

Articles

Montane-breeding Bird Distribution and Abundance Across National Parks of Southwestern Alaska

Courtney L. Amundson,* Colleen M. Handel, Daniel R. Ruthrauff, T. Lee Tibbitts, Robert E. Gill, Jr

U.S. Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, Alaska 99508

Abstract

Between 2004 and 2008, biologists conducted an inventory of breeding birds during May–June primarily in montane areas (>100 m above sea level) of Aniakchak National Monument and Preserve (Aniakchak NMP), Katmai National Park and Preserve (Katmai NPP), and Lake Clark National Park and Preserve (Lake Clark NPP) in southwestern Alaska. Observers conducted 1,021 point counts along 169 transects within 63 10-km × 10-km plots that were randomly selected and stratified by ecological subsection. We created hierarchical N-mixture models to estimate detection probability and abundance for 15 species, including 12 passerines, 2 galliforms, and 1 shorebird. We first modeled detection probability relative to observer, date within season, and proportion of dense vegetation cover around the point, then modeled abundance as a function of land cover composition (proportion of seven coarse-scale land cover types) within 300 m of the survey point. Land cover relationships varied widely among species but most showed selection for low to tall shrubs (0.2–5 m tall) and an avoidance of alpine and dwarf shrub–herbaceous cover types. After adjusting for species not observed, we estimated a minimum of 107 ± 9 species bred in the areas surveyed within the three parks combined. Species richness was negatively associated with elevation and associated land cover types. At comparable levels of survey effort ($n = 721$ birds detected), species richness was greatest in Lake Clark NPP (75 ± 12 species), lowest in Aniakchak NMP (45 ± 6 species), and intermediate at Katmai NPP (59 ± 10 species). Species richness was similar at equivalent survey effort ($n = 973$ birds detected) within the Lime Hills, Alaska Range, and Alaska Peninsula ecoregions (68 ± 8 ; 79 ± 11 ; 67 ± 11 , respectively). Species composition was similar across all three parks and across the three major ecoregions (Alaska Range, Alaska Peninsula, Lime Hills) that encompass them. Our results provide baseline estimates of relative abundance and models of abundance and species richness relative to land cover that can be used to assess future changes in avian distribution. Additionally, these subarctic montane parks may serve as signals of landscape change and barometers for the assessment of population and distributional changes as a result of warming temperatures and changing precipitation patterns.

Keywords: Alaska Peninsula; detection probability; landbirds; land cover associations; N-mixture models; population size; species richness

Received: June 12, 2017; Accepted: March 20, 2018; Published Online Early: March 2018; Published: June 2018

Citation: Amundson CL, Handel CM, Ruthrauff DR, Tibbitts TL, Gill RE Jr. 2018. Montane-breeding bird distribution and abundance across national parks of southwestern Alaska. *Journal of Fish and Wildlife Management* 9(1):180–207; e1944-687X. doi:10.3996/062017-JFWM-050

Copyright: All material appearing in the *Journal of Fish and Wildlife Management* is in the public domain and may be reproduced or copied without permission unless specifically noted with the copyright symbol ©. Citation of the source, as given above, is requested.

The findings and conclusions in this article are those of the author(s) and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

* Corresponding author: camundson@usgs.gov

Introduction

The Alaska Peninsula, dominated by the rugged, volcanic Aleutian Range, stretches approximately 800 km southwest from mainland Alaska to the Aleutian Island chain, separating the Bering Sea from the Pacific

Ocean. The Peninsula is an important stopover area for breeding and migrating birds, including a unique complement of alpine-nesting species (Murie 1959; Gill et al. 1981, 2015; Gill and Tomkovich 2004; Ruthrauff et al. 2007; Ruthrauff and Tibbitts 2009). Predominantly under federal ownership, the Alaska Peninsula and



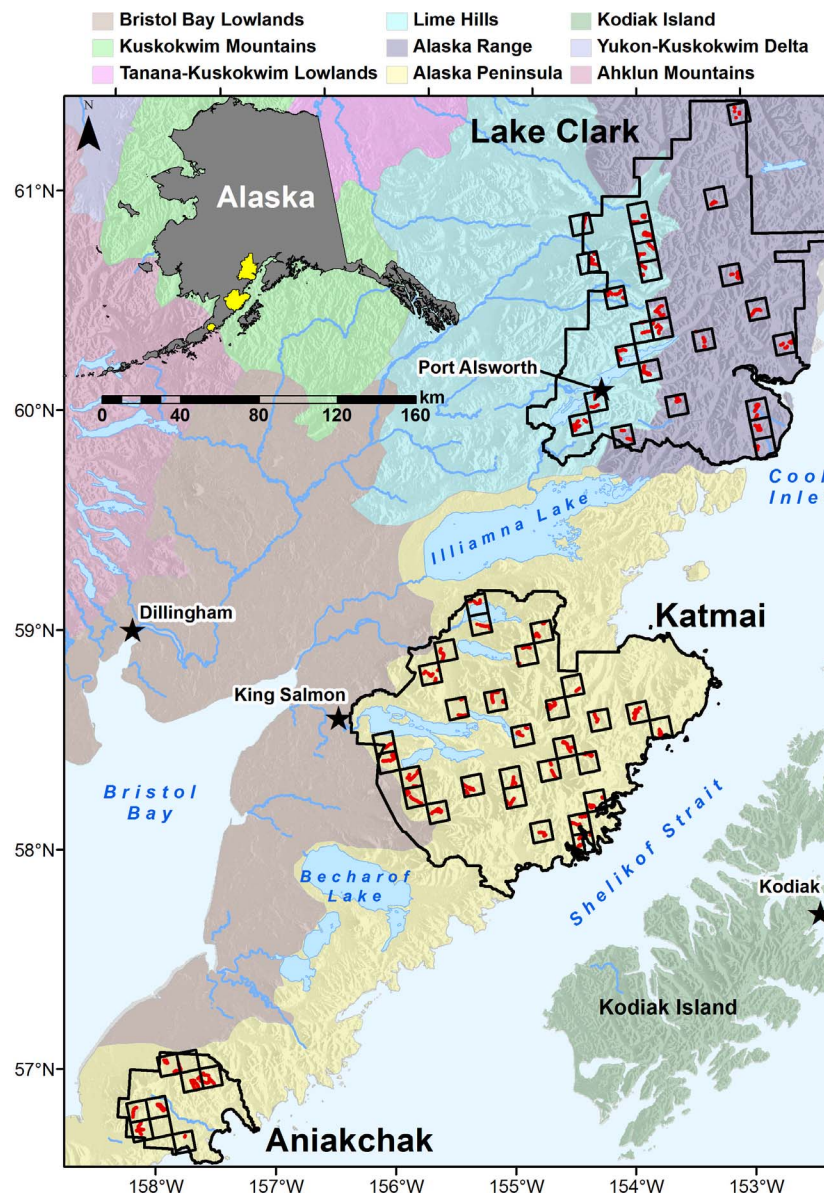


Figure 1. Distribution of ecoregions (Nowacki et al. 2001) and breeding-bird inventory sample plots (10 km × 10 km) with survey point locations (2004–2008) in Aniakchak National Monument and Preserve, Katmai National Park and Preserve (NPP), and Lake Clark NPP, Alaska. Black stars denote local human communities.

contiguous mainland portion of the Alaska Range include three National Parks and three National Wildlife Refuges. Aniakchak National Monument and Preserve (Aniakchak NMP), Katmai National Park and Preserve (Katmai NPP), and Lake Clark National Park and Preserve (Lake Clark NPP; hereafter, the parks) constitute three of the five units of the Southwest Alaska Network of National Parks and occupy the northern extent of the Peninsula and adjacent mainland (Figure 1). Among the most isolated and inaccessible units within the National Park system, the parks encompass a 5° latitudinal gradient and cover >35,500 km². Further, they span three Alaska climatic zones and encompass four ecoregions in which flora and fauna from the coastal Aleutian, interior boreal, low Arctic, and Pacific coastal zones converge (Murie 1959; Gallant et al. 1995). This

region is one of the most geographically active on the continent; numerous volcanoes and glaciers subject the landscape to high rates of natural disturbance.

The current climatic regime in southwestern Alaska, with mean annual temperatures close to 0°C, renders the area's flora and fauna particularly sensitive to small changes in temperature and precipitation. Increases in temperature and precipitation in alpine areas have already led to upslope shifts in treeline and changes in alpine vegetation communities elsewhere (Walther et al. 2005; Moritz et al. 2008), but changes in avian distribution may be heterogeneous in direction and magnitude. In the Sierra Nevada mountains, California, changes in precipitation led to downslope shifts in avian distributions while changes in temperature led to upward shifts in the same area; these avian shifts varied

in magnitude by species and site (Tingley et al. 2012). Consequently, montane species richness in the area has remained relatively constant over the past ≥ 80 y at mid-elevations but decreased at very low and very high elevations, suggesting heterogeneity in montane bird community responses to climate change (Tingley and Beissinger 2013). Southwestern Alaska is facing some of the largest predicted temperature anomalies and range-size contractions for montane birds in the world (La Sorte and Jetz 2010). Resource managers in Alaska have raised questions about potential effects of climate change on bird populations. Yet, to date, they have had little information with which to assess or plan for possible changes in distribution, abundance, or biodiversity.

Several earlier studies examined migratory birds breeding in or migrating through the Alaska Peninsula region (e.g., Murie 1959; Gill and Jorgensen 1979; Gill et al. 1981; Petersen 1981; Wilk and Wilk 1989; Ward et al. 1994; Adler 1997; Egan and Adler 2001), but most surveys and studies took place in coastal areas or along river corridors and lake shores of the lowlands adjacent to Bristol Bay. Seasonal, geographic, and taxonomic biases create an incomplete picture of the avian diversity, distribution, and abundance of breeding birds in the Alaska Peninsula region, particularly in montane-dominated vegetation types, which encompass much of the region's National Parks. To address this shortcoming, the National Park Service worked with the U.S. Geological Survey to conduct a comprehensive inventory of montane-breeding birds in Aniakchak NMP, Katmai NPP, and Lake Clark NPP as part of the National Park Service Inventory and Monitoring Program. Previous reports summarized those inventory data and described basic relationships between avian occurrence and vegetation (Ruthrauff et al. 2007; Ruthrauff and Tibbitts 2009). However, rugged terrain in all of the parks limited access to certain areas such that not all vegetation types or elevations were sampled relative to their occurrence in each park. In addition, preliminary analyses did not account for potential temporal or spatial correlation in the counts (cf. Thogmartin and Knutson 2007; Webster et al. 2008). Thus, preliminary abundance estimates could not be applied simply and reliably across park landscapes to estimate parkwide relative abundance or examine distribution patterns.

Our primary objective was to integrate data from recent inventories with land cover data to model abundance, species richness, and distribution of breeding birds across the parks, particularly in montane vegetation types. We built hierarchical models that incorporated detection probabilities to estimate density in relation to land cover attributes. We further modeled apparent species richness relative to elevation and land cover composition. Using these model-based approaches with environmental covariates accounted for potential bias arising from undersampling inaccessible areas and spatial correlation among sampled sites. We then used modeling results to construct maps of predicted density (for select species) and total species richness across park landscapes.

Methods

Previous reports described the study area, study design, and field methods in detail, and also provided basic data summaries (Ruthrauff et al. 2007; Ruthrauff and Tibbitts 2009). As a result, we only describe our modeling approaches in detail. We present standardized common bird species names throughout the text (Chesser et al. 2017); corresponding scientific names for all species detected during surveys are listed in Table 1.

Study area, survey design, and data collection

Ecoregions. The parks encompass portions of four major Alaska ecoregions: the Alaska Range, Lime Hills, Alaska Peninsula, and Bristol Bay Lowlands (Nowacki et al. 2001; Alaska Department of Fish and Game 2006; Figure 1). All ecoregions contain lowland tall shrub and forest, but vary in topography and vegetation types. The Alaska Range ecoregion, which includes the eastern half of Lake Clark NPP, is characterized by high peaks ($>3,900$ m) and very steep mountain slopes covered with glaciers, rocky slopes, and ice fields. The ecoregion contains discontinuous permafrost and sparse vegetation; dwarf shrub communities are common in wind-swept areas (Gallant et al. 1995). The Lime Hills ecoregion lies at the southwest end of the Alaska Range and includes the western half of Lake Clark NPP, with mountain peaks $>1,970$ m in elevation. This ecoregion is characterized by sharp mountain ridges and deep lakes; tall and low shrub communities dominate most areas, with bare ground or sparse vegetation at higher elevations. The Alaska Peninsula ecoregion is widespread across the parks, encompassing all of Aniakchak NMP and most of Katmai NPP. This ecoregion is defined by the Aleutian Range, which contains several glaciers and active volcanoes, and reaches 2,600 m in elevation. Semiarid alpine tundra dominates, but low shrubs, lichens, and grasslands also occur. The Bristol Bay Lowlands ecoregion, which only peripherally occurs along the western fringe of Katmai NPP, is characterized by flat-to-rolling moraine and outwash-mantled lowland <150 m in elevation. Moist and wet tundra dominates the landscape, interspersed with low and dwarf shrubs.

Inventory design. The inventory sampling frame consisted of a previously delineated 10-km $\times$ 10-km Geographic Information System grid that covered all three parks (Handel and Cady 2004). We considered areas within plots for inclusion in the inventory of montane-breeding birds if they were 1) within park boundaries, 2) >100 m mean elevation above sea level, 3) $<50^\circ$ mean slope, and 4) unglaciated. Following these criteria, we selected plots at random, and stratified them by ecological subsection (Shephard and Spencer 2000; Spencer 2001; Tande and Michaelson 2001) within each of the four sampled ecoregions (Nowacki et al. 2001; Figure 1). Mean elevation across the parks was >100 m above sea level in 91.0% of 25-ha cells in Katmai NPP, 93.5% of cells in Aniakchak NMP, and 99.3% of cells in Lake Clark NPP. Nevertheless, we revised plot selection in

Aniakchak NMP to include those with <100 m elevation to meet additional inventory objectives for that park. In Katmai NPP and Lake Clark NPP, we restricted the number of survey points in each subsection to between 10 and 60 units to avoid undersampling or oversampling geographically rare or extensive subsections, respectively. Observers conducted surveys at points placed at 500-m intervals along transects, which were oriented across gradients of elevation and vegetation type. Observers attempted to sample all subsections present in each plot within feasible logistical limits.

Field methods. The main purpose of the inventory was to identify and count birds breeding in montane areas of each park. Therefore, we conducted surveys from mid-May to early June, which coincided with peak courtship for most species. Observers recorded all birds detected during 10-min, unlimited-radius point counts (Ralph et al. 1995). Observers also recorded the approximate radial distance of each bird from the point, time elapsed from the start of the survey to detection, a suite of observation-specific information (e.g., sex, behavior, aural or visual detection), survey-specific information (wind speed, time of day, date, observer), and vegetation composition within 50 m or 150 m of the point, classified according to Viereck et al. (1992). The 10-min count duration allowed observers to detect species that typically breed at low densities (e.g., shorebirds, corvids, cranes; Table 1) and may not be detected within a standard 3- or 5-min count (Allredge 2007). We analyzed 5-min survey data for landbirds to minimize potential for undetected movement of birds, which could result in double-counting individuals. On Katmai NPP and Lake Clark NPP, observers did not record passerines during 10-min counts that targeted shorebirds and larger bodied species, but conducted a subsequent 5-min count immediately following the 10-min count to record detailed observations of passerines. On Aniakchak NMP, bird density was low and all species could be reliably recorded within the first 10-min count. All observers were trained and experienced in avian point-count methodology, distance estimation, and identification of birds in Alaska.

Detection probability

Using point-count information to estimate abundance of birds can be hampered by variable detection probability among species, dates, observation conditions, behaviors, vegetation types, and individuals (Buckland et al. 2001). We can reasonably account for much variation in perceptibility (p_d), or the ability to detect a bird given it has provided a cue, and availability (p_a), or the probability a bird has signaled its presence to the observer, by using careful study design and a combination of distance-sampling (Buckland et al. 2001) and time-removal methods (Farnsworth et al. 2002, 2005). In distance sampling, one records the approximate distance of a bird or group of birds from the observer. The analysis accounts for perceptibility by assuming maxi-

mum ability to detect cues occurs at the survey point and decreases as a function of distance from the observer. Distance sampling requires ≥ 60 –80 observations to estimate perceptibility reliably (Buckland et al. 2001).

Time-removal methods break the count period into shorter time intervals and apply a removal estimator to derive the proportion of the local (point) population that never signaled its presence to observers (e.g., did not sing; Farnsworth et al. 2002). During each short time period, animals are detected and then removed from the population; fewer animals are then available for detection in subsequent intervals. The decline in observations through time can be modeled to estimate the initial population size (Farnsworth et al. 2002). Combining these two methods makes various species observed during variable survey conditions comparable and allows relative abundance estimation for each species that should be strongly correlated with actual abundance (Amundson et al. 2014).

Detection probability models make several assumptions, including 1) the population is closed; 2) birds are not affected by the presence of an observer; and 3) there is no double-counting of individuals. Distance-sampling theory further generally assumes that 1) birds at the point are detected with certainty ($g[0] = 1$); 2) birds are detected at their original location (i.e., did not move toward or away from observer); and (3) distance measurements are exact. Basic time-removal methods assume that all 'easy to detect' individuals are detected during the first time interval and remaining birds have a constant per-minute probability of being detected. Combining distance-sampling and time-removal methods relaxes the assumption of perfect detection at the point and allows more accurate density estimates across the landscape. Birds observed flying overhead, participating in aerial chases or fights, or flying and landing within view of the observer may not be detected at their original location and could inflate density estimates. Therefore, we excluded birds exhibiting those behaviors from analyses with the exception of American pipit and Wilson's snipe, which regularly conduct aerial courtship displays within breeding territories.

Observers measured distance using a rangefinder either to the bird itself or to two landscape features that represented a range in which a bird was located. For example, a bird singing from a grove of trees could be measured as the midpoint between the nearest and furthest tree in the grove. Inherently, then, there will be some measurement error associated with distance estimates. We addressed some biases associated with measurement error by examining histograms of observations by distance and subsequently binning observations into distance categories by species (4–5 bins/species). We determined cutpoints based on the density of observations within a particular distance bin that minimized heaping, or the propensity of observers to round distances (e.g., 50 m, 100 m), which can strongly

Table 1. Survey length (SL; 5 or 10 min) and total number of individuals observed by species in three National Parks in southwestern Alaska (Aniakchak [ANIA] National Monument and Preserve [NMP], Lake Clark [LACL] National Park and Preserve [NPP], Katmai [KATM] NPP) and in four ecoregions within the parks (Alaska Peninsula [AP], Alaska Range [AR], Lime Hills [LH], and Bristol Bay Lowlands [BBL]) based on 1,021 surveys conducted during May–June, 2004–2008. We excluded observations from groups of >25 birds and individuals in directed flight to focus on birds breeding near survey points. We also excluded observations of passerines and landbirds that occurred after the first 5 min in Aniakchak NMP to be consistent with effort in Katmai and Lake Clark NPPs. Species are listed in taxonomic order (Chesser et al. 2017).

Common name	Scientific name	SL (min)	No. observed							Total
			Park			Ecoregion				
			ANIA	KATM	LACL	AP	AR	LH	BBL	
Trumpeter swan	<i>Cygnus buccinator</i>	5	0	0	37	0	33	4	0	37
Tundra swan	<i>Cygnus columbianus</i>	5	0	6	0	6	0	0	0	6
American wigeon	<i>Anas americana</i>	5	0	3	6	3	2	4	0	9
Mallard	<i>Anas platyrhynchos</i>	5	0	7	3	7	1	2	0	10
Northern shoveler	<i>Anas clypeata</i>	5	0	0	6	0	1	5	0	6
Northern pintail	<i>Anas acuta</i>	5	0	4	6	2	1	5	2	10
Green-winged teal	<i>Anas crecca</i>	5	0	3	13	3	3	10	0	16
Ring-necked duck	<i>Aythya collaris</i>	5	0	3	0	3	0	0	0	3
Greater scaup	<i>Aythya marila</i>	5	0	17	38	17	0	38	0	55
Lesser scaup	<i>Aythya affinis</i>	5	0	2	0	2	0	0	0	2
Harlequin duck	<i>Histrionicus histrionicus</i>	5	3	0	2	3	2	0	0	5
White-winged scoter	<i>Melanitta fusca</i>	5	0	0	4	0	4	0	0	4
Black scoter	<i>Melanitta americana</i>	5	0	2	6	2	0	6	0	8
Long-tailed duck	<i>Clangula hyemalis</i>	5	0	2	3	0	0	3	2	5
Common goldeneye	<i>Bucephala clangula</i>	5	0	1	7	1	0	7	0	8
Barrow's goldeneye	<i>Bucephala islandica</i>	5	0	4	5	2	0	5	2	9
Red-breasted merganser	<i>Mergus serrator</i>	5	0	2	4	2	4	0	0	6
Willow ptarmigan	<i>Lagopus lagopus</i>	5	30	41	39	71	19	20	0	110
Rock ptarmigan	<i>Lagopus muta</i>	5	16	52	23	68	10	13	0	91
White-tailed ptarmigan	<i>Lagopus leucura</i>	5	0	5	5	5	5	0	0	10
Horned grebe	<i>Podiceps auritus</i>	5	0	4	2	4	0	2	0	6
Red-necked grebe	<i>Podiceps grisegena</i>	5	0	2	0	2	0	0	0	2
Sandhill crane	<i>Antigone canadensis</i>	10	5	8	1	13	1	0	0	14
Black oystercatcher	<i>Haematopus bachmani</i>	10	1	0	0	1	0	0	0	1
Black-bellied plover	<i>Pluvialis squatarola</i>	10	0	5	0	5	0	0	0	5
American golden-plover	<i>Pluvialis dominica</i>	10	0	5	20	5	0	20	0	25
Pacific golden-plover	<i>Pluvialis fulva</i>	10	0	6	0	6	0	0	0	6
Semipalmated plover	<i>Charadrius semipalmatus</i>	10	30	16	9	46	0	9	0	55
Whimbrel	<i>Numenius phaeopus</i>	10	0	25	2	25	2	0	0	27
Hudsonian godwit	<i>Limosa haemastica</i>	10	0	1	0	1	0	0	0	1
Marbled godwit	<i>Limosa fedoa</i>	10	1	0	0	1	0	0	0	1
Surfbird	<i>Calidris virgata</i>	10	0	9	6	9	0	6	0	15
Dunlin	<i>Calidris alpina</i>	10	4	0	0	4	0	0	0	4
Rock sandpiper	<i>Calidris ptilocnemis</i>	10	21	0	0	21	0	0	0	21
Baird's sandpiper	<i>Calidris bairdii</i>	10	0	0	3	0	1	2	0	3
Least sandpiper	<i>Calidris minutilla</i>	10	7	22	7	27	1	6	2	36
Short-billed dowitcher	<i>Limnodromus griseus</i>	10	4	0	1	4	1	0	0	5
Wilson's snipe	<i>Gallinago delicata</i>	10	10	34	35	44	13	22	0	79
Spotted sandpiper	<i>Actitis macularia</i>	10	0	1	3	1	3	0	0	4
Wandering tattler	<i>Tringa incana</i>	10	0	0	5	0	4	1	0	5
Greater yellowlegs	<i>Tringa melanoleuca</i>	10	6	54	11	58	5	6	2	71
Lesser yellowlegs	<i>Tringa flavipes</i>	10	0	0	27	0	15	12	0	27
Red-necked phalarope	<i>Phalaropus lobatus</i>	10	19	0	14	19	0	14	0	33
Long-tailed jaeger	<i>Stercorarius longicaudus</i>	10	0	0	1	0	0	1	0	1
Bonaparte's gull	<i>Chroicocephalus philadelphia</i>	10	0	3	1	3	1	0	0	4
Mew gull	<i>Larus canus</i>	10	2	35	15	33	6	9	4	52
Glaucous-winged gull	<i>Larus glaucescens</i>	10	4	2	1	6	1	0	0	7
Red-throated loon	<i>Gavia stellata</i>	5	0	2	0	2	0	0	0	2
Pacific loon	<i>Gavia pacifica</i>	5	0	2	8	2	1	7	0	10
Common loon	<i>Gavia immer</i>	5	0	0	1	0	1	0	0	1
Bald eagle	<i>Haliaeetus leucocephalus</i>	10	1	5	1	6	1	0	0	7
Northern harrier	<i>Circus cyaneus</i>	10	4	7	0	9	0	0	2	11
Rough-legged hawk	<i>Buteo lagopus</i>	10	2	0	0	2	0	0	0	2
Golden eagle	<i>Aquila chrysaetos</i>	10	0	2	2	2	1	1	0	4

Table 1. Continued.

Common name	Scientific name	SL (min)	No. observed							Total
			Park			Ecoregion				
			ANIA	KATM	LACL	AP	AR	LH	BBL	
Short-eared owl	<i>Asio flammeus</i>	10	0	1	0	1	0	0	0	1
Downy woodpecker	<i>Picoides pubescens</i>	5	1	0	0	1	0	0	0	1
American three-toed woodpecker	<i>Picoides dorsalis</i>	5	0	1	4	1	0	4	0	5
Merlin	<i>Falco columbarius</i>	10	1	1	1	2	0	1	0	3
Olive-sided flycatcher	<i>Contopus cooperi</i>	5	0	0	4	0	4	0	0	4
Say's phoebe	<i>Sayornis saya</i>	5	0	0	2	0	1	1	0	2
Northern shrike	<i>Lanius excubitor</i>	10	0	1	1	1	1	0	0	2
Gray Jay	<i>Perisoreus canadensis</i>	10	0	2	12	2	3	9	0	14
Black-billed magpie	<i>Pica hudsonia</i>	10	3	0	8	3	2	6	0	11
Common raven	<i>Corvus corax</i>	10	8	9	7	17	6	1	0	24
Horned lark	<i>Eremophila alpestris</i>	5	1	25	30	24	4	26	2	56
Bank swallow	<i>Riparia riparia</i>	5	26	0	0	26	0	0	0	26
Black-capped chickadee	<i>Poecile atricapillus</i>	5	0	1	1	1	0	1	0	2
Boreal chickadee	<i>Poecile hudsonicus</i>	5	0	2	5	2	0	5	0	7
American dipper	<i>Cinclus mexicanus</i>	5	0	1	0	1	0	0	0	1
Ruby-crowned kinglet	<i>Regulus calendula</i>	5	0	4	55	4	19	36	0	59
Northern wheatear	<i>Oenanthe oenanthe</i>	5	0	0	2	0	2	0	0	2
Gray-cheeked thrush	<i>Catharus minimus</i>	5	2	0	7	2	3	4	0	9
Swainson's thrush	<i>Catharus ustulatus</i>	5	0	0	3	0	3	0	0	3
Hermit thrush	<i>Catharus guttatus</i>	5	85	154	108	236	84	24	3	347
American robin	<i>Turdus migratorius</i>	5	6	101	83	104	32	51	3	190
Varied thrush	<i>Ixoreus naevius</i>	5	0	16	56	16	21	35	0	72
American pipit	<i>Anthus rubescens</i>	5	22	88	88	108	49	39	2	198
Gray-crowned rosy-finch	<i>Leucosticte tephrocotis</i>	5	0	3	2	3	2	0	0	5
Pine grosbeak	<i>Pinicola enucleator</i>	5	0	3	0	3	0	0	0	3
White-winged crossbill	<i>Loxia leucoptera</i>	5	0	0	1	0	1	0	0	1
Common redpoll	<i>Acanthis flammea</i>	5	0	14	29	14	20	9	0	43
Hoary redpoll	<i>Acanthis hornemanni</i>	5	3	14	23	17	21	2	0	40
Lapland longspur	<i>Calcarius lapponicus</i>	5	10	15	10	25	0	10	0	35
Snow bunting	<i>Plectrophenax nivalis</i>	5	15	22	18	37	16	2	0	55
Northern waterthrush	<i>Parkesia noveboracensis</i>	5	0	4	7	4	6	1	0	11
Orange-crowned warbler	<i>Oreothlypis celata</i>	5	55	123	22	178	16	6	0	200
Yellow warbler	<i>Setophaga petechia</i>	5	0	22	40	22	39	1	0	62
Yellow-rumped warbler	<i>Setophaga coronata</i>	5	0	59	124	59	55	69	0	183
Wilson's warbler	<i>Cardellina pusilla</i>	5	119	195	93	314	70	23	0	407
American tree sparrow	<i>Spizelloides arborea</i>	5	4	124	132	124	39	93	4	260
Savannah sparrow	<i>Passerculus sandwichensis</i>	5	29	99	55	123	18	37	5	183
Fox sparrow	<i>Passerella iliaca</i>	5	39	232	136	264	116	20	7	407
Lincoln's sparrow	<i>Melospiza lincolni</i>	5	0	2	2	2	1	1	0	4
White-crowned sparrow	<i>Zonotrichia leucophrys</i>	5	10	95	91	105	37	54	0	196
Golden-crowned sparrow	<i>Zonotrichia atricapilla</i>	5	112	351	216	447	126	90	16	679
Dark-eyed junco	<i>Junco hyemalis</i>	5	0	41	111	41	39	72	0	152
Rusty blackbird	<i>Euphagus carolinus</i>	5	0	0	1	0	1	0	0	1

influence goodness-of-fit tests (Buckland et al. 2001). Additionally, outliers do little to assess the density function and may lead to poor fit within chosen distributions. Therefore, we eliminated the farthest 10% of observations from analysis for each species (Buckland et al. 2001).

Detection covariates. We considered a parsimonious set of covariates to refine perceptibility and availability in bird observations, and reduced those as necessary to avoid overfitting models for uncommon species (Table 2). We included date within season as a covariate on availability. We did not consider time of day because average survey time was similar among parks, ecoregions, and transects and availability is relatively stable

during the survey period for most species we examined (Thompson et al. 2017). We examined the effect of two groups of observers on perceptibility because some observers did not detect some species, leading to lack of model convergence when we examined observers individually. We did not have a priori hypotheses as to whether observers varied in their ability to detect a species. Therefore, we condensed observers into two groups based on similar ability to hear birds; to do this, we visually inspected detection curves for individual observers and compared perceptibility ($\pm 95\%$ CIs) estimated from models (described below) for several of the most common species that had been detected by all individuals. Observers recorded percent vegetation type

Table 2. Description and mean value of each covariate used in analyses of landbird and shorebird detection probability in three National Parks in southwestern Alaska (Aniakchak National Monument and Preserve, Lake Clark National Park and Preserve [NPP], Katmai NPP) based on surveys conducted during May–June, 2004–2008. Observers collected detection covariate data during surveys.

Variable	Mean (range)	Description
Perceptibility		
Observer	2 Observer groups: G1: Observers 1 and 2; G2: Observers 3, 4, and 5	All observers were trained and experienced in identification and distance estimation. Observers were combined into two groups based on similar hearing ability, determined from comparative analysis of detectability curves for the most common species.
Dense Cover	0.14 (0–1)	The total proportion of either a 50-m- (in closed habitats) or 150-m- (in open habitats) radius circle around the survey point covered by closed tall shrub, closed dwarf trees, and closed deciduous, mixed, or coniferous forest.
Availability		
Season date	144 (131–160)	The date of the survey within each season. Mean survey date (day 144) was 24 May.

(to third hierarchical level) using the Viereck et al. (1992) classification system for Alaska within a 150-m radius ($n = 779$ points) of each point except when visibility was obscured by trees or shrubs and could only be reliably estimated within a 50-m radius ($n = 242$ points). We defined Dense Cover as the total proportion of the survey circle covered by closed shrub >1.5 m tall, closed dwarf trees <3 m tall, and closed forest (deciduous, coniferous, or mixed) combined. We included this as a covariate on perceptibility under the hypothesis that an increase in tall, dense cover would reduce both visual and aural detections. We did not consider wind because surveys were only conducted during low-wind conditions (<20 km/h). We included only singing males in analyses for passerines that were primarily aurally detected to reduce heterogeneity in perceptibility. We included all birds of known and unknown sex for willow ptarmigan, rock ptarmigan, and Wilson's snipe because both sexes commonly vocalized, sex could not always be reliably determined, and sample sizes would otherwise have been too small to model.

Abundance

Our primary objectives were to 1) determine relationships between density, adjusted for imperfect detection, and each of several land cover types and physiographic factors for the species most commonly observed during the inventory; and 2) create predictions of relative abundance across the parks as a function of those relationships. We originally evaluated 14 fine-scale land cover classifications recorded by observers at each site as the basis of our assessment, but models were often overfit and unable to be extrapolated to unsurveyed areas, so we standardized classes between observed land cover types and the 2011 National Land Cover Database (NLCD) for Alaska (Homer et al. 2015). Correlations among observed fine-scale land cover classes and the NLCD were low (Text S1, *Supplemental Material*). Because certain land cover types (e.g., grass, ice and snow) were

rare and structurally similar to more common cover types (e.g., dwarf shrub, bare ground), we combined these cover types with others in the NLCD to reach seven coarse-scale land cover classes: Baresnow (bare ground and perennial ice and snow), Dshrubherb (mesic herbaceous cover and shrub cover <20 cm in height), Shrub (shrub cover >20 cm and <5 m in height), Dec (deciduous forest), Mixed (mixed deciduous–needleleaf forest), Spruce (needleleaf forest consisting of white *Picea glauca*, black *P. mariana*, or Sitka spruce *P. sitchensis*), and Water (emergent and woody wetlands and open water types including turbid and clear water). The resulting mean correlation between observer designations and the condensed NLCD classifications was 0.56 (Text S1, *Supplemental Material*).

The scale at which birds select land cover types can vary with landscape configuration, making scale important for assessing bird–land cover relationships. Research elsewhere across highly fragmented tracts of vegetation suggested that landscape composition at multiple scales ultimately determined occupancy at the local scale (Thogmartin and Knutson 2007; Thompson et al. 2014). Across the vast, intact landscapes of our study areas, however, use of a land cover type may be less sensitive to the scale at which it is assessed. Here, we examined avian selection of land cover types using a single 300-m-radius buffer around each survey point for all species. The land cover configurations surrounding individual survey points were relatively uniform, and the compositions of NLCD land cover within 150-m- and 800-m-radius buffers around each survey point were strongly correlated (correlation range = 0.58–0.90, $\bar{x}_r = 0.81$). The proportion of water within each buffer was the only land cover type with $r < 0.79$. Furthermore, the 300-m scale was large enough to feasibly predict density in similarly sized grid cells across the parks. Therefore, we assumed this scale was representative of the land cover types used by birds observed at each point.



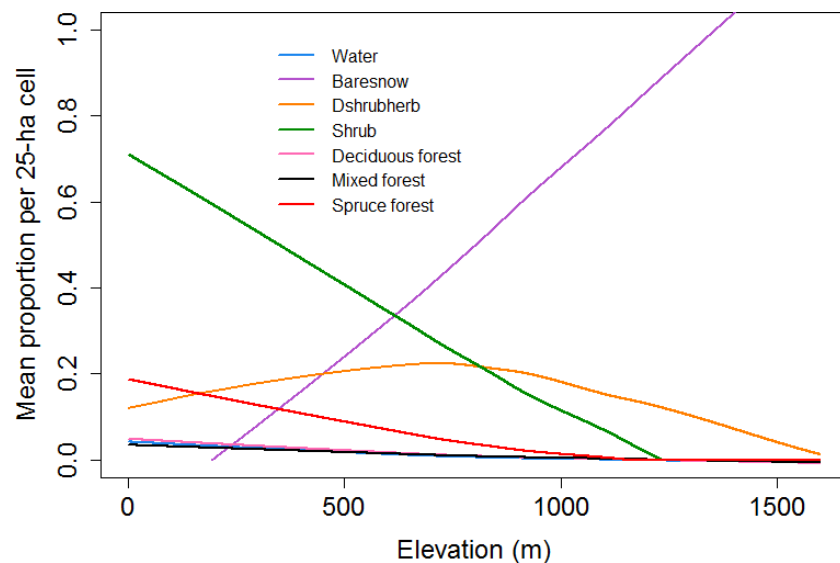


Figure 2. Loess-smoothed (degree and span = 1) plots of the mean proportion of seven major land cover classes relative to elevation (m) within 500-m $\times$ 500-m (25-ha) cells throughout Aniakchak National Monument and Preserve, Katmai National Park and Preserve (NPP), and Lake Clark NPP, in southwestern Alaska. Land cover classes were derived using the National Land Cover Dataset (Homer et al. 2015; Text S1, *Supplemental Material*).

Topographical and geomorphological variables affect microclimate and vegetation structure, especially in high-latitude areas (Young et al. 1997). These factors can then indirectly influence bird abundance and distribution (Jones 2001; Cintra and Naka 2012). Low elevations were characterized by forests and tall shrubs, with scattered wet and mesic herbaceous–graminoid meadows. Mid-elevation sites contained more low to tall shrubs, and upper elevations were predominantly characterized by dwarf shrubs and bare ground (Figure 2). Breeding birds are ultimately selecting for vegetation types rather than elevation per se; therefore, we included multiple land cover types as potential covariates in models, but excluded elevation because land cover types were strongly predictive of elevation in exploratory models (adjusted $R^2 = 0.53$). We used the *lsectpolyst* function in Geospatial Modelling Environment software (v. 7.2.0; Beyer 2012) to derive mean values for spatial covariates either from the NLCD or the National Elevation Dataset (Gesch 2007).

Multinomial mixture models. To estimate density, we modeled relative abundance adjusted for detection probability (p_d and p_a) and adjusted for the area surveyed for each species (raw data available in Data S1, *Supplemental Material*). We created a combined distance-sampling and time-removal model implemented in a Bayesian framework for analyses (Amundson et al. 2014). We estimated perceptibility (p_d) by modeling the scale parameter (σ) of the half-normal detection function in the distance analysis (Buckland et al. 2001). We estimated availability (p_a) at each point, i , with the removal model (Farnsworth et al. 2002), using three 100-s or 200-s time intervals for 5-min or 10-min counts, respectively.

We then modeled abundance (λ_i) as a Poisson distribution. Factors intrinsic to communities or populations (e.g., territoriality and constraints on dispersal), or extrinsic environmental factors (e.g., vegetation composition and landforms), can lead to clustering or overdispersion of birds across a landscape. To address these concerns, we 1) created nested random effects of points within transects (i.e., counts on points within a transect are likely similar), and 2) incorporated spatially structured environmental covariates. Despite numerous zeros in the data set, we did not incorporate a zero-inflation parameter because preliminary analyses suggested zero inflation reduced model fit and had negligible influences on resulting estimates or variance (C.L. Amundson, unpublished data). We linked combined detection probability to the process model such that latent abundance ($\hat{N}$) was characterized by a Poisson distribution of the expected count at each site (Kéry and Schaub 2012). We described observed counts at each site (Y_i) by a binomial distribution conditioned on the number of individuals that were available for detection (p_a) and detected (p_d). The expected count was a function of transect-specific random intercepts (α) and suite of fixed covariates (z_i). The general model was

$$Y_i \sim \text{Binomial}(p_d \times p_a, \hat{N}_i)$$

$$\hat{N}_i \sim \text{Poisson}(\lambda_i)$$

$$\log(\lambda_i) = \alpha[\text{transect}_i] + \beta_z \times z_i \quad (1)$$

We assigned random effects to normal distributions with mean 0 and precision τ , where precision is the inverse of the variance. We assigned variances and the half-normal shape parameter to uniform priors ranging

Table 3. Mean (range) values of land cover types and physiographic covariates (elevation, slope) used to determine criteria for distribution maps and assess bird–land cover relationships in Aniakchak National Monument and Preserve, Katmai National Park and Preserve (NPP), and Lake Clark NPP in southwestern Alaska. We report mean proportion of each land cover type by National Park and across all three parks for every 500-m $\times$ 500-m grid cell (25 ha) covered by a land cover type ($n_{\text{cells}} = 107,824$). We summarized mean land cover composition within a 300-m-radius buffer of each survey point (~ 28 ha; $n_{\text{points}} = 1,021$). We did not include cells that were classified as $>75\%$ open water or wetlands ($n = 6,562$ cells), $>80\%$ deciduous forest ($n = 381$ cells), $>55\%$ mixed forest ($n = 409$ cells), $>60^\circ$ mean slope ($n = 11,349$ cells), or <100 m mean elevation above sea level in Katmai NPP and Lake Clark NPP or $>1,600$ m above sea level for all parks ($n = 16,868$ cells). Land cover classes were derived using the National Land Cover Dataset (Homer et al. 2015; Text S1, *Supplemental Material*).

Covariate	Aniakchak	Katmai	Lake Clark	All parks	Survey points
Elevation (m)	268 (0–1244)	509 (100–1600)	791 (100–1600)	619 (0–1600)	480 (1–1598)
Slope ($^\circ$)	26.7 (0–60)	30.6 (0–60)	39.0 (0–60)	34.2 (0–60)	23.0 (0–63)
Bare/snow	0.18 (0–1)	0.29 (0–1)	0.43 (0–1)	0.35 (0–1)	0.14 (0–1)
Water	0.02 (0–0.75)	0.01 (0–0.75)	0.02 (0–0.75)	0.01 (0–0.75)	0.02 (0–0.74)
Dshrub/herb	0.32 (0–1)	0.23 (0–1)	0.12 (0–1)	0.19 (0–1)	0.29 (0–1)
Shrub	0.48 (0–1)	0.41 (0–1)	0.26 (0–1)	0.34 (0–1)	0.41 (0–1)
Dec	0.002 (0–0.29)	0.02 (0–0.8)	0.02 (0–0.79)	0.02 (0–0.8)	0.03 (0–0.76)
Mixed	0.000 (0–0.003)	0.007 (0–0.55)	0.03 (0–0.55)	0.02 (0–0.55)	0.03 (0–0.54)
Spruce	0.000 (0–0.004)	0.04 (0–1)	0.12 (0–1)	0.07 (0–1)	0.08 (0–1)

from 0 to 1,000 (Kéry 2010; Rota et al. 2011). For fixed effects, we specified vague normal prior distributions with mean 0 and $\tau = 0.001$ (variance = 1,000). We conducted 25,000–50,000 simulations using three Markov chains, thinned every 5 samples, and removed the first 10,000 simulations to facilitate convergence.

We conducted analyses in JAGS ver. 4.1.0 (Plummer 2003) called remotely from the package jagsUI (Kellner 2015) in Program R ver. 3.2.3 (R Core Team 2017). We assessed model convergence using the Gelman–Rubin potential scale reduction parameter, $\hat{R}$ where $\hat{R} = 1$ at convergence (Gelman and Rubin 1992). We accepted coefficient estimates with $\hat{R} < 1.1$. Finally, we examined goodness-of-fit of all models using posterior predictive checks (i.e., Bayesian P -values; Royle and Dorazio 2008). Bayesian P -values from 0.2 to 0.8, with 0.5 as the optimal value, suggest an acceptable fit to the data. We provide example R code for our model structure in Text S2 (*Supplemental Material*). We report breeding bird density per hectare by dividing $\hat{N}$ by the area surveyed and doubling estimates (i.e., assuming a 50:50 sex ratio) for all species except ptarmigan and Wilson’s snipe. We interpreted loess plots (span = 1, degree = 1) of predicted density against values of each land cover type.

Mapping distributions

We extrapolated density estimates across applicable areas within the parks based on the land cover types and physiographic factors affecting density. Despite randomly selecting survey plots and points within plots, sampling did not encompass the full range of land cover composition across the parks (Table 3). Therefore, we assumed survey data were representative of each park given several criteria and made predictions for cells that were 1) ≥ 100 m above sea level in Katmai NPP and Lake Clark NPP and $\leq 1,600$ m above sea level in all parks, 2) $\leq 75\%$ open water or wetlands, 3) $\leq 80\%$ deciduous forest, 4) $\leq 55\%$ mixed forest, and 5) $\leq 60^\circ$ mean slope. We created a 500-m $\times$ 500-m grid (25 ha)

across the parks and calculated the proportion of each land cover type within each cell using the `lsectpolrst` function in Geospatial Modelling Environment. We used cell-specific land cover proportions as values of a new data set.

The relatively fine resolution of our distribution maps ($\sim 107,000$ cells) prevented us from predicting N for each cell within Bayesian models as a result of computing power limitations. Instead, we derived 1,000 realizations of λ for each cell by exponentiating the model log-likelihood using cell-specific spatial covariate values and draws from a normal distribution for predicted α and β_z (see eq. 1) and their associated standard errors (Gelman and Hill 2007:363). We derived coefficients for map predictions from a model that pooled perceptibility across Dense Cover. Preliminary analyses suggested confounding between land cover effects on detection and abundance model components. Thus, using only coefficients for abundance from the full model that parsed contributions of dense vegetation to each model component would have biased predictions using our ad hoc cell-estimation method. We estimated overall and park-specific densities by calculating the mean and median values across grid cells and taking the 2.5 and 97.5 quantiles of the distribution of cell-specific means for each species. Similar to our point predictions, we doubled density estimates (assuming a 50:50 sex ratio) for all species except ptarmigan and Wilson’s snipe.

Species richness

We estimated species richness for each park and the three predominant ecoregions within park boundaries (Alaska Range, Lime Hills, and Alaska Peninsula); we did not include Bristol Bay Lowlands because only 17 points were sampled along its eastern edge (Figure 1). To ensure sampling effort was consistent across the parks, we included passerine and other landbird species observed during the 5-min surveys in Katmai NPP and Lake Clark NPP and during the first 5 min of Aniakchak



NMP surveys; we included shorebirds and low-density species recorded during the full 10-min surveys in all parks. We excluded birds in directed flight overhead and flocks of >25 birds (representing a natural break point in the counts) to focus on groups suspected of breeding near survey points. We estimated species richness using the 'vegetarian' package in Program R (version 1.2; Charney and Record 2015), which calculates the species accumulation rescaled by the mean number of individuals observed during surveys. This provides a smooth curve of the number of species observed in each group relative to sampling effort (i.e., the total no. of individuals observed; Colwell et al. 2004; Handel et al. 2009). We used the first-order jackknife method, which accounts for species missed during sampling, to estimate species richness (Burnham and Overton 1979). We examined differences in predicted species richness among parks and ecoregions by comparing mean richness $\pm$ 95% confidence intervals at levels of survey effort needed to detect 973 individual birds for Alaska Peninsula, Alaska Range, and Lime Hills ecoregions (no. observed in Alaska Range), and at levels to detect 721 individuals for each park (no. observed in Aniakchak NMP). We estimated overall species richness based on the total number of individuals observed ($n = 4,923$).

We examined factors affecting 'apparent' species richness (i.e., the no. of unique species observed at each site, uncorrected for detection probability) by creating a generalized linear model under a Poisson distribution and a log link with the number of species as the response variable and either elevation or the same suite of land cover covariates used for modeling species' abundance. We realized that analyzing naïve species counts without accounting for differences in detection probability would likely lead to biased estimates of species richness (McNew and Handel 2015). We expected, however, that modeled relationships of richness with elevation and land cover variables would be conservative, because detection probability would be greater at higher elevations with vegetation of lower stature, whereas species richness should show the reverse pattern. We truncated observations at a distance of 300 m from the observer to ensure that the species richness observed was derived on the same scale as the density maps. Unlike abundance estimation, we assumed that observations without recorded distances ($n = 188$) were within 300 m and included these in richness estimates. We then mapped species richness across applicable areas in the parks as described for mapping abundance based on land cover associations.

We estimated the similarity of species composition among ecoregions and parks using the Horn–Morisita (H–M) index of similarity in the 'vegetarian' package in Program R. The H–M index estimates the proportion of shared species among groups. We based inference on the Wolda (1981) adjusted H–M index of counts to reduce bias caused by overweighting highly abundant

species (Jost 2007). We conducted 1,000 bootstrap simulations to estimate standard errors for each group (Jost 2007). We present richness and similarity estimates $\pm$ 95% confidence intervals.

Results

Observers surveyed 1,021 points in 169 transects in 63 sample plots across the parks. Fewer observations and species were recorded in Aniakchak NMP ($n_{\text{points}} = 136$, $n_{\text{obs}} = 721$, $n_{\text{sp}} = 39$) than in Katmai NPP ($n_{\text{points}} = 468$, $n_{\text{obs}} = 2,229$, $n_{\text{sp}} = 71$) or Lake Clark NPP ($n_{\text{points}} = 417$, $n_{\text{obs}} = 1,973$, $n_{\text{sp}} = 78$). After eliminating birds in directed flight overhead and flocks of >25 birds, observers recorded 5,782 birds of 97 species (range = 1–815 observations/species). Records included 4,440 birds of 62 species during 5-min surveys (including most species of passerines and landbirds only during the first 5-min of the 10-min count at Aniakchak NMP) and 483 individuals of 35 low-density species (i.e., raptors, cranes, shorebirds, gulls, jaegers, owls, corvids) during 10-min surveys (Table 1). In Aniakchak NMP, yellow warbler ($n = 3$) was not included in species richness counts because it was detected for the first time during the second half of the 10-min survey.

Model results

We analyzed 2,674 observations from 15 species (12 passerines, 2 galliforms, and 1 shorebird). Analyses included 62–501 observations/species. In general, models fit these data well; posterior predictive checks averaged 0.53 (range = 0.44–0.61). Maximum truncated distance from the observer varied by species (Table 4). Cumulative perceptibility to 100 m from the observer ranged from 0.63 for Wilson's warbler to 0.96 for Wilson's snipe (Table 4). Singing frequency varied greatly among species; the estimated availability for detection during a given point count ranged from 0.52 to 0.97 and was greatest for warblers and lowest for American robin. We eliminated covariates on perceptibility for 7 species and covariates on both detection components for 1 species to improve model fit (Table S1, *Supplemental Material*). For remaining species, perceptibility was generally lower for Observer Group 2 and with increasing Dense Cover (4 species); availability decreased with season date for 3 species (Table S1, *Supplemental Material*).

Abundance models indicated a substantial association with land cover type for landbird species (Table S2, *Supplemental Material*). Land cover type models did not converge for Wilson's snipe, so we evaluated an elevation-only model (mean elevation within 300 m of the survey point) for that species. Several species were positively associated with low to tall shrub (Figure 3) and forested cover types, especially deciduous forest (Figure 4), but American pipits and rock ptarmigan were more positively associated with open land cover types such as dwarf shrub (Figure 5). Savannah and white-crowned sparrows, and to some extent American tree sparrows, also used lower elevation wetlands and areas with open

Table 4. Estimates of two components of detection probability, along with sample sizes and truncation distances (m) used in analysis, for 15 species of montane-breeding birds during surveys in three National Parks in southwestern Alaska (Aniakchak National Monument and Preserve, Katmai National Park and Preserve [NPP], Lake Clark NPP) during May–June, 2004–2008. Species modeled include willow ptarmigan *Lagopus lagopus*, rock ptarmigan *L. muta*, Wilson’s snipe *Gallinago delicata*, hermit thrush *Catharus guttatus*, American robin *Turdus migratorius*, American pipit *Anthus rubescens*, orange-crowned warbler *Oreothlypis celata*, yellow-rumped warbler *Setophaga coronata*, Wilson’s warbler *Cardellina pusilla*, American tree sparrow *Spizelloides arborea*, Savannah sparrow *Passerculus sandwichensis*, fox sparrow *Passerella iliaca*, white-crowned sparrow *Zonotrichia leucophrys*, golden-crowned sparrow *Z. atricapilla*, and dark-eyed junco *Junco hyemalis*. Availability (p_a ; $\pm$ 95% credible limits) is the probability of being available for detection (e.g., signaling the observer) during a 5-min (landbirds) or 10-min (Wilson’s snipe) point count. Perceptibility ($p_{d\ 100\ m}$; $\pm$ 95% credible limits) is the cumulative probability of being observed within 100 m of the observer, given birds were available for detection. The number of observations excludes birds in directed flight overhead, groups of ptarmigan >25 , as well as females and birds of unknown sex for all species except willow and rock ptarmigan and Wilson’s snipe.

Species	No. of observations	Truncation distance (m)	p_a	$p_{d\ 100\ m}$
Willow ptarmigan	91	432	0.53 (0.27, 0.79)	0.93 (0.91, 0.95)
Rock ptarmigan	73	500	0.59 (0.25, 0.85)	0.93 (0.92, 0.95)
Wilson’s snipe	62	600	0.85 (0.67, 0.95)	0.96 (0.94, 0.96)
Hermit thrush	217	280	0.85 (0.74, 0.92)	0.86 (0.82, 0.89)
American robin	143	300	0.52 (0.38, 0.67)	0.93 (0.89, 0.98)
American pipit	125	300	0.67 (0.56, 0.80)	0.88 (0.84, 0.91)
Orange-crowned warbler	148	150	0.96 (0.93, 0.99)	0.69 (0.61, 0.77)
Yellow-rumped warbler	144	150	0.95 (0.90, 0.98)	0.76 (0.67, 0.86)
Wilson’s warbler	280	175	0.97 (0.93, 0.98)	0.63 (0.57, 0.68)
American tree sparrow	202	175	0.81 (0.63, 0.95)	0.72 (0.67, 0.78)
Savannah sparrow	139	200	0.92 (0.85, 0.97)	0.76 (0.70, 0.82)
Fox sparrow	306	250	0.92 (0.87, 0.96)	0.80 (0.76, 0.83)
White-crowned sparrow	140	205	0.70 (0.47, 0.92)	0.82 (0.77, 0.88)
Golden-crowned sparrow	501	280	0.95 (0.93, 0.97)	0.86 (0.84, 0.88)
Dark-eyed junco	103	162	0.69 (0.52, 0.94)	0.76 (0.66, 0.86)

water (Figure 6); whereas, American pipits and rock ptarmigan were more abundant in alpine areas associated with bare ground and perennial ice and snow (Figure 7). American tree sparrows showed a nonlinear relationship with most land cover types, suggesting they selected a mosaic of open and closed vegetation. Wilson’s snipe were negatively associated with elevation (Figure 8). At sampled points, density for all species ranged from 0.004 to 0.19 breeding birds/ha and was lowest for Wilson’s snipe and greatest for Wilson’s warbler (Table 5). We predicted abundance for 15 species across 107,824 cells (26,956 km²) after removing 34,922 cells that did not meet inclusion criteria. Predicted mean density per hectare varied across parks; median density across parks ranged from 0.007 breeding birds/ha for willow ptarmigan to 0.12 breeding birds/ha for golden-crowned sparrows (Table S3, *Supplemental Material*). Distribution maps for each species are located in Figure S1 (*Supplemental Material*).

Species richness

Accounting for undetected species, overall species richness was 107 ± 9 species, given the total survey effort expended (Figure 9). Apparent richness averaged 3.3 species/survey point (range = 0–14, median = 3). Estimated species richness was lower in Aniakchak NMP than in either Katmai NPP or Lake Clark NPP at equal sampling efforts (721 observations; 44.5 ± 6.4 , 58.9 ± 9.9 , and 74.5 ± 12.1 species, respectively; Figure 9, upper panel). Estimated species richness was similar at equal survey effort (973 observations) within the Lime Hills,

Alaska Range, and Alaska Peninsula ecoregions (68.2 ± 8.1 ; 78.9 ± 10.9 ; 67.4 ± 10.6 , respectively; Figure 9, lower panel).

The proportion of shared species was large among ecoregions and parks. Estimated proportion of shared species ranged from 0.64 (95% CL = 0.59–0.69) between Aniakchak NMP and Lake Clark NPP to 0.88 (95% CL = 0.85–0.9) between Katmai NPP and Lake Clark NPP. Aniakchak NMP and Lake Clark NPP shared a lower proportion of species than other pairwise park groupings (Figure 10, left). Pairwise comparisons of the Alaska Peninsula, Alaska Range, and Lime Hills ecoregions found a large proportion of shared species between the Alaska Peninsula and the Alaska Range (0.90; 95% CL = 0.87–0.93), and lower similarity between each of these two ecoregions and the Lime Hills (AP–LH = 0.72, 95% CL = 0.67–0.77; AR–LH = 0.67, 95% CL = 0.62–0.71; Figure 10, right). Observers recorded 17, 7, and 1 unique (i.e., not detected in other units) species in the Alaska Peninsula, Alaska Range, and Lime Hills ecoregions, respectively; and they recorded 7, 11, and 15 unique species in Aniakchak NMP, Katmai NPP, and Lake Clark NPP, respectively (Table 1).

We included 4,416 individuals of 90 species in the Poisson model of apparent species richness. Omitting observations beyond 300 m from the observer excluded 7 unique species and 507 individuals from the analysis. Species richness decreased with increasing elevation (Figure 11), but incorporating individual land cover types improved model fit (adjusted $R^2 = 0.13$ and 0.24 for elevation and land cover models, respectively). Species

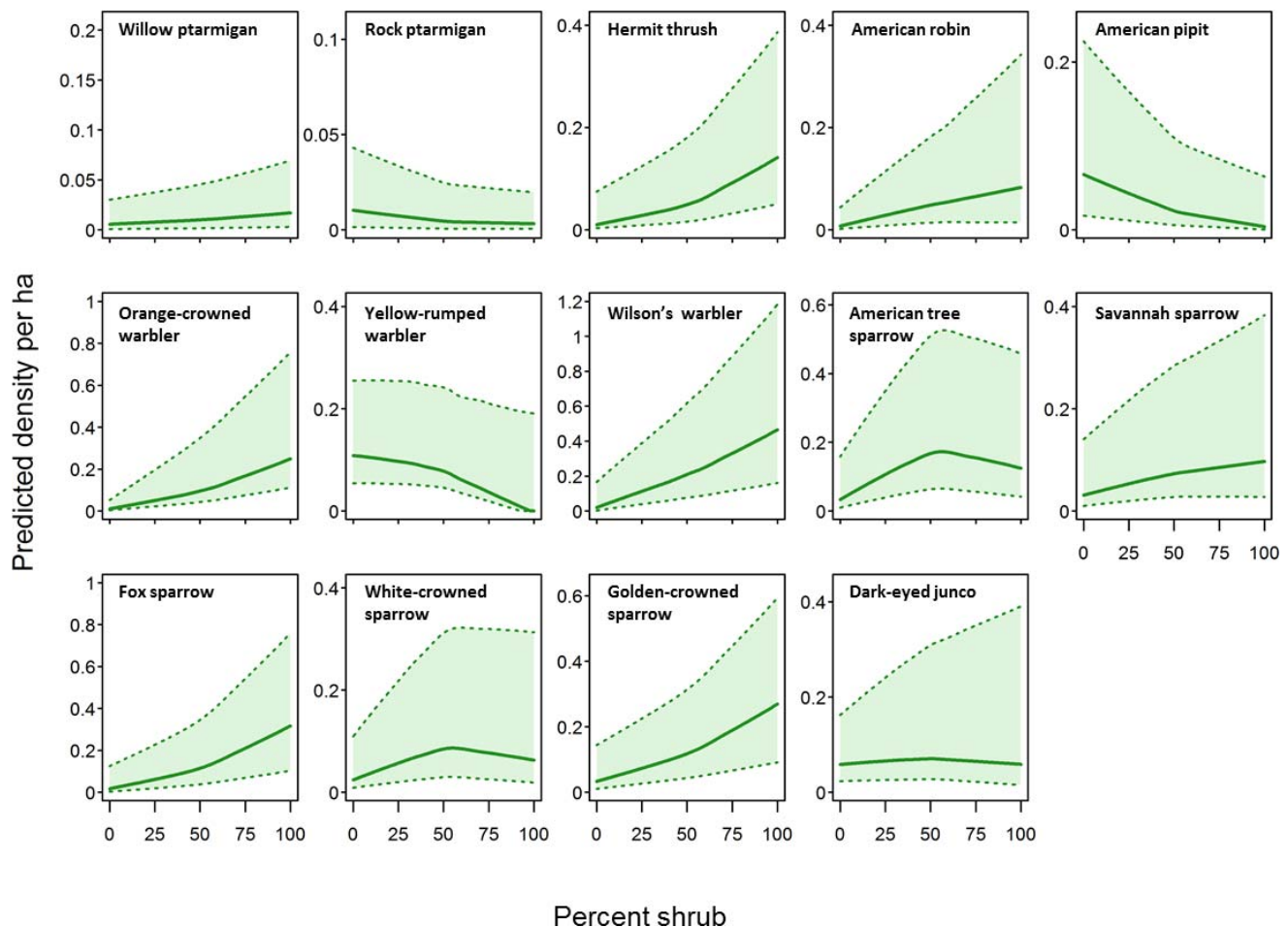


Figure 3. Predicted density per hectare of 14 landbird species surveyed during May–June, 2004–2008, at 1,021 points in three National Parks of southwestern Alaska (Aniakchak National Monument and Preserve, Katmai National Park and Preserve [NPP], Lake Clark NPP) relative to the proportion of shrub cover (0.2–5 m tall) within a 300-m radius around each point. Solid lines represent mean predicted values and shaded areas 95% credible intervals. Species modeled include willow ptarmigan *Lagopus lagopus*, rock ptarmigan *L. muta*, hermit thrush *Catharus guttatus*, American robin *Turdus migratorius*, American pipit *Anthus rubescens*, orange-crowned warbler *Oreothlypis celata*, yellow-rumped warbler *Setophaga coronata*, Wilson's warbler *Cardellina pusilla*, American tree sparrow *Spizelloides arborea*, Savannah sparrow *Passerculus sandwichensis*, fox sparrow *Passerella iliaca*, white-crowned sparrow *Zonotrichia leucophrys*, golden-crowned sparrow *Z. atricapilla*, and dark-eyed junco *Junco hyemalis*. Note that scale of y-axis varies among species.

richness was driven by positive associations with low to tall shrub and water and negative associations with dwarf shrub–herbaceous land cover and bare ground and perennial ice and snow (Figure 11). Species richness was not strongly associated with coniferous forest, but decreased with greater amounts of mixed forest and increased in areas with more deciduous forest (Figure 11). Consequently, the greatest predicted species richness was in riparian or lacustrine tall shrub communities, often near large lakes or on islands within lakes (Figure 12). The highest 5% of richness values were concentrated in Katmai NPP (54%) around Kulik Lake in the north and along the western river outlets of Lake Grosvenor and Naknek Lake in the central part of the park. Lake Clark NPP had 39% of the top 5% of richness values, which were concentrated in the northeast part of the park around the Stony and Telequana rivers (Figure S2,

Supplemental Material). Aniakchak NMP had the fewest (7%) cells with top richness values; these areas were concentrated along the Cinder River to the north and along the Meshik River and in low-elevation areas to the south (Figure S2, *Supplemental Material*).

Discussion

Species richness, as well as abundance of many individual species, increased with vegetation height and structure in our study. A global analysis of bird diversity in montane systems found that greatest avian diversity generally occurs in areas with the warmest and wettest conditions elevationally (McCain 2009). In high-latitude mountains, both temperature and precipitation typically decrease with increasing elevation, leading to a predicted pattern of concomitant declines in avian

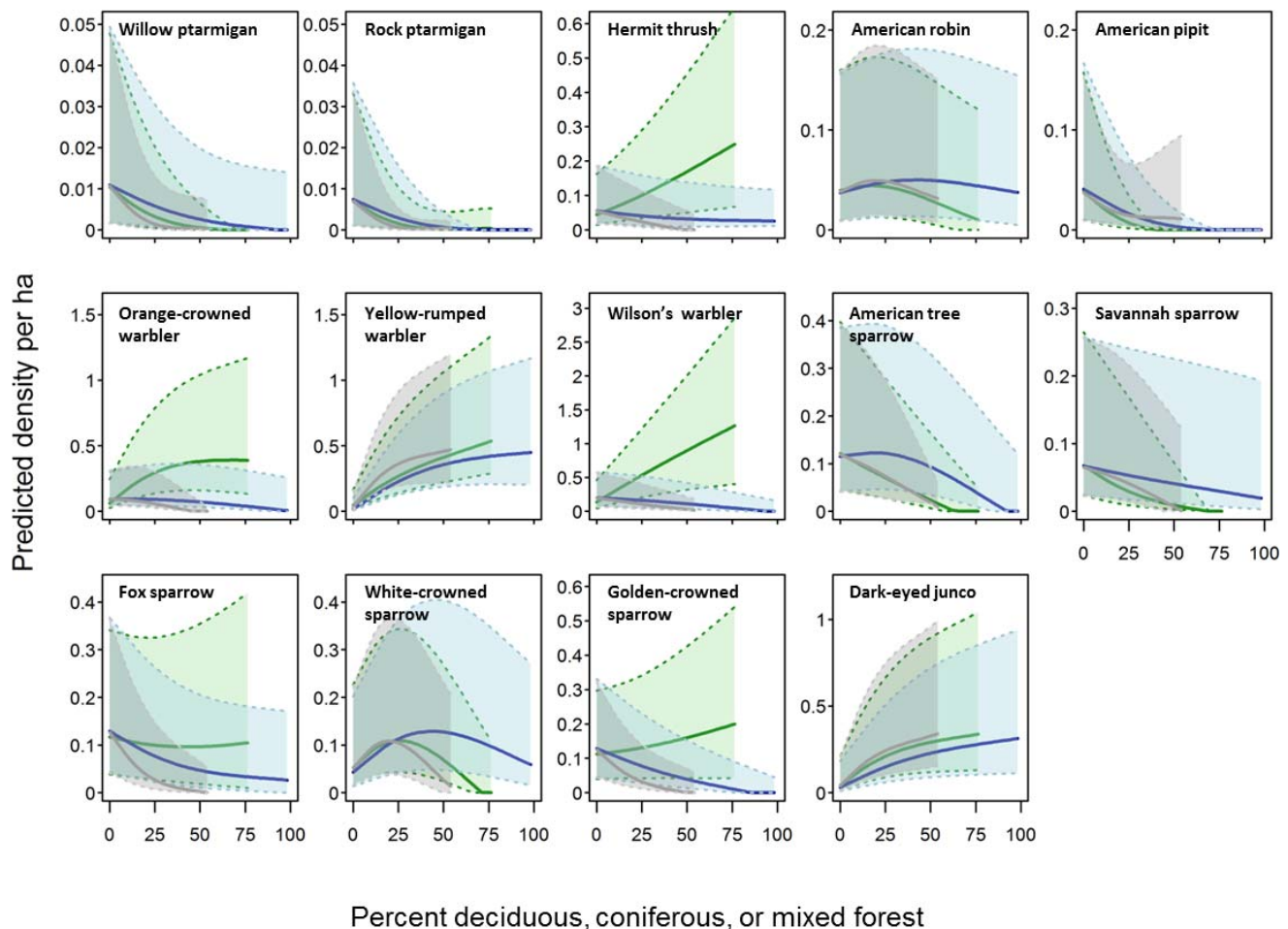


Figure 4. Predicted density per hectare of 14 landbird species surveyed during May–June, 2004–2008, at 1,021 points in three National Parks of southwestern Alaska (Aniakchak National Monument and Preserve, Katmai National Park and Preserve [NPP], Lake Clark NPP) relative to the proportion of deciduous forest (green), mixed deciduous–coniferous forest (gray), and coniferous forest (blue) within a 300-m radius around each point. Solid lines represent mean predicted values and shaded areas 95% credible intervals. Species modeled include willow ptarmigan *Lagopus lagopus*, rock ptarmigan *L. muta*, hermit thrush *Catharus guttatus*, American robin *Turdus migratorius*, American pipit *Anthus rubescens*, orange-crowned warbler *Oreothlypis celata*, yellow-rumped warbler *Setophaga coronata*, Wilson's warbler *Cardellina pusilla*, American tree sparrow *Spizelloides arborea*, Savannah sparrow *Passerculus sandwichensis*, fox sparrow *Passerella iliaca*, white-crowned sparrow *Zonotrichia leucophrys*, golden-crowned sparrow *Z. atricapilla*, and dark-eyed junco *Junco hyemalis*. Note that scale of y-axis varies among species.

diversity (McCain and Grytnes 2010). This pattern was strongly confirmed in our study and similar to that found in another montane park in Interior Alaska (Handel et al. 2009). Across broad latitudinal gradients, the best global predictors of avian species richness are topographical variability, which reflects heterogeneity in vegetation, and temperature (Davies et al. 2007). In our study, avian species richness conformed to this prediction in that the number of species increased with elevation span and vertical structure of available vegetation types within each park (i.e., greatest in Lake Clark NPP and lowest in Aniakchak NMP).

The strong relationship between species richness of breeding bird communities and foliage height diversity has long been recognized, particularly for passerines (e.g., MacArthur and MacArthur 1961; Karr and Roth 1971; Willson 1974; Tews et al. 2004). Taller shrubs and trees provide perches for singing, support for nest

structures, protection from inclement weather, concealment from nest predators, and important foraging substrates. In Alaska, many species of birds can be assigned to their predominant habitat type based on structure and height of the vegetation, topography of the terrain, and moisture content of the substrate (Kessel 1979).

Although our predictive models for abundance of individual species across the landscape were largely structured on such attributes, we were surprised to find that model coefficients for individual covariates did not reveal the expected relationships and led to less than useful conclusions for most species (Table S2, *Supplemental Material*). For example, American pipits are typically an alpine and open tundra species (Hendricks and Verbeek 2012). Concordantly, predicted abundance per point was positively associated with bare ground and perennial ice and snow, and dwarf shrub–herbaceous

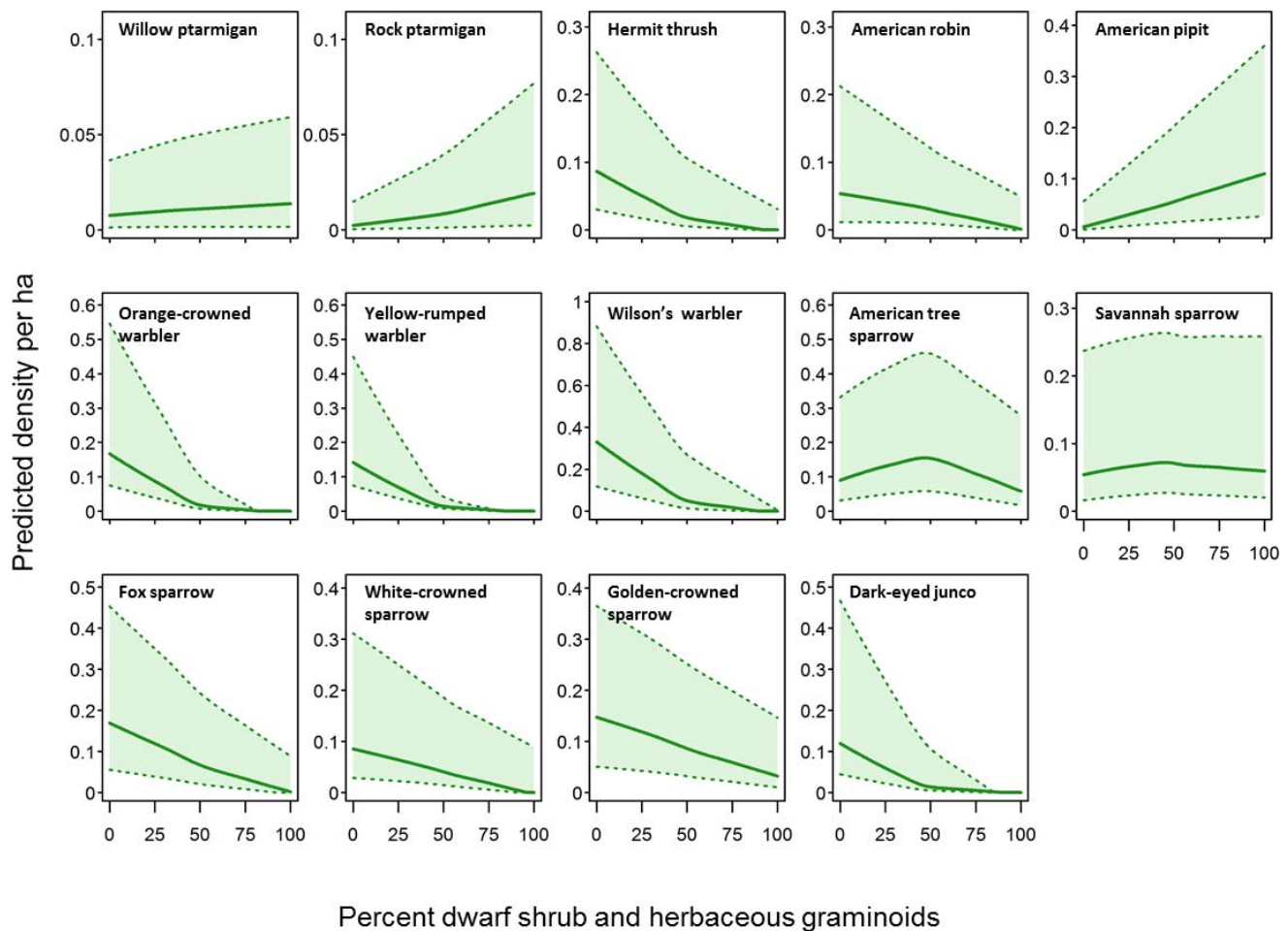


Figure 5. Predicted density per hectare of 14 landbird species surveyed during May–June, 2004–2008, at 1,021 points in three National Parks of southwestern Alaska (Aniakchak National Monument and Preserve, Katmai National Park and Preserve [NPP], Lake Clark NPP) relative to the proportion of dwarf-shrub and herbaceous-graminoid vegetation (Dshrubherb) within a 300-m radius around each point. Solid lines represent mean predicted values and shaded areas 95% credible intervals. Species modeled include willow ptarmigan *Lagopus lagopus*, rock ptarmigan *L. muta*, hermit thrush *Catharus guttatus*, American robin *Turdus migratorius*, American pipit *Anthus rubescens*, orange-crowned warbler *Oreothlypis celata*, yellow-rumped warbler *Setophaga coronata*, Wilson's warbler *Cardellina pusilla*, American tree sparrow *Spizelloides arborea*, Savannah sparrow *Passerculus sandwichensis*, fox sparrow *Passerella iliaca*, white-crowned sparrow *Zonotrichia leucophrys*, golden-crowned sparrow *Z. atricapilla*, and dark-eyed junco *Junco hyemalis*. Note that scale of y-axis varies among species.

land cover types. Nevertheless, model coefficients were equivocal for dwarf shrub–herbaceous cover types and negative for bare ground and perennial ice and snow (Table S2, *Supplemental Material*). Coefficients in linear models are measuring the effect of a one-unit change in a covariate while holding all other covariates constant. In our models, this is not possible because all land cover proportions sum to 1 for each point. Thus, we cannot have an increase in one cover type without a decrease in at least one other covariate value. We suspect our coefficient results are a special case of suppressor effects (Thompson and Levine 1997; Tu et al. 2008), whereby land cover types are only weakly linearly correlated (and thus not multicollinear in the traditional sense; Dormann et al. 2012), but intrinsically dependent upon one another. Therefore, at least some land cover types are explaining variance in one another rather than in avian abundance. As a consequence, covariates may exhibit

larger effect sizes and switching of coefficient signs (Tu et al. 2008; Knaeble and Dutter 2015). We therefore advise against referring to the strength or magnitude of individual coefficients in this study. Instead, land cover associations should be interpreted from predicted abundance plotted against point-specific land cover composition.

Most species evaluated had positive associations between bird abundance and the amount of shrub or deciduous forest around the point and avoided areas that were predominantly covered by low-statured vegetation, bare ground, or perennial snow and ice. In addition to rock ptarmigan, only the American pipit showed even a weakly positive association with the amount of dwarf shrub–herbaceous cover type present, despite its relatively common occurrence across the parks. Two of the species we examined, dark-eyed junco and yellow-rumped warbler, showed strong affinities to

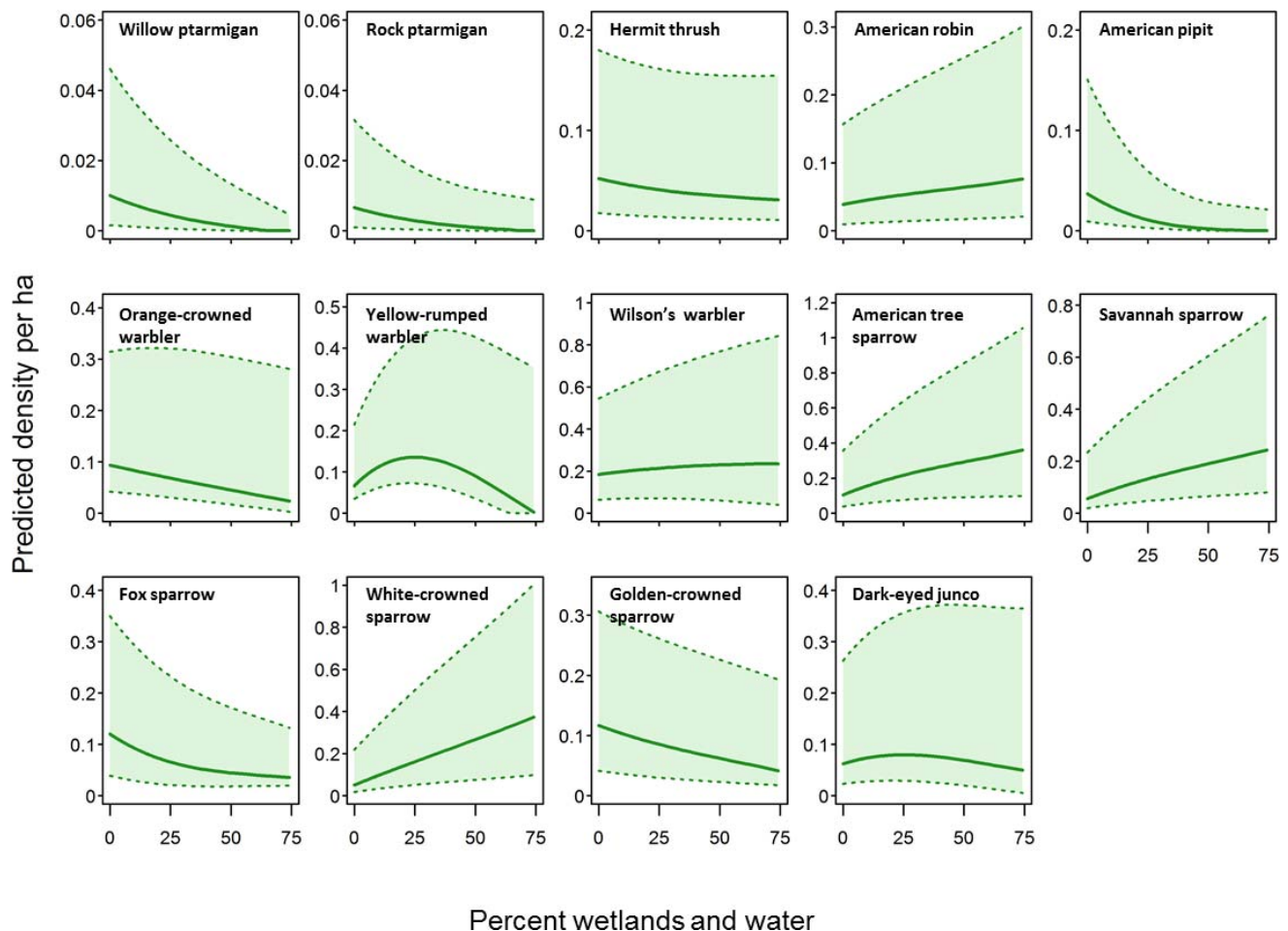


Figure 6. Predicted density per hectare of 14 landbird species surveyed during May–June, 2004–2008, at 1,021 points in three National Parks in southwestern Alaska (Aniakchak National Monument and Preserve, Katmai National Park and Preserve [NPP], Lake Clark NPP) relative to the proportion of wetlands and open water (e.g., lakes and rivers) within a 300-m radius around each point. Solid lines represent mean predicted values and shaded areas 95% credible intervals. Species modeled include willow ptarmigan *Lagopus lagopus*, rock ptarmigan *L. muta*, hermit thrush *Catharus guttatus*, American robin *Turdus migratorius*, American pipit *Anthus rubescens*, orange-crowned warbler *Oreothlypis celata*, yellow-rumped warbler *Setophaga coronata*, Wilson's warbler *Cardellina pusilla*, American tree sparrow *Spizelloides arborea*, Savannah sparrow *Passerculus sandwichensis*, fox sparrow *Passerella iliaca*, white-crowned sparrow *Zonotrichia leucophrys*, golden-crowned sparrow *Z. atricapilla*, and dark-eyed junco *Junco hyemalis*. Note that scale of y-axis varies among species.

forests of all types, and these two species are similarly allied with coniferous and mixed coniferous–deciduous forests elsewhere in Alaska as well as throughout their breeding ranges (Kessel 1989, 1998; Hunt and Flaspohler 1998; Nolan et al. 2002). In contrast, densities of hermit thrush, golden-crowned sparrow, and orange-crowned and Wilson's warblers were greater with increasing amounts of deciduous forest but negatively or neutrally related to increases in coniferous or mixed forest. All these species were more strongly affiliated with shrubs but tolerated patchy forested vegetation with a significant deciduous component, as they do elsewhere in Alaska (Kessel 1989, 1998). General land cover affinities of the remaining species were similar to those found elsewhere in Alaska (Kessel 1989, 1998; Van Hemert et al. 2006; Handel et al. 2009; Gibson 2011; Thompson et al. 2016). Both white-crowned sparrow and American robin were associated primarily with shrubs and tolerant

of moderate amounts of forest, whereas the shrub-loving fox, Savannah, and American sparrows were largely intolerant of forest. The sparrows were somewhat differentiated, however, in their varied associations with proximity to water.

In general, predictive models for abundance of species across the landscape were somewhat limited by the coarse level of attributes available in the 2011 NLCD land cover layer. For instance, the inability to differentiate height of low and tall shrubs was particularly significant, because several of the species we modeled occurred on our study area much more frequently in tall shrubs (hermit thrush, fox sparrow, Wilson's warbler) while others occurred more frequently in low shrubs (willow ptarmigan, American tree sparrow, Savannah sparrow) or wet meadow (Wilson's snipe; Ruthrauff et al. 2007; Ruthrauff and Tibbitts 2009). Lack of differentiation of dwarf shrub from herbaceous cover was less problematic

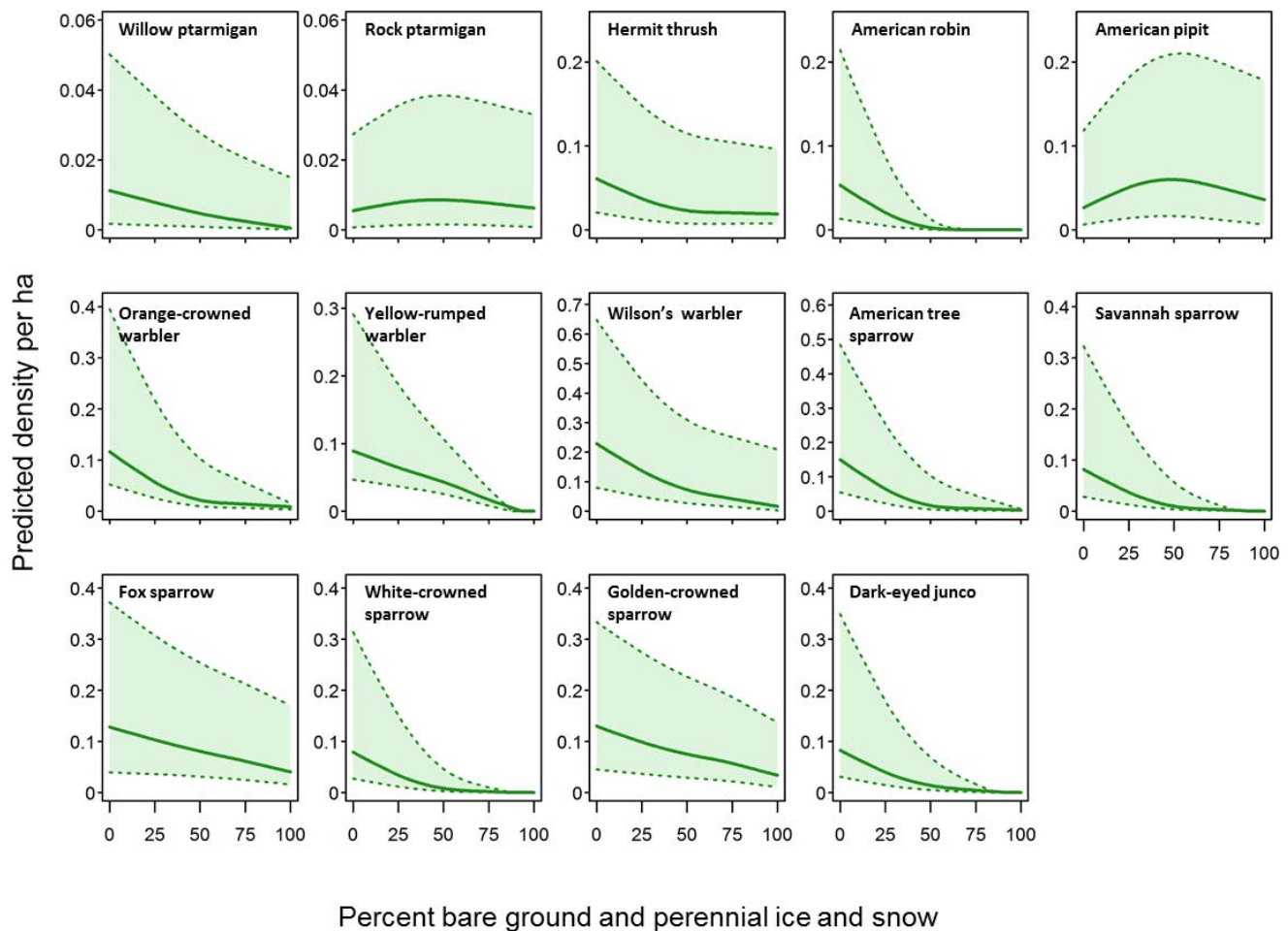


Figure 7. Predicted density per hectare of 14 landbird species surveyed during May–June, 2004–2008, at 1,021 points in three National Parks in southwestern Alaska (Aniakchak National Monument and Preserve, Katmai National Park and Preserve [NPP], Lake Clark NPP) relative to the proportion of bare ground and perennial ice and snow within a 300-m radius around each point. Solid lines represent mean predicted values and shaded areas 95% credible intervals. Species modeled include willow ptarmigan *Lagopus lagopus*, rock ptarmigan *L. muta*, hermit thrush *Catharus guttatus*, American robin *Turdus migratorius*, American pipit *Anthus rubescens*, orange-crowned warbler *Oreothlypis celata*, yellow-rumped warbler *Setophaga coronata*, Wilson's warbler *Cardellina pusilla*, American tree sparrow *Spizelloides arborea*, Savannah sparrow *Passerculus sandwichensis*, fox sparrow *Passerella iliaca*, white-crowned sparrow *Zonotrichia leucophrys*, golden-crowned sparrow *Z. atricapilla*, and dark-eyed junco *Junco hyemalis*. Note that scale of y-axis varies among species.

because most modeled species that occurred in one occurred in the other almost as frequently, except for Wilson's snipe, which uses wet meadow, or rock ptarmigan and American pipit, which both occurred predominantly in drier dwarf shrub at higher elevations (Ruthrauff et al. 2007; Ruthrauff and Tibbitts 2009). Adding elevation to these models could have theoretically helped refine these relationships, but we found that it generally failed to add much resolution because of its strong correlation with land cover type, which we found more informative.

Species richness and composition were similar among the three predominate ecoregions in the parks, which somewhat followed park boundaries (Figure 1). Small samples in the Bristol Bay Lowlands, which occurred in very limited extent in Katmai NPP, precluded any meaningful inference on species richness or similarity. Comparisons among individual parks revealed greater

differences from north to south in both species richness and species composition, which was not surprising given that the parks span 5° of latitude, connecting the boreal biome of Interior Alaska to the tundra biome of the Alaska Peninsula. The parks shared many of the same species found during recent inventories of the rugged Kenai Fjords National Park (Van Hemert et al. 2006), which lies 250 km west of Lake Clark NPP, and the Alaska Peninsula/Becharof National Wildlife Refuge (Savage and Payne 2012), which encompasses the lowlands along Bristol Bay adjacent to Katmai NPP and Aniakchak NMP. The parks differed significantly from Kenai Fjords National Park; however, in the complete or near absence of species strongly affiliated with the Pacific coast rainforests, such as rufous hummingbird *Selasphorus rufus*, Steller's jay *Cyanocitta stelleri*, and chestnut-backed chickadee *Poecile rufescens*. Similarly, the parks lacked or hosted only low densities of a large complement of

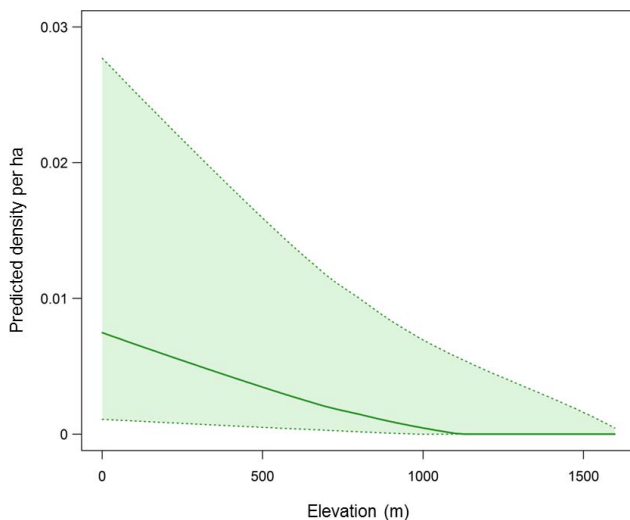


Figure 8. Predicted density per hectare of Wilson's snipe *Gallinago delicata* surveyed during May–June, 2004–2008, at 1,021 points in three National Parks in southwestern Alaska (Aniakchak National Monument and Preserve, Katmai National Park and Preserve [NPP], Lake Clark NPP) relative to elevation (m) within a 300-m radius around each point. Solid lines represent mean predicted values and shaded areas 95% credible intervals.

waterfowl and shorebirds that occurred commonly on the Refuge lowlands.

We used individuals detected during point counts, excluding those in directed flight, in large flocks, and beyond 300 m of the observer, as a general indication of species that were most likely regular breeders in each park. Given these criteria, each park hosted a unique

complement of species that did not occur regularly on the others. The majority of species unique to any park were generally uncommon in Alaska, or lowland water- or wetland-dependent species more common on the adjacent Alaska Peninsula/Becharof National Wildlife Refuge. Lake Clark NPP hosted the most species (15) not found regularly in either of the other two parks. Unique species, especially within the Alaska Range ecoregion portion of Lake Clark, included a few associated with coniferous forests of boreal Interior Alaska—olive-sided flycatcher, white-winged crossbill, and Swainson's thrush. Additionally, several typical alpine-nesting species—northern wheatear, Say's phoebe, wandering tattler, and Baird's sandpiper—were observed during point counts only in Lake Clark NPP, which hosts the highest mean elevation and greatest amounts of glaciated and bare ground area of the parks. Several species associated with deep lakes were also unique to the Alaska Range portion of Lake Clark NPP, including trumpeter swan, long-tailed duck, white-winged scoter, and common loon. All of these species except trumpeter swan, Say's phoebe, and northern wheatear were observed in the other parks peripherally to the point counts, suggesting that they may also breed there in very low densities.

Our analysis of birds recorded during point counts suggests that 107 ± 9 species breed regularly in montane regions across the parks. Species richness curves were not at asymptotes for individual parks, however, and additional survey effort would likely increase richness estimates. The species richness map suggests riparian areas and south-facing u-shaped mountain valleys attract a wide diversity of bird species (Figure 12). These areas align with the distribution of shrub cover, with which many of the individual species

Table 5. Estimated densities (birds per hectare) of 15 species of montane-breeding birds on points surveyed in three National Parks in southwestern Alaska (Aniakchak National Monument and Preserve, Katmai National Park and Preserve [NPP], Lake Clark NPP) during May–June, 2004–2008. Species modeled include willow ptarmigan *Lagopus lagopus*, rock ptarmigan *L. muta*, Wilson's snipe *Gallinago delicata*, hermit thrush *Catharus guttatus*, American robin *Turdus migratorius*, American pipit *Anthus rubescens*, orange-crowned warbler *Oreothlypis celata*, yellow-rumped warbler *Setophaga coronata*, Wilson's warbler *Cardellina pusilla*, American tree sparrow *Spizelloides arborea*, Savannah sparrow *Passerculus sandwichensis*, fox sparrow *Passerella iliaca*, white-crowned sparrow *Zonotrichia leucophrys*, golden-crowned sparrow *Z. atricapilla*, and dark-eyed junco *Junco hyemalis*. Densities represent means (95% credible limits), corrected for detection probability, across all of the points sampled within each park and in all parks combined.

Species	Density per hectare			
	All parks	Aniakchak	Katmai	Lake Clark
Willow ptarmigan	0.02 (0.01, 0.03)	0.02 (0.01, 0.04)	0.02 (0.009, 0.04)	0.02 (0.008, 0.03)
Rock ptarmigan	0.01 (0.006, 0.03)	0.01 (0.007, 0.03)	0.02 (0.008, 0.04)	0.005 (0.003, 0.01)
Wilson's snipe	0.004 (0.003, 0.006)	0.006 (0.003, 0.009)	0.005 (0.003, 0.007)	0.003 (0.002, 0.005)
Hermit thrush	0.05 (0.04, 0.06)	0.05 (0.04, 0.07)	0.06 (0.05, 0.08)	0.04 (0.03, 0.05)
American robin	0.04 (0.02, 0.07)	0.05 (0.02, 0.11)	0.04 (0.02, 0.05)	0.04 (0.02, 0.08)
American pipit	0.04 (0.03, 0.05)	0.05 (0.02, 0.09)	0.04 (0.03, 0.05)	0.03 (0.02, 0.04)
Orange-crowned warbler	0.09 (0.07, 0.12)	0.07 (0.06, 0.11)	0.15 (0.12, 0.2)	0.03 (0.02, 0.05)
Yellow-rumped warbler	0.08 (0.06, 0.10)	0.004 (0, 0.02)	0.07 (0.05, 0.10)	0.11 (0.08, 0.14)
Wilson's warbler	0.19 (0.16, 0.22)	0.18 (0.14, 0.24)	0.25 (0.21, 0.31)	0.11 (0.09, 0.14)
American tree sparrow	0.11 (0.08, 0.15)	0.02 (0.002, 0.09)	0.12 (0.09, 0.15)	0.13 (0.09, 0.19)
Savannah sparrow	0.06 (0.05, 0.08)	0.06 (0.04, 0.09)	0.08 (0.06, 0.1)	0.04 (0.03, 0.06)
Fox sparrow	0.11 (0.10, 0.14)	0.05 (0.04, 0.08)	0.16 (0.13, 0.2)	0.08 (0.06, 0.1)
White-crowned sparrow	0.06 (0.04, 0.11)	0.03 (0.003, 0.1)	0.06 (0.04, 0.09)	0.07 (0.04, 0.15)
Golden-crowned sparrow	0.11 (0.1, 0.13)	0.11 (0.09, 0.14)	0.14 (0.13, 0.17)	0.08 (0.07, 0.09)
Dark-eyed junco	0.06 (0.03, 0.09)	0.02 (0.004, 0.06)	0.04 (0.02, 0.06)	0.09 (0.06, 0.15)

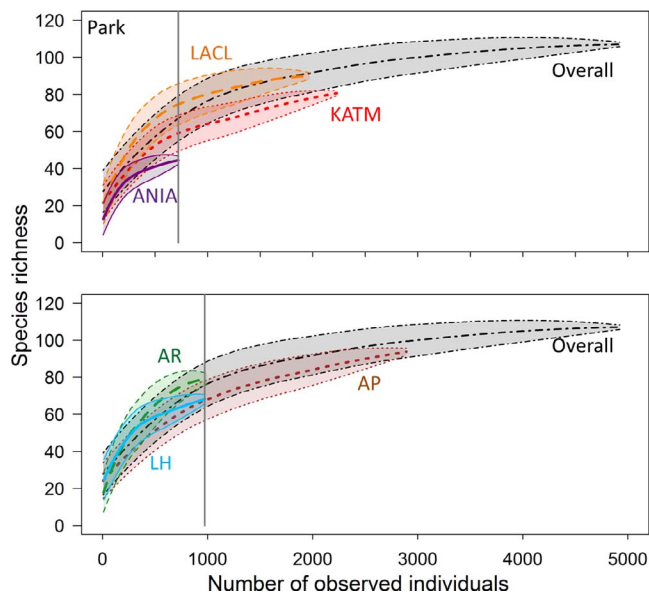


Figure 9. Predicted species richness relative to survey effort (cumulative no. of individuals observed) for individual parks (**upper panel**) and predominant ecoregions within parks (**lower panel**) during the breeding season in southwestern Alaska. Inventories were conducted during May–June, 2004–2008, in three National Parks: Aniakchak National Monument and Preserve (ANIA), Katmai National Park and Preserve [NPP] (KATM), and Lake Clark NPP (LACL). These parks encompassed large portions of three ecoregions: Lime Hills (LH), Alaska Range (AR), and Alaska Peninsula (AP). Predicted species richness increased with the number of individuals detected during surveys and did not reach an asymptote for any park or ecoregion. Shaded regions indicate 95% confidence intervals based on bootstrapping. Vertical gray lines represent levels of effort at which we compared species richness among ecoregions and parks. A list of species encountered during surveys can be found in Table 1.

we modeled were strongly associated. Species richness was greatest in Lake Clark NPP and lowest in Aniakchak NMP, and species composition was least similar between these two parks. The landscape of Aniakchak NMP has largely been shaped by volcanic activity of the Aniakchak caldera, which formed only approximately 3,500 y ago. The terrain is characterized by young soils covered with successional young vegetation types. Approximately 40% of the landscape is covered by dwarf and low shrubs and the park contains no coniferous and very little deciduous forest. Aniakchak NMP also has lower mean elevation and a smaller elevational range than either Lake Clark NPP or Katmai NPP. The low diversity of terrestrial vegetation types and restricted elevational gradient may explain why species diversity was lowest in Aniakchak NMP. The species found in Aniakchak NMP are largely a subset of those that occur in nearby Katmai NPP; 95% of species ever recorded in Aniakchak NMP have also been confirmed in Katmai NPP (Ruthrauff and Tibbitts 2009).

Our analysis of species richness did not incorporate detection probability, which varied among the species

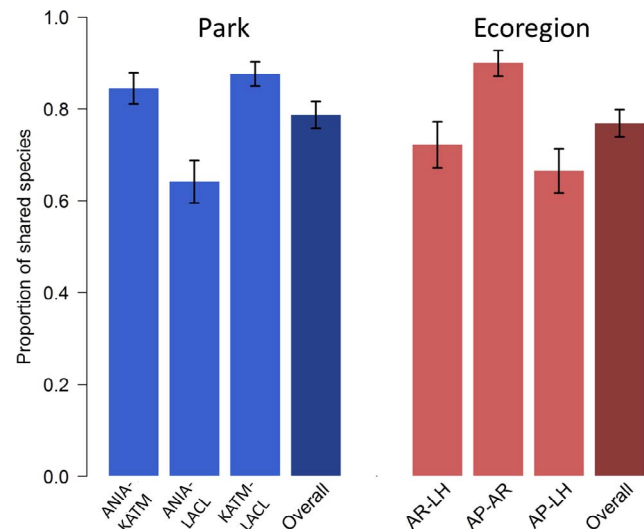


Figure 10. Similarity of avian species composition during the breeding season within three National Parks in southwestern Alaska (**left**) and the portions of three predominant ecoregions that they include (**right**), based on surveys conducted during May–June, 2004–2008. The three parks inventoried include Aniakchak National Monument and Preserve (ANIA), Katmai National Park and Preserve (NPP; KATM), and Lake Clark NPP (LACL), which together encompass portions of the Alaska Peninsula (AP), Alaska Range (AR), and Lime Hills (LH) ecoregions. Pairwise and overall comparisons were based on Horn–Morisita’s index of similarity, which estimates the proportion of species shared among groups. Error bars represent 95% confidence intervals based on bootstrapping.

we examined and was always <100%. This is a limitation to our analysis and may positively bias estimates of richness to land cover types occupied by species with greater detection probabilities. Recently, Colwell et al. (2012) implemented methods to estimate site-specific species richness while correcting for undetected species. Although we tried this approach, richness was so low that models were unable to reach convergence at either the point or transect level. Thus, we could only examine apparent richness and acknowledge that the assumption of equal detectability among species and survey sites is likely violated.

Density estimation

Raw counts (i.e., no. of birds observed per point count) on the parks were generally similar for a given species to those recorded during a recent inventory of the adjacent Alaska Peninsula/Becharof National Wildlife Refuge (Sesser and Jehle 2005) and on the Seward Peninsula in northwestern Alaska (Thompson et al. 2016), both of which are more representative of the subarctic tundra biome. In contrast, estimated densities, corrected for detection probability using similar techniques to ours, were much greater (2–20×) for most species in the Yukon–Charley Rivers National Preserve (NP) in Interior Alaska than densities in our study area (Handel et al. 2009). These discrepancies likely reflect real differences in

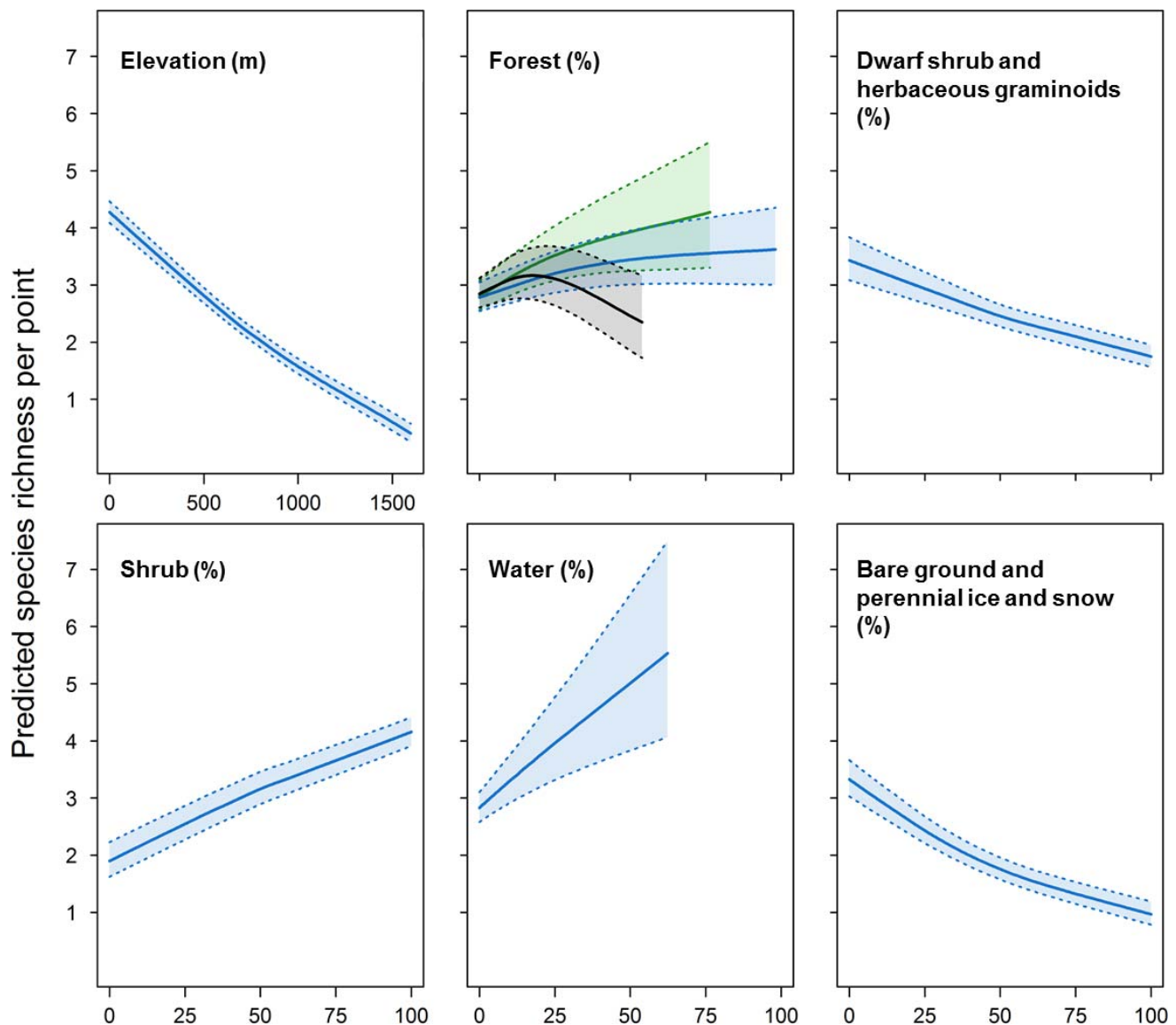


Figure 11. Predicted mean breeding-bird species richness from models incorporating either land cover type or elevation within 300 m of the observer on 1,021 points surveyed during May–June, 2004–2008 in three National Parks in southwestern Alaska (Aniakchak National Monument and Preserve, Katmai National Park and Preserve [NPP], Lake Clark NPP). Solid lines represent mean predicted values and shaded areas 95% confidence intervals. The forest plot represents three types: deciduous forest (green), mixed deciduous–coniferous forest (gray), and coniferous forest (blue). A list of species encountered during surveys can be found in Table 1.

abundance that exist between core breeding areas in large contiguous areas of boreal forest in Interior Alaska and the peripheral fingers of boreal forest that occur in southwestern Alaska. In contrast, densities were similar for fox sparrow and Wilson’s warbler but approximately 10 times greater for hermit thrush in the southwestern Alaska parks than in Yukon–Charley Rivers NP, which reflects the importance of shrubs in the tundra biome. Density of common species varied widely by individual park, and though we are confident these represent real differences, we cannot rule out that they may be due in part to year effects because we surveyed parks in different years.

We conducted a post hoc analysis to explore our ability to predict abundance and distribution by examining two species that, to date, have not been observed in Aniakchak NMP (Ruthrauff and Tibbitts 2009; Sullivan et al. 2009): dark-eyed junco and yellow-rumped warbler. Juncos and yellow-rumped warblers are usually associated with forest and sometimes tall shrubs (Hunt and Flaspohler 1998; Kessel 1998; Nolan et al. 2002), which are both largely absent from Aniakchak NMP. Our models predicted approximately 2.5 dark-eyed junco pairs/km² (6,140 total pairs) and 0.75 yellow-rumped warbler pairs/km² (1,741 total pairs) in Aniakchak NMP. Occurrence predictions were largely influenced by the predominance

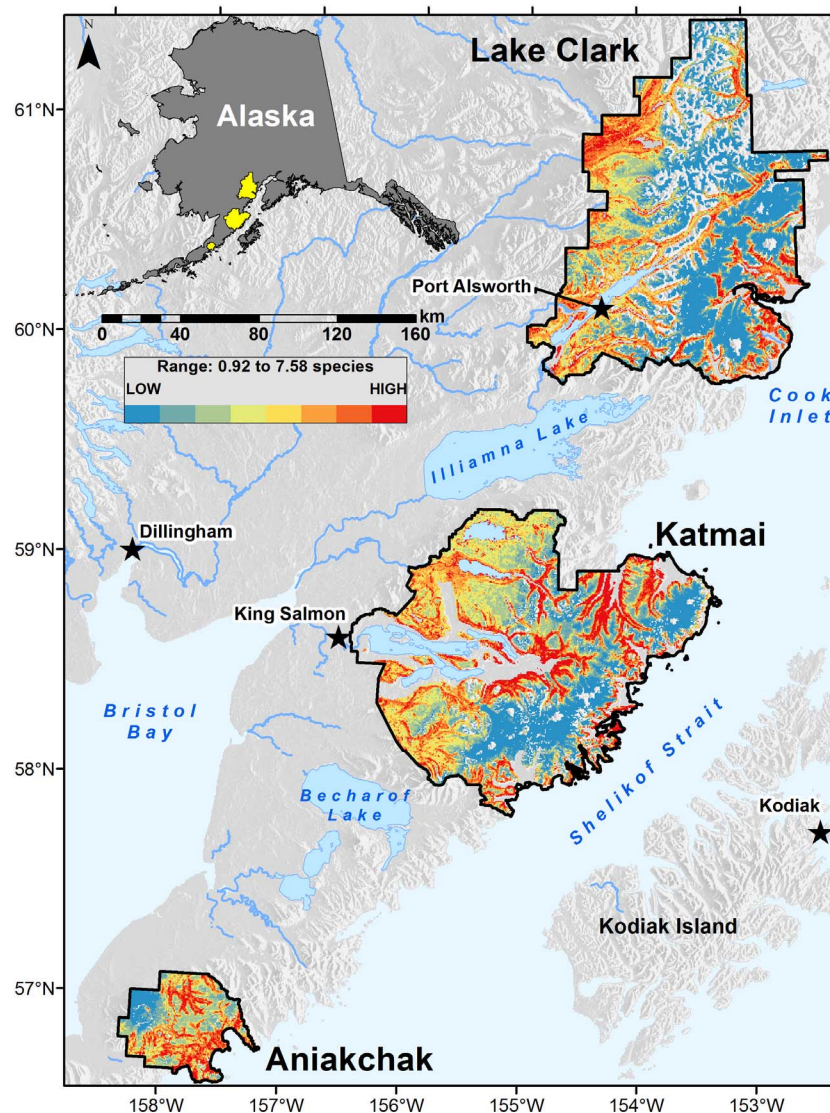


Figure 12. Estimated species richness of breeding birds within 25-ha cells in three National Parks in southwestern Alaska (Aniakchak National Monument and Preserve, Lake Clark National Park and Preserve [NPP], Katmai NPP) based on surveys conducted during May–June, 2004–2008. We included only observations of birds within 300 m of each survey point. Naïve richness does not account for undetected species and should be considered an index to true richness. We did not include cells that were classified as >75% open water or wetlands ($n = 6,562$ cells), >80% deciduous forest ($n = 381$ cells), >55% mixed forest ($n = 409$ cells), >60° mean slope ($n = 11,349$ cells), or <100 m mean elevation above sea level in Katmai NPP and Lake Clark NPP or >1,600 m above sea level for all parks ($n = 16,868$ cells). Black stars denote local human communities. A list of species encountered during surveys can be found in Table 1.

of shrub (0.2–5 m) cover type categorized by the NLCD in this park. It is likely that the coarse land cover classifications used to map relative density are too general for areas of unique geophysical nature such as Aniakchak NMP or too unrefined to distinguish features (e.g., shrub height) that are critical for a given species. Alternatively, we may not have included other environmental characteristics important to these two species that have precluded their colonization to date in this area. Thus, our predictions of density and distribution are likely appropriate for most species, but are generalized by coarse-scale land cover types and should be ground-truthed whenever possible.

Detection probability

It was important to correct for detection for all species analyzed. Counts underestimated abundance by 18–51% within 100 m of the observer, and perceptibility often varied spatially. In general, perceptibility was reduced in areas with more dense vegetation cover around the observer. This finding is similar to that of a study evaluating perceptibility relative to boreal forest density in Alberta, Canada (Yip et al. 2017). Perceptibility rates from distance sampling were similar to those from other published studies in Alaska (Kissling and Garton 2006; Handel et al. 2009; Hoekman and Lindberg 2012) and montane areas elsewhere (Kotliar et al. 2007), although

direct comparisons could not be easily made because truncation distances varied.

Species-specific availability estimates were lower, but generally consistent with a recent inventory conducted in Interior Alaska that observed many of the same species (Handel et al. 2009). Our inventory focused on montane-nesting species, especially shorebirds; therefore, timing of surveys likely started earlier than the peak singing period for some songbird species, thereby reducing their availability. Nevertheless, three species (American robin, American pipit, golden-crowned sparrow) evaluated showed a negative association with season date, suggesting surveys were conducted at or after peak detectability for these species.

Recently, Thompson et al. (2017) evaluated detection probability (the combination of perceptibility, availability, and the probability of presence; Nichols et al. 2009) of landbirds in similar open land cover types in northwestern Alaska using audio recording devices. Peak detection probability for the 10 species in common with this study was much greater than we observed. Thompson et al.'s (2017) estimates were for detection of the species, whereas ours were for an individual of a given species; thus, their detection probabilities would be expected to be greater than ours for any species for which multiple individuals are typically singing in a survey area. In a companion study in northwestern Alaska, direct comparisons of birds detected by a human observer and an audio recorder revealed that perceptibility was greater for the observer (0.58) than the acoustic recorder (0.48) within 100 m and that 91% of the birds missed by the audio recorder were beyond that distance (Vold et al. 2017). Thus, to make valid comparisons of abundance between different studies, it is important to control for the effective area sampled as well as relative detection probability as it applies to either the species or individual. Our methods can account for issues related to both timing and area surveyed; thus, resulting density estimates would only be biased if the proportion of birds not present during surveys varied through space or by year because only one park was surveyed per year. We based timing of surveys each year on phenological stage and bird cues and we completed surveys in a short season interval, so we suspect the entire breeding population was present on the breeding grounds during surveys.

Conclusions

This inventory, the first that we are aware of conducted in the parks, provides valuable baseline information for assessing climate-change-mediated shifts in richness, abundance, and distribution, and guiding future monitoring efforts and management actions. Climate change in Alaska is currently resulting in rapid glacier loss, shrub expansion, and changes in plant phenology and growing season duration throughout subarctic and Arctic areas (Hinzman et al. 2005). Further, studies have shown upward elevational shifts in shrubline and treeline that vary relative to available moisture (Lloyd and Fastie 2002;

Lloyd 2005; Dial et al. 2016), with some evidence of concordant shifts in avian distributions (Tingley et al. 2012). Consequences of these vegetation shifts remain largely unknown, but large-scale simulations suggest that both diversity and abundance of montane-breeding species will decrease as a result (Sekercioglu et al. 2008; Stralberg et al. 2016).

Supplemental Material

Please note: The *Journal of Fish and Wildlife Management* is not responsible for the content or functionality of any supplemental material. Queries should be directed to the corresponding author for the article.

Data S1. Data and metadata for the analysis of 14 landbird and one shorebird species surveyed May–June, 2004–2008, at 1,021 points within three National Parks in southwestern Alaska (Aniakchak National Monument and Preserve [NMP], Katmai National Park and Preserve [NPP], Lake Clark NPP). Data are provided for the following species: willow ptarmigan *Lagopus lagopus*, rock ptarmigan *L. muta*, Wilson's snipe *Gallinago delicata*, hermit thrush *Catharus guttatus*, American robin *Turdus migratorius*, American pipit *Anthus rubescens*, orange-crowned warbler *Oreothlypis celata*, yellow-rumped warbler *Setophaga coronata*, Wilson's warbler *Cardellina pusilla*, American tree sparrow *Spizelloides arborea*, Savannah sparrow *Passerculus sandwichensis*, fox sparrow *Passerella iliaca*, white-crowned sparrow *Zonotrichia leucophrys*, golden-crowned sparrow *Z. atricapilla*, and dark-eyed junco *Junco hyemalis*.

Found at DOI: <http://dx.doi.org/10.3996/062017-JFWM-050.S1> (92 KB ZIP).

Table S1. Model coefficients (SE) of factors affecting detection probability for breeding landbirds during May–June, 2004–2008 in Aniakchak National Monument and Preserve (NMP), Katmai National Park and Preserve (NPP), and Lake Clark NPP, Alaska. Perceptibility is the probability of being observed within the maximum truncation distance, given birds were available for detection aurally or visually during 5-min (landbirds) or 10-min (Wilson's snipe *Gallinago delicata*) point-count surveys. Intercepts and coefficients are on the log scale. Covariates include season date, the proportion of a 50-m- or 150-m-radius circle around the survey point covered by dense shrub or forest cover (Dense Cover), and two levels of observer hearing ability (Sigma obs G1 and G2; half-normal distribution). Observers with similar coefficients from a model including separate effects for each observer were pooled to create the groups. Bold text denotes coefficients with 95% credible limits that do not overlap zero. We evaluated Wilson's snipe with simpler models without covariates and eight landbird species without perceptibility covariates after initial models suggested overfit. Additional species modeled include willow ptarmigan *Lagopus lagopus*, rock ptarmigan *L. muta*, hermit thrush *Catharus guttatus*, American robin *Turdus migratorius*, American pipit *Anthus rubescens*, orange-crowned warbler *Oreothlypis celata*, yellow-



rumped warbler *Setophaga coronata*, Wilson's warbler *Cardellina pusilla*, American tree sparrow *Spizelloides arborea*, Savannah sparrow *Passerculus sandwichensis*, fox sparrow *Passerella iliaca*, white-crowned sparrow *Zonotrichia leucophrys*, golden-crowned sparrow *Z. atricapilla*, and dark-eyed junco *Junco hyemalis*.

Found at DOI: <http://dx.doi.org/10.3996/062017-JFWM-050.S2> (13 KB XLSX).

Table S2. Log-linear coefficients (SE) for environmental covariates associated with abundance of 14 landbird and one shorebird species in Aniakchak National Monument and Preserve (NMP), Katmai National Park and Preserve (NPP), and Lake Clark NPP, southwestern Alaska, surveyed at 1,021 points during 2004–2008. Bold text denotes coefficients with 95% credible intervals that do not overlap zero. We evaluated Wilson's snipe *Gallinago delicata* with a simpler elevation-only model. Mean intercept across transects is provided for each species (Mu). Additional species modeled include willow ptarmigan *Lagopus lagopus*, rock ptarmigan *L. muta*, hermit thrush *Catharus guttatus*, American robin *Turdus migratorius*, American pipit *Anthus rubescens*, orange-crowned warbler *Oreothlypis celata*, yellow-rumped warbler *Setophaga coronata*, Wilson's warbler *Cardellina pusilla*, American tree sparrow *Spizelloides arborea*, Savannah sparrow *Passerculus sandwichensis*, fox sparrow *Passerella iliaca*, white-crowned sparrow *Zonotrichia leucophrys*, golden-crowned sparrow *Z. atricapilla*, and dark-eyed junco *Junco hyemalis*.

Found at DOI: <http://dx.doi.org/10.3996/062017-JFWM-050.S3> (10 KB XLSX).

Table S3. Predicted density (per ha) of 15 species of breeding birds across selected 25-ha grid cells surveyed in Aniakchak National Monument and Preserve (NMP), Katmai National Park and Preserve (NPP), and Lake Clark NPP, Alaska, 2004–2008. We derived estimates and associated error from 1,000 bootstrap realizations of the model coefficients and standard errors (SEs). We present mean and median predicted cell values with 95% confidence intervals. Species modeled include willow ptarmigan *Lagopus lagopus*, rock ptarmigan *L. muta*, Wilson's snipe *Gallinago delicata*, hermit thrush *Catharus guttatus*, American robin *Turdus migratorius*, American pipit *Anthus rubescens*, orange-crowned warbler *Oreothlypis celata*, yellow-rumped warbler *Setophaga coronata*, Wilson's warbler *Cardellina pusilla*, American tree sparrow *Spizelloides arborea*, Savannah sparrow *Passerculus sandwichensis*, fox sparrow *Passerella iliaca*, white-crowned sparrow *Zonotrichia leucophrys*, golden-crowned sparrow *Z. atricapilla*, and dark-eyed junco *Junco hyemalis*.

Found at DOI: <http://dx.doi.org/10.3996/062017-JFWM-050.S4> (10 KB XLSX).

Figure S1. Predicted density (ha^{-1}) maps of 14 landbird and 1 shorebird species surveyed May–June, 2004–2008, at 1,021 points within three National Parks in southwestern Alaska (Aniakchak National Monument and Preserve [NMP], Katmai National Park and Preserve [NPP], Lake Clark NPP). Species modeled include willow ptarmigan

Lagopus lagopus, rock ptarmigan *L. muta*, Wilson's snipe *Gallinago delicata*, hermit thrush *Catharus guttatus*, American robin *Turdus migratorius*, American pipit *Anthus rubescens*, orange-crowned warbler *Oreothlypis celata*, yellow-rumped warbler *Setophaga coronata*, Wilson's warbler *Cardellina pusilla*, American tree sparrow *Spizelloides arborea*, Savannah sparrow *Passerculus sandwichensis*, fox sparrow *Passerella iliaca*, white-crowned sparrow *Zonotrichia leucophrys*, golden-crowned sparrow *Z. atricapilla*, and dark-eyed junco *Junco hyemalis*.

Found at DOI: <http://dx.doi.org/10.3996/062017-JFWM-050.S5> (10,633 KB PDF).

Figure S2. Areas of three National Parks in southwestern Alaska (Aniakchak National Monument and Preserve [NMP], Lake Clark National Park and Preserve [NPP], Katmai NPP) that were above (red) or below (blue) the 95th percentile (≥ 4 species/25 ha based on 107,824 25-ha cells) for avian species richness based on habitat modeling of surveys conducted during May–June, 2004–2008. We included only observations of birds within 300 m of each survey point and cells that met inclusion criteria (see Methods). Apparent richness does not account for undetected species and should be considered an index to true richness. In Lake Clark NPP, richness was greatest in the northeast around the Stony and Telequana rivers (A). In Katmai NPP, richness was greatest around Kulik Lake in the north (B) and along the western river outlets of Lake Grosvenor and Naknek Lake (C). In Aniakchak NMP, areas of greatest richness were concentrated along the Cinder River to the north (D) and along the Meshik River and in low-elevation areas to the south (E). A list of species encountered during surveys can be found in Table 1.

Found at DOI: <http://dx.doi.org/10.3996/062017-JFWM-050.S6> (1323 KB TIF).

Text S1. Accuracy comparison of two land cover layers (the National Land Cover Dataset and a layer provided by the Alaska Natural Heritage Program) available for the Alaska Peninsula, Alaska. We assessed accuracy of land cover layers derived from satellite imagery relative to land cover data collected by observers during avian surveys at 1,021 sites within three National Parks (Aniakchak National Monument and Preserve [NMP], Katmai National Park and Preserve [NPP], and Lake Clark NPP) in southwestern Alaska, May–June, 2004–2008.

Found at DOI: <http://dx.doi.org/10.3996/062017-JFWM-050.S7> (1454 KB DOCX).

Text S2. Jags code (Plummer 2003) called from Program R (R Core Team 2017) to recreate estimates of abundance and detection probability for landbirds surveyed within three National Parks (Aniakchak National Monument and Preserve [NMP], Katmai National Park and Preserve [NPP], and Lake Clark NPP) in southwestern Alaska, May–June, 2004–2008.

Found at DOI: <http://dx.doi.org/10.3996/062017-JFWM-050.S8> (24 KB DOCX).

Reference S1. Adler CD. 1997. Avian studies at Becharof Lake, Alaska Peninsula/Becharof National Wild-



life Refuge, Alaska, June–September, 1997. Unpublished Report. King Salmon: Alaska Peninsula/Becharof National Wildlife Refuge.

Found at DOI: <http://dx.doi.org/10.3996/062017-JFWM-050.S9> (17,249 KB PDF).

Reference S2. Egan RC, Adler CD. 2001. A progress report: landbird breeding and fall migration monitoring at Mother Goose Lake, Alaska Peninsula National Wildlife Refuge, Alaska, June–September 2000. Unpublished Report. King Salmon: Alaska Peninsula/Becharof National Wildlife Refuge.

Found at DOI: <http://dx.doi.org/10.3996/062017-JFWM-050.S10> (26,615 KB PDF).

Reference S3. Gibson DD. 2011. Nesting shorebirds and landbirds of Interior Alaska. Unpublished Contract Report. Anchorage: U.S. Geological Survey, Alaska Science Center.

Found at DOI: <http://dx.doi.org/10.3996/062017-JFWM-050.S11> (2064 KB PDF).

Reference S4. Wilk RJ, Wilk KI. 1989. Floral and faunal inventory of selected wildlife habitats and other observations in the Alaska Peninsula National Wildlife Refuge, 1985–87, Part I: quantitative assessment. Unpublished Report. King Salmon: Alaska Peninsula/Becharof National Wildlife Refuge.

Found at DOI: <http://dx.doi.org/10.3996/062017-JFWM-050.S12> (1580 KB PDF).

Archived Material

Please note: The Journal of Fish and Wildlife Management is not responsible for the content or functionality of any archived material. Queries should be directed to the corresponding author for the article.

To cite this archived material, please cite both the journal article (formatting found in the Abstract section of this article) and the following recommended format for the archived material.

Reference A1. Alaska Department of Fish and Game. 2006. Our wealth maintained: a strategy for conserving Alaska's diverse wildlife and fish resources. Juneau: Alaska Department of Fish and Game. Archived in WebCite®: <http://www.webcitation.org/6wisLhh1h>

Reference A2. Farnsworth GL, Nichols JD, Sauer JR, Fancy SG, Pollock KH, Shriner SA, Simons TR. 2005. Statistical approaches to the analysis of point count data: a little extra information can go a long way. Pages 736–743 in Ralph CJ, Rich TD, editors. General Technical Report PSW-GTR-191. Albany, California: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. Archived in WebCite®: <http://www.webcitation.org/6wisSSKqc>

Reference A3. Gallant AL, Binnian EF, Omernik JM, Shasby MB. 1995. Ecoregions of Alaska. U.S. Geological Survey Professional Paper No. 1567. Denver, Colorado:

U.S. Department of Interior, U.S. Geological Survey. Archived in WebCite®: <http://www.webcitation.org/6wisW9KEB>

Reference A4. Handel CM, Cady MN. 2004. Alaska Landbird Monitoring Survey: protocol for setting up and conducting point count surveys. Sponsored by Boreal Partners in Flight. Unpublished Protocol. Anchorage: U.S. Geological Survey, Alaska Science Center. Archived in WebCite®: <http://www.webcitation.org/6wisZGI5v>

Reference A5. Hendricks P, Verbeek NA. 2012. American pipit (*Anthus rubescens*). Account 95 in Rodewald PG, editor. The birds of North America. Ithaca: Cornell Lab of Ornithology. Archived in WebCite®: <http://www.webcitation.org/6wkCesj6s>

Reference A6. Hoekman ST, Lindberg MS. 2012. Point transect sampling for monitoring passerine birds in Denali National Park and Preserve: an assessment of 2002–2008 pilot data. Natural Resource Technical Report NPS/CAKN/NRTR-2012/589. Fort Collins, Colorado: National Park Service. Archived in WebCite®: <http://www.webcitation.org/6wise3Rbl>

Reference A7. Hunt PD, Flaspohler DJ. 1998. Yellow-rumped warbler (*Setophaga coronata*). Account 376 in Rodewald PG, editor. The birds of North America. Ithaca, New York: Cornell Lab of Ornithology. Archived in WebCite®: <http://www.webcitation.org/6wkCoUwhq>

Reference A8. Knaeble B, Dutter S. 2015. Reversals of least-squares estimates and model-independent estimation for directions of unique effects. arXiv preprint:1503.02722. Archived in WebCite®: <http://www.webcitation.org/6wisfSagt>

Reference A9. Nolan V Jr, Ketterson ED, Cristol DA, Rogers CM, Clotfelter ED, Titus RC, Schoech SJ, Snajdr E. 2002. Dark-eyed junco (*Junco hyemalis*). Account 716 in Rodewald PG, editor. The birds of North America. Ithaca, New York: Cornell Lab of Ornithology. Archived in WebCite®: <http://www.webcitation.org/6wkCvXMxj>

Reference A10. Nowacki G, Spencer P, Fleming M, Brock T, Jorgenson T. 2001. Unified ecoregions of Alaska: 2001. U.S. Geological Survey, Open-file Report 02-297. Archived in WebCite®: <http://www.webcitation.org/6wisIU5vG>

Reference A11. Ralph CJ, Droege S, Sauer JR. 1995. Managing and monitoring birds using point counts: standards and applications. Pages 161–168 in Ralph CJ, Sauer JR, Droege S, editors. Monitoring bird populations by point counts. General Technical Report PSW-GTR-149. Albany, California: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. Archived in WebCite®: <http://www.webcitation.org/6wisobNB6>

Reference A12. Ruthrauff DR, Tibbitts TL. 2009.



Inventory of breeding birds in Aniakchak National Monument and Preserve. Unpublished Report NPS/AKRSWAN/NRTR-2009/186. Anchorage: U.S. Geological Survey, Alaska Science Center. Archived in WebCite®: <http://www.webcitation.org/6wisrojsc>

Reference A13. Ruthrauff DR, Tibbitts TL, Gill RE Jr, Handel CM. 2007. Inventory of montane-nesting birds in Katmai and Lake Clark National Parks and Preserves. Unpublished Report NPS/AKRSWAN/NRTR-2007/02. Anchorage: U.S. Geological Survey, Alaska Science Center. Archived in WebCite®: <http://www.webcitation.org/6wisvWTqQ>

Reference A14. Savage SE, Payne KJ. 2012. Alaska Landbird Monitoring Survey activities at the Alaska Peninsula/Becharof National Wildlife Refuge, Alaska Peninsula, Alaska, June 2012. Unpublished Report. King Salmon: U.S. Fish and Wildlife Service. Archived in WebCite®: <http://www.webcitation.org/6wisvgGrY>

Reference A15. Sesser K, Jehle G. 2005. Alaska Landbird Monitoring Survey: Alaska Peninsula/Becharof National Wildlife Refuge, 9–28 June, 2004. Unpublished Technical Report. King Salmon: U.S. Fish and Wildlife Service. Archived in WebCite®: <http://www.webcitation.org/6wit1mbXp>

Reference A16. Shephard ME, Spencer P. 2000. Ecological subsections of Katmai National Park & Preserve, Alagnak Wild River. Unpublished Report. Anchorage: National Park Service, Alaska Region Inventory and Monitoring Program. Archived in WebCite®: <http://www.webcitation.org/6wit4rU5d>

Reference A17. Spencer P. 2001. Ecological subsections of Lake Clark National Park & Preserve. Unpublished Report. Anchorage: National Park Service, Alaska Region Inventory and Monitoring Program. Archived in WebCite®: <http://www.webcitation.org/6wit7qkm0>

Reference A18. Tande G, Michaelson J. 2001. Ecological subsections of Aniakchak National Monument & Preserve, Alaska. Unpublished Report to National Park Service. Anchorage: Alaska Region Inventory and Monitoring Program. Archived in WebCite®: <http://www.webcitation.org/6witFfwh5>

Reference A19. Van Hemert CR, Handel CM, Cady MN, Terenzi J. 2006. Summer inventory of landbirds in Kenai Fjords National Park. National Park Service Report NPS/AKRSWAN/NRTR-2006/04. Archived in WebCite®: <http://www.webcitation.org/6yPIRycow>

Reference A20. Viereck LA, Dyrness CT, Batten AR, Wenzlick KJ. 1992. The Alaska vegetation classification. General Technical Report PNW-GTR-286. Portland, Oregon: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. Archived in WebCite®: <http://www.webcitation.org/6witKEs4b>

Acknowledgments

We thank C. Van Hemert, B. Thompson, T. Hamon, L. Pajot, J. Morse, M. Fitz, P. Farrell, D. Ward, M. Dementyev, and N. Senner for field assistance. Katmai National Park and Preserve (NPP), Lake Clark NPP, and Aniakchak National Monument and Preserve provided lodging and logistics support and for this we especially thank J. Putera, L. Alsworth, T. Jones, and H. Lons. Pilots L. Alsworth, P. Huckleberry, A. Johnson, and S. Hermens ensured safe transport of personnel. A. Bennett helped initiate and procure funding for the inventories. M. Sheppard and T. Wilson with the Southwest Network of Alaska Parks provided additional support. D. Haukos, S. Thompson, C. Van Hemert, and two anonymous reviewers provided helpful feedback on earlier drafts. Funding for analysis was provided by the Natural Resource Preservation Project through the U.S. Geological Survey. This research used resources provided by the Core Science Analytics, Synthesis, and Libraries Advanced Research Computing group at the U.S. Geological Survey.

Any use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. Government.

References

- Adler CD. 1997. Avian studies at Becharof Lake, Alaska Peninsula/Becharof National Wildlife Refuge, Alaska, June–September, 1997. Unpublished Report. King Salmon: Alaska Peninsula/Becharof National Wildlife Refuge (see *Supplementary Material*, Reference S1, <http://dx.doi.org/10.3996/062017-JFWM-050.S9>).
- Alaska Department of Fish and Game. 2006. Our wealth maintained: a strategy for conserving Alaska's diverse wildlife and fish resources. Juneau: Alaska Department of Fish and Game (see *Archived Material*, Reference A1, <http://www.webcitation.org/6wisLhh1h>); also available: <http://www.adfg.alaska.gov/index.cfm?adfg=species.wapview> (January 2018).
- Aldredge MW. 2007. A field evaluation of distance measurement error in auditory avian point count surveys. *Journal of Wildlife Management* 71:2759–2766.
- Amundson CL, Royle JA, Handel CM. 2014. A hierarchical model combining distance sampling and time removal to estimate detection probability during avian point counts. *The Auk: Ornithological Advances* 131:476–494.
- Beyer HL. 2012. Geospatial modelling environment. Version 0.7.2.0. (software). Available: <http://www.spatalecolgy.com/gme> (January 2018).
- Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L. 2001. Introduction to distance sampling: estimating abundance of biological populations. Oxford, United Kingdom: Oxford University Press.
- Burnham KP, Overton WS. 1979. Robust estimation of population size when capture probabilities vary among animals. *Ecology* 60:927–936.



- Charney N, Record S. 2015. Package 'vegetarian': Jost diversity measures for community data. R package version 1.2. Available: <https://CRAN.R-project.org/package=vegetarian> (January 2018).
- Chesser, RT, Burns KJ, Cicero C, Dunn JL, Kratter AW, Lovette IJ, Rasmussen PC, Remsen JV, Jr., Rising JD, Stotz DF, Winker, K. 2017. Fifty-eighth supplement to the American Ornithological Society's check-list of North American birds. The Auk: Ornithological Advances 134:751–773.
- Cintra R, Naka LN. 2012. Spatial variation in bird community composition in relation to topographic gradient and forest heterogeneity in a Central Amazonian rainforest. International Journal of Ecology Article ID: 435671. DOI: [dx.doi.org/10.1155/2012/435671](https://doi.org/10.1155/2012/435671)
- Colwell RK, Chao A, Gotelli NJ, Lin S-Y, Mao CX, Chazdon RL, Longino JT. 2012. Models and estimators linking individual-based and sample-based rarefaction, extrapolation, and comparison of assemblages. Journal of Plant Ecology 5:3–21.
- Colwell RK, Mao CX, Chang J. 2004. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. Ecology 83:2717–2727.
- Davies RG, Orme CDL, Storch D, Olson VA, Thomas GH, Ross SG, Ding T-S, Rasmussen PC, Bennett PM, Owens IPF, Blackburn TM, Gaston KJ. 2007. Topography, energy and the global distribution of bird species richness. Proceedings of the Royal Society B 274:1189–1197.
- Dial RJ, Smeltz TS, Sullivan PF, Rinas CL, Timm K, Geck JE, Tobin SC, Golden TS, Berg EC. 2016. Shrubline but not treeline advance matches climate velocity in montane ecosystems of south-central Alaska. Global Change Biology 22:1841–1856.
- Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, Marquéz JRG, Gruber B, Lafourcade B, Leitão PJ, Münkemüller T, McClean C, Osborne PE, Reineking B, Schröder B, Skidmore AK, Zurell D, Lautenbach S. 2012. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 35:1–20.
- Egan RC, Adler CD. 2001. A progress report: landbird and fall migration monitoring at Mother Goose Lake, Alaska Peninsula National Wildlife Refuge, Alaska, June–September 2000. Unpublished Report. King Salmon: Alaska Peninsula/Becharof National Wildlife Refuge (see *Supplemental Material*, Reference S2, [http://dx.doi.org/10.3996/062017-JFWM-050.S10](https://dx.doi.org/10.3996/062017-JFWM-050.S10)).
- Farnsworth GL, Nichols JD, Sauer JR, Fancy SG, Pollock KH, Shriner SA, Simons TR. 2005. Statistical approaches to the analysis of point count data: a little extra information can go a long way. Pages 736–743 in Ralph CJ, Rich TD, editors. General Technical Report PSW-GTR-191. Albany, California: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station (see *Archived Material*, Reference A2, <http://www.webcitation.org/6wisSSKqc>); also available: https://www.fs.fed.us/psw/publications/documents/psw_gtr191/Asilomar/pdfs/736-743.pdf (January 2018).
- Farnsworth GL, Pollock KH, Nichols JD, Simons TR, Hines JE, Sauer JR. 2002. A removal model for estimating detection probabilities from point-count surveys. The Auk 119:414–425.
- Gallant AL, Binnian EF, Omernik JM, Shasby MB. 1995. Ecoregions of Alaska. U.S. Geological Survey Professional Paper No. 1567. Denver, Colorado: U.S. Department of Interior, U.S. Geological Survey (see *Archived Material*, Reference A3, <http://www.webcitation.org/6wisW9KEB>); also available: <https://pubs.er.usgs.gov/publication/pp1567> (January 2018).
- Gelman A, Hill J. 2007. Data analysis using regression and multilevel/hierarchical models. New York: Cambridge University Press.
- Gelman A, Rubin D. 1992. Inference from interactive simulation using multiple sequences. Statistical Science 7:457–511.
- Gesch DB. 2007. The national elevation dataset. Pages 99–118 in Maune D, editor. Digital elevation model technologies and applications: the DEM user's manual. 2nd edition. Bethesda, Maryland: American Society for Photogrammetry and Remote Sensing.
- Gibson DD. 2011. Nesting shorebirds and landbirds of Interior Alaska. Unpublished Contract Report. Anchorage: U.S. Geological Survey, Alaska Science Center (see *Supplemental Material*, Reference S3, [http://dx.doi.org/10.3996/062017-JFWM-050.S11](https://dx.doi.org/10.3996/062017-JFWM-050.S11)).
- Gill RE Jr, Jorgensen PD. 1979. A preliminary assessment of timing and migration of shorebirds along the northcentral Alaska Peninsula. Studies in Avian Biology 2:113–123.
- Gill RE Jr, Petersen MR, Jorgensen PD. 1981. Birds of the northcentral Alaska Peninsula, 1976–1980. Arctic 34:286–306.
- Gill RE Jr, Tomkovich PS, Dementyev MN. 2015. Breeding ecology of wandering tattlers *Tringa incana*: a study from south-central Alaska. Wader Study 122:99–114.
- Gill RE Jr, Tomkovich PS. 2004. Subarctic alpine nesting by Baird's sandpipers *Calidris bairdii*. Wader Study Group Bulletin 104:39–50.
- Handel CM, Cady MN. 2004. Alaska Landbird Monitoring Survey: protocol for setting up and conducting point count surveys. Sponsored by Boreal Partners in Flight. Unpublished Protocol. Anchorage: U.S. Geological Survey, Alaska Science Center (see *Archived Material*, Reference A4, <http://www.webcitation.org/6wisZGI5v>); also available: https://alaska.usgs.gov/science/biology/bpif/monitor/ALMSprotocol_2004.pdf (June 2017).
- Handel CM, Swanson SA, Nigro DA, Matsuoka SM. 2009. Estimation of avian population sizes and species richness across a boreal landscape in Alaska. Wilson Journal of Ornithology 121:528–547.
- Hendricks P, Verbeek NA. 2012. American pipit (*Anthus rubescens*). Account 95 in Rodewald PG, editor. The birds of North America. Ithaca: Cornell Lab of Ornithology (see *Archived Material*, Reference A5, <http://www.webcitation.org/6wkCesj6s>); also avail-

- able: <http://bna.birds.cornell.edu/bna/species/yerwar>. doi.org/ 10.2173/bna.95 (June 2017).
- Hinzman LD, Bettez ND, Bolton WR, Chapin FS, Dyurgerov MB, Fastie CL, Griffith B, Hollister RD, Hope A, Huntington HP, Jensen AM, Jia GJ, Jorgenson T, Kane DL, Klein DR, Kofinas G, Lynch AH, Lloyd AH, McGuire AD, Nelson FE, Oechel WC, Osterkamp TE, Racine CH, Romanovsky VE, Stone RS, Stow DA, Sturm M, Tweedie CE, Vourlitis GL, Walker MD, Walker DA, Webber PJ, Welker JM, Winker KS, Yoshikawa K. 2005. Evidence and implications of recent climate change in northern Alaska and other Arctic regions. *Climatic Change* 72:251–298.
- Hoekman ST, Lindberg MS. 2012. Point transect sampling for monitoring passerine birds in Denali National Park and Preserve: an assessment of 2002–2008 pilot data. Natural Resource Technical Report NPS/CAKN/NRTR-2012/589. Fort Collins, Colorado: National Park Service (see *Archived Material*, Reference A6, <http://www.webcitation.org/6wise3Rbl>); also available: <https://irma.nps.gov/DataStore/Reference/Profile/2185664> (June 2017).
- Homer CG, Dewitz JA, Yang L, Jin S, Danielson P, Xian G, Coulston J, Herold ND, Wickham JD, Megown K. 2015. Completion of the 2011 National Land Cover Database for the conterminous United States—representing a decade of land cover change information. *Photogrammetric Engineering and Remote Sensing* 81:345–354.
- Hunt PD, Flaspohler DJ. 1998. Yellow-rumped warbler (*Setophaga coronata*). Account 376 in Rodewald PG, editor. *The birds of North America*. Ithaca, New York: Cornell Lab of Ornithology (see *Archived Material*, Reference A7, <http://www.webcitation.org/6wkCoUwhq>); also available: <http://bna.birds.cornell.edu/bna/species/yerwar>. doi.org/ 10.2173/bna.376 (June 2017).
- Jones JJ. 2001. Habitat selection studies in avian ecology: a critical review. *The Auk* 118:557–562.
- Jost L. 2007. Partitioning diversity into independent alpha and beta components. *Ecology* 88:2427–2439.
- Karr JR, Roth RR. 1971. Vegetation structure and avian diversity in several New World areas. *American Naturalist* 105:423–435.
- Kellner K. 2015. jagsUI: a wrapper around rjags to streamline JAGS analyses. R package version 1.3.1. Available: <https://cran.r-project.org/web/packages/jagsUI/index.html> (June 2017).
- Kéry M. 2010. *Introduction to WinBUGS for ecologists*. New York: Academic Press.
- Kéry M, Schaub M. 2012. *Bayesian population analysis using WinBUGS: a hierarchical perspective*. New York: Academic Press.
- Kessel B. 1979. Avian habitat classification for Alaska. *Murrelet* 60:86–94.
- Kessel B. 1989. *Birds of the Seward Peninsula, Alaska*. Fairbanks: University of Alaska Press.
- Kessel B. 1998. *Habitat characteristics of some passerine birds in western North American taiga*. Fairbanks: University of Alaska Press.
- Kissling ML, Garton EO. 2006. Estimating detection probability and density from point-count surveys: a combination of distance and double-observer sampling. *The Auk* 123:735–752.
- Knaeble B, Dutter S. 2015. Reversals of least-squares estimates and model-independent estimation for directions of unique effects. arXiv preprint:1503.02722 (see *Archived Material*, Reference A8, <http://www.webcitation.org/6wisfSagt>); also available: <https://arxiv.org/abs/1503.02722> (June 2017).
- Kotliar NB, Kennedy PL, Ferree K. 2007. Avifaunal responses to fire in southwestern montane forests along a burn severity gradient. *Ecological Applications* 17:491–507.
- La Sorte FA, Jetz W. 2010. Projected range contractions of montane biodiversity under global warming. *Proceedings of the Royal Society B* 277:3401–3410.
- Lloyd AH. 2005. Ecological histories from Alaskan tree lines provide insight into future change. *Ecology* 86:1687–1695.
- Lloyd AH, Fastie CL. 2002. Spatial and temporal variability in the growth and climate response of treeline trees in Alaska. *Climatic Change* 52:481–509.
- MacArthur RH, MacArthur JW. 1961. On bird species diversity. *Ecology* 42:594–598.
- McCain CM. 2009. Global analysis of bird elevational diversity. *Global Ecology and Biogeography* 18:346–360.
- McCain CM, Grytnes J-A. 2010. Elevational gradients in species richness. *Encyclopedia of life sciences (ELS)*. Chichester: John Wiley & Sons, Ltd. doi.org/ 10.1002/9780470015902.a0022548.
- McNew LB, Handel CM. 2015. Evaluating species richness: biased ecological inference results from spatial heterogeneity in detection probabilities. *Ecological Applications* 25:1669–1680.
- Moritz C, Patton JL, Conroy CJ, Parra JL, White GC, Beissinger SR. 2008. Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science* 322:261.
- Murie OB. 1959. *Fauna of the Aleutian Islands and Alaska Peninsula*. North American Fauna 61.
- Nichols JD, Thomas L, Conn PB. 2009. Inferences about landbird abundance from count data: recent advances and future directions. Pages 201–235 in Thomsen DL, Cooch, EG, Conn PB, editors. *Modeling demographic processes in marked populations USA*: Springer. Also available: DOI 10.1007/978-0-387-78151-8_9 (April 2018).
- Nolan V Jr, Ketterson ED, Cristol DA, Rogers CM, Clotfelter ED, Titus RC, Schoech SJ, Snajdr E. 2002. Dark-eyed junco (*Junco hyemalis*). Account 716 in Rodewald PG, editor. *The birds of North America*. Ithaca, New York: Cornell Lab of Ornithology (see *Archived Material*, Reference A9, <http://www.webcitation.org/6wkCvXMxj>); also available: <https://birdsna.org/Species-Account/bna/species/daejun>. doi.org/ 10.2173/bna.716 (June 2017).
- Nowacki G, Spencer P, Fleming M, Brock T, Jorgenson T. 2001. *Unified ecoregions of Alaska: 2001*. U.S. Geolog-

- ical Survey, Open-file Report 02-297 (see *Archived Material*, Reference A10, <http://www.webcitation.org/6wisIU5vG>); also available: <http://agdc.usgs.gov/data/usgs/erosafo/ecoreg/> (June 2017).
- Petersen MR. 1981. Populations, feeding ecology and molt of Steller's eiders. *Condor* 83:256–262.
- Plummer M. 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003), March 20–22, Vienna, Austria. ISSN 1609-395X. Available: <https://www.r-project.org/conferences/DSC-2003/Drafts/Plummer.pdf> (June 2017).
- R Core Team. 2017. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. Available: <http://www.R-project.org/> (June 2017).
- Ralph CJ, Droege S, Sauer JR. 1995. Managing and monitoring birds using point counts: standards and applications. Pages 161–168 in Ralph CJ, Sauer JR, Droege S, editors. *Monitoring bird populations by point counts*. General Technical Report PSW-GTR-149. Albany, California: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station (see *Archived Material*, Reference A11, <http://www.webcitation.org/6wisobNB6>); also available: https://www.fs.fed.us/psw/publications/documents/wild/gtr149/pg161_168.pdf (January 2018).
- Rota CT, Fletcher RJ Jr, Evans JM, Hutto RL. 2011. Does accounting for imperfect detection improve species distribution models? *Ecography* 34:659–670.
- Royle JA, Dorazio RM. 2008. *Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities*. New York: Elsevier/Academic Press.
- Ruthrauff DR, Tibbitts TL. 2009. Inventory of breeding birds in Aniakchak National Monument and Preserve. Unpublished Report NPS/AKRSWAN/NRTR-2009/186. Anchorage: U.S. Geological Survey, Alaska Science Center (see *Archived Material*, Reference A12, <http://www.webcitation.org/6wisrojsc>); also available: http://alaska.usgs.gov/science/biology/shorebirds/pdfs/RuthrauffD_2009_ANIA_BreedingBirdsFinalReport_090121.pdf (June 2017).
- Ruthrauff DR, Tibbitts TL, Gill RE Jr, Handel CM. 2007. Inventory of montane-nesting birds in Katmai and Lake Clark National Parks and Preserves. Unpublished Report NPS/AKRSWAN/NRTR-2007/02. Anchorage: U.S. Geological Survey, Alaska Science Center (see *Archived Material*, Reference A13, <http://www.webcitation.org/6wisvWTqQ>); also available: <https://pubs.er.usgs.gov/publication/70174837> (June 2017).
- Savage SE, Payne KJ. 2012. Alaska Landbird Monitoring Survey activities at the Alaska Peninsula/Becharof National Wildlife Refuge, Alaska Peninsula, Alaska, June 2012. Unpublished Report. King Salmon: U.S. Fish and Wildlife Service (see *Archived Material*, Reference A14, <http://www.webcitation.org/6wisygGrY>); also available: <http://www.arlis.org/docs/vol1/FWS/A/876052506.pdf> (June 2017).
- Sekercioglu CH, Schneider SH, Fay JP, Loarie SR. 2008. Climate change, elevational range shifts, and bird extinctions. *Conservation Biology* 22:140–50.
- Sesser K, Jehle G. 2005. Alaska Landbird Monitoring Survey: Alaska Peninsula/Becharof National Wildlife Refuge, 9–28 June, 2004. Unpublished Technical Report. King Salmon: U.S. Fish and Wildlife Service (see *Archived Material*, Reference A15, <http://www.webcitation.org/6wit1mbXp>); also available: <http://www.arlis.org/docs/vol1/B/58450993.pdf> (June 2017).
- Shephard ME, Spencer P. 2000. Ecological subsections of Katmai National Park & Preserve, Alagnak Wild River. Unpublished Report. Anchorage: National Park Service, Alaska Region Inventory and Monitoring Program (see *Archived Material*, Reference A16, <http://www.webcitation.org/6wit4rU5d>); also available: www.arlis.org/docs/vol1/122443531.pdf (June 2017).
- Spencer P. 2001. Ecological subsections of Lake Clark National Park & Preserve. Unpublished Report. Anchorage: National Park Service, Alaska Region Inventory and Monitoring Program (see *Archived Material*, Reference A17, <http://www.webcitation.org/6wit7qkm0>); also available: www.arlis.org/docs/vol1/122456496.pdf (June 2017).
- Stralberg D, Matsuoka SM, Handel CM, Bayne EM, Schmiegelow FKA, Hamman A. 2016. Biogeography of boreal passerine range dynamics in western North America: past, present, and future. *Ecography* 39:001–017.
- Sullivan BL, Wood CL, Iliff MJ, Bonney RE, Fink D, Kelling S. 2009. eBird: a citizen-based bird observation network in the biological sciences. *Biological Conservation* 142:2282–2292.
- Tande G, Michaelson J. 2001. Ecological subsections of Aniakchak National Monument & Preserve, Alaska. Unpublished Report to National Park Service. Anchorage: Alaska Region Inventory and Monitoring Program (see *Archived Material*, Reference A18, <http://www.webcitation.org/6witFfwh5>); also available: http://accs.uaa.alaska.edu/files/vegetation-ecology/Publications/2001/Ecological_Subsections_of_Aniakchak_National_Monument.pdf (June 2017).
- Tews J, Brose U, Grimm V, Tielborger K, Wichmann MC, Schwager M, Jeltsch F. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography* 31:79–92.
- Thogmartin WE, Knutson MG. 2007. Scaling local species-habitat relations to the larger landscape with a hierarchical spatial count model. *Landscape Ecology* 22:61–75.
- Thompson FT, Levine DU. 1997. Examples of easily explainable suppressor variables in multiple regression research. *Multiple Linear Regression Viewpoints* 24:11–13.
- Thompson SJ, Arnold TW, Amundson CL. 2014. A multiscale assessment of tree avoidance by prairie birds. *The Condor: Ornithological Applications* 116:303–305.

- Thompson SJ, Handel CM, McNew LB. 2017. Autonomous recording devices reveal complex patterns in avian detection probability and presence in the subarctic. *Journal of Wildlife Management* 81:1228–1241.
- Thompson SJ, Handel CM, Richardson RM, McNew LB. 2016. When winners become losers: predicted nonlinear responses of Arctic birds to increasing woody vegetation. *PLoS ONE* 11(11):e0164755.
- Tingley MW, Beissinger SR. 2013. Cryptic loss of montane avian richness and high community turnover over 100 years. *Ecology* 94:598–609.
- Tingley MW, Koo MS, Moritz C, Rush AC, Beissinger SR. 2012. The push and pull of climate change causes heterogeneous shifts in avian elevational ranges. *Global Change Biology* 18:3279–3290.
- Tu Y-K, Gunnell DJ, Gilthorpe MS. 2008. Simpson's paradox, Lord's paradox, and suppression effects are the same phenomenon—the reversal paradox. *Emerging Themes in Epidemiology* 5:2.
- Van Hemert CR, Handel CM, Cady MN, Terenzi J. 2006. Summer inventory of landbirds in Kenai Fjords National Park. National Park Service Report NPS/AKRSWAN/NRTR-2006/04 (see *Archived Material*, Reference A19, <http://www.webcitation.org/6yPIRycow>); also available: <http://www.arlis.org/docs/vol1/USGS/2006/76815051.pdf> (April 2018).
- Viereck LA, Dyrness CT, Batten AR, Wenzlick KJ. 1992. The Alaska vegetation classification. General Technical Report PNW-GTR-286. Portland, Oregon: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station (see *Archived Material*, Reference A20, <http://www.webcitation.org/6witKEs4b>); also available: http://www.fwspubs.org/doi/suppl/10.3996/112015-JFWM-116/suppl_file/112015-jfwm-116.s1.pdf (January 2018).
- Vold ST, Handel CM, McNew LB. 2017. Comparison of acoustic recorders and field observers for monitoring tundra bird communities. *Wildlife Society Bulletin* 41:566–576.
- Walther G-R, Beißner S, Pott R. 2005. Climate change and high mountain vegetation shifts. Pages 77–96 in Broll G, Keplin B, editors. *Mountain ecosystems: studies in treeline ecology*. Heidelberg, Germany: Springer.
- Ward DH, Stehn RA, Derksen DV. 1994. Response of staging brant to disturbance at the Izembek Lagoon, Alaska. *Wildlife Society Bulletin* 22:220–228.
- Webster RA, Pollock KH, Simons TR. 2008. Bayesian spatial modeling of data from avian point count surveys. *Journal of Agricultural, Biological, and Environmental Statistics* 13:121–139.
- Wilk RJ, Wilk KI. 1989. Floral and faunal inventory of selected wildlife habitats and other observations in the Alaska Peninsula National Wildlife Refuge, 1985–87, Part I: quantitative assessment. Unpublished Report. King Salmon: Alaska Peninsula/Becharof National Wildlife Refuge (see *Supplemental Material*, Reference S4, <http://dx.doi.org/10.3996/062017-JFWM-050.S12>).
- Willson MF. 1974. Avian community organization and habitat structure. *Ecology* 55:1017–1029.
- Wolda H. 1981. Similarity indices, sample size and diversity. *Oecologia* 50:296–302.
- Yip DA, Bayne EM, Solymos P, Campbell J, Proppe D. 2017. Sound attenuation in forest and roadside environments: implications for avian point-count surveys. *Condor* 119:73–84.
- Young KL, Woo M-K, Edlund SA. 1997. Influence of local topography, soils, and vegetation on microclimate and hydrology at a high Arctic site, Ellesmere Island, Canada. *Arctic and Alpine Research* 29:270–284.