public lands within the USA is particularly amenable to cooperative and adaptive management strategies (Scott et al. 2001, Aycrigg et al. 2013). Management of U.S. public lands varies among agencies with differing conservation and other land-use mandates. The Protected Areas Database of the United States (USGS-GAP 2012) has identified four general categories of protection status (GAP status). Here we focus our assessment on land parcels with intermediate conservation mandates (GAP status 2 or 3) that have the greatest likelihood of allowing changes in management practices by agencies; e.g., through the management of natural disturbance on GAP status 2 and 3 lands and the management of extractive uses on GAP status 3 lands (see Appendix A for definitions). These two categories provide a higher degree of flexibility for the implementation of management recommendations relative to GAP status 1 lands, where land is managed to maintain biodiversity, and GAP status 4 lands, which have no permanent protection. We further limit our assessment to GAP status 2 and 3 lands in the western portion of the contiguous USA administered by two agencies: Bureau of Land Management (BLM) and the United States Forest Service (USFS). The BLM administers primarily shrub, steppeland, and savanna systems at lower elevations located west of the 98th meridian, whereas the USFS administers primarily forest and woodland systems at higher elevations throughout the USA (Aycrigg et al. 2013). As 17% of all lands within the contiguous USA are under the stewardship of these two agencies, there is the opportunity to substantively affect conservation through the development of management recommendations on a large collection of lands already under public ownership (Aycrigg et al. 2013).

Here we use citizen-science data to assess ecological stewardship responsibilities over the complete annual cycle for 308 bird species occurring on GAP status 2 and 3 lands administered by the BLM and USFS west of the 98th meridian within the contiguous USA (Fig. 1). By focusing on the western portion of the contiguous USA, we examine stewardship responsibilities within a geographic region where, across the annual cycle, species with shared migration strategies (La Sorte et al. 2014) have opportunities to occur on lands administered by both agencies. Our aim is to develop a basis for understanding how changes in species' spatial associations with lands under different administrative and management mandates should inform broad-scale policy within and among agencies. Our goal is to identify opportunities, based on well-defined groups of species, in which interagency cooperation may be the most beneficial. Specifically, we identify species that occur consistently across the annual cycle on public lands administered by one agency, and species whose seasonal movements result in changes in stewardship responsibilities. Using weekly distributional estimates based on data from the eBird citizen-science database (Sullivan et al. 2014), we assess how ecological stewardship responsibilities, defined as a species' percentage total probability of occurrence on GAP status 2 and 3 lands administered by the BLM and USFS, change over time, and if there are groups of species with similar opportunities for interagency cooperation based on shared seasonal patterns. We would expect GAP status 3 lands, which have a lower protection mandate, but are much more numerous than GAP status 2 lands (Aycrigg et al. 2013), to play a more substantial stewardship role across the annual cycle. We would also expect, for both GAP status 2 and 3 lands, migratory species breeding in forested environments to switch between the higher-elevation USFS administered lands in the summer to the lower-elevation BLM administered lands in the winter. We test these predictions by summarizing geographic characteristics of species with shared stewardship relationships to determine which factors are the most relevant in defining each group. Finally, we develop recommendations for adapting management policies within these areas to provide the greatest overall benefits for avian populations in western North America.

Methods

Data sources

We use two primary data sources to assess spatio-temporal patterns of stewardship responsibilities within the western contiguous USA with fine spatial and temporal resolution. The data sources are information rich, making the identification and description of patterns challenging. By focusing on GAP status 2 and 3 lands administered by the BLM and USFS in the west, our study extent is simplified into four separate geographic regions of interest, which we identify as BLM 2, BLM 3, USFS 2, and USFS 3 (Fig. 1). Within

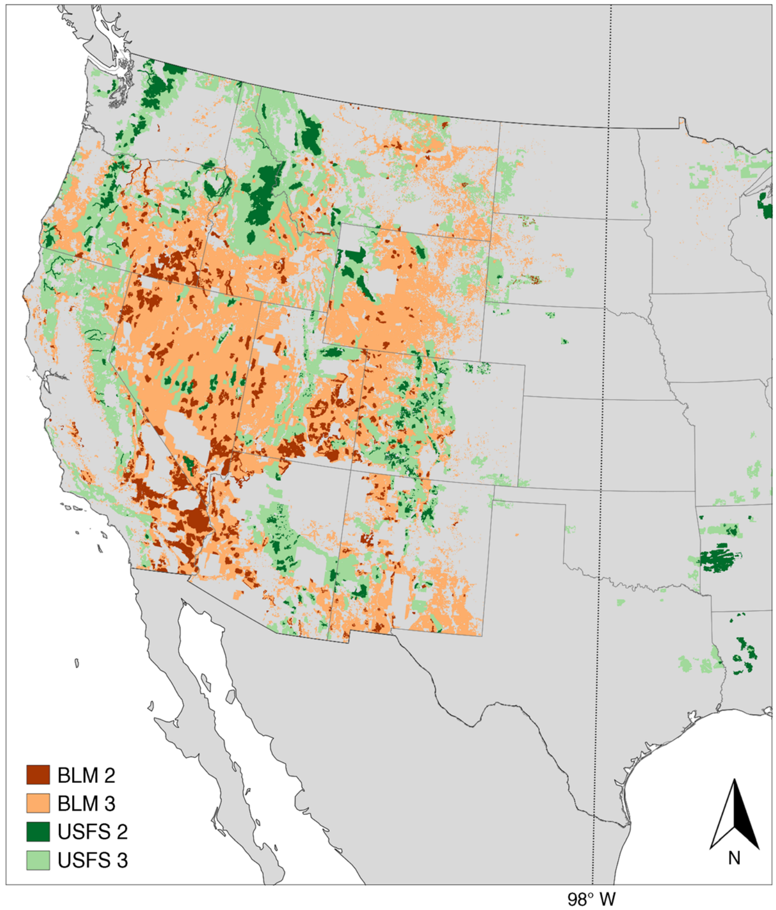

FIG. 1. GAP status 2 and 3 lands administered by the Bureau of Land Management (BLM) and the United States Forest Service (USFS) within the contiguous USA. The data is from the Protected Areas Database of the United States, version 1.3. The map projection is Albers equal area. Only lands located west of the 98th meridian were considered in the analysis.

these regions, our goal is to derive ecologically meaningful species groupings that can be used to identify opportunities for full life cycle conservation and management planning. We do this in three steps: first, we group species based on their overall seasonal patterns of occurrence within the geographic extent of the study area (Fig. 1). Within these groups, we then generate a parsimonious division of species into secondary groups that contain cohesive weekly stewardship trajectories on GAP status 2 lands administered by the BLM and the USFS, and GAP status 3 lands administered by the BLM and the USFS. Here the goal is to capture the main sources of variation in seasonal trajectories within GAP status 2 and GAP status 3 lands between the BLM and USFS, and to identify situations where geographic movements over the annual cycle may result in changes in stewardship responsibilities. Lastly, to support interpretation, we develop geographic descriptions of species within these secondary groups.

We estimated weekly probability of occurrence within the contiguous USA for 441 species of North American birds using spatiotemporal exploratory models (STEM; Fink et al. 2010) with occurrence information from the eBird citizen-science database (Sullivan et al. 2014). To represent species' distributions uniformly across the study area, STEM estimates of probability of occurrence were rendered at 933 688 points from a geographically stratified random design (SRD). The geographically stratified random points are distributed within a geographic coordinate system at a density of ~1 per 3 × 3 km area within the contiguous USA. From these points, we used 506 525 that were located west of the 98th meridian. For STEM analyses, we fit each model using complete eBird checklists that were collected under the "traveling count" and "stationary count" protocols from 1 January 2004 to 31 December 2011. We restricted data to those with transect distances ≤8.1 km, start times to daylight hours between 0500 and 2000, and with total search times to <3 hours.

STEM uses a multi-scale strategy to differentiate between local and global-scale spatiotemporal structure, which is achieved by creating a randomized ensemble of overlapping local models, each based on data from a restricted geographic and temporal extent (Fink et al. 2010). STEM learns the associations between observed patterns of bird occurrence (eBird data) and local land-cover characteristics (Fry et al. 2011). These models are then used to make estimates of each species' distribution throughout the year based on local land-cover characteristics. For each species, a separate model was fit, and species' probabilities of occurrence were estimated for single days at weekly intervals across the contiguous USA for all 52 weeks of a calendar year. Variation in detectability associated with the search effort for individual searches was controlled by assuming that all effort predictors (search time, transect length, time of day, number of observers, and protocol) were constant and additively associated with the true occupancy probability. The quantity we used to estimate species distributions is defined as the probability that a typical eBird participant will detect the species on a search from 0700 to 0800 while traveling 1 km on the given day at the given location. This quantity is a relative measure of species occupation.

Locations of protected areas within the contiguous USA were obtained from the Protected Areas Database of the United States (PAD-US), version 1.3 (USGS-GAP 2012). From the 87 686 uniquely identified land parcels in PAD-US, we limited our assessment to 1207 terrestrial land parcels (area $\sim 4.2 \times 10^5$ km^2) that were administered by the BLM or USFS west of the 98th meridian within the contiguous USA, that were assigned GAP status of 2 or 3, and contained >2 SRD points (Fig. 1).

Stewardship analysis

Our stewardship assessment documented variation in seasonal patterns of occurrence among species' core populations within and among land stewardship categories. To identify core populations, we first created probability thresholds to remove SRD points at which species had low probabilities of occurrence during a given week, and second, we created thresholds to remove weeks for which the species' probability of occurrence was very low. More specifically, for each species and week, we excluded SRD points with probabilities of occurrence that were below the 80% percentile of the distribution of probabilities of occurrence for that week. We then used weekly frequency of occurrence across all SRD points to identify and remove weeks with low numbers of points with probabilities of occurrence >0 (Appendix B: Fig. B1). Occurrences at SRD points during these weeks were often related to the presence of vagrants, events of little relevance to our assessment. We determined frequency of occurrence threshold values based on consistencies identified across species' weekly frequency of occurrence plots (Appendix B: Fig. B1). For broadly occurring migratory and nonmigratory species, our criteria meant that we used a frequency of occurrence threshold of at least 8000 SRD points ($n =$ 393 species). For range-restricted species with limited migratory behavior, no threshold was applied ($n = 39$ species). For range-restricted species with stronger migratory behavior, we used a threshold of at least 2500 SRD points ($n = 9$ species).

After removing SRD points and weeks, we placed each of the 441 species into one of three seasonal guilds based on their seasonal patterns of occurrence within the contiguous USA. The first guild contained species that occurred during the breeding and nonbreeding season (year-round), the second guild was composed of species that occurred primarily during the breeding season (Summer), and the third guild contained species that occurred primarily during the nonbreeding season (Winter). Note that Year-round species included both nonmigratory species and short-distance migrants; Summer species were primarily long-distance migrants that moved to tropical areas south of the United States during the nonbreeding season. Seasonal patterns of occurrence of nine species that did not breed or winter in the study area but primarily passed through the study area during migration were poorly represented and excluded from further analysis.

We then estimated for each species the weekly stewardship responsibilities among the four land stewardship categories (BLM 2, BLM 3, USFS 2, and USFS 3). We defined stewardship responsibility as the proportion of the total probability of occurrence west of the 98th meridian (Fig. 1) identified in each category for each week (Appendix B: Fig. B1). This approach first summed probabilities of occurrence across all SRD points that occurred west of the 98th meridian, and then calculated proportions based on probabilities of occurrence summed across SRD points located within the four land stewardship categories west of the 98th meridian. The resulting proportions provided a standardized measure of occurrence among species within the region, allowing for a cross-taxa analysis.

We examined how these weekly proportions changed over time, in combination with the frequency of occurrence plots, to identify species that occurred on few SRD points, resulting in seasonal land stewardship associations that were poorly represented across the complete annual cycle (Appendix B: Fig. B1). This procedure resulted in a total of 308 species remaining for further analysis with 214 classified as Year-round, 75 as Summer, and 19 as Winter (Appendix C). We summarized weekly stewardship responsibilities over time for species in each seasonal guild using generalized additive mixed models (GAMM) with species as a random effect (Wood 2006).

Stewardship cluster identification and analysis

We used hierarchical cluster analysis to identify groups of species within each seasonal guild whose stewardship responsibilities changed in a similar fashion over time. The resulting groups we termed stewardship clusters. We first generated, for each species, a vector that captures weekly associations between BLM or USFS lands. Taking values -1 or 1, this vector encodes which agency's land holds a greater proportion of total predicted probability of occurrence, with -1 indicating USFS and 1 indicating BLM. Weeks excluded from analysis based on the thresholding procedures are assigned 0. When values in the preference vector for a species switch from one week to the next between -1 and 1, there has been a switch from the USFS to the BLM, and between 1 and -1 there has been a switch from the

BLM to the USFS. We measured the similarity between the preference vectors for all unique species pairs, computed as Euclidean distances. We generated clusters from the resulting similarity matrix using the unweighted pairgroup method with arithmetic averages. Lastly, we applied an adaptive branch pruning technique to identify the prominent clusters of species for each seasonal guild (Langfelder et al. 2008).

We identified 84 species from the 308 that were considered birds of conservation concern (USFWS 2008) or threatened and endangered.[4] We used permutation tests to determine if these species occurred randomly among stewardship clusters. Specifically, we calculated the observed proportion of species with this classification within each group. We then resampled without replacement species' classifications 9999 times. Where these observed proportions occurred within the distributions of permutation-based proportions allowed us to estimate the probability of the observed proportion occurring by chance alone.

We estimated geographic characteristics of species within each stewardship cluster using six variables that described each species' geographic location, elevation, and geographic extent within the contiguous USA west of the 98th meridian. For geographic location, we used the latitude and longitude of the SRD points at which they occurred. We calculated the weighted mean location for each species and week where weights were species' probabilities of occurrence at the SRD points. This approach provided weekly centroids of occurrence within the region. For elevation, we extracted elevation data at 30 arc-second resolution ($\sim$1 km at the Equator) for each of the SRD points (USGS 2008). We then calculated the weighted mean elevation for each species and week where weights were species' probabilities of occurrence at the SRD points. We further summarized vertical location by calculating for each species the mean and standard deviation of elevation across weeks; the first measure estimated annual elevation, and the second the annual variation in elevation. We further summarized location by calculating the annual centroid based on the average latitude and longitude of the weekly centroids. We also calculated the standard deviation of the latitudes of the weekly centroids. The first measure provided an estimate of the overall location of species' distributions within the study area during the annual cycle, and the second an estimate of the degree of latitudinal movement during the annual cycle, which we interpret as a measure of migratory behavior. Geographic extent within the study area for each species was based on the week with the greatest number of SRD points with probabilities of occurrence >0. This measure provided an estimate of each species' maximum geographic extent within the region during their annual cycle.

To determine if these characteristics in combination differed among stewardship clusters within each seasonal guild, we first used MANOVA with the Pillai–Bartlett statistic. If there was evidence for differences among stewardship clusters ($P < 0.10$), we then applied a linear discriminant function analysis to determine how the combination of characteristics differed among the stewardship clusters within each seasonal guild.

All analysis was conducted in R, version 3.0.2 (R Development Core Team 2014). GAMM was implemented using the gamm4 library (Wood and Scheipl 2014). The adaptive branch pruning technique was implemented using the dynamicTreeCut library (Langfelder et al. 2008). The linear discriminant function analysis was implemented using the discrimin function in the ade4 library (Dray and Dufour 2007).

Results

When we summarized the percentages of species' total probabilities of occurrence weekly, the 308 species had higher percentages on GAP status 3 than GAP status 2 lands for both the BLM and USFS (Fig. 2). Percentages peaked on average during the breeding seasons; this was particularly pronounced for USFS lands and especially with GAP status 3, with peaks approaching 15% on average (Fig. 2). When summarized by seasonal guild, the 214 Year-round species were strongly associated on average with GAP status 3 lands, though with a weaker peak during the breeding season (Fig. 2; Appendix C). In contrast, the breeding season peak for the 75 Summer species was especially pronounced, with birds on USFS 3 lands showing the strongest peak on average, followed by birds on BLM 3 and USFS 2 lands (Fig. 2; Appendix C). The lowest proportions were found for the 19 Winter species, with peaks of limited average strength occurring, as expected, outside the breeding season (Fig. 2; Appendix C).

Year-round species

Stewardship relationships within each seasonal guild followed a few general patterns, as identified by the hierarchical cluster analysis. For Year-round species, there were three prominent stewardship clusters on GAP status 2 lands (Fig. 3), and three prominent stewardship clusters on GAP status 3 lands (Fig. 4). In both cases, the majority of species had a strong BLM association that was consistent across the annual cycle (cluster 1; "BLM breeding"), which was followed by species that had a strong USFS association that peaked during the breeding season (cluster 2; "USFS breeding"). A minority of species had associations that switched between the BLM during the nonbreeding season and the USFS during the breeding season (cluster 3; "Switchers").

Geographic location most strongly differentiated the stewardship clusters for Year-round species both for GAP status 2 and GAP status 3 lands (Table 1; Appendix B: Figs. B2 and B3). Cluster 1 species (BLM breeding) were more southern in location and cluster 2 species (USFS breeding) were more northern in location on average throughout the year. We found limited evidence of seasonal latitudinal movements by bird species in stewardship clusters 1 or 2, suggesting little migratory behavior. In contrast, the locations of cluster

[4] http://www.fws.gov/endangered/

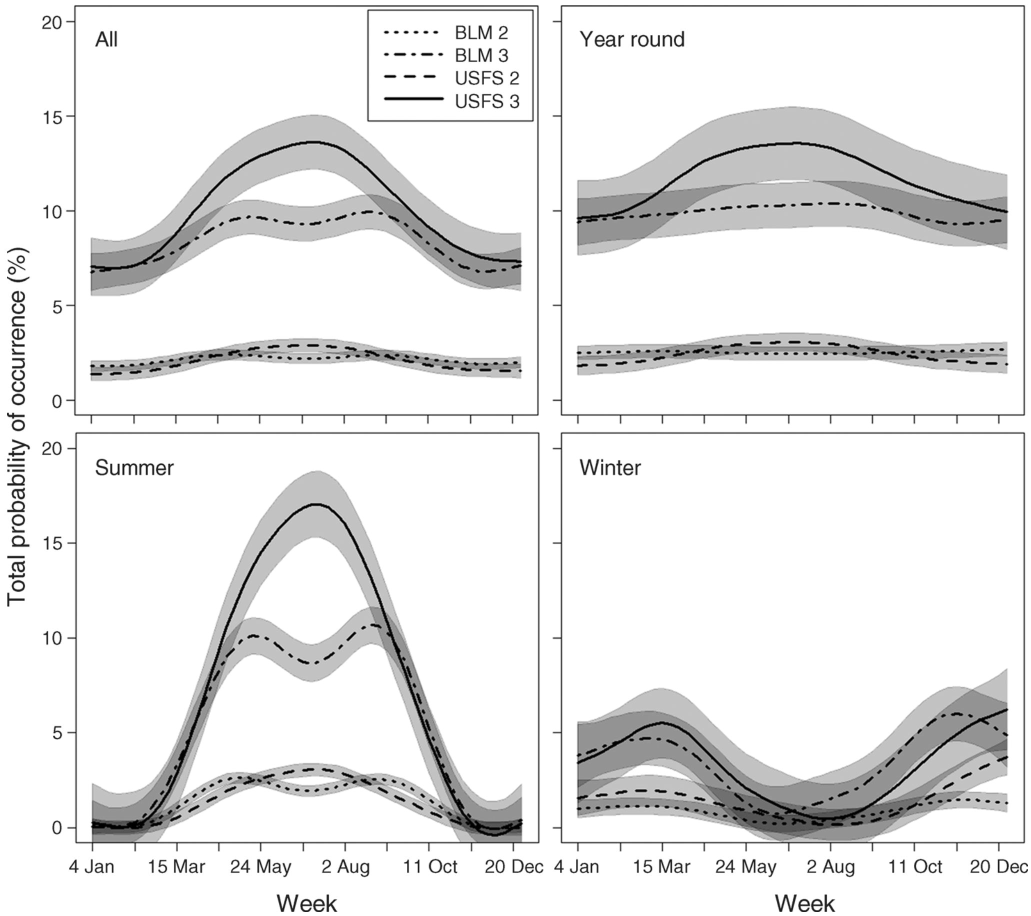

FIG. 2. Weekly total percentage probability of occurrence for All species ($n = 308$), Year-round species ($n = 214$), Summer species ($n = 75$), and Winter species ($n = 19$) on GAP status 2 or 3 lands administered by the Bureau of Land Management (BLM) and the United States Forest Service (USFS) west of the 98th meridian within the contiguous USA. Regression lines and shaded areas show the fitted response and 95% confidence bands of generalized additive mixed models with species as a random effect. Probability of occurrence for each species is estimated weekly for the combined period 2004–2011.

3 species (Switchers) showed stronger seasonal latitudinal movements, suggesting more significant migratory behavior. Elevation played a secondary role, differentiating stewardship clusters for both GAP status 2 and GAP status 3 lands. Cluster 1 species (BLM breeding) occurred at lower elevations from cluster 2 species (USFS breeding) on average across the annual cycle (Table 1; Appendix B: Fig. B4). Cluster 3 species (Switchers) occurred at lower elevations on average during the nonbreeding season, with a strong gain in elevation during the breeding season, especially on GAP status 2 lands. Range size played a secondary role differentiating stewardship clusters for both GAP status 2 and 3 lands. Cluster 3 species (Switchers) had larger maximum geographic extents on average within the study area, especially on GAP status 2 lands (Table 1; Appendix B: Fig. B4).

Summer species

Summer species fell into three prominent stewardship clusters for GAP status 2 lands (Fig. 3) and two prominent stewardship clusters for GAP status 3 lands (Fig. 4). In both cases, the majority of species had a strong USFS association that peaked considerably during the breeding season (cluster 1; USFS breeding), which was followed by species that had a strong BLM association that also peaked considerably during the breeding season (cluster 2; BLM breeding). For nine species on GAP status 2 lands, associations peaked on USFS lands during the breeding season, but switched to peak on BLM lands during spring and autumn migration (cluster 3; Switchers).

Elevation, range size, and geographic location most strongly differentiated stewardship clusters for Summer species on GAP status 2 lands (Table 1; Appendix B: Figs. B2–B4). All three clusters showed evidence of latitudinal movements, with the breeding ranges of cluster 1 and 3 species occurring north of cluster 2 species on average. Cluster 1 species (USFS breeding) occurred at higher elevations, cluster 2 species (BLM breeding) at lower elevations, and cluster 3 species (Switchers) at intermediate elevations on average;

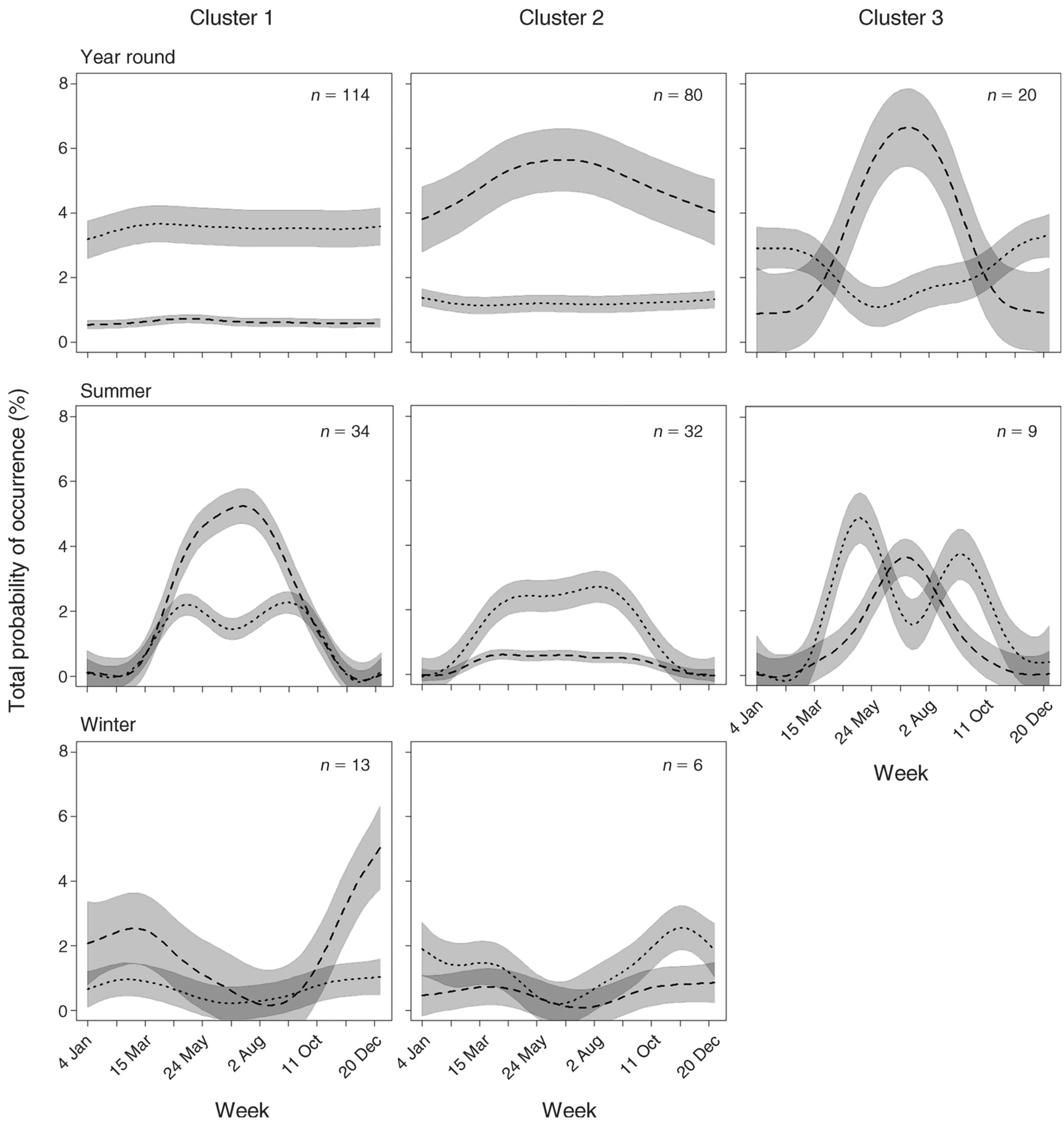

FIG. 3. Weekly total percentage probability of occurrence for Year-round species ($n = 214$), Summer species ($n = 75$), and Winter species ($n = 19$) on GAP status 2 lands west of the 98th meridian within the contiguous USA administered by the Bureau of Land Management (BLM; dotted lines) and the United States Forest Service (USFS; dashed lines) for groups of species identified based on a hierarchical cluster analysis of their weekly stewardship relationships (see *Methods* for details; n is number of species in each group). Regression lines and shaded areas show the fitted response and 95% confidence bands of generalized additive mixed models with species as a random effect. Probability of occurrence for each species is estimated weekly for the combined period 2004–2011.

elevations peaked roughly during the middle of the breeding season for all except cluster 3 species (Switchers) with a peak occurring late in the season. Cluster 1 species (USFS breeding) had the smallest and Cluster 3 species (Switchers) the largest maximum geographic extent within the study area on average (Table 1; Appendix B: Fig. B4).

For Summer species on GAP status 3 lands, elevation and geographic location most strongly differentiated stewardship clusters (Table 1; Appendix B: Figs. B2–B4). Cluster 1 species (USFS breeding) occurred at higher elevations and cluster 2 species (BLM breeding) at lower elevations on average. Cluster 1 species (USFS breeding) were more northern in location on average during the breeding season, with evidence for latitudinal movements. Cluster 2 species (BLM breeding) were more southern in location on average during the breeding season, with evidence for more limited

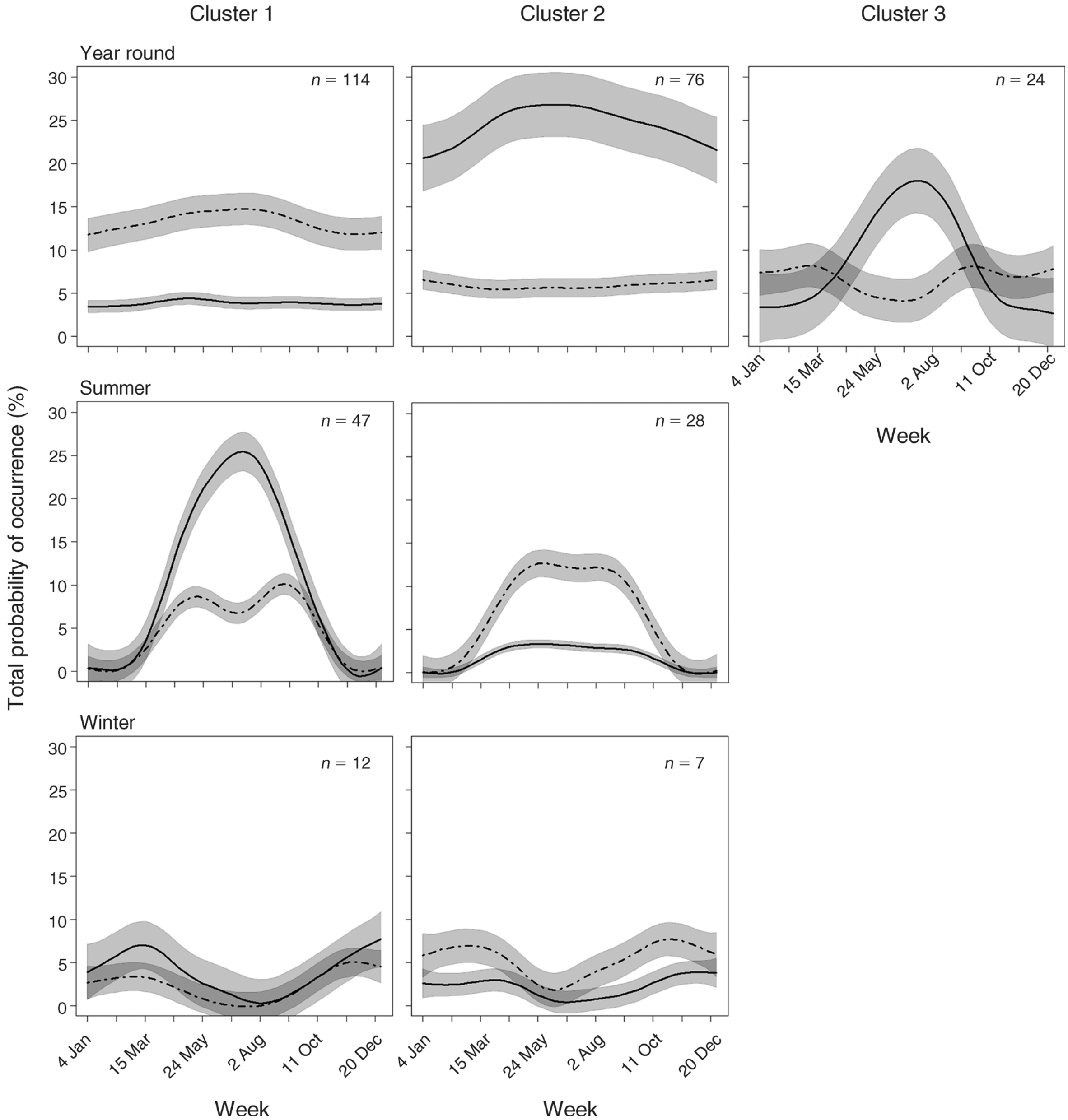

FIG. 4. Weekly total percentage probability of occurrence for Year-round species ($n = 214$), Summer species ($n = 75$), and Winter species ($n = 19$) on GAP status 3 lands west of the 98th meridian within the contiguous USA administered by the Bureau of Land Management (BLM; dot-dash lines) and the United States Forest Service (USFS; solid lines) for groups of species identified based on a hierarchical cluster analysis of their weekly stewardship relationships (see *Methods* for details; n is number of species in each group). Regression lines and shaded areas show the fitted response and 95% confidence bands of generalized additive mixed models with species as a random effect. Probability of occurrence for each species is estimated weekly for the combined period 2004–2011.

latitudinal movements. Range size differed little between the two clusters.

Winter species

Winter species fell into two prominent stewardship clusters for both GAP status 2 (Fig. 3) and GAP status 3 lands (Fig. 4). In both cases, the majority of species had a peak USFS association during the nonbreeding season (cluster 1) and a minority of species had a peak BLM association during the nonbreeding season (cluster 2). However, the overall associations were weak and the differences between the USFS and BLM were minor with no evidence for species that switched between lands under jurisdiction of the two agencies.

The stewardship clusters for Winter species were poorly differentiated by our geographic variables, especially on GAP status 2 lands (Table 1). On GAP status 3 lands, geographic location most strongly

Table 1. MANOVA Pillai–Bartlett statistics (Λ) and approximate F tests and standardized canonical coefficients and eigenvalues (λ) for six geographic variables discriminating species among stewardship clusters.

	GAP status 2			GAP status 3		
Class and variable	Pillai–Bartlett	Canonical function 1	Canonical function 2	Pillai–Bartlett	Canonical function 1	Canonical function 2
Year-round						
Elevation mean	$\Lambda = 0.521$	−0.007	0.434	$\Lambda = 0.484$	−0.042	0.057
Elevation SD	$F_{12,414} = 12.16$	0.084	0.223	$F_{12,414} = 11.02$	0.083	0.376
Longitude mean	$P < 0.001$	−0.339	0.015	$P < 0.001$	0.037	0.424
Latitude mean		−1.121	−0.041		−1.029	0.248
Latitude SD		0.249	0.508		0.318	0.462
Range size		0.288, $\lambda = 0.361$	0.499, $\lambda = 0.161$		0.282, $\lambda = 0.331$	−0.022, $\lambda = 0.154$
Summer						
Elevation mean	$\Lambda = 0.577$	0.919	0.118	$\Lambda = 0.426$	−0.722	
Elevation SD	$F_{12,136} = 4.49$	0.423	−0.560	$F_{6,68} = 8.41$	0.049	
Longitude mean	$P < 0.001$	0.073	−0.590	$P < 0.001$	−0.132	
Latitude mean		0.274	−0.015		−0.669	
Latitude SD		0.371	0.658		−0.496	
Range size		−0.668, $\lambda = 0.493$	0.231, $\lambda = 0.084$		0.460, $\lambda = 0.426$	
Winter						
Elevation mean	$\Lambda = 0.259$	0.212		$\Lambda = 0.684$	0.591	
Elevation SD	$F_{6,12} = 0.698$	−0.091		$F_{6,12} = 4.34$	0.630	
Longitude mean	$P = 0.657$	−0.429		$P = 0.015$	0.193	
Latitude mean		−0.856			−1.968	
Latitude SD		−0.168			−1.416	
Range size		−0.255, $\lambda = 0.259$			0.214, $\lambda = 0.684$	

Notes: Species were identified by three classes: Year-round, Summer, and Winter. (See *Methods* for details and descriptions of variables.)

differentiated stewardship clusters (Table 1; Appendix B: Figs. B2 and B3). Cluster 1 species were more northern in location and cluster 2 species were more southern in location on average during the nonbreeding season within the study area. Elevation and range size played secondary roles differentiating stewardship clusters (Table 1; Appendix B: Fig. B4). Cluster 1 species occurred at higher elevations and had smaller maximum geographic extents on average.

Conservation status

When considering the 84 species identified as birds of conservation concern or threatened and endangered (Appendix C), there was no evidence that the distributions of these species within the three seasonal guilds differed from what would be expected by chance (Appendix D). Among the stewardship clusters, only Year-round species in cluster 2 (USFS breeding) for GAP status 2 and 3 lands showed evidence of differences; fewer species identified as birds of conservation concern or threatened and endangered occurred within these clusters than expected by chance (Appendix D).

Discussion

Our results provide the first empirical evaluation of seasonal public land use by North American birds and highlight the value of citizen-science data in conservation science. Our findings document the rich seasonal variation in ecological stewardship responsibilities for a large number of bird species on GAP status 2 and 3 lands administered by the BLM and USFS. We identified suites of species that shared similar seasonal associations with lands administered by these agencies, including species characterized by a notable "switching" pattern where they occurred on lands administered by the two agencies at different times of the annual cycle. Even though the collections of public lands we examined occur across a limited spatial extent and do not represent all of the ecological systems found within the contiguous USA (Aycrigg et al. 2013), our findings suggest these areas support, in some cases, substantial proportions of species' distributions and are important for the health of continental bird populations (NABCI 2011). Our findings also suggest that more species would benefit from management efforts on public lands throughout the year, rather than efforts directed only toward species during the breeding season.

Our findings indicate that species whose associations switched between agencies across the annual cycle can be classified into two groups: (1) Year-round species that moved from high-elevation USFS lands during the summer to lower-elevation BLM lands during the winter (GAP status 2 and 3); and (2) Summer species that occurred primarily on higher-elevation USFS lands during the breeding season and lower-elevation BLM lands during spring and autumn migrations (GAP status 2 only). Species that switched between agencies' lands were primarily migratory and had relatively broad distributions. Examples of Year-round switching species include Mountain Bluebird (*Sialia currucoides*) and Red-naped Sapsucker (*Sphyrapicus nuchalis*), both of which breed in high-elevation coniferous and aspen forests and migrate to lower elevations in the western USA in winter (Appendix C; see Plate 1). Summer switchers include Black-headed Grosbeak (*Pheucticus melanocephalus*), Wilson's Warbler (*Cardelina pusilla*), Western Wood-Pewee (*Contopus sordidus*), and other western forest-breeding species (Appendix C; see Plate 1) that likely rely on lower-elevation riparian habitats during migration to Neotropical wintering areas (Skagen et al. 1998, Finch and Yong 2000, DeLong et al. 2005).

In addition to species whose primary stewardship relationships switched during their annual cycles, our results identified suites of species that are dependent on public lands under single agency management. The largest cluster of Year-round species occurred primarily on BLM GAP status 2 and 3 lands, which support $\geq$25% of the average weekly distribution within the contiguous USA for 36 species, including 19 species of conservation concern (Appendix C). The largest cluster of Summer species that were dependent on a single agency were those occurring on USFS lands. Similarly, USFS GAP status 2 and 3 lands support $\geq$25% of the average weekly distribution within the contiguous USA for 25 species, including six species of conservation concern (Appendix C). Because multiple species have high dependence on these lands, policy-level action by these agencies has the potential to substantially enhance their conservation.

The need for cooperation has been identified as a conservation and management necessity from local to global scales (Sodhi et al. 2011), not only when designing and managing terrestrial protected areas (McNeely 1994), but also when considering the control and management of invasive species (Lodge et al. 2006), and efforts to mitigate the consequences of climate change (Novacek and Cleland 2001). The interaction of policies, interests, and transaction costs among organizations may determine the quality of cooperative arrangements and their ability to achieve conservation and management objectives (Bode et al. 2011). Approaches for supporting cooperation have been broadly identified and in some cases successfully implemented within (Valdez et al. 2006) and among countries (Agrawal 2000). The potential complexity of these cooperative arrangements is well illustrated by conservation efforts that must consider an organism's complete annual cycle, in which species may occur on areas at different times of the year administered by different agencies having potentially disparate management intents.

To provide broad-scale and comprehensive management strategies for North American birds, especially migratory birds, our results identify the need for directed cooperation between the BLM and USFS. For the short-distance migratory species that occur year-round within the contiguous USA, BLM and USFS GAP status 2 and 3 lands are both important, suggesting that cooperative efforts considering the requirements of these species throughout their annual cycles would benefit a significant component of their populations. For long-distance migratory species that winter south of the USA, the need is especially acute for improved cooperative efforts across BLM and USFS GAP status 2 lands. Although GAP status 2 lands cover a more limited spatial extent, they offer long-term protections for high-elevation forest habitats used for breeding.

Many long-distance migratory species that breed in temperate regions of North America have shown intervals of decline over the past several decades (Robbins et al. 1989, Sauer and Link 2011) and will require targeted management efforts to stabilize their populations (Rich et al. 2004). Improved management for these species is particularly urgent, as these declines are likely to be exacerbated in the future through continuing climate change (Møller et al. 2008, Carey 2009) and especially land-use/land-cover change in the tropics (Jetz et al. 2007). Many species whose populations have declined have persisted through periphery populations on mountain tops or other in situ macro-refuges (Ashcroft 2010) where anthropogenic activities have been minimal or absent (Channell and Lomolino 2000). The public lands considered in this study, particularly the high-elevation USFS lands, may play a similar role for birds under global warming (La Sorte and Jetz 2010).

Our findings provide a framework for U.S. federal agencies to better address their shared responsibilities for bird populations across the annual cycle. For example, our findings inform the memorandums of understanding between the BLM, USFS, and U.S. Fish and Wildlife Service directed under Executive Order 13186 (*Responsibilities of Federal Agencies to Protect Migratory Birds*),[5] signed in 2001 (NABCI 2011). Our results specifically allow both the BLM and USFS to consider impacts of projects under federal jurisdiction on migratory bird populations and habitats across the full annual cycle. For example, fire management policies on high-elevation USFS GAP status 2 lands (i.e., wilderness areas) can have a disproportionate effect on forest breeding birds in summer, whereas livestock grazing and energy development on GAP status 3 (multiple use) BLM lands can affect these same species in winter, as well as many other lower-elevation species year-round. Our findings suggest that an absence of cooperative efforts between these agencies will most greatly affect 29 migratory species on GAP status 2 lands and 24 migratory species on GAP status 3 lands (see Appendix C).

Future assessments of ecological stewardship responsibilities for birds or other taxa would benefit from consideration of areas that are managed by other public or private organizations, which in total represent a much more complex scenario for fostering cooperation (Golodetz and Foster 1997). Considering public–private partnerships in the eastern USA is particularly important where protected areas are more at risk of conversion and the representation of ecological systems

[5] ceq.hss.doe.gov/nepa/regs/eos/eo13186.html

PLATE 1. (Upper left) Mountain Bluebird (*Sialia currucoides*) and (upper right) Red-naped Sapsucker (*Sphyrapicus nuchalis*), species that breed in high-elevation forests and migrate to lower elevations in winter. (Lower left) Black-headed Grosbeak (*Pheucticus melanocephalus*) and (lower right) Wilson's Warbler (*Cardelina pusilla*), species that breed in western forests that use lower elevation habitats during migration to Neotropical wintering grounds. Photo credits: B. L. Sullivan and C. Wood (Red-naped Sapsucker).

within protected areas is less redundant (Aycrigg et al. 2013). Future assessments that provide an international perspective would also be highly beneficial, especially for long-distance migrants that winter in the Caribbean and Central and South America and only occur within our study area during the breeding season or as transients during migration. International conservation planning has the potential to increase conservation benefits while reducing financial costs and the quantity of area requiring protection (Kark et al. 2009). For long-distance migratory birds, identifying current threats to migration stopover habitat and wintering areas outside the USA is likely to be as critical as identifying breeding areas for increased protection within the USA (Wilson et al. 2007, Berlanga et al. 2012). International assessments could summarize annual associations within protected areas, as done in this study, or within other ecologically or politically relevant geographic features. Such work could be used to prioritize areas that, when considered across the full annual cycle, provide the greatest overall benefits to the greatest number of migratory species now or under future global change scenarios.

The specific types of results that we present in this paper are dependent on the availability of information on species' occurrences at fine spatial and temporal resolutions, and our study was facilitated by the availability of a single set of data that covered the area of interest. Nevertheless, there are several ways in which our study has implications into areas where these conditions are not met. First, as the geographic resolution of the eBird database continues to improve, the feasibility of implementing such assessments in other regions of the world is increasing (Sullivan et al. 2014). Recent extensions to STEM demonstrate how eBird data can be used to produce seamless estimates of species distributions across hemispherical spatial extents despite the fact that these observational data are irregularly, and often very sparsely distributed (Fink et al. 2013, 2014). It is therefore conceivable that, in the not too distant future, studies such as this one may be replicated at much broader geographic extents, although likely with coarser-resolution distributional estimates in areas of low data density. We believe that such coarser-resolution information, used within the same framework of analysis, may be useful for the purpose of understanding stewardship responsibilities among larger management units, i.e., among countries, states, or provinces. This opens up the possibility of replicating this analysis in other parts of the world to identify opportunities to coordinate full life cycle, international biodiversity management efforts. Lastly, our results reinforce the importance of creating larger data sets from country-specific monitoring data, as are found in Europe, where eBird-like data are being gathered by a series of national-level programs.

By considering geographic occurrences of birds during the entirety of their annual cycles, we provide a scientific basis for more detailed and comprehensive assessments of stewardship responsibilities that may lead to better-informed management and policy decisions. The stewardship relationships distinguished in our analysis reflect how avian migration strategies and the location of breeding and wintering grounds and migration routes interact with the unique geographical distributions of public lands in the western USA. Slowing or even reversing population declines of birds within the USA may depend on shifts in current policy and management on these lands. Toward this end, our findings support the development of a cooperative interagency framework that considers the temporal and spatial dynamics of avian distributions and the long-term requirements of these species under global environmental change.

Acknowledgments

We thank T. Fredericks, J. Ward, and K. Webb for assistance with data acquisition and preparation, A. Dhondt, M. Iliff, and D. Winkler for valuable discussions, and two anonymous reviewers for constructive comments. We are grateful to the many eBird participants for their contributions. This work was funded by the Leon Levy Foundation, Wolf Creek Foundation, and the National Science Foundation (IIS-1125098 and IIS-1017793) with computing support from CNS-1059284, OCI-1053575, and DEB-110008.

Literature Cited

Agrawal, A. 2000. Adaptive management in transboundary protected areas: the Bialowieza National Park and Biosphere Reserve as a case study. Environmental Conservation 27:326–333.

Albers, H. J., A. W. Ando, and M. Batz. 2008. Patterns of multi-agent land conservation: crowding in/out, agglomeration, and policy. Resource and Energy Economics 30:492–508.

Ashcroft, M. B. 2010. Identifying refugia from climate change. Journal of Biogeography 37:1407–1413.

Aycrigg, J. L., A. Davidson, L. K. Svancara, K. J. Gergely, A. McKerrow, and J. M. Scott. 2013. Representation of ecological systems within the protected areas network of the continental United States. PLoS ONE 8:e54689.

Bagchi, R., et al. 2013. Evaluating the effectiveness of conservation site networks under climate change: accounting for uncertainty. Global Change Biology 19:1236–1248.

Berlanga, H., et al. 2012. Saving our shared birds: partners in flight tri-national vision for landbird conservation. Cornell Lab of Ornithology, Ithaca, New York, USA.

Bode, M., W. Probert, W. R. Turner, K. A. Wilson, and O. Venter. 2011. Conservation planning with multiple organizations and objectives. Conservation Biology 25:295–304.

Butchart, S. H. M., et al. 2012. Protecting important sites for biodiversity contributes to meeting global conservation targets. PLoS ONE 7:e32529.

Butchart, S. H. M., et al. 2010. Global biodiversity: indicators of recent declines. Science 328:1164–1168.

Carey, C. 2009. The impacts of climate change on the annual cycles of birds. Philosophical Transactions of the Royal Society B 364:3321–3330.

Channell, R., and M. V. Lomolino. 2000. Dynamic biogeography and conservation of endangered species. Nature 403:84–86.

Chape, S., M. D. Spalding, and M. D. Jenkins. 2008. The world's protected areas: status, values and prospects in the twenty-first century. University of California Press, Berkeley, California, USA.

DeLong, J. P., S. W. Cox, and N. S. Cox. 2005. A comparison of avian use of high- and low-elevation sites during autumn migration in central New Mexico. Journal of Field Ornithology 76:326–333.

Dray, S., and A. B. Dufour. 2007. The ade4 package: implementing the duality diagram for ecologists. Journal of Statistical Software 22:1–20.

Faaborg, J., et al. 2010*a*. Conserving migratory land birds in the New World: Do we know enough? Ecological Applications 20:398–418.

Faaborg, J., et al. 2010*b*. Recent advances in understanding migration systems of New World land birds. Ecological Monographs 80:3–48.

Fairfax, S. K., L. Gwin, M. A. King, L. Raymond, and L. A. Watt. 2005. Buying nature: the limits of land acquisition as a conservation strategy, 1780–2004. MIT Press, Cambridge, Massachusetts, USA.

Finch, D. M., and W. Yong. 2000. Landbird migration in riparian habitats of the middle Rio Grande: a case study. Studies in Avian Biology 20:88–89.

Fink, D., T. Damoulas, N. E. Bruns, F. A. La Sorte, W. M. Hochachka, and C. P. Gomes. 2014. Crowdsourcing meets ecology: hemisphere-wide spatiotemporal species distribution models. AI Magazine 35(2):19–30. http://dx.doi.org/10.1609/aimag.v35i2.2533

Fink, D., T. Damoulas, and J. Dave. 2013. Adaptive spatio-temporal exploratory models: hemisphere-wide species distributions from massively crowdsourced eBird data. Twenty-Seventh AAAI Conference on Artificial Intelligence (AAAI-13), Bellevue, Washington, USA.

Fink, D., W. M. Hochachka, B. Zuckerberg, D. W. Winkler, B. Shaby, M. A. Munson, G. Hooker, M. Riedewald, D. Sheldon, and S. Kelling. 2010. Spatiotemporal exploratory models for broad-scale survey data. Ecological Applications 20:2131–2147.

Fry, J. A., G. Xian, S. Jin, J. A. Dewitz, C. G. Homer, L. Yang, C. A. Barnes, N. D. Herold, and J. D. Wickham. 2011. Completion of the 2006 National Land Cover Database for the conterminous United States. Photogrammetric Engineering and Remote Sensing 77:858–864.

Golodetz, A. D., and D. R. Foster. 1997. History and importance of land use and protection in the North Quabbin Region of Massachusetts (USA). Conservation Biology 11:227–235.

Hole, D. G., S. G. Willis, D. J. Pain, L. D. Fishpool, S. H. M. Butchart, Y. C. Collingham, C. Rahbek, and B. Huntley. 2009. Projected impacts of climate change on a continent-wide protected area network. Ecology Letters 12:420–431.

Jetz, W., D. S. Wilcove, and A. P. Dobson. 2007. Projected impacts of climate and land-use change on the global diversity of birds. PLoS Biology 5:1211–1219.

Kark, S., N. Levin, H. S. Grantham, and H. P. Possingham. 2009. Between-country collaboration and consideration of costs increase conservation planning efficiency in the Mediterranean Basin. Proceedings of the National Academy of Sciences USA 106:15368–15373.

Karl, T. R., and K. E. Trenberth. 2003. Modern global climate change. Science 302:1719–1723.

Langfelder, P., B. Zhang, and S. Horvath. 2008. Defining clusters from a hierarchical cluster tree: the Dynamic Tree Cut package for R. Bioinformatics 24:719–720.

La Sorte, F. A., D. Fink, W. M. Hochachka, A. Farnsworth, A. D. Rodewald, K. V. Rosenberg, B. L. Sullivan, D. W. Winkler, C. Wood, and S. Kelling. 2014. The role of atmospheric conditions in the seasonal dynamics of North American migration flyways. Journal of Biogeography 41:1685–1696.

La Sorte, F. A., and W. Jetz. 2010. Projected range contractions of montane biodiversity under global warming. Proceedings of the Royal Society B 277:3401–3410.

Lodge, D. M., et al. 2006. Biological invasions: recommendations for U.S. policy and management. Ecological Applications 16:2035–2054.

Mascia, M. B., and S. Pailler. 2011. Protected area downgrading, downsizing, and degazettement (PADDD) and its conservation implications. Conservation Letters 4:9–20.

McNeely, J. A. 1994. Protected areas for the 21st century: working to provide benefits to society. Biodiversity and Conservation 3:390–405.

Meyer, W. B., and B. L. Turner. 1992. Human-population growth and global land-use/cover change. Annual Review of Ecology and Systematics 23:39–61.

Møller, A. P., D. Rubolini, and E. Lehikoinen. 2008. Populations of migratory bird species that did not show a phenological response to climate change are declining. Proceedings of the National Academy of Sciences USA 105:16195–16200.

NABCI. 2011. The state of the birds 2011 report on public lands and waters. Department of Interior, Washington, D.C., USA.

Novacek, M. J., and E. E. Cleland. 2001. The current biodiversity extinction event: scenarios for mitigation and recovery. Proceedings of the National Academy of Sciences USA 98:5466–5470.

Pereira, H. M., and D. H. Cooper. 2006. Towards the global monitoring of biodiversity change. Trends in Ecology and Evolution 21:123–129.

Pressey, R. L., M. Cabeza, M. E. Watts, R. M. Cowling, and K. A. Wilson. 2007. Conservation planning in a changing world. Trends in Ecology and Evolution 22:583–592.

R Development Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rich, T. D., et al. 2004. Partners in Flight North American landbird conservation plan. Cornell Lab of Ornithology, Ithaca, New York, USA.

Robbins, C. S., J. R. Sauer, R. S. Greenberg, and S. Droege. 1989. Population declines in North-American birds that migrate to the neotropics. Proceedings of the National Academy of Sciences USA 86:7658–7662.

Rodrigues, A. S. L., et al. 2004. Global gap analysis: priority regions for expanding the global protected-area network. BioScience 54:1092–1100.

Sauer, J. R., and W. A. Link. 2011. Analysis of the North American Breeding Bird Survey using hierarchical models. Auk 128:87–98.

Scott, J. M., F. W. Davis, R. G. McGhie, R. G. Wright, C. Groves, and J. Estes. 2001. Nature reserves: Do they capture the full range of America's biological diversity? Ecological Applications 11:999–1007.

Skagen, S. K., C. P. Melcher, W. H. Howe, and F. L. Knopf. 1998. Comparative use of riparian corridors and oases by migrating birds in southeast Arizona. Conservation Biology 12:896–909.

Sodhi, N. S., R. Butler, W. F. Laurance, and L. Gibson. 2011. Conservation successes at micro-, meso- and macroscales. Trends in Ecology and Evolution 26:585–594.

Sullivan, B. L., et al. 2014. The eBird enterprise: an integrated approach to development and application of citizen science. Biological Conservation 169:31–40.

USFWS. 2008. Birds of conservation concern 2008. United States Department of Interior, Fish and Wildlife Service, Division of Migratory Bird Management, Arlington, Virginia, USA.

USGS. 2008. Global Land Survey Digital Elevation Model (GLSDEM). Global Land Cover Facility, College Park, Maryland, USA.

USGS-GAP. 2012. Protected Areas Database of the United States (PAD-US) Version 1.3. U.S. Geological Survey (USGS) Gap Analysis Program (GAP), Moscow, Idaho, USA.

Valdez, R., J. C. Guzman-Aranda, F. J. Abarca, L. A. Tarango-Arambula, and F. C. Sanchez. 2006. Wildlife conservation and management in Mexico. Wildlife Society Bulletin 34:270–282.

Vitousek, P. M., C. M. Dantonio, L. L. Loope, M. Rejmanek, and R. Westbrooks. 1997. Introduced species: a significant component of human-caused global change. New Zealand Journal of Ecology 21:1–16.

Wilson, K. A., et al. 2007. Conserving biodiversity efficiently: What to do, where, and when. PLoS Biology 5:e223.

Wood, S. N. 2006. Generalized additive models: an introduction with R. Chapman and Hall/CRC, Boca Raton, Florida, USA.

Wood, S. N., and F. Scheipl. 2014. gamm4: Generalized additive mixed models using mgcv and lme4. R package version 0.2-2. R Foundation for Statistical Computing, Vienna, Austria.

Supplemental Material

Ecological Archives

Appendices A–D are available online: http://dx.doi.org/10.1890/14-0702.1.sm