



RESEARCH ARTICLE

Breeding habitat associations and predicted distribution of an obligate tundra-breeding bird, Smith's Longspur

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ABSTRACT

Smith's Longspur (*Calcarius pictus*) is a species of conservation concern which breeds in Arctic habitats that are expected to be especially vulnerable to climate change. We used bird presence and habitat data from point-transect surveys conducted at 12 sites across the Brooks Range, Alaska, 2003–2009, to identify breeding areas, describe local habitat associations, and identify suitable habitat using a predictive model of Smith's Longspur distribution. Smith's Longspurs were observed at seven sites, where they were associated with a variety of sedge–shrub habitats composed primarily of mosses, sedges, tussocks, and dwarf shrubs; erect shrubs were common but sparse. Nonmetric multidimensional scaling ordination of ground cover revealed positive associations of Smith's Longspur presence with sedges and mosses and a negative association with high cover of shrubs. To model predicted distribution, we used boosted regression trees to relate landscape variables to occurrence. Our model predicted that Smith's Longspurs may occur in valleys and foothills of the northeastern and southeastern mountains and in upland plateaus of the western mountains, and farther west than currently documented, over a predicted area no larger than 15% of the Brooks Range. With climate change, shrubs are expected to grow larger and denser, while soil moisture and moss cover are predicted to decrease. These changes may reduce Smith's Longspur habitat quality and limit distribution in the Brooks Range to poorly drained lowlands and alpine plateaus where sedge–shrub tundra is likely to persist. Conversely, northward advance of shrubs into sedge tundra may create suitable habitat, thus supporting a northward longspur distribution shift.

Keywords: *Calcarius pictus*, sub-Arctic, predictive distribution model, climate change, Brooks Range, Alaska

Asociaciones del hábitat reproductivo y distribución predicha de *Calcarius pictus*, un ave de reproducción obligada en la tundra

RESUMEN

Calcarius pictus es una especie de interés para la conservación que se reproduce en hábitats del ártico y se espera que sea especialmente vulnerable al cambio climático. Usamos datos del hábitat y de presencia de aves tomados de censos en transectos por puntos conducidos entre 2003 y 2009 en 12 sitios a través de Brooks Range, Alaska, para identificar las áreas reproductivas, describir las asociaciones locales del hábitat e identificar hábitat apropiado usando un modelo predictivo de la distribución de *C. pictus*. Hicimos observaciones de la especie en siete sitios, donde estuvo asociada con una variedad de hábitats de pastos y arbustos compuestos principalmente por musgos, gramíneas y arbustos enanos; los arbustos erectos eran comunes pero dispersos. Una ordenación por escalamiento multidimensional no métrico de la cobertura del terreno reveló una asociación positiva entre la presencia de *C. pictus* y la de gramíneas y musgos, y una asociación negativa con una alta cobertura de arbustos. Para modelar la distribución predicha usamos árboles de regresión mejorada para relacionar las variables del paisaje con la presencia de aves. Nuestro modelo predijo que *C. pictus* puede encontrarse en los valles y piedemontes de las montañas del noreste y sureste, en las mesetas de las montañas del occidente y mucho más hacia el occidente de lo que está documentado actualmente, en un área predicha no mayor al 15% de Brooks Range. Con el cambio climático se espera que los arbustos se hagan más grandes y densos, y que la humedad del suelo y la cobertura de musgos disminuyan. Estos cambios podrían reducir la calidad del hábitat de *C. pictus* y limitar su distribución en Brooks Range a tierras bajas pobremente drenadas y a mesetas alpinas donde es probable que persista la tundra de gramíneas. Por el contrario, el avance hacia el norte de los arbustos dentro de la tundra de gramíneas podría crear hábitat apropiado y promovería un cambio en la distribución hacia el norte.

Palabras clave: Alaska, Brooks Range, *Calcarius pictus*, cambio climático, modelo predictivo de distribución, subártico

INTRODUCTION

Climatically driven changes in vegetation are projected to alter avian habitats and distributions worldwide (Crick 2004). Arctic birds are particularly vulnerable because ecosystem and habitat changes are expected to be accelerated and dramatic at northern latitudes (Arctic Climate Impact Assessment 2004, North American Bird Conservation Initiative 2010). For example, in the Fennoscandian mountain range of northern Europe, 64% of common bird species associated with montane tundra and subalpine forests have declined in numbers between 2002 and 2012, concomitant with increased summer temperatures and precipitation that have likely changed vegetative features (Lehikoinen et al. 2013). The potential effects of climate change may be especially important for species that are already of conservation concern (North American Bird Conservation Initiative 2010). Unfortunately, for many Arctic-breeding bird species, distribution and details of habitat preference are still not well known, making it difficult to link climate change to resultant habitat change to bird distribution (Boreal Partners in Flight 1999).

Smith's Longspur (*Calcarius pictus*) is a species of conservation concern that breeds in Arctic and sub-Arctic regions of western and central North America. In spring, Smith's Longspurs migrate from the southern Great Plains to breed along the northern edge of the tundra–forest transition zone from the southern shores of Hudson Bay in Ontario, Canada, to the central Brooks Range in northern Alaska, United States. Small, isolated breeding populations have also been documented above the tree line in alpine tundra meadows in south-central and southeast Alaska, and northern British Columbia, Canada (Briskie 2009).

Due to its remote breeding areas, current understanding of Smith's Longspur distribution, habitat associations, and population status is limited to anecdotal accounts and local studies at a few accessible locations. Previous studies of Smith's Longspurs on their breeding grounds focused primarily on their behavior and reproductive physiology (Meddle et al. 2003, Briskie 2009). Studies addressing habitat are primarily from central Canada (Jehl 1968); there are few accounts documenting occurrence and habitat associations in western Canada and Alaska. In Alaska, Smith's Longspurs have been documented breeding at the northern edge of the forest–tundra transition zone in moist, hummocky tundra and wet sedge habitats in the valleys and foothills of the Brooks Range, and in high-elevation valleys in the Wrangell–St. Elias Mountains (Hines 1963, Sage 1976, Kessel and Gibson 1978, Gotthardt and Jansen 2004). Current broad-scale monitoring programs in northern Alaska, such as the Breeding Bird Survey or Alaska Landbird Monitoring Survey (ALMS), insufficiently assess Smith's Longspur populations (Boreal Partners in Flight 1999, Rich et al. 2004).

The majority of the Alaskan population of Smith's Longspurs is thought to breed in the Brooks Range, most of which is managed by federal agencies that are tasked with protecting migratory birds and species of conservation concern. However, without information on distribution, even basic monitoring programs cannot be effectively implemented (Thogmartin and Knutson 2007). In order to provide land managers with information on explanatory environmental variables of Smith's Longspur distribution, we analyzed habitat associations at two scales across the Brooks Range. At a local scale, we described breeding habitat and vegetative groundcover associated with Smith's Longspur presence. On a broad landscape scale, we surveyed sites across the Brooks Range to document Smith's Longspur presence, and used occurrence data with landscape variables to predict where other suitable breeding areas might be found across the ecoregion. The predictive model and analysis of habitat associations can be used to: (1) identify areas of potentially suitable habitat across the Brooks Range, (2) refine future survey efforts for Smith's Longspurs, and (3) generate hypotheses about future conservation challenges, including predicted changes in the tundra–forest transition zone interface due to a changing climate (Virkkala et al. 2013).

METHODS

Study Area

The Brooks Range ecoregion (15.6 million ha; Nowacki et al. 2001) encompasses the northernmost mountain range in North America and is almost entirely above the Arctic Circle (Figure 1). It extends 1,200 km from the Yukon Territory, Canada, westward through Alaska to within 100 km of the Chukchi Sea. The rugged, barren mountains of the Brooks Range (elevations 500–2,600 m) separate interior boreal forests in the south from treeless Arctic tundra to the north. The area is remote and mostly undeveloped, with only a few scattered communities and one road (Dalton Highway). In addition, the region includes nearly 8.5 million ha of designated Wilderness managed by the U.S. Fish and Wildlife Service and National Park Service, thereby limiting travel to and within sites. We accessed remote study sites using fixed-wing aircraft, and traveled between routes using inflatable canoes and on foot; only one site was accessible from the Dalton Highway.

Field Data

We surveyed 12 sites across the Brooks Range for Smith's Longspurs during 2 main efforts (hereafter referred to as Park and focused surveys) in June 2003–June 2009 (Figure 1, Table 1). Our surveys fell within a geographical area between 66.46° and 69.40° N latitudes (258-km extent), and 141.10° and 156.23° W longitudes (639-km extent),

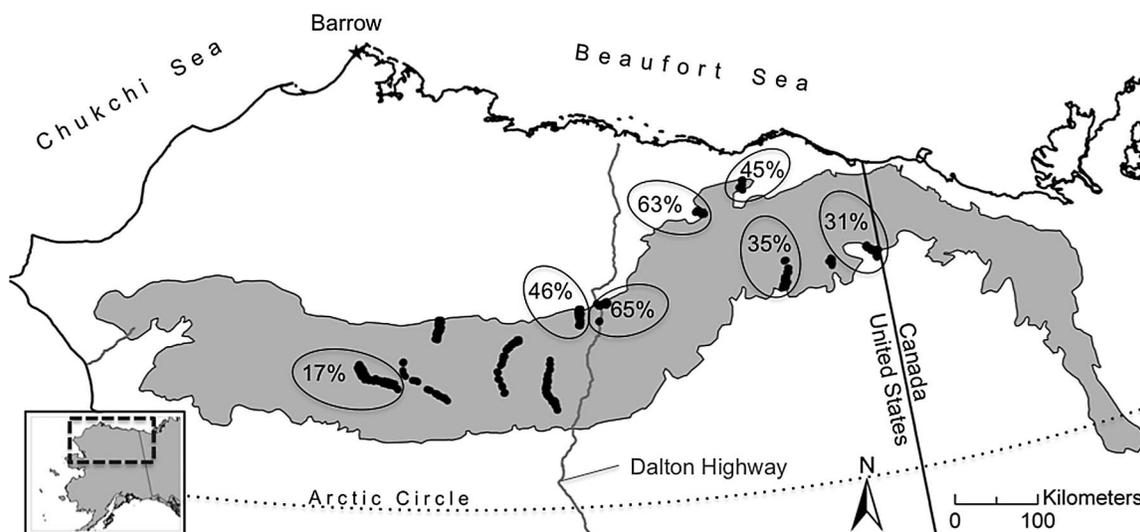


FIGURE 1. The Brooks Range ecoregion (grey area) and points surveyed ($n = 1,124$) for Smith's Longspurs in 2003–2009 at 12 study sites; from west to east: Noatak, Alatna, Killik, John, North Fork Koyukuk, Itkillik, Atigun Gorge, Canning, Sunset Pass, Sheenjek, Coleen, and Firth. Smith's Longspurs were detected in the 7 circled sites at 248 points; numbers represent the percentage of points in each site where longspurs were present.

with coordinates based on the North American Datum 1983. We conducted Park surveys in June 2003–June 2005 within Gates of the Arctic National Park and Preserve as part of a study on the distribution, diversity, abundance, and habitat of all bird species within six major river corridors. From west to east, the six Park study sites included Noatak, Alatna, Killik, John, North Fork Koyukuk, and Itkillik. The primary objective of focused surveys, conducted in 2006–2009, was to locate Smith's Longspurs in areas of historical observations or regions thought to have suitable habitat. Six focused surveys were located east of the Dalton Highway within the Arctic National Wildlife Refuge, and included Atigun Gorge, Canning, Sunset Pass, Sheenjek, Coleen, and Firth. Although survey sites were not randomly selected, our primary goal was to collect presence and absence data in a systematic manner to best

inform our models of predicted distribution (Pineda and Lobo 2009), given the extreme logistical constraints of working in Alaska's Brooks Range.

Although the objectives of the 2 efforts were different, survey design and methods were identical for all 12 sites (Figure 1). Study site boundaries and point arrays were created in ArcMap 9.3 (ESRI 2008). The size and shape of study sites varied due to differences among the valleys sampled and access limitations. Within each site we placed a 500-m grid array from which sampling points were selected; the first point was randomly selected and all subsequent points were sampled sequentially. The number of routes per site was based on the number of available survey days (dependent on logistics of getting to and from each site). As a result, each site had 6–15 survey routes, with each route consisting of 10–12 points (Table 1). With

TABLE 1. Location and descriptions of 12 sites surveyed for Smith's Longspurs in the Brooks Range, Alaska, 2003–2009.

Site	No. routes (points) surveyed	Starting coordinates		Ending coordinates		Elevation range (m)	Habitat
		Latitude	Longitude	Latitude	Longitude		
Noatak	15 (187)	N67.596	W155.231	N67.858	W156.352	487–619	Tundra
Alatna	8 (72)	N67.900	W155.080	N67.890	W155.080	263–879	Tundra & forest
Killik	10 (72)	N68.151	W154.168	N68.360	W153.996	516–631	Tundra
John	14 (119)	N67.550	W152.230	N68.130	W151.750	275–755	Tundra & forest
N. Fork Koyukuk	17 (156)	N67.350	W150.750	N67.860	W150.890	304–575	Forest
Itkillik	9 (104)	N68.250	W149.992	N68.433	W149.909	643–811	Tundra
Atigun Gorge	7 (97)	N68.470	W149.290	N68.480	W149.160	744–1,114	Tundra
Canning	5 (40)	N69.343	W146.096	N69.396	W146.157	330–575	Tundra
Sunset Pass	5 (55)	N69.658	W144.729	N69.581	W144.772	435–730	Tundra
Sheenjek	8 (96)	N68.716	W143.826	N68.434	W143.903	656–800	Tundra & forest
Coleen	3 (37)	N68.621	W142.451	N68.656	W142.450	375–816	Tundra & forest
Firth	6 (89)	N68.661	W141.091	N68.738	W141.336	530–687	Tundra & forest

this design, sampling effort was constant within a study site, but varied among sites. During field surveys, inaccessible points such as those on cliffs or in rivers were dropped and replaced with the next sequential point(s). For focused surveys, we similarly dropped points with >50% forest cover to omit areas where Smith's Longspurs were unlikely to occur based on prior observations. As a result, sampling effort differed between Park and focused surveys because Park surveys included many forested points.

Smith's Longspur presence/absence. We conducted point-transect bird surveys from June 1 to June 27 between 02:30 and 09:00 Alaska Daylight Time under conditions of good visibility, little or no precipitation, and light winds, in accordance with protocols of the Alaska Landbird Monitoring Survey (ALMS; http://alaska.usgs.gov/science/biology/bpif/monitor/alms/ALMSprotocol_2004.pdf). At each survey point we conducted one 10-min count (Buckland et al. 2001), during which we recorded individuals of all bird species detected by sight and sound out to an unlimited distance. We made an effort to track individuals to avoid recording the same individual more than once or at multiple points. Distances to each observation were measured using laser rangefinders.

Points at which we detected the species were classified as "presence" points; all other points were classified as "absence" points. As part of another study (Wild 2014), we analyzed point surveys using distance sampling (Buckland et al. 2001) and time-removal (Farnsworth et al. 2002) methods to determine detectability and thus increase our confidence in "presence" versus "absence." Detection probability within a 10-min interval was high (0.90 ± 0.04 SE) within 100 m of survey points (Matsuoka et al. 2014). Effective distance radius was 112 m (95% CI = 95–132 m).

Local habitat variables. We recorded ground cover characteristics on 100-m radius plots centered on bird survey points. We visually estimated percent cover for different tree species, shrubs, forbs, sedges, mosses, lichens, water, and bare ground within each plot. We also estimated average height for willow (*Salix* spp.) and birch (*Betula* spp.) shrubs that were >20 cm high. Only plants with $\geq 5\%$ ground cover within the plot were recorded. For sedges, we distinguished between tussock and nontussock growth forms; a tussock was defined as a clump of grass or sedge ≥ 15 cm in diameter at the base and ≥ 7 cm in height. The composition of ground cover was recorded at the species or genus level, but forb species present in <5% of plots were grouped into a miscellaneous herb category for analysis (Table 2).

To focus on potentially suitable habitat and account for differences in study design, forested points from Park surveys were not included in our local habitat association analyses; we used 762 plots with $\leq 50\%$ forest cover

(longspurs present, $n = 182$; absent, $n = 580$). In addition, habitat data from one site were not available for analysis, resulting in a smaller dataset than was used for distribution modeling. The count of Smith's Longspurs at each point was used as a continuous variable to examine local habitat associations. Means, standard deviations (SD), and maximum cover for local habitat variables were calculated for points where Smith's Longspurs were present and absent.

Distribution Model Variables

In order to build a distribution model based on landscape-scale characteristics, we used additional variables extracted for each presence and absence point using available spatial data in ArcMap 9.3 (ESRI 2008). We generated seven variables for use in analyses: ecotype, surface geology, distance to coast, distance to river, elevation, slope, and aspect. Ecotype was a categorical variable and included 36 ecosystem classes from Ecosystems of Northern Alaska (http://www.uspermfrosts.org/reports/NoAK_Ecosystems_tabloid_med.pdf). This predictive ecosystem model classified 30-m² raster cells based on vegetation, bedrock geology, topography, and physiognomy (alpine, upland, lowland, riverine, and coastal). Unfortunately, the spatial extent of this ecotype data did not cover the southeastern edge of our study area. Despite the lack of complete coverage, we used ecotype because it provided greater discrimination among tundra and shrub communities than other available vegetation datasets. Surface geology also was a categorical variable, and included classes differentiating major geologic deposits (alluvial, fluvial, moraine, and drift) and their sources (coastal, glacial, and mountain). These data were derived from a digital version of the U.S. Geological Survey (USGS) surface geology map of Alaska (Karlstrom et al. 1964) at a scale of 1:1,584,000. Topographical variables were continuous, and included elevation, slope, aspect, distance to river, and distance to coastline. Elevation, slope, and aspect were derived from the 60-m² raster USGS National Elevation Dataset (National Park Service 1999). We used the ESRI Digital Chart of the World (ESRI 1993) at 1:1,000,000 scale to calculate distances to ocean coasts and rivers. The Arctic Ocean has a cooling effect on inland temperatures, particularly when sea-ice is present (Bhatt et al. 2010); distance to coastline was included to reflect the important effect of colder temperatures on habitat characteristics and bird distribution.

Analyses

Local habitat associations. We used nonmetric multidimensional scaling ordination (Kruskal 1964) to visually depict similarities and differences between ground cover at presence and absence points; points are arranged within the multidimensional space to fit dissimilarity distance values. This ordination is well suited for exploring habitat

TABLE 2. Mean \pm SD cover, maximum cover (in parentheses), and frequency of occurrence (%) values for local habitat ground cover components within a 100 m radius of nonforested points surveyed for birds in the Brooks Range, Alaska, June 2003–June 2009. Results were grouped by Smith's Longspur occurrence (present, $n = 182$ points; absent, $n = 580$ points). Frequency of occurrence is the percentage of presence or absence points where the ground cover type was found.

Cover type	Mean cover (maximum cover)		Frequency	
	Present	Absent	Present	Absent
Trees			10	20
Deciduous trees ^a	<0.1 \pm 0 (<0.1)	0 \pm 2 (23)	1	6
Black spruce (<i>Picea mariana</i>)	Not present	0 \pm 1 (16)	0	4
White spruce (<i>P. glauca</i>)	<0.1 \pm 0 (0.1)	0 \pm 2 (14)	9	14
Shrubs			92	97
Willow (<i>Salix</i> spp.)	13 \pm 13 (59)	20 \pm 21 (90)	83	90
Birch (<i>Betula</i> spp.)	7 \pm 10 (48)	15 \pm 17 (95)	54	72
Alder (<i>Alnus</i> spp.)	0 \pm 1 (14)	2 \pm 7 (80)	2	12
Labrador tea (<i>Rhododendron</i> spp.)	1 \pm 4 (20)	2 \pm 5 (56)	18	33
Blueberry (<i>Vaccinium uliginosum</i>)	3 \pm 5 (31)	4 \pm 7 (48)	37	49
Buffaloberry (<i>Shepherdia canadensis</i>)	Not present	0 \pm 1 (17)	0	3
Dwarf shrubs			94	81
Lapland rosebay (<i>Rhododendron lapponicum</i>)	2 \pm 5 (35)	1 \pm 4 (60)	34	20
Lingonberry (<i>Vaccinium vitis-idaea</i>)	2 \pm 5 (48)	3 \pm 8 (68)	19	26
Crowberry (<i>Empetrum nigrum</i>)	1 \pm 4 (38)	1 \pm 3 (25)	14	16
<i>Dryas</i> spp.	12 \pm 17 (80)	7 \pm 12 (80)	75	52
Dwarf willow (<i>Salix</i> spp.)	9 \pm 9 (45)	4 \pm 8 (60)	73	40
Bearberry (<i>Arctostaphylos</i> spp.)	1 \pm 3 (18)	2 \pm 4 (44)	15	25
Heather (<i>Cassiope</i> spp.)	2 \pm 5 (40)	1 \pm 3 (39)	23	12
Forbs			46	33
Miscellaneous herbs ^b	2 \pm 4 (35)	1 \pm 3 (32)	28	12
Horsetail (<i>Equisetum</i> spp.)	3 \pm 8 (55)	2 \pm 7 (70)	31	24
Sedges			93	66
Tussock	13 \pm 18 (80)	17 \pm 25 (100)	62	53
Nontussock	23 \pm 22 (100)	8 \pm 18 (99)	81	29
Other				
Mosses	67 \pm 30 (100)	38 \pm 32 (100)	97	90
Lichens	9 \pm 12 (67)	5 \pm 10 (62)	69	51
Bare ground ^c	2 \pm 7 (60)	1 \pm 6 (70)	20	10
Water ^d	6 \pm 17 (96)	5 \pm 13 (90)	27	28

^a Paper birch (*Betula neoalaskana*), balsam poplar (*Populus balsamifera*), and quaking aspen (*P. tremuloides*).

^b *Andromeda polifolia*, bear flower (*Boykinia richardsonii*), fireweed (*Chamerion angustifolium*), dwarf fireweed (*C. latifolium*), lousewort (*Pedicularis* spp.), and wintergreen (*Pyrola* spp.).

^c Sand, gravel, mud, soil, and talus.

^d River, creek, lake, and pond.

relationships because it assumes no underlying distribution of the data and allows for correlated variables commonly found in community data (McCune and Grace 2002). It is a useful tool for assessing bird–habitat relationships (Lent and Capen 1995, Reinkensmeyer et al. 2007, Jobin and Falardeau 2010), in part because the user can rotate and center the ordination to any configuration; in our case we centered on the strongest gradient of Smith's Longspur occurrence.

To build the ordination, we used PC-ORD (version 5.0; McCune and Mefford 1999), with a random starting configuration in the autopilot mode, to test ordinations with up to four axes. We selected Sørensen distance, most often used with community data, to calculate dissimilarity values (McCune and Grace 2002). The remaining mismatch between ranked distance order and distance

between points in the ordination space is reported as stress, and reflects the poor fit of the ordination. Stress values >30 indicate that the ordination is no different from random and should not be interpreted (McCune and Grace 2002); values of 10–20 are typical for ecological data and are considered acceptable. We ran 50 Monte Carlo simulations to determine the probability that our final stress value could have been achieved by chance (McCune and Grace 2002). The coefficient of determination, R^2 , was calculated for each axis to reflect the variability that the axis explained. Pearson's correlation coefficients (r) were used to characterize the relationships among ordination axes and Smith's Longspur occurrence, ground cover components, and landscape variables. We present unsquared r -values to reflect strength as well as direction (+ or –) of correlations with each axis, and use

vector arrows to visually depict strength and direction of the strongest correlations within the multidimensional ordination.

The ordination calculated dissimilarity distance values for each of the survey points based on percent cover values of local habitat variables, and arranged the points within a predetermined number of dimensions to fit with the ranked dissimilarity. The optimum solution was sought through an iterative process to maximize fit while maintaining the interpretability of the data by obtaining the fewest dimensions. After the ordination was made, we overlaid Smith's Longspur occurrence information (presence/absence and count) and the five continuous topographic variables (elevation, slope, aspect, distance to coast, and distance to river) to aid interpretation of the ordination and to identify the strongest associations between occurrence and habitat characteristics.

Distribution modeling. We used survey results and landscape data to develop an exploratory species distribution model to predict occurrence and suitable habitat using gradient-boosted regression trees (BRT), a sophisticated form of classification and regression tree analysis. Classification and regression trees are considered powerful techniques for exploring and describing ecological data because they can model complex relationships using both continuous and categorical variables without sensitivity to outliers, data transformations, or missing predictor values (De'ath and Fabricius 2000). Instead of building one large tree, BRT applies boosting to build and combine hundreds of small trees in an ensemble model (De'Ath 2007, Elith et al. 2008), thereby improving performance through model averaging (Schapire and Singer 1999). BRT is a machine-learning algorithm that recursively creates hundreds of simple trees in a forward, stepwise process; each additional tree is built to model the remaining residuals while existing trees are left unchanged. With BRT, overfitting is controlled through optimizing the number of trees, the learning rate, and tree complexity. BRT has been used to model ecological relationships (Leathwick et al. 2006, Tanneberger et al. 2010), and is a top performer among techniques for predicting species distributions (Elith et al. 2006, Heikkinen et al. 2012). We used BRT to predict Smith's Longspur occurrence for the Alaska portion of the Brooks Range ecoregion, expanded by a 10-km buffer (15.5 million ha). Within the ecoregion, we assumed that sites would have similar biological communities, climate, and geographical characteristics, and therefore that distribution could be predicted using occurrence and landscape associations from select study sites.

Because our study sites were primarily in river valleys, many common and prevalent landscapes were not surveyed, such as mountain peaks and ridges, talus hillsides, and high glacial basins and passes. Prediction beyond the valleys that we studied was an extrapolation

beyond the inference space of our sampling design, because study sites were selected nonrandomly to survey large river valleys (Park surveys) and to increase our chances of finding Smith's Longspurs (focused surveys). To reduce the effect of the sampling bias introduced into our distribution model and to sample other habitats within the region, we randomly created an additional 1,000 background points within the ecoregion prediction area using Hawth's Tools in ArcMap 9.3 (Beyer 2008). Background points were treated as absence points and were similar to the pseudoabsence points that are commonly used in predictive species distribution models (Elith and Leathwick 2009).

Prior to building the species distribution model, we randomly withheld 30% of the presence points and 30% of the absence points to use as an evaluation dataset. To build the model, we used the remaining Smith's Longspur survey data, the background points, and the seven landscape variables. To account for unequal sample sizes of presence ($n = 173$) and absence points ($n = 641$ survey + 1,000 background), we balanced the weights of these occurrence classes for BRT analysis (Barbet-Massin et al. 2009). We used a maximum of six nodes per tree to allow for interactions among variables. To achieve good model fit without overfitting, the final number of trees was determined internally by optimizing lift using 10-fold cross-validation. To interpret the BRT results, landscape variables important to the model were ranked according to their relative contribution to variation in the model, and partial dependence plots were created to view the relationships between individual variables and predicted occurrence: positive scores indicated support for presence, whereas negative scores indicated support for absence (Elith et al. 2008).

We evaluated the species distribution model by its ability to correctly predict presence or absence. To do this, we used the previously withheld evaluation dataset (presence, $n = 75$ points; absence, $n = 275$ points). For each of these points, we applied the predictive model to calculate occurrence scores and compared them to survey results to calculate the area under the curve (AUC). This threshold-independent measure assessed the ability of our predictive model to assign higher occurrence scores to presence points than absence points (Pearce and Ferrier 2000, Fielding and Bell 2002). AUC scores range from 0.0 to 1.0, where a score of 1.0 indicates perfect discrimination, a score of 0.7 indicates acceptable discrimination, and 0.5 indicates discrimination that is no better than random (Manel et al. 2001). We calculated AUC using ROC_AUC software (<http://lec.wzw.tum.de/index.php?id=67&L=1> 2004). We also evaluated our predictive distribution model using classification matrix measures that are threshold dependent. From the classification matrix, we calculated the true presence rate, false presence rate (commission

TABLE 3. Pearson's correlations (r) of variables with the 3 axes of the nonmetric multidimensional scaling (NMS) ordination of local ground cover measured on unforested habitat plots centered on points surveyed for Smith's Longspurs in the Brooks Range, Alaska, in June 2007–June 2009. Only variables with $r \geq |0.20|$ (shown in bold) for at least 1 of the 3 axes are shown.

Variable	Axis 1	Axis 2	Axis 3
Smith's Longspur	0.10	0.21	-0.37
Deciduous trees	-0.14	-0.28	-0.03
White spruce	-0.05	-0.23	0.03
Willow	-0.52	-0.20	0.20
Willow height	-0.40	-0.77	-0.10
Birch	0.22	-0.12	0.46
Birch height	0.19	-0.29	0.13
Blueberry	0.30	-0.05	0.06
Labrador tea	0.38	-0.05	0.20
Alder	0.06	-0.22	0.05
Lingonberry	0.30	-0.05	0.06
Heather	0.10	0.25	-0.22
Bear berry	-0.25	-0.10	0.14
Dwarf willow	-0.03	0.23	-0.19
<i>Dryas</i> spp.	-0.20	0.24	-0.05
Tussock sedge	0.63	-0.01	0.18
Nontussock sedge	0.31	0.34	-0.57
Mosses	0.38	0.09	-0.64
Lichens	0.23	0.28	-0.27
Bare ground	-0.11	0.31	-0.08
Distance to coast	-0.33	-0.35	0.56
Elevation	0.13	0.49	-0.22
Slope	0.12	0.23	0.01

error), true absence rate, false absence rate (omission error), and overall percentage correct (Kohavi and Provost 1998).

To examine Smith's Longspur occurrence across the ecoregion, we produced a predicted distribution map from the BRT distribution model. First, we created a square grid of points and extracted landscape variables for each point in the grid. This grid, called the prediction grid, covered the ecoregion study area with 1 km spacing between points. Second, we applied the BRT model to the prediction grid to calculate an occurrence score based on the landscape variables for each point. Using GIS, we converted the prediction grid into a 1-km² raster to create a predictive map for the occurrence of Smith's Longspurs. Finally, we classified the resulting continuous occurrence prediction scores into predicted presence or absence for the distribution map using two threshold occurrence scores. Occurrence scores at or above the threshold were classified as presence. Threshold values were calculated from the classification matrix values and selected because of their good performance (Schröder and Richter 1999, Jimenez-Valverde and Lobo 2007). To identify a broad area of predicted occurrence and potentially suitable habitat, we used a threshold of 0.20, where the true presence rate equaled the true absence rate, in order to balance extent of

occurrence and area of occupancy (Rondinini et al. 2006). We also used a higher threshold of 0.39, which maximized the sum of the true presence and absence rates, to identify areas with high probability of occurrence or highly suitable habitats (Liu et al. 2005).

RESULTS

Smith's Longspurs were patchily distributed at both the landscape and local scale. We surveyed 1,124 points within 12 sites for occurrence. We detected Smith's Longspurs at 7 sites (Figure 1). Of the 762 points surveyed in nonforested habitats, we detected Smith's Longspurs at 30% ($n = 248$). Frequency of occurrence at survey points within sites where longspurs were detected ranged from 17% to 65% (Figure 1).

Sites at which we detected Smith's Longspurs included 2 river valleys situated within the tundra–forest transition zone (Sheenjek, Firth), and 5 large tundra valleys; 4 were along the northern front of the Brooks Range (Itkillik, Atigun Gorge, Canning, Sunset Pass) and 1 was along an east-flowing river (Noatak) in the westernmost study site (Figure 1). Smith's Longspurs occurred at elevations from 331 m to 1,109 m (645 ± 163 m) across the range of elevations sampled (263–1,114 m). The average slope where they were found was $12^\circ \pm 12^\circ$; 30% of presence plots had a slope $<5^\circ$.

Local Habitat Associations

Within the points that we sampled, habitats were composed of many of the same ground-cover species, but at variable levels of percent cover (Table 2). Smith's Longspurs were most frequently associated with willow shrubs, dwarf willow, *Dryas* spp., nontussock sedges, and mosses. Representing differences in vegetation composition among nonforested plots, the 3 axes of the ordination cumulatively explained 86% of the variation in ground cover (axis 1: $r^2 = 0.27$; axis 2: $r^2 = 0.33$; axis 3: $r^2 = 0.26$; final stress = 14.8; $P < 0.02$). Axis 1 had a negligible correlation with Smith's Longspur presence and separated tussock habitats with birch and ericaceous shrubs from tall willow habitats (Table 3). Axes 2 and 3 had the strongest correlations with Smith's Longspur occurrence and were used to display the ordination (Table 3, Figure 2). Axis 2 separated nontussock sedge and dwarf shrub habitats from tall shrub and woodland habitats; Axis 3 separated nontussock sedge habitats with more moss cover from habitats with greater cover of willow, birch, and Labrador tea. Plots in which Smith's Longspurs occurred were clustered in the middle and lower part of the ordination, reflecting an association with greater cover of mosses and nontussock sedges, and to a lesser degree with cover of lichens, dwarf willow, *Dryas* spp., and heather. Correlation with environmental variables showed that these associated

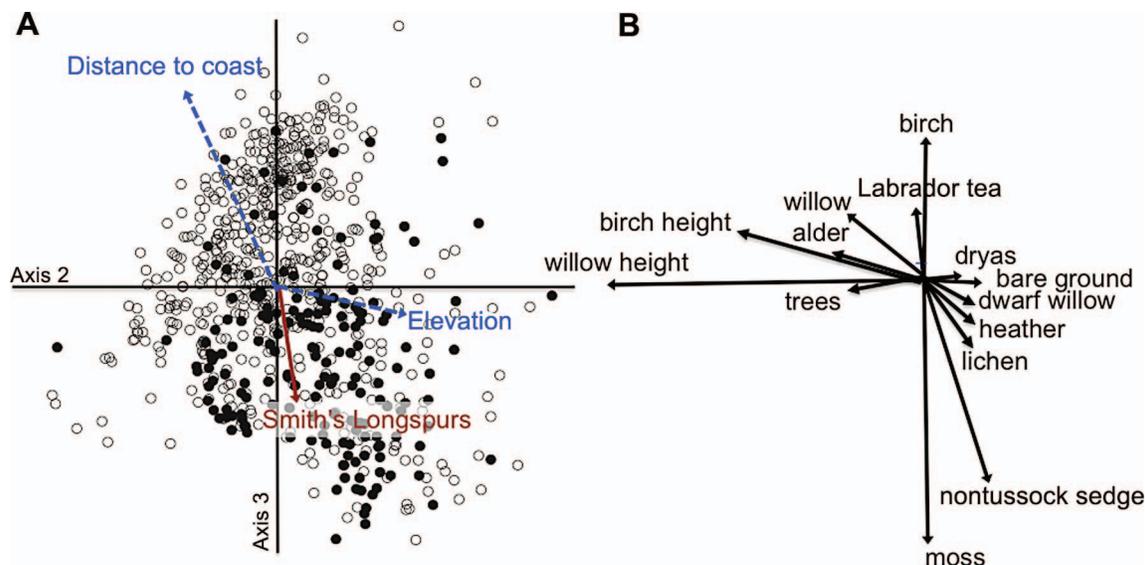


FIGURE 2. (A) Axis 2 vs. axis 3 of the 3-dimensional nonmetric multidimensional scaling (NMS) ordination of ground cover measured at nonforested local habitat plots where Smith's Longspurs were present (●; $n = 182$) and absent (○; $n = 580$) in the Brooks Range, Alaska, USA. Plots were situated in the diagram by NMS according to the similarity of ground cover composition. After the points were arranged in the ordination, we used landscape variables to help interpret patterns within the ordination; vector arrows show the strength and direction of correlations with Smith's Longspur occurrence (red line) and landscape characteristics (blue dashed line). Habitats in which longspurs occurred are clustered in the middle and lower part of the ordination, correlating with higher elevation habitats or those closer to the coast. (B) The corresponding NMS vector diagram shows the strength and direction of correlations of ground cover components (black lines) with longspur presence/absence. Only components with $r \geq |0.2|$ are shown, reflecting a positive association of longspurs with moss and sedge cover, and a negative association with birch, willow, and alder cover.

habitats were found closer to the northern coastline and at higher elevations. Although a few presence points had more shrub cover, there was a general negative association with greater cover of birch, willow, and alder shrubs.

Predicted Distribution

Our distribution model successfully predicted Smith's Longspur occurrence (AUC = 0.86; Figure 3) across the Brooks Range ecoregion (Figure 1). At the 0.20 threshold, the overall correct classification rate was 75%; of the points used to evaluate our predictive map, 56 of the 75 presence points were classified correctly (true presence rate, 75%), as well as 206 of the 275 absence points (true absence rate, 75%). At this lower threshold (0.20), we predicted occurrence in 15% (~2.3 million ha) of the 15.5 million ha study area. Most of these presence predictions had a low probability of occurrence: 47% of the points where presence was predicted had occurrence scores between 0.20 and 0.29 (27% = 0.30–0.39; 15% = 0.40–0.49; 7% = 0.50–0.59; 3% = 0.60–0.69; and only 1% ≥ 0.70). Using a threshold of 0.39 to identify areas with a higher probability of occurrence, we predicted only 4% (641,700 ha) of the Brooks Range ecoregion to have Smith's Longspurs present. At the 0.39 threshold, the overall correct classification rate was 85%; of the points used to evaluate our predictive map, 41 of the 75 presence points were

classified correctly (true presence rate, 55%), as well as 256 of the 275 absence points (true absence rate, 85%). The higher threshold resulted in fewer commission errors ($n = 19$; 7%) and more omission errors ($n = 34$; 45%) than were found using the lower threshold. At the higher threshold (0.39), the majority of presence predictions had occurrence scores close to the threshold: 61% of the points where presence was predicted had occurrence scores between 0.39 and 0.49 (26% = 0.50–0.59; 10% = 0.60–0.69; 3% = 0.70–0.79; and <1% ≥ 0.80).

Our BRT model contained 312 trees and used all 7 landscape variables to model occurrence. BRT scored the relative importance of variables based on their contribution to reducing variance in the model: ecotype (100), distance to coast (93), elevation (73), distance to river (66), surface geology (61), slope (60), and aspect (50). Smith's Longspurs were positively associated with sedge and shrub tundra ecotypes and negatively associated with barrens, water, and forest ecotypes (Figure 4). Only two of the surface geology classes, lightly modified moraine and moderately modified moraine, were positively associated with Smith's Longspur presence. Partial dependence plots for topographical variables depicted an association with points within 250 km of the coast, ~400–1,000 m above sea level, and <1,500 m from rivers, with weaker support for sites <100 m from rivers (Figure 5). North- and east-

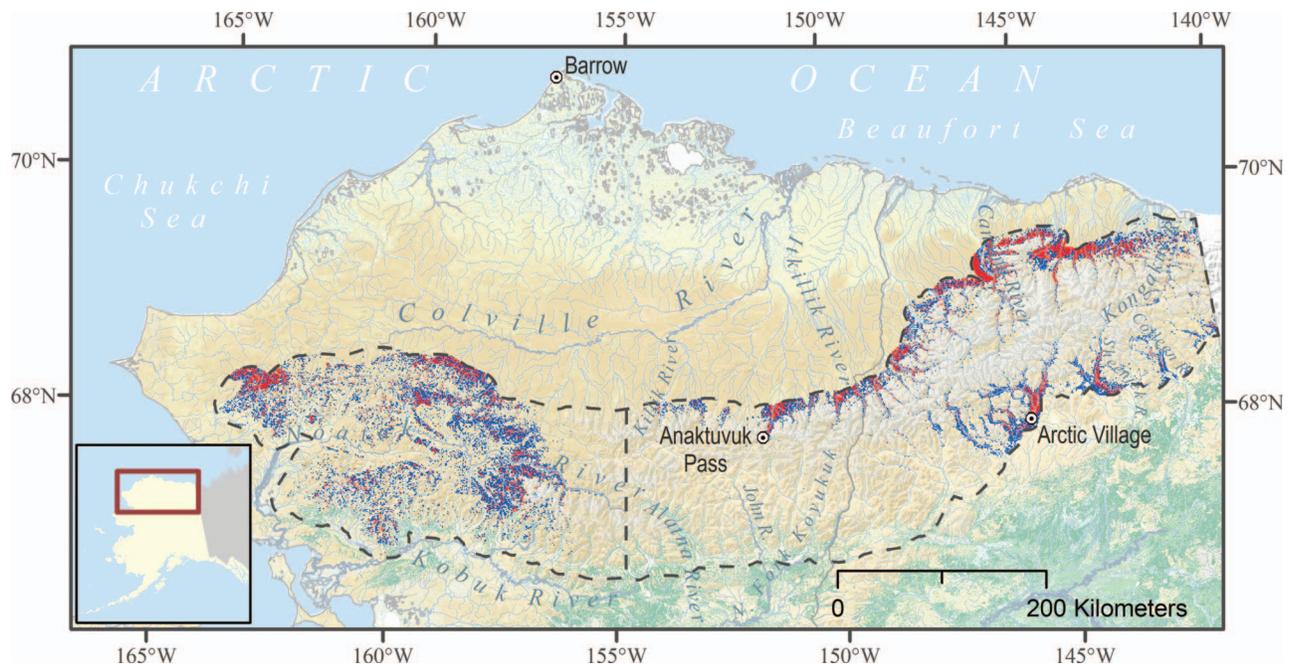


FIGURE 3. Predicted distribution of the Smith's Longspur in the Brooks Range, Alaska (AUC = 0.86; overall correct classification of evaluation data = 75%), identifying associations with uplands in the west and valleys and hillsides in the east. AUC is the area under the curve; this threshold-independent measure assesses the ability of our predictive model to assign higher occurrence scores to presence points than absence points. Within the ecoregion study area (black dashed line), areas of predicted occurrence are shown in blue and red. Blue areas represent potentially suitable habitat, but had low longspur occurrence scores of 0.20–0.39. Red areas also represent suitable habitat and had high occurrence scores (≥ 0.39). The ecoregion was divided to separate the western region, where Smith's Longspur occurrence is less certain.

facing slopes up to 35° were associated with longspur presence, with the strongest association for sites with $<5^\circ$ slope.

With our distribution map (Figure 3), we predicted that Smith's Longspurs would breed in several areas in the Brooks Range. Large areas of predicted presence were located in the eastern Brooks Range, primarily within the river valleys and foothill slopes along the northern front of the mountains from the Kongakut River to the Killik River; along the southern front, Smith's Longspur occurrence was predicted in several large river valleys from the Canadian border to just west of Arctic Village. In the west, presence was predicted primarily in upland areas and broad mountain passes surrounding the large Noatak River valley.

DISCUSSION

As in previous accounts of Smith's Longspurs, we found that their overall occurrence was low across the landscape of the Brooks Range. However, Smith's Longspurs were patchily distributed and locally abundant within various tundra-associated habitats in broad tundra valleys and on low-mountain slopes. The broad valleys along the northeastern edge of the Brooks Range ecoregion (Nowacki et al.

2001) likely support the largest numbers of Smith's Longspurs in the ecoregion; the northeastern edge is where we found the highest densities during our surveys (Wild 2014). In other parts of the ecoregion, few birds were detected during surveys, predicted distribution was patchy, and densities were lower.

Habitat Associations

At both the local and landscape scale, Smith's Longspurs were associated with heterogeneous land cover of sedge and shrub habitats. Correspondence between local habitat characteristics and ecotype on the landscape scale indicated that local-scale studies were useful for informing models of longspur distribution (Thogmartin and Knutson 2007). In general, Smith's Longspurs were associated with ground cover characterized by sedges and mosses with variable amounts of dwarf and low shrub habitat; patches of dense shrubs or trees were sometimes present interspersed within sedge–shrub tundra, but sites with large patches of closed shrub cover appeared to be avoided. Because Smith's Longspurs typically walk on the ground to forage in sedges, mosses, and dwarf shrubs (Irving 1960, Sage 1976, Briskie 2009), we expected to find the species associated with a variety of sedge tundra and dwarf shrub cover. However, their association with willow shrubs was

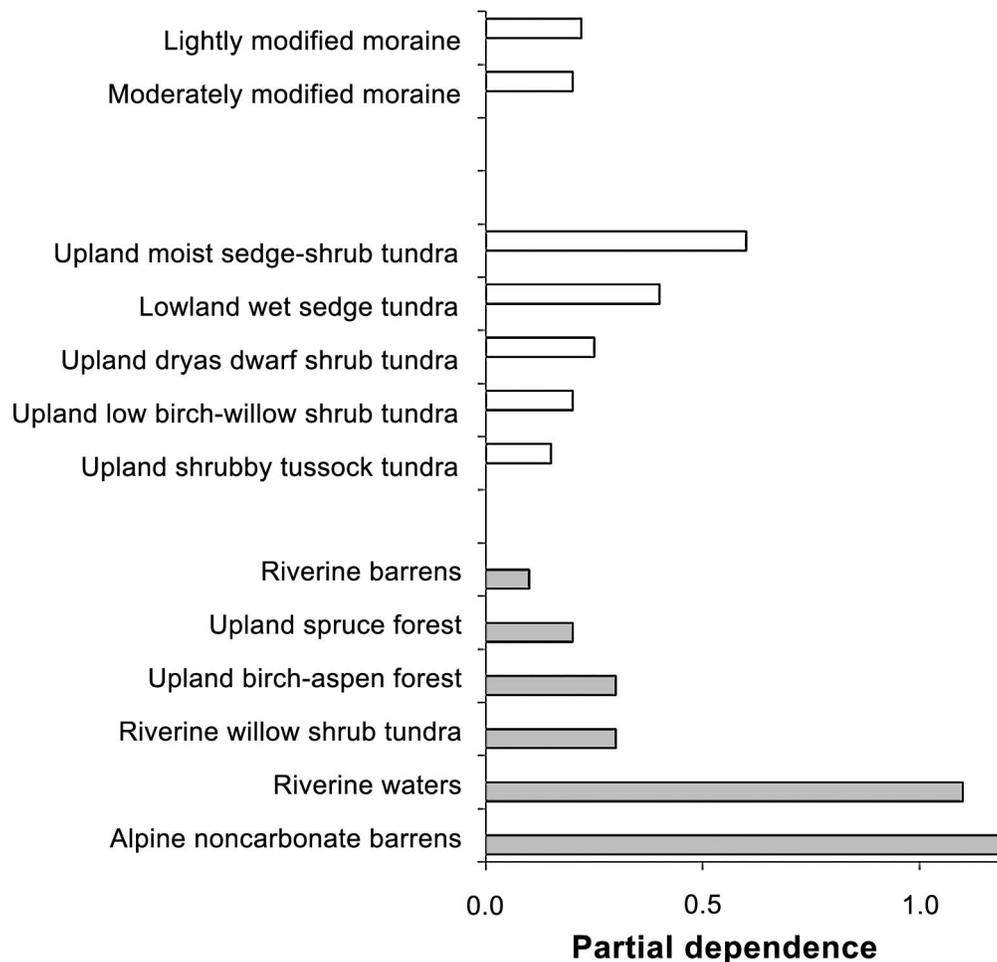


FIGURE 4. Partial dependence scores for surface geology and ecotype classes from a boosted regression tree (BRT) analysis of Smith's Longspur distribution in the Brooks Range, Alaska. White bars show positive partial dependence and indicate the variables associated with Smith's Longspurs. Gray bars show negative partial dependence and reflect a negative association with Smith's Longspurs. The partial dependence was an index of the presence/absence comparison in relative units; it was interpreted as high to low. Categories with partial dependence $< |0.1|$ are not shown.

unexpected and may simply reflect the widespread nature of shrubs in the ecoregion. There is likely some maximum threshold of shrub cover that is used by Smith's Longspurs, which merits further study.

Shrubs provide vertical structure with cover for nests, protection from predators, refuge during inclement weather, and perches for broadcasting songs and observing intruders (Jehl 1968). However, the use of different shrub communities for foraging is not well understood. For example, we found that riparian ecotypes were negatively associated with Smith's Longspur presence, yet birds were occasionally observed making foraging trips into riparian shrub habitats (T. Wild personal observation); proximity to riparian shrub habitats may be important at a larger scale than that measured. Shrub habitats will likely become more widespread and denser in response to climate change (Tape et al. 2006); further investigations into the relation-

ship between shrubs and breeding ecology should explore thresholds of shrub cover use and the suitability of different types of shrub habitats.

At the local scale, habitat at many of the absence points was similar to that at presence points, which may indicate either that suitable habitat was not saturated by Smith's Longspurs or that there were unmeasured factors that limited longspur occurrence. It is possible that the habitat in those absence plots was suitable, but that birds were not detected due to their behavior, observer error, survey timing, or survey conditions. However, we attempted to maximize detectability by adequately training personnel, timing surveys to correspond with peaks in singing, and conducting surveys in good weather. In addition, the open tundra habitats and conspicuousness of singing males led to high detectability within the 100-m sampling radius ($P = 0.9$). It is possible that landscape mosaic is an important

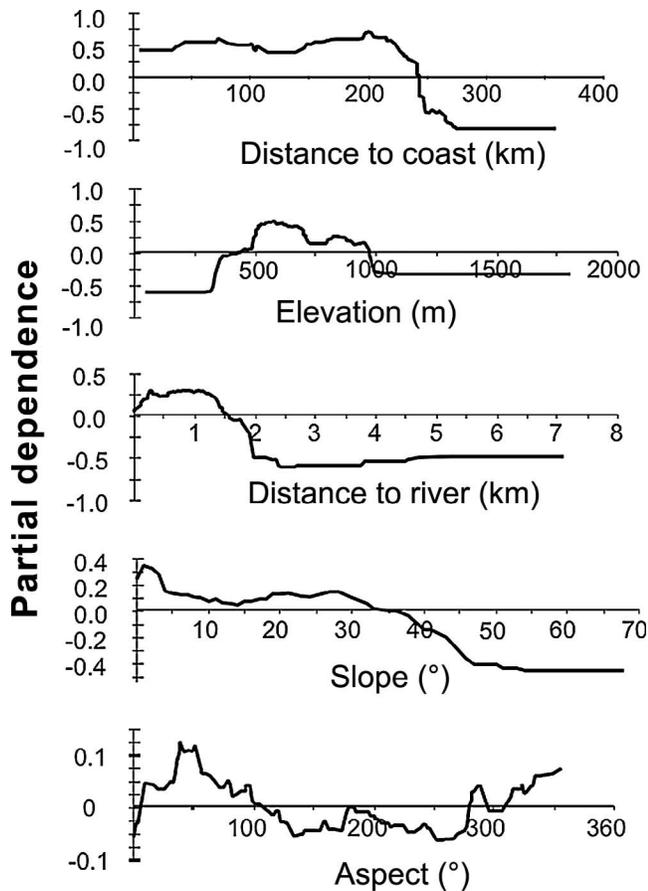


FIGURE 5. Partial dependence plots of topographical variables from a boosted regression tree (BRT) analysis of Smith's Longspur distribution in the Brooks Range, Alaska. The graphs show the individual relationship of topographic variables with the occurrence of Smith's Longspurs: positive values suggest longspurs are associated with those features, and negative values suggest the opposite.

habitat variable that we did not measure. Smith's Longspurs may select breeding areas based on habitat composition beyond the scale of 100-m radius plots; 29% of presence points had birds detected only at 100–200 m, suggesting that the habitat mosaic operates at a scale larger than our plots. Finally, Smith's Longspurs are not territorial, but form neighborhoods of interbreeding males and females within large home ranges (males: 9.4–30.9 ha; females: 5.4–19.5 ha; Briskie 2009). The number of birds in a neighborhood is likely influenced by the landscape composition and area of suitable habitat (Jehl 1968). Because of their polygynandrous breeding system, a mosaic of local habitats may be preferred over more homogenous landscapes on a neighborhood rather than a territory scale. Questions of habitat suitability and saturation remain important for conservation and management, and future research efforts should assess the effects of scale and habitat heterogeneity on the occupancy,

abundance, home range size, and breeding success of Smith's Longspurs.

Predicted Distribution

Based on our model, we predicted that Smith's Longspurs could range across a wide portion of the Brooks Range, but that their distribution would be limited because rugged mountains and other unsuitable habitats such as forests, barren ridges, rivers, and lakes characterize much of the ecoregion. When we used a lower threshold of occurrence to identify a broad area of potentially suitable habitat, the percentage of correct presence predictions was 75%; however, the tradeoff was an increase (from 7% to 25%) in commission error (mistakenly thought to be present) rates. Although missed detections can result in higher commission rates, the high detectability of Smith's Longspurs suggests that this was not the case. We would expect some level of false presence (commission) predictions because of the patchy, "uncommon" occurrence of the species and evidence that some suitable habitats are not occupied at the local scale. Indeed, presence points had generally low probabilities of occurrence. Although increased commission errors in distribution modeling can lead to overestimating a species' distribution (Rondinini et al. 2006, Pineda and Lobo 2009), our intent was to take a broad-scale, regional approach to our prediction model in order to focus future surveys in areas of potentially suitable habitat for Smith's Longspurs. In addition, areas of false presence predictions could stimulate future studies to determine why apparently suitable habitats are not occupied. For instance, social factors such as breeding in neighborhoods and site fidelity may influence patterns of occupancy. Site selection could also be influenced by local, ephemeral environmental conditions, such as snowmelt or flooding early in the breeding season.

Conversely, when we used a higher threshold of occurrence in the model, the area predicted to be suitable was reduced from 2.3 million ha to 641,700 ha. Using the higher threshold excluded areas that were less suitable for Smith's Longspurs, as shown by fewer commission errors; however, this was at the expense of an increase (from 25% to 45%) in omission errors (mistakenly thought to be absent). Although omission errors due to missed detections can lead to underestimating areas of suitable habitat, this estimate was likely closer to the true area of occupancy given our knowledge of local breeding areas and the patchy distribution of Smith's Longspurs; some predicted areas of occurrence coincided with known or probable breeding areas (Gotthardt and Jansen 2004).

Although large forested valleys and rugged mountains in the Brooks Range limit suitable habitat, our model predicted that Smith's Longspurs might occur in many of the valleys and foothills not surveyed during our study. For

example, the model predicted presence in the southeastern valleys, including areas where breeding longspurs have previously been observed (Kessel and Schaller 1960, Spindler et al. 1980). However, due to the gap in coverage of the most important variable, ecotype, our model could not differentiate among habitats in this area; therefore, predicted presence in the forested parts of these valleys is likely false. In the northeastern region, large areas of predicted presence suggest that Smith's Longspurs may also be found farther north than previously thought, in adjacent portions of the Brooks Foothills ecoregion (Nowacki et al. 2001).

In the valleys west of Anaktuvuk Pass, our model predicted presence in only a few small areas along the northern edge of the central Brooks Range. Anaktuvuk Pass was once thought to mark the western extent of the Smith's Longspur breeding range (Sage 1976); reasons for their absence in the valleys farther west are not clear. Our surveys in this region were limited to navigable river valleys, leaving the broad tundra passes and headwater valleys unsurveyed. Suitable habitat may exist in upland areas that were not identified in our model due to the limited extent of our surveys. In addition, the high importance assigned to distance to coastline may be driving down prediction scores due to the shape of the coastline in relation to the Brooks Range. Predicted absence in the tundra valleys and uplands immediately west of Anaktuvuk Pass should be confirmed with more targeted surveys in this area.

Our model identified many areas in the montane uplands of the western Brooks Range, far outside the presumed western boundary of the species' range (Gotthardt and Jansen 2004), as potentially suitable habitat for Smith's Longspurs. To date, most of this area has not been surveyed for breeding landbirds, and the extent of the species' western distribution remains uncertain. Although we had no test data from the region, an inventory of montane-nesting birds in the western and central Brooks Range in 2001–2003 detected Smith's Longspurs in areas where we predicted presence (Tibbitts et al. 2005). Anecdotal reports also suggest that Smith's Longspurs are breeding near the northern edge of the ecoregion near the headwaters of the Utukok and Colville Rivers (P. Reynolds personal communication). Focused surveys in the western Brooks Range are needed to refine our understanding of Smith's Longspur distribution in that region.

Our predicted distribution reflected the bias toward valleys and did not fully represent potentially suitable habitat which may be found in tundra basins and passes at higher elevations with greater distances to rivers. The ability of our model to identify these areas was not reflected in our evaluation measures, because our evaluation data came from the same study sites that were used

to make the predictions and therefore had the same biases. However, with so little known about Smith's Longspur distribution, our intent was to develop a model to understand habitat associations and locate potential breeding areas. Species distribution modeling is an iterative process (Elith and Leathwick 2009); future work should refine our predictive model by incorporating new information on presence and absence and spatial landscape data as they become available.

Climate Change

Dramatic changes associated with climate warming are predicted for northern Alaska, including advance of the tree line, increased shrub abundance and growth, and decreased moss cover and soil moisture (Hinzman et al. 2005, Euskirchen et al. 2009). Climatically driven changes to vegetation communities have already been documented; shrubs are becoming larger and more abundant (Tape et al. 2006, Euskirchen et al. 2009). Shrubs, particularly willow, birch, and alder, are primarily increasing in valleys and on hill slopes, especially south-facing slopes. It is likely that shrubs have already increased in some areas where Smith's Longspurs occur. As conditions in the tundra increasingly favor shrub and tree growth, more open tundra habitats may be lost, which could impact breeding habitat for longspurs and other open-country species. We found that longspurs used tundra habitats that sometimes had patches of willows and birch; however, they were not found in areas with large expanses of dense shrubs. How Smith's Longspurs respond to increasing shrub densities will depend largely on the patterns of shrub growth and the persistence of sedges and mosses in the understory. In fact, increasing shrub growth in sedge–tundra habitats could form the sedge–shrub tundra preferred by Smith's Longspurs. However, a reduction in soil moisture and moss cover may drastically alter preferred habitat. As the climate gets warmer and drier, sedge–shrub tundra will likely persist in poorly drained lowlands and moist alpine basins. Conversely, suitable sedge–shrub tundra may follow the northern advance of the tundra–forest transition zone, and Smith's Longspur distribution could adapt to the shifting distribution of preferred habitat. In recent years, breeding Smith's Longspurs have been documented along the Dalton Highway north of the Brooks Range (Meddle et al. 2003), and as far north as the transition from the foothills to the flat coastal plain (T. Wild personal observation), indicating that northern habitats may be more suitable than previously assumed. In northern Europe, even common bird species associated with tundra habitats are showing indications of population declines, corresponding to increased summer temperatures and precipitation in the region (Lehikoinen et al. 2013). Increased abundances of birds with southerly origins are expected

with increased Arctic willow thickets, because of increased arthropod abundance associated with shrubbiness; however, changes in avian community composition may be at the expense of local generalists (Sokolov et al. 2012, Rich et al. 2013). The extent to which Smith's Longspurs will persist in increasingly shrubby sites or occupy new sites is uncertain and may be confounded by apparent breeding-site fidelity (Jehl 1968, A. Powell personal observation).

This study was the first effort to characterize the breeding habitat and distribution of Smith's Longspurs across a large geographic area. The identified breeding areas and associated habitat characteristics can serve as a guide for developing future studies on habitat requirements and sensitivity of this species to shrub encroachment. Additionally, the predicted distribution models provide a sampling frame for further field validation of the species' distribution across the ecoregion, providing a critical baseline for monitoring and conservation in a changing climate.

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