**Surveys**

**Inventory of Lowland-Breeding Birds on the Alaska Peninsula**

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**Abstract**

We conducted the first systematic inventory of birds in the lowlands (areas ≤100 m above sea level) of the Alaska Peninsula during summers of 2004–2007 to determine their breeding distributions and habitat associations in this remote region. Using a stratified random survey design, we allocated sample plots by elevation and land cover with a preference for wetland cover types used by shorebirds, a group of particular interest to land managers. We surveyed birds during 10-min counts at 792 points across 52, 5 km × 5 km sample plots distributed from south of the Naknek River (58.70°N,157.00°W) to north of Port Moller (56.00°N,160.52°W). We detected 95 bird species including 19 species of shorebirds and 34 species (36% of total) considered at the time to be of conservation concern for the land managers in the region. The most numerous shorebirds on point counts were dunlin *Calidris alpina*, short-billed dowitcher *Limnodromus griseus*, and Wilson’s snipe *Gallinago delicata*. We found the breeding-season endemic marbled godwit *Limosa fedoa beringiae* at 20 plots within a 3,000-km² area from north of Ugashik Bay to just north of Port Heiden and east to the headwaters of the Dog Salmon and Ugashik rivers. The most abundant passerines on point counts were American tree sparrow *Spizelloides arborea*, Lapland longspur *Calcarius lapponicus*, and savannah sparrow *Passerculus sandwichensis*. Sandhill crane *Antigone canadensis*, glaucous-winged gull *Larus glaucescens*, and greater scaup *Aythya marila* were also relatively abundant. We categorized habitat associations for 30 common species and found that lowland herbaceous vegetation supported wetland-focused species including sandhill crane, marbled godwit, short-billed dowitcher, and dunlin; whereas, dwarf shrub-ericaceous vegetation supported tundra-associated species such as willow ptarmigan *Lagopus lagopus*, rock sandpiper *Calidris ptilocnemis*, and American pipit *Anthus rubescens*. Tall shrub vegetation was important to several species of warblers and sparrows, as well as one species of shorebird (greater yellowlegs *Tringa melanoleuca*). We found that point counts augmented with incidental observations provided an almost complete inventory of lowland-breeding species on the study area. These data form a baseline to monitor any future changes in bird distribution and abundance on the Alaska Peninsula.

**Keywords:** abundance; Alaska; distribution; lowlands, passerines; shorebirds; waterfowl

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Introduction

The Alaska Peninsula encompasses about 6.5 million ha, a vast region that stretches from the shores of Alaska’s largest lake, Iliamna Lake, south to Bechevin Bay (Figure 1). The terrain has been shaped by volcanoes, glaciers, and oceans, resulting in a rugged and varied landscape that provides abundant breeding, wintering, and staging habitat for resident and migratory birds. The Aleutian Range with its many active volcanoes forms the spine of the Alaska Peninsula and separates the flat marshy northern side from the steep rocky southern side. Bays and estuaries along Bristol Bay in the north are shallow and muddy in contrast to the south shore’s deep, clear waters. The boreal forest barely reaches the Alaska Peninsula in the north; consequently, tundra- and shrub-land cover types dominate the region. A cool maritime climate prevails, but the weather is dynamic and strong winds are common in all seasons. A large portion of the Alaska Peninsula (62% of lands) was retained in 1980 by the federal government through the Alaska National Interest Lands Conservation Act. Thus, land management responsibilities are held primarily by the National Park Service and the U.S. Fish and Wildlife Service (USFWS) with the remainder of the State of Alaska (25%) and several Native Corporations (13%; Figure 1).

In the >100 y between 1874 and 1980, 16 scientific expeditions and surveys included some documentation of birds on the Alaska Peninsula (Table S1 and references therein, Supplemental Material). After the creation of the Alaska Peninsula and Becharof National Wildlife Refuges in 1980 and up to the time of this inventory in 2004, standardized surveys and in-depth studies of birds at specific locations had been conducted (Table S1, Supplemental Material). In general, the majority of these past and more recent efforts occurred on the north and central Alaska Peninsula in coastal areas or along river corridors and lake shores and focused on waterfowl (e.g., Platte and Butler 1995; Larned 2008; Dau and Mallek 2009), seabirds (e.g., Bartonek and Gibson 1972; Levandowski and Savage 2004), and bald eagles Haliaeetus leucocephalus (Savage and Hodges 2006; Table S1, Supplemental Material). Only a few studies occurred away from major waterbodies in spring (late April–early June) when lowland-breeding birds initiate nesting and are at their most detectable. Studies that focused on lowland-breeding shorebirds, a sizeable component of the Alaska Peninsula avifauna and a group of management concern to USFWS due to population declines or
uncertain population trends (ASG 2008; Andres et al. 2012), have been few and limited in geographic and taxonomic scope. Past shorebird studies included a comprehensive assessment of shorebird occurrence and breeding status in coastal meadows adjacent to Nelson Lagoon (Gill et al. 1981), an assessment of records and a field trip to obtain specimens for the description of the Alaska subspecies of marbled godwits *Limosa fedoa beringiae* (Gibson and Kessel 1989), a brief nest search for marbled godwits (North and Tucker 1992), a habitat assessment for marbled godwits at Godwit Valley (Mehall-Niswander 1997), and a pilot study to assess survey methods for shorebirds (Wightman et al. 2002).

The godwit studies provided the first description of the subspecies (Gibson and Kessel 1989) and information to generate a rough population estimate of about 3,000 birds (Gratto-Trevor 2000). Beringian marbled godwits breed only on the Alaska Peninsula about 2,500 km away from the next-closest breeding population of marbled godwits on the central prairies of Canada (Gratto-Trevor 2000). The breeding range on the Alaska Peninsula is described as the lowlands adjacent to Ugashik Bay south toward Port Heiden (Gibson and Kessel 1989; Mehall-Niswander 1997).

In the late 20th century, widespread declines in many populations of North American birds led to the development of national plans for bird conservation (e.g., Brown et al. 2000; Rich et al. 2004). The USFWS was mandated in most of these plans to develop action items that would work to curtail population declines in migratory birds. A unifying feature of all these plans was their encouragement to develop science-based monitoring programs that could provide information on the status and trends of bird populations. This information would then be available to land managers for decision-making and monitoring. Prior to the early 2000s, no broad scale, multispecies inventory had been attempted on the Alaska Peninsula. But, in the early 2000s, National Park Service Southwest Area Network and the USFWS Alaska Peninsula and Becharof National Wildlife Refuges each committed to develop geographically broad-scale programs to inventory and monitor birds on the Alaska Peninsula. The National Park Service Southwest Area Network’s inventory took place in 2004–2006 and 2008 and focused on the montane areas (i.e., lands >100 m in elevation) of three parks in the region (Lake Clark, Katmai, and Aniakchak [Ruthrauff et al. 2007; Ruthrauff and Tibbitts 2009; Amundson et al. 2018]). The inventory described herein complements the National Park Service’s efforts by focusing on the extensive lowlands (defined as all lands <100 m in elevation) in the same region. Goals and methods differ only slightly between the montane inventories and this study; thus, the combined results provide a comprehensive view of the breeding avifauna of the north and central Alaska Peninsula that is not limited by elevation, land cover type, accessibility, or land ownership. These inventories provide baseline information necessary to evaluate any future changes in avifauna and vegetation, which is particularly useful in this era of declining populations and changing environmental conditions (Lawler 2009; Martinuzzi et al. 2016; Thompson et al. 2016). Our objectives for this inventory were to 1) establish baseline information on distribution and abundance of breeding birds in lowland areas of the Alaska Peninsula, with an emphasis on shorebirds (Scolopacidae, Charadriidae); 2) describe habitat associations of breeding birds; and 3) establish a more complete baseline of the distribution and abundance of marbled godwits for future monitoring.

**Methods**

**Study area**

The study area consisted of lowlands on the Alaska Peninsula (hereafter, “the peninsula”), extending from the northern boundary of the Alaska Peninsula and Becharof National Wildlife Refuges south to the peninsula’s tip (Figure 1). Lowlands occur primarily on the north side of the peninsula, where they create an ecoregion known as the Bristol Bay–Nushagak Lowlands (Gallant et al. 1995), but there are also small pockets of lowlands on the south coast along the Gulf of Alaska. Lowland areas are characterized by ponds, lakes, and meandering rivers surrounded by extensive wet or mesic meadows. These meadows are vegetated primarily by sedges (e.g., *Carex* spp., *Eriophorum* spp.) and grasses (mostly *Calamagrostis canadensis*), and interspersed with patches of low and dwarf shrub vegetation dominated by dwarf birch *Betula nana*, sweet gale *Myrica gale*, and dwarf ericaceous shrubs (e.g., *Rhododendron tomentosum*). Smaller lakes and ponds are filled with emergent plants like buckbean *Menyanthes trifoliata* and horsetail *Equisetum* spp. Areas with even slight topographic relief contain dense thickets of willows *Salix* spp. and green alder *Alnus viridis*. Well-drained areas with hummocks and low hills support tundra heath communities where carpets of crowberry *Empetrum nigrum* are interspersed with patches of bare ground, lichen, and dwarf willow (e.g., *Salix rotundifolia*). The largest town on the peninsula is Naknek (544 inhabitants in 2010; [http://live.laborstats.alaska.gov/cen/dparea.cfm](http://live.laborstats.alaska.gov/cen/dparea.cfm)) located downriver of the town of King Salmon (374 inhabitants in 2010), which hosts the main airport in the region as well as the headquarters of the Alaska Peninsula and Becharof National Wildlife Refuges. Numerous smaller villages and seasonal camps are scattered along both coasts and along river corridors. Roads exist only in the immediate vicinity of towns and villages; thus, local people and visitors use motor boats and small aircraft to travel to inland sites.

**Sampling design**

We used a stratified random sampling design based on elevation and land cover to select sampling units. The sampling universe included all lowlands from Naknek River near King Salmon to the tip of the peninsula (Figure 2). We used an existing Geographic Information System grid of Alaska composed of 10 km ×
10 km plots that had been used in other landbird surveys in the state (Handel and Cady 2004; Tibbitts et al. 2005). We divided the grid into smaller units (i.e., 5 km \( \times \) 5 km plots) that could be sampled more easily, given that common land-cover features (e.g., sloughs, rivers) would put large portions of most 10-km plots off-limits to observers on foot. We retained all plots that had \( \geq 15\% \) of their area, \( \leq 100 \text{ m} \) in elevation (based on the National Elevation Dataset, 1:24,000 scale; https://nationalmap.gov/elevation.html). For the area north of Port Moller (Figure 2), we calculated land cover composition of the resulting lowlands within each plot based on the digital land-cover map from the Bristol Bay Mapping Project (Wibbenmeyer et al. 1982) that had been created from Landsat Multispectral Scanner imagery with a 50-m pixel resolution. We grouped the Mapping Project’s 15 land cover types into 8 general types that described known bird habitats in Alaska: shallow water, barren, persistent emergent wetlands (a combination of “Marsh–Very Wet Bog” and “Wet Bog–Wet Meadow”), heath, shrub, tundra, a group of rare lowland cover types in the region (“Conifer Forest,” “Mixed Forest,” “Mixed Deciduous,” and “Closed Shrub Graminoid”), and a group of inaccessible and unknown cover types (“Deep Clear Water,” “Snow–Cloud–Light–Barren,” “Offshore–Shallow–Sedimented,” “Offshore–Deep–Clear”). For the area south of Port Moller, we used wetland symbols on U.S. Geological Survey topographic maps (1:63,360 scale) to delineate polygons of persistent emergent wetlands. We then classified each plot into one of two strata based on the amount of persistent wetlands that they contained because lowland-breeding shorebirds in Alaska usually associate with this land cover type (ASG 2008). Specifically we identified 1) lowland plots dominated by persistent emergent wetlands (hereafter, “wet plots”), with great potential to host shorebirds (\( \geq 25\% \) of a plot’s lowlands were covered by persistent emergent wetlands); and 2) lowland plots dominated by drier and shrubbier cover types (hereafter, “dry plots”), with low potential (\( < 25\% \) of lowlands contained persistent emergent wetlands).

Figure 2. Distribution of study plots for the inventory of lowland-breeding birds on the Alaska Peninsula, 2004–2007. The lowland sampling universe is shaded green. Blue squares denote surveyed wet plots (\( \geq 25\% \) cover of wetlands), brown squares show surveyed dry plots (\( < 25\% \) of wetlands), and black squares show plots selected for sampling during the plot selection process, but not surveyed. All nonsurveyed plots are on the south Alaska Peninsula. Towns depicted by red dots.
From this sampling frame of 256 wet and 1,006 dry plots, we systematically selected 64 sample plots including 32 in each host class (Figure 2). This necessitated selecting wet plots at four times the frequency of dry plots. We chose this unequal sample scheme because we had limited resources for field work and knew that shorebirds (and most lowland-breeding species) were more likely to be associated with wetlands. In addition, we systematically selected four plots (three wet and one dry) along the Meshik and Ugashik river corridors to increase sampling within the range of marbled godwits. Our goal was to survey a minimum of 15 points in each of these 68 plots; to minimize the probability of detecting the same individual on consecutive points, we spaced points along transects at 500-m intervals. Prior to going into the field, we sketched potential transect routes onto plots maps that depicted land cover polygons. We drew transect routes to cross gradients of elevation and land cover with the 15 points allocated in proportion to the extent of each land cover type. The logistics of accessing plots and crossing natural barriers sometimes made it difficult to follow the predesigned transect routes, and in those instances, we rerouted transects in the field.

We accessed sampled plots (see below) using helicopters (33 plots), fixed-wing aircraft (15 plots), and inflatable canoes that had been transported to upstream drop-off points by fixed-wing aircraft (5 plots). Distance of surveyed plots from King Salmon ranged from 40 to 353 km. In 2004, most plots were north of the Ugashik River except one plot at Cinder Lagoon and three plots on the Meshik River (Figure 2; Table S2, Supplemental Material). In 2005, the addition of helicopter transportation allowed us to reach plots from the mouth of Becharof Lake south to Port Heiden including one on the Gulf of Alaska side of the Peninsula. In 2006, we completed the remaining plots north of the Ugashik River plus one on the Meshik River and one south of Mount Aniakchak. In 2007, we surveyed exclusively south of Port Heiden on the Bristol Bay side of the Peninsula. Survey teams usually camped on plots for one to two nights, but sometimes only made day trips if the aircraft was parked at a nearby fuel cache or if crews required helicopter assistance to access portions of the plots (e.g., points across unfordable rivers).

Data collection

We conducted fieldwork during May and early June to coincide with the period of peak courtship and singing activity of breeding birds, particularly shorebirds. We conducted surveys during daylight hours and suspended them whenever fog, rain, or wind hampered our ability to detect birds. Birds were sampled by unlimited distance point-count (Ralph et al. 1995) and variable-circular-plot methods (Buckland et al. 2001, 2004). We worked in two-person field crews, in which the primary observer searched visually and aurally for birds and called out detections to the recorder, who kept track of elapsed time and watched for birds that might have been missed by the primary observer. For each plot, we maintained standardized lists of presence, general abundance, and breeding status of birds detected while walking between points and at other times during each plot visit, and compiled these incidental data along with point-count data.

For each detection of a shorebird or a potential avian predator of shorebird adults, chicks, or eggs (i.e., raptor, crane, gull, corvid, shrike) during the 10-min count, we recorded species, number of individuals, time of detection, radial distance of the bird(s) from the sample point, and whether the initial detection was aural or visual. When possible, we collected additional data on plumage, behavior, vocalization(s), and interactions with other birds to help assign sex and breeding status. We used rangefinders to estimate radial distance to individual birds and, if we only heard an individual, we recorded the possible range of its location using intervals. We estimated these intervals using rangefinders by measuring the distance to landmarks on either side of the calling bird. For birds at extreme distances, or in places where a rangefinder had difficulty measuring a distance (e.g., unvegetated lakes), we recorded the possible range of their locations using topographic features referenced on 1:63,360 scale U.S. Geological Survey maps. For all other avian species (waterfowl, ptarmigan, waterbirds, passerines), we recorded only the number of individuals within or beyond a 50-m radius of the point during the 10-min count.

At the start of each 10-min count, we recorded averaged Global Positioning System location and positional error, date, time of day, observer, recorder, slope, aspect, estimated wind speed using the Beaufort scale, and sky condition. We also recorded the percent cover of all vegetation types within 50 m of the point if in dense vegetation (e.g., alder thickets, \( n = 96 \) points) and 150 m of the point in open vegetation (e.g., sedge meadows, \( n = 607 \) points). Observers used laser rangefinders to determine the 50-m or 150-m radius around a point and then visually estimated percent cover of the different vegetation types with the circle. We classified wetlands according to types described in the National Wetland Inventory (Cowardin et al. 1979) and classified vegetation to at least Level II of the Alaska Vegetation Classification System (Viereck et al. 1992): water, bare ground, herbaceous-wet, herbaceous-dry, dwarf shrub-willow (shrubs <20 cm tall, not ericaceous), dwarf shrub-ericaceous (shrubs <20 cm tall), low shrub (shrubs 20 cm to 1.5 m tall), tall shrub (shrubs \( \geq 1.5 \) m tall), and forest. We eliminated forest cover from summaries because we only recorded it at one point. We also took four digital photographs of vegetation at each point looking in the four cardinal directions to create a baseline for any future studies of vegetation change. Observers spent 1–2 d on each plot hiking between 5 and 22 km for a total of 578 km traversed during searches for birds. Most point counts
(90%) were conducted between 1000 and 1800 hours. The remainder of counts were conducted between 1800 and 2230 hours (10%) and before 0800 hours (<1%).

Species lists, distribution, and conservation status

We annotated the list of birds detected during the inventory with breeding status (i.e., confirmed breeder, presumed breeder based on behavior, presumed breeder based on breeding range, nonbreeding migrant) and detection method (i.e., detected on plots via point counts or incidentally). We then mapped the presence or absence per plot of each species to visualize distributions. To assess whether some species co-occurred more or less than expected by chance (i.e., to identify species assemblages), we used the ‘cooccur’ package in Program R (version 1.3; Griffith et al. 2016), which calculates the probability of significant pairwise associations between pairs of species if they were to distribute themselves randomly and independently of each other (after Veech 2013). The model then uses the expected frequency of co-occurrence between each pair of species to determine whether they co-occur less or more than expected by chance at an alpha level of 0.05. We conducted this analysis on the two species groups with sufficient sample sizes: shorebirds within 150 m of points and passerines within 50 m of points. These truncated distances approximately controlled for detection differences among species.

We identified the species of conservation concern on our list in two time periods—near the time of fieldwork (1999 to 2008) and more currently (2008 to 2018). We based the conservation status on designations from five conservation organizations: Audubon Alaska (Stenhouse and Senner 2005; Warnock 2017), Partners in Flight (Rich et al. 2004; Rosenberg et al. 2016), U.S. Fish and Wildlife Service (USFWS 2008, 2011), Alaska Shorebird Group (ASG 2008, In review), and Boreal Partners in Flight (BPIF 1999, In review). We used these multiple schemes because each incorporated slightly different benchmarks to designate categories of conservation concern and focused on different species groups; taken together, these plans formed a comprehensive view of the conservation status of the peninsula’s breeding avifauna in the 5 y pre- and post-inventory. Finally, to evaluate whether we detected near the true number of lowland-breeding species on the peninsula, we compared our list to a long-term summary of spring and summer bird records on the peninsula curated by the Alaska Peninsula and Becharof National Wildlife Refuges that includes information from earlier expeditions (Table S1, Supplemental Material), USFWS field camps, local birdwatchers, and eBird (Sullivan et al. 2009). For poorly documented birds on the summary list, we used range maps from the Birds of North America series to determine whether they were breeders (Rodewald 2015).

Relative abundance, species richness, and habitat associations

We calculated relative abundance and apparent species richness as mean number of individuals and mean number of species detected per 10-min unlimited-distance point counts, respectively. We report these metrics by survey area and stratum, the latter to broadly examine the effect of wetland cover on bird occurrence. We also summarized bird–habitat associations at the finer scale of points by comparing the mean percent cover of each vegetation type on the subset of points where a species was detected to the mean percent cover of each vegetation type at all points. We considered species to be strongly positively associated with a vegetation type when the points where they occurred contained double the average percent cover of all points. Similarly, we considered species to have avoided vegetation types when points where they occurred contained half the average percent cover at all points. We evaluated these metrics for species that occurred within 150 m (shorebirds and avian predators) or 50 m (all other species) of ≥10 points (n = 30 species). These assessments are not a definitive analysis of bird use of peninsula habitats because they do not take into account variable detection probabilities introduced by differences in vegetation structure, or possible inaccuracies in percent cover estimates introduced by assuming percent cover values within 50 m of densely vegetated points corresponded to percent cover within 150 m of those points (an artifact of our data collection methods). Rather, we present them here as an overview of possible vegetation affinities of birds in the region to help guide future analyses and study designs.

Results

Survey effort and conditions

We conducted surveys during 13 May–2 June 2004, 8 May–2 June 2005, 10–31 May 2006, and 16–26 May 2007 (Table S2, Supplemental Material). We surveyed 52 of the 68 plots (31 wet lowland, 21 dry lowland) that had been allocated through the sampling design (Figure 2), but we were logistically unable to survey 16 plots (8 wet lowland, 8 dry lowland) located between Port Moller and Bechevin Bay. Annually, we sampled between 10 and 16 plots (Table S2, Supplemental Material). Overall, we conducted 792 point counts (482 in wet lowland plots, 310 in dry lowland plots), representing 132 h of survey time. Observers surveyed an average of 15.5 ± 0.55 standard error (SE; range = 10–21) points per plot in wet lowlands and 14.8 ± 0.59 SE (range = 7–21) points per plot in dry lowlands. Spring and early summer conditions during the years of the inventory did not deviate significantly from the 20-y average at the King Salmon weather station (the closest station with continuous records), although May air temperatures and precipitation were slightly warmer and wetter in both 2004 and 2005, and slightly warmer and drier in
2006 (Table S3, Supplemental Material), as compared with average. Observation conditions on survey days were fair to good (i.e., winds ≤ Beaufort 4 and visibility ≥300 m) for the majority (96%) of point counts and poor (i.e., winds ≥ Beaufort 4 and fog) on relatively few (4%).

Species lists
We detected 95 species, including 19 species of shorebirds (20% of total species), 17 species of avian predators (18%), 33 species of waterbirds (35%), and 26 species of land- and song-birds (27%; Table 1). We determined that 82 of the 95 species, including 14 of the 19 shorebird species, were breeding in the lowlands of the peninsula based on the presence of nests or young (32 species as confirmed breeders), singing males or flight displays (42 presumed breeders), or birds present within their documented breeding range (8 presumed breeders). We determined that the remaining species were either migrants en route to breeding areas farther north (n = 11) given their known breeding ranges (e.g., emperor goose Chen canagica, semipalmated sandpiper Calidris pusilla), or species that breed in marine habitats on the peninsula (n = 2; black-legged kittiwake Rissa tridactyla, Aleutian tern Onychoprion aleuticus). About one-third of the species (36 of 95) were considered species of conservation concern by one or more organizations at the time of the inventory, including 10 species of shorebirds (Table 1). Many species of concern were relatively common on the inventory (i.e., occurring on ≥50% of plots; n = 13), including three species of shorebirds (Table S4, Supplemental Material). Both past and current species of concern that we rarely encountered (i.e., detected on ≤2 plots; Table 1) comprised Arctic and subarctic breeders (e.g., emperor goose, long-tailed duck Clangula hyemalis, whimbrel Numenius phaeopus), montane- and boreal-breeders (e.g., rock ptarmigan Lagopus muta, Hudsonian godwit Limosa haemastica), and species that habitually occur in low densities (e.g., golden eagle Aquila chrysaetos, peregrine falcon Falco peregrinus). Based on the USFWS compilation of bird records on the peninsula and Birds of North America breeding range maps (Rudowalad 2015), we estimated that we may have missed five species on the inventory, including Sabine’s gull Xema sabini, Bonaparte’s gull Chroicocephalus philadelphia, olive-sided flycatcher Contopus cooperi, violet-green swallow Tachycineta thalassina, and rusty blackbird Euphagus carolinus.

Species distribution and co-occurrence
In general, we usually detected species that were abundant, large-bodied, or highly vocal during point counts instead of incidentally (Table 1). For example, we detected tundra swans Cygnus columbianus on point counts at 33 plots and incidentally on only 4 plots. In contrast, we detected uncommon and usually silent species (e.g., short-eared owls Asio flammmeus) fairly equally by either method, and we tended to detect habitat specialists incidentally (e.g., red-breasted merganser Mergus serrator, belted kingfisher Megaceryle alcyn). We detected most species of shorebirds, including marbled godwits, during point counts. About one-third of the species (n = 36), with representatives from various bird taxonomic groups, occurred on over half the plots (e.g., tundra swan, willow ptarmigan Lagopus mutus, Pacific golden-plover Pluvialis fulva; Table 1). The most widely distributed species were mallard Anas platyrhynchos, northern pintail A. acuta, sandhill crane Antigone canadensis, short-billed dowitcher Limnodromus griseus, Wilson’s snipe Gallinago delicata, mew gull Larus canus, and savannah sparrow Passerellus sandwichensis; all of these occurred on 92–98% of the plots (Table 1; Figure S1, Supplemental Material). In contrast, we detected 21 species on only a single plot and 4 species on only two plots (Table 1; Figure S1, Supplemental Material). These rarely detected species included mostly migrants or habitat specialists. Other regional patterns included one breeding species found only on the north coast (rock sandpiper Calidris ptilocnemis) and many breeding species absent from the southern third of the survey area (i.e., between Port Heiden and Port Moller: greater white-fronted goose Anser albifrons, black-bellied plover Pluvialis squatarola, marbled godwit, western sandpiper Calidris mauri, long-tailed jaeger Stercorarius longicaudus, northern goshawk Accipiter gentilis, pelican Pelecanus onocrotalus, American dipper Cinclus mexicanus, gray-cheeked thrush Catharus minimus, yellow warbler Setophaga petechia, and yellow-rumped warbler S. coronata; Figure S1, Supplemental Material). In contrast, only two breeding species were absent on surveys of the northern third of the survey area (i.e., north of Egegik: harlequin duck Histrionicus histrionicus, black-billed magpie Pica hudsonia). We encountered marbled godwits from Pike Lake south to Reindeer Creek and from near the Bering Sea coast east to Lower Ugashik Lake and the western flank of Mount Ainekchak (Figure 3). In addition, we recorded a single alarm-calling marbled godwit as it flew past Shosky Creek about 50 km north of our next-closest detections of marbled godwits; we could not confirm if this bird was breeding on the plot.

Co-occurrence analysis included 13 of the 19 shorebird species with sufficient sample size (i.e., those with >1% chance of co-occurrence with other species) for a total of 66 species pair comparisons. Most pairwise comparisons yielded random results (62%) and all significant co-occurrences were mostly positive (30%; i.e., these pairs occurred together on points significantly more often than expected by chance) rather than negative (8%; Figure S2, Supplemental Material). Least sandpipers Calidris minutilla, marbled godwits, Wilson’s snipe, short-billed dowitchers, and dunlin Calidris alpina all positively co-occurred with each other. At the other end of the spectrum, semipalmated plovers Charadrius semipalmatus exhibited mostly random associations with other shorebird species except for significantly negative co-occurrences with short-billed dowitchers and Wilson’s
Table 1. Species recorded during the inventory of lowland-breeding birds on the Alaska Peninsula, 2004–2007, their observed breeding status, conservation status, and distribution among survey plots. Values in bold indicate species that occurred on ≥50% of total plots. Species are listed in taxonomic order (AOU 1998; Chesser et al. 2017).

| Common name          | Scientific name          | Breeding status | Conservation status | Number of plots | Proportion of total plots (n = 52) |
|----------------------|--------------------------|-----------------|---------------------|----------------|-----------------------------------|
| **Waterfowl**        |                          |                 |                     |                |                                   |
| Emperor goose        | Chen canagica            | X, 1            | —                   | 1              | 0.02                              |
| Greater white-fronted goose | Anser albifrons    | CB              | —                   | 15             | 0.22                              |
| Cackling goose       | Branta hutchinsii        | X               | —                   | 1              | 0.04                              |
| Canada goose         | Branta canadensis        | B               | 1                   | 5              | 0.17                              |
| Tundra swan          | Cygnus columbianus      | CB              | —                   | 33             | 0.67                              |
| Northern shoveler    | Spatula clypeata         | B               | —                   | 14             | 0.27                              |
| Gadwall              | Mareca strepera          | B               | —                   | 5              | 0.17                              |
| Eurasian wigeon      | Anas penelope           | B               | —                   | 1              | 0.02                              |
| American wigeon      | Anas americana          | CB              | —                   | 23             | 0.46                              |
| Mallard              | Anas platyrhynchos      | CB              | —                   | 34             | 0.92                              |
| Northern pintail     | Anas acuta              | CB              | —                   | 31             | 0.92                              |
| Green-winged teal    | Anas crecca             | B               | 1                   | 24             | 0.71                              |
| Canvasback           | Aythy a valisineria     | B               | —                   | 26             | 0.91                              |
| Greater scaup        | Aythy a marila          | B               | 2                   | 9              | 0.31                              |
| Harlequin duck       | Histrionicus histrionicus | B         | 5                   | —              | 0.10                              |
| Surf scoter          | Melanitta perspicilata  | X               | —                   | 1              | 0.02                              |
| White-winged scoter  | Melanitta fusca         | B               | 2                   | 6              | 0.27                              |
| Black scoter         | Melanitta nigra        | 1, 2            | 18                  | 8              | 0.50                              |
| Long-tailed duck     | Clangula hyemalis       | R               | 1                   | —              | 0.02                              |
| Bufflehead           | Bucephala albeola       | B               | —                   | 1              | 0.04                              |
| Common goldeneye     | Bucephala clangula      | X               | —                   | 1              | 0.02                              |
| Barrow’s goldeneye   | Bucephala islandica     | B               | —                   | 1              | 0.02                              |
| Common merganser     | Mergus merganser        | B               | —                   | —              | 0.06                              |
| Red-breasted merganser | Mergus serrat            | B               | —                   | 5             | 0.33                              |
| **Ptarmigan**        |                          |                 |                     |                |                                   |
| Willow ptarmigan     | Lagopus lagopus         | CB              | 1, 2                | 37             | 0.88                              |
| Rock ptarmigan       | Lagopus muta            | B               | 1, 2                | —              | 1.00                              |
| **Grebes and cranes**|                          |                 |                     |                |                                   |
| Horned grebe         | Podiceps auritus        | B               | —                   | 3              | 0.06                              |
| Red-necked grebe     | Podiceps grisegena      | B               | 2                   | 4              | 0.31                              |
| Sandhill crane       | Antigone canadensis     | CB              | —                   | 48             | 0.94                              |
| **Shorebirds**       |                          |                 |                     |                |                                   |
| Black-bellied plover  | Pluvialis squatarola    | B               | —                   | 17             | 0.33                              |
| Pacific golden-plover | Pluvialis fulva        | CB              | 1                   | 22             | 0.50                              |
| Semipalmated plover  | Charadrius semipalmatus | CB              | —                   | 9              | 0.31                              |
| Whimbrel             | Numenius phaeopus       | X, 1            | 1                   | —              | 0.02                              |
| Hudsonian godwit     | Limosa haemastica       | X               | 1, 2                | —              | 0.02                              |
| Marbled godwit       | Limosa fedoa beringiae  | B               | 1, 2                | 18             | 0.38                              |
| Black turnstone      | Arenaria melanoccephala | R               | 1, 2                | 5              | 0.15                              |
| Dunlin               | Calidris alpina         | CB              | 1, 2                | 40             | 0.77                              |
| Rock sandpiper       | Calidris ptilocnemis    | CB              | 1, 2                | 4              | 0.08                              |
| Least sandpiper      | Calidris minutilla      | CB              | —                   | 47             | 0.90                              |
| Pectoral sandpiper   | Calidris melanotos      | X               | —                   | 1              | 0.02                              |
| Semipalmated sandpiper | Calidris pusilla       | X               | —                   | 1              | 0.02                              |
| Western sandpiper    | Calidris mauri          | B               | 1, 2                | 4              | 0.10                              |
| Short-billed dowitcher | Limnodromus griseus    | CB              | 1, 2                | 47             | 0.94                              |
| Wilson’s snipe       | Gullino delcata         | CB              | —                   | 51             | 0.98                              |
| Spotted sandpiper    | Actitis macularis       | R               | —                   | —              | 0.04                              |
| Wandering tattler    | Tringa incana          | X               | 1                   | —              | 0.02                              |
| Greater yellowlegs   | Tringa melanoleuca     | CB              | —                   | 35             | 0.75                              |
| Red-necked phalarope | Phalaropus lobatus      | CB              | —                   | 27             | 0.67                              |
| Jaegers, gulls, and terns |               |                 |                     |                |                                   |
| Parasitic jaeger     | Stercorarius parasiticus | CB              | —                   | 39             | 0.83                              |
| Long-tailed jaeger   | Stercorarius longicaudus | B             | —                   | 14             | 0.40                              |
| Black-legged kitiwake | Rissa tridactyla      | X               | —                   | —              | 0.02                              |
| Mew gull             | Larus canus            | CB              | —                   | 42             | 0.92                              |
| Glaucous-winged gull | Larus glaucescens      | CB              | —                   | 39             | 0.81                              |
| Aleutian tern        | Onychoprion aleuticus  | X               | 1, 2                | 3              | 0.08                              |
| Arctic tern          | Sterna paradisaea      | CB              | 1                   | 37             | 0.83                              |
snipe. Of the passerine species with sufficient sample size to analyze (18 of 25 species for a total of 115 species pairs), most pairwise comparisons were random (44%), although almost as many were significantly positive (39%) while fewer were negative (17%). Orange-crowned warbler *Oreothlypis celata*, American robin *Turdus migratorius*, common redpoll *Acanthis flammea*, golden-crowned sparrow *Zonotrichia atricapilla*, yellow warbler, and Wilson’s warbler *Cardellina pusilla* all positively co-occurred while Lapland longspur *Calcarius lapponicus*...
and savannah sparrow stood out for their negative co-occurrences with other songbirds, except with each other.

**Relative abundance on point counts**

We recorded 15,600 individual birds of 74 species on the 10-min, unlimited distance point counts (Table 2). These included 4,814 shorebirds (30.9% of individuals on point counts), 2,897 avian predators (18.6%), and 7,889 individuals of other species (50.6%). About 12% of species (9 of 74) dominated point-count detections and occurred at average levels of 0.9–1.5 birds/point (Table 2); these included (in order of decreasing abundance): dunlin, sandhill crane, Lapland longspur, savannah sparrow, Wilson’s snipe, short-billed dowitcher, greater scaup Aythya marila, American tree sparrow Spizelloides arborea, and glaucous-winged gull Larus glaucescens. Marbled godwits were relatively more abundant in the southern half of their range, with up to 1.6 birds/point in the lowlands adjacent to and southeast of Cinder Lagoon (Figure 3). The majority of species detected on point counts (89%) were present in both wet and dry lowland plots (Table 2); exceptions were species represented by a single or few individuals (e.g., Eurasian wigeon Anas penelope, peregrine falcon). We detected similar numbers of species and individuals per point in both wet and dry lowland plots; an average of $8.7 \pm 0.1$ SE species per point on wet plots, $8.1 \pm 0.2$ SE species on dry plots, and $20.8 \pm 1.0$ SE individuals per point on wet plots and $18.0 \pm 1.1$ SE individuals on dry plots. Species composition differed between strata, however, with more species and individuals of shorebirds (20% more species and 30% more individuals) and avian predators (12% and 20%) on point counts in wet than dry plots (Table 2). Conversely, there were more species (8%) and more individuals (10%) of the mixed species group of ‘other birds’ in dry than wet plots; these differences were due to the presence in dry plots of more individual ducks, thrushes, warblers, and all sparrows except savannah sparrow (Table 2). For the subset of shorebirds to which we assigned sex during point counts via plumage characteristics or behavioral cues (2,317 of 3,450 detections), we classified the vast majority as males (97%) and only a few as females (1%) or male–female pairs (2%). For the subset of avian predators to which we assigned sex (330 of 1,617...
detections), we classified 8% as males, 4% as females, and 88% as pairs. Although not measured directly, most passerine detections involved singing males as noted by observers on plot forms.

**Distribution of vegetation**

Across the study area, low shrub was the most common vegetation type and encountered on 53% of all points (Figure S3, Supplemental Material). Other fairly common vegetation types were water (24% of points), herbaceous-wet (32%), herbaceous-dry (36%), dwarf shrub-ericaceous (39%), and tall shrub (26%). In contrast, bare ground and dwarf shrub-willow were rare, occurring on 3% and 7% of all points, respectively. Common occurrence translated into relatively high percent cover for low shrub and dwarf shrub-ericaceous, but not for the other common vegetation types (Figure 4). When present, bare ground and dwarf shrub-willow covered just small areas at points. We encountered all vegetation types in plots from both strata, but in different proportions. At least twice as many points contained herbaceous-wet habitat in wet plots than dry plots whereas the opposite was true for bare ground, dwarf shrub-willow, and dwarf shrub-ericaceous (Table 3). There also tended to be slightly greater occurrences of water and herbaceous-dry in wet plots and more low shrub and tall shrub in dry plots. Wet plots contained relatively more (i.e., greater percent cover) of the herbaceous vegetation types than dry plots (Figure 4, Table 3); whereas, dry plots contained twice as much dwarf shrub-ericaceous and tall shrub vegetation. Percent cover of the remaining vegetation types did not differ substantially between strata, including the commonly encountered low shrub type and the less common land-cover types such as water, bare ground, and dwarf shrub-willow (Table 3).

**Associations between birds and habitats**

Some species showed strong associations with particular vegetation types. For example, points at which we recorded semipalmated plovers and American pipits *Anthus rubescens* generally had over twice the percent cover of bare ground than all points sampled across the study area (Table 4); whereas, the water-obligate red-necked phalarope *Phalaropus lobatus* and species that forage in or above open water, such as Arctic tern *Sterna paradisaea* and tree swallow *Tachycineta bicolor*, were positively associated with points with more water. Even though low shrub was commonly encountered and extensively covered points on the survey area, the majority of species were found in this cover type either slightly less or in accordance with its average overall abundance (Table 4). Only two species (American tree sparrow and white-crowned sparrow *Zonotrichia leucomystax*) were strongly positively associated with low shrub; and one species (rock sandpiper) stood out among other species with its low association with low shrub. A suite of passerines (including hermit thrush *Catharus guttatus*, common redpoll, fox sparrow *Passerella iliaca*, golden-crowned sparrow, orange-crowned warbler, and Wilson’s warbler) was strongly associated with tall shrub, whereas up to 15 species appeared to avoid tall shrub; notably, western sandpiper and rock sandpiper were not detected on points with any tall shrub. Three species of shorebirds (Pacific golden-plover, western sandpiper, rock sandpiper) and one passerine (American pipit) were positively associated with dwarf shrub-ericaceous. Sandhill crane and short-billed dowitcher were the only two species strongly positively associated with herbaceous-wet and many of the passerines and one of the shorebirds (rock sandpiper) appeared to avoid this vegetation cover type. No species were strongly positively associated with herbaceous-dry and a few, mostly passerines, appeared to avoid it. Dwarf shrub-willow, a rare habitat, was attractive to willow ptarmigan, black-bellied plover, marbled godwit, and Lapland longspur and unattractive to western sandpiper, rock sandpiper, and many passerines. Species in the shorebird assemblage tended to use points with less bare ground and dwarf shrub-willow and more low shrub and herbaceous-wet and -dry than other shorebirds. Species in the songbird assemblage used points with more tall shrub than the other songbirds. Overall, the survey points at which marbled godwits occurred were dominated by herbaceous habitats, low shrub, and dwarf shrub-willow.

**Discussion**

Our inventory of breeding birds across the north and central lowlands of the Alaska Peninsula (a 400 km × 150 km area) provides the first systematic assessment of distribution, relative abundance, and vegetation associations of birds in this remote region. These baseline data can be used to monitor future changes in bird and vegetation communities. The 95 species of birds detected represent a substantial portion of the overall Alaskan avifauna (Gabrielson and Lincoln 1959; Kessel and Gibson 1978) and were divided almost equally among waterfowl (24 species), shorebirds (19), and passerines (25). This differed slightly from the composition of avifauna in adjacent uplands in Katmai National Park and Preserve and Aniakchak National Monument and Preserve (Ruthrauff et al. 2007; Ruthrauff and Tibbits 2009; Amundson et al. 2018), which supported fewer waterfowl (19 species) and shorebirds (17), but more passerines (35 species). Even so, there was an 82% overlap in species detected between our lowland inventory and the upland inventories, indicating (not surprisingly) that most species in the region are distributed fairly continuously up to their elevation limits. Generally, the drier uplands lacked some of the rarer waterfowl found in the lowlands (e.g., canvasback *Aythya valisineria*) and hosted shorebird and passerine species that associate with dwarf shrub mats in the alpine zone (i.e., American golden-plover *Pluvialis dominica*, Baird’s sandpiper *Calidris bairdii*, horned lark *Eremophila alpestris*, snow bunting *Plectrophenax nivalis*).
### Table 2. Comparison of average abundance (number of individuals per point) of birds on 10-min, unlimited distance point counts at all points and at points in the two sampling strata (wet plots with ≥25% cover of wetlands; dry plots with <25% of wetlands) during the inventory of lowland-breeding birds on the Alaska Peninsula, 2004–2007. Values in bold indicate occurrences of >0.50 birds/point. Species are listed in taxonomic order (AOU 1998; Chesser et al. 2017).

| Common name* | Scientific name | Total birds detected | Average abundance (SE) | Average abundance | Average abundance |
|--------------|-----------------|----------------------|-------------------------|------------------|------------------|
| Greater white-fronted goose | Anser albifrons | 82 | 0.104 (0.024) | 0.108 | 0.097 |
| Cackling goose | Branta hutchinsii | 4 | 0.005 (0.004) | 0.008 | — |
| Canada goose | Branta canadensis | 14 | 0.018 (0.009) | 0.025 | 0.006 |
| Unidentified goose | — | 2 | 0.003 (0.003) | 0.004 | — |
| Tundra swan | Cygnus columbianus | 173 | 0.218 (0.025) | 0.243 | 0.181 |
| Northern shoveler | Spatula clypeata | 100 | 0.126 (0.043) | 0.187 | 0.032 |
| Gadwall | Mareca strepera | 23 | 0.029 (0.009) | 0.039 | 0.013 |
| Eurasian wigeon | Anas penelope | 2 | 0.003 (0.003) | 0.004 | — |
| American wigeon | Anas americana | 113 | 0.143 (0.033) | 0.102 | 0.206 |
| Mallard | Anas platyrhynchos | 147 | 0.186 (0.030) | 0.195 | 0.171 |
| Northern pintail | Anas acuta | 153 | 0.193 (0.032) | 0.257 | 0.094 |
| Green-winged teal | Anas crecca | 86 | 0.109 (0.021) | 0.104 | 0.116 |
| Greater scap | Aythya marila | 758 | 0.957 (0.364) | 0.822 | 1.168 |
| White-winged scoter | Melanitta fusca | 59 | 0.074 (0.033) | 0.021 | 0.158 |
| Black scoter | Melanitta nigra | 158 | 0.199 (0.050) | 0.081 | 0.384 |
| Bufflehead | Bucephala albeola | 3 | 0.004 (0.004) | 0.010 | — |
| Red-breasted merganser | Mergus serrator | 15 | 0.019 (0.008) | 0.025 | 0.010 |
| Red-throated loon | Gavia stellata | 1182 | 1.473 (0.083) | 2.006 | 0.645 |
| Greater yellowlegs | Tringa melanoleuca | 184 | 0.232 (0.019) | 0.205 | 0.274 |
| Black-bellied plover | Pluvialis squatarola | 72 | 0.091 (0.015) | 0.062 | 0.135 |
| Pacific golden-plover | Pluvialis fulva | 100 | 0.126 (0.015) | 0.104 | 0.161 |
| Semipalmated plover | Charadrius semipalmatus | 23 | 0.029 (0.007) | 0.010 | 0.058 |
| Red-necked grebe | Podiceps grisegena | 55 | 0.069 (0.014) | 0.085 | 0.045 |
| Northern goshawk | Accipiter gentilis | 1 | 0.001 (0.001) | — | 0.003 |
| Belted kingfisher | Megaceryle alcyon | 2 | 0.003 (0.002) | 0.004 | — |
| Short-eared owl | Asio flammeus | 27 | 0.034 (0.007) | 0.048 | 0.013 |
| Red-throated loon | Gavia stellata | 32 | 0.040 (0.009) | 0.050 | 0.026 |
| Arctic tern | Sterna paradisaea | 236 | 0.298 (0.042) | 0.357 | 0.206 |
| Greater yellowlegs | Tringa melanoleuca | 184 | 0.232 (0.019) | 0.205 | 0.274 |
| Red-throated loon | Gavia stellata | 32 | 0.040 (0.009) | 0.050 | 0.026 |
| Northern harrier | Circus cyaneus | 57 | 0.072 (0.011) | 0.068 | 0.077 |
| Northern pintail | Anas acuta | 153 | 0.193 (0.032) | 0.257 | 0.094 |
| Red-throated loon | Gavia stellata | 1182 | 1.473 (0.083) | 2.006 | 0.645 |
| Red-throated loon | Gavia stellata | 32 | 0.040 (0.009) | 0.050 | 0.026 |
| Northern goshawk | Accipiter gentilis | 1 | 0.001 (0.001) | — | 0.003 |
| Red-throated loon | Gavia stellata | 32 | 0.040 (0.009) | 0.050 | 0.026 |
| Red-throated loon | Gavia stellata | 1182 | 1.473 (0.083) | 2.006 | 0.645 |
| Red-throated loon | Gavia stellata | 32 | 0.040 (0.009) | 0.050 | 0.026 |
| Northern goshawk | Accipiter gentilis | 1 | 0.001 (0.001) | — | 0.003 |
| Northern goshawk | Accipiter gentilis | 1 | 0.001 (0.001) | — | 0.003 |
| Northern goshawk | Accipiter gentilis | 1 | 0.001 (0.001) | — | 0.003 |
| Northern goshawk | Accipiter gentilis | 1 | 0.001 (0.001) | — | 0.003 |
| Northern goshawk | Accipiter gentilis | 1 | 0.001 (0.001) | — | 0.003 |
Table 2. Continued.

| Common namea | Scientific name               | All points (n = 792) | Wet (n = 482) | Dry (n = 310) |
|--------------|--------------------------------|----------------------|--------------|--------------|
|              |                                | Total birds detected | Average abundance (SE) | Average abundance | Average abundance |
| Common raven | Corvus corax                   | 0.120 (0.015)        | 0.114        | 0.129        |
| Tree swallow | Tachycineta bicolor            | 0.289 (0.104)        | 0.363        | 0.174        |
| Bank swallow | Riparia riparia                | 0.049 (0.016)        | 0.058        | 0.035        |
| Black-capped chickadee | Poecile atricapillus    | 0.008 (0.004)        | 0.006        | 0.010        |
| Gray-cheeked thrush | Catharus minimus        | 0.005 (0.003)        | 0.006        | 0.003        |
| Hermit thrush | Catharus guttatus             | 0.330 (0.032)        | 0.193        | 0.542        |
| American robin | Turdus migratorius         | 0.279 (0.023)        | 0.205        | 0.394        |
| Eastern yellow wagtail | Motacilla tschutschensis    | 0.001 (0.001)        | —           | 0.003        |
| American pipit | Anthus rubescens             | 0.063 (0.010)        | 0.029        | 0.116        |
| Common redpoll | Carduelis flammea           | 0.326 (0.031)        | 0.344        | 0.297        |
| Lapland longspur | Calcarius lapponicus       | 1.352 (0.058)        | 1.376        | 1.316        |
| American tree sparrow | Spizelloides arborea    | 0.885 (0.045)        | 0.722        | 1.139        |
| Savannah sparrow | Passerellus sandwichensis   | 1.169 (0.047)        | 1.272        | 1.010        |
| Fox sparrow | Passerilla iliaca           | 0.134 (0.016)        | 0.102        | 0.184        |
| White-crowned sparrow | Zonotrichia leucophrys  | 0.356 (0.028)        | 0.307        | 0.432        |
| Golden-crowned sparrow | Zonotrichia atricapilla | 0.600 (0.038)        | 0.398        | 0.913        |
| Orange-crowned warbler | Vermivora celata       | 0.254 (0.024)        | 0.158        | 0.403        |
| Yellow warbler | Dendroica petechia           | 0.071 (0.013)        | 0.039        | 0.119        |
| Yellow-rumped warbler | Dendroica coronata     | 0.003 (0.002)        | 0.002        | 0.003        |
| Wilson’s warbler | Wilsonia pusilla            | 0.302 (0.030)        | 0.249        | 0.384        |
| Unidentified songbird | —                          | 0.001 (0.001)        | —           | 0.002        |

a See Table 1 for scientific names.

Uplands also hosted forest-dwelling passerine species not present in our lowland survey area (e.g., boreal chickadee Poecile hudsonicus, varied thrushIxoreus naevius).

Our list and relative abundance rankings of breeding birds were similar to those compiled 25 y previously on the central peninsula by Gill et al. (1981) during their intensive study of birds in coastal and lowland areas surrounding Port Moller, Herendeen Bay, and Nelson Lagoon (essentially the southern edge of our survey area). The few notable differences between this earlier study and our inventory were their lack of breeding American robins and American tree sparrows and their abundance of breeding western sandpipers. These differences were notable because American robins and American tree sparrows occurred in relatively large numbers across the length and breadth of our survey area, and the western sandpipers closest to Port Moller that we encountered were about 250 km north. These different observation patterns suggest that Port Moller represents a fairly new boundary to the breeding range in Alaska of American robins and American tree sparrows, and that western sandpipers may have a disjunct breeding range on the peninsula. The pattern of American robins and American tree sparrows support the idea proposed by Maley et al. (2003) that these two species have just recently started to extend their range south along the peninsula. The distribution of marbled godwits that we mapped encompassed all discrete areas where the species had previously been documented either breeding or suspected to be breeding (Gibson and Kessel 1989; North and Tucker 1992; Mehall-Niswander 1997; Maley et al. 2003; Gill et al. 2004), but it also extended the known breeding range substantially eastward to include the eastern slopes of the Aleutian Range near Lower Ugashik Lake. Marbled godwits were especially common on plots in the lowlands east and south of Cinder River. If our observation of a single alarm-calling bird northwest of Becharof Lake (58.196°N, 156.797°W) represents breeding there, then that would be a 50-km northward extension of the documented breeding range and thus warrants further investigation. A significant number of species and subspecies of concern were confirmed as breeding or suspected breeding during our surveys. The shorebirds were placed on these lists due to unknown population trends (dunlin, western sandpiper), restricted breeding distributions (marbled godwit, black turnstone Arenaria melanecephala, short-billed dow-
itcher), and conservation concerns elsewhere in their annual range (Pacific golden-plover, rock sandpiper; Stenhouse and Senner 2005; ASG 2008).

Habitat associations of species detected on the inventory fit patterns previously described for these species in Alaska (BPIF 1999, In review; ASG 2008, In review). Habitat associations of species were also consistent between lowland and upland areas on the peninsula (see figure 7 in Ruthrauff et al. 2007 and appendix 7 in Ruthrauff and Tibbits 2009; Amundson et al. 2018). For the 17 species that overlapped among the lowland and upland inventories (i.e., 10 species shared among our inventory, Aniakchak, and Katmai–Lake Clark; 7 additional species between our inventory and Katmai–Lake Clark), most were positively associated with the same habitats across studies. There were a few exceptions, however—willow ptarmigan were found most frequently in dwarf shrub-ericaceous cover type in the lowland inventory and herbaceous and low shrub cover types in the upland inventories. Mew gulls were mostly associated with herbaceous-wet cover types in the lowland inventory, but with low shrub and dwarf shrub cover types in the upland inventories. Habitat associations of marbled godwits on survey points mirrored that found by Mehall-Niswander (1997) in an intensive study of the species’ behavior at Godwit Lake (57.33°N, 157.33°W) in the northern portion of their breeding range. In that study, breeding marbled godwits used herbaceous

**Figure 4.** Percent cover of vegetation types on all points ($n = 792$) and on points in the wet ($\geq 25\%$ cover of wetlands; $n = 482$) and dry ($<25\%$ of wetlands; $n = 310$) sampling strata during the inventory of lowland-breeding birds on the Alaska Peninsula, 2004–2007. Box plots show median (horizontal vertical line), mean (dotted horizontal line), quartiles (open box), and 10th and 90th percentiles of values (whiskers).
Table 4. Mean (SD) percent cover of vegetation types within a 50- or 150-m-radius circle of all points surveyed within the study area and points where each avian species was detected during the inventory of lowland-breeding birds on the Alaska Peninsula, 2004–2007. Number of points at which we detected each species is shown in parentheses.

| Species area (n) | Study area (792) | Pacific golden-plover Pluvialis fulva (20) | Semipalmated plover Charadrius semipalmatus (11) | Greater yellowlegs Tringa melanoleuca (35) | Marbled godwit Limosa fedoa beringiae (48) | Western sandpiper Calidris mauri (11) | Least sandpiper Calidris minutilla (332) | Rock sandpiper Calidris ptilocnemis (13) | Dunlin Calidris alpina (417) | Short-billed dowitcher Limnodromus griseus (220) | Wilson’s snipe Gallinago delicata (503) | Red-necked phalarope Phalaropus lobatus (93) | Mew gull Larus canus (109) | Glaucous-winged gull Larus glaucescens (36) | Arctic tern Sterna paradisaea (19) | Parasitic jaeger Stercorarius parasiticus (23) | Tree swallow Tachycineta bicolor (14) | Hermit thrush Catharus guttatus (32) | American pipit Anthus rubescens (12) | Common redpoll Carduelis flammea (44) | Lapland longspur Calcarius lapponicus (162) | American tree sparrow Spizella arborea (90) | Savannah sparrow Passerculus sandwichensis (189) | Fox sparrow Passerella iliaca (13) | White-crowned sparrow Zonotrichia leucophrys (30) | Golden-crowned sparrow Zonotrichia atricapilla (35) | Orange-crowned warbler Vermivora celata (26) | Wilson’s warbler Wilsonia pusilla (56) |
|-----------------|-----------------|---------------------------------------------|-----------------------------------------------|---------------------------------------------|---------------------------------------------|---------------------------------------------|---------------------------------------------|---------------------------------------------|---------------------------------------------|---------------------------------------------|---------------------------------------------|---------------------------------------------|---------------------------------------------|---------------------------------------------|---------------------------------------------|---------------------------------------------|---------------------------------------------|---------------------------------------------|---------------------------------------------|---------------------------------------------|---------------------------------------------|---------------------------------------------|---------------------------------------------|---------------------------------------------|
| Water           | 3.6 (8.5)       | 0.8 (2.4)                                  | 3.5 (9.9)                                   | 5.6 (9.9)                                  | 3.2 (6.2)                                  | 4.0 (9.9)                                  | 5.6 (9.9)                                   | 3.5 (9.9)                                  | 5.6 (9.9)                                  | 3.2 (6.2)                                  | 4.0 (9.9)                                  | 5.6 (9.9)                                  | 3.2 (6.2)                                  | 4.0 (9.9)                                  | 3.5 (9.9)                                   | 3.2 (6.2)                                  | 4.0 (9.9)                                  | 5.6 (9.9)                                  | 3.5 (9.9)                                   | 3.2 (6.2)                                  | 4.0 (9.9)                                  |
| Bare ground     | 0.6 (5.8)       | 5.8 (13.3)                                 | 5.0 (10.7)                                  | 5.3 (10.6)                                 | 5.0 (11.7)                                 | 5.5 (11.7)                                 | 5.3 (10.6)                                  | 5.0 (10.7)                                 | 5.3 (10.6)                                 | 5.0 (11.7)                                 | 5.5 (11.7)                                 | 5.3 (10.6)                                 | 5.0 (11.7)                                 | 5.3 (10.6)                                  | 5.0 (11.7)                                 | 5.3 (10.6)                                 | 5.0 (11.7)                                 | 5.3 (10.6)                                  | 5.0 (11.7)                                 | 5.3 (10.6)                                  |
| Herbaceous-wet  | 14.0 (28.3)     | 18.3 (30.1)                                | 26.4 (42.0)                                | 21.7 (37.5)                                | 27.4 (43.2)                                | 4.5 (15.1)                                  | 18.3 (30.1)                                | 21.7 (37.5)                                | 27.4 (43.2)                                | 4.5 (15.1)                                  | 18.3 (30.1)                                | 21.7 (37.5)                                | 27.4 (43.2)                                | 4.5 (15.1)                                  | 18.3 (30.1)                                | 21.7 (37.5)                                | 27.4 (43.2)                                | 4.5 (15.1)                                  | 18.3 (30.1)                                | 21.7 (37.5)                                |
| Herbaceous-dry  | 15.7 (28.3)     | 11.3 (29.0)                                | 12.7 (26.0)                                | 13.4 (29.2)                                | 12.9 (27.5)                                | 15.0 (20.5)                                 | 18.3 (30.1)                                | 13.4 (29.2)                                | 12.9 (27.5)                                | 15.0 (20.5)                                 | 18.3 (30.1)                                | 13.4 (29.2)                                | 12.9 (27.5)                                | 15.0 (20.5)                                 | 18.3 (30.1)                                | 13.4 (29.2)                                | 12.9 (27.5)                                | 15.0 (20.5)                                 | 18.3 (30.1)                                | 13.4 (29.2)                                |
| Dwarf shrub-willow | 3.9 (16.3)    | 0 (0)                                      | 5.0 (16.6)                                 | 3.0 (13.5)                                 | 11.3 (27.0)                                | 0 (0)                                      | 0 (0)                                      | 3.0 (13.5)                                 | 11.3 (27.0)                                | 0 (0)                                      | 0 (0)                                      | 0 (0)                                      | 3.0 (13.5)                                 | 11.3 (27.0)                                | 0 (0)                                      | 0 (0)                                      | 3.0 (13.5)                                 | 11.3 (27.0)                                | 0 (0)                                      |
| Dwarf shrub-ericaceous | 22.9 (34.2) | 41.8 (40.8)                               | 36.4 (41.2)                                | 22.4 (33.7)                                | 5.3 (15.0)                                 | 55.5 (33.4)                                | 4.8 (9.3)                                  | 5.8 (13.3)                                 | 2.5 (12.5)                                 | 15.8 (29.6)                                 | 19.7 (29.9)                                | 7.0 (18.0)                                 | 13.6 (24.0)                                | 12.5 (21.5)                                | 5.6 (9.9)                                  | 3.2 (6.2)                                  | 4.0 (9.9)                                  | 5.6 (9.9)                                  | 3.2 (6.2)                                  |
| Low shrub       | 22.7 (31.7)     | 24.1 (32.7)                                | 7.7 (15.4)                                 | 17.9 (27.9)                                | 24.4 (35.8)                                | 18.2 (21.5)                                | 5.3 (15.0)                                 | 18.6 (28.6)                                | 18.5 (27.7)                                | 14.8 (21.4)                                 | 10.1 (27.1)                                | 3.4 (11.6)                                 | 18.5 (27.7)                                | 14.8 (21.4)                                | 10.1 (27.1)                                | 3.4 (11.6)                                  | 18.5 (27.7)                                | 14.8 (21.4)                                | 10.1 (27.1)                                |
| Tall shrub      | 10.6 (24.0)     | 1.5 (4.6)                                  | 1.4 (4.5)                                  | 11.3 (20.6)                                | 5.1 (11.7)                                 | 0 (0)                                      | 5.6 (9.9)                                  | 3.2 (6.2)                                  | 4.0 (9.9)                                  | 5.6 (9.9)                                  | 3.2 (6.2)                                  | 4.0 (9.9)                                  | 5.6 (9.9)                                  | 3.2 (6.2)                                  | 4.0 (9.9)                                  | 5.6 (9.9)                                  | 3.2 (6.2)                                  | 4.0 (9.9)                                  | 5.6 (9.9)                                  | 3.2 (6.2)                                  | 4.0 (9.9)                                  |

Mean (SD) percent cover of vegetation types within a 50- or 150-m-radius circle of all points surveyed within the study area and points where each avian species was detected during the inventory of lowland-breeding birds on the Alaska Peninsula, 2004–2007. Number of points at which we detected each species is shown in parentheses.
habitats 60% of the time and open low shrub habitat 40% of the time during 107 h of focal observations.

Overall abundances of birds on lowland point counts were relatively high (8.14 ± 0.18 SE to 8.74 ± 0.13 SE birds/point, in plots within the wet and dry strata, respectively) when compared with similar surveys of breeding birds in montane areas north of our survey area (6.64 ± 0.17 SE birds/point at Lake Clark and Katmai National Parks and Preserves; Ruthrauff et al. 2007), and in the Arctic (5.63 ± 0.13 SE birds/point in the Arctic Network of National Parks; Tibbitts et al. 2005). In contrast, abundances were similar or slightly lower than those found in adjacent montane areas on the central peninsula (9.38 ± 0.56 SE birds/point at Aniakchak National Monument and Preserve; Ruthrauff and Tibbitts 2009). Bird abundance is usually greater at lower elevations and latitudes and these detection patterns likely reflect the presence of more diverse vegetation types (Guo et al. 2013). We estimated that our inventory worked well for documenting the broad-scale presence and distribution of almost all lowland-breeding birds on the peninsula; for the five species that we missed (based on our comparison with the USFWS compiled list and *Birds of North America* range maps), most are usually associated with boreal forest, which is a habitat that occurred only on one plot of our survey area. Our methods also appeared suitable for measuring relative abundance and habitat associations of species that were commonly encountered, but were less effective for measuring these same variables for species that occurred in low densities or only in discrete vegetation types (e.g., mergansers on streams, grosbeaks in forests). These latter groups are likely better assessed with techniques that maximize survey effort (e.g., area searches, more points and plots) and focus on habitats of the species of interest. Finally, the differences we noted in species composition between wet and dry strata will require adjustments in future analyses of population density.

By design, we timed the inventory to coincide with the peak in courtship displays and territorial behavior for shorebirds and passerines. The preponderance of males and displaying shorebirds and songbirds in the sample data indicates that surveys were appropriately timed for those groups. Nevertheless, we suspect that some species were underdetected because of mismatch between field work and migration timing. For the species that typically arrive in Alaska in April (e.g., northern pintail, green-winged teal *Anas crecca*) or in June (e.g., spotted sandpiper *Actitis macularius*, alder flycatcher *Empidonax alnorum*) all measures of abundance and distribution are likely biased low. Finally, the short duration of plot visits and nature of conducting a point-count survey (i.e., moving steadily between points) precluded us from thoroughly investigating the breeding status of many species. For example, we did not have time to observe singing birds and track them back to their nests; thus, we discovered most nests and young opportunistically. Based on our knowledge of bird behavior in Alaska, however, along with locations of nest records curated by the Alaska Peninsula and Becharof National Wildlife Refuges, we are confident we correctly assigned breeding status for all species on our inventory list.

We recommend further analyses of these data to generate predicted distributions relative to land cover (after Amundson et al. 2018). We encourage completion of the remaining 16 lowland plots between Port Moller and the southern tip of the peninsula to fill gaps in our knowledge about bird distribution and abundance in this area. Information obtained from the southern plots would also help delineate the southern extent of some species’ breeding ranges, particularly the few that we encountered exclusively in the central lowlands (e.g., black-billed magpie, rock sandpiper). Finally, future monitoring of the Alaska Peninsula lowlands would be informative for species that reach their geographic range limit within the study area (e.g., greater white-fronted goose, black-bellied plover, marbled godwit, yellow warbler, yellow-rumped warbler) and those whose distributions occur at the transition zone between boreal forest and tundra ecoregions located at the northern edge of our study area (e.g., greater scaup, Hudsonian godwit). Monitoring distribution dynamics of species at the edge of their range can provide insights into how species are responding to changing climate and environmental conditions (Geber 2011).

Data that support the findings in this paper are available in Tibbitts et al. (2018) including tables and their associated metadata of spatial information (e.g., plot locations, transect and point locations), presence and absence of species on plots (i.e., the information that was used to create the maps in Figure S1), details of bird observations on point transects (e.g., distance from point, bird behavior), and percent cover of vegetation types at individual points.

**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.

**Table S1.** Summary of past (1847–2004) scientific expeditions and surveys on the Alaska Peninsula by season and subregion that provide information on birds and were conducted prior to the start of the inventory of lowland-breeding birds on the Alaska Peninsula, 2004–2007. Listed are published studies and unpublished reports by the U.S. Fish and Wildlife Service and the National Park Service. Studies in Katmai National Park and Preserve are not included here because they are well-documented elsewhere.

Found at DOI: [https://doi.org/10.3996/082017-JFWM-070.S1](https://doi.org/10.3996/082017-JFWM-070.S1) (19 KB DOCX).

**Table S2.** Characteristics of the 52 sample plots that we surveyed during the inventory of lowland-breeding birds on Alaska Peninsula, 2004–2007. Latitude and longitude of plot centroids are presented in WGS 84 datum and plots are ordered from north to south. Note that plot 1357 was surveyed in 2 different y.
Included are species detected on the 52 sample plots (% plot value from Table 2). Not included are species detected on ≤2 plots with no evidence of breeding; these excluded species are listed in Table 1.

Table S4. Past (1999–2008) and current (2008–2018) conservation status of species recorded during the inventory of lowland-breeding birds on the Alaska Peninsula, 2004–2007, and their percent occurrence on inventory of lowland-breeding birds on the Alaska Peninsula in fall. Anchorage, Alaska: U.S. Fish and Wildlife Service Migratory Bird Management Office. Unpublished Report.

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Reference S3. Dau CP, Mallek EJ. 2009. Aerial survey of Emperor Geese and other waterbirds in Southwestern Alaska, spring 2009. Anchorage, Alaska: U.S. Fish and Wildlife Service Migratory Bird Management Office. Unpublished Report.

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Found at DOI: https://doi.org/10.3996/082019-JFWM-070.S21 (16.7 MB PDF); also available at http://www.arlis.org/docs/vol1/USGS/Papers/S13-Wibbenmeyer_et_al_1982.pdf.

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