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*RESEARCH ARTICLE*

# Combined analysis of roadside and off-road breeding bird survey data to assess population change in Alaska

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## ABSTRACT

Management interest in North American birds has increasingly focused on species that breed in Alaska, USA, and Canada, where habitats are changing rapidly in response to climatic and anthropogenic factors. We used a series of hierarchical models to estimate rates of population change in 2 forested Bird Conservation Regions (BCRs) in Alaska based on data from the roadside North American Breeding Bird Survey (BBS) and the Alaska Landbird Monitoring Survey, which samples off-road areas on public resource lands. We estimated long-term (1993–2015) population trends for 84 bird species from the BBS and short-term (2003–2015) trends for 31 species from both surveys. Among the 84 species with long-term estimates, 11 had positive trends and 17 had negative trends in 1 or both BCRs; negative trends were primarily found among aerial insectivores and wetland-associated species, confirming range-wide negative continental trends for many of these birds. Three species with negative trends in the contiguous United States and southern Canada had positive trends in Alaska, suggesting different population dynamics at the northern edges of their ranges. Regional population trends within Alaska differed for several species, particularly those represented by different subspecies in the 2 BCRs, which are separated by rugged, glaciated mountain ranges. Analysis of the roadside and off-road data in a joint hierarchical model with shared parameters resulted in improved precision of trend estimates and suggested a roadside-related difference in underlying population trends for several species, particularly within the Northwestern Interior Forest BCR. The combined analysis highlights the importance of considering population structure, physiographic barriers, and spatial heterogeneity in habitat change when assessing patterns of population change across a landscape as broad as Alaska. Combined analysis of roadside and off-road survey data in a hierarchical framework may be particularly useful for evaluating patterns of population change in relatively undeveloped regions with sparse roadside BBS coverage.

*Keywords:* Alaska, boreal forest, Breeding Bird Survey, hierarchical model, Pacific Coast rainforest, passerines, population trends, shorebirds

**Analyse combinée des données d'inventaire des oiseaux nicheurs sur route et hors route pour évaluer les variations de populations en Alaska**

## RÉSUMÉ

L'intérêt pour la gestion des oiseaux de l'Amérique du Nord se concentre de plus en plus sur les espèces qui se reproduisent en Alaska et au Canada, où les habitats subissent des modifications rapides en réponse à des facteurs climatiques et anthropiques. Nous avons utilisé une série de modèles hiérarchiques afin d'estimer les taux de variation des populations dans deux régions de conservation des oiseaux (RCO) en Alaska à partir des données du Relevé des oiseaux nicheurs (BBS) de l'Amérique du Nord sur route et du Relevé des oiseaux terrestres de l'Alaska, qui échantillonnent les zones hors route sur les terres publiques. Nous avons estimé les tendances des populations à long terme (1993–2015) de 84 espèces d'oiseaux à partir du BBS et les tendances à court terme (2003–2015) de 31 espèces à partir des deux relevés. Parmi les 84 espèces avec des estimations à long terme, 11 avaient des tendances positives et 17 avaient des tendances négatives dans une ou les deux RCO; les tendances négatives impliquaient principalement les insectivores aériens et d'autres espèces associées aux milieux humides, confirmant les tendances négatives à l'échelle du contient pour plusieurs espèces. Trois espèces avec des tendances négatives dans la région contigüe des États-Unis et du sud du Canada avaient des tendances positives en Alaska, suggérant une dynamique des populations différente à la limite nord de leur aire de répartition respective. Les tendances des populations régionales en Alaska différaient pour plusieurs espèces, particulièrement celles représentées par différentes sous-espèces dans les deux RCO, lesquelles sont séparées par des chaînes de montagnes accidentées et couvertes de glace. L'analyse des données sur route et hors route dans un modèle hiérarchique conjoint avec des paramètres partagés a permis d'améliorer la précision des estimations de tendances et a suggéré une différence liée aux routes dans les tendances des populations

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sous-jacentes chez plusieurs espèces, particulièrement dans la RCO de la Forêt intérieure du Nord-Ouest. L'analyse combinée met en évidence l'importance de considérer la structure des populations, les barrières physiographiques et l'hétérogénéité spatiale dans les modifications de l'habitat lors de l'évaluation des patrons de variation des populations à travers un paysage aussi vaste que l'Alaska. L'analyse combinée des données des relevés sur route et hors route dans un cadre hiérarchique peut être particulièrement utile pour évaluer les patrons de variation des populations dans des régions relativement peu développées avec une couverture limitée du BBS sur route.

*Mots-clés :* Alaska, forêt boréale, Relevé des oiseaux nicheurs, modèle hiérarchique, forêt pluviale de la côte du Pacifique, passereaux, tendances des populations, limicoles

## INTRODUCTION

Alaska, USA, hosts a unique and important breeding avifauna by virtue of its position at the northwestern extremity of the North American continent, proximity to Asia, and zoogeographic history (Kessel and Gibson 1978, Gibson and Withrow 2015). This region not only serves as the terminus for multiple migratory pathways from North and South America, but also supports avian populations migrating north from nonbreeding areas in Oceania, Australasia, Antarctica, and Africa (e.g., Johnson et al. 1997, Gill et al. 2005, 2013, Winker et al. 2007, McIntyre et al. 2008, Irwin et al. 2011, Robertson et al. 2011, Bairlein et al. 2012). During the past half-century, the highest rates of climatic warming in North America have occurred in Alaska and northwestern Canada (Trenberth et al. 2007, Clegg and Hu 2010), and the resulting physical and biotic changes are altering the distribution and composition of vegetation and ecosystem processes across the landscape (Dial et al. 2007, 2016, Kasichke et al. 2010, Barrett et al. 2011, Hinzman et al. 2013, Jorgenson et al. 2013, Chapin et al. 2015, Csank et al. 2016).

Despite the importance of Alaskan breeding grounds for North American birds and the rapid changes occurring in their habitats, little information is available on avian population trends; monitoring data exist only for some raptors (e.g., Ritchie et al. 2003, Witter and Mangipane 2011, Fackler et al. 2014) and for waterfowl and other waterbirds (e.g., Mallek and Groves 2011, Stehn et al. 2013, Wilson 2015) from periodic, mostly aerial surveys. Although the road-based North American Breeding Bird Survey (BBS) has served as one of most important long-term monitoring programs for more than 400 bird species on the continent (Sauer et al. 2013, 2017a, 2017b), coverage in Alaska and northern Canada has been relatively sparse and geographically restricted due to the paucity of both roads and observers in remote areas. Thus, BBS analyses of regional and continental population trends have traditionally been limited to a core area of survey routes extending only as far north as southern Canada (Sauer et al. 2013, 2017a, 2017b).

During the 1980s and 1990s, several seminal studies, some based on analyses of BBS data from temperate latitudes, raised concerns about recent, rapid declines of many migrant landbird populations (Robbins et al. 1989, Terborgh 1989, Hagan and Johnston 1992, DeGraaf and Rappole 1995). Questions arose as to whether such population declines were also occurring in Alaska and northern Canada or if, alternatively, distributions could be shifting northward. Other studies in temperate North America and in Europe have found a strong signal of recent northward range shifts in breeding bird populations correlated with climatic warming (Thomas and Lennon 1999, Hitch and Leberg 2007, Devictor et al. 2008, Bradshaw et al. 2014, Virkkala and Lehikoinen 2014, Virkkala et al. 2014, Gillings et al. 2015). Migrants are important components of ecological communities in northern regions, where the magnitude and velocity of climate change are the highest, and thus may be particularly vulnerable to decoupling of climatic conditions on breeding and nonbreeding grounds and mistiming of migration (Robinson et al. 2009). Species can differ widely in their rate and type of response to climate change, such as shifts in phenology or distribution (Auer and Martin 2013, Bradshaw et al. 2014, Gillings et al. 2015), and may not be able to compensate completely. One might then expect differences among northern species in population trends related to migratory behavior or other life-history traits.

To understand how trajectories of bird populations in Alaska compared with those elsewhere on the continent, members of Boreal Partners in Flight, a regional working group of the international coalition, began 2 concerted efforts in 1993 to gather population trend data (Handel 2000). The first effort was to recruit qualified observers to maximize annual coverage of roadside BBS routes in Alaska, since coverage had been geographically sparse and temporally sporadic. Inferences about regional population trends derived solely from roadside surveys, however, could be inaccurate if trends in roadside habitats, detectability, or the populations themselves differed from trends in these parameters across the rest of the landscape (Bart et al. 1995, Johnson 2000, Sauer et al. 2005, Harris and Haskell 2007). Thus, a second effort was also begun to design, test, and implement a complementary monitoring program for birds breeding in the extensive public off-road areas of Alaska. In 2003, the Alaska Landbird Monitoring Survey (ALMS) was established on a voluntary, collabora-



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tive basis to determine avian population trends on federal and state resource lands, which comprise about two-thirds of the 1.5 million $km^2$ in Alaska (Handel 2000).

To maximize the efficiency of this large-scale monitoring program (Johnson 2000), initial off-road survey efforts were concentrated in the 2 predominantly forested Bird Conservation Regions (BCRs) among the 5 that occur in Alaska (U.S. NABCI Committee 2000). The Northwestern Interior Forest BCR (NW Interior Forest) encompasses more than half of the landmass of Alaska, and its vast taiga habitats form the northwestern extent of the boreal forest region that extends across Canada. The narrow coastal Northern Pacific Rainforest BCR (N Pacific Rainforest) in southeastern and south-central Alaska constitutes the northernmost extent of the largest temperate rainforest in the world (Alaback 2007) and is separated from the continental interior forests by a series of rugged, glaciated mountain ranges. These 2 BCRs support distinct avifaunas, and many polytypic species in Alaska are represented by interior continental and Pacific coastal populations (Gibson and Withrow 2015). Patterns of genetic divergence in many North American species show a split between a western coastal lineage and an eastern lineage related to the long periods of boreal fragmentation that occurred during the Pleistocene (Weir and Schluter 2004, Ruegg et al. 2006, Topp et al. 2013). Thus, we hypothesized that population trends could differ for some species between these 2 BCRs because of differing zoogeographic affinities and potential differences in demography in breeding and nonbreeding areas.

Here, we present the first analysis of avian population trends in interior and Pacific coastal Alaska based on data from the roadside BBS (since 1993) and off-road ALMS (since 2003). Given the high costs of surveying birds in remote areas, we were particularly interested in the prospects of obtaining accurate assessments of population trends through a combination of roadside and off-road surveys. We analyzed the data in a series of individual and joint hierarchical models (Sauer and Link 2011) to account for differences in protocols and sampling design between the 2 surveys. Our models were constructed to address the following questions: (1) Are population trends in remote, off-road areas of vast, protected public resource lands concordant with those in areas sampled by the geographically restricted roadside BBS in Alaska? (2) Can estimates of population trends be improved by analyzing roadside and off-road data together in joint hierarchical models? (3) Do population trends differ between Pacific coastal rainforests and Alaskan interior boreal forests, particularly for polytypic species represented by different subspecies in the 2 BCRs? (4) Do species with significantly declining population trends at temperate latitudes show similar declines at the northern extent of their ranges? Answers to these questions should help to optimize the design of monitoring programs for other northern regions and also to determine the appropriate geographic scale at which inferences about population trends should be drawn to gain insights into potential underlying causes.

## METHODS

### Sampling Frames

In Alaska, the BBS sampling frame included the limited system of roads at least 40 km long to accommodate 50 stops (survey points) placed 800 m apart, with routes selected randomly when possible along these roads (Sauer et al. 2013). Although a few roadside routes were established as early as 1968 in Alaska, early effort was minimal and sporadic; a concerted effort was begun in 1993 to survey a consistent number of routes each year, including a few routes along navigable stretches of slow-moving rivers.

The ALMS sampling frame consisted of a $10 \times 10$ $km^2$ grid of sampling blocks from the Alaska–Canada border (141°W) across mainland Alaska; blocks were assigned a random order within the sampling frame. Within each sampling block, we established a $5 \times 5$ grid of 25 points whose southwestern-most point was offset from the corner of the block by a randomly selected set vector consistently across the state (Handel and Cady 2004). Sampling points within each grid were spaced 250 m apart in closed, forested habitats and 500 m apart in more open habitats. These distances were selected to minimize travel distance between points while also minimizing the potential for double-counting the same individual birds at adjacent survey points. The sampling design was a stratified random design, with strata based on BCRs in Alaska (U.S. NABCI Committee 2000). The initial sampling frame consisted of all blocks within the boundaries of federal and state resource lands; potential sampling blocks were then restricted to those deemed reasonably accessible (by foot, boat, or small plane) based on criteria developed by each land management unit (which could be driven by regulation, cost, or safety). Blocks with any survey point within 1 km of an accessible area were included in the sampling frame.

We initially allocated the number of ALMS blocks to be sampled within each participating land management unit in proportion to its area within the BCR. We then selected potential sampling blocks for the unit based on the randomized order of blocks within the unit. A minimum of 15 of the 25 points in a block had to be available for surveying birds (i.e. not in large lakes or rivers, on glaciers or icefields, on terrain too unsafe to survey, etc.) or the next block in randomized order within the land management unit was selected for sampling (see additional details in Handel and Cady 2004).

Three sets of sampling units that had been established several years previously were added to the ALMS sampling



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frame. These included 7 transects within Tetlin National Wildlife Refuge with 12–28 points per transect; 13 transects in Chugach State Park and large parklands of the Municipality of Anchorage with 12–13 points per transect; and 2 transects in Klondike Gold Rush National Historical Park with 12–13 points per transect. Points were spaced 250 m apart with starting locations randomly selected from accessible areas. We also included a set of 11 minigrids established for general monitoring in Denali National Park and Preserve (NPP) that had 19–25 points each, spaced 500 m apart. The first ALMS blocks were surveyed in 2003, and additional samples were added in subsequent years as resources allowed and additional cooperators joined the program. To increase overall sample size for trend estimation, the general protocol was to survey half of the blocks each in alternate years, but some were sampled annually and a few less frequently as logistics and resources allowed.

For this study, we restricted our analyses to ALMS and BBS samples from the NW Interior Forest and N Pacific Rainforest BCRs because of limited survey effort in the other, tundra-dominated BCRs (Figure 1). Temporally, our analyses included BBS routes sampled since 1993 and ALMS blocks sampled since 2003. Geographic coverage by both the BBS and ALMS varied between the 2 BCRs.

## Survey Methods

Surveys for both the BBS and ALMS were generally conducted between June 10 and June 30 to ensure that all late-arriving migrants had arrived, although surveys could be done during early June in southeastern Alaska and as late as 7 July in more northern regions. Each BBS was conducted by an experienced volunteer birder during a single morning starting 30 min before local sunrise and was completed within 6.5 hr. The observer recorded all birds seen or heard at each stop within a 400-m radius during a 3-min period.

ALMS surveys usually started within 30 min after sunrise, but no earlier than 0300 hours Alaska Daylight Time, and ended no later than 5 hr after sunrise; surveys in a block usually required 2–3 days to complete, depending on habitat, terrain, and number of points. At each of the points in the survey block, a single observer recorded all birds seen or heard within a 10-min period out to an unlimited distance, along with distance of the bird from the observer, its behavior, and time of detection. Distance (measured with a laser rangefinder when possible) was recorded in 10-m intervals to 100 m, in 25-m intervals from 101 m to 150 m, in 50-m intervals in open habitats from 151 m to 400 m, or as >150 m or >400 m in closed or open habitats, respectively. Time of detection was recorded in the following intervals: 0–3 min, 3–5 min, 5–8 min, or 8–10 min. Observers recorded behavior and mode of detection (singing, calling, drumming, booming, flight-displaying, flying over, nesting, visual), as well as the age and sex of each bird when possible (Handel and Cady 2004). For ALMS analysis, we excluded birds in direct flight over the survey area and any known juvenile birds.

For both surveys, observers recorded the date, time of day, air temperature, wind conditions, and sky conditions at the beginning and end of each survey. For the ALMS, time of day was also recorded at each point. For both surveys, counts were only conducted under favorable weather conditions (no to little precipitation or wind). Observers had to have good hearing and eyesight and were required to complete training programs in visual and aural identification of birds. ALMS observers also received field training in distance estimation, navigation and use of GPS, and safety in remote areas. For the ALMS, points within a block could be surveyed by different observers within and among years. For the BBS, a single observer surveyed all 50 stops on a route each year and was encouraged to survey the same route for multiple years.

## Statistical Analysis

We constructed a series of hierarchical models to estimate population trends of birds from BBS and ALMS data independently and then jointly. For our analysis of ALMS data, we selected a subset of landbird and shorebird species for which we had sufficient numbers of both ALMS blocks and BBS routes per BCR to estimate trends ($n \geq 14$ each). We treated BCRs as strata and the roadside and off-road areas sampled by the BBS and ALMS, respectively, as substrata. Our generalized linear mixed models allowed year, stratum, and factors affecting detection probability (observer for both BBS and ALMS; day within season and time of day for ALMS) to be governed by parameters that were random variables; the hierarchical structure incorporated the various levels at which data were collected. In the BBS hierarchical model (Sauer and Link 2011), counts of a species on routes, $Y_{i,j,t}$ ($i$ for stratum, $j$ for unique combinations of route and observer, $t$ for year), were considered independent, overdispersed Poisson random variables with means, $\lambda_{i,j,t}$, that were log-linear functions of explanatory variables:

$$\log(\lambda_{i,j,t}) = S_i + \beta_i(t - t^*) + \omega_j + \gamma_{i.t} + \eta I_{j,t} + \varepsilon_{i,j,t}. \quad (1)$$

Explanatory variables for BBS data included stratum-specific intercepts ($S$) and slopes ($\beta$, relative to baseline year $t^*$), unique observer–route combinations ($\omega$), year ($\gamma$), first-year observer effects ($\eta$) with an indicator variable ($I$) that was 1 for an observer's first year of a survey on a route and 0 otherwise, and overdispersion effects ($\varepsilon$).

In the ALMS hierarchical model, abundances of species at individual points, $N_{i,j,t}$ ($i$ for stratum, $j$ for point, $t$ for year), were modeled as independent, overdispersed Pois-



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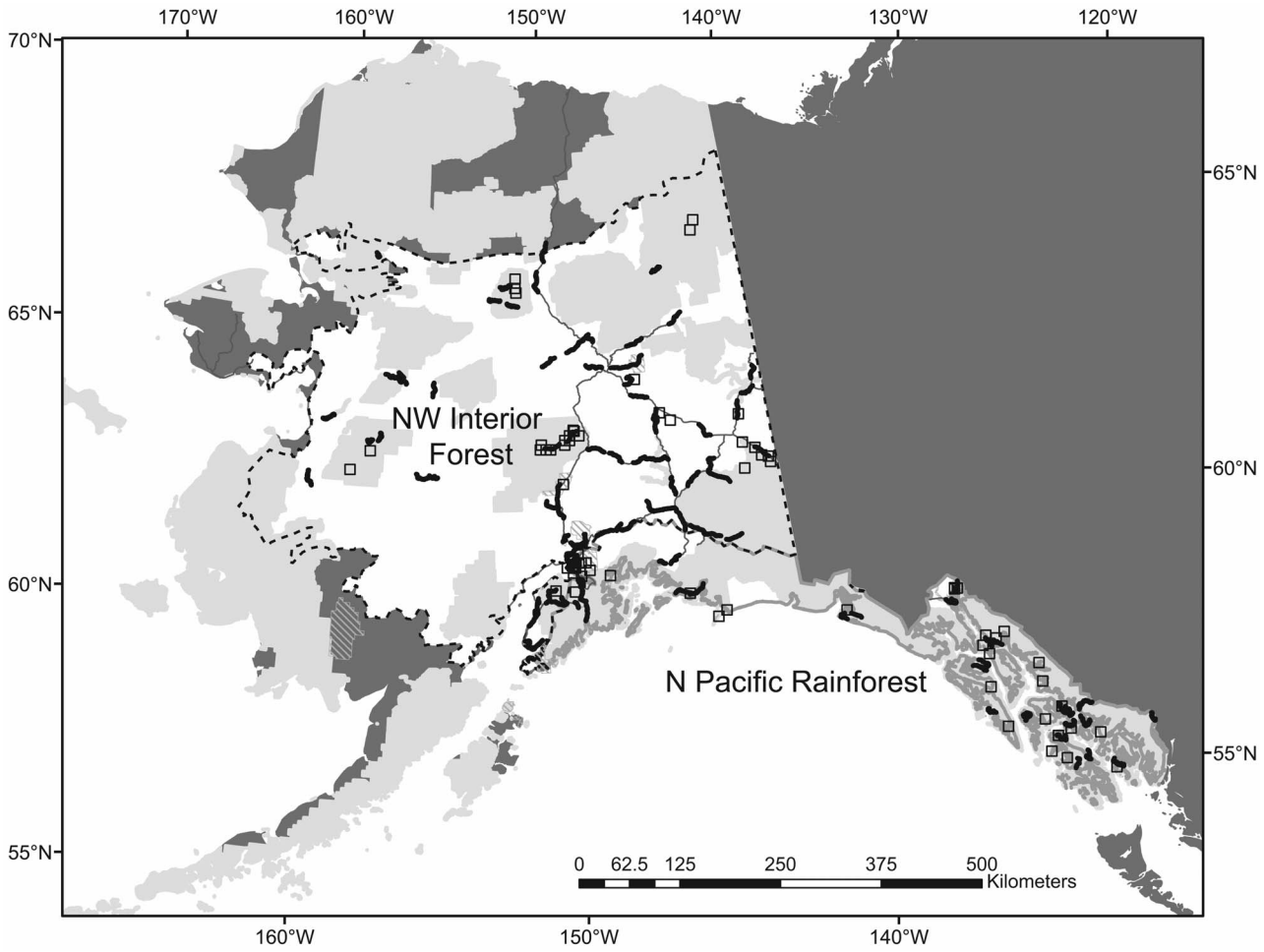



**FIGURE 1.** Location of roadside Breeding Bird Survey (BBS) routes (thick lines; 1993–2015) and off-road Alaska Landbird Monitoring Survey blocks (open squares; 2003–2015) sampled in the Northwestern (NW) Interior Forest (white, dashed border) and Northern (N) Pacific Rainforest (white, gray border) Bird Conservation Regions in Alaska, USA. Areas of federal (light gray) and state (cross-hatched) conservation and resource lands administered by the USDA Forest Service, U.S. Fish and Wildlife Service, National Park Service, Bureau of Land Management, Department of Defense, and State of Alaska are shown for the entire state relative to lands under other jurisdictions (dark gray). Major roads (thin lines) are concentrated in east-central and south-central Alaska, but local roads and a few slow-moving rivers were used for the BBS in other areas.

son random variables with means, $\lambda_{i,j,t}$, that similarly were log-linear functions of explanatory variables:

$$\log(\lambda_{i,j,t}) = S_i + \beta_i(t - t^*) + \tau_b + \gamma_{i.t} + \varepsilon_{i,j,t}. \quad (2)$$

Explanatory variables for ALMS data included stratum-specific intercepts ($S$) and slopes ($\beta$, relative to baseline year $t^*$), block ($\tau$) and year ($\gamma$) effects, and overdispersion effects ($\varepsilon$). For all analyses, the baseline year was set to 2010, the midpoint of the ALMS survey period. Block-specific intercepts were modeled as random effects to account for similarities among points within blocks (Amundson et al. 2014). The ALMS protocol allowed point-specific counts to be modeled at a different hierarchical level as a function of covariates explaining 2 aspects of detection probability, $p_a$ (availability, given presence) and $p_d$ (perception, given availability), following Amundson et al. (2014). Briefly, the number of individuals available for sampling (*navail*) was modeled as a binomial random variable with sample size $N$ and probability of availability for detection $p_a$:

$$navail_{i,j,t} \sim Binomial(N_{i,j,t}, p_{a_{i,j,t}}). \quad (3)$$

The observed number of birds per point, $Y$, was modeled as a binomial random variable with sample size *navail* and probability of detection $p_d$, given availability:

$$Y_{i,j,t} \sim Binomial(navail_{i,j,t}, p_{d_{i,j,t}}). \quad (4)$$

We constructed a time-removal model to estimate $p_a$, given the number of detections in 3 time intervals (0–3, 3–



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5, and 5–10 min) of the 10-min counts. We included point-level covariates for day within season and time of day (both linear, scaled, and centered) with a logit function. We modeled $p_d$ as a function of the distance of the bird from the observer with the half-normal detection function and no adjustment terms. First, we truncated all observations at 150 m. Scale parameters were estimated for each observer within a BCR with >60 detections of a given species; observers with fewer detections were assigned a single scale parameter for that BCR, with the assumption that detection probability would be influenced primarily by differences in the openness of habitats between the 2 BCRs and that estimates of density would be robust to pooling (Buckland et al. 2001).

We also conducted a joint hierarchical analysis that modeled the BBS (1993–2015) and ALMS (2003–2015) data at separate levels, but with shared parameters in a single framework, incorporating roadside and off-road areas as substrata within each BCR stratum. We modeled BBS counts and ALMS abundances as described by equations (1) through (4) above, but with shared random year effects ($\gamma_{i,t}$) for the 2 surveys within each BCR, based on the assumption that interannual variation in abundance would be driven by broad environmental patterns and therefore would be similar between roadside and off-road substrata within a region. We allowed the underlying trends to differ between roadside and off-road areas within a given BCR by adding a stratum-specific roadside effect ($\rho_i$) for the BBS surveys ($\beta_{BBS,i} = \beta_{ALMS,i} + \rho_i$). All other parameters were survey- and stratum-specific as described for the independent models.

We implemented the models in a Bayesian framework using JAGS 4.2.0 (Plummer 2003) called from R 3.3.1 (R Core Team 2016) with package R2jags 0.5-7 (Su and Yajima 2015). Following Sauer and Link (2011), for the BBS, we gave parameters $S_i$, $\eta$, $\beta_i$, and $\rho_i$ diffuse (essentially flat) normal distributions (mean = 0, variance = $10^6$), and treated observer–route effects ($\omega$), year effects ($\gamma$), and overdispersion effects ($\varepsilon$) as mean-zero normal random variables. We assigned all variances diffuse inverse gamma prior distributions by setting scale and shape parameters to 0.001. Following Amundson et al. (2014) for the ALMS, we assigned nested point-within-block intercepts and observer groups as normal distributions with mean $\mu$ and associated precision (variance$^{-1}$). For $\mu$ hyperparameters and coefficients for availability effects (date and time of day), we specified vague normal prior distributions (mean = 0, variance = $10^2$); for variances, we specified uniform priors ranging from 0 to $10^3$ at the $\sigma$ scale. Variances of effects for observer–route ($\sigma^2_\omega$), block ($\sigma^2_\tau$), and overdispersion ($\sigma^2_\varepsilon$) within each substratum (survey type) did not vary among strata, but the variance of the year effects ($\sigma^2_{\gamma_i}$) was allowed to vary among strata (BCRs). We discarded the first 10,000 iterations from each Markov chain as burn-in, then ran an additional 10,000 iterations to estimate the posterior distributions. For the ALMS analysis, we ran 2 Markov chains and tested for model convergence using the Gelman-Rubin diagnostic, considering values of $\hat{R}$ between 1.0 and 1.1 to be acceptable (Gelman and Rubin 1992). To assess goodness-of-fit for detectability parameters, we used Bayesian *P*-values from the predictive distributions (Gelman et al. 1996), considering values close to 0.5 to indicate good fit (Kéry 2010). For each parameter, we provide the median and 95% credible intervals (CI) from the posterior distributions.

For each independent model and the joint model, we followed Sauer and Link (2011) and derived annual estimates of abundance for each substratum (survey area) within a given stratum (BCR) by exponentiating sums of stratum, trend, and year effects, scaled by the proportion of routes or blocks in substratum $k$ within stratum $i$ in which the species was observed ($z_{i,k}$). We also added the respective variance components for each substratum ($\sigma^2 = \sigma^2_\omega$ [observer–route] + $\sigma^2_{\varepsilon_k}$ [overdispersion] for BBS; $\sigma^2 = \sigma^2_{obs}$ [observer] + $\sigma^2_{\varepsilon_k}$ [overdispersion] for ALMS) to account for asymmetries arising from the log-normal distribution of the estimated means. Annual estimates of abundance per substratum were thus estimated as:

$$n_{i,t,k} = z_{i,k}\exp\left(S_{i,k} + \beta_{i,k}(t - t^*) + \gamma_{i,t} + 0.5\sigma^2\right), \quad (5)$$

where $n_{i,t,k}$ for the BBS was an index of the abundance of birds per 50-stop route (uncorrected for detection probability) and for the ALMS was the estimated abundance per point (corrected for detection probability) within stratum $i$ during year $t$. Similarly, following Sauer and Link (2011), we estimated the stratum- and substratum-specific trend during a given period as the geometric mean of proportional change in population size, expressed as a percentage. The trend from year $t_a$ to year $t_b$ was $100(B_{i,k} - 1)$%, where:

$$B_{i,k} = \left\{\frac{n_{i,t_b,k}}{n_{i,t_a,k}}\right\}^{\frac{1}{t_b - t_a}}. \quad (6)$$

We derived initial estimates for long-term (1993–2015) and short-term (2003–2015) BBS trends as period-specific estimates from a single independent analysis of all of the BBS data. Similarly, we derived initial estimates for short-term (2003–2015) ALMS trends from an independent analysis of ALMS data. The joint hierarchical model incorporated all data available from both surveys, but we estimated trends for the period when both substrata were sampled (2003–2015).

Credible intervals were used to evaluate the significance of differences in estimated trends between species and regions. If 95% CIs did not overlap in a comparison, we considered the difference to be significant, and trends were considered significantly different from zero if the



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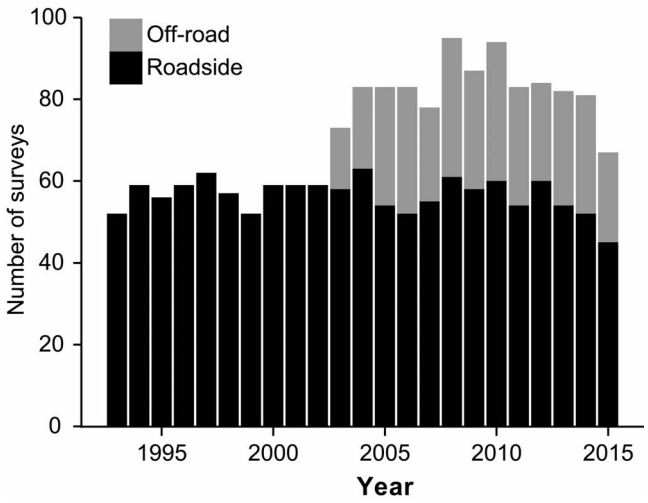



**FIGURE 2.** Annual survey effort for roadside Breeding Bird Surveys and off-road Alaska Landbird Monitoring Surveys (ALMS) in the Northwestern Interior Forest and Northern Pacific Rainforest Bird Conservation Regions in Alaska, 1993–2015. Note that ALMS blocks are typically surveyed biennially.

95% CIs did not include zero. We compared trends by species (1) for BBS results between BCRs for the short-term and long-term estimates; (2) between BBS and ALMS data for the short-term estimates; and (3) between BCRs for polytypic and monotypic species using BBS and ALMS data. We then evaluated the differences in trends from the BBS and ALMS as estimated by the joint model, and examined increases in precision associated with the joint model. Finally, we compared trends from our Alaskan data with results from the core BBS survey area in the contiguous U.S. and southern Canada (Sauer et al. 2013).

## RESULTS

Observers conducted surveys on 54 roadside BBS routes (2,700 unique points) in the NW Interior Forest BCR and 27 roadside routes (1,350 unique points) in the N Pacific Rainforest BCR in Alaska between 1993 and 2015. The total number of 50-stop roadside surveys completed was 866 in NW Interior Forest and 434 in N Pacific Rainforest. In off-road areas, observers conducted surveys in 44 blocks (828 unique points) in NW Interior Forest and 28 blocks (529 unique points) in N Pacific Rainforest between 2003 and 2015. The average number of points surveyed per block was 18 ± 1 (SE). The total number of individual point-count surveys completed in off-road areas was 3,570 in NW Interior Forest and 2,343 in N Pacific Rainforest. Survey effort was fairly consistent across years (Figure 2).

### Long-term vs. Short-term Roadside Population Trends

We estimated long-term population change for 84 species in 1 or both of the forested BCRs in Alaska based on roadside BBS data from 1993 to 2015 (Appendix Table 2). Among these, 17 species showed significantly negative trends and 11 species had significantly positive trends in 1 or both regions (i.e. 95% CIs did not include zero). None of these, however, showed opposing trends between the 2 regions. Among the species with negative trends, most were associated with moist or wetland forest habitats, particularly in NW Interior Forest. Notable among these were the Canada Goose (*Branta canadensis*), Red-necked Grebe (*Podiceps grisegena*), Lesser Yellowlegs (*Tringa flavipes*), Olive-sided Flycatcher (*Contopus cooperi*), Western Wood-Pewee (*C. sordidulus*), Alder Flycatcher (*Empidonax alnorum*), all 5 swallow species that occur regularly in Alaska, Blackpoll Warbler (*Setophaga striata*), and Savannah Sparrow (*Passerculus sandwichensis*). Positive trends were found for 7 species in N Pacific Rainforest, most of which were strongly associated with mature coniferous forests, e.g., Red-breasted Sapsucker (*Sphyrapicus ruber*), Northern Flicker (*Colaptes auratus*), Pacific-slope Flycatcher (*Empidonax difficilis*), Red Crossbill (*Loxia curvirostra*), and Townsend's Warbler (*Setophaga townsendi*). Only 4 species had significant long-term positive trends in NW Interior Forest, including both kinglets (Golden-crowned Kinglet [*Regulus satrapa*] and Ruby-crowned Kinglet [*R. calendula*]), which were associated with mature coniferous forests, and 2 shrub-associated sparrows (Chipping Sparrow [*Spizella passerine*] and Lincoln's Sparrow [*Melospiza lincolnii*]).

Among 36 species for which we could determine long-term BBS trends in both BCRs, 4 had negative trends in both BCRs, including the Olive-sided Flycatcher, Western Wood-Pewee, Violet-green Swallow (*Tachycineta thalassina*), and Savannah Sparrow, none showed positive trends in both BCRs, and none had a positive trend in 1 BCR but a negative trend in the other (Appendix Table 2). For 13 species, the trend was significantly positive ($n = 7$) or negative ($n = 6$) on long-term BBS routes in one BCR but stable in the other; 95% CIs overlapped for all but 5 of these. The remaining 19 species had no significant long-term trend in either BCR.

Among the species monitored on BBS routes with sufficient sample sizes during 2003–2015, most that demonstrated long-term negative (10 of 13) or positive trends (6 of 9) also showed significant population trends during the short-term period (Supplemental Material Table S1). All of these species showed long- and short-term trends in the same direction, except the Ruby-crowned Kinglet, which showed a significant short-term negative trend of –3.6% per year but a significant long-term positive trend of 1.6% per year in NW Interior Forest.



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**TABLE 1.** Comparisons of annual percent change (% $yr^{-1}$) in populations of 31 species of shorebirds and landbirds from roadside Breeding Bird Surveys and off-road Alaska Landbird Monitoring Surveys in 2 Bird Conservation Regions (BCRs) of Alaska, USA, 2003–2015, based on independent hierarchical models. For each species, we present number of routes surveyed (*n*) and the median and 95% credible intervals (CIs) for the annual percent change; **boldface** font indicates those for which 95% CIs did not overlap zero. Trends are presented only for species recorded on ≥14 routes in a region, unless 95% CIs were precise enough to detect trend of 5% $yr^{-1}$ (cf. Sauer et al. 2003). Scientific names of species are given in Appendix Table 2. Species noted with an asterisk (*) are represented by different subspecies in the 2 BCRs in Alaska (cf. Gibson and Withrow 2015), but not all had samples sufficient for comparative analysis.

| | Northwestern Interior Forest BCR | | | | | | | | Northern Pacific Rainforest BCR | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Roadside | | | | Off-road | | | | Roadside | | | | Off-road | | | |
| Species | *n* | Median | 2.5% | 97.5% | *n* | Median | 2.5% | 97.5% | *n* | Median | 2.5% | 97.5% | *n* | Median | 2.5% | 97.5% |
| Rufous Hummingbird | | | | | | | | | 19 | 0.8 | −2.2 | 3.3 | 24 | **−7.5** | **−13.5** | **−3.2** |
| Wilson's Snipe | 44 | −0.6 | −3.1 | 1.6 | 24 | −6.5 | −12.6 | 1.8 | | | | | | | | |
| Lesser Yellowlegs | 32 | **−5.3** | **−8.5** | **−2.2** | 17 | **−9.2** | **−15.0** | **−0.6** | | | | | | | | |
| Red-breasted Sapsucker | | | | | | | | | 16 | 3.3 | −3.0 | 10.3 | 18 | **10.2** | **6.6** | **14.4** |
| Olive-sided Flycatcher | 39 | **−2.8** | **−5.3** | **−0.3** | 19 | **−17.9** | **−25.1** | **−8.8** | 16 | **−3.4** | **−7.4** | **−0.7** | | | | |
| Western Wood-Pewee* | 24 | −3.8 | −7.6 | 2.3 | 17 | 8.5 | −4.0 | 26.4 | | | | | | | | |
| Alder Flycatcher | 46 | −1.8 | −3.9 | 0.1 | 35 | 2.1 | −2.1 | 6.2 | 19 | −0.7 | −5.3 | 4.0 | | | | |
| Pacific-slope Flycatcher | | | | | | | | | 15 | **2.7** | **0.3** | **6.1** | 19 | 0.3 | −1.8 | 3.0 |
| Tree Swallow | 35 | −4.6 | −10.3 | 1.6 | 14 | −0.5 | −10.9 | 22.1 | | | | | | | | |
| Black-capped Chickadee | 37 | −1.5 | −5.6 | 2.9 | 20 | 1.6 | −4.3 | 7.9 | | | | | | | | |
| Chestnut-backed Chickadee | | | | | | | | | 19 | −0.4 | −4.2 | 2.8 | 24 | 2.4 | −1.9 | 7.1 |
| Boreal Chickadee | 42 | 0.2 | −4.2 | 4.7 | 27 | −1.6 | −8.1 | 4.9 | | | | | | | | |
| Pacific Wren | | | | | | | | | 18 | −0.5 | −3.1 | 2.4 | 24 | −0.7 | −2.7 | 1.5 |
| Golden-crowned Kinglet* | | | | | | | | | 22 | −1.9 | −7.5 | 4.1 | 21 | **−5.4** | **−9.2** | **−1.5** |
| Ruby-crowned Kinglet* | 45 | **−3.6** | **−6.7** | **−0.6** | 34 | 1.4 | −2.9 | 4.4 | 22 | −3.0 | −6.8 | 0.3 | 22 | −2.1 | −4.4 | 0.8 |
| Swainson's Thrush* | 45 | **1.7** | **0.0** | **3.7** | 36 | **3.1** | **0.5** | **5.5** | 22 | 1.3 | −0.9 | 3.5 | 13 | −2.2 | −6.0 | 2.1 |
| Hermit Thrush* | 37 | 2.7 | −1.5 | 7.0 | 31 | −5.3 | −10.7 | 0.7 | 23 | 0.4 | −1.4 | 2.3 | 28 | **2.9** | **0.7** | **5.4** |
| American Robin* | 46 | 1.3 | −0.2 | 2.9 | 38 | **3.1** | **0.9** | **5.4** | 23 | **3.1** | **0.8** | **5.6** | 22 | −3.5 | −7.9 | 0.5 |
| Varied Thrush* | 45 | 0.6 | −2.4 | 3.6 | 26 | 3.0 | −2.5 | 8.6 | 23 | −0.4 | −2.8 | 2.1 | 27 | 0.5 | −1.6 | 2.4 |
| Orange-crowned Warbler* | 44 | **−2.9** | **−5.4** | **−0.3** | 43 | 1.8 | −1.1 | 5.1 | 23 | −1.1 | −3.2 | 2.2 | 28 | **6.0** | **3.5** | **8.9** |
| Yellow Warbler* | 45 | **6.6** | **2.8** | **10.8** | 31 | **7.5** | **2.3** | **15.8** | 23 | 0.4 | −3.0 | 3.0 | 15 | 3.2 | −5.6 | 11.0 |
| Blackpoll Warbler | 35 | **−5.4** | **−9.3** | **−0.5** | 14 | 10.4 | −8.9 | 23.3 | | | | | | | | |
| Yellow-rumped Warbler* | 46 | −0.7 | −3.0 | 1.7 | 36 | −0.3 | −3.0 | 2.5 | 20 | 0.5 | −2.0 | 2.7 | 15 | **−6.2** | **−11.0** | **−1.3** |
| Townsend's Warbler | 23 | −2.3 | −7.0 | 2.1 | | | | | 21 | **4.2** | **1.3** | **7.2** | 20 | **5.3** | **3.0** | **8.5** |
| Wilson's Warbler | 46 | **−4.5** | **−6.6** | **−2.4** | 39 | −3.7 | −8.2 | 0.1 | 22 | 0.3 | −2.5 | 3.4 | 26 | 2.0 | −0.4 | 4.9 |
| Savannah Sparrow | 38 | **−5.0** | **−7.6** | **−2.5** | 33 | 4.0 | −0.8 | 8.7 | | | | | | | | |
| Fox Sparrow* | 46 | −0.6 | −3.3 | 1.7 | 35 | **7.6** | **3.2** | **11.7** | 23 | **2.0** | **0.2** | **3.9** | 13 | −2.0 | −6.2 | 2.3 |
| Lincoln's Sparrow* | 43 | **3.8** | **0.6** | **7.2** | 32 | **5.8** | **2.4** | **10.5** | 21 | 0.0 | −2.7 | 4.0 | 18 | 2.1 | −0.4 | 4.8 |
| White-crowned Sparrow* | 46 | **−3.0** | **−5.2** | **−0.7** | 38 | −2.2 | −5.0 | 0.7 | | | | | | | | |
| Dark-eyed Junco* | 46 | 0.3 | −1.6 | 2.3 | 41 | 0.6 | −1.4 | 2.8 | 23 | −0.2 | −2.6 | 2.4 | 24 | **3.6** | **0.2** | **7.3** |
| Rusty Blackbird | 20 | 1.3 | −3.9 | 8.9 | 14 | 6.5 | −1.6 | 16.5 | | | | | | | | |

### Short-term Population Trends in Off-road vs. Roadside Areas

We estimated short-term (2003–2015) population changes for the off-road substratum in comparison with the roadside substratum for 31 shorebird and landbird species in 1 or both BCRs based on independent models of ALMS and BBS data (Table 1, Figure 3). In the NW Interior Forest, roadside and off-road trends were concordant in direction for 16 of 24 species, being significantly negative for 2 species (Lesser Yellowlegs and Olive-sided Flycatcher), significantly positive for 3 species (Swainson's Thrush [*Catharus ustulatus*], Yellow Warbler [*Setophaga petechia*], and Lincoln's Sparrow), and stable (i.e. with 95% CIs overlapping zero) for 11 species. Negative trends in the Wilson's Warbler (*Cardellina pusilla*) and White-crowned Sparrow (*Zonotrichia leucophrys*) were evident but not as strong in the off-road as in the roadside substratum. The Savannah Sparrow had a significant negative roadside trend but a nonoverlapping stable trend in the off-road substratum; the Fox Sparrow (*Passerella iliaca*) had a significant positive trend in the off-road substratum but was stable in roadside areas. Trends for the remaining 3 species were significantly positive or negative in 1 substratum and apparently stable in the other, but 95% CIs overlapped. No species had a significant negative trend in 1 substratum but a significant positive trend in the other.

In the N Pacific Rainforest, roadside and off-road trends were concordant in direction for 9 of 19 species, being



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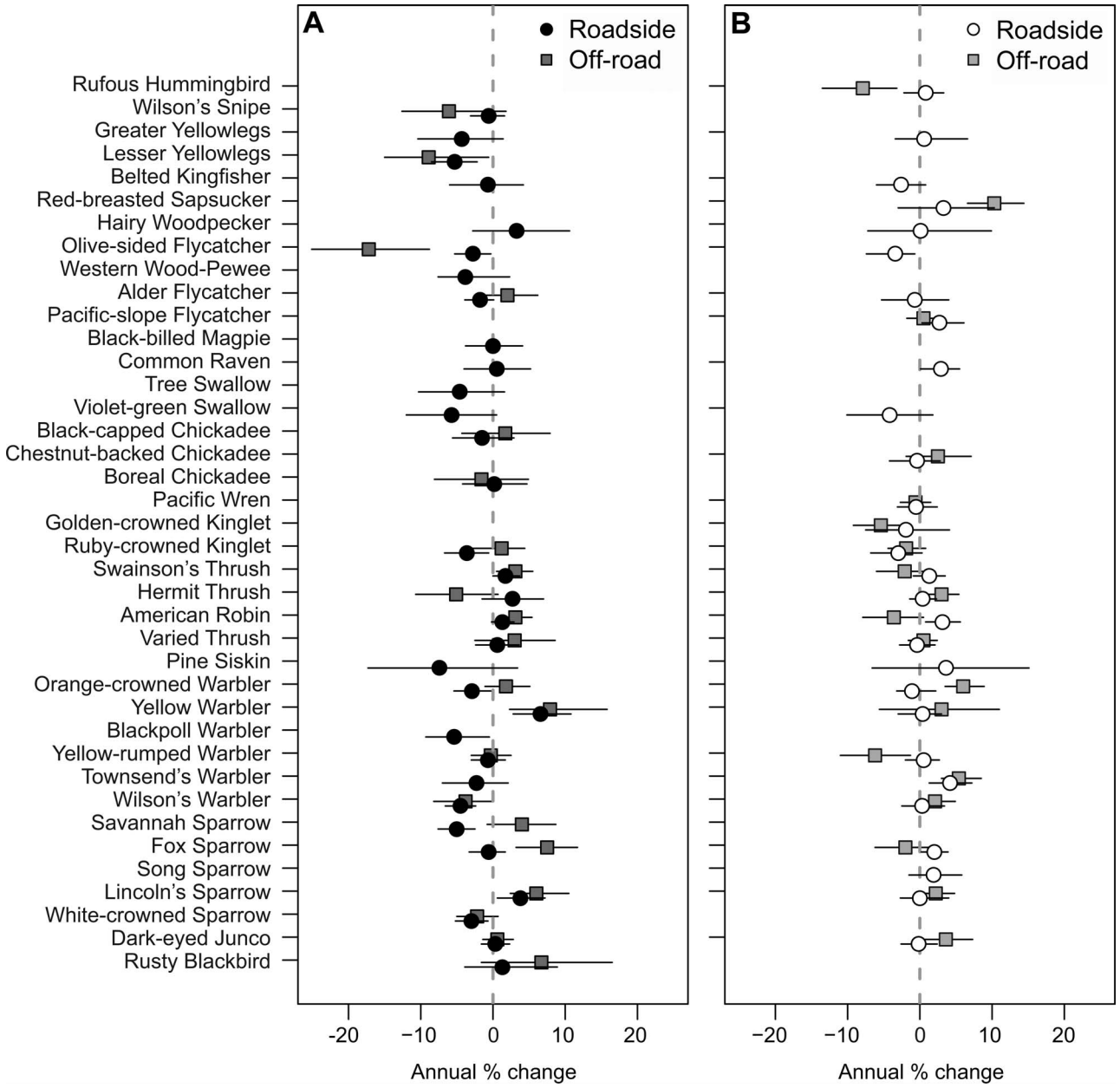



**FIGURE 3.** Annual percent change (median ± 95% CI) in populations of 39 species of shorebirds and landbirds on roadside Breeding Bird Surveys (circles) and off-road Alaska Landbird Monitoring Surveys (squares) in the (**A**) Northwestern Interior Forest and (**B**) Northern Pacific Rainforest Bird Conservation Regions in Alaska, USA, between 2003 and 2015. Estimates are from independent hierarchical models for each survey.

significantly positive for the Townsend's Warbler and stable for 8 species (Table 1). The Rufous Hummingbird (*Selasphorus rufus*) had a significant negative trend in the off-road substratum but a nonoverlapping stable trend along roadsides. The American Robin (*Turdus migratorius*) and Orange-crowned Warbler (*Oreothlypis celata*) were stable in the off-road and roadside substratum, respectively, but exhibited a significant, nonoverlapping positive trend in the other. Trends for the remaining 7 species were significantly positive or negative in 1 substratum and stable in the other, but with overlapping 95% CIs.

### Trends from Independent vs. Joint Hierarchical Models

We analyzed BBS and ALMS data from 2003 to 2015 together in joint hierarchical models for the same 31 landbird and shorebird species as above and compared



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estimates of population trends (Supplemental Material Table S2) with corresponding estimates derived from the independent models of each survey dataset analyzed separately (Table 1). The mean difference in estimated trends (from joint model vs. independent models) among species within BCRs was a negligible 0.004% $yr^{-1}$ (95% CI: –0.4% to 0.4%; range: –7.5% to +6.0%) for the off-road substratum and –0.05% $yr^{-1}$ (95% CI: –0.7% to 0.6%; range: –4.0% to +2.6%) for the roadside substratum; 95% CIs for corresponding estimates from joint and independent models overlapped for every species, signaling consistency between the 2 methods. The 95% CIs of the estimates, however, were 2.6% $yr^{-1}$ narrower (95% CI: 3.7% to 1.6%) for the off-road substratum and 1.2% $yr^{-1}$ narrower (95% CI: 1.5% to 0.8%) for the roadside substratum from the joint models vs. the independent models, indicating an increased precision in estimates from the joint models.

The joint models allowed us to test specifically for a difference in trend slope between roadside and off-road substrata within the BCRs; we found that 10 of 24 species (42%) in the NW Interior Forest and 6 of 19 species (32%) in the N Pacific Rainforest had a differential roadside slope parameter (ρ) for which the 95% CIs did not include zero (Supplemental Material Table S2), providing evidence of a roadside effect on underlying population trends. The 16 trend estimates for which the joint model identified a difference in slope included those for all 6 species whose roadside and off-road estimates from the independent models differed significantly, plus an additional 10 species whose estimates from independent models had overlapping 95% CIs for the 2 substrata.

### Differences in BCR Trends for Polytypic vs. Monotypic Species

Two of 16 polytypic species with different subspecies in interior and coastal Alaska that were monitored in both BCRs exhibited significantly different long-term roadside trends (nonoverlapping 95% CIs) in NW Interior Forest vs. N Pacific Rainforest: the Canada Goose (–3.4% $yr^{-1}$ vs. stable) and Ruby-crowned Kinglet (+1.6% $yr^{-1}$ vs. stable). Among 20 monotypic species monitored in both BCRs, the Glaucous-winged Gull (*Larus glaucescens*) and Wilson's Warbler had significant negative trends in NW Interior Forest but were stable in N Pacific Rainforest; the Townsend's Warbler exhibited a significant positive trend in N Pacific Rainforest but was apparently stable in NW Interior Forest.

In the off-road substratum, 11 of 12 species monitored in both BCRs were polytypic (Table 1). Among these, the American Robin and Fox Sparrow both had a positive trend (+3.1% $yr^{-1}$ and +7.6% $yr^{-1}$, respectively) in NW Interior Forest and a stable trend with nonoverlapping 95% CIs in N Pacific Rainforest; the Hermit Thrush (*Catharus guttatus*) showed the opposite pattern (stable vs. +2.9% $yr^{-1}$). For 6 polytypic species, the trend was significantly positive ($n = 5$) or negative ($n = 1$) in 1 BCR and stable in the other, but 95% CIs overlapped. Two polytypic and the single monotypic species had no significant trends in the off-road substratum of either BCR.

### Trends in Alaska vs. the Contiguous U.S. and Southern Canada

Among the 84 species for which we estimated population change from roadside BBS data in Alaska (1993–2015), 21 had positive trends and 33 had negative trends (long-term: 1966–2011, short-term: 2001–2011, or both) at lower latitudes of North America, based on a recent analysis of BBS data from the contiguous U.S. and southern Canada (Sauer et al. 2013). Among the 21 species with positive BBS trends at lower latitudes, only the Common Raven (*Corvus corax*) also had a positive trend in the roadside BBS substratum in Alaska, while the Canada Goose and Cliff Swallow (*Petrochelidon pyrrhonota*) had negative trends. The other 18 species had no significant trends. In contrast, among the 33 species with negative BBS trends at lower latitudes, 11 also had negative trends in the roadside BBS substratum in Alaska (Lesser Yellowlegs, Olive-sided Flycatcher, Western Wood-Pewee, Alder Flycatcher, Bank Swallow [*Riparia riparia*], Barn Swallow [*Hirundo rustica*], Orange-crowned Warbler, Blackpoll Warbler, Wilson's Warbler, Savannah Sparrow, and White-crowned Sparrow), 4 had positive trends (Northern Flicker, Pacific-slope Flycatcher, Golden-crowned Kinglet, and Chipping Sparrow), and 18 had no significant trends. Among the species with negative BBS trends at lower latitudes, 2 had negative trends in the off-road but not the roadside substratum in Alaska (Rufous Hummingbird and Golden-crowned Kinglet).

## DISCUSSION

At the onset of this study, one of our initial goals was to develop a method to analyze data from the roadside and off-road surveys combined to increase power to detect regional population trends in Alaska. We expected that species composition and relative abundance might differ between the substrata within a given BCR due to potential differences in habitat (Wellicome et al. 2014), but did not expect population trends to differ markedly within a given BCR. Roadside and off-road trends were concordant for most species, but did differ significantly for some species in each BCR, although never in opposite directions. In contrast, we did expect population trends to differ between the 2 BCRs, and our analysis confirmed significant differences in regional population trends for several species. Comparisons of BBS population trends in Alaska with those from more southern latitudes of North America suggested concordant range-wide negative trends for



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several species, but also provided evidence that trends may differ for some species at the northern extents of their ranges. Combining analyses of off-road and roadside data from Alaska in a joint hierarchical model increased the precision of trend estimates while allowing separate estimates for each substratum of interest, suggesting that this approach might prove valuable in other regions where population trends might be expected to vary between roadside and off-road areas.

### Trends in Roadside vs. Off-road Substrata in BCRs

The occurrence of significant, concordant trends in the roadside and off-road substrata within each BCR suggests that broad regional factors may be at play for several species, such as wetland-related declines for Lesser Yellowlegs and Olive-sided Flycatchers in NW Interior Forest, shrub-related increases for Swainson's Thrushes, Yellow Warblers, and Lincoln's Sparrows in NW Interior Forest, and increases in Townsend's Warblers in maturing conifers of the N Pacific Rainforest. Given the restricted geographic distribution of roads and the vast expanses of protected resource areas in Alaska, however, finding disparate population trends for some species in the roadside vs. off-road substratum was not completely unexpected for either BCR. It is important to note that we did not find any species with significantly opposing trends in roadside and off-road areas; differences were either a matter of magnitude or consisted of a significant trend in one substratum and an apparently stable trend in the other. Failure to detect a trend in one substratum that was detected in the other could have been a result of low power to do so, particularly given the relatively short time series (13 yr) during which the 2 surveys have been in simultaneous operation.

Some disparities in population trends between roadside and off-road areas were likely related to recent differential changes in habitats within the substrata. In the NW Interior Forest BCR in Alaska, there was a 44% increase in the human population between 1990 and 2016 (http://live.laborstats.alaska.gov/pop/), with concomitant urban development along the limited network of roads used by the BBS. In response to increased traffic, there was a statewide effort during that period to increase safety by widening road corridors and reducing roadside vegetation (Atkinson et al. 2014). Elsewhere in North America, differential increases in urbanization or changes in vegetation along roadsides relative to off-road areas have been identified as potential sources of bias in the use of BBS data for monitoring regional populations due to changes in breeding habitats (Bart et al. 1995, Keller and Scallan 1999). Changes along roadsides can also result in decreased detectability of birds due to increased traffic (Simons et al. 2007, Pacifici et al. 2008, Griffith et al. 2010, but see Lituma and Buehler 2016), higher mortality associated with traffic (Summers et al. 2011), and other negative impacts on breeding birds in response to anthropogenic noise itself (Habib et al. 2007, Francis et al. 2011, Halfwerk et al. 2011). Such effects might at least partially explain significant negative trends along roadsides but not in off-road areas for some species (Orange-crowned Warbler, Savannah Sparrow), or a reduced or lack of a positive trend along roadsides compared with trends found off-road (American Robin, Yellow Warbler, Fox Sparrow). Off-road areas sampled in the NW Interior Forest BCR occurred primarily in National Wildlife Refuges, National Parks and Preserves, and State Parks, where habitat management was minimal; thus, off-road avian population trends likely better represented responses to broader environmental change (Mizel et al. 2016).

Different factors were likely at play in the N Pacific Rainforest BCR, which is almost completely isolated from the continental road system and has had limited human population growth (5% from 1990 to 2016; http://live.laborstats.alaska.gov/pop/). Fewer differences in trends occurred between the roadside and off-road substrata, and trends were inconsistent in the direction of the effect. In this BCR, habitat management on public lands is a more pervasive influence than development along roadside corridors. The expansive Tongass National Forest, which dominates southeastern Alaska, consists of a complex matrix of natural and modified landscapes, reflecting its multiple-use management (Tongass National Forest 2016). Birds breeding in this region vary markedly in abundance relative to the age of forest stands and specific silvicultural treatments, such as gapping and thinning (Dellasalla et al. 1996), but numerical responses have also been found to vary with time since treatment (Matsuoka et al. 2012). Patterns of positive and negative trends cannot be explained by any single directional response to age or structure of the forest. For example, Red-breasted Sapsuckers (positive trend) and Golden-crowned Kinglets (negative trend) both occur in greatest abundance in old-growth forests (>150 yr old), whereas Orange-crowned Warblers (positive trend) are most abundant in young growth (Dellasalla et al. 1996). Of note, negative trends in off-road areas of Rufous Hummingbirds and Golden-crowned Kinglets were concordant with negative continental trends in more southern portions of their breeding range (Sauer et al. 2013). Thus, changes in avian abundance in the expansive off-road substratum of this region that were not well reflected by the roadside BBS would be best examined relative to changes in habitat across the BCR.

As part of the ALMS protocol, detailed information on habitat at each survey point is collected during the first year of the survey and subsequently every 10 yr or whenever a major disturbance has occurred (Handel and Cady 2004). Analysis of changes in avian abundance



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relative to changes in habitat would enhance our understanding of whether differences in avian population trends reflect responses to breeding habitat directly or to some other factor locally or outside their breeding range. Similarly, collecting habitat data periodically along BBS routes, as recommended by a peer review panel (O'Connor et al. 2000), would allow us to determine the extent to which BBS population trends are associated with changes in roadside habitats. In Alaska, Cotter and Andres (2000) characterized the major vegetation cover types at each individual stop on 62 BBS routes during 1996 and 1997. Repetition of these vegetation surveys would provide valuable insights into whether avian population trends may be attributable to long-term changes in habitats. Comparative analyses of population trends in roadside and off-road substrata relative to habitat are particularly important in Alaska because of the vast expanses of public resource lands and the great disparity in potential habitat changes between these lands and those sampled from roadside corridors. Further stratification of public lands by degree or types of habitat management may also help us understand avian population trends.

### Regional Differences in Trends of Monotypic and Polytypic Species

Our results highlight the importance of incorporating a spatial component into any analysis of Alaskan population trends. Analysis of BBS data collected outside Alaska has been designed in part to address the effects of spatial sampling imbalance on estimates of population change, particularly at the edges of a species' range (Link and Sauer 2002, Sauer and Link 2011, Bled et al. 2013), but analysts have also long recognized the importance of understanding regional patterns of population change to facilitate management and conservation at the local level (Peterjohn and Sauer 1994, Herkert 1995). We found significant differences in regional population trends for several species, some monotypic and others represented by different subspecies in the 2 forested BCRs of Alaska, which are separated by steep mountain ranges and major icefields. For example, based on long-term BBS data, the Lesser Canada Goose (*B. c. parvipes*) population sampled in the NW Interior Forest BCR showed a significant negative trend (–3.4% $yr^{-1}$), whereas the Dusky (*B. c. occidentalis*) and Vancouver (*B. c. fulva*) Canada Goose populations breeding in the N Pacific Rainforest BCR were stable or slightly increasing, consistent with recent results from the North American Waterfowl Breeding and Population Habitat Survey (U.S. Fish and Wildlife Service 2016). In contrast, the nominate subspecies of Ruby-crowned Kinglet (*R. c. calendula*), which breeds in the NW Interior Forest, experienced a significant positive trend (+1.6% $yr^{-1}$), while the coastal *R. c. grinnelli* population remained stable. However, several monotypic species, such as the Townsend's Warbler and Wilson's Warbler, also showed long-term roadside trends that differed significantly between the 2 BCRs, but never in opposing directions.

We also found a pattern of a significant positive trend in the off-road substratum of the interior but not the coastal population for several polytypic species, most notably the American Robin (+3.1% $yr^{-1}$) and Fox Sparrow (+7.6% $yr^{-1}$), which may have reflected rapid northward range expansion in the continental inland populations relative to the more restricted Pacific coastal populations. Distributional patterns show a general divergence between populations of boreal species in interior and Pacific coastal Alaska, which has been linked to post-Pleistocene expansion from disjunct eastern and western refugia (Avise and Walker 1998, Johnson and Cicero 2004, Weir and Schluter 2004, Lovette 2005, Ruegg et al. 2006, Topp et al. 2013). Northwestward range expansion may be continuing for many species in response to climatic warming, as predicted by Stralberg et al. (2015).

### Comparisons with Trends in the Contiguous U.S. and Southern Canada

Most (65%) of the 54 species with data from Alaska that have shown long-term (45-yr) or short-term (10-yr) population trends in the core BBS area (Sauer et al. 2013) had no significant trends in either the roadside or the off-road substratum in Alaska. It is likely, however, that the duration of the Alaskan surveys has not yet been sufficient to detect similar trends for most populations. Within the complement of the species that did show trends in Alaska, most (14 of 19) had trends that were concordant with those on the rest of the continent, suggesting that the same dynamics were influencing their populations range-wide. The strongest signals were negative trends for a group of species associated in Alaska with wetland habitats, including the Lesser Yellowlegs, several flycatchers, several swallows, and the Blackpoll Warbler. In Alaska, boreal lakes and wetlands have been shrinking and drying in response to climatic warming (Roach et al. 2011, Hinzman et al. 2013, Jepsen et al. 2013). Negative trends in populations of aerial insectivores have been widely attributed to parallel declines in insect abundance, although whether changes in insect populations have occurred on the breeding grounds or elsewhere during the annual cycle is still being questioned and may vary among species (Nebel et al. 2010, Fraser et al. 2012, Nocera et al. 2012, Paquette et al. 2014). It is notable that the Rusty Blackbird (*Euphagus carolinus*), a boreal wetland species that has suffered a severe long-term population decline in more southerly portions of its range, particularly in the east (Greenberg and Droege 1999, Sauer et al. 2013), showed no indication of a negative trend in Alaska during our period of analysis. Our finding of a relatively stable



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population in Alaska is consistent with a lack of evidence for a decline in the neighboring Mackenzie Valley, Northwest Territories, Canada, between the 1970s and 2006 (Machtans et al. 2007). Understanding the linkages between invertebrate prey abundance in Alaskan wetlands and avian adult survival and reproduction would provide important insights into how populations of wetland-dependent species will be affected by continued rapid warming in boreal habitats.

We found evidence that populations might be increasing at the northern edge of the breeding range while declining elsewhere on the continent for only 3 species (Northern Flicker, Pacific-slope Flycatcher, and Chipping Sparrow). Several other species (e.g., Yellow-bellied Flycatcher [*Empidonax flaviventris*], Tennessee Warbler [*Oreothlypis peregrina*], and Cape May Warbler [*Setophaga tigrina*]) have recently been expanding their breeding ranges from northwestern Canada into Alaska (Gibson and Withrow 2015), but these species have as yet been too sparsely detected in Alaska to be monitored by either the BBS or ALMS. An analysis of climatic suitability for 80 boreal passerine species has projected that the barrier currently formed by the northwestern cordillera will be weakened as climate change improves conditions for breeding, likely leading to breeding range expansion into the boreal interior of Alaska for many more species by the end of this century (Stralberg et al. 2016).

### Hierarchical Analysis of Roadside and Off-road Surveys

We found the hierarchical modeling framework to be ideal for analyzing population trends while accounting for differences in sampling design, survey protocols, spatial correlation, and sources of detectability bias in the roadside BBS and off-road ALMS surveys. Addressing these nuisance factors is an inherent challenge in combined analysis of point count data from programs with disparate protocols (Nichols et al. 2009, Reidy et al. 2011). Importantly, failure to account for variation in detection probability can lead to biased estimates of abundance and erroneous conclusions about population trends (Pollock et al. 2002, Rosenstock et al. 2002, Thompson 2002). Some covariates, such as habitat structure (or elevation, as a proxy for habitat), can affect both abundance and detectability of birds, so distinguishing their effects on detection is essential for unbiased estimates of abundance (Bibby et al. 1992, Kéry et al. 2005, Kéry 2008).

Key components of detection probability (availability for detection, perceptibility) for most passerines breeding in boreal and sub-Arctic regions of North America are strongly affected by date, time of day, and habitat structure (Schmidt et al. 2013, Sólymos et al. 2013, Amundson et al. 2014, Thompson et al. 2016). For several long- and short-distance migrants breeding in interior Alaska, timing of spring arrival was strongly affected by interannual variation in air temperature during a recent 15-yr period (Mizel et al. 2017). Failure to account for effects on detectability of covariates such as climate-related advances in phenology, with concomitant seasonal changes in singing rates, or structural changes in habitat, with changes in perceptibility, can be problematic in long-term monitoring programs, particularly if there is a directional change in these covariates. Although we did not model interannual variation in availability or perceptibility in our analysis of our relatively short time series of off-road surveys, hierarchical models can readily accommodate such covariates explicitly to estimate long-term effects on both abundance and the observation process.

When we analyzed the data from roadside and off-road surveys together in the joint hierarchical model, the precision of estimates generally increased compared with that from the analysis of the 2 datasets independently. The joint structure allowed for separate intercepts (abundance) and slopes (underlying trend) for the roadside and off-road substrata in both BCRs, but it also incorporated shared parameters for random year effects within each BCR. This served to improve the overall mean precision of period-specific trend estimates. Residual interannual variation in abundance most likely reflected variation in regional weather patterns, which can be pronounced in northern regions (Mizel et al. 2017). These conditions would not likely vary between roadside and off-road substrata within a particular BCR, but this assumption deserves more careful scrutiny.

An initial goal of establishing the ALMS was to complement the existing roadside BBS, which was limited by the sparse road system in Alaska, and to increase power to detect regional population trends by increasing sample sizes and overall spatial coverage of the surveys. Combining data from the 2 surveys to produce a single estimate of population trend for each species in the state or even by BCR will be more complicated than initially envisioned. A primary concern is that the current ALMS covers only a portion of the Alaskan off-road areas, focusing on accessible areas of variably protected public lands; estimates of relative avian densities in the roadside and off-road substrata as well as their geographic sizes for proper weighting of trends are difficult to obtain given differences in protocols and the expansive areas in Alaska that are virtually inaccessible for surveys or unsuitable for breeding birds (e.g., massive glaciers, icefields, and rugged mountain ranges). However, our combined analysis has shown that important insights can be gained through comparing population-level results from the 2 surveys across the northern landscape. These complementary long-term monitoring programs can provide important information on range expansions (or contractions) and



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changes in abundance at the northern edge of the continent, particularly if coupled with information on population structuring and on habitat and environmental factors that may influence demographic processes. Such insights will be invaluable for guiding conservation and management decisions.

For other northern and western regions that have relatively sparse coverage by the roadside BBS and large expanses of less developed lands, we suggest that establishing a parallel off-road breeding bird survey, such as the ALMS, may be useful for increasing power and for validating the applicability of the BBS for monitoring regional population change. We also stress the importance of periodically collecting stop-level habitat data along roadside routes to be able to control for changes in roadside vegetation structure, urbanization, and detectability of birds, so that their effects on counts can be distinguished from actual changes in avian abundance across the broader landscape. Coupling the roadside BBS with a set of off-road surveys would further allow estimation of and control for effects of detection probability, which may be particularly important to measure as breeding phenology advances and habitats become altered in response to climatic change.

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**Author contributions:** C.M.H. and J.R.S. conceived the idea and design, formulated the questions asked, developed the methods, analyzed the data, and contributed resources and funding. C.M.H. wrote the paper with input from J.R.S.

**Data deposits:** Data used for this analysis are available with associated metadata at www.pwrc.usgs.gov/bbs/ (BBS) and doi:10.5066/F7XW4H88 (ALMS).

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**APPENDIX TABLE 2.** Long-term (1993–2015) annual percent change (% $yr^{-1}$) in bird populations on roadside Breeding Bird Surveys in 2 Bird Conservation Regions (BCRs) of Alaska, USA. For each species, we present number of routes surveyed (*n*) and the median and 95% credible intervals (CIs) for the annual percent change; **boldface** font indicates those for which 95% CIs did not overlap zero. Trends are presented only for species recorded on ≥14 routes in a region. Species noted with an asterisk (*) are represented by different subspecies in the 2 BCRs in Alaska (cf. Gibson and Withrow 2015), but not all had samples sufficient for comparative analysis.

| | | Northwestern Interior Forest BCR | | | | Northern Pacific Rainforest BCR | | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | Scientific name | *n* | Median | 2.5% | 97.5% | *n* | Median | 2.5% | 97.5% |
| Canada Goose* | *Branta canadensis* | 30 | **−3.4** | **−6.0** | **−0.9** | 18 | 2.1 | -0.9 | 5.0 |
| American Wigeon | *Anas americana* | 36 | 1.2 | −0.8 | 3.3 | | | | |
| Mallard | *Anas platyrhynchos* | 38 | 1.1 | −1.1 | 3.8 | 16 | 0.3 | −3.1 | 3.7 |
| Northern Shoveler | *Anas clypeata* | 23 | −1.1 | −4.7 | 2.0 | | | | |
| Northern Pintail | *Anas acuta* | 28 | −0.5 | −3.9 | 3.5 | | | | |
| Green-winged Teal | *Anas crecca* | 37 | 0.5 | −1.3 | 3.0 | | | | |
| Ring-necked Duck | *Aythya collaris* | 16 | 1.4 | −2.8 | 5.3 | | | | |
| Bufflehead | *Bucephala albeola* | 25 | −0.6 | −2.7 | 1.8 | | | | |
| Common Goldeneye | *Bucephala clangula* | 26 | −0.1 | −2.1 | 2.1 | | | | |
| Common Merganser | *Mergus merganser* | 15 | 0.2 | −5.6 | 5.1 | 21 | −1.0 | −3.0 | 0.8 |
| Ruffed Grouse* | *Bonasa umbellus* | 21 | −0.1 | −2.9 | 3.2 | | | | |
| Red-necked Grebe | *Podiceps grisegena* | 23 | **−2.5** | **−4.0** | **−1.1** | | | | |
| Rufous Hummingbird | *Selasphorus rufus* | | | | | 22 | 0.4 | −0.4 | 1.2 |
| Wilson's Snipe | *Gallinago delicata* | 58 | −0.1 | −0.7 | 0.7 | 15 | −0.6 | −1.7 | 0.6 |
| Spotted Sandpiper | *Actitis macularius* | 43 | −0.1 | −1.2 | 1.0 | 16 | 1.2 | −0.8 | 4.0 |
| Solitary Sandpiper | *Tringa solitaria* | 35 | −1.3 | −2.7 | 0.2 | | | | |
| Greater Yellowlegs | *Tringa melanoleuca* | 22 | −1.4 | −3.0 | 0.5 | 20 | 0.0 | −1.3 | 1.4 |
| Lesser Yellowlegs | *Tringa flavipes* | 49 | **−2.0** | **−3.1** | **−1.0** | | | | |
| Herring Gull | *Larus argentatus* | 34 | 0.0 | −1.7 | 2.0 | | | | |
| Glaucous-winged Gull | *Larus glaucescens* | 15 | **−5.3** | **−9.8** | **−1.7** | 23 | 1.0 | −1.1 | 3.4 |
| Common Loon | *Gavia immer* | 28 | −0.3 | −1.5 | 0.9 | 16 | −1.2 | −3.1 | 0.6 |
| Great Blue Heron | *Ardea herodias* | | | | | 15 | −1.7 | −3.6 | 0.4 |
| Bald Eagle | *Haliaeetus leucocephalus* | 37 | 0.4 | −1.5 | 1.8 | 26 | 0.5 | −0.3 | 1.2 |
| Northern Harrier | *Circus cyaneus* | 24 | −0.5 | −2.8 | 1.5 | | | | |
| Northern Goshawk | *Accipiter gentilis* | 15 | 1.3 | −1.2 | 4.0 | | | | |
| Red-tailed Hawk | *Buteo jamaicensis* | 34 | 0.4 | −1.0 | 1.8 | | | | |
| Great Horned Owl | *Bubo virginianus* | 31 | −0.9 | −2.6 | 0.8 | | | | |
| Belted Kingfisher | *Megaceryle alcyon* | 34 | −0.2 | −1.5 | 1.1 | 26 | −0.9 | −1.8 | 0.1 |
| Red-breasted Sapsucker | *Sphyrapicus ruber* | | | | | 20 | **2.0** | **0.5** | **3.6** |
| Downy Woodpecker* | *Picoides pubescens* | 25 | −0.7 | −2.8 | 1.1 | | | | |
| Hairy Woodpecker* | *Picoides villosus* | 31 | 1.2 | −0.5 | 2.9 | 23 | −1.0 | −2.6 | 0.9 |



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**APPENDIX TABLE 2.** Continued.

| Species | Scientific name | Northwestern Interior Forest BCR | | | | Northern Pacific Rainforest BCR | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | *n* | Median | 2.5% | 97.5% | *n* | Median | 2.5% | 97.5% |
| American Three-toed Woodpecker | *Picoides dorsalis* | 28 | −0.4 | −2.7 | 2.3 | | | | |
| Northern Flicker* | *Colaptes auratus* | 40 | −0.4 | −1.5 | 0.8 | 14 | **1.3** | **0.0** | **2.9** |
| American Kestrel | *Falco sparverius* | 17 | −0.9 | −3.7 | 2.5 | | | | |
| Merlin | *Falco columbarius* | 27 | 0.4 | −2.6 | 2.5 | | | | |
| Olive-sided Flycatcher | *Contopus cooperi* | 50 | **−1.2** | **−2.0** | **−0.5** | 23 | **−1.3** | **−2.3** | **−0.4** |
| Western Wood-Pewee* | *Contopus sordidulus* | 34 | **−1.7** | **−2.8** | **−0.3** | 15 | **−4.0** | **−8.2** | **−1.3** |
| Alder Flycatcher | *Empidonax alnorum* | 58 | **−0.8** | **−1.3** | **−0.3** | 23 | −0.4 | −1.5 | 0.7 |
| Hammond's Flycatcher | *Empidonax hammondii* | 27 | 0.6 | −0.8 | 1.9 | | | | |
| Pacific-slope Flycatcher | *Empidonax difficilis* | | | | | 20 | **0.9** | **0.2** | **1.6** |
| Say's Phoebe | *Sayornis saya* | | | | | 15 | −2.7 | −7.5 | 1.0 |
| Gray Jay | *Perisoreus canadensis* | 58 | 0.7 | −0.2 | 1.6 | | | | |
| Steller's Jay | *Cyanocitta stelleri* | | | | | 22 | −0.4 | −1.3 | 0.5 |
| Black-billed Magpie | *Pica hudsonia* | 28 | 0.0 | −1.1 | 1.2 | | | | |
| Northwestern Crow | *Corvus caurinus* | | | | | 21 | 0.6 | −0.3 | 1.4 |
| Common Raven | *Corvus corax* | 57 | 0.3 | −0.8 | 1.4 | 28 | **1.2** | **0.5** | **2.0** |
| Tree Swallow | *Tachycineta bicolor* | 49 | −1.3 | −2.7 | 0.2 | 25 | **−2.2** | **−4.0** | **−0.8** |
| Violet-green Swallow | *Tachycineta thalassina* | 42 | **−2.0** | **−3.6** | **−0.4** | 20 | **−1.8** | **−3.5** | **−0.3** |
| Bank Swallow | *Riparia riparia* | 47 | **−2.8** | **−4.5** | **−1.0** | | | | |
| Cliff Swallow | *Petrochelidon pyrrhonota* | 33 | **−3.4** | **−5.2** | **−1.4** | | | | |
| Barn Swallow | *Hirundo rustica* | | | | | 15 | **−2.7** | **−4.0** | **−1.0** |
| Black-capped Chickadee | *Poecile atricapillus* | 47 | −0.3 | −1.3 | 0.9 | | | | |
| Chestnut-backed Chickadee | *Poecile rufescens* | | | | | 22 | 0.1 | −0.8 | 1.0 |
| Boreal Chickadee | *Poecile hudsonicus* | 51 | 0.3 | −0.7 | 1.6 | | | | |
| Red-breasted Nuthatch | *Sitta canadensis* | | | | | 15 | −0.9 | −3.1 | 1.3 |
| Brown Creeper | *Certhia americana* | | | | | 22 | 0.4 | −1.9 | 2.6 |
| Pacific Wren | *Troglodytes pacificus* | | | | | 21 | 0.2 | −0.4 | 0.9 |
| Golden-crowned Kinglet* | *Regulus satrapa* | 14 | **6.2** | **1.4** | **13.3** | 26 | 0.1 | −1.2 | 1.5 |
| Ruby-crowned Kinglet* | *Regulus calendula* | 56 | **1.6** | **0.7** | **2.5** | 27 | −0.3 | −1.2 | 0.5 |
| Swainson's Thrush* | *Catharus ustulatus* | 59 | 0.3 | −0.1 | 0.8 | 28 | 0.5 | −0.1 | 1.0 |
| Hermit Thrush* | *Catharus guttatus* | 48 | 0.9 | −0.1 | 2.0 | 28 | 0.3 | −0.3 | 0.8 |
| American Robin* | *Turdus migratorius* | 59 | 0.3 | −0.1 | 0.7 | 28 | 0.0 | −0.5 | 0.5 |
| Varied Thrush* | *Ixoreus naevius* | 57 | −0.5 | −1.2 | 0.3 | 28 | −0.3 | −1.0 | 0.3 |
| Pine Grosbeak | *Pinicola enucleator* | 37 | −1.3 | −2.8 | 0.4 | | | | |
| Red Crossbill | *Loxia curvirostra* | | | | | 19 | **7.1** | **2.9** | **12.1** |
| White-winged Crossbill | *Loxia leucoptera* | 48 | 3.0 | −0.1 | 6.4 | 15 | −0.9 | −3.9 | 1.9 |
| Pine Siskin | *Spinus pinus* | 30 | 1.4 | −1.5 | 4.5 | 26 | 0.8 | −1.5 | 3.2 |
| Northern Waterthrush | *Parkesia noveboracensis* | 53 | −0.3 | −1.0 | 0.7 | 14 | 0.9 | −0.5 | 2.3 |
| Orange-crowned Warbler* | *Oreothlypis celata* | 56 | −0.6 | −1.3 | 0.1 | 27 | **−1.0** | **−1.7** | **−0.4** |
| Common Yellowthroat | *Geothlypis trichas* | | | | | 15 | 1.0 | −0.5 | 2.5 |
| Yellow Warbler* | *Setophaga petechia* | 58 | 0.4 | −0.4 | 1.2 | 26 | 0.4 | −0.4 | 1.1 |
| Blackpoll Warbler | *Setophaga striata* | 50 | **−2.3** | **−3.4** | **−1.1** | | | | |
| Yellow-rumped Warbler* | *Setophaga coronata* | 58 | 0.3 | −0.3 | 0.9 | 24 | 0.3 | −0.3 | 0.9 |
| Townsend's Warbler | *Setophaga townsendi* | 29 | −1.1 | −2.6 | 0.2 | 27 | **1.7** | **0.9** | **2.6** |
| Wilson's Warbler | *Cardellina pusilla* | 58 | **−1.7** | **−2.3** | **−1.0** | 27 | 0.0 | −0.7 | 0.8 |
| Chipping Sparrow | *Spizella passerina* | 20 | **4.8** | **3.0** | **6.9** | | | | |
| Savannah Sparrow | *Passerculus sandwichensis* | 52 | **−1.9** | **−2.6** | **−1.1** | 19 | **−1.3** | **−2.1** | **−0.5** |
| Fox Sparrow* | *Passerella iliaca* | 57 | 0.3 | −0.3 | 1.0 | 28 | **0.8** | **0.3** | **1.3** |
| Song Sparrow* | *Melospiza melodia* | | | | | 24 | 0.3 | −0.5 | 1.2 |
| Lincoln's Sparrow* | *Melospiza lincolnii* | 51 | **1.0** | **0.1** | **1.9** | 28 | −0.2 | −1.0 | 0.7 |
| White-crowned Sparrow* | *Zonotrichia leucophrys* | 59 | **−1.6** | **−2.2** | **−1.0** | | | | |
| Golden-crowned Sparrow | *Zonotrichia atricapilla* | 18 | −0.6 | −1.5 | 0.2 | | | | |
| Dark-eyed Junco* | *Junco hyemalis* | 59 | −0.1 | −0.6 | 0.4 | 28 | 0.0 | −0.6 | 0.6 |
| Rusty Blackbird | *Euphagus carolinus* | 34 | 0.4 | −1.2 | 2.2 | | | | |



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