



# Ecological determinants of avian distribution and abundance at Rankin Inlet, Nunavut in the Canadian Arctic

Kevin A. Hawkshaw<sup>1,2</sup> · Lee Foote<sup>1</sup> · Alastair Franke<sup>2,3,4</sup>

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## Abstract

Large areas of the Arctic remain poorly surveyed, creating biological knowledge gaps as scientists and managers grapple with issues of increasing resource extraction and climate change. We modelled spatiotemporal patterns in abundance for avian species in the low Arctic ecosystem near the community of Rankin Inlet, Nunavut, from 2015 to 2017. We employed six habitat covariates, including terrain ruggedness and freshwater cover, and contrasted the influence of elevation with distance from coast, as well as the normalized difference vegetation index (NDVI; a proxy for vegetative productivity) with the normalized difference water index (NDWI; a proxy for vegetation water content). Our results most clearly show the importance of low elevation, large amounts of freshwater and high vegetative productivity for Arctic birds at relatively local scales (<1 km<sup>2</sup>). Although NDVI more consistently appeared in competitive models of abundance, NDWI was particularly important in predicting abundance for shorebirds, ducks, Tundra Swans (*Cygnus columbianus*) and Lapland Longspurs (*Calcarius lapponicus*), demonstrating that it may be a more influential habitat covariate than NDVI for species that frequent habitats with wet vegetation. We also documented apparent shifts in habitat between early and late summer for geese, which were more strongly associated with freshwater later in the season, likely due to the presence of flightless juveniles and moulting adults at that time. Our study illustrates a relatively easy to implement survey methodology for avian species, provides baseline information for an Arctic study area that had not previously been surveyed intensively, and includes species that are underrepresented in previous literature.

**Keywords** Habitat associations · Arctic · Birds · Density surface modelling · Distance sampling

## Introduction

Although wildlife studies are common in the Arctic, they are spatially clumped, and potentially cannot be generalized (Metcalf et al. 2018). Studies tend to differ in variables measured, methodology, spatiotemporal scale, approach to handling detection error, and in selection of habitat covariates or other drivers of distribution and abundance. Baseline data and knowledge of habitat or climatic factors affecting populations of Arctic avifauna are increasingly important given recent declines of some species (Rosenberg et al. 2019; Smith et al. 2020), increased resource extraction in many areas (Haley et al. 2011) and climate change (Meredith et al. 2019).

Habitat plays an important role in the distribution of Arctic birds, in many cases mediating biotic and abiotic drivers of reproductive success and abundance. Vegetation, for example, provides nesting habitat (Boal and Andersen 2005; Peterson et al. 2014; Boelman et al. 2015), forage for

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✉ Kevin A. Hawkshaw  
hawkshaw@ualberta.ca

<sup>1</sup> Department of Renewable Resources, University of Alberta, GSB 751, Edmonton, Alberta T6G0N4, Canada

<sup>2</sup> Arctic Raptors Project, Box 626, Rankin Inlet, Nunavut, Canada

<sup>3</sup> Nunavut Wildlife Cooperative Research Unit, Rankin Inlet, Nunavut, Canada

<sup>4</sup> Department of Biological Sciences, University of Alberta, CW 405, Edmonton T6G2E9, Alberta, Canada

herbivores (Cadieux et al. 2005), and supports arthropod prey for insectivores (Pérez et al. 2016). Although avian species are thought to migrate to the Arctic in part due to lower nest predation risk (McKinnon et al. 2010), predation nonetheless remains an important driver of reproductive success for many bird species (Bêty et al. 2001; Smith et al. 2007). Topography and the availability of freshwater potentially mediate interactions with predators, and therefore drive habitat associations (Stahl and Loonen 1997; Lecomte et al. 2009; Anderson et al. 2014). Despite the potential value of topography to breeding birds, measures such as terrain ruggedness have only rarely been included in studies of Arctic bird distributions (e.g., Robinson et al. 2014). Coastal areas in the Arctic are often subject to climatic gradients in temperature and wind that impact local ecosystem processes (Rouse 1991), and marine food sources are important to many coastal species (Eberl and Picman 1993). Recent work has highlighted the vulnerability of Arctic habitat components to climate change, for example, drying of tundra ponds (Smol and Douglas 2007) and proliferation of tall vegetation (Bjorkman et al. 2018), which may positively or negatively influence the abundance of Arctic birds in the long term.

Although breeding bird surveys are commonplace in the Arctic, there has been considerable heterogeneity in methodology, and significant gaps in knowledge remain (Smith et al. 2020). An important aspect of effective wildlife surveys is accounting for detectability. Without this, abundance estimates can be biased, and, if detection varies spatially within a study area, abundance estimates can be biased spatially as well (Marques et al. 2007). Distance sampling is a well-known survey technique that accounts for detectability by modelling the relationship between observation distance and probability of detection (Buckland et al. 2015). Several extensions of distance sampling analyses exist for spatiotemporal modelling of survey counts (e.g., Oedekoven et al. 2014; Bachl et al. 2019), but one of the most common is density surface modelling (DSM; Miller et al. 2013), a two-stage approach that first fits a detection function to distance sampling data, and then models survey counts on the basis of spatial or temporal covariates. DSM has been used to model the abundance and distribution of a wide array of organisms, from cetaceans (Roberts et al. 2016) to seabirds (Winiarski et al. 2014) to ungulates (Valente et al. 2016) to benthic invertebrates (Katsanevakis 2007) to land birds (Camp et al. 2020), and has shown to be a flexible and effective alternative in species distribution modelling. Distance sampling has been used previously in studies of Arctic land birds (e.g., Amundson et al. 2014; Robinson et al. 2014); however, to our knowledge, distance sampling in combination with DSM has not.

In this study, we investigated habitat associations of avian species and groups breeding on the west coast of Hudson Bay, near the community of Rankin Inlet, Nunavut. We used

multiple habitat measures from remotely sensed datasets to model avian habitat associations, including terrain ruggedness, elevation, distance to coast, freshwater cover, normalized difference vegetation index (NDVI), and normalized difference water index (NDWI), and accounted for changes in abundance across and within years. NDVI is a widely used index of vegetation greenness that is correlated with vegetative biomass, cover and diversity in Arctic ecosystems (Raynolds et al. 2006; Laidler et al. 2008; Nilsen et al. 2013), and has been used in past investigations of avian habitat associations (Pellissier et al. 2013; Robinson et al. 2014). Arctic study areas are frequently characterized by saturated or intermittently flooded habitats, or those with very small water bodies (e.g., ponds), which exist at scales finer than the resolution of satellite imagery (Muster et al. 2012). Because wet habitats are known to be frequented by Arctic birds (Latour et al. 2005; Slattery and Alisauskas 2007), we also used NDWI in competing DSMs. NDWI is generally correlated with NDVI but is further able to represent variation in vegetation water content (Gao 1996), which can reflect local differences in soil moisture and water table depth (De Alwis et al. 2007; Tagesson et al. 2013).

In general, we predicted that birds would associate with vegetated areas containing large amounts of freshwater, and those occurring at low elevations near the coast due to the availability of forage and nesting habitat, as well as refuges from predation. We also explored interactions between habitat and temporal covariates based on previous literature support and ecological rationale. We predicted that songbird and shorebird species would increase in abundance at low elevations near the coast later in the summer as individuals aggregated into post-breeding flocks and prepared for southward migration (Connors et al. 1979; Hussell and Montgomerie 2002; Wheelwright and Rising 2008). We predicted that warm and dry conditions would lead to stronger associations between geese and freshwater (Robinson et al. 2014), and that geese would be more strongly associated with freshwater later in the summer to reduce predation risk to flightless juveniles and moulting adults. Our study includes species poorly represented in Arctic literature (e.g., Sandhill Cranes *Antigone canadensis*) and species of current conservation concern due to population declines (e.g., shorebirds; Rosenberg et al. 2019; Smith et al. 2020).

## Materials and methods

### Study area

Surveys were conducted in the area surrounding Rankin Inlet, Nunavut, Canada (62.81°N, 92.09°W) from 2015 to 2017. This study area represents approximately 2500 km<sup>2</sup> of coastal tundra and marine habitat typical of the low Arctic,

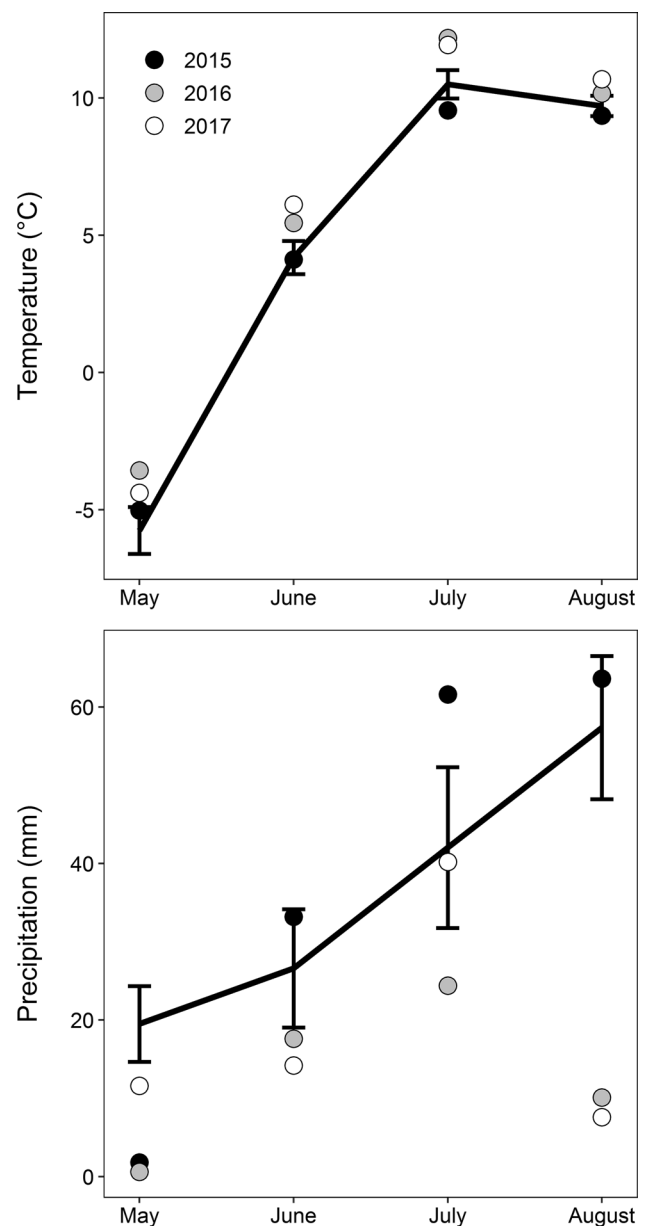
containing a diversity of wet meadows, dwarf shrubs, dry eskers, rocky ridges, tidal flats and sea cliffs. The diversity of avian life observed can be found in Online Resource 1. Readers can refer to Court et al. (1988) for general descriptions of natural history of this study area.

Monthly temperatures in Rankin Inlet, Nunavut for May, June, July and August average  $-5.75$  °C,  $4.19$  °C,  $10.50$  °C and  $9.72$  °C, respectively. On average, monthly precipitation increases as summer progresses in Rankin Inlet, ranging from  $19.50$  mm in May to  $57.35$  mm in August. Among our years of study, 2016 and 2017 were warm and dry, while 2015 represented conditions closer to average, if not relatively cool and wet for the June–August period (Fig. 1). Temperature and precipitation data were collected at the Rankin Inlet Airport (Environment and Climate Change Canada).

### Distance sampling

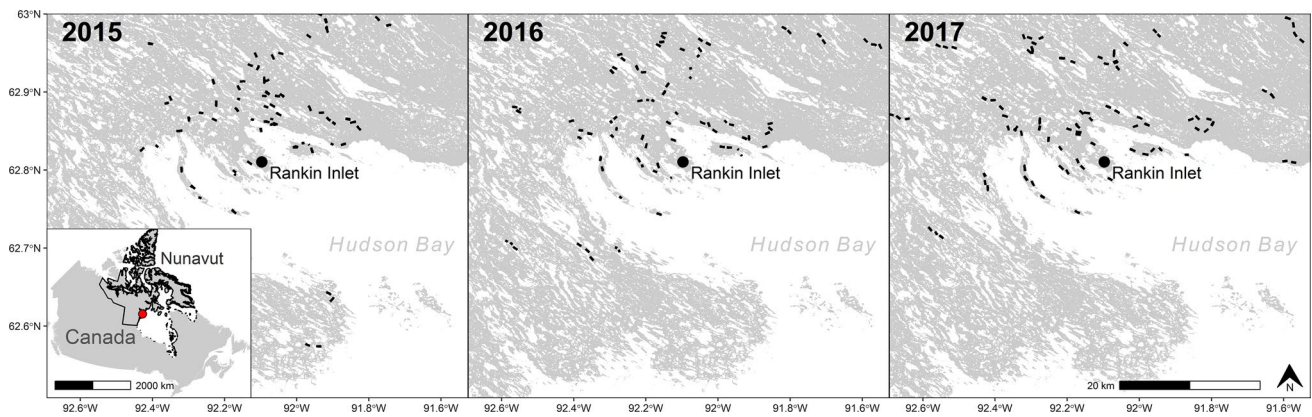
We used distance sampling transects (Buckland et al. 2015), each approximately 1 km in length, to estimate habitat associations of avian species and groups. We generated random start points at the start of each field season and surveyed approximately two transects per day spanning the period from spring melt to the start of outward migration for many avian species. Among years, the sampling period was similar; in 2015, surveys were conducted from June 7 to August 19, in 2016 from May 26 to August 22 and in 2017 from May 29 to August 21. Within each year, sampling was classified into two periods: period one included transects sampled prior to July 11 and period two included those sampled on or after (hereafter termed early and late summer, respectively). This date roughly corresponds to the division between incubation and brood rearing for most avian species in our study area (pers. obs.) and thus was a logical cut-off when investigating how habitat associations and abundance might change within year. All transects were replicated before and after this date, and a small number of transects were sampled three times per season. In total, 498 distinct transect visits were made to 225 transect locations. Time of day of surveys ranged from 9:00 to 20:00. Although we sampled a different collection of transects in each year (Fig. 2), data exploration revealed that the range of habitat covariates sampled was very similar.

Our analysis involved a two-step process: (1) we modelled the probability of detection of each species or group as a function of distance and detection covariates and (2) we modelled spatiotemporal variation in our survey counts while accounting for the probability of detection estimated in step one. The first step involved estimating the relationship between observation distance and probability of detection. We collected bearing and distance data for all observations using a compass and a laser rangefinder, and



**Fig. 1** Monthly mean temperature (upper panel) and total precipitation (lower panel) during May–August in Rankin Inlet, Nunavut from 2015 to 2017, with the 30 year averages (1980–2010) represented by the black line and the error bars representing 95% confidence intervals

subsequently calculated perpendicular distance from the transect line (as recorded by handheld Global Positioning System: GPSmap 62s, Garmin Ltd.). We modelled only those species for which we had the recommended minimum 60 observations (Buckland et al. 2001) and in some cases combined species into groups to attain the minimum threshold. In other cases, we combined species into groups because we expected similar habitat associations (e.g., gulls, loons *Gavia* spp., geese). For geese, we dropped observations of



**Fig. 2** Maps of Rankin Inlet study area displaying the spatial distribution of avian distance sampling transects surveyed from 2015 to 2017. Black bars represent individual transects, and note that each transect

was repeated a minimum of twice during a season. Inset map displays the spatial location of the study area (red circle) within Nunavut, Canada

>5 individuals observed in flight as they were presumed to be migrating through the study area and would have confounded our attempts to describe habitat associations.

We followed the recommendations of Thomas et al. (2010) and modelled combinations of key functions (half-normal, hazard rate, uniform) and adjustment terms in our detection functions. Also, detection covariates were included in candidate models as follows: day of the year, time of day, terrain ruggedness (standard deviation in elevation; scale corresponded to that used in subsequent spatial modelling, see section on Density surface modelling), and wind speed on a 0–3 scale of increasing severity (upper limit ~30-km/h). We generally avoided sampling on days with poor weather conditions, but wind was difficult to avoid without creating large time gaps in sampling. A single observer was responsible for all avian observations and associated detection covariates.

The best-fitting detection function for each species or group was selected by comparing Akaike's Information Criterion corrected for small sample size (AICc) for the suite of candidate models and selecting the competitive model ( $\Delta\text{AICc} < 2$ ) with the fewest parameters for subsequent spatiotemporal modelling. If detection functions with different covariates were competitive, we further fit a function including both covariates and retained it if it provided an improvement in  $\text{AICc} > 2$ . Detection functions were fit using the package *Distance* (Miller et al. 2019) in the R statistical environment (R Core Team 2020).

### Density surface modelling

The second step of our analysis, density surface modelling (DSM), modelled our count data as a function of spatial and temporal covariates, and incorporated the previously estimated probability of detection into an offset term. Analyses

were conducted using the R package *dsm* (Miller et al. 2020). Although we used all observations to fit detection functions, we restricted our spatiotemporal analyses to data collected between June 7 and August 19, as this was the consistent sampling period across all years.

We included combinations of six habitat variables in our candidate DSMs, as follows: ruggedness, NDVI, NDWI, proportion freshwater cover, distance from coast and elevation. All models included ruggedness and freshwater, as well as year, period and their interaction as factor covariates. We compared models containing NDVI to models containing NDWI, and models containing elevation to those containing distance from coast. Based on prior evidence and ecological rationale, we also included interaction terms in candidate models as follows: for geese freshwater  $\times$  period and freshwater  $\times$  year terms, and for songbird species and shorebirds elevation  $\times$  period and distance from coast  $\times$  period. Data exploration proceeded according to the protocol of Zuur et al. (2010), and we ensured collinearity among predictors included in a given model was  $|r| \leq 0.6$ . We standardized all continuous covariates prior to analyses.

Because habitat can vary along a line transect, during DSM analyses they are typically divided into smaller segments. In our study, segment length corresponded to roughly twice the truncation distance used when modelling the detection function for a given species or group (Petersen et al. 2011); thus, our sampling units were approximately square. For songbirds and shorebirds, segment length was approximately 250 m, for ducks, geese and gulls approximately 500 m, and for Tundra Swans, Sandhill Cranes (*Cygnus columbianus*), loons and Common Eiders (*Somateria mollissima*) transects were not split into segments unless a given transect was greater than 1050 m. We fit models with a full random effect structure corresponding to our sampling design, including random intercepts for a given

transect visit and a given transect (segments were nested within transect visits, which were nested within transects). For Tundra Swans, Sandhill Cranes, loons and Common Eiders, a minority of transects were split into segments, and we therefore fit only random intercepts for transect identity. For the remaining species and groups, we retained the full random effects structure in all models unless they produced poor diagnostics, in which case we reduced complexity and refit with a single random effect term for transect identity.

For each habitat index, data were extracted from 30-m resolution rasters. Ruggedness and elevation were extracted from a digital elevation map (original resolution: 16 m, vertical resolution: 5 m, Natural Resources Canada 2015), and we obtained NDVI and NDWI rasters derived from Landsat 8 images from Google Earth Engine (8-day composite images from July 12 to 20, 2018 in both cases; Gorelick et al. 2017). Freshwater cover was estimated using a surface water layer (resolution: 25 m; Natural Resources Canada 2016). Habitat variables were calculated over moving windows of size  $270 \times 270$  m,  $510 \times 510$  m and  $990 \times 990$  m, which approximated the segment size used for each species or group. The goal was to ensure habitat covariates corresponded to individual transect segments with minimal overlap between segments. A distance from the coast raster was calculated based on a land layer (resolution: 25 m; Natural Resources Canada 2019). Note that for distance from the coast, inland areas have positive distances, while nearshore islands in Hudson Bay were assigned negative distances. Habitat covariates were then extracted at the midpoint of each transect segment. For NDVI and NDWI, we masked all water bodies prior to applying the moving window calculations.

Depending on model diagnostics, we modelled segment counts with either negative binomial or Tweedie response distributions. We compared candidate models for each species or group by AICc and drew inference from competitive models ( $\Delta\text{AICc} < 2$ ). In the case of nested competitive models, we drew inference from the simplest nested model. The additional terms included in more complex, nested models are generally non-informative when AICc indicates statistical equivalence (Arnold 2010). Due to the large number of species and groups modelled here, in cases where there were multiple, non-nested competitive models but inference was identical between them, we present one model for brevity. The full suite of models fit to each species or group can be found in Online Resource 2 and AICc comparison tables in Online Resource 3. Models to be compared by AICc were fit using maximum likelihood (ML), and competitive models were refit using restricted maximum likelihood (REML) prior to presentation and interpretation (Zuur et al. 2009). We ensured good visual fit of our models using standard diagnostic plots, including quantile–quantile plots and plots of randomized quantile residuals (Dunn and Smyth 1996).

## Results

### Detection functions

Overall, we recorded 2942 observations of 6221 individual birds from 33 species (Online Resource 1). Detection of American Pipits (*Anthus rubescens*), Horned Larks (*Eremophila alpestris*), Savannah Sparrows (*Passerculus sandwichensis*), shorebirds, geese and Sandhill Cranes were affected by detection covariates in selected models, with pipits and Savannah Sparrows less detectable in more rugged terrain, larks less detectable later in the day and later in summer, shorebirds and cranes more detectable later in summer, and geese less detectable on surveys with higher wind scores (Table 1). Common Eiders were also less detectable later in summer, but there was minor overlap of the 95% confidence intervals for this term with zero. The best-fitting detection function for Tundra Swans included a positive effect of ruggedness, but there was substantial overlap of the 95% confidence interval with zero for this term and a simpler model including no covariates narrowly missed the  $\Delta\text{AICc} < 2$  threshold ( $\Delta\text{AICc} = 2.04$ ), so we retained the latter in our spatiotemporal models.

### Habitat associations

#### Vegetation indices

In general, NDVI rather than NDWI was present in competitive DSMs. NDVI was positively related to Horned Lark, redpoll (*Acanthis* spp.; minor overlap of the 95% confidence interval with zero), Savannah Sparrow and Sandhill Crane abundance, and NDWI did not appear in competitive DSMs for any of these species (Fig. 3; Table 2). Duck (not including Common Eider) abundance was positively related to NDWI (minor overlap of the 95% confidence interval with zero), and NDVI did not appear in competitive DSMs for ducks. For geese, NDVI had no substantial effect on abundance, and NDWI did not appear in the best-fitting DSM. For gulls, we found a small negative influence of NDVI on abundance (minor overlap of the 95% confidence interval with zero), and NDWI did not appear in the best-fitting DSM. Tundra swan, Lapland Longspur (*Calcarius lapponicus*) and shorebird abundance was positively related to NDWI (minor overlap of the 95% confidence interval with zero for swans), and NDVI did not appear in competitive DSMs for any of these species. Loon and American Pipit abundance was unrelated to NDVI or NDWI, and Common Eider abundance was negatively related to both covariates.

**Table 1** Summary information for selected detection functions for species and groups surveyed in the Rankin Inlet study area from 2015 to 2017. Indicated is the species/guild, number of observations (N), truncation distance, key function and adjustment terms added (Key+adj, with the number of adjustment terms indicated in parentheses), covariate term if present along with its coefficient estimates and their 95% confidence intervals (in parentheses), average probability of detection ( $P_{det}$ ) and 95% confidence intervals (in parentheses)

Species/group	N	Truncation (m)	Ind	Key + adj	Term	Estimate	$P_{det}$	CvM
American Pipit	300	105	467	Half-normal	Ruggedness	<b>-0.14 (-0.21, -0.07)</b>	0.59 (0.54, 0.65)	0.63
Horned Lark	298	110	448	Half-normal	Time of day	<b>-0.20 (-0.37, -0.03)</b>	0.60 (0.54, 0.65)	0.71
					Day of year	<b>-0.13 (-0.24, -0.03)</b>		
Redpoll	83	130	153	Uniform + cosine (1)			0.55 (0.49, 0.62)	0.35
Lapland Longspur	183	105	336	Uniform + cosine (1)			0.58 (0.53, 0.63)	0.87
Savannah Sparrow	158	95	243	Half-normal	Ruggedness	<b>-0.29 (-0.46, -0.12)</b>	0.56 (0.49, 0.64)	0.89
Shorebird	100	130	210	Hazard rate	Day of year	<b>0.38 (0.06, 0.70)</b>	0.51 (0.37, 0.65)	0.99
Duck	114	230	282	Half-normal			0.68 (0.57, 0.80)	0.77
Goose	314	250	1104	Half-normal	Wind	<b>-0.20 (-0.33, -0.06)</b>	0.57 (0.52, 0.62)	0.24
Gull	499	250	964	Hazard rate			0.53 (0.45, 0.60)	0.94
Tundra Swan	88	400	309	Half-normal			0.73 (0.58, 0.88)	0.81
Sandhill Crane	334	320	732	Half-normal	Day of year	<b>0.12 (0.01, 0.23)</b>	0.62 (0.56, 0.68)	0.83
Loon	85	340	136	Half-normal			0.59 (0.48, 0.70)	0.81
Common Eider	69	330	298	Half-normal	Day of year	-0.33 (-0.75, 0.09)	0.56 (0.43, 0.68)	0.73

### Elevation and distance from coast

Elevation was present more often in competitive DSMs than distance from coast. Savannah Sparrows, shorebirds, geese, gulls, Tundra Swans, Sandhill Cranes, loons and Common Eiders were more abundant at low elevations, and distance from coast did not appear in competitive DSMs for any of these groups (Fig. 3; Table 2). American Pipit abundance was also negatively related to both elevation and distance from coast (minor overlap of the 95% confidence interval with zero in both cases). Redpoll abundance was unrelated to elevation or distance from coast. Lapland Longspurs were more abundant inland, and although the best-fitting model included the interaction between distance from coast and sampling period, the 95% confidence interval for this term had wide overlap of zero. Elevation did not appear in competitive DSMs for longspurs. There was some evidence for a shift to lower elevation, coastal habitat in late summer for Horned Larks. Duck abundance was negatively related both to distance from coast and elevation.

### Freshwater

Ducks, geese, gulls, Tundra Swans and loons were more abundant in areas with high freshwater cover (Fig. 3; Table 2; minor overlap of the 95% confidence interval with

zero for geese and one competitive duck model). In addition, geese became more abundant in areas with more freshwater later in summer, and the interaction between freshwater and year did not appear in the best-fitting DSM for geese. American Pipit, redpoll, Lapland Longspur, Savannah Sparrow, shorebird, Sandhill Crane, and Common Eider abundance was unrelated to freshwater. Horned Larks were less abundant in areas with more freshwater.

### Ruggedness

American Pipits, redpolls and geese were more abundant in areas with rugged terrain, while ducks were more abundant in areas with flat terrain (Fig. 3; Table 2; minor overlap of the 95% confidence interval with zero for geese). Lapland Longspur, Savannah Sparrow, Horned Lark, shorebird, gull, Sandhill Crane and loon abundance was unrelated to ruggedness. Competitive models for Common Eider abundance indicated differing effects of ruggedness; in the model including NDVI, eider abundance was positively related to ruggedness, while in the model including NDWI, this relationship was weakened considerably (minor overlap of the 95% confidence interval with zero). These differing effects are likely due to the fact that NDWI was correlated with ruggedness to a greater degree than NDVI.

## Temporal changes in abundance

American Pipit, shorebird, Common Eider and loon abundance was stable across all years and sampling periods (Fig. 4). Horned Lark and redpoll abundance was lower in late summer 2016, while Savannah Sparrows and Sandhill Cranes were more abundant in late summer 2017. Lapland Longspurs were less abundant in late summer 2015 and to a lesser degree in late summer 2016 as well. Duck and Tundra Swan abundance was generally stable but was lower in late summer 2017, while goose abundance was particularly low in late summer 2015 and late summer 2017. Gulls were more abundant in late summer 2015.

## Discussion

### Habitat associations of avian species and groups in the Arctic

Among the general conclusions that can be drawn from our study is the importance of areas with high freshwater cover, low elevation and high vegetative productivity as habitat for breeding tundra birds, generally according with our predictions. The abundance of freshwater that characterizes many Arctic study areas provides foraging habitat for birds as well as refuges from predation (Petersen 1990; Ruggles 1994; Stickney et al. 2002; Slattery and Alisauskas 2007). Unsurprisingly waterfowl such as ducks (not including Common Eiders), geese and swans, as well as loons and gulls were all more abundant in areas with greater freshwater cover. We also found that geese had stronger associations with freshwater later in summer, as adults were likely moulting and juveniles remained flightless. This accords with the results of Stahl and Loonen (1997), who found Barnacle Goose (*Branta leucopsis*) habitat use with respect to freshwater during brood rearing to vary, in their case annually, with predation risk. Lecomte et al. (2009) showed that the availability of freshwater on the tundra is also important for providing nearby drinking water to incubating geese, and that nesting success with respect to freshwater varied with annual moisture conditions, raising the possibility that geese might respond to moisture conditions in terms of their annual habitat use as well (Robinson et al. 2014). However, we did not find strong evidence for shifts in annual habitat use with regards to freshwater. It is possible that the gradient in moisture conditions across years did not permit effective investigation of this phenomenon, and it is also possible that freshwater is less limiting in our study area, which is located on the generally low-lying Hudson Bay coast. Previous study has revealed a drying trend for high-latitude ponds and lakes (Smol and Douglas 2007), which would logically have adverse effects upon species relying on freshwater.

Perhaps surprisingly, we did not find positive associations between shorebirds and freshwater cover. Our study area is coastal, and given the strong negative relationship between elevation and shorebird abundance, shorebirds may have associated with marine habitat instead. In addition, the most common shorebird identified on our surveys, the Semipalmated Plover (*Charadrius semipalmatus*), is known to breed on dry, pebbled substrates (Nguyen et al. 2003; Nol and Blanken 2014) that likely decrease the presence of freshwater in the immediate area around a nest. Lastly, much of the freshwater in the Arctic is below the scale generally captured in satellite imagery (Muster et al. 2012), and the positive relationship between shorebird abundance and NDWI hints at the possibility that shorebirds were associating with very small water bodies, or areas with wet soils. Only one species appeared to avoid areas with high freshwater cover, the Horned Lark, which generally accords with descriptions of its preferred habitat as dry or barren (Beason 1995).

The effects of elevation or distance from the coast on avian abundance were almost universally negative. For species such as loons, gulls or Common Eiders, which utilize marine food sources, this association is intuitive, and gulls also exploit anthropogenic food sources (e.g., landfill, discarded bycatch from fishing; Staniforth 2002; Weiser and Powell 2010) from the hamlet of Rankin Inlet itself, which is coastal within the study area (Fig. 2). Higher abundance in low, coastal habitats is consistent with previous study on shorebirds (Saalfeld et al. 2013) and various waterfowl (Conkin and Alisauskas 2013), and it is likely that this relationship is driven by the greater availability of suitable habitat in low, coastal areas, for example, wetlands (bogs, fens), river deltas or tidal habitats.

Elevation is strongly correlated with distance from coast in our study area ( $R \sim 0.8$ ), and yet it was elevation that was most often found in competitive DSMs. This may be because elevation can account for subtleties in the landscape, such as wide coastal lowlands or river valleys which may drive habitat associations for some species rather than simply proximity to coast. In addition, elevation may have better accounted for the sampling of nearshore islands in Hudson Bay, which were assigned negative distance from coast.

Only a single species was positively associated with elevation or distance from the coast, the Lapland Longspur, which accords with prior study by Andres (2006), which showed a heavily longspur-biased songbird population was more abundant at higher elevations in a study area on the Ungava Peninsula. While the mechanism for this association is unknown, it is possible that this is a form of habitat partitioning, because other songbird species generally had negative responses to elevation or distance from coast. As these species all largely consume invertebrates during the breeding season (Custer et al. 1986; Beason 1995; Knox and Lowther 2000; Hussell and Montgomerie 2002; Wheelwright and

Rising 2008; Hendricks and Verbeek 2012), competition may in part dictate their spatial distributions.

The use of coastlines by migrating birds has been long known (Alerstam and Pettersson 1977) and has been noted for some of the species modelled in our study (Connors et al. 1979; Hussell and Montgomerie 2002; Wheelwright and Rising 2008). However, we found limited evidence for coastward shifts in the distributions of songbirds and shorebirds later in the summer. Only Horned Larks showed some evidence of a shift to lower, coastal habitats later in summer. The general lack of a shift may reflect the fact that songbirds and shorebirds were already more abundant in low, coastal areas. Possibly this is also an artefact of our sampling design. We used July 11 as the division between early and late summer sampling, but it is likely that migratory flocking in most species occurs substantially later than this date; thus, we were not able to detect coastward shifts in abundance.

Our study compared DSMs containing NDVI or NDWI, which can both be expected to generally track the vegetative productivity of an area; however, NDWI is more specifically a proxy for vegetation water content (Gao 1996), which may further represent variation in soil moisture and underlying hydrology (De Alwis et al. 2007; Tagesson et al. 2013). This is particularly important for study areas such as ours, which contains substantial variation in water availability that may not be detected by satellite imagery (Muster et al. 2012). NDWI was particularly important in predicting abundance for Lapland Longspurs, shorebirds, ducks (excluding Common Eiders) and Tundra Swans. For the latter three, the fact that models including NDWI rather than NDVI were more competitive is perhaps unsurprising. Tundra Swans and some duck species (e.g., Northern Pintails, the second most common species observed in this group; Online Resource 1) are known consumers of very wet vegetation (e.g., graminoids in wet meadows, emergent or aquatic vegetation; Monda et al. 1994; Clark et al. 2014) and would be expected to frequent habitats featuring plants with high water content. Shorebirds are insectivorous, and areas with ample soil moisture or small water bodies also support abundant invertebrate prey (Bolduc et al. 2013; Cameron and Buddle 2017). Lapland Longspurs, on the other hand, are frequently described as an upland songbird, and indeed in this and other studies have more frequently been found further inland at higher elevations (Andres 2006). It might be expected that longspurs would therefore frequent areas with comparatively dry or sparse vegetation, but it appears the opposite is the case in our study area. We note that the model coefficient for NDWI was approximately 1/3 that of distance from coast in longspurs, so the latter is the far more powerful determinant of abundance.

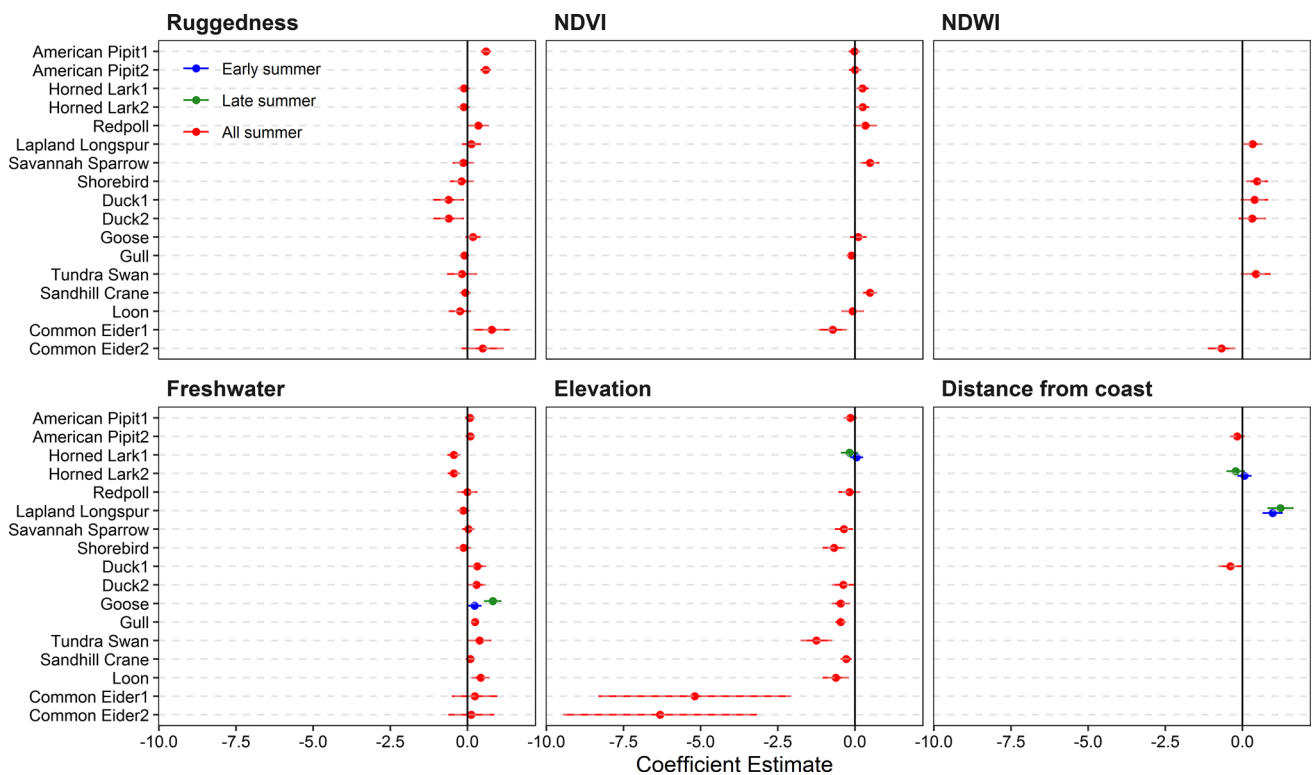
For both NDVI and NDWI, effects on abundance were generally positive or neutral as expected, with only Common Eiders showing negative associations with both metrics.

Common Eiders have been shown to avoid nesting habitats with high levels of cover, even though nests in these habitats benefit from lower cost of thermoregulation (Fast et al. 2007), possibly because these habitats reduce predator detection (Noel et al. 2005). This may be reflected in their avoidance of areas with more productive vegetation. Surprisingly, we did not find positive associations between geese and NDVI or NDWI, despite their herbivorous diet and previously demonstrated associations with wet meadows and wetlands (Cadieux et al. 2005; Slattery and Alisauskas 2007). We suggest that this may be an idiosyncrasy specific to study areas such as ours where geese frequently nest on cliffs. These areas are generally low NDVI or NDWI because they contain bare rock or are otherwise sparsely vegetated. Geese in our study area likely divide their time among vegetated (where they forage) and non-vegetated (where they nest) areas, which would explain why we did not find an association with either measure of vegetation. On the other hand, we did find positive associations between NDVI and the generally herbivorous Sandhill Cranes, and also for three songbird species: Horned Larks, Savannah Sparrows and redpolls. Various vegetation types are used by songbirds; for example, shrubs for nesting (Peterson et al. 2014; Boelman et al. 2015) and canopy-dwelling insect prey (Boelman et al. 2015; Pérez et al. 2016), and seeds and berries are also important diet components when arthropods are less available (White and West 1977; Custer and Pitelka 1978; Norment and Fuller 1997).

To our knowledge, this is the first usage of NDWI in modelling avian habitat in the Arctic, although it has been used to characterize tundra vegetation in previous study (Riihimäki et al. 2019). Given there was more support for DSMs including NDWI rather than NDVI for some species and groups, NDWI may be an important variable to include in future studies of avian distribution. The general trend for Arctic vegetation under climate warming has been towards general greening (Jenkins et al. 2020) and taller growth forms (Bjorkman et al. 2018). This is likely to have varying effects upon Arctic birds (Thompson et al. 2016), perhaps benefitting those that utilize shrub cover for nesting or foraging (Boelman et al. 2015). Based on the results of our study, Savannah Sparrows, redpolls, Horned Larks, Lapland Longspurs, Tundra Swans, shorebirds and ducks might be predicted to benefit from a greener Arctic on account of their positive relationships with vegetation indices.

Ruggedness is less commonly studied as a habitat metric for Arctic birds, but nonetheless can influence habitat associations when vertical structure improves protection from terrestrial predators (Anderson et al. 2014). Conversely, some species prefer nesting habitats that allow for high visibility (i.e., minimal topography) in order to increase the detectability of predators (Haynes et al. 2014). Geese (generally Canada Geese *Branta canadensis*; Online Resource 1) and





**Fig. 3** Parametric model coefficients and 95% confidence intervals for habitat covariates. Avian survey data collected during the summers of 2015–17 at Rankin Inlet, Nunavut. All covariates were standardized prior to analyses. Blue indicates a given estimate is specific to early summer, green is specific to late summer, and red indicates that the effect is pooled across the entire summer. Habitat covariates were modelled at the 270×270 m scale for songbird species and shorebirds, 510×510 m for ducks, geese and loons, and 990×990 m for Common Eiders, swans, cranes and loons. American Pipit (*Anthus*

*rubescens*), Horned Lark (*Eremophila alpestris*), redpoll (*Acanthis* spp.), Lapland Longspur (*Calcarius lapponicus*), Savannah Sparrow (*Passerculus sandwichensis*), Tundra Swan (*Cygnus columbianus*), Sandhill Crane (*Antigone canadensis*), Common Eider (*Somateria mollissima*). NDVI (normalized difference vegetation index), NDWI (normalized difference water index). In some cases, there were multiple competitive density surface models for a given species or group, and these models are noted with a number

Common Eiders were positively associated with rugged terrain, likely due to their use of cliffs for nesting. Cliffs in our study area are frequently home to raptors (Peregrine Falcon *Falco peregrinus* and Rough-legged Hawk *Buteo lagopus*) in addition to geese and eiders, and previous study has shown geese to nest in association with some raptor species (Tremblay et al. 1997; Quinn et al. 2003), apparently for the benefit of protection against terrestrial nest predators such as Arctic Foxes (*Vulpes lagopus*). This highlights a potential extension of our study: including potential relationships with predators explicitly in our models. Previous study has also shown songbird abundance to be reduced in the vicinity of raptor nests (Meese and Fuller 2008), and so the response to active raptor nests may be species or group specific.

### Temporal changes in abundance

Although summer represents the most favourable time of year in the Arctic for reproduction, abiotic factors can have a large impact on reproductive output (Jehl Jr and Hussell

1966; Skinner et al. 1998; Chmura et al. 2018). The patterns in abundance we found during our years of study were mixed relative to temperature and precipitation (Figs. 1, 4), and in general, there were few congruencies in abundance patterns across years and sampling periods among our species and groups, which likely indicates that population drivers are species or group specific.

Abundance of some songbirds declined from early to late summer, which is not intuitive given presumed brood production. Rather, this pattern may actually reflect declines in singing behaviour later in the year (Thompson et al. 2017), rather than a decline in abundance per se. Although our distance sampling analysis attempted to account for reduced detection later in the breeding season via detection distance, because detection of songbirds was primarily aural, non-singing birds may have been “unavailable” for detection, and thus, the assumption of 100% detection on the transect line may have been violated (Bachler and Liechti 2007). For this reason, we did not present density estimates for the avian species and groups

**Table 2** Density surface modelling (DSM) results for all species and groups surveyed in the Rankin Inlet, Nunavut study area from 2015 to 2017. Included information is the response distribution (Dist; tw for Tweedie and nb for negative binomial) used in the modelling, proportion deviance explained (Dev), number of observations ( $N$ ) and number of non-zero observations ( $N > 0$ ). Summary information for model terms is also included for each model, separated into fixed and random effects. For fixed effects, coefficient estimates are reported, along with their 95% confidence intervals (in parentheses). Random effects were modelled as smooth terms in the *dsm* package, so we

report the estimated degrees of freedom of the smooth and the associated  $p$  value. In some cases, there were multiple competitive DSMs for a given species or group, and models are noted with a number. Fixed effects with 95% confidence intervals not overlapping zero are bolded. American Pipit (*Anthus rubescens*), Horned Lark (*Eremophila alpestris*), redpoll (*Acanthis* spp.), Lapland Longspur (*Calcarius lapponicus*), Savannah Sparrow (*Passerculus sandwichensis*), Tundra Swan (*Cygnus columbianus*), Sandhill Crane (*Antigone canadensis*), Common Eider (*Somateria mollissima*). NDVI (normalized difference vegetation index), NDWI (normalized difference water index)

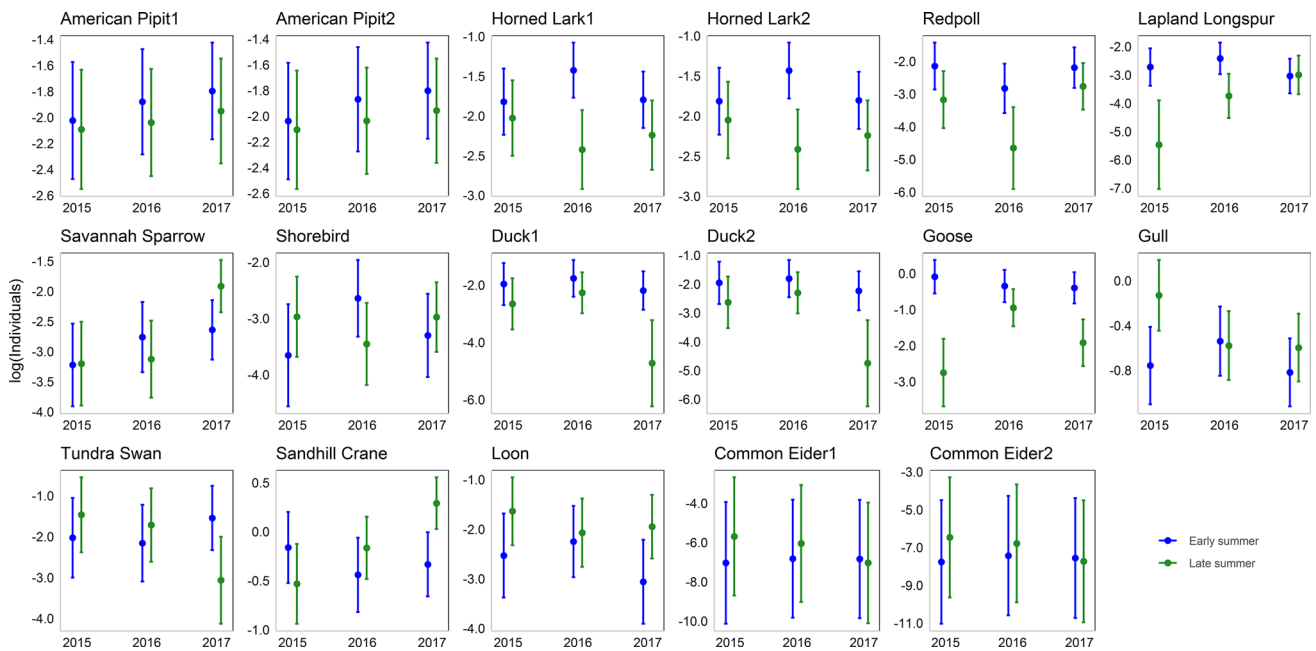
Model	Intercept	Ruggedness	NDVI	NDWI	Freshwater	Freshwater: late summer
American Pipit 1	-12.40 (-12.85, -11.95)	<b>0.60 (0.44, 0.77)</b>	-0.02 (-0.21, 0.16)		0.08 (-0.08, 0.23)	
American Pipit 2	-12.42 (-12.87, -11.97)	<b>0.59 (0.42, 0.76)</b>	0 (-0.20, 0.20)		0.09 (-0.07, 0.25)	
Horned Lark 1	-12.09 (-12.51, -11.67)	-0.11 (-0.31, 0.09)	<b>0.24 (0.04, 0.45)</b>		<b>-0.44 (-0.65, -0.24)</b>	
Horned Lark 2	-12.08 (-12.50, -11.67)	-0.12 (-0.32, 0.08)	<b>0.25 (0.04, 0.46)</b>		<b>-0.44 (-0.65, -0.24)</b>	
Redpoll	-12.58 (-13.30, -11.87)	<b>0.35 (0.01, 0.69)</b>	0.33 (-0.05, 0.71)		0 (-0.33, 0.32)	
Lapland Longspur	-13.00 (-13.66, -12.34)	0.13 (-0.18, 0.45)		<b>0.33 (0.03, 0.63)</b>	-0.13 (-0.34, 0.07)	
Savannah Sparrow	-13.33 (-14.01, -12.64)	-0.14 (-0.48, 0.20)	<b>0.48 (0.18, 0.79)</b>		0.03 (-0.17, 0.23)	
Shorebird	-14.10 (-15.01, -13.19)	-0.19 (-0.57, 0.19)		<b>0.47 (0.12, 0.83)</b>	-0.13 (-0.37, 0.12)	
Duck1	-13.71 (-14.44, -12.97)	<b>-0.61 (-1.11, -0.12)</b>		0.39 (-0.06, 0.83)	<b>0.31 (0.02, 0.60)</b>	
Duck2	-13.70 (-14.44, -12.97)	<b>-0.61 (-1.10, -0.11)</b>		0.31 (-0.13, 0.76)	0.29 (0.00, 0.58)	
Goose	-11.78 (-12.25, -11.32)	0.18 (-0.07, 0.43)	0.11 (-0.16, 0.37)		0.23 (-0.01, 0.46)	<b>0.59 (0.29, 0.90)</b>
Gull	-12.36 (-12.71, -12.02)	-0.10 (-0.26, 0.05)	-0.11 (-0.27, 0.04)		<b>0.24 (0.11, 0.38)</b>	
Tundra Swan	-14.88 (-15.85, -13.90)	-0.18 (-0.67, 0.31)		0.43 (-0.05, 0.91)	<b>0.39 (0.01, 0.77)</b>	
Sandhill Crane	-12.68 (-13.04, -12.31)	-0.07 (-0.25, 0.11)	<b>0.49 (0.26, 0.71)</b>		0.09 (-0.06, 0.24)	
Loon	-15.06 (-15.90, -14.21)	-0.24 (-0.60, 0.12)	-0.08 (-0.44, 0.29)		<b>0.43 (0.13, 0.72)</b>	
Common Eider 1	-19.45 (-22.55, -16.35)	<b>0.78 (0.20, 1.37)</b>	<b>-0.72 (-1.18, -0.27)</b>		0.24 (-0.50, 0.98)	
Common Eider 2	-20.17 (-23.44, -16.91)	0.49 (-0.19, 1.18)		<b>-0.68 (-1.13, -0.24)</b>	0.12 (-0.62, 0.87)	
Model	Elevation	Elevation: late summer	Coast	Coast: late summer	2016	2017
American Pipit 1	-0.15 (-0.36, 0.06)				0.14 (-0.45, 0.74)	0.23 (-0.35, 0.81)
American Pipit 2			-0.17 (-0.41, 0.07)		0.17 (-0.43, 0.77)	0.24 (-0.35, 0.82)
Horned Lark 1	0.05 (-0.16, 0.26)	-0.23 (-0.55, 0.09)			0.40 (-0.14, 0.93)	0.02 (-0.52, 0.56)
Horned Lark 2			0.06 (-0.17, 0.29)	-0.28 (-0.61, 0.05)	0.38 (-0.16, 0.92)	0.01 (-0.53, 0.55)

**Table 2** (continued)

Model	Elevation	Elevation: late summer	Coast	Coast: late summer	2016	2017
Redpoll	-0.18 (-0.54, 0.17)				-0.69 (-1.72, 0.35)	-0.05 (-1.00, 0.90)
Lapland Longspur			<b>0.98 (0.65, 1.31)</b>	0.25 (-0.20, 0.71)	0.31 (-0.54, 1.15)	-0.32 (-1.19, 0.56)
Savannah Sparrow	<b>-0.36 (-0.65, -0.07)</b>				0.46 (-0.43, 1.35)	0.58 (-0.25, 1.42)
Shorebird	<b>-0.68 (-1.05, -0.32)</b>				1.01 (-0.10, 2.13)	0.35 (-0.80, 1.51)
Duck1			<b>-0.39 (-0.78, -0.01)</b>		0.20 (-0.75, 1.15)	-0.23 (-1.19, 0.74)
Duck2	<b>-0.38 (-0.74, -0.02)</b>				0.15 (-0.80, 1.10)	-0.28 (-1.24, 0.69)
Goose	<b>-0.46 (-0.75, -0.18)</b>				-0.26 (-0.90, 0.38)	-0.31 (-0.94, 0.32)
Gull	<b>-0.47 (-0.64, -0.30)</b>				0.22 (-0.24, 0.68)	-0.06 (-0.52, 0.40)
Tundra Swan	<b>-1.25 (-1.77, -0.73)</b>				-0.13 (-1.44, 1.18)	0.48 (-0.74, 1.71)
Sandhill Crane	<b>-0.28 (-0.46, -0.11)</b>				-0.28 (-0.80, 0.24)	-0.17 (-0.66, 0.31)
Loon	<b>-0.62 (-1.05, -0.19)</b>				0.28 (-0.80, 1.36)	-0.53 (-1.70, 0.64)
Common Eider 1	<b>-5.19 (-8.31, -2.08)</b>				0.21 (-1.25, 1.68)	0.20 (-1.24, 1.64)
Common Eider 2	<b>-6.32 (-9.46, -3.17)</b>				0.33 (-1.14, 1.81)	0.21 (-1.24, 1.65)

Model	Late summer	2016: late summer	2017: late summer	Transect visit	Transect	Dist	N	N>0	Dev
American Pipit 1	-0.07 (-0.62, 0.49)	-0.09 (-0.83, 0.65)	-0.09 (-0.82, 0.64)	38.41 0.15	72.28 <0.001	tw	1784	221	0.35
American Pipit 2	-0.07 (-0.62, 0.49)	-0.10 (-0.84, 0.64)	-0.09 (-0.82, 0.64)	38.89 0.14	72.85 <0.001	tw	1784	221	0.36
Horned Lark 1	-0.21 (-0.79, 0.38)	-0.79 (-1.61, 0.02)	-0.24 (-1.02, 0.54)	67.57 <0.001	46.23 0.01	tw	1784	226	0.33
Horned Lark 2	-0.23 (-0.82, 0.35)	-0.75 (-1.57, 0.07)	-0.20 (-0.98, 0.58)	67.66 <0.001	46.17 0.01	tw	1784	226	0.33
Redpoll	-1.03 (-2.15, 0.09)	-0.79 (-2.63, 1.04)	0.46 (-1.01, 1.92)	0 0.99	0 0.88	nb	1784	67	0.11
Lapland Longspur	<b>-2.75 (-4.34, -1.15)</b>	1.42 (-0.27, 3.11)	<b>2.79 (1.13, 4.44)</b>	37.65 0.09	62.62 0.01	tw	1784	142	0.59
Savannah Sparrow	0.02 (-0.75, 0.80)	-0.39 (-1.46, 0.68)	0.70 (-0.21, 1.61)		82.43 <0.001	tw	1784	126	0.40
Shorebird	0.69 (-0.25, 1.62)	<b>-1.50 (-2.76, -0.23)</b>	-0.36 (-1.60, 0.88)		66.26 <0.001	tw	1784	85	0.45
Duck 1	-0.69 (-1.70, 0.32)	0.19 (-1.10, 1.47)	-1.85 (-3.70, 0.01)		59.07 <0.001	tw	1015	79	0.51
Duck 2	-0.68 (-1.69, 0.33)	0.18 (-1.11, 1.47)	-1.84 (-3.69, 0.01)		59.45 <0.001	tw	1015	79	0.51
Goose	<b>-2.66 (-3.62, -1.70)</b>	<b>2.06 (0.97, 3.15)</b>	1.14 (-0.02, 2.30)		77.46 <0.001	tw	1015	177	0.45
Gull	<b>0.63 (0.21, 1.05)</b>	<b>-0.67 (-1.24, -0.09)</b>	-0.41 (-0.97, 0.16)	0.02 0.92	68.59 <0.001	nb	1015	350	0.29
Tundra Swan	0.56 (-0.73, 1.85)	-0.12 (-1.91, 1.66)	<b>-2.08 (-3.90, -0.27)</b>		13.37 0.80	nb	607	62	0.39
Sandhill Crane	-0.37 (-0.87, 0.13)	0.65 (-0.03, 1.32)	<b>0.99 (0.37, 1.62)</b>		55.47 <0.001	tw	607	219	0.31
Loon	0.89 (-0.14, 1.93)	-0.72 (-2.11, 0.67)	0.22 (-1.22, 1.66)		25.44 0.10	nb	607	67	0.36
Common Eider 1	<b>1.35 (0.21, 2.49)</b>	-0.58 (-2.12, 0.96)	-1.55 (-3.16, 0.05)		27.53 <0.001	tw	607	45	0.80
Common Eider 2	<b>1.30 (0.14, 2.46)</b>	-0.65 (-2.21, 0.90)	-1.47 (-3.08, 0.14)		28.31 <0.001	tw	607	45	0.80



**Fig. 4** Combined effects of year, period and their interaction on the abundance of avian species and guilds, along with 95% confidence intervals, plotted on the scale of the linear predictor (i.e., the logarithm of abundance when all other covariates in the model and the offset were set to their means and effect of the random component of the model was removed). Blue indicates early summer and green indicates late summer. Avian survey data collected during the summers of 2015–17 at Rankin Inlet, Nunavut. American Pipit (*Anthus*

*rubescens*), Horned Lark (*Eremophila alpestris*), redpoll (*Acanthis* spp.), Lapland Longspur (*Calcarius lapponicus*), Savannah Sparrow (*Passerculus sandwichensis*), Tundra Swan (*Cygnus columbianus*), Sandhill Crane (*Antigone canadensis*), Common Eider (*Somateria mollissima*). NDVI (normalized difference vegetation index), NDWI (normalized difference water index). In some cases, there were multiple competitive density surface models for a given species or group, and these models are noted with a number

modelled here, and comparisons between early and late summer abundance for songbirds have to be interpreted in the context of possible variation in availability. For species that are large and more likely to be detected visually, this was less likely an issue, and additionally our line transect protocol resulted in many songbirds being detected as they flushed in front of the observer, perhaps maintaining this assumption. Future studies should explore variation in availability using double observer surveys or time removal protocol (Amundson et al. 2014; Buckland et al. 2015). For the sake of accurate songbird density estimates, we recommend surveys be conducted in early summer, when male songbirds in particular have high detectability. However, if breeding productivity is of interest, and intensive nest searching and monitoring are not possible, then late season surveys are a necessity. In general, late season abundance was more variable than early season abundance across taxa in our study (Fig. 4), which may reflect the fact that late season abundance had considerable input from within-season breeding.

To conclude, we estimated habitat associations for multiple avian species and groups over three breeding seasons in the area surrounding Rankin Inlet, Nunavut, employing to our knowledge the first application of density surface

modelling to Arctic land birds. Low elevation, large amounts of freshwater, and high vegetative productivity were the most consistent determinants of high avian abundance. In addition, NDWI emerged as an alternative to NDVI for characterizing habitat for several species and groups. Much of the available research on the habitat associations of Arctic avifauna is dated, qualitative and/or relies on studies completed at more southerly locations. Analyses such as those we have demonstrated here offer necessary updates and new approaches to basic research questions (CAFF, see Christensen et al. 2013) regarding Arctic birds and the biotic and abiotic drivers of their distribution and abundance. Birds are frequently cited as an effective indicator for biodiversity and ecosystem health because of their positions at higher trophic levels and the ease with which surveys can be conducted (Carignan and Villard 2002; Gregory 2006). Although wildlife studies are lacking throughout large areas of the circumpolar Arctic (Metcalf et al. 2018), available data suggest some Arctic-breeding birds are in decline (e.g., shorebirds; Smith et al. 2020). Our study provides information on habitat associations for some species that are under-represented in previous literature in a geographic region that is equally poorly represented, addressing knowledge gaps

and demonstrating methodological tools that can be widely applied across the Arctic.

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**Data availability** The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval** All applicable international, national and/or institutional guidelines for the care and use of animals were followed.

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