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TRENDS IN LANDBIRD DENSITY AT TWO NATIONAL PARKS IN FRAGMENTED, MIXED-USE LANDSCAPES OF THE PACIFIC NORTHWEST

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ABSTRACT—National parks play a key role in conserving species by providing landscapes where threats from anthropogenic disturbance are reduced. In a recent study of 3 large wilderness parks in the Pacific Northwest, nearly all landbird species were found to be stable or increasing. Nonetheless, contemporary results from the Breeding Bird Survey and mark-recapture studies fuel concerns that some landbirds in the Pacific Northwest are trending in sync with many North America species in widespread decline. Although landbird populations might be thriving in large parks with extensive old-growth forest, those in smaller parks with less intact wilderness and higher ratios of edge-to-interior habitat might reflect the stressors inherent in more human-dominated landscapes. We conducted landbird point-count surveys from 2005 to 2016 in 2 national historical parks situated in the more human-dominated landscapes of this region, San Juan Island National Historical Park and Lewis and Clark National Historical Park. Established primarily to protect cultural resources, these parks lack old-growth forest and consist of relatively small parcels embedded in fragmented, multi-use landscapes. Here, we apply recent developments in point-count analysis to estimate trends in population density for 50 landbird species commonly detected in these small parks, including lagged effects of precipitation and temperature on the annual density of each species, and effects of survey conditions on species detection. All but 3 species exhibited stable densities in both parks, and more than half of the populations analyzed clearly increased in density over the study period. Notable exceptions were single-park declines in Olive-sided Flycatcher (*Contopus cooperi*), Northern Flicker (*Colaptes anratus*), and Hutton's Vireo (*Vireo huttoni*). Annual variation in population density was often related to climate, with generally positive responses to a recent deficit in annual precipitation-as-snow, and more variable responses to higher mean spring temperature. These results reinforce trends estimated for 3 large national parks in the Pacific Northwest, suggesting recent stability of landbird populations in parks of this region, independent of park size or setting.

Key words: bird trends, climate, edge effects, Lewis and Clark National Historical Park, San Juan Island National Historical Park

National parks and other protected areas throughout the world play a key role in conserving bird species (Venter and others 2014), by providing landscapes where threats from anthropogenic habitat loss, habitat degradation and hunting pressure are reduced or eliminated (Watson and others 2014; Runge and others 2015). Although protected areas will

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continue to face climatic changes, the effects of those changes might vary with context. For example, projected changes in climate through 2070 are predicted to increase the potential for birds to colonize national parks in the United States (Wu and others 2018). For many bird species, residing within protected areas might reduce some of the risks associated with climate change (Gauzere and others 2016). One example is especially pertinent to the Pacific Northwest, where national parks protect a substantial portion of the region's remaining old-growth forest (Bolsinger and Waddell 1993; Moeur and others 2011); in this region, the microhabitats provided by those protected forests appear to have buffered the negative effects of climate change for certain bird species sensitive to increasing temperatures (Betts and others 2017). In keeping with this result, we found evidence for recent stability in landbird populations breeding in 3 large wilderness parks of this region; specifically, most landbird populations were stable or increasing in our analysis of trends from 2005 to 2014 in Mount Rainier National Park, North Cascades National Park Complex, and Olympic National Park (Ray and others 2017a).

Concerns persist, however, about landbird trends in the Pacific Northwest (Rockwell and others 2017), where local declines have been inferred from Breeding Bird Survey data (Sauer and others 2017) and mark-recapture monitoring efforts (Rockwell and others 2017). Bolstering local concerns are more general concerns about the effects of climate change and other stressors on birds worldwide (Huntley and others 2008; Şekercioğlu and others 2008; Tingley and others 2012; Newbold and others 2013; Bregman and others 2014; Loss and others 2015; Mayor and others 2017). Even as landbird populations in large, intact wilderness areas in the Pacific Northwest appear to be thriving, populations in more fragmented, human-modified landscapes may face greater threats (Marzluff and Ewing 2001; Devictor and others 2007; Zurita and others 2012). Although large parks clearly provide more habitat and consequently can support greater numbers of birds than small parks, the size, wilderness characteristics, and higher ratio of interior-to-edge habitat in larger parks might also provide enhanced protections for wildlife (e.g., Cantú-Salazar and Gaston 2010; Santangeli and others 2017). It is unclear whether smaller parks in landscapes that are more heavily modified by humans might conserve bird populations as effectively as large wilderness parks.

We assessed data from 2 non-wilderness parks in the Pacific Northwest to see if the overarching pattern of stable or increasing bird populations reported by Ray and others (2017a) would also be reflected in much smaller parks embedded in mixed-use landscapes with a substantially greater human footprint. San Juan Island National Historical Park (SAJH) and Lewis and Clark National Historical Park (LEWI) are largely characterized by natural habitat, but were established primarily to protect historical resources. Compared to the wilderness parks, these historical parks are lacking in old-growth forest and are more exposed to threats associated with non-wilderness landscapes, such as habitat alteration on adjacent lands and the invasion of alien species (Lewis and Sharpe 1987).

In 2005, the National Park Service North Coast and Cascades Inventory and Monitoring Network (NCCN) began monitoring landbird populations in 5 National Parks, under a peer-reviewed protocol (Siegel and others 2007) that has served as a model for other resource-monitoring efforts within the NCCN and in other networks. Landbird monitoring is part of a suite of monitoring activities designed to track "vital signs" related to NPS resources (Fancy and others 2009; Weber and others 2009). Landbird populations were identified as vital signs by the NPS because several aspects of terrestrial ecosystem change can be inferred efficiently by monitoring trends in these species, which occupy relatively high trophic positions and provide important ecological functions such as seed dispersal and insect control. Here, we apply recent developments in point-count analysis to estimate trends in population density for 50 landbird species commonly detected in SAJH and/or LEWI as part of the NCCN landbird monitoring program. Accounting for components of detection probability, we estimate trends over time and explore lagged effects of precipitation and temperature on the annual density of these species in each park. We hypothesized that breeding bird densities would increase in these parks following years with warmer spring temperature and lower precipitation-as-snow.

Methods

With the goal of monitoring population trends in multiple species, breeding-season point-counts were conducted biennially at dozens of points in each historical park under a protocol detailed in Siegel and others (2007), Saracco and others (2014), and Ray and others (2017a, 2017b). Surveys were conducted in SAJH in odd years from 2005 to 2015, and in LEWI in even years from 2006 to 2016, as part of a larger project including annual surveys in each of the 3 large wilderness parks of the NCCN: Mount Rainier National Park (MORA), North Cascades National Park Complex (NOCA) and Olympic National Park (OLYM). To minimize variability among years related to the observation process, surveys were conducted by trained observers. To minimize variability due to seasonal processes, surveys were timed to coincide with the peak in breeding (vocalizing) activities for most species. All surveys of SAJH and LEWI were conducted between 21 May and 6 June.

Study Area and Sampling Frame

Both historical parks are located in coastal lowland habitats (Fig. 1). The sampling frame for SAJH included 2 separate parcels: American Camp on the southwest shore of San Juan Island, and the central portion of British Camp on the northwest shore (Table 1). The sampling frame for LEWI included Fort Clatsop and most of Cape Disappointment, as well as Sunset Beach and an adjacent parcel termed the Yeon Property (Table 1). Forested areas in SAJH were dominated by Douglas-fir (*Pseudotsuga menziesii*), mixed conifer (coniferous forest with canopy <80% Douglas-fir), and Red Alder (*Alnus rubra*). SAJH also included substantial grasslands, dunes, and developed areas with lawns and other landscaping. Habitats in LEWI varied somewhat by parcel, but forested areas were generally dominated by Sitka Spruce (*Picea sitchensis*), Western Hemlock (*Tsuga heterophylla*), Douglas-fir, Shore Pine (*Pinus contorta* ssp. *contorta*), and Red Alder, with willows (*Salix* spp.) and other shrubs typically dominating forest gaps and wetlands.

Survey and Habitat Covariates

Each park was surveyed at point-count stations distributed in a grid (Fig. 1), with roughly 350 m between points. At each point,

TABLE 1. Area of each park unit surveyed.

Park	Total area (ha)	Parcel	Area (ha)
SAJH	710	American Camp	505
		British Camp	205
LEWI	1216	Fort Clatsop	522
		Cape Disappointment	564
		Sunset Beach	90
		Yeon Property	39

an observer recorded the species of each bird detected during a 5- or 7-min survey, along with detection distance and time interval, enabling analyses that account for birds present but undetected (Royle and others 2004; Alldredge and others 2007; Amundson and others 2014). Surveys were lengthened from 5 to 7 min in 2011, to expand options for modeling detection probability. Potential covariates of detection and abundance were also recorded during surveys, including point coordinates, observer, date, time, ambient noise level, presence of forest cover, and group size (number of birds detected at once and acting as a unit or flock).

We hypothesized that years of heavy snow and cooler spring temperatures could delay initiation of breeding and result in food scarcity or weather-related nest failure early in the nesting season (Hahn and others 2004; Pereyra 2011; Mathewson and others 2012), leading to lower recruitment and lagged effects of lower breeding-bird abundance in the subsequent year (DeSante 1990). To test this hypothesis, we selected ClimateWNA as a source of "scale-independent" data, resolving climate at each point-count station (Wang and others 2016). To characterize spring conditions, we selected mean spring temperature (*MST*, the average daily temperature from 1 March through 31 May) and annual precipitation-as-snow (*PAS*, millimeters of snow falling between 1 August and 31 July). Specifically, we calculated *MST* and *PAS* as anomalies, relative to 1971–2000 normals, under the expectation that breeding and recruitment would be inversely related to snowfall and directly related to temperature (Ray and others 2017a, 2017b). For surveys in year t, lag-1 *MST* was the mean temperature anomaly from 1 March to 31 May of year t-1, and lag-1 *PAS* was the snowfall anomaly from 1 Aug of year t-2 to 31 July of year t-1. Following Graham (2003), we considered simultaneous effects of these corre-
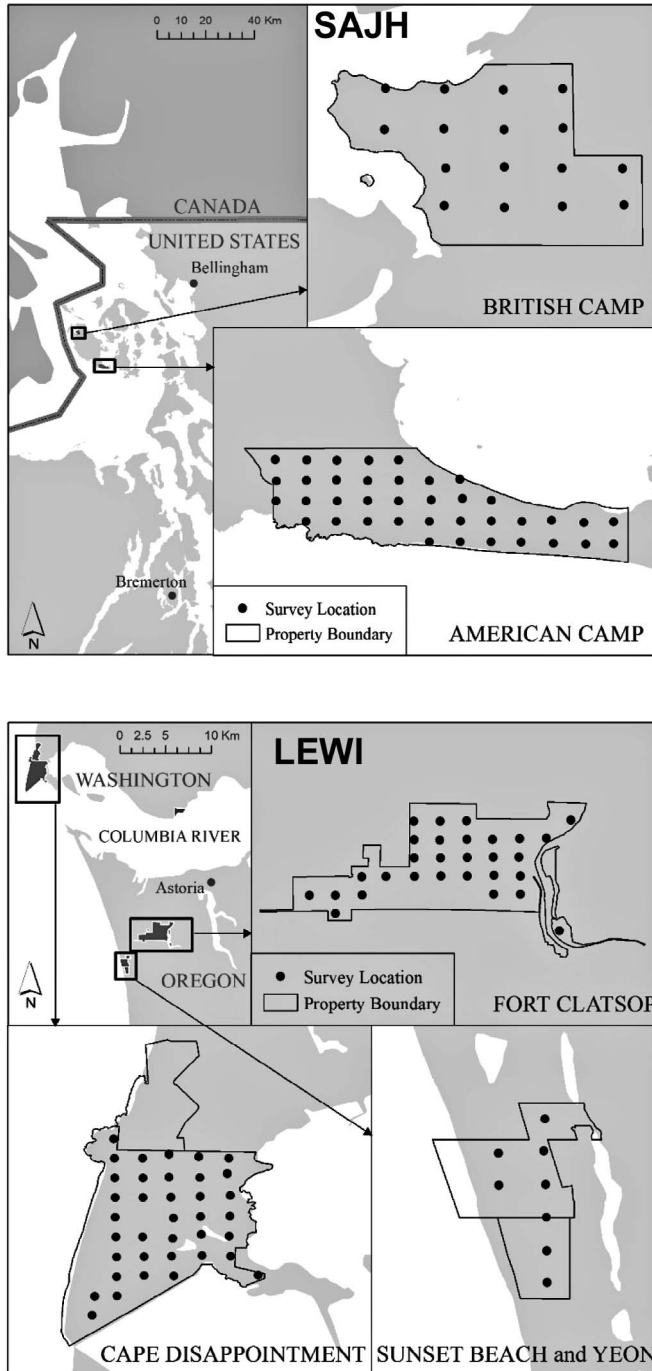
FIGURE 1. Distribution of surveyed park units and point-count stations (dots) in San Juan Island National Historical Park (SAJH, upper panel) and Lewis and Clark National Historical Park (LEWI, lower panel). Point-count stations were typically 350 m apart. A higher density of stations (not shown) was surveyed during the first year of point counts in each park (see Table 3).

TABLE 2. Models used to estimate parameters controlling detection probability and abundance of landbird populations in each park from 2005 to 2016; q, σ and λ control p_a, p_d and N, respectively. PAS = lagged precipitation-as-snow and $rMST$ = lagged residual mean spring temperature, as described in text. Subscripts k and t are point-count station and year, respectively.

Model	Sub-model	Linear predictor
Basic	Availability	$\mathrm{logit}(q_{kt}) = \alpha_0$
	Perceptibility	$\log(\sigma_{kt}) = \log(\sigma_0)$
	Abundance	$\log(\lambda_{kt}) = \beta_0 + \beta_1 year_t$
Climate	Availability	$\mathrm{logit}(q_{kt}) = \alpha_0$
	Perceptibility	$\log(\sigma_{kt}) = \log(\sigma_0)$
	Abundance	$\log(\lambda_{kt}) = \beta_0 + \beta_1 year_t + \beta_2 PAS_{k,t-1} + \beta_3 rMST_{k,t-1}$

lated predictors by replacing MST with residual MST ($rMST$), the residuals of a linear regression of MST on PAS.

Analyses

Temporal trends in population density and effects of covariates on species detection and density were estimated for each park using a Bayesian hierarchical modeling framework outlined briefly here and detailed in Ray and others (2017a, 2017b). The hierarchy involves 1 level at which the count of birds (y) is a function of the number of birds available for detection (n) and the probability that each will be detected (p_d), and another level at which p_d is a function of potential covariates like observer identity and day of year. The number of birds available is also a function of the number present (N) and the probability that each bird present makes itself available for detection (p_a) through vocalization or other conspicuous behaviors (Amundson et al. 2014).

Data from multiple count intervals were used to generate individual detection histories modeled in a closed-population framework to characterize p_a (Alldredge and others 2007). We followed Farnsworth and others (2002) in modeling availability from time-removal data, in which each detection was assigned to 1 of 3 count intervals (<3, 3–5 or >5 min), and subsequent detections of the same individual were ignored. We modeled availability as a function of point- and/or year-specific covariates, x_{kt}, as $\mathrm{logit}(q_{kt}) = \alpha_0 + \sum_x \alpha_x x_{kt}$, where q is the per-minute probability of a bird's failure to be vocal, conspicuous, or otherwise available for detection, and subscripts k and t denote point and year. To characterize p_d, we first dropped about 10% of the farthest (least accurate) detections of each species to obtain the maxi-

mum effective detection distance (per Kéry and Royle 2016) and then sorted the remaining detection distances into variable-width bins, equalizing the number of detections in each bin (Amundson and others 2014). We followed Buckland and others (2001) in modeling the probability of detecting a bird in distance bin b using the half-normal distribution, which is controlled by shape parameter σ, the decay rate of detections with distance. We then modeled σ as a function of point- and year-specific covariates as $\log(\sigma_{kt}) = \log(\sigma_0) + \sum_x \alpha_x x_{kt}$.

We combined these models of p_a and p_d with a model of N in an "N-mixture" or binomial mixture model of the count y. N-mixture models typically embed a Poisson model of λ (expected N) in a binomial model of y, providing a hierarchical extension of generalized linear models to allow for structure in parameters at each hierarchical level (Royle 2004). Here, we follow Amundson and others (2014) by linking a Poisson model of λ as a function of environmental covariates with 2 binomial models expressing detection as functions of q and σ. Our "basic" model (Table 2) featured a log-linear trend in λ and no covariates of detection, whereas our "climate" model added fixed effects of PAS and $rMST$ on λ.

As detailed in Ray and others (2017a, 2017b), we assumed no prior information about the distribution of values that each unknown parameter might take; for example, our uninformative prior for α_0 was normal with mean 0 and variance 100. We used the JAGS programmable platform (Plummer 2003) for Markov chain Monte Carlo (MCMC) simulation to characterize the posterior probability distribution of each parameter. MCMC randomly samples the joint parameter space while requiring that successive sample parameter values generally increase the probability of obtaining the observed data given

TABLE 3.   Survey effort by year and park.

| Year | Number of point-count surveys | | Survey minutes per point |
	SAJH	LEWI	
2005	109		5
2006		81[1]	5
2007	54		5
2008		68	5
2009	54		5
2010		71	5
2011	54		7
2012		71	7
2013	54		7
2014		74[2]	7
2015	54		7
2016		73	7
Total	379	438	

[1] Of these 81 points, 8 in Cape Disappointment State Park and 2 in Dismal Nitch were retired after 2006, and data from these 10 retired points were omitted from all LEWI analyses, including survey-effort adjustments.
[2] The YEON parcel and its 3 point-count stations were added to LEWI after 2012.

the proposed model. Using 3 chains of 100,000 samples each, we discarded 50,000 initial samples and thinned the remaining samples by 50 to obtain 3000 uncorrelated samples from the posterior distribution of each parameter. We assessed the convergence of parameter estimates using the Gelman-Rubin potential scale reduction parameter, R-hat, and visual inspection of MCMC summaries provided by JAGS. For convergent estimates of each focal parameter, we present the expected value and 95% Bayesian credible interval (CRI), which contains the value of the focal parameter with a subjective probability of 0.95. Components of model fit were characterized using Bayesian P-values generated from posterior predictive distributions, suggesting good fit for P near 0.5 and inadequate fit for $P < 0.1$ or $P > 0.9$. We called JAGS remotely using *jagsUI* (Kellner 2015) from the R environment for statistical computing (R Core Team 2017), and used R for all other analyses and plots.

MCMC simulation resulted in an estimate of N for every point in every year, including the non-survey years in each park and points surveyed only in the 1st year of each study (Table 3). We excluded, however, 10 point-count stations surveyed in LEWI in 2006 that fell outside the final sampling frame. These 10 points included 8 in the northern portion of the Cape Disappointment peninsula and 2 in the separate parcel called Dismal Nitch. The scope of

inference for LEWI does not include Dismal Nitch or the narrow, northern reach of Cape Disappointment.

In addition to fitting the coefficients (β) in Table 2, we estimated annual population density (N/ha) averaged over all point-count stations within a park unit (1 or more parcels within a park) by dividing the sum of N across all stations in the unit by the number of stations in the unit and the effective area surveyed at each station. Effective area surveyed varied with detection distance for each species.

For comparison with estimates of annual population density, we also present raw annual counts corrected for survey effort and rescaled for presentation. Specifically, the raw count for species x in year t, y_{xt}, was corrected for effort as $y_{xt}{}^c = y_{xt}/P_t/M_t$, where P_t was the number of points surveyed and M_t was the number of minutes surveyed per point in year t. Counts corrected for survey effort were then rescaled as $y_{xt} = y_{xt}{}^c/\min_{nz}(y_{xt}{}^c)$, where $\min_{nz}(y_{xt}{}^c)$ was the smallest non-zero value of $y_{xt}{}^c$.

RESULTS

From 2005 to 2016, we completed 817 point-count surveys at 163 points in SAJH and 76 points in LEWI (after excluding 10 points in LEWI that fell outside the final sampling frame). These counts resulted in the detection of 111 species across the 2 parks, including 7428 individuals of 98 species in SAJH and 7224 individuals of 89 species in LEWI (Table 4; note: refer to this table for the scientific names of bird species mentioned in this article). Counts of zero, where no species were detected, did not occur in these parks. Most detections (97.67% in SAJH and 98.30% in LEWI) were of individual birds, and most flocks were composed of non-landbirds such as the Glaucous-winged Gull (in both parks) and Caspian Tern (in LEWI). Although seabirds, shorebirds and waterfowl were commonly detected, most (85) of the 111 species detected were landbirds (Table 4).

Climatic Variation during the Monitoring Period

Our metrics of spring conditions, precipitation-as-snow (*PAS*), and mean spring temperature (*MST*), varied roughly in opposition (Fig. 2), with the annual *PAS* anomaly (upper left panel) generally rising from 2004 to 2009 and then falling from 2011 to 2015, and conversely for the
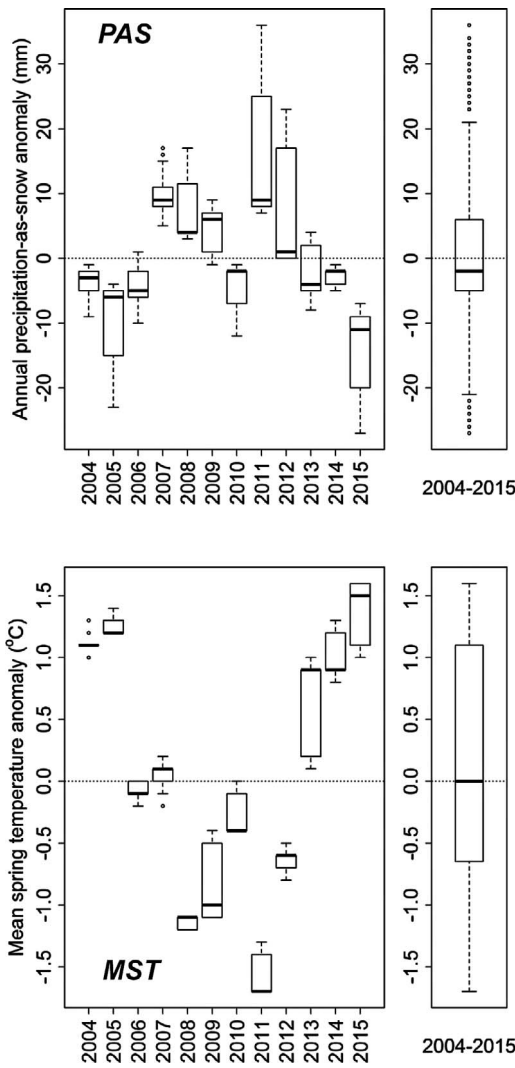
FIGURE 2. Anomalies in precipitation-as-snow (*PAS*, upper panel) and mean spring temperature (*MST*, lower panel) during the landbird monitoring period, lagged by 1 year to allow for demographic response to breeding habitat conditions.

annual *MST* anomaly (lower left panel). The *PAS* anomaly during 2004 to 2015 was somewhat lower than its 1971 to 2000 normals (upper right panel), whereas the *MST* anomaly was consistent with its 1971 to 2000 normals (lower right panel). Thus, snows were lighter but springs were not warmer than the long-term average during our monitoring period. In contrast, mountain parks during this period experienced both lighter snows and warmer springs (Ray

and others 2017a). Relative to the mountain parks, the historical parks are located at lower elevations in more coastal climates. Although historical parks experienced a range of anomalies in *MST* comparable to the mountain parks (Ray and others 2017a), they experienced a much smaller range of anomalies in *PAS*, reflecting the smaller range of (lagged) *PAS* received annually from 2004 to 2015: 6–44 mm in SAJH and 13–83 mm in LEWI, but 19–2992 mm across all survey points in the mountain parks.

Fitted Models

We successfully fitted models to data from 50 of the species detected, including 40 species in SAJH, 39 in LEWI, and 29 in both parks (Table 5). Our models estimated missing data from non-survey years within the monitoring period, but avoided extrapolation outside the monitoring period. Thus, trends in SAJH were estimated for the period 2005 to 2015, whereas trends in LEWI were estimated for the period 2006 to 2016.

Models that included more covariates than our default, "basic" model were less likely to be supported (Table 5). For example, of 40 species fitted to the basic model in SAJH, 8 (20%) were not fitted to the climate model because parameter estimates failed to converge. Models that included covariates of detection also were rarely supported by our data. Effects of hour or day on species availability were never supported, and covariates of perceptibility were supported in only 2 cases: forest cover reduced Dark-eyed Junco detection, and ambient noise reduced American Robin detection. Observer effects were difficult to implement because the observer covariate was missing whenever surveys were not conducted, which was every 2nd year in these parks. When a single value for "observer" was assigned to all station-years with missing data, that value became the most common "observer" in the dataset, biasing results from a random-effects model. However, 1 change in model structure greatly improved models for several species: for Hermit Warbler in LEWI, and for Barn Swallow, European Starling, and Cedar Waxwing in SAJH, poor model fit or lack of convergence was alleviated by narrowing the scope of inference to include only those parcels where the focal species was detected. Such "habitat specialists" were easy to accommodate

TABLE 4.   Species identified during point-count surveys conducted biennially from 2005 to 2015 at San Juan Island National Historical Park (SAJH) and from 2006 to 2016 at Lewis and Clark National Historical Park (LEWI).

			Total count	
Species code	Common name	Scientific name	SAJH	LEWI
CACG	Cackling Goose	*Branta hutchinsii*	0	1
CANG	Canada Goose	*Branta canadensis*	137	74
WODU	Wood Duck	*Aix sponsa*	0	1
BWTE	Blue-winged Teal	*Spatula discors*	2	0
MALL	Mallard	*Anas platyrhynchos*	13	22
GWTE	Green-winged Teal	*Anas crecca*	1	0
SUSC	Surf Scoter	*Melanitta perspicillata*	55	0
CAQU	California Quail	*Callipepla californica*	44	0
RNEP	Ring-necked Pheasant	*Phasianus colchicus*	6	1
PBGR	Pied-billed Grebe	*Podilymbus podiceps*	0	3
BTPI	Band-tailed Pigeon	*Patagioenas fasciata*	11	35
EUCD	Eurasian Collared-Dove	*Streptopelia decaocto*	10	9
MODO	Mourning Dove	*Zenaida macroura*	29	0
VASW	Vaux's Swift	*Chaetura vauxi*	5	1
ANHU	Anna's Hummingbird	*Calypte anna*	1	12
RUHU	Rufous Hummingbird	*Selasphorus rufus*	80	32
VIRA	Virginia Rail	*Rallus limicola*	0	2
BLOY	Black Oystercatcher	*Haematopus bachmani*	4	0
AMGP	American Golden-Plover	*Pluvialis dominica*	1	0
KILL	Killdeer	*Charadrius vociferus*	7	3
WHIM	Whimbrel	*Numenius phaeopus*	0	2
COMU	Common Murre	*Uria aalge*	8	0
PIGU	Pigeon Guillemot	*Cepphus columba*	35	0
RHAU	Rhinoceros Auklet	*Cerorhinca monocerata*	52	0
WEGU	Western Gull	*Larus occidentalis*	0	31
CAGU	California Gull	*Larus californicus*	1	1
GWGU	Glaucous-winged Gull	*Larus glaucescens*	726	141
CATE	Caspian Tern	*Hydroprogne caspia*	1	366
PALO	Pacific Loon	*Gavia pacifica*	11	2
COLO	Common Loon	*Gavia immer*	4	1
DCCO	Double-crested Cormorant	*Phalacrocorax auritus*	5	3
PECO	Pelagic Cormorant	*Phalacrocorax pelagicus*	14	85
BRPE	Brown Pelican	*Pelecanus occidentalis*	0	184
GBHE	Great Blue Heron	*Ardea herodias*	3	3
TUVU	Turkey Vulture	*Cathartes aura*	5	3
OSPR	Osprey	*Pandion haliaetus*	1	7
BAEA	Bald Eagle	*Haliaeetus leucocephalus*	71	35
RTHA	Red-tailed Hawk	*Buteo jamaicensis*	7	3
NOPO	Northern Pygmy-Owl	*Glaucidium gnoma*	0	1
BADO	Barred Owl	*Strix varia*	0	1
BEKI	Belted Kingfisher	*Megaceryle alcyon*	5	1
RBSA	Red-breasted Sapsucker	*Sphyrapicus ruber*	1	0
DOWO	Downy Woodpecker	*Picoides pubescens*	0	12
HAWO	Hairy Woodpecker	*Picoides villosus*	13	20
NOFL	Northern Flicker	*Colaptes auratus*	33	29
PIWO	Pileated Woodpecker	*Dryocopus pileatus*	24	7
PEFA	Peregrine Falcon	*Falco peregrinus*	0	8
OSFL	Olive-sided Flycatcher	*Contopus cooperi*	61	67
WEWP	Western Wood-Pewee	*Contopus sordidulus*	3	11
WIFL	Willow Flycatcher	*Empidonax traillii*	1	0
HAFL	Hammond's Flycatcher	*Empidonax hammondii*	2	1
DUFL	Dusky Flycatcher	*Empidonax oberholseri*	1	0
PSFL	Pacific-slope Flycatcher	*Empidonax difficilis*	300	423
HUVI	Hutton's Vireo	*Vireo huttoni*	9	50
CAVI	Cassin's Vireo	*Vireo cassinii*	35	2
WAVI	Warbling Vireo	*Vireo gilvus*	83	59
STJA	Steller's Jay	*Cyanocitta stelleri*	1	75

TABLE 4. Continued.

Species code	Common name	Scientific name	Total count SAJH	Total count LEWI
AMCR	American Crow	*Corvus brachyrhynchos*	199	312
CORA	Common Raven	*Corvus corax*	70	67
TRES	Tree Swallow	*Tachycineta bicolor*	1	10
VGSW	Violet-green Swallow	*Tachycineta thalassina*	9	56
NRWS	Northern Rough-winged Swallow	*Stelgidopteryx serripennis*	16	8
CLSW	Cliff Swallow	*Petrochelidon pyrrhonota*	2	2
BARS	Barn Swallow	*Hirundo rustica*	70	70
BCCH	Black-capped Chickadee	*Poecile atricapillus*	1	59
CBCH	Chestnut-backed Chickadee	*Poecile rufescens*	186	213
BUSH	Bushtit	*Psaltriparus minimus*	14	4
RBNU	Red-breasted Nuthatch	*Sitta canadensis*	162	33
BRCR	Brown Creeper	*Certhia americana*	69	55
ROWR	Rock Wren	*Salpinctes obsoletus*	1	0
HOWR	House Wren	*Troglodytes aedon*	265	0
PAWR	Pacific Wren	*Troglodytes pacificus*	75	481
MAWR	Marsh Wren	*Cistothorus palustris*	0	130
BEWR	Bewick's Wren	*Thryomanes bewickii*	35	48
GCKI	Golden-crowned Kinglet	*Regulus satrapa*	67	215
SWTH	Swainson's Thrush	*Catharus ustulatus*	259	742
AMRO	American Robin	*Turdus migratorius*	606	368
VATH	Varied Thrush	*Ixoreus naevius*	26	11
EUST	European Starling	*Sturnus vulgaris*	70	29
CEDW	Cedar Waxwing	*Bombycilla cedrorum*	44	68
EVGR	Evening Grosbeak	*Coccothraustes vespertinus*	1	18
HOFI	House Finch	*Haemorhous mexicanus*	108	2
PUFI	Purple Finch	*Haemorhous purpureus*	90	159
RECR	Red Crossbill	*Loxia curvirostra*	231	52
PISI	Pine Siskin	*Spinus pinus*	107	3
AMGO	American Goldfinch	*Spinus tristis*	309	80
SPTO	Spotted Towhee	*Pipilo maculatus*	269	36
CHSP	Chipping Sparrow	*Spizella passerina*	21	0
CCSP	Clay-colored Sparrow	*Spizella pallida*	1	0
VESP	Vesper Sparrow	*Pooecetes gramineus*	10	0
SAVS	Savannah Sparrow	*Passerculus sandwichensis*	368	21
SOSP	Song Sparrow	*Melospiza melodia*	161	273
WCSP	White-crowned Sparrow	*Zonotrichia leucophrys*	328	118
GCSP	Golden-crowned Sparrow	*Zonotrichia atricapilla*	1	0
DEJU	Dark-eyed Junco	*Junco hyemalis*	107	154
RWBL	Red-winged Blackbird	*Agelaius phoeniceus*	126	112
BHCO	Brown-headed Cowbird	*Molothrus ater*	277	114
BRBL	Brewer's Blackbird	*Euphagus cyanocephalus*	1	0
OCWA	Orange-crowned Warbler	*Oreothlypis celata*	269	141
NAWA	Nashville Warbler	*Oreothlypis ruficapilla*	1	0
MGWA	MacGillivray's Warbler	*Geothlypis tolmiei*	1	5
COYE	Common Yellowthroat	*Geothlypis trichas*	44	116
AMRE	American Redstart	*Setophaga ruticilla*	1	0
YEWA	Yellow Warbler	*Setophaga petechia*	20	70
YRWA	Yellow-rumped Warbler	*Setophaga coronata*	45	19
BTYW	Black-throated Gray Warbler	*Setophaga nigrescens*	67	112
TOWA	Townsend's Warbler	*Setophaga townsendi*	99	7
HEWA	Hermit Warbler	*Setophaga occidentalis*	0	165
WIWA	Wilson's Warbler	*Cardellina pusilla*	96	373
WETA	Western Tanager	*Piranga ludoviciana*	61	113
BHGR	Black-headed Grosbeak	*Pheucticus melanocephalus*	39	150

TABLE 5.   Models, as described in Table 2, fitted to species commonly detected in each park or parcel. "No" indicates that the species was detected too rarely to support convergence of model parameter estimates.

Species code[1]	SAJH Basic[2]	SAJH Climate[2]	LEWI Basic	LEWI Climate
CAQU	Yes	No	No	No
BTPI	No	No	Yes	Yes
MODO	Yes	No	No	No
RUHU	Yes	Yes	Yes	Yes
BAEA	Yes	Yes	Yes	Yes
HAWO	No	No	Yes	No
NOFL	No	No	Yes	Yes
OSFL	Yes	Yes	Yes	Yes
PSFL	Yes	Yes	Yes	Yes
HUVI	No	No	Yes	Yes
CAVI	Yes	No	No	No
WAVI	Yes	Yes	Yes	Yes
STJA	No	No	Yes	Yes
AMCR	Yes	Yes	Yes	Yes
CORA	Yes	Yes	Yes	No
BARS	Yes, AMCA[3]	Yes, AMCA	No	No
BCCH	No	No	Yes	Yes
CBCH	Yes	Yes	Yes	Yes
RBNU	Yes	Yes	Yes	Yes
BRCR	Yes	Yes	Yes	Yes
HOWR	Yes	Yes	No	No
PAWR	Yes	Yes	Yes	Yes
MAWR	No	No	Yes	Yes
BEWR	No	No	Yes	No
GCKI	Yes	Yes	Yes	Yes
SWTH	Yes	Yes	Yes	Yes
AMRO	Yes, Noise[4]	Yes	Yes, Noise	Yes
EUST	Yes, AMCA	No	No	No
CEDW	Yes, AMCA	No	No	No
HOFI	Yes	Yes	No	No
PUFI	Yes	Yes	Yes	Yes
PISI	Yes	Yes	No	No
AMGO	Yes	Yes	Yes	Yes
SPTO	Yes	Yes	Yes	No
SAVS	Yes	Yes	Yes	No
SOSP	Yes	Yes	Yes	Yes
WCSP	Yes	Yes	Yes	Yes
DEJU	Yes, Forest[5]	Yes	Yes, Forest	Yes
RWBL	Yes	Yes	Yes	Yes
BHCO	Yes	Yes	Yes	Yes
OCWA	Yes	Yes	Yes	Yes
COYE	Yes	No	Yes	Yes
YEWA	Yes	No	Yes	Yes
YRWA	Yes	No	No	No
BTYW	Yes	Yes	Yes	Yes
TOWA	Yes	Yes	No	No
HEWA	No	No	Yes, FOCL[6]	Yes, FOCL
WIWA	Yes	Yes	Yes	Yes
WETA	Yes	Yes	Yes	Yes
BHGR	No	No	Yes	Yes

[1] See Table 4 for species code definitions
[2] See Table 2 for descriptions of the Basic and Climate models.
[3] Species detected only in the American Camp (AMCA) parcel of SAJH; species data were used to develop a model specific to AMCA.
[4] Basic models for AMRO included a well-supported effect of noise on detection.
[5] Basic models for DEJU included a well-supported effect of forest cover on detection.
[6] Species detected only in the Fort Clatsop (FOCL) parcel of LEWI; species data were used to develop a model specific to FOCL.
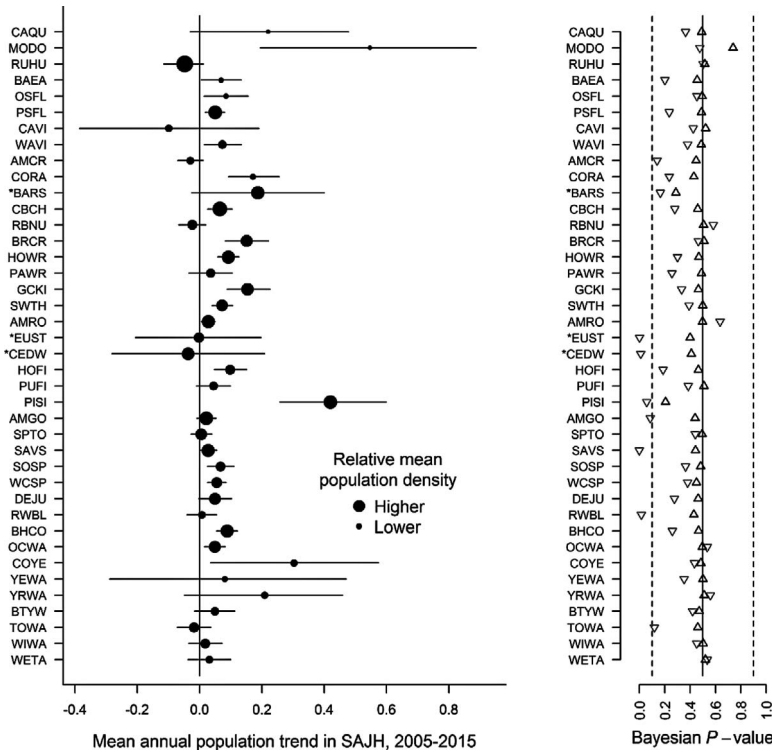
FIGURE 3. Population trend estimates with 95% credible intervals (left-hand panel) and metrics of model fit (right-hand panel) for species in San Juan Island National Historical Park (SAJH). Species are listed top to bottom in taxonomic order, using abbreviations defined in Table 4. Asterisks indicate species observed and modeled only in the American Camp portion of SAJH. Bayesian P-values (right-hand panel) distinguish fit to the sub-model of species availability (upright triangles) from fit to the overall model of detectability after including effects of species perceptibility (inverted triangles). Population density (relative to other species graphed) is indicated by the relative size of dots in the left-hand panel.

in these fragmented parks, comprising discrete parcels that could be dropped where the focal species was rarely or never detected.

Trends in San Juan Island National Historical Park

Point-count surveys conducted in odd-numbered years from 2005 to 2015 in San Juan Island National Historical Park (SAJH) resulted in the detection of 79 landbird species along with several seabirds, shorebirds and waterfowl (Table 4). The Glaucous-winged Gull (count = 726) was the most common bird detected during point counts, followed by the American Robin (count = 606). Just under half (*n* = 32) of the landbird species detected in SAJH were recorded fewer than 17 times each, too infrequently to support our models of detectability and population trend. The Yellow Warbler, detected only

20 times in SAJH, was the most rarely detected species to support our models, but trends could not be estimated for 7 species with total counts higher than 20: Chipping Sparrow (count = 21), Pileated Woodpecker (24), Varied Thrush (26), Bewick's Wren (35), Northern Flicker (33), Black-headed Grosbeak (39) and Red Crossbill (231). In Red Crossbill, flocking behavior likely introduced unmodeled heterogeneity in detection probability that precluded the convergence of parameter estimates or contributed to poor model fit.

We estimated mean annual trends in population density (Fig. 3) as stable or increasing during the monitoring period for each of the 40 landbird species analyzed in SAJH. Trends were clearly positive for almost half of these species, and no declines were supported. In Appendix 1, we quantify the maximum detection distance

(d_{max}), effective survey area, mean population density (N/ha) and associated 95% credible interval (CRI), mean annual trend in abundance (N/year) and associated 95% CRI, and 2 components of model fit: Bayesian P-values for the sub-models of species availability and overall detectability.

Estimates of N/ha scaled inversely with maximum detection distance and ranged from 0.012 for both Mourning Dove and California Quail, to 1.439 for Chestnut-backed Chickadee and 3.187 for Rufous Hummingbird (Appendix 1). However, the density of hummingbirds was likely overestimated owing to their unusual attraction to observers, which might result in low detection distances that inflate density estimates.

Our default detection model assumed constant availability and perceptibility of a species, corresponding to constant q and σ. We evaluated fit for each component of detection using Bayesian P-values (Fig. 3, right-hand panel), distinguishing fit to the model of availability (upright triangles) from fit to the model incorporating perceptibility (inverted triangles). Results suggest that constant availability was an acceptable assumption for every species modeled (Bayesian P-values were close to 0.5), and constant perceptibility was an adequate assumption for the vast majority of species. However, extreme Bayesian P-values signal that the default model of perceptibility was less than adequate for at least 6 of the 40 species (European Starling, Cedar Waxwing, Savannah Sparrow, Red-winged Blackbird, Pine Siskin, and American Goldfinch). Flocking behavior likely contributed to poor model fit in most of those 6 species. For the European Starling, Cedar Waxwing, and Barn Swallow, convergence of parameter estimates was achieved by censoring data from British Camp, where these species were not detected. For these 3 species, counts and density estimates are reported only for the American Camp portion of SAJH.

In addition to fitting a linear trend to the annual data for each focal species in SAJH (Fig. 3), we also estimated mean annual population density as N_t/ha using our "basic" models (Fig. 4). The mean trajectory (solid line) for almost every species suggests stability or increase over the monitoring period, with the possible exception of Rufous Hummingbird, Cassin's Vireo, American Crow, and Red-breasted Nuthatch. However, the 95% credible intervals on each time series of population density suggest at least the potential for stable dynamics in every species.

We also plotted effort-adjusted counts for each focal species in SAJH (Fig. 5) for comparison with modeled estimates of trend and population density. Effort varied with the number of points accessed each year (by chance and due to the reduction in point-count station density after the 1st year of surveys) and with the number of count intervals per survey (increased in 2011 from 2 to 3 intervals or from 5 to 7 min). Although counts are temporally sparse in the SAJH dataset, and do not reflect effects of detection probability and covariates, we see at least general congruence when comparing modeled estimates of annual population density (Fig. 4) with effort-adjusted counts (Fig. 5). Species with rising estimates of density over the monitoring period tend to have rising counts, and vice versa. Species with more variable counts generally exhibit more variable mean estimates of density associated with wider 95% credible intervals. The rescaled number of birds counted (Fig. 5) varies less among species than the estimated population size (Fig. 4) owing to variation among species in effective detection distance (effective survey area).

Trends in Lewis and Clark National Historical Park

Point-count surveys conducted in even-numbered years from 2006 to 2016 in Lewis and Clark National Historical Park (LEWI) resulted in the detection of 71 landbird species along with several seabirds, shorebirds, and waterfowl (Table 4). Swainson's Thrush (count = 742) was the most common bird detected during point counts, followed by Pacific Wren (count = 481). Over 1/3 ($n = 27$) of the landbird species detected in LEWI were recorded fewer than 20 times each during the monitoring period, too infrequently to support our analyses. Hairy Woodpecker, detected only 20 times in LEWI, was the most rarely detected species to support our models, but trends could not be estimated for 5 (often flocking) species with higher total counts: European Starling ($n = 29$), Red Crossbill ($n = 52$), Violet-green Swallow ($n = 56$), Barn Swallow ($n = 70$), and Cedar Waxwing ($n = 68$).

Mean annual trends in population density (Fig. 6) were estimated as stable or increasing during the monitoring period for all but 3 of 39 landbird species commonly detected in LEWI.
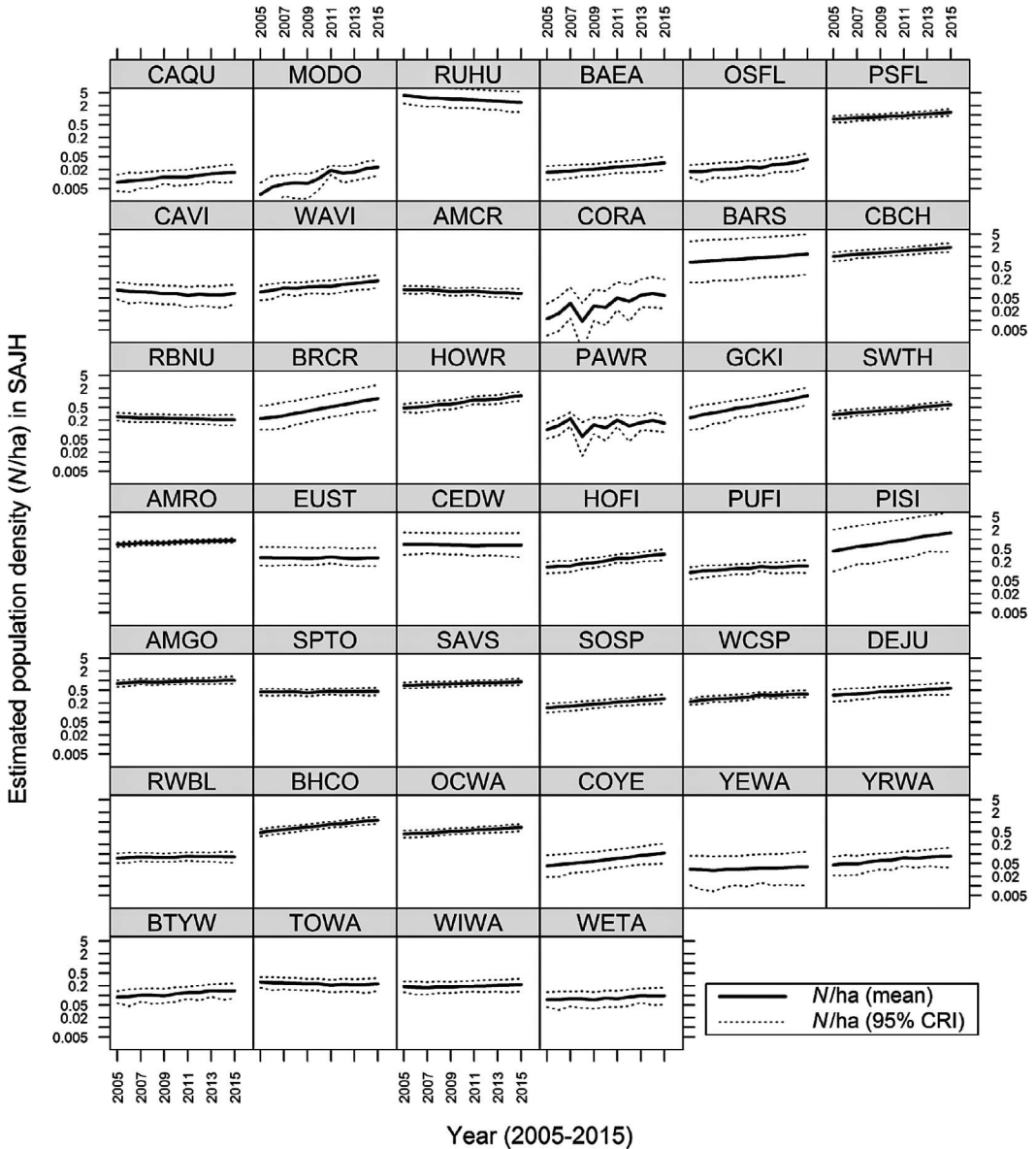
FIGURE 4.   Yearly estimates of population density (*N*/ha) for 40 species commonly detected in San Juan Island National Historical Park (SAJH). Density estimates, summarized here on a log$_{10}$ scale by means (solid lines) and 95% credible intervals (dotted lines), were based on the "basic" models listed in Table 2. BARS, EUST, and CEDW densities apply only to American Camp.

Trends were clearly positive for at least 20 of these species, but declines were supported for Northern Flicker (Fig. 7), Olive-sided Flycatcher, and Hutton's Vireo. Estimates of mean *N*/ha ranged from 0.023 for Common Raven to 2.230 for Chestnut-backed Chickadee and 2.884 for Rufous Hummingbird (Appendix 2). Constant availability appeared to be an acceptable assumption for every species modeled (Fig. 6), but assuming constant perceptibility resulted in poor detection-model fit for about 6 (15%) of the 39 species (Bald Eagle, Marsh Wren, Common Yellowthroat, White-crowned Sparrow, Dark-eyed Junco, and Red-winged Blackbird).
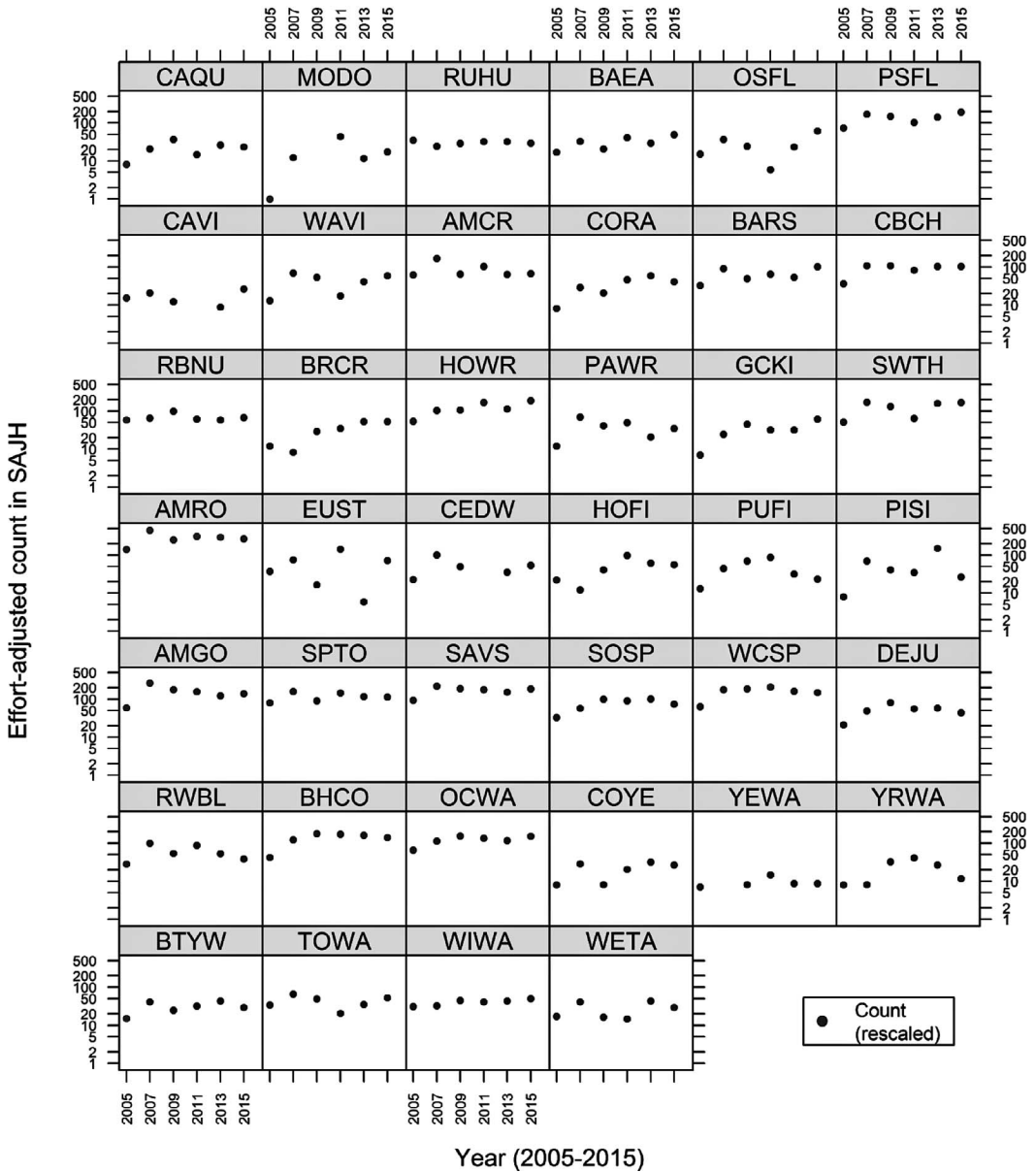
FIGURE 5.   Effort-adjusted counts for 40 species commonly detected in San Juan Island National Historical Park (SAJH). Surveys in SAJH were conducted in odd-numbered years. Counts per point and minute surveyed were rescaled for comparison on a log_{10} scale by setting the lowest non-zero count to 1. Counts are missing for even-numbered years when surveys were not conducted in this park, and counts of zero are not plotted. BARS, EUST, and CEDW counts apply only to American Camp.

Mean annual population density estimates (Fig. 8) suggest general stability or increase over the monitoring period, with the possible exception of Rufous Hummingbird, Northern Flicker, Olive-sided Flycatcher, Hutton's Vireo, and Red-breasted Nuthatch. However, the 95% CRI on each time series of population density suggests at least the potential for stable dynamics in every species except the Olive-sided Flycatcher.
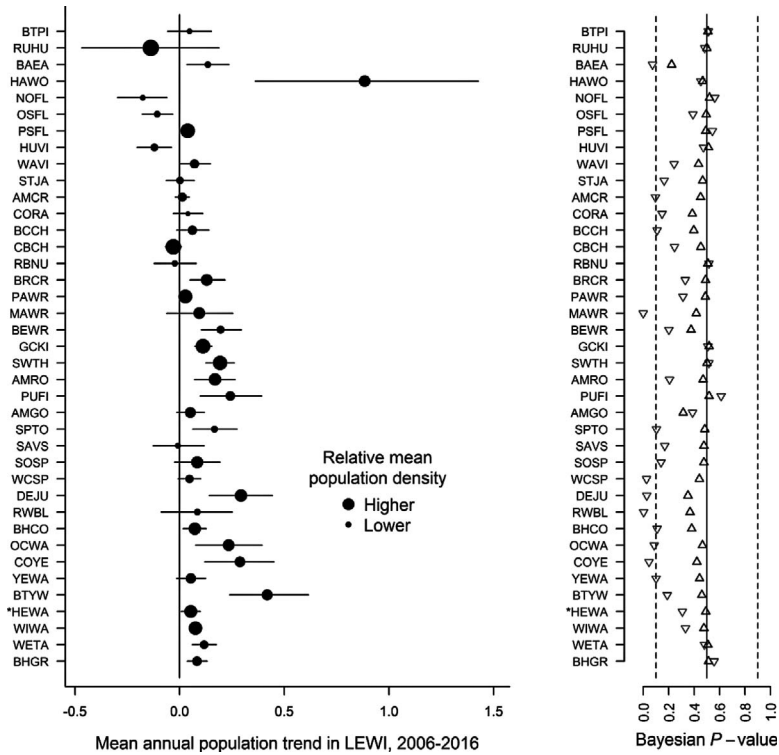
FIGURE 6. Population trend estimates with 95% credible intervals (left-hand panel) and metrics of model fit (right-hand panel) for species in Lewis and Clark National Historical Park (LEWI). Species are listed top to bottom in taxonomic order, using abbreviations defined in Table 4. Asterisks indicate species observed and modeled only in the Fort Clatsop portion of LEWI. Bayesian *P*-values (right-hand panel) distinguish fit to the sub-model of species availability (upright triangles) from fit to the overall model of detectability after including effects of species perceptibility (inverted triangles).

Effort-adjusted counts (Fig. 9) show general congruence with modeled estimates of annual population density, as in SAJH (Fig. 5). The general concordance between effort-adjusted counts and modeled trend estimates that account for imperfect detection implies that effort-adjusted counts might be suggestive of trends for species that we could not fit to our models, so we note here that effort-adjusted counts for the flocking and rare species mentioned above did not appear to trend more negatively than those shown in Figure 5 and Figure 9. However, trend estimates can be strongly influenced by a high or low count in a single year, as exemplified by counts for the Warbling Vireo, which appeared to decline consistently from 2006 to 2014, followed by a dramatic increase in 2016. Uncertainty in the Warbling Vireo trend is reflected in the broad 95% CRI for its trajectory of population densities (Fig. 8), as well as the

zero at one end of its 95% CRI for trend (0.000–0.147; Fig. 6, Appendix 2). Similarly, effort-adjusted counts for rarely detected and flocking species often appear variable owing to the lower signal-to-noise in small or correlated numbers. Note also that Hermit Warbler counts-per-effort appear higher than other species in Figure 9 mainly because effort was lowest for this species after censoring data from all parcels outside Fort Clatsop to reflect the localized distribution of this species.

Effects of Climate in the Historical Parks

Annual anomalies in *PAS* explained substantial variation in population density for 9 species in SAJH and 7 species in LEWI (Fig. 10). Effects of *PAS* varied among parks, however, with unanimously negative effects in SAJH and almost evenly divided (4 positive and 3 nega-

FIGURE 7. Northern Flicker (shown) was 1 of 3 species estimated to have declined in LEWI from 2006 to 2016. No declines were detected in SAJH, and Northern Flicker declines in LEWI were not related to lagged precipitation-as-snow or mean spring temperature. Photo by Rob McCay.

tive) effects in LEWI. After accounting for effects of *PAS*, residual effects of *MST* also varied among parks. Residual *MST* (*rMST*) had predominantly negative effects in SAJH (7 negative and 2 positive) and predominantly positive effects in LEWI (2 negative and 5 positive). Larger effect sizes also tended to be associated with larger credible intervals on the effect size for *rMST* (Fig. 10). Together, these results suggest that longer time-series are needed to clarify effects of climate in these coastal parks.

It was rare for estimates of trend to be appreciably affected by the addition of climate covariates. However, for some species in the historical parks, such as Barn Swallow in American Camp at SAJH, there was strong support for a positive trend only after accounting for effects of climate. To investigate the generality of this effect, we tested for correlation between paired trends estimated using basic versus climate models for each park (Table 4). Pearson's product-moment correlation was high

and significant for each test ($\rho = 0.70$, $t = 5.39$, $df = 30$, $P << 0.001$ for SAJH; $\rho = 0.58$, $t = 4.04$, $df = 32$, $P < 0.001$ for LEWI), showing little effect of our climate metrics on trend estimates.

DISCUSSION

We estimated that nearly all of the breeding populations analyzed in SAJH or LEWI have been stable or increasing between 2005 and 2016. The 50 species suitable for our analyses represent a large proportion (59%) of the 85 landbird species detected at least once in our surveys of these 2 parks. These results from 2 smaller parks in mixed-use landscapes are consistent with a previous finding of mainly stable or increasing trends in landbird populations across the 3 large wilderness parks of this region over approximately the same time period (Ray and others 2017a). Stability in the mountain parks was evident even when allowing for trends specific to each elevational stratum, providing no clear evidence for up-slope range adjustments. The largely stable or increasing densities we found in these low-elevation parks also fail to support up-slope range adjustments in response to climatic drivers.

Effects of annual variation in climate were less evident in these low-elevation, coastal parks than in the nearby mountain parks (Ray and others 2017a). In SAJH, however, years of lower breeding density followed years of higher snowfall, in keeping with results from the mountain parks. Thus, the slight depression in recent snowfall in this region, relative to the long-term average, might have contributed to the generally favorable trends we found. Of course, effects of climate in these breeding habitats might be masked, for migratory species, by other effects of climate in non-breeding habitats (Nott and others 2002). However, we saw no difference in the number or direction of trends when comparing migrant with resident species: for example, declining species were split between residents like Hutton's Vireo and migrants like Olive-sided Flycatcher, and in this case the migrant exhibited one of the strongest apparent responses to local precipitation-as-snow.

In addition to climate, there are many possible drivers that might explain our results. The most obvious differences between the historical and wilderness parks in this region involve park size
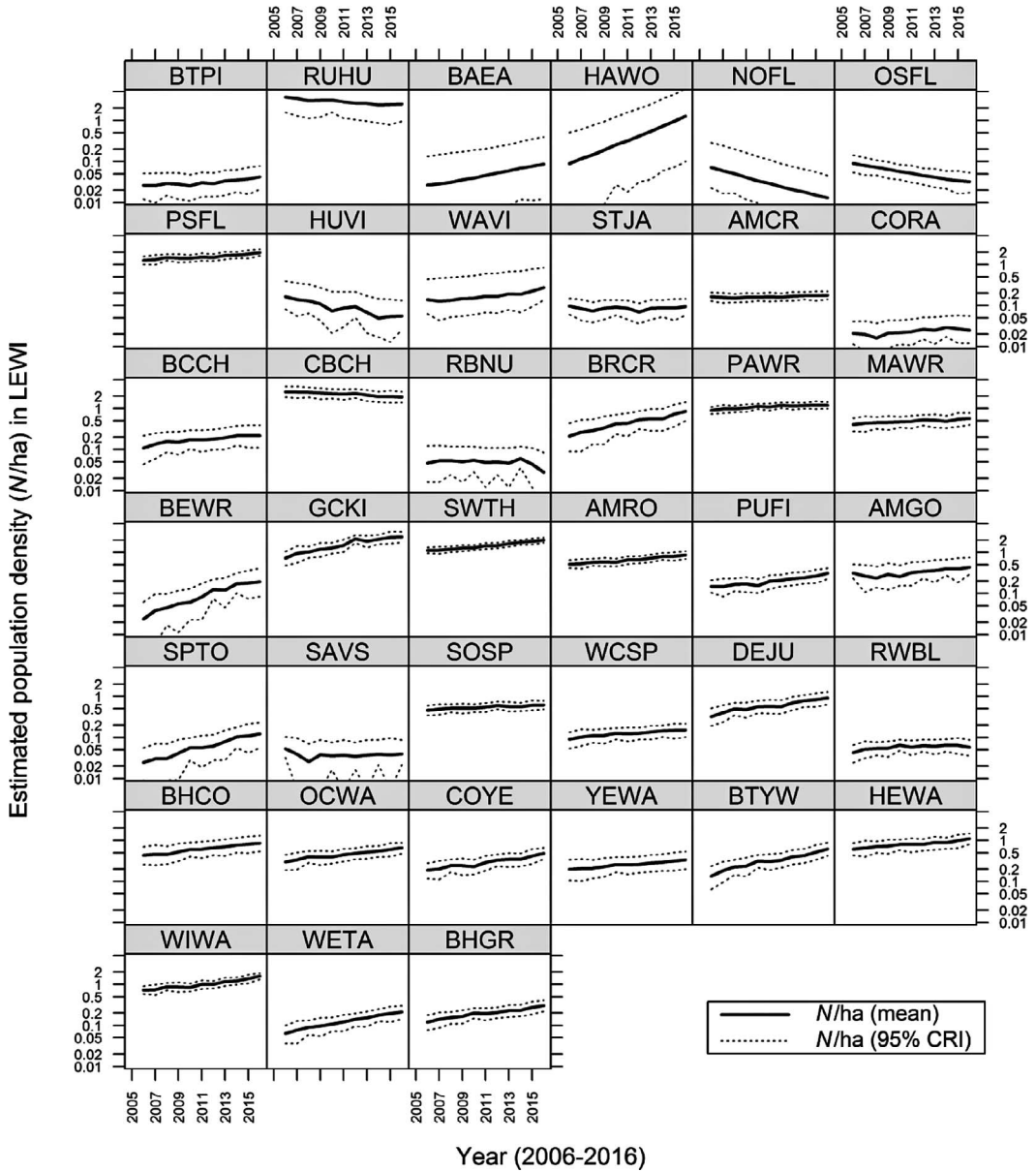
FIGURE 8. Yearly estimates of population density (N/ha) for 39 species commonly detected in Lewis and Clark National Historical Park (LEWI). Density estimates, summarized here on a $\log_{10}$ scale by means (solid lines) and 95% credible intervals (dotted lines), were based on the "basic" models listed in Table 2. HEWA densities apply only to Fort Clatsop.

and habitat quality. We might expect these smaller parks in mixed-use landscapes to show weaker evidence of population growth for several reasons, including their higher potential for edge effects and their lack of climate-modulating old-growth forest (Betts et al.

2017). However, positive trends in landbird densities in these historical parks were at least as common as in the wilderness parks, evidence of suitable conditions for most of these bird species. By generating annual species density estimates from the broad spectrum of habitat
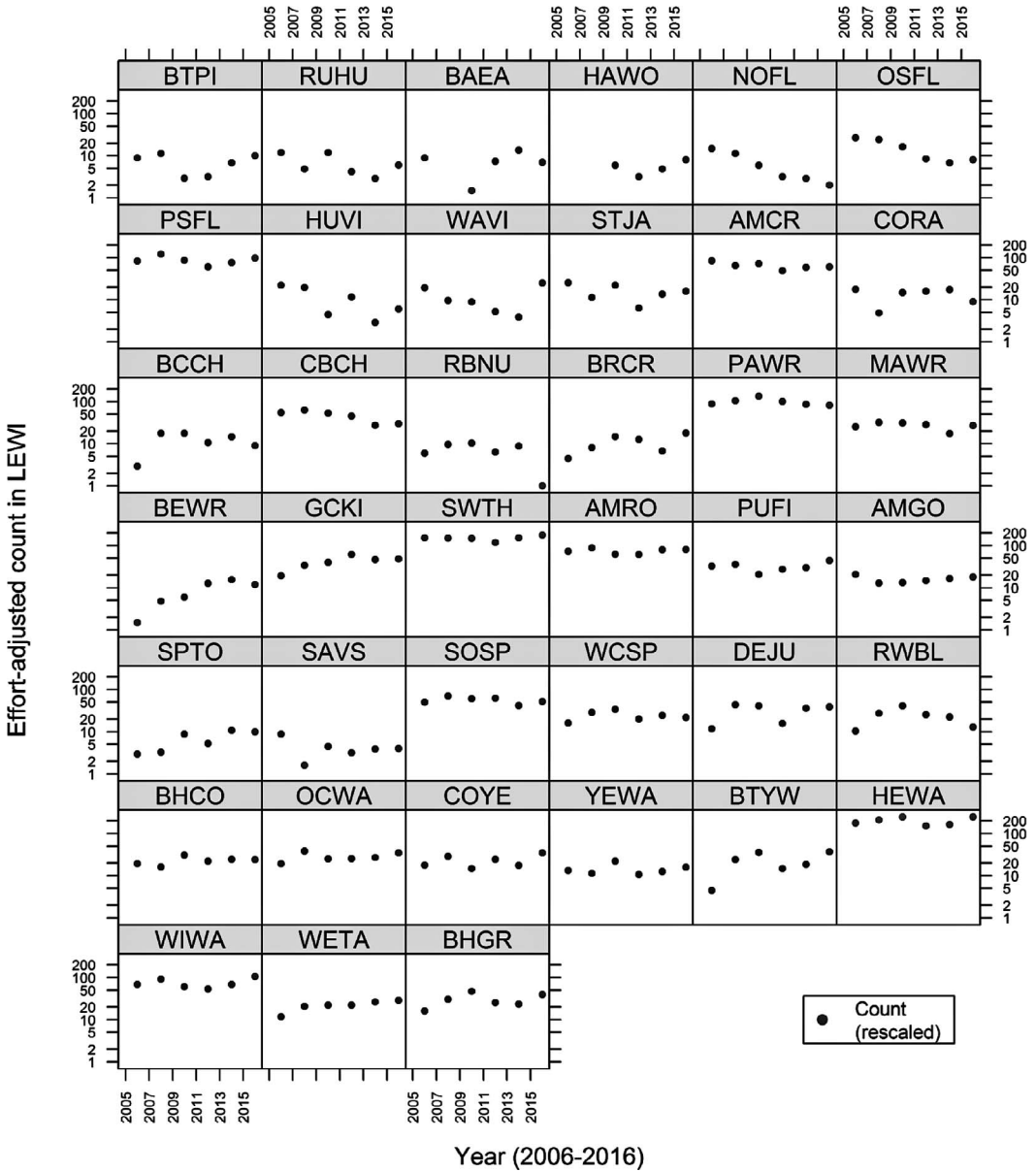
FIGURE 9.   Effort-adjusted counts for 39 species commonly detected in Lewis and Clark National Historical Park (LEWI). Surveys in LEWI were conducted in even-numbered years. Counts per point and minute surveyed were rescaled for comparison on a $\log_{10}$ scale by setting the lowest non-zero count to 1. Counts are missing for odd-numbered years when surveys were not conducted in this park, and counts of zero are not plotted. HEWA densities apply only to Fort Clatsop.

types in this national park network, we have demonstrated that many landbird species have responded positively to recent conditions, regardless of park size and setting. Our comparisons between historical and wilderness parks should be appropriate given that our results derive from a monitoring project designed specifically to estimate trends in population density using methods consistent across parks (Siegel and others 2007).
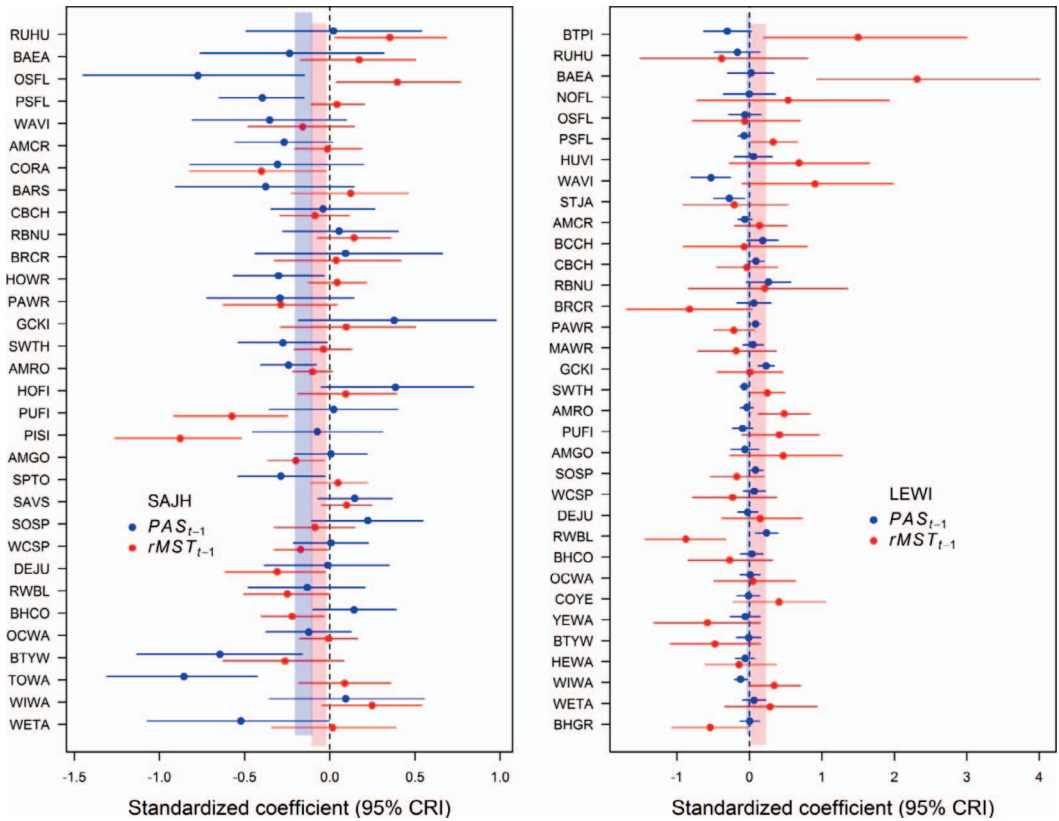
FIGURE 10.   Linear effects of climate in 1 year on breeding landbird density estimates for the following year in SAJH (left-hand panel) and LEWI (right-hand panel). For each species, effects of local precipitation-as-snow (*PAS*, blue symbols) and residual mean spring temperature (*rMST*, red symbols) are displayed as means (dots) and 95% CRIs (horizontal lines). $\bar{x} \pm s\bar{x}$ for the fitted coefficient of *PAS* across species (light blue vertical bars) was predominantly negative only in SAJH and was nearly 0 in LEWI. $\bar{x} \pm s\bar{x}$ for the fitted coefficient of *rMST* across species (light red vertical bars) was generally negative in SAJH and positive in LEWI.

Several landbird species that were common in these 2 historical parks were absent or rare in data from the wilderness parks, such as White-crowned Sparrow, Song Sparrow, Orange-crowned Warbler, Chestnut-backed Chickadee, Savannah Sparrow, American Goldfinch, Spotted Towhee, Purple Finch, and Red-winged Blackbird. This finding underscores the potential value of these historical parks as bird habitat within the national park network, as well as their value as a target for landbird monitoring to extend inference to additional species. Differences between mountain and lowland park habitats might explain these distinctions in landbird communities. In the rain shadow of the Olympic Mountains, SAJH includes small but important examples of coastal prairie and Garry Oak woodlands, plant communities that are rather rare in western Washington (Atkinson and Sharpe 1985) and have been noted for hosting regionally unusual bird communities (Lewis and Sharpe 1987; Siegel and others 2009). LEWI includes lowland wetlands as well as coastal and upland forests, and also represents the southernmost extent of NCCN habitats monitored for landbird trends (Siegel and others 2007). To the extent that these habitats are locally rare, SAJH and LEWI might be especially important for conserving certain bird populations. Alternatively, SAJH and LEWI might represent the variety of habitats offered by lowland protected areas, which would elevate the importance of monitoring landbirds in these 2 parks (Siegel and others 2007).

Source-sink dynamics might also contribute to landbird community structure in historical parks. Immigration from surrounding areas could mask poor local recruitment and yield positive population trends even for sink habitat. It is also possible that immigration from sources in the immediate vicinity of these historical parks might be limited if, for example, surrounding habitats are more degraded than those inside the parks. In this case, these historical parks might be serving as a source for some species, allowing for metapopulation or meta-community dynamics in which mixed-use landscapes offer habitats that are sufficiently productive to help generate regional stability (Hanski and Gilpin 1997; Holyoak and others 2005).

Unfortunately, not all positive trends signal a healthy community. The Brown-headed Cowbird is an obligate nest parasite that is clearly increasing in both of these historical parks. Cowbirds have already been implicated in the local decline of MacGillivray's Warbler in SAJH (Lewis and Sharpe 1987), and are capable of deleteriously affecting populations of numerous songbird species, including flycatchers and vireos as well as warblers. The invasion of the European Starling, first reported in the San Juan Islands in 1959 (Lewis and Sharpe 1987), also appears to be have been secured: Starling densities at SAJH were stable from 2005 to 2015 in our analysis.

Our estimates of population trends in these 2 parks were in general agreement with other results from this region, with few exceptions. We found evidence for decline in only 3 species (Northern Flicker, Olive-sided Flycatcher, and Hutton's Vireo), and each of these apparent declines was limited to 1 park (LEWI). Similarly, Northern Flicker and Olive-sided Flycatcher results from the mountain-parks study of 2005 to 2014 showed a decline in some parks but not others (Ray and others 2017a, 2017b). Across the state of Washington, results from the 2005 to 2015 Breeding Bird Survey showed stability in Norther Flicker populations, but decline in Olive-sided Flycatcher populations (Sauer and others 2017). Hutton's Vireo was too rare in data from mountain parks to allow trend estimation, but BBS data supported a state-wide decline that was non-significant. Of the species increasing across the state in the BBS analysis, 9 occurred with sufficient frequency for us to analyze trend in at least 1 of the historical parks. Of those 9, 7 trended positively in at least 1 historical park (Bald Eagle and Warbling Vireo trended positively in both parks) and 2 showed no trend in our analysis. Of the species declining across the state in the 2005–2015 BBS analysis, 5 occurred with sufficient frequency for our analyses. Of those 5, we found only mixed support for decline in 2 species, Olive-sided Flycatcher as summarized above and Rufous Hummingbird. The 95% CRI for trend in Rufous Hummingbird was almost wholly negative in SAJH, but there was less evidence for decline in LEWI, similar to our previous finding that the trend for this species was nearly negative in only 1 of the 3 mountain parks (Ray and others 2017a). Of the remaining 3 species in decline state-wide during 2005 to 2015, we found no evidence for decline in the Savannah Sparrow or Barn Swallow in these 2 small parks, but we found strong support for increasing densities of Brown-headed Cowbird, as reported above. Although we did not detect park-specific declines in several species that have declined state-wide, our estimates are at least in agreement with nation-wide projections for birds in the national parks; Wu and others (2018) projected that colonizations will outpace extinctions in the parks through mid-century as a result of climate change.

Differences among analyses in trend estimates might derive from differences between locations in the processes affecting bird densities as well as differences in assumptions and methods of analysis. Our estimates of trend were based on a generalized linear regression through estimates of population size that account for detection probability, whereas the BBS trends that we cite were based on a geometric mean estimator sensitive to trend endpoints and applied to indices of population size without correction for detection probability (Sauer and Link 2011). There are many ways to account for detection probability to improve estimates of population density, and we have chosen an approach suited to situations in which only a single visit to each point-count station is feasible during the breeding season (Amundson and others 2014). We adopted this approach because the scale of our sampling frame (5 parks in the NCCN) precluded multiple visits during the short breeding season, given the monitoring resources available. However, single-visit studies cannot estimate variation in detection probability

throughout the breeding season (Schmidt and others 2013; Mizel and others 2017), limiting our ability to isolate trends in abundance. For example, if we estimated N during a period of low detection probability in 1 year and during a period of high detection probability in the next year, we would be more likely to infer a trend in population size than if detection probability were truly constant. To minimize variation in detection probability within a season, our surveys were timed to coincide with the local peak in territorial breeding behavior. To minimize variation in detection probability among years, survey crews were trained and tested in bird identification and distance estimation (Siegel and others 2007). Distance-based estimates of population density can be sensitive to the distribution of detection distances, and the sparse data available from our biennial surveys in these small parks make it difficult to generate a smooth histogram of detection distances for each year. Therefore, we assumed a constant detection probability and characterized the detection-distance distribution using data from all detections of a species from a park, across all years, after censoring the farthest 10% of detections according to common practice (Kéry and Royle 2016). If detection distance actually trends over time, then our approach will confound trends in abundance and detection, a problem that also afflicts analyses that do not account for detection probability.

Despite these possible sources of bias or error in trend detection, we found a remarkable degree of concordance in trends between historical parks and the large wilderness parks studied in Ray and others (2017a). All but 3 species modeled exhibited stable densities in both historical parks, and more than half of the populations analyzed clearly increased in density over the study period. Although annual variation in population density was often related to climate in our analyses, the generally positive trends in these low-elevation populations do not support the up-slope range retraction often predicted as a response to warming trends (Freeman and Class Freeman 2014). The trends we report here for landbirds breeding in relatively small parks in mixed-use landscapes were generally more positive than statewide trends reported for the same period. In keeping with nationwide projections by Wu and others (2018), our results suggest that even relatively

small protected areas might serve as important bird habitat in the contemporary climate of this region.

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APPENDIX 1. Results from "basic" models (summarized in Tables 2 and 5 of the main text) fitted to breeding landbird point-count data from San Juan Island National Historical Park, 2005–2015.

Species code	d_{max} (m)	Effective area surveyed (ha)	Density (N/ha)		Annual trend (N/y)		Bayesian P-values	
			$\bar{x}$	95% CRI	$\bar{x}$	95% CRI	Availability	Detectability
CAQU	254	20.27	0.012	(0.008, 0.019)	0.220	(–0.030, 0.478)	0.492	0.365
MODO	181	10.29	0.012	(0.008, 0.019)	0.547	(0.195, 0.887)	0.739	0.476
RUHU	30	0.28	3.187	(1.811, 6.788)	–0.048	(–0.115, 0.012)	0.515	0.502
BAEA	375	44.18	0.023	(0.015, 0.032)	0.069	(0.005, 0.133)	0.456	0.201
OSFL	199	12.44	0.025	(0.016, 0.037)	0.085	(0.014, 0.156)	0.494	0.454
PSFL	80	2.01	0.954	(0.798, 1.143)	0.050	(0.018, 0.080)	0.489	0.235
CAVI	107	3.60	0.072	(0.038, 0.117)	–0.099	(–0.386, 0.190)	0.522	0.425
WAVI	117	4.30	0.120	(0.078, 0.172)	0.073	(0.015, 0.133)	0.488	0.381
AMCR	228	16.33	0.082	(0.064, 0.103)	–0.030	(–0.070, 0.011)	0.448	0.140
CORA	386	46.81	0.037	(0.017, 0.117)	0.171	(0.093, 0.255)	0.429	0.235
BARS	93	2.72	0.894	(0.215, 3.827)	0.187	(–0.026, 0.400)	0.287	0.166
CBCH	61	1.17	1.439	(1.107, 1.822)	0.065	(0.025, 0.105)	0.461	0.280
RBNU	126	4.99	0.228	(0.173, 0.290)	–0.023	(–0.067, 0.020)	0.506	0.583
BRCR	77	1.86	0.508	(0.246, 1.291)	0.151	(0.083, 0.221)	0.509	0.466
HOWR	68	1.45	0.769	(0.562, 0.993)	0.092	(0.058, 0.126)	0.468	0.300
PAWR	95	2.84	0.150	(0.098, 0.217)	0.036	(–0.034, 0.105)	0.490	0.256
GCKI	48	0.72	0.605	(0.328, 1.023)	0.154	(0.088, 0.226)	0.466	0.334
SWTH	126	4.99	0.439	(0.357, 0.535)	0.072	(0.040, 0.106)	0.500	0.392
AMRO	152	7.26	0.812	(0.710, 0.920)	0.028	(0.005, 0.050)	0.498	0.636
EUST	142	6.33	0.264	(0.169, 0.544)	–0.002	(–0.206, 0.197)	0.400	0.001
CEDW	84	2.22	0.669	(0.346, 1.548)	–0.037	(–0.281, 0.208)	0.410	0.011
HOFI	124	4.83	0.223	(0.165, 0.299)	0.098	(0.047, 0.151)	0.466	0.187
PUFI	146	6.70	0.124	(0.087, 0.165)	0.045	(–0.010, 0.099)	0.510	0.385
PISI	94	2.78	0.920	(0.260, 4.137)	0.420	(0.258, 0.599)	0.206	0.058
AMGO	97	2.96	0.945	(0.785, 1.130)	0.021	(–0.009, 0.052)	0.439	0.085
SPTO	112	3.94	0.449	(0.366, 0.545)	0.005	(–0.027, 0.039)	0.494	0.441
SAVS	105	3.46	0.816	(0.687, 0.958)	0.027	(–0.001, 0.055)	0.442	0.001
SOSP	163	8.35	0.202	(0.156, 0.256)	0.067	(0.025, 0.110)	0.484	0.365
WCSP	104	3.40	0.314	(0.271, 0.381)	0.055	(0.025, 0.085)	0.450	0.381
DEJU	85	2.27	0.465	(0.324, 0.646)	0.049	(–0.003, 0.102)	0.464	0.277
RWBL	216	14.66	0.081	(0.061, 0.105)	0.007	(–0.040, 0.054)	0.429	0.016
BHCO	103	3.33	0.789	(0.639, 0.955)	0.088	(0.054, 0.121)	0.467	0.260
OCWA	109	3.73	0.540	(0.437, 0.651)	0.049	(0.015, 0.082)	0.496	0.536
COYE	195	11.95	0.070	(0.039, 0.134)	0.303	(0.035, 0.574)	0.485	0.434
YEWA	151	7.16	0.035	(0.012, 0.090)	0.081	(–0.289, 0.471)	0.501	0.353
YRWA	129	5.23	0.066	(0.037, 0.105)	0.209	(–0.049, 0.459)	0.511	0.560
BTYW	82	2.11	0.115	(0.081, 0.171)	0.049	(–0.016, 0.113)	0.472	0.419
TOWA	82	2.11	0.233	(0.154, 0.320)	–0.018	(–0.072, 0.036)	0.461	0.118
WIWA	95	2.84	0.196	(0.136, 0.273)	0.018	(–0.035, 0.072)	0.502	0.453
WETA	110	3.80	0.084	(0.052, 0.139)	0.031	(–0.038, 0.100)	0.520	0.536

APPENDIX 2.   Results from "basic" models (summarized in Tables 2 and 5 of the main text) fitted to breeding landbird point-count data from Lewis and Clark National Historical Park, 2006–2016.

Species code	d_{max} (m)	Effective area surveyed (ha)	Density (N/ha)		Annual trend (N/y)		Bayesian P-values	
			$\bar{x}$	95% CRI	$\bar{x}$	95% CRI	Availability	Detectability
BTPI	205	13.20	0.031	(0.018, 0.053)	0.047	(–0.057, 0.151)	0.507	0.511
RUHU	22	0.15	2.884	(1.416, 6.216)	–0.138	(–0.468, 0.188)	0.499	0.483
BAEA	361	40.94	0.050	(0.008, 0.217)	0.134	(0.035, 0.235)	0.222	0.073
HAWO	96	2.90	0.455	(0.038, 2.080)	0.883	(0.361, 1.426)	0.467	0.452
NOFL	206	13.33	0.034	(0.013, 0.133)	–0.176	(–0.297, –0.060)	0.521	0.561
OSFL	224	15.76	0.055	(0.038, 0.079)	–0.107	(–0.179, –0.033)	0.494	0.390
PSFL	73	1.67	1.539	(1.315, 1.791)	0.039	(0.009, 0.067)	0.492	0.543
HUVI	99	3.08	0.093	(0.047, 0.229)	–0.121	(–0.203, –0.040)	0.513	0.473
WAVI	124	4.83	0.174	(0.080, 0.595)	0.071	(0.000, 0.147)	0.435	0.242
STJA	132	5.47	0.085	(0.056, 0.121)	0.002	(–0.064, 0.070)	0.467	0.164
AMCR	206	13.33	0.163	(0.136, 0.196)	0.013	(–0.021, 0.045)	0.451	0.095
CORA	250	19.63	0.023	(0.013, 0.045)	0.040	(–0.031, 0.111)	0.385	0.147
BCCH	103	3.33	0.174	(0.104, 0.283)	0.061	(–0.015, 0.140)	0.397	0.108
CBCH	49	0.75	2.230	(1.765, 2.783)	–0.030	(–0.068, 0.009)	0.452	0.245
RBNU	102	3.27	0.049	(0.026, 0.105)	–0.023	(–0.122, 0.079)	0.507	0.515
BRCR	53	0.88	0.469	(0.283, 0.763)	0.130	(0.049, 0.217)	0.489	0.330
PAWR	91	2.60	1.091	(0.947, 1.241)	0.028	(0.002, 0.053)	0.488	0.312
MAWR	78	1.91	0.485	(0.365, 0.614)	0.094	(–0.062, 0.254)	0.416	0.001
BEWR	86	2.32	0.100	(0.054, 0.187)	0.196	(0.104, 0.295)	0.375	0.201
GCKI	44	0.61	1.581	(1.219, 1.990)	0.112	(0.072, 0.154)	0.518	0.507
SWTH	102	3.27	1.466	(1.300, 1.644)	0.193	(0.125, 0.261)	0.501	0.515
AMRO	113	4.01	0.664	(0.560, 0.778)	0.169	(0.071, 0.264)	0.470	0.206
PUFI	120	4.52	0.204	(0.154, 0.268)	0.242	(0.098, 0.392)	0.518	0.612
AMGO	52	0.85	0.328	(0.231, 0.539)	0.051	(–0.014, 0.118)	0.314	0.387
SPTO	95	2.84	0.065	(0.033, 0.110)	0.166	(0.062, 0.274)	0.483	0.104
SAVS	88	2.43	0.038	(0.021, 0.075)	–0.008	(–0.127, 0.117)	0.476	0.169
SOSP	110	3.80	0.545	(0.450, 0.649)	0.084	(–0.025, 0.193)	0.476	0.139
WCSP	152	7.26	0.125	(0.092, 0.161)	0.047	(–0.008, 0.101)	0.441	0.025
DEJU	84	2.22	0.600	(0.436, 0.822)	0.293	(0.141, 0.443)	0.352	0.027
RWBL	211	13.99	0.058	(0.043, 0.078)	0.085	(–0.088, 0.251)	0.367	0.002
BHCO	70	1.54	0.623	(0.429, 0.916)	0.072	(0.017, 0.127)	0.381	0.109
OCWA	83	2.16	0.461	(0.352, 0.591)	0.234	(0.076, 0.394)	0.466	0.086
COYE	91	2.60	0.302	(0.223, 0.395)	0.288	(0.120, 0.451)	0.421	0.045
YEWA	103	3.33	0.258	(0.173, 0.380)	0.053	(–0.015, 0.124)	0.443	0.101
BTYW	96	2.90	0.335	(0.238, 0.465)	0.418	(0.238, 0.615)	0.461	0.188
HEWA	90	2.54	0.812	(0.617, 1.037)	0.053	(0.007, 0.099)	0.491	0.307
WIWA	80	2.01	1.036	(0.870, 1.215)	0.075	(0.046, 0.106)	0.476	0.332
WETA	118	4.37	0.131	(0.094, 0.174)	0.117	(0.060, 0.175)	0.508	0.481
BHGR	140	6.16	0.202	(0.155, 0.258)	0.083	(0.036, 0.132)	0.512	0.557