Broad-scale changes in tundra-nesting bird abundance in response to hyperabundant geese

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Abstract. Environmental changes can propagate through food webs in complex ways via trophic cascades. In the North American Arctic, hyperabundant populations of geese are causing significant habitat change and the resulting trophic cascades are known to impact plant and invertebrate communities. However, the potential impacts on other tundra-nesting birds are not fully understood. Here, we evaluate the impacts of light geese (Snow Geese, Chen caerulescens, and Ross’ Goose, Chen rossii) populations on other tundra-nesting birds, using count data collected during bird surveys conducted at varying distances from light goose colonies across the Canadian Arctic. From a dataset of 920 12–16 ha plots distributed across the Canadian Arctic, we identified 527 that were within 200 km of the mapped extent of known light goose colonies. After accounting for regional variation, we demonstrate that densities of most Cover-Nesting Shorebirds and passerines are depressed in the vicinity of light goose colonies. We suggest that these trends are the results of the combined effects of goose-induced changes in habitat and predator–prey interactions. These direct and indirect effects of light geese could be contributing to the declines experienced by some tundra-nesting bird populations in parts of their range. Ongoing climate-related changes to habitat, predators, and arthropods could interact with this effect of geese to further alter the suitability of tundra habitats for Arctic-breeding birds, in additive or even unanticipated ways.

Key words: community ecology; hyperabundant; nest-site selection; predator–prey; shorebird; Snow Goose; trophic cascade.

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INTRODUCTION

The response of ecosystems to environmental changes can be complex, with indirect effects sometimes operating across non-adjacent trophic levels. These apparent trophic cascades can operate through top-down and bottom-up forces (Kagata and Ohgushi 2006) and can have profound effects on ecosystem structure and function (Hebblewhite et al. 2005, Ripple et al. 2014). In temperate systems, anthropogenically elevated herbivore populations can initiate these cascades, altering songbird (Allombert et al. 2005a, Martin et al. 2011) and invertebrate (Allombert et al. 2005b) communities through changes to vegetation structure. Arctic systems are less complex (Gauthier et al. 2011, Legagneux et al. 2012), highly connected (Wirta et al. 2015), and experiencing rapid environmental change (Post et al. 2009, Collins et al. 2013), potentially leaving them more susceptible to herbivore-induced trophic cascades. Understanding the ecosystem effects of trophic cascades is important for multispecies conservation so that
management of hyperabundant populations can acknowledge the conservation requirements of other species.

During the last century, populations of northern-breeding geese have increased dramatically (Batt 1997, Kerbes et al. 2014), primarily as a result of food subsidies in their overwintering areas, from changing agricultural practices (Batt 1997, Jefferyes et al. 2004, Abraham et al. 2005a). In an attempt to curb the growth of light goose (Lesser and Greater Snow Goose, and Ross’ Goose Chen caerulescens caerulescens, C. c. atlanticus, Chen rossii, respectively) populations, hunting bag limits and seasons were liberalized to include spring hunts. These measures have not succeeded in reducing population sizes (Alisauskas et al. 2011). Recent estimates of Central and Eastern Arctic light goose breeding colonies indicate that breeding populations increased by more than 400% between 1973 and 2008 (Kerbes et al. 2014). Total population estimates that include breeding and non-breeding birds show larger increases, and suggest that the population may now be greater than 15 million individuals (Alisauskas et al. 2011). In some areas, these hyperabundant populations of light geese have significantly altered their breeding habitats (Kotanen and Jefferyes 1997, Jefferyes et al. 2006, Flemming et al. 2019), and these changes could cascade through other components of Arctic ecosystems.

Around light goose breeding colonies, the effects of intensive goose foraging on plant (Cargill and Jefferyes 1984, Srivastava and Jefferyes 2002) and invertebrate communities (Milakovic et al. 2001, Milakovic and Jefferyes 2003) are known, but the potential indirect effects on other sympatric taxa, less so (Flemming et al. 2016). The highly vegetated tundra habitats used by geese also provide breeding habitat for many other bird species, especially migratory shorebirds (Brown et al. 2007). In many tundra habitats, shorebirds represent the most species-rich component of the avifauna (Meltote et al. 2007). Significant population declines have been documented in several Arctic-breeding shorebird species (Andres et al. 2012) making them a high conservation priority (Johnston et al. 2015). Many Arctic-nesting passerines also overlap with geese and shorebirds in their choice of habitat (Latour et al. 2005, Walker et al. 2015). Negative impacts of hyperabundant light geese on these sympatric birds have been suggested (Sammler et al. 2008, Hines et al. 2010, Flemming et al. 2016), but the extent and mechanisms remain largely unknown.

Where light goose foraging is intensive, the height and coverage of vegetation are reduced (Abraham et al. 2005b, Conkin and Alisauskas 2017). Many small-bodied tundra-nesting birds select sites with tall (>30 cm) vegetation to conceal their nests from predators (Smith et al. 2007a), so these goose-induced changes in vegetation structure could reduce the availability of suitable nesting habitat. Over a 25-yr period in the vicinity of a light goose colony, Savannah Sparrow (Passerculus sandwichensis) nesting density declined by 77% and the area of their preferred nesting habitat, grassland–shrub, declined by 63% (Rockwell et al. 2003). Also, generalist predators can be attracted to light goose colonies as a source of food (McKinnon et al. 2013), increasing the risk of predation for other birds nesting nearby. Near a light goose colony on Bylot Island, Nunavut, American Golden-Plover (Pluvialis dominica) occurrence and the survival probability of artificial shorebird nests increased as a function of distance from the colony while predator occurrence decreased (Lamarre et al. 2017). Combined, the effects of habitat alteration and predation could result in lower abundances of shorebirds and passerines at large spatial scales, potentially contributing to a broader conservation issue.

Here, we evaluate the hypothesis that hyperabundant light geese are indirectly decreasing the abundance of sympatric birds. Using survey data from plots at varying distances from goose colonies across the Canadian Arctic, we tested the prediction that the densities of shorebirds and passerines would increase as a function of distance from goose colonies and that this trend would be more pronounced for species that select concealed nest sites than for species that use nesting sites with little vegetative concealment. Conversely, we expected to see the densities of predators decrease with increasing distance from colonies. We provide evidence that, at the scale of the Canadian Arctic, light goose colonies are associated with reduced densities of Cover-Nesting Shorebirds and passerines, and discuss the implications of this finding with respect to the conservation status of Arctic birds.
MATERIALS AND METHODS

Bird surveys

Bird surveys were conducted in plots distributed across the Canadian Arctic. Plot selection followed the methods of the Arctic Program for Regional and International Shorebird Monitoring (PRISM), a program designed to assess the population status of shorebirds across the North American Arctic (Bart et al. 2002; Fig. 1). Briefly, plots were selected from within regions and stratified by habitat type, with a disproportionate number of plots selected from the wetland stratum (typically six wetland plots for each three vegetated upland plots, and one sparsely vegetated upland plot). In some cases, plots were also selected to delineate significant environmental features such as the Mackenzie Valley. Regions encompassed an area that could feasibly be accessed by helicopter in a single season, and also followed approximate geographical (e.g., islands) or habitat boundaries (e.g., separating expansive barren areas from more suitable habitats) based on the broad habitat types from the Circumpolar Arctic Vegetation Map (CAVM Team 2003).

Following PRISM protocols, surveys occurred during the late-courtship to early incubation period for shorebirds (typically centered around mid- to late-June), when birds had settled on their breeding territories but remained conspicuous through territorial displays (see Bart and Johnson 2012). During surveys, two observers separated by 25 m walked systematically through the plots (typically 12 ha but sometimes 16 ha) using a GPS to ensure complete coverage, with surveys lasting approximately 90 min. Observers recorded the numbers and species of

Fig. 1. Locations of Arctic Program for Regional and International Shorebird Monitoring Program survey plots situated within 200 km of light goose colonies in each region across the Canadian Arctic. The regions are A, Mackenzie; B, South Archipelago; C, North Archipelago; D, Central Ellesmere; E, Queen Maud Gulf; F, North Hudson Barrens; G, Southwest Hudson Barrens; H, Northwest Hudson Barrens; I, Southampton; J, Eastern Foxe Basin; K, Quebec.
all birds seen using the plot. We assumed that probability of detecting birds was constant across sites and over time, so that our counts are believed to represent a constant fraction of their true density.

For the purposes of plot selection, each plot was assigned to a habitat category at the landscape scale using remote-sensing data. However, on the ground, the coverage of habitat types within the plot varied. During the surveys, two trained observers estimated the proportional cover of three general habitat types (upland, lowland, and permanent water) and adjusted their estimates after discussion and comparison at the end of the survey. Upland habitats consisted of vegetated mesic and sparsely vegetated xeric areas, while lowlands were heavily vegetated hygric to hydric habitats. Permanent water included ponds, lakes, and rivers.

Since plots were distributed throughout the Canadian Arctic, many were thousands of kilometers away from the nearest goose breeding areas. We hypothesized that any effect of geese on sympatric birds would decline to zero at a threshold distance away from the colony; analyzing results from plots well beyond this distance could lead to spurious results related to species’ ranges and correlated biogeographic patterns in bird densities. To isolate the effects of geese per se, we excluded from analysis any plots that were >200 km from the edge of a known goose colony. Previous site-specific studies have found goose-related effects on vegetation extend 17–19 km (Conkin and Alisauskas 2017; R. F. Rockwell et al., unpublished data) from colonies, while effects on predators extend to 10.5 km from colonies (Lamarre et al. 2017). We therefore expected that a 200 km cutoff would capture effects of goose grazing well beyond the previously identified thresholds while at the same time avoiding confounding regional effects. To account for any range-specific effects, we removed plots for species that fell outside of the species’ range and visually verified that PRISM counts conformed to ranges outlined by Birds of North America maps.

In the analyses, we examined patterns within this 200 km buffer in an attempt to locate a threshold distance for effects of geese (see Data analyses). We acknowledge that pre- and post-breeding light geese can have pronounced effects on habitat far outside the boundaries of the breeding colonies (Conkin and Alisauskas 2017). Thus, some of our plots outside of colonies were nevertheless within areas of altered habitat, weakening our ability to test our prediction and making our approach a conservative test of the effects of geese.

We treated bird species separately in our analyses but also assigned species to one of four categories to aid in testing our hypotheses and interpreting our results (Table 1). Some shorebird species conceal their nests in the tall vegetation of moist and wet lowlands; these species are categorized as cover-nesting. In contrast, Open-Nesting Shorebirds use sparsely vegetated upland habitat and select unconcealed nest sites with an unimpeded view of the surrounding area (Smith et al. 2007a). We predicted that the habitat changes arising from goose grazing would have a greater impact on cover-nesting vs. open-nesting species. Two passerine species were abundant (n > 100 sightings) across all regions: Lapland Longspur (Calcarius lapponicus) and Savannah Sparrow. Both rely on cover for nest building and often breed in sedge meadow (a lowland habitat type). Other passerines were too uncommon (n < 100 sightings) for analysis. American Golden-Plover and Black-bellied Plover (Pluvialis squatarola), both open-nesting species, were lumped for analyses owing to small sample sizes. Baird’s Sandpiper (Calidris bairdii) was also included in order to increase the number of open-nesting species. Finally, we classified aerial predators as any species that has been known to prey upon goose eggs or goslings, and depredate shorebird or passerine nests. The number of predatory birds encountered was generally low (Long-tailed Jaeger, 35; Parasitic Jaeger, 15; Glaucous Gull, 28), so these were lumped across species for analyses.

Goose colony surveys

The locations and sizes of light goose breeding colonies have been monitored at 5- to 10-yr intervals throughout the Canadian Arctic by the Canadian Wildlife Service and the United States Fish and Wildlife Service (Kerbes et al. 2014). Colonies are photographed from airplanes and digitized images are inspected manually to determine the outer limits of the distribution of nesting birds (Kerbes et al. 2014). The colony
boundaries used here for analyses represent the cumulative outermost edge of the areas within which geese were observed to breed between 2002 and 2009 (K. Meeres and J. Ingram, unpublished data). The location of the coastline was obtained from the Global Administrative Areas database (Hijmans et al. 2010).

**Data analyses**

For each PRISM plot, we measured the distance from the plot edge to the nearest coastline and to the edge of the nearest goose colony polygon using the gDistance function in the rgeos package Version 3.0 (Bivand and Rundel 2014). We then visually assessed whether plots were situated within a goose colony. To test for covariates of bird abundance, we used generalized additive models with a negative binomial distribution to account for overdispersion. We first tested for multicollinearity among predictor variables. The proportions of upland and lowland habitat within plots were highly negatively correlated ($r > -0.8$), and few plots contained significant permanent water ($11.7 \pm 17.4$), so we included only the proportion of lowland habitat as a predictor in all models. We also included a fixed effect of square-root-transformed distance to coast in all models because wetland habitat is most often associated with coastal areas (Brown et al. 2007) and shorebird abundance can decline as a function of increased distance to coast (Johnson and Herter 1989, Morrison 1997, Bart et al. 2012). Region and an offset of the log-transformed plot area were included in all models as fixed effects to account for geographic variation in abundance and differences in plot sizes, respectively. We tested models with species (eight individual shorebird species, lumped into seven groups; two passerines; three predators, lumped into one group) and species group (Cover-Nesting Shorebirds, Open-Nesting Shorebirds, passerines, and aerial predators).

To identify if distance to goose colony influenced bird abundance, we tested models with a fixed effect of the natural spline of the square-root-transformed distance to nearest goose colony. Since each species has slightly different habitat preferences (e.g., lowland with high concealment, lowland with low concealment), we expected species-specific responses to habitat-related changes associated with distance to goose colonies. We also expected a distance threshold beyond which the effects of geese on habitat and sympatric species were negligible. We therefore tested models with interactions between species/species groups and the natural spline of square-root-transformed distance to goose colony (distance to colony × species).

We used Akaike’s information criterion to test the performance of models with and without distance to goose colony and individual species vs. species groups and used a likelihood ratio test to

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**Table 1. Broad classification of birds seen during Arctic Program for Regional and International Shorebird Monitoring Program plot surveys and included in our analyses.**

| Classification                                | Common name     | Species name         | References supporting classification                        |
|-----------------------------------------------|-----------------|----------------------|-------------------------------------------------------------|
| Shorebird, lowland habitat preferring, cover-nesting | Dunlin           | *Calidris alpina*    | Cunningham et al. (2016), Flemming et al. (2019)            |
|                                                | Pectoral Sandpiper | *Calidris melanotos* | Farmer et al. (2013), Cunningham et al. (2016)             |
|                                                | Red-necked Phalarope | *Phalaropus lobatus* | Walpole et al. (2008)                                       |
|                                                | Red Phalarope    | *Phalaropus fulicarius* | Smith et al. (2007a, b), Cunningham et al. (2016)        |
|                                                | Semipalmated Sandpiper | *Calidris pusilla*   | Jehl (2006)                                                 |
|                                                | White-rumped Sandpiper | *Calidris fuscicollis* | Smith et al. (2007a, b)                                     |
| Shorebird, upland habitat preferring, open-nesting | American Golden-Plover | *Pluvialis dominica* | Johnson and Connors (2010)                                 |
|                                                | Baird’s Sandpiper | *Calidris bairdii*   | Parmelee et al. (1967)                                      |
|                                                | Black-bellied Plover | *Pluvialis squatarola* | Smith et al. (2007a)                                       |
| Passerine, lowland habitat preferring, cover-nesting | Lapland Longspur | *Calcarius lapponicus* | Sammler et al. (2008)                                      |
|                                                | Savannah Sparrow | *Passerculus sandwichensis* | Sammler et al. (2008)                                   |
| Generalist egg and shorebird predator          | Glaucous Gull    | *Larus hyperboreus*  | Béty et al. (2002), Weiser and Powell (2010)                |
|                                                | Long-tailed Jaeger | *Stercorarius longicaudus* | Taylor (1974)                                              |
|                                                | Parasitic Jaeger | *Stercorarius parasiticus* | Haven and Lee (1999)                                     |
identify significant predictors. All models were ranked using Akaike’s information criterion corrected for sample size ($\text{AIC}_c$; Burnham and Anderson 2002). We considered models within 2 $\text{AIC}_c$ units of the top model as supported and competing for the best top model (Burnham and Anderson 2002).

To identify a distance threshold at which goose colony had no effect on species abundance, we performed a segmented analysis on the predicted species-specific trends using the lavielle function from the adehabitatLT package in R. This function calculates the break point at which goose colony had little or no effect on bird abundance. All statistical analyses were conducted using R Version 3.3.1 (R Core Team 2017).

RESULTS

Plot summary

Our dataset comprised 527 plots distributed widely across the Canadian Arctic but situated within 200 km of 19 distinct light goose colonies (Fig. 1). All surveys were conducted over 11 yr between 5 June and 21 July 1995–2016 (Table 2, Fig. 1). For the 14 species, we counted a total of 5849 individuals for which the total density ranged from 0 to 775 (92.49 ± 81.56) pairs per km². An additional 60 species were observed infrequently (in fewer than 30 plots or 3 regions) and were not included in analyses (Appendix S1: Table S1).

Model results

The top model relating bird abundance to distance from a goose colony included a fixed effect of species, the natural spline of distance from the nearest goose colony, and an interaction between the two. This model ranked well above all other models on the basis of $\text{AIC}_c$ (Table 2). Distance from coast ranged from 0.02 to 168.57 km (mean ± standard deviation, 19.10 ± 26.96) and negatively influenced bird abundance ($X^2_{12} = 64.18$, $P < 0.001$). In contrast, bird abundance was positively related to the proportion of lowland within a plot ($X^2_{12} = 80.14$, $P < 0.001$). The proportion of lowland varied from 0% to 100% (53.2 ± 38.4) and was not related to distance to coast ($r = −0.11$) or distance to colony ($r = −0.11$). For the 14 species we tested, regional variation ($X^2_{12} = 82.81$, $P < 0.001$) in bird density ranged from 48.45 ± 30.52 individuals per km² in the Southwest Hudson Barrens (Table 3, Fig. 1, area G) to 104.38 ± 65.89 in the Queen Maud Gulf (Fig. 1, area E). There was also significant interspecific variation in abundance ($X^2_{12} = 2056.14$, $P < 0.001$). Lapland Longspur (1927 total individuals across all plots) and Red Phalarope ($Phalaropus fulicarius$, 1063) were most abundant, and Black-bellied Plover and American Golden-Plover (119 combined) were less so.

Overall, we found a species-specific effect of distance from the nearest goose colony on bird abundance (distance × species interaction, $X^2_{20} = 135.60$, $P < 0.001$). We identified different relationships between distance to colony and abundance for open-nesting species, cover-nesting species, passerines, and aerial predators (Table 4). As expected, after accounting for proportion of lowland habitat in the plots and distance to coastline, most Cover-Nesting Shorebird and passerine species increased in abundance with

Table 2. Model selection results for the densities of shorebirds, passerines, and Generalist Aerial Predators observed in 527 plots situated across the Canadian Arctic.

| Model                                                                 | $K$ | Adjusted R-squared | $\text{AIC}_c$ | $\Delta\text{AIC}_c$ | $W_c$ |
|-----------------------------------------------------------------------|-----|--------------------|----------------|----------------------|-------|
| lowl+sqrt(cst_dist)+ns(sqrt(col_dist))+species+Reg+                 | 43  | 0.38               | 11,295.93      | 0.00                 | 1.00  |
| ns(sqrt(col_dist)):species+offset(log(area))                         |     |                    |                |                      |       |
| lowl+sqrt(cst_dist)+species+Reg+offset(log(area))                    | 21  | 0.37               | 11,387.93      | 92.00                | 0.00  |
| lowl+sqrt(cst_dist)+species_group+Reg+offset(log(area))             | 14  | 0.36               | 11,498.80      | 202.9                | 0.00  |
| lowl+sqrt(cst_dist)+ns(sqrt(col_dist))+species_group+               | 22  | 0.35               | 11,501.76      | 205.8                | 0.00  |
| Reg+offset(log(area))                                               |     |                    |                |                      |       |
| Null                                                                 | 2   | 0.00               | 12,862.04      | 1566.1               | 0.00  |

Notes: Fixed effects include lowland (%; lowl), natural spline of coast distance (km; cst_dist), colony distance (km; col_dist), species (individual species; species), spec_group (grouped species: cover-nesting, open-nesting, passerine, predator), region (Reg), and interactions between lowland and species, and colony distance and species. Each model included an offset for the log area of each plot.
distance from goose colony up to a peak at which point the abundances evened out or declined (Fig. 2). The nature and degree of the response, however, varied among species, as did the threshold distance implied by the break point.

Open-Nesting Shorebird abundances varied little with distance from goose colony. Plover abundance changed marginally with distance from goose colony, and Baird’s Sandpiper abundance slowly increased to a peak at which point it declined (Fig. 3). Conversely, Generalist Aerial Predator abundance decreased slightly with distance from nearest goose colony.

**DISCUSSION**

We investigated whether proximity to light goose breeding colonies affects the abundance of shorebirds, passerines, and Generalist Aerial Predators. Within 200 km of goose colonies, the abundances of both passerines and four cover-nesting shorebird species, all of which use vegetated lowland habitat to varying degrees for nesting, increased as a function of distance from goose colony. The abundance of open-nesting species that nest in upland habitat with little vegetative cover changed less so. These results suggest that a reduction in vegetative cover, such as that arising from goose-induced habitat alteration, is driving the observed trends in cover-nesting bird abundances. The results presented here are the first to suggest that the trophic cascades initiated by light geese are affecting tundra-nesting bird communities at a landscape scale at goose colonies across the Canadian Arctic. We propose that these reduced abundances could arise through at least three mechanisms:

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**Table 3.** Variation in survey years and bird densities (mean ± standard deviation) among PRISM regions and associated light goose abundances as estimated by Kerbes et al. (2014).

| PRISM region             | Year surveyed       | Density (per km²) | Light goose abundance |
|-------------------------|---------------------|-------------------|-----------------------|
| Eastern Foxe Basin      | 1996, 1997, 2003, 2004 | 89.25 ± 83.74     | 1,618,600             |
| Mackenzie               | 2005, 2006, 2007, 2008, 2009 | 99.81 ± 73.85   | 3200                  |
| North Hudson Barrens    | 2015                | 58.61 ± 42.22     | 126,438               |
| North West Hudson Barrens | 2016              | 48.12 ± 31.16     | 0                     |
| Queen Maud Gulf         | 2005, 2006, 2010    | 104.38 ± 65.89    | 2,790,193             |
| South Archipelago       | 2012                | 52.38 ± 51.22     | 427,000               |
| South West Hudson Barrens | 2015              | 43.45 ± 30.52     | 724,500               |
| Southampton             | 2004, 2006          | 71.92 ± 42.01     | 939,700               |

**Table 4.** Distance from goose colony break points at which bird densities change.

| Species                        | Distance of break point (km) | Within density (birds/km²) | Outside density (birds/km²) | Magnitude of difference outside: within (birds/km²) |
|-------------------------------|-----------------------------|---------------------------|-----------------------------|-----------------------------------------------|
| Passerines                    |                             |                           |                             |                                               |
| Lapland Longspur              | 5                           | 9.59                      | 15.57                       | 1.62                                          |
| Savannah Sparrow              | 7                           | 5.25                      | 7.78                        | 1.48                                          |
| Cover-Nesting Shorebirds      |                             |                           |                             |                                               |
| Dunlin                        | 34                          | 2.63                      | 2.81                        | 1.07                                          |
| Pectoral Sandpiper            | 15                          | 3.51                      | 5.33                        | 1.52                                          |
| Red-necked Phalarope          | 8                           | 6.30                      | 5.31                        | 0.84                                          |
| Red Phalarope                 | 117                         | 14.10                     | 32.23                       | 2.29                                          |
| Semipalmated Sandpiper        | 25                          | 4.19                      | 8.98                        | 2.14                                          |
| White-rumped Sandpiper        | 13                          | 8.85                      | 14.17                       | 1.60                                          |
| Open-Nesting Shorebirds       |                             |                           |                             |                                               |
| Plover species                | 51                          | 1.10                      | 1.63                        | 1.48                                          |
| Baird’s Sandpiper             | 12                          | 0.51                      | 0.65                        | 1.28                                          |
| Generalist Aerial Predators   | 88                          | 0.60                      | 0.45                        | 0.75                                          |

Notes: Densities of passerines, Cover-Nesting Shorebirds, Open-Nesting Shorebirds, and Generalist Aerial Predators within and outside the break points of distance from goose colony. Bolded test is total per group.
Habitat effects, effects on generalist nest predators, and effects on the birds' arthropod prey.

**Habitat effects**

Geese are well known to reduce the coverage of sedges and grasses and increase the extent of exposed substrate in areas that they use heavily (Flemming et al. 2019). These areas include, but are not necessarily limited to, the breeding colony areas. Adult Snow and Ross' Geese uproot vegetation to build nests (Conkin and Alisauskas 2017) and forage intensively in these areas during incubation; however, broods can move up to 60 km beyond the colony (Hughes et al. 1994, Mainguy et al. 2006, Slattery and Alisauskas 2007) removing above-ground vegetation as they disperse. In the Hudson Bay lowlands (northern Manitoba), Rockwell et al. (unpublished data) documented goose shoot-pulling up to 19 km from a goose colony. Similarly, Conkin and Alisauskas (2017) found a negative relationship between distance from light goose colony and the proportion of exposed peat up to 17 km from colonies in the Central Canadian Arctic. Thus, light geese can reduce the coverage of heavily vegetated habitats within and surrounding their colonies, and this

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**Fig. 2.** Density (birds per km²) of passerines and Cover-Nesting Shorebirds in relation to distance from nearest light goose colony (km). Black lines represent the predicted fit, and gray shading represents the standard error. Vertical lines represent the break point calculated using a segmented analysis.
gradient of grazing pressure could relate to a gradient of habitat suitability for sympatric species.

We found that bird abundance was positively correlated with the proportion of lowland habitat present in plots. Many shorebird and passerine species select wet sedge-dominated sites for nesting and, specifically, select nest sites with higher vegetative cover that conceals nests from predators (Smith et al. 2007a, Walpole et al. 2008, Cunningham et al. 2016). In the Arctic Coastal Plain of Alaska, habitat suitability for eight species of shorebird was found to be positively related to the proportional cover of lowland habitat (Saalfeld et al. 2013). Snow and Ross’ Geese also nest in wet, lowland areas (Batt 1997, Lecomte et al. 2008) and forage in wet sedge meadows (Jefferies and Rockwell 2002, Jefferies et al. 2006, Slattery and Alisauskas 2007, Conkin and Alisauskas 2017). At the regional scale, we found that bird density was typically higher in regions with high goose abundance further supporting the spatial overlap between shorebirds and geese (Flemming et al. 2016).

Intensive grazing and grubbing in and around light goose colonies can, however, reduce the proportional cover of graminoid (grass and sedge spp.) habitats (Jefferies et al. 2006, Fleming et al. 2019) and the height of vegetation (O et al. 2006, Flemming et al. 2019), thereby limiting the availability of habitat used by some shorebirds for nesting. For instance, near a light goose colony in Cape Churchill, Manitoba Sammler et al. (2008) found densities of Cover-Nesting Shorebirds and passerines were ~60% lower in goose-altered habitat than in intact sedge meadow habitat. Similarly, Hines et al. (2010a, b) found a positive relationship between all shorebird and passerine abundance and increased distance from goose colony (up to 10 km) at a light goose colony situated in the Western Canadian Arctic.

We found significant species-specific effects of colony distance on bird abundances for several species. Specifically, the abundances of four Cover-Nesting Shorebirds and both passerines were positively related up to 200 km from the nearest light goose colony, with a threshold of maximum abundance for passerines at 9 km and the affected cover-nesting species at 8 km from colonies. In contrast, the abundances of all open-nesting species were influenced up to 32 km from colonies and both Plover species experienced little change. The open-nesting species, American Golden-Plover, Black-bellied Plover, and Baird’s Sandpiper, all nest in dry upland habitats and select nest sites with varying degrees of low vegetative cover (Moskoff and Montgomery 2002, Smith et al. 2007a). The elevated ridges where these species nest are often sparsely vegetated with Dryas spp. and lichens, and lateral concealment seems neutral or avoided in nest-site selection (Smith et al. 2007a). A reduction in the extent or height of graminoids should therefore have less impact on these species than for cover-nesting species.

The species-specific thresholds we identified may be due to flexibility in nest-site selection.
exhibited by individual species. Savannah Sparrows, for instance, were influenced up to 7 km from goose colonies, beyond which their abundance was 1.48 times greater. Across its large breeding range, this species selects a wide variety of nesting habitats from hayed fields to scrub-willow-dominated habitat (Wheelwright and Rising 2008) and so may be flexible in its habitat selection. However, near a goose colony situated in the Hudson Bay lowlands, both Rockwell et al. (2003) and Peterson et al. (2013) documented declines of over 75% in Savannah Sparrow occupancy along with significant declines in the areal extent of their primary nesting habitat over 25 and 36 yr periods, respectively, suggesting that this species may still be affected and local effects can be pronounced.

The affected Cover-Nesting Shorebirds varied in their threshold (8–25 km from colony) and magnitude of change (1.52:1–2.29:1 bird/km² outside: within). White-rumped Sandpiper (Calidris fuscicollis), which were influenced up to 13 km from colonies, can be generalist in their nest-site selection, nesting in habitats ranging from damp sedge-dominated areas to drier sedge and scrub-dominated sites (Flemming et al. 2019). Both Red-necked Phalarope (Phalaropus lobatus; Wallpole et al. 2008) and Pectoral Sandpiper (Calidris melanotos; Cunningham et al. 2016) nest in lowland sedge-dominated wet meadows and therefore may be prone to goose-induced changes in vegetation height or lateral concealment in sedge-dominated meadows.

Flexibility in habitat selection could make species less susceptible to goose-induced habitat alteration. Red Phalaropes select either concealed nest sites in sedge meadow, or open nest sites in coastal areas; the latter sometimes at high density in association with aggressive species such as gulls or terns (Egevang et al. 2004, Smith et al. 2007b). Additionally, some birds nesting in a goose colony could be afforded protection from satiated predators (Baldwin et al. 2011, Kellett and Alisauskas 2011), but this benefit may be offset by interspecific conflicts (Baldwin et al. 2011). Through fecal deposition, geese could also be altering wetland water chemistry (Mariash et al. 2018) and thus food availability as has been suggested elsewhere (Alisauskas and Kellett 2014). Combined, these effects may explain the unexpected high densities of Red Phalaropes seen in a small number of plots within goose colonies; however, these hypotheses require further investigation.

**Predator effects**

Generalist Aerial Predator abundance declined marginally as a function of distance from goose colony, largely due to low sightings and significant variation in predator abundance within goose colonies. This may be due to regional variability in our plot surveys, which may be capturing changes in prey availability. Lamarre et al. (2017) determined that the frequency of aerial predator occurrence was negatively related to distance from the centroid of a light goose colony up to 8.5 and 10.5 km when lemming abundance was low and high, respectively. Since our survey data span seven regions and 10+ yr, we were not able to account for the effect of lemming cycles which could significantly affect the spatial distribution of predators. When lemmings are scarce, avian predator abundance may be depressed by higher Arctic fox (Vulpes lagopus) predation on nests (Gauthier et al. 2015, Lamarre et al. 2017). Lemming abundance can also mediate the importance of alternative food sources such as goose eggs to aerial predators (Béty et al. 2002) and therefore their spatial distribution around a colony. During low lemming years, the break point at distance from colony can decrease by up to 2 km compared to during high lemming abundance (Lamarre et al. 2017). Our surveys conducted within light goose colonies could have occurred during regional peak or low lemming years and therefore aerial predator abundance may be more variable.

Nevertheless, aerial predator abundance was small, ~27% higher within 20 km from colonies, and 62% higher within 40 km of goose colonies. This elevated aerial predator abundance could influence Cover-Nesting Shorebird and passerine settlement strategies, nest success, and ultimately nest density. When faced with high predation risk, birds may abandon their nests or not nest altogether (Lima 2009). In the vicinity of goose colonies, Cover-Nesting Shorebirds and passerines may be choosing not to nest or suffering higher nest predation rates resulting in lower overall nest densities (Flemming et al. 2019).

**Prey availability**

We have hypothesized that the trends we report here are due to the combined effects of...
habitat loss and increased risk of predation near light goose colonies; however, bird communities could also be responding to goose-induced variation in prey availability, which we did not measure. Invertebrate communities upon which shorebirds and passerines prey may have lower abundances (Milakovic and Jefferies 2003) and diversities (Milakovic et al. 2001) in goose-influenced areas, forcing these birds to forage in areas further from colonies. At the local scale, tundra-nesting shorebirds do not appear to select nest sites based on prey availability (Smith et al. 2007a, Walpole et al. 2008). Studies relating arthropod abundance to habitat use by birds at larger spatial scales have not yet been conducted; as such, this hypothesis warrants further investigation.

Conclusions

Arctic habitats are experiencing changes such as the northward movement of shrub communities due to rising temperatures (Post et al. 2009) and therefore may be sensitive to further pressures imposed by intensive grazing. Arctic-nesting light goose populations have exploded and, in some areas, may initiate trophic cascades by altering vegetation (Abraham et al. 2005a, b) and habitat important for invertebrate communities (Milakovic et al. 2001, Milakovic and Jefferies 2003). Our results show that the effects of these cascades extend further than previously thought and that other important and distinctive components of Arctic avian communities are also affected. We suggest these impacts are the products of goose-induced changes to habitat and, potentially, Generalist Aerial Predator populations. The downstream effects of hyperabundant light geese on other trophic levels may have been underestimated and could be contributing, in part, to the regional declines observed in many tundra-nesting bird species. Future studies to elucidate the effects of geese on the reproductive success of sympatric birds would help to further clarify the magnitude of the issue. Current monitoring and research on goose abundance and population dynamics should also continue so that shorebird management decisions can be made in relation to future goose population changes.

Human-induced habitat alteration at shorebird non-breeding sites and climate change across their ranges are currently thought to be the greatest threats to tundra-breeding shorebirds (Thomas et al. 2006, Studds et al. 2017). In northern areas, climate-driven changes to habitat, predators, and arthropods could interact with goose effects to further alter the suitability of tundra habitats for Arctic-breeding birds, in additive or even unanticipated ways (Flemming et al. 2016). A comprehensive understanding of the current and future effects of geese on sympatric birds is essential as populations of tundra-breeding shorebirds continue to decline.

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Literature Cited

Abraham, K. F., R. L. Jefferies, and R. T. Alisauskas. 2005a. The dynamics of landscape change and snow geese in mid-continent North America. Global Change Biology 11:841–855.
Abraham, K. F., R. L. Jefferies, and R. Rockwell. 2005b. Goose-induced changes in vegetation and land cover between 1976 and 1997 in an arctic coastal marsh. Arctic, Antarctic and Alpine Research 37:269–275.
Alisauskas, R. T., and D. K. Kellett. 2014. Age-specific in situ recruitment of female King Eiders estimated with mark-recapture. Auk 131:129–140.
Alisauskas, R. T., R. F. Rockwell, K. W. Dufour, E. G. Cooch, G. Zimmerman, K. L. Drake, J. O. Leafloor, T. J. Moser, and E. T. Reed. 2011. Harvest, survival, and abundance of midcontinent lesser snow geese relative to population reduction efforts. Wildlife Monographs 179:1–42.
Allombert, S., A. Gaston, and J. Martin. 2005a. A natural experiment on the impact of overabundant deer on songbird populations. Biological Conservation 126:1–13.

Allombert, S., S. Stockton, and J. Martin. 2005b. A natural experiment on the impact of overabundant deer on forest invertebrates. Conservation Biology 19:1917–1929.

Andres, B. A., P. A. Smith, R. G. Morrison, C. L. Gratto-Trevor, S. C. Brown, and C. A. Friis. 2012. Population estimates of North American shorebirds, 2012. Wader Study Group Bulletin 119:178–192.

Baldwin, F. B., R. T. Alisauskas, and J. O. Leafloor. 2011. Nest survival and density of Cackling Geese (Branta hutchinsii) inside and outside a Ross’s Goose (Chen rossii) colony. Auk 128:404–414.

Bart, J., B. Andres, S. Brown, G. Donaldson, B. Harrington, and H. Johnson. 2002. The Program for Regional and International Shorebird Monitoring (PRISM). www.shorebirdplan.org/wp-content/uploads/2013/01/PRISMOverview1_02.pdf

Bart, J., S. Brown, B. A. Andres, R. Platte, and A. Manning. 2012. Chapter 4 in J. Bart and V. H. Johnston, editors. Arctic shorebirds in North America: a decade of monitoring. Studies in Avian Biology Series 44. University of California Press, Berkeley, California, USA.

Bart, J. and V. Johnston. 2012. Arctic shorebirds in North America: a decade of monitoring. Studies in Avian Biology Series 44. University of California Press, Berkeley, California, USA.

Batt, B. D. J., editor. 1997. Arctic ecosystems in peril: report of the Arctic Goose Habitat Working Group. Arctic Goose Joint Venture Special Publication. U.S. Fish and Wildlife Service, Washington, D.C., USA and Canadian Wildlife Service, Ottawa, Ontario, Canada.

Béty, J., G. Gauthier, E. Korpimaki, and J. Giroux. 2002. Shared predators and indirect trophic interactions: lemming cycles and arctic-nesting geese. Journal of Animal Ecology 71:88–98.

Bivand, R., and C. Rundel. 2014. rgeos: interface to Geometry Engine—Open Source (GEOS). R package version 0.3-6. http://CRAN.R-project.org/package=rgeos

Brown, S., J. Bart, R. B. Lanctot, J. A. Johnson, S. Kendall, D. Payer, and J. Johnson. 2007. Shorebird abundance and distribution on the coastal plain of the Arctic National Wildlife Refuge. Condor 109:1–14.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer, New York, New York, USA.

Cargill, S., and R. L. Jefferies. 1984. The effects of grazing by lesser snow geese on the vegetation of a sub-arctic salt-marsh. Journal of Applied Ecology 21:669–686.

CAVM Team. 2003. Circumpolar Arctic Vegetation Map (scale 1:7 500 000). Conservation of Arctic Flora and Fauna (CAFF) Map No. 1. U.S. Fish and Wildlife Service, Anchorage, Alaska, USA.

Collins, M., et al. 2013. Long-term climate change: projections, commitments and irreversibility. In T. F. Stocker, et al. editors. Climate change 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK and New York, New York, USA.

Conkin, J., and R. T. Alisauskas. 2017. Conversion of tundra to exposed peat habitat by snow geese (Chen caerulescens caerulescens) and Ross’s geese (C. rossii) in the central Canadian Arctic. Polar Biology 40:563–576.

Cunningham, J. A., D. C. Kesler, and R. B. Lanctot. 2016. Habitat and social factors influence nest-site selection in Arctic-breeding shorebirds. Auk 133:364–377.

Egevang, C., K. Kampp, and D. Boertmann. 2004. The breeding association of red phalaropes with Arctic Terns: response to a redistribution of terns in a major Greenland colony. Waterbirds 27:406–410.

Farmer, A., R. T. Holmes, and F. A. Pitelka. 2013. Pectoral Sandpiper (Calidris melanotos). In A. Poole, editor. The Birds of North America Online. Cornell Lab of Ornithology, Ithaca, New York, USA.

Flemming, S. A., A. Calvert, E. Nol, and P. A. Smith. 2016. Do hyperabundant Arctic-nesting geese pose a problem for sympatric species? Environmental Reviews 24:1–10.

Flemming, S. A., E. Nol, L. V. Kennedy, and P. A. Smith. 2019. Hyperabundant herbivores limit habitat availability and influence nest site selection of Arctic-breeding birds. Journal of Applied Ecology. https://doi.org/10.1111/1365-2664.13336

Gauthier, G., D. Bertaux, J. Béty, A. Tarroux, J. F. Therryrien, L. McKinnon, P. Legagneux, and M. C. Cadieux. 2011. The tundra food web of Bylot Island in a changing climate and the role of exchanges between ecosystems. Ecoscience 18:223–235.

Gauthier, G., P. Legagneux, M.-A. Valiquette, M.-C. Cadieux, and J.-F. Therrien. 2015. Diet and reproductive success of an Arctic generalist predator: interplay between variations in prey abundance, nest site location, and intraguild predation. Auk 132:735–747.
Haven, W. R., and D. S. Lee. 1999. Parasitic Jaeger (Stercorarius parasiticus). In A. Poole, editor. The Birds of North America Online. Cornell Lab of Ornithology, Ithaca, New York, USA.

Hebblewhite, M., C. A. White, C. G. Nietvelt, J. A. McKenzie, T. E. Hurd, J. M. Fryxell, S. E. Bayley, and P. C. Paquet. 2005. Human activity mediates a trophic cascade caused by wolves. Ecology 86:2135–2144.

Hijmans, R., N. Garcia, and J. Wieczorek. 2010. GADM: database of global administrative areas. www.gadm.org/country

Hines, J. E., P. B. Latour, and C. S. Machtans. 2010. The effects on lowland habitat, breeding shorebirds and songbirds in the Banks Island Migratory Bird Sanctuary Number 1 by the growing colony of Lesser Snow Geese (Chen caerulescens caerulescens). Canadian Wildlife Service Occasional Paper 118, Environment Canada, Canadian Wildlife Service, Ottawa, Ontario, Canada.

Hughes, R. J., A. Reed, and G. Gauthier. 1994. Space and habitat use by greater snow goose broods on Bylot Island, Northwest Territories. Journal of Wildlife Management 58:536.

Jefferies, R. L., A. Jano, and K. F. Abraham. 2006. A biotic agent promotes large-scale catastrophic change in the coastal marshes of Hudson Bay. Journal of Ecology 94:234–242.

Jefferies, R., and R. Rockwell. 2002. Foraging geese, vegetation loss and soil degradation in an Arctic salt marsh. Applied Vegetation Science 5:7–16.

Jefferies, R. L., R. Rockwell, and K. F. Abraham. 2004. Agricultural food subsidies, migratory connectivity and large-scale disturbance in arctic coastal systems: a case study. Integrative and Comparative Biology 44:130–139.

Jehl, J. R. 2006. Coloniality, mate retention, and nest-site characteristics in the semipalmated sandpiper. Wilson Journal of Ornithology 118: 478–484.

Johnson, O. W., and P. G. Connors. 2010. American Golden-Plover (Pluvialis dominica). In A. Poole, editor. The Birds of North America Online. Cornell Lab of Ornithology, Ithaca, New York, USA.

Johnson, S. R., and D. R. Herter. 1989. The birds of the Beaufort Sea. BP Exploration (Alaska) Inc., Anchorage, Alaska, USA.

Johnston, V., et al. 2015. Arctic Migratory Birds Initiative (AMBI): workshop plan 2015–2019. CAFF Strategies Series No. 6. Conservation of Arctic Flora and Fauna, Akureyri, Iceland.

Kagata, H., and T. Ohgushi. 2006. Bottom-up trophic cascades and material transfer in terrestrial food webs. Ecological Research 21:26.

Kellett, D. K., and R. T. Alisauskas. 2011. Clutch size and nest survival of Cackling Geese in a Lesser Snow and Ross’s Goose colony. Waterbirds 34:400–411.

Kerbes, R. H., K. M. Meeres, and R. T. Alisauskas. 2014. Surveys of nesting lesser snow geese and Ross’s geese in Arctic Canada, 2002-2009. Arctic goose joint venture special publication. U.S. Fish and Wildlife Service, Washington, D.C., USA, and Canadian Wildlife Service, Ottawa, Ontario, Canada.

Kotanen, P. M., and R. L. Jefferies. 1997. Long-term destruction of sub-arctic wetland vegetation by lesser snow geese. Ecoscience 4:179–182.

Lamarre, J.-F., P. Legagneux, G. Gauthier, E. T. Reed, and J. Béty. 2017. Predator-mediated negative effects of overabundant snow geese on arctic-nesting shorebirds. Ecosphere 8:e01788.

Latour, P. B., C. S. Machtans, and G. W. Beyersbergen. 2005. Shorebird and passerine abundance and habitat use at a High Arctic breeding site: Creswell Bay, Nunavut. Arctic 58:55–65.

Lecomte, N., G. Gauthier, and J.-F. Giroux. 2008. Breeding dispersal in a heterogeneous landscape: the influence of habitat and nesting success in greater snow geese. Oecologia 155:33–41.

Legagneux, P., et al. 2012. Disentangling trophic relationships in a high arctic tundra ecosystem through food web modeling. Ecology 93:1707–1716.

Lima, S. L. 2009. Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. Biological Reviews 84:485–513.

Mainguy, J., G. Gauthier, J.-F. Giroux, and J. Béty. 2006. Gosling growth and survival in relation to brood movements in Greater Snow Geese (Chen caerulescens atlantica). Auk 123:1077.

Mariash, H. L., P. A. Smith, and M. Mallory. 2018. Decemberal response of Arctic freshwaters to burgeoning goose populations. Ecosystems 21:1230–1243.

Martin, T. G., P. Arcese, and N. Scheerder. 2011. Browsing down our natural heritage: deer impacts on vegetation structure and songbird populations across an island archipelago. Biological Conservation 144:459–469.

McKinnon, L., D. Berteaux, G. Gauthier, and J. Béty. 2013. Predator-mediated interactions between preferred, alternative and incidental prey in the arctic tundra. Oikos 122:1042–1048.

Meloftpfe, H., et al. 2007. Effects of climate variation on the breeding ecology of Arctic shorebirds. Meddelelser om Grønland, Bioscience 59. Danish Polar Center, Copenhagen, Denmark.

Milakovic, B., T. Carleton, and R. Jefferies. 2001. Changes in midge (Diptera: Chironomidae)
populations of sub-arctic supratidal vernal ponds in response to goose foraging. Ecoscience 8:58–67.

Milakovic, B., and R. Jefferies. 2003. The effects of goose herbivory and loss of vegetation on ground beetle and spider assemblies in an Arctic supratidal marsh. Ecoscience 10:57–65.

Morrison, R. I. G. 1997. The use of remote sensing to evaluate shorebird habitats and populations on Prince Charles Island, Foxe Basin, Canada. Arctic 50:55–75.

Moskoff, W., and R. Montgomeri. 2002. Baird’s Sandpiper (Calidris bairdii). In A. Poole, editor. The Birds of North America. Cornell Lab of Ornithology, Ithaca, New York, USA.

O, P. C., P. M. Kotanen, and K. F. Abraham. 2006. Geese and grazing lawns: responses of the grass Festuca rubra to defoliation in a subarctic coastal marsh. Canadian Journal of Botany 84:1732–1739.

Parmeelee, D. F., H. A. Stephens, and R. H. Schmidt. 1967. The birds of Southeastern Victoria Island and adjacent small islands. National Museum of Canada, Ottawa, Ontario, Canada.

Peterson, S. L., R. F. Rockwell, C. R. Witte, and D. N. Koons. 2013. The legacy of destructive Snow Goose foraging on supratidal marsh habitat in the Hudson Bay Lowlands. Arctic, Antarctic, and Alpine Research 45:575–583.

Post, E., et al. 2009. Ecological dynamics across the arctic associated with recent climate change. Science 325:1335–1338.

R Development Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ripple, W. J., et al. 2014. Status and ecological effects of the world’s largest carnivores. Science 343:151.

Rockwell, R., C. Witte, R. Jefferies, and P. Weatherhead. 2003. Response of nesting snow goose sparrow to 25 years of habitat change in a snow goose colony. Ecoscience 10:33–37.

Saafield, S. T., R. B. Lanctot, S. C. Brown, D. T. Saalfeld, J. A. Johnson, B. A. Andres, and J. R. Bart. 2013. Predicting breeding shorebird distributions on the Arctic Coastal Plain of Alaska. Ecosphere 4:16.

Sammler, J. E., D. E. Andersen, and S. K. Skagen. 2008. Population trends of tundra-nesting birds at Cape Churchill, Manitoba, in relation to increasing goose populations. Condor 110:325–334.

Slattery, S. M., and R. T. Alisauskas. 2007. Distribution and habitat use of Ross’s and Lesser snow geese during late brood rearing. Journal of Wildlife Management 71:2230.

Smith, P. A., H. G. Gilchrist, and J. N. M. Smith. 2007a. Effects of nest habitat, food, and parental behavior on shorebird nest success. Condor 109:15–31.

Smith, P. A., H. G. Gilchrist, J. N. M. Smith, and E. Nol. 2007b. Annual variation in the benefits of a nesting association between Red Phalaropes (Phalaropus fulicarius) and Sabine’s Gulls (Xema sabini). Auk 124:276–290.

Srivastava, D., and R. Jefferies. 2002. Intertidal plant communities of an Arctic salt marsh: the influence of isostatic uplift and herbivory. Ecoscience 9:112–118.

Studds, C. E., et al. 2017. Rapid population decline in migratory shorebirds relying on Yellow Sea tidal mudflats as stopover sites. Nature Communications 8:14895.

Taylor, P. S. 1974. Summer populations and food ecology of jaegers and snowy owls on Bathurst Island, N.W.T. Dissertation. University of Alberta, Edmonton, Alberta, Canada.

Thomas, G. H., R. B. Lanctot, and T. Szekely. 2006. Can intrinsic factors explain population declines in North American breeding shorebirds? A comparative analysis. Animal Conservation 9:252–258.

Walker, B. G., S. L. Meddle, L. M. Romero, M. M. Landys, J. Reneerkens, and J. C. Wingfield. 2015. Breeding on the extreme edge: modulation of the adrenocortical response to acute stress in two High Arctic passerines: stress response in two high Arctic passerines. Journal of Experimental Zoology Part A: Ecological Genetics and Physiology 323:266–275.

Walpole, B., E. Nol, and V. Johnston. 2008. Breeding habitat preference and nest success of Red-necked Phalaropes on Niglintgak Island, Northwest Territories. Canadian Journal of Zoology 86:1346–1357.

Weiser, E. L., and A. N. Powell. 2010. Does garbage in the diet improve reproductive output of glaucous gulls? Condor 112:530–538.

Wheelwright, N. T., and J. D. Rising. 2008. Savannah Sparrow (Passerculus sandwichensis). In A. Poole, editor. The Birds of North America. Cornell Lab of Ornithology, Ithaca, New York, USA.

Wirita, H. K., E. J. Vesterinen, P. A. Hambäck, E. Weingartner, C. Rasmussen, J. Reneerkens, N. M. Schmidt, O. Gilg, and T. Roslin. 2015. Exposing the structure of an Arctic food web. Ecology and Evolution 5:3842–3856.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2785/full