RESEARCH ARTICLE

Hyperabundant herbivores limit habitat availability and influence nest site selection of Arctic-breeding birds

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Abstract

1. Understanding an organism's habitat selection and behavioural flexibility in the face of environmental change can help managers plan for future conservation of that species. Hyperabundant tundra-nesting geese are influencing Arctic environments through their foraging activities. Goose-induced habitat change in Arctic wetlands may influence the availability of habitat for numerous shorebird species that breed sympatrically with geese.

2. We explore whether goose-induced habitat alteration affects shorebird breeding density and nest site selection. Using habitat data collected at sites with High, Moderate and Low goose influence, and samples collected during two periods separated by 11 years, we document the habitat characteristics influenced by geese. We describe the habitat characteristics preferred by shorebirds and relate their availability to goose influence and shorebird density. Finally, we examine whether shorebird nest site selection has changed over time and whether shorebirds select nest sites differently in habitat influenced by geese.

3. We document spatial and temporal changes in sedge meadow habitat and lateral concealment relating to goose influence. The availability of sedge meadow habitat and the degree of lateral concealment declined with increasing goose influence, and also declined at two sites over the 11 years of the study.

4. Densities of both cover- and open-nesting shorebirds were highest where goose influence was lowest. At sites with Low goose influence, cover-nesting shorebirds selected nest sites with more sedge meadow and concealment than at sites with Moderate and High goose influence, presumably because these high-quality sites were more available.

5. Synthesis and applications. Intensive foraging by a colony of hyperabundant geese is limiting the availability of preferred nesting habitat and densities of sympatric-nesting shorebirds. Where goose-induced habitat alteration is pronounced shorebird species that select concealed nest sites are nesting in areas with lower concealment and less sedge meadow. Studies examining the degree to which these effects scale up to impact the population sizes of declining shorebirds should be considered a future research priority. Moreover, management strategies for geese should incorporate the habitat needs of sympatric species and

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reinvigorate efforts for goose population reduction in order to achieve the population targets articulated by management agencies.

**KEYWORDS**
Arctic, habitat alteration, habitat availability, nest site selection, overabundant, Ross’ goose, shorebird, snow goose

# 1 | INTRODUCTION

Species vary in their flexibility of habitat selection, from generalists to specialists, with specialists being less flexible and more susceptible to change (Devictor, Julliard, & Jiguet, 2008; Owens & Bennett, 2000). By understanding an organism’s habitat selection and flexibility in the face of environmental change, managers can plan for future conservation actions.

Projected climate-related changes such as rising temperatures, longer growing seasons and expanding shrub communities (Post et al., 2009) are expected to profoundly impact Arctic environments, increasing the need to understand habitat selection among northern wildlife. Typically, tundra vegetation changes at a relatively slow rate (Forbes, Ebersole, & Strandberg, 2001; Jorgenson, Hoef, & Jorgenson, 2010); however, in the last 20 years, some North American Arctic and sub-Arctic vegetation communities have experienced significant and rapid change (Abraham, Jefferies, & Rockwell, 2005; Batt, 1997; Kotanen & Jefferies, 1997). In addition to climate-related changes, increasingly abundant breeding and staging lesser snow (Chen caerulescens caerulescens) and Ross’ goose (Chen rossii) have altered wetland habitats through their foraging activities (Abraham et al., 2005; Batt, 1997; Kerbes, Kotanen, & Jefferies, 1990). Intensive grazing of above-ground vegetation, and grubbing (e.g. probing beneath ground to consume the plants’ rhizomes) by geese can deplete the energy reserves of forage plants and impede their growth (Batt, 1997; Jefferies, Rockwell, & Abraham, 2004; Srivastava & Jefferies, 1996). In extreme cases, when tundra vegetation is removed by intensive foraging, the result can be an alternate stable habitat state of exposed substrate or moss carpet (Srivastava & Jefferies, 1996).

Goose-induced habitat alteration in Arctic wetlands has the potential to influence the availability of habitat for shorebirds that breed sympatrically with geese (Flemming, Calvert, Nol, & Smith, 2016; Sammler, Andersen, & Skagen, 2008; Swift, Rodewald, & Senner, 2017). Many shorebirds nest among grasses and sedges in graminoid-dominated habitats (Cunningham, Kesler, & Lanctot, 2016; Saalfeld et al., 2013; Smith, Gilchrist, & Smith, 2007) to conceal their nests from predators (Smith et al., 2007). By doing so, some species increase their nest survival (Bentzen et al., 2017; Walpole, Nol, & Johnston, 2008) and may receive thermoregulatory benefits (Miller, Nol, Nguyen, & Turner, 2015). If removal of vegetative cover by geese limits the availability of preferred habitats, then birds may forgo nesting or select habitat that makes them more susceptible to predation.

Understanding how geese influence habitat characteristics, how shorebirds select habitat and the degree to which the two processes interact can allow for better management of these species and their environment. Here, we explore these questions using habitat data collected at three study areas in Arctic North America with High, Moderate and Low goose influence. First, we tested whether geese have landscape-level effects on habitat availability. We predicted that the proportions of moss carpet habitat would be highest and sedge meadow habitat and vegetation concealment lowest in areas with High goose influence. We also tested for habitat change over time, using habitat data collected during two periods separated by 11 years. We predicted that we would find a decline in the proportion of sedge meadow habitat and concealment at the study area with Moderate goose influence but no change at the study area with Low goose influence.

We then used habitat data collected at shorebird Nest, Non-use and Random Sites to identify the habitat characteristics preferred by shorebirds, their availability and the resulting influence on shorebird nest density. Finally, we examined whether shorebird nest site selection has changed over time and whether shorebirds select nest sites differently in habitat influenced by geese. We predicted that the density of shorebirds that select nest sites in vegetation that conceals their nests (i.e. cover-nesters) would be highest in the study area with Low goose influence and that the nests at the study area with Moderate and High goose influence would have lower concealment than at the study area with Low goose influence. By contrast, we expected to see no change in the density of shorebirds that selected exposed nest sites with little vegetation (i.e. open-nesters) and no difference in their habitat characteristics among study areas.

# 2 | MATERIALS AND METHODS

## 2.1 | Study areas and species

We conducted fieldwork from late May to early August, in various years between 2000 and 2017 at three study areas: two within the East Bay Migratory Bird Sanctuary on Southampton Island, Nunavut and one on Coats Island, Nunavut, Canada. Light geese are believed to be the dominant herbivores present in this region. Other herbivores such as Cackling Goose (Branta hutchinsii), caribou and lemming (absent from Coats Island) are present, but in lower numbers relative to light geese. Moreover, the abundance of these other herbivores has not increased enough over time, to explain the reductions in vegetation that we attribute to geese. The principal egg
predators in the region are arctic fox (Vulpes lagopus) followed by Parasitic Jaeger (Stercorarius parasiticus); Glaucous Gull (Larus hyperboreus) are also present, but we have not observed them depredating nests.

The first study area (6 km²) is situated within a Lesser Snow Goose colony (63°55′N, 81°55′W; Figure S1) that has been linked to changes in graminoid-dominated and mesic lowland habitats and their conversion to bare peat and moss (Fontaine & Mallory, 2011; K. Abraham, unpubl. data). The East Bay Mainland (63°59′N, 81°40′W) study area comprises a 12-km² area and is situated approximately 10 km east of the goose colony. At Coats Island (62°51′N, 82°29′W), approximately 135 km away, the 12-km² study area has no permanent goose breeding colony; however, the study area is used for staging and moulting (Kerbes, Meeres, & Alisauskas, 2014, S.A. Flemming pers. obs). Combined, these areas represent a gradient of goose use from High (goose colony) to Moderate (East Bay Mainland), to Low (Coats Island).

We quantified the differences in goose use between our three study areas through a survey of goose faecal pellets. From 2014 to 2017, we counted all goose faecal pellets (old and new) in two 1-m² plots within 5 m of the 356 sites selected at random for habitat surveys (see below).

2.2 Study species, nest searching and densities

Across the study areas, eight tundra-nesting shorebird species are common breeders: Dunlin (Calidris alpina), Semipalmated Sandpiper (Calidris pusilla), White-rumped Sandpiper (Calidris fuscicollis), Red Phalarope (Phalaropus fulicarius), Black-bellied Plover (Pluvialis squatarola), American Golden-Plover (Pluvialis dominica), Semipalmated Plover (Charadrius semipalmatus) and Ruddy Turnstone (Arenaria interpres). We located the nests of these species using behavioural observations and by flushing the incubating bird from the nest while walking. We marked the location of each nest (±3 m) with a Global Positioning System (GPS) and wooden tongue depressors placed ~10 m from the nest cup.

To obtain estimates of nesting densities of shorebirds, we intensively searched 300 × 400 m plots throughout the breeding season at each of the study areas (High use area: n = 2 plots, Moderate: n = 3 and Low: n = 3). During intensive nest searches, individual surveyors searched all portions of each plot. Plots were searched during six visits each season and we averaged 4.1 hr per visit; a level of search effort that is considered sufficient to find nearly all nests that persist for multiple visits (Smith, Bart, Lanctot, McCaffery, & Brown, 2009).

2.3 Habitat survey locations and years

We conducted habitat surveys at the study areas over 17 years; however, due to the inter-annual variation in field support and number of nesting shorebirds, our habitat sampling effort varied among years and study areas. From 2015 to 2017, we collected habitat data at locations drawn randomly from within the High, Moderate and Low goose influence areas (Random Sites; see Table 3 for sample sizes). Using these data, we characterized the availability of habitats within each of the study areas to explore how geese influence the habitats important for nesting shorebirds. A subset of 85 of these Random Sites had been surveyed previously, prior to 2005, at the Moderate and Low study areas only (i.e. habitat surveys were not completed at the High study area in these earlier years). We identified temporal changes in habitat that may have resulted from goose foraging by comparing habitat measures between these two sampling periods, and refer to these 85 sites as Temporal Sites when making these comparisons.

To explore spatial and temporal patterns in shorebirds’ nest site selection, we completed habitat surveys at all shorebird nest sites found within the Moderate and Low study areas (few nests were found at the High study area) from 2000 to 2004 and from 2014 to 2016 (Nest Sites). In addition to measuring habitat characteristics at Nest Sites, we also conducted surveys at sites within 5 m of the Nest Site to provide a finer scale indication of habitat preference (Jones, 2001), and refer to these as Non-use Sites. In all years, we conducted habitat surveys during the last 2 weeks of July, once breeding efforts were complete.

2.4 Habitat surveys

During Random, Temporal, Nest and Non-use Site habitat surveys, we measured habitat characteristics by estimating the proportional cover of habitat within a 75 m² circle surrounding the Nest or Random Site and identifying the dominant habitat category (sedge meadow, SM; upland, Upl; scrub willow, SW; exposed substrate, ES; moss carpet, MC; water, Wa; Table S1). Following Smith et al. (2007), we also estimated lateral concealment using 12 cm diameter discs, which were covered in 1 cm grids and placed at the point of interest. We estimated the proportion (±5%) of the vertically oriented discs obscured when viewed from a distance of 5 m and height of 40 cm (approximating the height of an arctic fox), from each cardinal direction. We also recorded the height (in mm) and type of each ground cover type that was touching the disc at each cardinal direction.

2.5 Statistical methods

2.5.1 Goose use and habitat alteration

Using Random Sites data, we tested for differences in goose faecal pellet abundance using an ANOVA with study area (High, Moderate, Low) and dominant habitat type (Upl, SM, MC, SW, ES) as fixed effects. To test for differences in concealment and cover height between study areas, we conducted a MANOVA with study area, dominant habitat type and an interaction between the two as fixed effects. To determine which cover type was driving the observed trends, we conducted ANOVAs on each cover type with study area as the fixed effect and height (mm) as the response variable.

We were interested in determining the effect of goose use on lateral concealment within each habitat type after accounting for between area variations in concealment. To evaluate this, we used a
linear mixed effects model with lateral concealment as the response variable, and faecal pellet count, dominant habitat type and an interaction between the two latter variables as predictors. To account for variation between the two study periods, we included study area as a random effect.

2.6 | Habitat availability

2.6.1 | Spatial patterns

To identify the availability of each dominant habitat type, we used Random Sites data and determined and the frequency at which each dominant habitat type occurred within each study area. Proportions of habitats within the 75 m² surveyed at each Random Site were highly correlated, so we used a principal components analysis (PCA) to reduce the number of variables. Principal components analyses revealed three principal components that explained 60.82% of the variation among sampling points (Table 1). The first principal component (PC1) described a gradient from low sedge meadow and low lateral concealment (positive PC values) to high sedge meadow and high lateral concealment (negative PC values). The second principal component (PC2) explained a gradient of water (negative) to dry upland habitat (positive). PC3 described a gradient of moss carpet (negative) to water (positive). We used a MANOVA to test for differences in the scores derived from the first three principal components with study area (High, Moderate, Low) as a fixed effect.

2.6.2 | Temporal trends

We used Temporal Sites data to identify changes in habitat that occurred between the two study periods (prior to 2005 and revisited 2015–2016). We computed scores for both sets of sites using the PCA described above, and then performed a MANOVA on the scores from the first three principal components. We included study period, study area (Moderate use and Low use only; no habitat available for the four most common species (Semipalmated Sandpiper and Dunlin, at the Low use study area, and White-rumped Sandpiper as cover-nesting species because they selected nest sites in vegetation that concealed their nests. We classified American Golden-Plover, Black-bellied Plover, Semipalmated Plover and Ruddy Turnstone as open-nesting species because they selected exposed nest sites with little vegetation. We used a linear mixed effects model with PC1 as the response variable, and study area (Low, Moderate), survey scale (Nest Site, Non-use Site) and an interaction between the two as fixed effects. To account for any species-specific variation in selection, we included species as a random effect.

2.7 | Habitat selection and nest density

2.7.1 | Spatial patterns

Using the Nest Sites data, we classified the preferred nesting habitat of each shorebird species as the dominant habitat type (i.e. greatest proportional cover in the 75 m² surveyed patch) that was used most frequently across all study areas. To identify how shorebirds select nest sites across study areas, we tested for differences in PCA scores computed from Random Sites (responses: PC1, PC2, PC3) between survey scales (Nest, Non-use, Random Sites) of individual shorebirds using MANOVAs.

We were also interested in comparing habitat variables between Nest and Non-use Sites among study areas; however, the number of shorebird nests per species and study area was insufficient for analysis. We therefore lumped species into “cover-nesting” and “open-nesting” categories. Based on our results and previous studies (Cunningham et al., 2016; Smith et al., 2007), we classified Red Phalarope, Dunlin, Semipalmated Sandpiper and White-rumped Sandpiper as cover-nesting species because they selected nest sites in vegetation that concealed their nests. We classified American Golden-Plover, Black-bellied Plover, Semipalmated Plover and Ruddy Turnstone as open-nesting species because they selected exposed nest sites with little vegetation. We used a linear mixed effects model with PC1 as the response variable, and study area (Low, Moderate), survey scale (Nest Site, Non-use Site) and an interaction between the two as fixed effects. To account for any species-specific variation in selection, we included species as a random effect.

2.7.2 | Temporal trends

As habitat availability changes, the habitat selected by nesting shorebirds could change or not, depending on shorebirds’ ability to mitigate the changes through habitat selection. We tested for temporal change in the nesting habitat selected by shorebirds between periods by contrasting habitat at shorebird nest sites prior to 2005 and 2014–2016. Adequate sample sizes (>20/period) of Nest Sites were available for the four most common species (Semipalmated Sandpiper and Dunlin, at the Low use study area, and White-rumped Sandpiper and Black-bellied Plover at the Moderate area). For each species, we tested for temporal shifts in habitat use between study periods using species-specific MANOVAs, with the PC scores as response variables.

2.7.3 | Shorebird Nest density

We tested for variation in shorebird nest density (nests per ha within the intensively searched plots) among the three study areas using a general linear model with a Poisson distribution. In this model, we included study area, species’ cover type (cover, open), year and surveys were conducted at the High use study area prior to 2005) and an interaction between the two as fixed effects.
plot, with an interaction between cover type and study area as fixed effects.

Statistical tests were performed in R version 3.2.4 (R Core Team, 2016). All MANOVAs were significant (Table S2), so we report the results of all post hoc ANOVAs.

3 | RESULTS

3.1 | Goose use and habitat alteration

Random Sites data revealed that goose pellet counts differed among study areas and habitat types (Table 2). As expected, the High goose area (16.54 ± 3.06; M ± SE pellets per 1 m² plot) had the highest faecal pellet count, followed by the Moderate (11.11 ± 2.51), and Low goose areas (1.75 ± 0.29). The moss carpet habitat type (23.29 ± 5.77) contained the greatest number of faecal pellets, followed by exposed substrate (13.03 ± 4.00), scrub willow (7.91 ± 2.46) and sedge meadow (7.20 ± 1.63).

Study area, dominant habitat type and an interaction between the two influenced concealment and the height of vegetation surrounding Random Sites (Table 2). After accounting for multiple tests, concealment was highest at the Low goose use area, driven largely by increases in graminoid height and to a lesser extent willow, and Avens height, but not moss, or rock height (Table 2; Figure 1b). Goose use as measured by faecal pellet count influenced lateral concealment but this effect was dependent on habitat type (F₁,₃₅₀: 3.30, p < 0.001), specifically, the proportions of sedge meadow (F₁,₃₅₀: 13.46, p < 0.001; Figure 1c).

3.2 | Habitat availability

3.2.1 | Spatial patterns

The frequency of dominant habitat types within the 75 m² circles surveyed at Random Sites varied among study areas (Table 3). Upland habitat, exposed substrate, and moss carpet were the dominant habitat types at the High goose study area, while water was dominant at the Moderate, and sedge meadow at the Low. As predicted, the frequency of both exposed substrate and moss carpet was highest at the High goose study area and lowest at the Low goose study area, while the opposite was true of sedge meadow habitat. Principal component scores also varied among study areas.

| TABLE 2 | Results of ANOVAs exploring variation in goose influence, habitat and shorebird nest density among study areas, habitat types and temporal periods |
|---------------------------------|-----------------|-----------------|-----------------|-----------------|
| Category                        | Response        | Effect          | df, n           | F-value        | p-value        |
| Goose influence                 | Pellet count    | Study area      | 2, 226          | 26.27          | <0.001         |
|                                |                 | Habitat type    | 2, 226          | 7.13           | <0.001         |
| Habitat characteristics         | Lateral concealment | Study area      | 2, 268          | 64.51          | <0.001         |
|                                |                 | Habitat type    | 4, 268          | 9.11           | <0.001         |
|                                |                 | Study area × habitat type | 8, 268 | 4.66 | <0.001 |
|                                | Cover height    | Study area      | 2, 268          | 25.16          | <0.001         |
|                                |                 | Habitat type    | 4, 268          | 16.84          | <0.001         |
|                                |                 | Study area × habitat type | 8, 268 | 3.75 | <0.01  |
| Cover type variation among study areas | Graminoid     | Study area      | 2, 392          | 62.57          | <0.001         |
|                                |                 | Study area      | 2, 86           | 6.07           | <0.001         |
|                                |                 | Study area      | 2, 89           | 15.84          | <0.001         |
|                                |                 | Study area      | 2, 95           | 2.02           | 0.14           |
|                                |                 | Study area      | 2, 52           | 0.67           | 0.42           |
| Habitat variation among study areas | PC1           | Study area      | 2, 353          | 58.25          | <0.001         |
|                                |                 | Study area      | 2, 353          | 0.12           | 0.88           |
|                                |                 | Study area      | 2, 353          | 2.59           | 0.08           |
| Habitat change between collection periods | PC1           | Study area      | 1, 204          | 20.53          | <0.001         |
|                                |                 | Temporal period | 1, 204          | 30.09          | <0.001         |
|                                |                 | Study area      | 1, 204          | 1.32           | 0.25           |
|                                |                 | Temporal period | 1, 204          | 0.10           | 0.75           |
|                                |                 | Study area      | 1, 204          | 19.87          | <0.001         |
|                                |                 | Temporal period | 1, 204          | 11.17          | <0.001         |
| Shorebird Nest density          | Study area      | 2, 39           | 16.23           | <0.001         |
|                                | Cover type      | 1, 39           | 8.33            | <0.01          |
|                                | Study area × nesting type | 2, 39 | 5.09 | <0.05 |

Significant effects are in bold.
Scores suggested that the proportion of sedge meadow and amount of lateral concealment (PC1) were lowest at the High goose area and highest at the Low area (Table 2; Figure 2); however, PC2 and PC3 scores did not differ among study areas.

### 3.2.2 Temporal trends

Using the Temporal Sites, and after accounting for habitat differences among study areas, we found that habitat differed between sample periods (Table 2; Figure 3). For both areas, sedge meadow and concealment (PC1) decreased and water (PC2) increased between the two time periods. Unexpectedly however, these differences were not greater at the Moderate use area versus the Low ($p > 0.05$; Figure 3).

### 3.3 Habitat selection and nest density

#### 3.3.1 Spatial and temporal trends

Each shorebird species exhibited clear preference for nesting in one of the six dominant habitat types (Table 3). American Golden-Plover and Black-bellied plover preferred upland, Ruddy Turnstone and Semipalmated Plover preferred exposed substrate, and Red Phalarope, Dunlin, White-rumped Sandpiper and Semipalmated Sandpiper preferred sedge meadow habitat.

Principal component scores differentiated Nest Sites of each shorebird species from Non-use and Random Sites (Table 2; Figure 4), and this selection did not change over time for the four species we tested ($p > 0.05$). All four cover-nesting species selected Nest Sites
with more sedge meadow and lateral concealment (negative values of PC1) than Non-use and Random Sites, while the open-nesting Semipalmated Plover selected sites with less sedge meadow and concealment (Table 4). Two cover-nesting species (Red Phalarope and Dunlin) and two open-nesting species (American Golden-Plover and Ruddy Turnstone) had higher PC2 scores than Non-use and Random Sites. Three cover-nesting species plus Semipalmated Plover selected Nest Sites with less moss carpet and more water than Non-use and Random Sites. As predicted, cover-nesting species selected Nest Sites with more sedge meadow and concealment (i.e. lower PC1 scores) than Non-use Sites ($F_{1,569} = 46.79, p < 0.001$), and these Nest Sites had more sedge meadow and concealment at the Low goose use study area than at the Moderate ($F_{1,569} = 14.78, p < 0.001$; Figure 5). Open-nesting species at the Moderate goose use study area selected Nest Sites with slightly less sedge meadow and concealment (PC1) than at the Low ($F_{1,232} = 4.35, p < 0.04$), but these indices did not differ between Nest and Non-use Sites ($F_{1,232} = 2.38, p = 0.12$), or by an interaction between study areas and survey scale ($F_{1,232} = 0.32, p = 0.57$).

### 3.3.2 Nest density

Shorebird nest density varied by study area, cover type, and a study area by cover type interaction (Table 3). Cover- and open-nesting shorebird densities were significantly higher at the Low goose area (cover: $0.27 \pm 0.21$ per ha; open: $0.07 \pm 0.05$ per ha) than at the High

![Figure 2](https://via.placeholder.com/150)

**Figure 2** Principal components scores for habitat data collected at Random Sites at three study areas varying in goose influence. Ellipses show the 95% confidence limits for each area.

![Figure 3](https://via.placeholder.com/150)

**Figure 3** Variation in PC scores ($M \pm SE$) between two time periods at Random and Nest Sites situated at Low and Moderate goose influence study areas.
DISCUSSION

We demonstrate significant impacts of geese on both the abundance and habitat use of nesting shorebirds and add to the growing body of evidence that hyperabundant populations of light geese breeding in North America are significantly altering tundra habitats and impacting sympatric species (Flemming et al., 2016; Sammler et al., 2008; Swift et al., 2017). When preferred habitat is altered or becomes limited, birds may search for suitable habitat elsewhere, resulting in locally depressed nest densities (Martin, Arcese, & Scheerder, 2011). Alternatively, birds could nest in non-preferred habitat (Chen, Liu, Yan, & An, 2011; Cornelius, 2008) with possible consequences for their reproductive success (Battin, 2004; Demeyrier, Lambrechts, Perret, & Grégoire, 2016). We found both patterns in our results. Cover-nesting shorebird densities were lowest in our study area with the greatest goose influence. Individuals that nested in these goose-affected areas selected nest sites with less sedge meadow and concealment than at the less affected area, possibly suggesting some behavioural flexibility in nest site selection. As concealment of nests can be an important predictor of success for some tundra birds (Bentzen et al., 2017; Walpole et al., 2008), shorebirds nesting in sites with less nest concealment may be more susceptible to

![FIGURE 4 Principal component scores of habitat for shorebird Nest, Non-use and Random Sites across study areas. Ellipses show the 95% confidence limits](image)

**TABLE 4** MANOVA results showing the difference between PC scores for Shorebird Nest, Non-use and Random Sites, for three principal components of open- and cover-nesting shorebird species

| Species                  | df, n | PC1        | p-value | PC2        | p-value | PC3        | p-value |
|--------------------------|-------|------------|---------|------------|---------|------------|---------|
| Cover-nesters            |       |            |         |            |         |            |         |
| White-rumped Sandpiper   | 2, 505| 63.159     | <0.001  | 1.465      | 0.232   | 1.547      | 0.214   |
| Semipalmated Sandpiper   | 2, 625| 166.740    | <0.001  | 2.217      | 0.110   | 11.058     | <0.001  |
| Red Phalarope            | 2, 408| 50.350     | <0.001  | 6.463      | 0.002   | 10.045     | <0.001  |
| Dunlin                   | 2, 450| 106.770    | <0.001  | 8.340      | <0.001  | 16.961     | <0.001  |
| Open-nesters             |       |            |         |            |         |            |         |
| American Golden-Plover   | 2, 409| 0.390      | 0.678   | 59.193     | <0.001  | 0.264      | 0.768   |
| Black-bellied plover     | 2, 424| 0.073      | 0.930   | 56.339     | <0.001  | 0.051      | 0.950   |
| Semipalmated Plover      | 2, 396| 5.839      | 0.003   | 0.058      | 0.944   | 13.931     | <0.001  |
| Ruddy Turnstone          | 2, 422| 3.049      | 0.048   | 6.075      | 0.003   | 1.393      | 0.250   |

Significant effects are in bold.

(cover: 0.01 ± 0.03 per ha; open: 0.00 ± 0.00 per ha) and Moderate areas (cover: 0.02 ± 0.04 per ha; open: 0.01 ± 0.03 per ha)
areas have 29% more bare ground, 30% more moss and 32% less sedge cover than intact areas (Sammler et al., 2008), and grazing geese have reduced the proportions of sedge (−37%) and scrub habitat (−61%; Peterson, Rockwell, Witte, & Koons, 2013). At our study areas, intensive use of the goose colony and post-hatching dispersal of family groups to our Moderate use area, along with the preferential use of certain habitats as seen in the faecal pellet counts, can explain the gradient of (presumed) habitat disturbance we see among areas and habitat types.

The temporal patterns in habitat condition reported here present a less clear signal of goose disturbance over the time period explored. Our Moderate and Low goose use areas both experienced similar declines in the extent of sedge meadow habitat and lateral concealment over ~11 years. In late July, we routinely observe flocks of up to 350 and 1,000 non-breeding and molting light geese at the Low and Moderate use areas (S.A. Flemming and L.V. Kennedy pers. obs.), respectively, suggesting they are used for molting or staging by geese breeding elsewhere. The local declines in sedge meadow and lateral concealment that we report for the Moderate and Low use areas may therefore reflect the influence of geese that do not breed locally.

Although the declines are similar, it is important to recall that the indices for sedge meadow and lateral concealment at the Low goose use area remain well above those at the Moderate area. Indeed, values recorded at the Moderate area prior to 2005 are similar to those recorded during the present period at the Low use area. This could reflect that much of the habitat alteration at the Moderate goose use area happened prior to our earlier habitat surveys.

Fontaine and Mallory (2011) already documented conversion of sedge meadow to exposed substrate and peat around the High and Moderate use study areas in 2001, before we measured habitat in 2004. Between 1997 and 2014, the entire Southampton Island breeding population of light geese increased by 44%, while the colonies near our study areas (East Bay and Coral Harbour colonies) increased by 85% (Kerbes et al., 2014; J. Leafloor, unpubl. data). Thus, although the population growth in this region is still substantial and ongoing, it is less rapid than the exponential growth that occurred range-wide prior to the 2000s (e.g. Alisauskas et al., 2011).

4.2 Shorebird nest site availability

The densities of "cover-nesting" shorebirds that use vegetation to conceal their nests from predators (Cunningham et al., 2016; Smith et al., 2007) were ~20 and ~15 times greater at the Low goose influence area compared to the High and Moderate areas respectively. Species such as the Red Phalarope, Semipalmated Sandpiper, Dunlin and White-rumped Sandpiper preferred nest sites with greater coverage of sedge meadow and higher lateral concealment. Cover-nesting shorebird densities may therefore be limited by the availability of sedge meadow within the goose colony (dominant at only 3% of Random Sites) and the low lateral concealment (0%, on average) provided there. Semipalmated Sandpiper and Dunlin nested in graminoid-dominated patches, while White-rumped Sandpiper and

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**FIGURE 5** Variation in PC1 scores (M ± SE) at Nest and Non-use Sites for cover- and open-nesting shorebirds at Low and Moderate goose influence study areas.
Red Phalarope preferred sites that provided significantly higher than average lateral concealment (32% and 59% concealment respectively). We propose that these species are avoiding goose-altered habitat because nest sites with suitable attributes are limited. Comparable results have been reported in the Hudson Bay Lowlands where cover-nesting shorebirds and passerines were 3.23 and 2.44 times more abundant in intact versus altered habitat respectively (Sammler et al., 2008).

Similarly, the density of open-nesting species was eight times higher at the Low goose study area compared to the Moderate area, and no open-nesting species were found nesting at the High area. In the Arctic, “open-nesting” shorebirds select nest sites that provide unimpeded views of predators, relying on distraction displays and crypsis to avoid predation (Smith et al., 2007). Thus, changes in the amount of lateral concealment or sedge meadow prevalence, for example from goose grazing, should not affect nest site choice for these species. American Golden-Plover and Black-bellied Plover primarily nested in upland, a habitat type used infrequently by geese based on faecal pellet counts, while Semipalmated Plover and Ruddy Turnstone preferred sites with exposed substrate and selected nest sites with less sedge meadow and concealment than the mean for Random Sites. Instead of habitat effects, the absence of these open-nesting species within areas heavily used by geese could reflect an increased abundance of predators in these areas. Lamarre, Legagneux, Gauthier, Reed, and Béty (2017) found that the frequencies of occurrence of American Golden-Plovers were ~40% and ~20% higher far from a goose colony compared to within the centre of the colony during high and low lemming years, respectively, demonstrating a link between occupancy and predation risk, irrespective of habitat.

4.3 Nest site flexibility

To test for behavioural flexibility, we examined whether shorebirds that chose to nest, changed their habitat selection when available habitat became limiting. For the four species for which we could test this, we found that the nest site selection remained constant between 11 years, while the availability of sedge meadow and lateral concealment declined. This suggests that habitat selection is inflexible and changing habitat conditions could lead to fewer individuals finding suitable nesting sites. In the Hudson Bay Lowlands where goose effects have been studied in detail, an 84% decline in shrub habitat was mirrored by an ~80% decline in the density of Savannah Sparrows that prefer to nest in this habitat (Peterson, Rockwell, Witte, & Koons, 2014).

Despite birds’ constant habitat preferences, we found differences in nest site habitat across our study areas, suggesting habitat limitation. Cover-nesting species selected nest sites with less sedge meadow and concealment at the Moderate use area compared to the Low, presumably because of a lack of availability of sites with high proportions of sedge meadow habitat and high concealment. Since vegetation height and concealment can be positively correlated with nest survival for Arctic birds (Bentzen et al., 2017; Walpole et al., 2008), cover-nesting shorebird nests in goose-affected areas may suffer higher predation rates. Artificial nest experiments in the Arctic support this relationship between concealment and nest survival; during the early nesting season artificial nests with 0% concealment suffer daily survival rates up to 20% lower than nests with 50% concealment (Bentzen et al., 2017).

5 CONCLUSIONS

5.1 Management and future considerations

Goose-induced habitat alteration appears to be limiting the availability of habitat for shorebirds, resulting in lower nest densities and individuals nesting in non-preferred habitat, potentially leaving them more susceptible to predation. The recent declines in Arctic-breeding shorebird populations (Zöckler, Lanctot, Brown, & Syroechkovskiy, 2013) particularly in the eastern and central Arctic (Andres et al., 2012; Bart, Brown, Harrington, & Morrison, 2007; Smith et al., 2012) underscores the urgency for conserving in these regions. Habitat loss elsewhere in the range and climate change are considered the biggest threats to Arctic shorebirds (Thomas, Lanctot, & Szekely, 2006); however, goose-induced habitat alteration could be a contributing factor that has not yet been assessed adequately to understand its impacts range-wide. Known lesser snow goose colonies occupy a relatively small proportion of the North American Arctic (Flemming et al., 2016); however, our results indicate that breeding geese can alter habitat well beyond the confines of the colony. Furthermore, non-breeding light geese may influence habitat anywhere within their range, which covers approximately 26% of the Arctic in North America and includes large fractions of the Arctic's wetlands, where a majority of shorebirds breed (Flemming et al., 2016).

The magnitude of effects that goose-related habitat impacts will have on Arctic-breeding shorebirds depends on the shorebird species’ preferred habitat and degree of specialization. Our results suggest that cover-nesting, sedge meadow specialists may be more susceptible to goose-induced alteration, while upland specialists may be less so. Elevated predator numbers in the vicinity of breeding geese may nevertheless impact these upland specialists; a hypothesis that requires further verification. Although a warming Arctic may promote the growth of the graminoid vegetation important for cover-nesting species (Gauthier et al., 2013), goose-altered habitat may be slow or unable to respond (Jefferyes, Jano, & Abraham, 2006). Predicting how Arctic habitats change with both climate- and goose-related effects, and how shorebird populations will respond to these changes at broad scales, should be a priority focus for future research. Moreover, management strategies for geese should incorporate the habitat needs of sympatric species and reinvigorate efforts for goose population reduction in order to achieve the population targets articulated by management agencies.
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AUTHORS’ CONTRIBUTIONS

S.A.F., E.N. and P.A.S. conceived the analytical approach; S.A.F., L.V.K. and P.A.S. led collection of data; S.A.F. completed analyses and wrote the manuscript, with L.V.K., P.A.S. and E.N. contributing significantly to revisions. All authors declare no conflict of interest and gave final approval for publication.

DATA ACCESSIBILITY

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.3ds11g5 (Flemming, Kennedy, Nol, & Smith, 2018).

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REFERENCES

Abraham, K., Jefferies, R., & Rockwell, R. (2005). 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., Rockwell, R. F., Dufour, K. W., Cooch, E. G., Zimmerman, G., Drake, K. L., & Reed, E. T. (2011). Harvest, survival, and abundance of midcontinent lesser snow geese relative to population reduction efforts. Wildlife Monographs, 179, 1–42. https://doi.org/10.1002/wmon.5

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

Bart, J., Brown, S., Harrington, B., & Morrison, R. I. G. (2007). Survey trends of North American shorebirds: Population declines or shifting distributions? Journal of Avian Biology, 38, 73–82. https://doi.org/10.1111/j.2007.0908-8857.03698.x

Batt, B. D. J., Arctic Goose Habitat Working Group, U.S. Fish and Wildlife Service. (1997). Arctic ecosystems in peril: Report of the Arctic Goose Habitat Working Group. Washington, DC: U.S. Fish and Wildlife Service.

Battin, J. (2004). When good animals love bad habitats: Ecological traps and the conservation of animal populations: Ecological traps. Conservation Biology, 18, 1482–1491.

Bentzen, R., Dinsmore, S., Liebezeit, J., Robards, M., Streever, B., & Zack, S. (2017). Assessing development impacts on Arctic nesting birds using real and artificial nests. Polar Biology, 40, 1527–1536.

Chen, J.-N., Liu, N.-F., Yan, C., & An, B. (2011). Plasticity in nest site selection of Black Redstart (Phoenicurus ochruros): A response to human disturbance. Journal of Ornithology, 152, 603–608.

Conkin, J., & Alisauskas, R. T. (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.

Cornelius, C. (2008). Spatial variation in nest-site selection by a secondary cavity-nesting bird in a human-altered landscape. The Auk, 110, 615–626.

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

Demeyrier, V., Lambrechts, M. M., Perret, P., & Grégoire, A. (2016). Experimental demonstration of an ecological trap for a wild bird in a human-transformed environment. Animal Behaviour, 118, 181–190.

Devictor, V., Julliard, R., & Jiguet, F. (2008). Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. Oikos, 117, 507–514.

Flemming, S. A., Calvert, A., Nol, E., & Smith, P. A. (2016). Do hyper-abundant Arctic-nesting geese pose a problem for sympatric species? Environmental Reviews, 24, 393–402. https://doi.org/10.1139/er-2016-0007

Flemming, S. A., Kennedy, L. V., Nol, E., & Smith, P. A. (2018). Data from: Hyperabundant herbivores limit habitat availability and influence nest site selection of Arctic-breeding birds. Dryad Digital Repository, https://doi.org/10.5061/dryad.3ds11g5

Fontaine, A. J., & Mallory, M. L. (2011). Detection and classification of land cover classes of Southampton Island, Nunavut, using landsat ETM+data. Environment Canada, (Ottawa).

Forbes, B. C., Ebersole, J. J., & Strandberg, B. (2001). Anthropogenic disturbance and patch dynamics in circumpolar arctic ecosystems. Conservation Biology, 15, 954–969.

Gauthier, G., Bety, J., Cadieux, M.-C., Legagneux, P., Doiron, M., Chevalier, C., ... Bertaux, D. (2013). Long-term monitoring at multiple trophic levels suggests heterogeneity in responses to climate change in the Canadian Arctic tundra. Philosophical Transactions of the Royal Society B – Biological Sciences, 368, 20120482.

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

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

Jones, J. (2001). Habitat selection studies in avian ecology: A critical review. The Auk, 118, 557.

Jorgenson, J. C., Hoef, J. M. V., & Jorgenson, M. T. (2010). Long-term recovery patterns of arctic tundra after winter seismic exploration. Ecological Applications, 20, 205–221.

Kerbes, R., Kotanen, P., & Jefferies, R. (1990). Destruction of wetland habitats by lesser snow geese – A keystone species on the west-coast of Hudson-Bay. Journal of Applied Ecology, 27, 242–258.

Kerbes, R. H., Meeres, K. M., & Alisauskas, R. T. (2014). Surveys of nesting lesser snow geese and Ross’s geese in Arctic Canada, 2002–2009. Washington, DC/Ottawa, Canada: Arctic Goose Joint Venture Special Publication, U.S. Fish and Wildlife Service/Canadian Wildlife Service.

Kotanen, P., & Jefferies, R. (1997). Long-term destruction of sub-arctic wetland vegetation by lesser snow geese. Ecoscience, 4, 179–182.

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

Leafloor, J. O., Moser, T. J., & Batt, B. D. J. (Eds.). (2012). Evaluation of special management measures for midcontinent lesser snow geese and Ross’s geese. Arctic Goose Joint Venture Special Publication. U.S. Fish and Wildlife Service, Washington, DC and Canadian Wildlife Service, Ottawa, ON.
Martin, T. G., Arcese, P., & Scheerder, N. (2011). Browsing down our natural heritage: Deer impacts on vegetation structure and songbird populations across an island archipelago. Biological Conservation, 144, 459–469.

Miller, V., Nol, E., Nguyen, L. P., & Turner, D. M. (2015). Habitat selection and nest success of the Upland Sandpiper (Bartramia longicauda) in Ivavik National Park, Yukon, Canada. The Canadian Field-Naturalist, 128, 341.

Owens, I. P., & Bennett, P. M. (2000). Ecological basis of extinction risk in birds: Habitat loss versus human persecution and introduced predators. Proceedings of the National Academy of Sciences of the United States of America, 97, 12144–12148.

Peterson, S. L., Rockwell, R. F., Witte, C. R., & Koons, D. N. (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.

Peterson, S. L., Rockwell, R. F., Witte, C. R., & Koons, D. N. (2014). Legacy effects of habitat degradation by lesser snow geese on nesting Savannah Sparrows. The Condor, 116, 527–537.

Post, E., Forchhammer, M. C., Bret-Harte, M. S., Callaghan, T. V., Christensen, T. R., Elberling, B., … Aastrup, P. (2009). Ecological dynamics across the arctic associated with recent climate change. Science, 325, 1355–1358.

R Core Team. (2016). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Saalfeld, S. T., Lanctot, R. B., Brown, S. C., Saalfeld, D. T., Johnson, J. A., Andres, B. A., & Bart, J. R. (2013). Predicting breeding shorebird distributions on the Arctic Coastal Plain of Alaska. Ecosphere, 4, art16.

Samelius, G., & Alisauskas, R. T. (2009). Habitat alteration by geese at a large arctic goose colony: Consequences for lemmings and voles. Canadian Journal of Zoology, 87, 95–101.

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

Smith, P. A., Bart, J., Lanctot, R. B., McCaffery, B. J., & Brown, S. (2009). Probability of detection of nests and implications for survey design. Condor, 111, 414–423.

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

Smith, P. A., Gratto-Trevor, C. L., Collins, B. T., Fellows, S. D., Lanctot, R. B., Liebezeit, J., … Gates, H. R. (2012). Trends in abundance of Semipalmated Sandpipers: Evidence from the Arctic. Waterbirds, 35, 106–119.

Srivastava, D., & Jefferies, R. (1996). A positive feedback: Herbivory, plant growth, salinity, and the desertification of an Arctic salt-marsh. Journal of Ecology, 84, 31–42.

Swift, R. J., Rodewald, A. D., & Senner, N. R. (2017). Breeding habitat of a declining shorebird in a changing environment. Polar Biology, 40, 1777–1786.

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

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

Zöckler, C., Lanctot, R., Brown, S., & Syroechkovskiy, E. (2013). Waders (Shorebirds). In Arctic Report Card 2012. Retrieved from http://www.Arctic.noaa.gov/reportcard

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