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RESEARCH ARTICLE

Legacy effects of habitat degradation by Lesser Snow Geese on nesting Savannah Sparrows

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ABSTRACT

Increased growth of the midcontinental population of Lesser Snow Geese (*Chen caerulescens caerulescens*) has led to overgrazing and habitat degradation at their Arctic and sub-Arctic breeding grounds. This habitat degradation has been shown to induce a trophic cascade that negatively affects plant, insect, and other avian species that share these habitats. In conjunction with a long-term study of the impacts of Lesser Snow Geese on habitat, we examined the dual influences of climate and long-term habitat change on the nesting occurrence of Savannah Sparrows near Churchill, Manitoba, Canada. Using multistate occupancy models, we found that variability in early-summer temperature and precipitation modulated year-to-year variability in nesting occurrence and detection probabilities. Extreme warm and wet conditions in early summer can benefit breeding Savannah Sparrows across the landscape. However, such events have not been prevalent enough to override the ~80% decline in Savannah Sparrow nesting occurrence over 36 yr. This dramatic decline can be attributed to the legacy of Lesser Snow Goose foraging, which has led to an 84% reduction in preferred shrub habitat for nesting Savannah Sparrows. Management actions targeted at reducing Lesser Snow Goose abundance and habitat restoration will be needed to allow sympatric Savannah Sparrows and functionally similar species to recover.

Keywords: beneficial climate effects, habitat degradation, hyperabundant species, overabundant species, passerine, trophic cascade, waterfowl

Effets hérités de la dégradation de l'habitat par *Chen caerulescens caerulescens* sur la nidification de *Passerculus sandwichensis*

RÉSUMÉ

La croissance accrue de la population du centre du continent de *Chen caerulescens caerulescens* a conduit au surbroutage et à la dégradation de l'habitat dans ses quartiers de nidification arctiques et subarctiques. Il a été démontré que cette dégradation de l'habitat induit une cascade trophique qui affecte négativement les plantes, les insectes et d'autres espèces aviaires qui partagent ces habitats. Conjointement avec une étude à long terme des impacts de *C. caerulescens caerulescens* sur l'habitat, nous avons examiné la double influence du climat et de la modification de l'habitat à long terme sur la fréquence de nidification de *Passerculus sandwichensis* près de Churchill, au Manitoba, Canada. En utilisant des modèles multi-états d'occupation, nous avons constaté que la variabilité de la température et des précipitations au début de l'été modulait la variabilité de la fréquence de nidification et des probabilités de détection d'année en année. Des conditions chaudes et humides extrêmes au début de l'été peuvent être bénéfiques pour les individus nicheurs de *P. sandwichensis* à travers le paysage. Toutefois, de tels événements n'ont pas été suffisamment répandus pour contrecarrer le déclin de ~80% de la fréquence de nidification de *P. sandwichensis* en 36 ans. Ce déclin dramatique peut être attribuable à l'héritage du broutage de *C. caerulescens caerulescens*, lequel a conduit à une réduction de 84% de l'habitat d'arbustaie préféré des individus nicheurs de *P. sandwichensis*. Des actions de gestion ciblant la réduction de l'abondance de *C. caerulescens caerulescens* et la restauration de l'habitat seront nécessaires pour permettre le rétablissement de *P. sandwichensis* et d'espèces similaires sympatriques.

Mots-clés: cascade trophique, dégradation de l'habitat, effets bénéfiques du climat, espèce surabondante, passereau, sauvagine

INTRODUCTION

Human-induced trophic cascades have had direct and indirect effects on biodiversity and ecosystems at both regional and local scales (Lindberg et al. 1998, Pace et al. 1999, Österblom et al. 2007). Although reports of trophic cascades are most common in marine environments (e.g., Merrick et al. 1997, Estes et al. 1998), they also occur in terrestrial ecosystems (e.g., Polis et al. 2000, Croll et al. 2005). One striking example is the impact that hyper-abundant Lesser Snow Geese (*Chen caerulescens caerulescens*; hereafter ''Snow Geese'') have on Arctic ecosystems (Heffernan et al. 2014).

Over the past 40 yr, the midcontinent population of Snow Geese has grown by 5–14% yr^{-1} (Alisauskas et al. 2011), which has been attributed to anthropogenic modifications of their wintering grounds and migratory routes. In these regions, increased agricultural production of rice and cereal-grain crops has led to drastic changes in the landscape, as well as in the energy available to migrating and wintering Snow Geese (Jefferies et al. 2004, 2006). Commensurate with these changes, the establishment of 1.5 million ha of U.S. National Wildlife Refuges across the Mississippi and Central flyways may have offered Snow Geese extra protection from hunting (Abraham et al. 2005). Recently, there has been increased interest in converting set-aside Conservation Reserve Program lands to the production of corn for expanding ethanol projects in the central and midwestern United States (Mehaffey et al. 2011), which may exacerbate the problem of growing Snow Goose populations by providing them with even more food subsidies (Secchi et al. 2009, Wiens et al. 2011). In combination, these land modifications maintain high annual survival of adult Snow Geese, fueling population growth (Abraham et al. 2005, Alisauskas et al. 2011, Koons et al. 2014).

An overabundance of Snow Geese and associated foraging pressures during spring migration and on their northern breeding grounds has led to severe degradation of >35,000 ha of salt-marsh habitat along the western Hudson Bay lowlands (Jano et al. 1998, Jefferies and Rockwell 2002, Jefferies et al. 2006). In turn, this leads to deleterious effects on the biodiversity of plant, insect, and avian communities (Jefferies et al. 1979, Bazely and Jefferies 1986, Hik et al. 1992, Srivastava and Jefferies 1995, Milakovic et al. 2001, Milakovic and Jefferies 2003, Rockwell et al. 2003, 2009, Abraham et al. 2005, 2012).

The Savannah Sparrow (*Passerculus sandwichensis*) was once a common nesting species in the La Pérouse Bay area (Weatherhead 1979). By 1999, however, degradation of their habitat by Snow Geese had led to a reduction of ~75% in nesting densities compared with the 1970s, when Snow Geese were less abundant (Rockwell et al. 2003). Since the 1990s, most Snow Geese have moved to healthier vegetated sites in the larger Cape Churchill region (Cooch et al. 2001, Aubry et al. 2013), potentially allowing the local vegetation and animal communities to rebound. Yet severe grubbing by Snow Geese removes the insulating layer of graminoid swards, exposing dark soils that result in higher soil temperatures and increased evapotranspiration. This allows salts from deeper soils of the historical Tyrrell Sea to be drawn and concentrated at the surface. Increased soil salinity, in turn, leads to increased mortality of dwarf shrubs (i.e. *Salix* spp. and *Betula* spp.; Iacobelli and Jefferies 1991). With reduced vegetative cover, spring floods cause erosion that exacerbates the problem, which has led to continued loss of high-quality shrub habitat long after most of the Snow Goose colony has moved to greener pastures (there is now <1 nesting pair of Snow Geese ha^{-1} in the immediate vicinity of La Pérouse Bay). In most other regions across the Arctic, however, climate warming is benefiting the expansion of shrub species, which could eventually help Savannah Sparrows recover, once habitat degradation by Snow Geese has ceased. Unfortunately, habitat degradation along La Pérouse Bay continues to occur (see Peterson et al. 2013).

Here, we focus on the impact these habitat changes have on the robust and adaptable Savannah Sparrow in relation to climatic variation, using long-term spot-mapping data and a multistate occupancy model. Although habitat has continued to deteriorate, we predict that warmer weather conditions can benefit Savannah Sparrows by providing them with earlier access to remaining habitat and increase their breeding propensity, potentially offsetting some of the negative impacts caused by overabundant Snow Geese.

METHODS

Study Area

Study plots were located on coastal salt-marsh and shrub (supratidal) wetland habitat near La Pérouse Bay, ~30 km east of Churchill, Manitoba, Canada (58°52.3′N, 93°41.0′W). The study area is part of the western Hudson Bay Lowlands and within the northern boundary of Canada's Wapusk National Park (Figure 1). Vegetation on the study area is characterized by dwarf shrubs (i.e. *Salix* spp. and *Betula* spp.), salt-marsh grasses (e.g., *Puccinellia phryganodes*), and sedges (e.g., *Carex subspathacea*). With increased grazing, grubbing, and shoot pulling of the preferred graminoids by Snow Geese (Jefferies et al. 2003), larger extents of hypersaline soils have become more common throughout the general area (Iacobelli and Jefferies 1991, Srivastava and Jefferies 1995, Jefferies and Rockwell 2002). Time-series photographs reveal the extent of habitat damage (see Figure 2), and summaries of vegetation change are provided in the results below (for details, see Peterson et al. 2013).

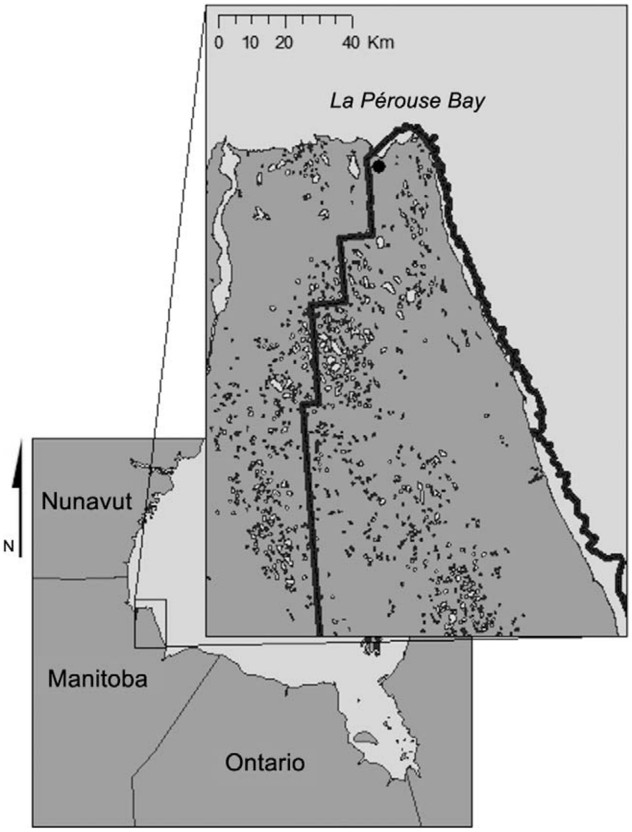

FIGURE 1. Map of the study area's location ~30 km east of Churchill, Manitoba, Canada. The general study area (58°52.3′N, 93°41.0′W) is identified by the black dot at the north end of Wapusk National Park (outlined by dark line).

Study Species

The Savannah Sparrow displays breeding philopatry and has been considered a habitat generalist throughout the majority of its range (Wheelwright and Rising 2008), potentially allowing it to better cope with local environmental change than specialist sparrow species (Dornak et al. 2013). Although Savannah Sparrows nest in tall grasses through most of their range, at the northern end of the range they use dwarf shrubs (Rotenberry and Knick 1999, Wheelwright and Rising 2008). Historical data on their widespread breeding on the study area (Weatherhead 1979) make them good indicators of shrub habitat quality. In the north, where shrubs replace the large swards of grass preferred for nesting on the prairies, the loss of high-quality shrub habitat induced by Snow Geese could have direct consequences for Savannah Sparrows (Rockwell et al. 2003).

FIGURE 2. A photographic time series of the area surrounding "Randy's observation tower" immediately east of our study area, documenting the extensive intertidal habitat damage caused by Snow Geese. Damage to our supratidal study area has also been severe, but not quite as extreme (Peterson et al. 2013). From top to bottom are photos taken in 1984, 1997, and 2011.

Survey Plots

Nest searching for Savannah Sparrows was conducted on 5 study plots, which were set up in a grid system of 250-m^2 cells (note that the 50 × 50 m grid cells should instead have been reported as 250 m^2 in Peterson et al. 2013). These included a 7-ha portion of the original study site established in 1976 by Weatherhead (1979) for investigating the relationship between mating systems of Savannah Sparrows and habitat quality (i.e. the eastern sector consisting of low-lying shrub habitat; for further details, see Rockwell et al. 2003, Peterson 2012). In addition to the 7-ha portion of the "Weatherhead" plot, 4 "paired" study plots were established in 1999, representing heavily degraded habitats (2 plots, one 3 ha and the other 5 ha) and marginally intact habitats (2 plots, one 3 ha and the other 5 ha) that were adjacent and representative of the habitats surrounding La Pérouse Bay at the time (Figure 1; Peterson 2012).

Nest searching was conducted in 1976 and 1977 on the Weatherhead plot, and in 1999, 2000, 2010, and 2011 on all 5 study plots (a total of 92 grid cells). During Weatherhead's (1979) intensive study of Savannah Sparrows, nest searches of each grid cell took place every 2 days by moving methodically from cell to cell along each grid column. These ground searches were augmented by color marking of individuals and daily behavioral observations of both marked and unmarked individuals. In 1999 and 2000, 1 to 3 observers conducted nest searches in a similar fashion every 4 to 5 days; in 2010 and 2011, 3 or 4 observers conducted nest searches every 5 to 7 days. In every year, any active nest, fresh nest bowl (current season only), or nest under construction was noted and marked with a small, uniquely labeled wooden stake. A GPS point was taken for each nest from 1999 onward. Any breeding behavioral cues (e.g., aerial displays, singing males, contact and warning chip notes, mousing [i.e. running on ground], broken wing display) of Savannah Sparrows were also recorded and assisted observers in finding nests. Nests were also found by searching patches of shrub and grass cover suspected of concealing a nest under construction (as indicated in a previous survey occasion) despite the absence of the species at the time of a given survey. All nests found were revisited every 2 to 7 days to document nest activity and survival.

Prior to 2010, nest searching began in late May and extended into late July. In 2010 and 2011, nest searching did not begin until mid-June because of inclement weather events (i.e. blizzards) in late May and early June that delayed avian phenology, but nonetheless, nests and nesting behavior were not detected until at least the second occasion, and searching continued until no new nests were found on successive sampling occasions (mid-July to late July). For data analysis, we considered the first occasion to be when the first nest was found each year. In 1999, 2000, 2010, and 2011, the numbers of sampling occasions were 5, 9, 4, and 5, respectively. For 1976 and 1977, only summary data were available on whether nests were found in a grid cell. As such, data were collapsed into a single occasion for the early years, providing information about nesting occurrence but no direct information about detection probability (see below).

Data Analysis

We initially attempted to model our detection history data by using a robust-design multistate occupancy model (MacKenzie et al. 2009) in Program MARK (Cooch and White 2006), but we could not obtain model convergence given the absence of occupancy data for the long periods of time between study periods. We thus opted to use the single-season, multistate occupancy model to examine variation in nesting occupancy rates using space- and time-varying covariates, assuming that all grid cells were closed to changes in occupancy status over a given season (Nichols et al. 2007). Given the difficulty in finding ground-nesting passerine nests and the strong possibility that we did not find all Savannah Sparrow nests present on the study plot, we focused on 3 alternative observation states relevant to our objectives: (a) no detection of nest or breeding activity (state $=0$); (b) detection of breeding behavior, which may include mousing, broken wing display, copulation, incessant chipping (singing males not included, because some territories may be held with no attendant females present), repeated circling of entire cell, and carrying nesting material (state $=1$); or (c) detection of a fresh nest bowl found with or without eggs, or a partial nest bowl under construction within a grid cell (state $=2$). Under the multistate occupancy framework, the lack of detecting a nest or breeding activity (state 0) does not necessarily imply that these activities were not present; the true state could be any of the 3 states described above. For example, if "breeding behavior" was detected, the true state could be 1 (e.g., in the breeding initiation phase) or a nest may have already been present (state 2) but we were unable to detect it. Only the highest-ranking state (2: a nest was found) is unambiguous.

Use of these observations in the multistate occupancy model allowed us to estimate ψ^1, the probability that a grid cell was occupied by ≥ 1 Savannah Sparrow displaying breeding behavior that did or did not nest (true state $=1$ or 2); ψ^2, the probability that ≥ 1 nest occurred within a grid cell for a particular year, given that evidence of breeding was seen at the site (true state $=2 \mid$ true state $=1$ or 2); p^1, the probability of detecting site occupancy, given a true state of behavioral evidence; p^2, the probability of detecting nesting, given that it occurred; and δ, the probability that evidence of nesting was found, given that breeding behavior was detected and nesting occurred, which accounts for the misclassification of the true state being 2. Given the limited information available for 1976 and 1977, we had to fix p^1 to zero in these years. We modeled p^2 in 1976 and 1977 using the habitat and climate attributes in relation to other years in which occurrence records were kept for each nest-searching occasion (see below).

We predicted a decline in Savannah Sparrow nest occupancy rates over time because of the impacts that overabundance of Snow Geese and associated foraging activities have on plant cover. To address this hypothesis, we considered the effects of 5 habitat measurements on the multistate occupancy parameters described above, each of which varied by grid cell and study period. The proportion of barren ground (bprop) was considered because Snow Goose foraging has led to an increase in barren ground over time, and a loss of ground cover with extended areas of hypersaline soils. In turn, this has led to increased mortality of shrub assemblages and a decrease in the proportion of shrub cover (sprop) that Savannah Sparrows depend on for nesting cover. As shrub cover is lost, shrub patch size (spatch) decreases, which contributes to the loss of connectivity and increases the patch size of barren ground (bpatch) as well as the distance between suitable shrub habitat patches for nesting (dist). We did not consider patches of graminoids in our analyses because Savannah Sparrows do not use them for nesting on our study area, but they do select nesting sites with small clumps of graminoids underneath shrubs (spatiotemporal changes in these habitat metrics are detailed in Peterson et al. 2013).

In addition to habitat conditions, we also wanted to account for possible effects of climatic conditions on nesting occurrence and our ability to detect a nest or breeding behavior. Given available climate data from the Churchill Meteorological Station ($\sim$30 km west of the study area), we considered the effects of the number of days with a high temperature below 0°C in June (cdays), the mean temperature in June (meanT), the number of precipitating days in June (daysppt), and total June precipitation (totppt) on annual variation in detection probabilities. In addition to these climate covariates, we also considered the effects of the number of days above 0°C (gdays; using mean temperature of each day) and the cumulative degrees for days above 0°C (i.e. growing degree days: gdd) in the months of May and June on the occupancy parameters. These latter covariates contribute to when available nesting habitat for Savannah Sparrows becomes snow-free and green (Aubry et al. 2013). We used the aforementioned "monthly" measures of climate because the weather on any given day at our coastal study area can be different than that in the town of Churchill, but interannual conditions tend to be similar over the scale of a month. Given the different methods and nest-searching efforts among years, we also considered a generic "year" effect (modeled as a factor) for detection parameters.

To compare models with alternative parameterizations of the space- and time-varying covariate structures for the occupancy and detection parameters, we used Akaike's Information Criterion adjusted for small sample size ($\mathrm{AIC_c}$; Akaike 1973). To avoid overly complex models, we modeled constant probabilities of detection across sampling occasions within a year. Using a tiered approach to model selection, we proceeded by examining null (no spatial or temporal variation in a given parameter), univariate, additive, and plausible interactive effects of the climate covariates on p^1, p^2, and δ across years, one at a time. Separately, we compared null and univariate effects of the habitat covariates on each of the detection probabilities. We then compared models with combinations of the climate and habitat covariates that were most supported in the previous model tiers (or generic year effects), but we never allowed related covariates (e.g., bprop and sprop) to enter the same model, because of their multicollinearity. After identifying the best model structure for the detection parameters, we went through the same variable-selection process for the occupancy parameters (ψ^1 and ψ^2). Given the limited information for 1976 and 1977 (see above), the use of space- and time-varying covariates allowed us to gain important insight into Savannah Sparrow nest-occupancy dynamics (see Ball et al. 2005) during the earliest years of the study, when Snow Geese had not yet altered shrub habitat (Peterson et al. 2013). To examine the robustness of our results to study design, we reran our top model on data from just the Weatherhead plot, where Savannah Sparrows were studied during all 3 study periods (as opposed to just the latter 2 periods on the paired plots).

All models were run using binomially distributed errors, the logit-link function, and the simulated annealing optimization routine in RMark (Laake and Rexstad 2008). Simulated annealing is effective at finding the global maximum likelihood in multistate data that may have multiple local maxima. Derived estimates of the unconditional probability that nesting occurred within 1 of the grid cells was calculated as the product of ψ^1 and ψ^2. Given that a grid cell equaled the average size of a Savannah Sparrow nesting territory in the region (P. Weatherhead personal communication), $\psi^1 \times \psi^2$ can also be interpreted as the expected proportion of potential Savannah Sparrow territories where a nest was successfully built each year (Nichols et al. 2007, MacKenzie et al. 2010).

RESULTS

Savannah Sparrow Trends

Over 36 yr of study at the long-term Weatherhead plot, the naive density of located Savannah Sparrow nests decreased by 75%. On the Weatherhead plot, 3.43 and 2.00 nests $\mathrm{ha^{-1}}$ were located in 1976 and 1977, respectively, but nest density dropped to 0.86 nests $\mathrm{ha^{-1}}$ by 1999. After 1999, however, there were no notable changes in nest densities (0.57, 1.00, and 0.86 nests $\mathrm{ha^{-1}}$ in 2000, 2010, and 2011, respectively). Because methods and personnel changed across the years of study, and because renests could not be distinguished from first nests, the naive density of located nests should nevertheless be interpreted cautiously. We therefore focus on the more robust results for changes in Savannah Sparrow "nesting occurrence" below, for which spatial

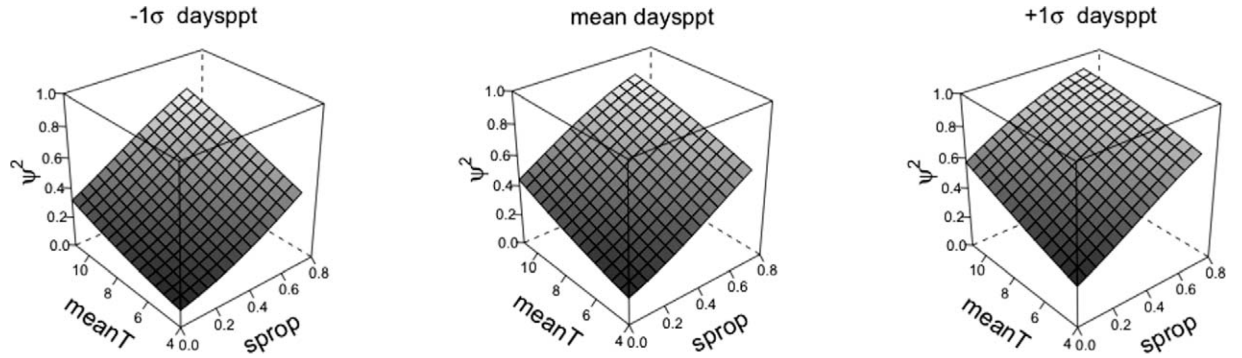

FIGURE 3. Estimated probabilities of nest occurrence in a study grid cell at La Pérouse Bay, Manitoba, Canada, given site occupancy by birds that were at least displaying behavioral evidence of breeding (ψ^2), in relation to the grid- and year-specific proportionate shrub cover (sprop) and annual measures of mean temperature in June (meanT in °C). Shown from left to right are the relationships across an additional predictor variable: low (–1 SD), mean, and high (+1 SD) values of the number of days with precipitation in June of each year (daysppt).

and temporal variation in detection of nests or nesting behavior was accounted for, to the best of our abilities.

We additionally note that at the Breeding Bird Survey (BBS) route ~30 km west of our study area in Churchill (no. 45100; https://www.pwrc.usgs.gov/bbs/), where few Snow Geese nest and habitat damage by migrants is less severe, the surveyed number of Savannah Sparrows did not change between 1977 and 2012 ($F = 1.88$, $P = 0.19$ for a simple time-trend regression). This indicates that any decline in breeding Savannah Sparrows may be restricted to the coastal lowlands, where they sympatrically co-occur with a Snow Goose colony.

Nest Occupancy Estimates

Our comparison of multistate occupancy models with various effects of habitat and climate covariates (see above) supported positive effects of mean temperature in June of each year on p^1 ($\beta_{\text{meanT}} = 0.25$, 95% confidence interval [CI]: 0.11 to 0.38), p^2 ($\beta_{\text{meanT}} = 0.25$, 95% CI: 0.18 to 0.33), and δ ($\beta_{\text{meanT}} = 0.29$, 95% CI: 0.10 to 0.47). In addition, the number of precipitating days in June of each year had a negative effect on p^1 ($\beta_{\text{daysppt}} = -0.22$, 95% CI: –0.32 to –0.12), but a positive effect on δ ($\beta_{\text{daysppt}} = 0.20$, 95% CI: 0.02 to 0.39). Models with other combinations of covariates (e.g., habitat effect), year effects, and null effects had greater AIC_c scores and were thus not supported by the data.

Using the most supported model structures for p^1, p^2, and δ presented above, we next modeled variation in the occupancy parameters (ψ^1 and ψ^2). The top model indicated that the proportion of barren ground in a grid cell had a strong negative effect on ψ^1 across time and space of the study ($\beta_{\text{bprop}} = -9.84$, 95% CI: –15.72 to –3.96). Moreover, the proportion of shrub cover had a positive effect on ψ^2 across time and space (Figure 3; $\beta_{\text{sprop}} = 2.89$, 95% CI: 0.51 to 5.28), as did the mean temperature ($\beta_{\text{meanT}} = 0.18$, 95% CI: 0.07 to 0.30) and number of precipitating days in June of each year (Figure 3; $\beta_{\text{daysppt}} = 0.19$, 95% CI: 0.07 to 0.32; for covariate values in years when Savannah Sparrows were studied, see Table 1). The addition of other covariates to this model led to an increase in ΔAIC_c (Table 2), and models with different covariates (e.g., measures of habitat fragmentation) all had $\Delta\text{AIC}_c > 11$. Less precise but qualitatively similar results were attained when we ran the top model on long-term data for only the Weatherhead plot, indicating robustness of our findings to the study design.

Given our top model, climate change could potentially benefit Savannah Sparrows at the northern edge of their range. Mean daily temperature (meanT) and number of precipitating days in June (daysppt) have increased slightly since 1943 ($\beta_{\text{year}} = 0.03$, $P < 0.05$ and $\beta_{\text{year}} = 0.05$, $P < 0.05$, respectively). However, the temporal patterns of these climatic variables are better described as being stochastic in the vicinity of our study area ($R^2 = 0.07$, $\text{CV} = 0.30$ and $R^2 = 0.04$, $\text{CV} = 0.36$, respectively). Over the course of our long-term study, the sharp increase in the average amount of barren ground (bprop) and associated decrease in the proportional cover of shrubs (sprop; see Table 1) led to a precipitous decline in the unconditional probability of Savannah Sparrow nesting occurrence ($\psi^1 \times \psi^2$; Figure 4). However, in years (like 1999) when early-summer conditions are extremely warm and wet (see Table 1), early availability and green-up of existing habitat can lead to moderately high Savannah Sparrow nesting occurrence and partially offset the effect of habitat loss caused by Snow Geese (Figures 3 and 4).

DISCUSSION

In conjunction with a long-term study of Snow Goose impacts on coastal marsh habitat along the Hudson Bay lowlands, we examined the dual influences of climate and

TABLE 1. Annual study-area means (and SD, range) of climate and habitat covariates included in the top multistate occupancy model for Savannah Sparrow nests presented in Table 2: proportion of barren ground (bprop), proportion of shrub cover (sprop), mean temperature in June (meanT), and number of precipitating days in June (dayssppt) (for further clarification of covariate definitions, see text).

Year	bprop	sprop	meanT (°C)	dayssppt
1976	0.26 (0.07, 0.12–0.43)	0.49 (0.12, 0.27–0.68)	7.37	11
1977	0.26 (0.07, 0.12–0.43)	0.49 (0.12, 0.27–0.68)	8.78	11
1999	0.62 (0.14, 0.20–0.90)	0.19 (0.07, 0.04–0.38)	10.71	12
2000	0.62 (0.14, 0.20–0.90)	0.19 (0.07, 0.04–0.38)	4.20	10
2010	0.78 (0.13, 0.51–0.99)	0.08 (0.05, 0.00–0.20)	7.65	5
2011	0.78 (0.13, 0.51–0.99)	0.08 (0.05, 0.00–0.20)	7.70	7

habitat change on the nesting occurrence of Savannah Sparrows over 36 yr. Both habitat and climate are known to play strong roles in regional as well as microhabitat nesting decisions in passerine species (Gratto and Cooke 1987, Morton 1994, Martin 2001, Hendricks 2003, Martin et al. 2009). Our results indicate that both factors can also affect passerine nesting occurrence, which is a function of changes in both population abundance and individual breeding decisions.

Attaining unbiased insight into the effects of habitat and climate on nesting occurrence rates is nevertheless challenging, because both variables can affect the probability of detecting at least 1 nest or bird exhibiting breeding behavior, given that they actually occur at a given site. For example, one might expect that thick habitat cover would negatively affect detection of nesting or breeding activity (and vice versa; Thompson 2002), but we found no such effects. In low-lying dwarf shrub environments, detection of passerine nests and breeding activity may not be as variable as in a more heterogeneous environment with larger extents of grass and shrub cover or taller willow (*Salix* spp.) shrubs. Consistent with other avian studies (e.g., Thompson et al. 2014), however, weather conditions influenced our ability to detect nests and nesting behavior. Detection probabilities were higher in years with generally favorable weather during nest searches (warm and little rainfall), perhaps because breeding pairs were more active in such conditions.

The advantage of multistate occupancy models is that one can estimate the true state of occupancy (in our case, nesting occurrence) by conditioning on detection probabilities and the variables that influence detection (MacKenzie 2005, Nichols et al. 2007). By doing so, we found that mean temperature and rainfall in June positively influenced ψ^2, the probability of nest occurrence given site occupancy by birds that were at least displaying behavioral evidence of breeding (Figure 3). By influencing melt of the snowpack and vegetation growth, these weather variables advance the availability of habitat and may therefore influence a Savannah Sparrow's decision to breed or not at

TABLE 2. Comparison of the top 10 multistate occupancy models for surveyed grid cells ($n = 92$) at La Pérouse Bay, Manitoba, Canada, in the summers of 1976, 1977, 1999, 2000, 2010, and 2011. Variables within these top-ranking models included proportion of barren ground (bprop), proportion of shrub cover (sprop), number of days with a high temperature below 0°C in June (cdays), mean temperature in June (meanT), and number of precipitating days in June (dayssppt). *K* is the number of parameters estimated in a model, Dev is the model deviance, and ΔAIC_c is the difference between a model's AIC_c and that of the top-ranked model.

Model	*K*	Dev	ΔAIC_c
ψ^1(bprop), ψ^2(sprop + meanT + dayssppt), p^1(meanT + dayssppt), p^2(meanT), δ(meanT + dayssppt)	14	1,788.76	0.00
ψ^1(bprop), ψ^2(sprop + meanT + dayssppt), p^1(meanT + dayssppt), p^2(meanT + dayssppt), δ(meanT + dayssppt)	15	1,786.76	0.15
ψ^1(bprop + cdays), ψ^2(sprop + meanT + dayssppt), p^1(meanT + dayssppt), p^2(meanT + dayssppt), δ(meanT + dayssppt)	16	1,785.07	0.61
ψ^1(bprop + cdays), ψ^2(sprop + dayssppt), p^1(meanT + dayssppt), p^2(meanT + dayssppt), δ(meanT + dayssppt)	15	1,788.22	1.60
ψ^1(bprop), ψ^2(sprop + meant + dayssppt), p^1(meanT + dayssppt), p^2(meanT), δ(meanT)	13	1,793.01	2.10
ψ^1(bprop), ψ^2(meanT + dayssppt), p^1(meanT + dayssppt), p^2(meanT + dayssppt), δ(meanT + dayssppt)	14	1,793.34	4.58
ψ^1(bprop + cdays), ψ^2(meanT + dayssppt), p^1(meanT + dayssppt), p^2(meanT + dayssppt), δ(meanT + dayssppt)	15	1,792.42	5.81
ψ^1(bprop + cdays), ψ^2(dayssppt), p^1(meanT + dayssppt), p^2(meanT + dayssppt), δ(meanT + dayssppt)	14	1,794.76	6.00
ψ^1(bprop + cdays), ψ^2(sprop + meanT), p^1(meanT + dayssppt), p^2(meanT + dayssppt), δ(meanT + dayssppt)	15	1,794.20	7.59
ψ^1(bprop), ψ^2(sprop + meanT), p^1(meanT + dayssppt), p^2(meanT + dayssppt), δ(meanT + dayssppt)	14	1,796.37	7.61

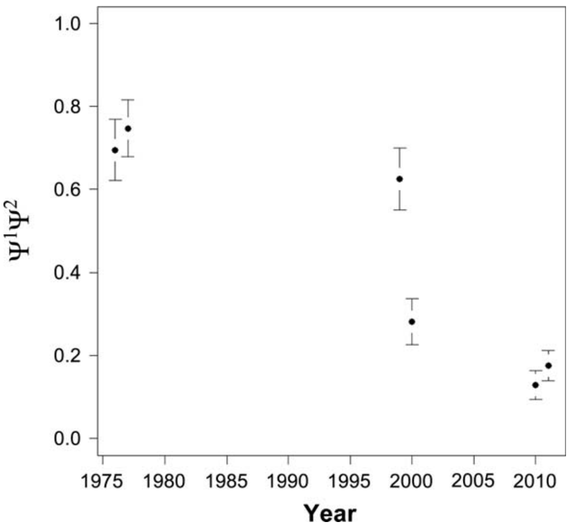

FIGURE 4. Derived estimates of the unconditional probability that nesting occurred within surveyed grid cells at La Pérouse Bay, Manitoba, Canada, in each year of the study ($\psi^1 \times \psi^2$), based on climate and habitat conditions (bars around annual mean estimates are 95% confidence intervals).

our high-latitude coastal site, where the climate window for rearing offspring is short. Temperature and precipitation regimes are highly stochastic along the Hudson Bay Lowlands (see above) and may help explain the episodic year-to-year fluctuations in passerine nesting at high latitudes. For example, June of 1999 was unusually warm (mean = 10.7°C), and that may have promoted greater nesting by Savannah Sparrows than the already degraded habitat would have supported in average June temperatures (6.5°C), indicating the potential for climate extremes to at least partially offset the effects of habitat degradation on nesting occurrence (Figures 3 and 4). Colder-than-average conditions in 2000 (4.2°C) at least partially influenced the ~55% reduction in nesting occurrence between successive years (Figure 4). However, June temperatures in the other years of the study were 0.9–2.3°C above average, and the region has experienced a slight increase in temperature and precipitation since the 1940s, but this subtle trend is largely overridden by large amounts of climatic stochasticity at our coastal study area (see above). Thus, climate change cannot explain the observed long-term decline in Savannah Sparrow nesting occurrence at La Pérouse Bay. The immediate focus should therefore be on the role of changes in preferred habitat conditions.

Contrary to habitat preferences in more southern regions of their breeding range, where they tend to avoid woody vegetation (Ribic and Sample 2001, Bakker et al. 2002, Grant et al. 2004, Graves et al. 2010, Thompson et al. 2014), Savannah Sparrows in the north prefer to nest in patches of low-lying willow, dwarf birch (*Betula glandulosa*), or sweet gale (*Myrica gale*) shrubs, always building the nest at the base of a shrub (Rotenberry and Knick 1999, Wheelwright and Rising 2008, Peterson 2012). Thus, it is not surprising that we found higher conditional probabilities of nesting occurrence in areas with large amounts of shrub cover (Figure 3).

In the 1970s, La Pérouse Bay was bounded by a band of healthy and productive supratidal salt-marsh habitat with large patches of shrub habitat that supported >3 Savannah Sparrow nests ha^{-1} (Rockwell et al. 2003). Since then, however, the overabundance of Snow Geese at La Pérouse Bay and their destructive foraging behaviors have led to an 84% reduction in shrub cover and an associated 3-fold increase in the amount of barren ground (Peterson et al. 2013). Although most of the ~35,000 breeding pairs of Snow Geese left La Pérouse Bay throughout the 1990s in search of greener pastures in the surrounding Cape Churchill region, where numbers have grown to >50,000 pairs (Cooch et al. 2001, Koons et al. 2014), hypersalinity of soils and erosion induced by groundcover loss continue to degrade the habitat (Peterson et al. 2013). As predicted, we found that this legacy that Snow Geese leave on the land continues to affect Savannah Sparrows and was largely responsible for the ~80% decline in nesting occurrence over 36 yr (Figure 4).

The consequences of further habitat degradation by Snow Geese will not only affect the generalist Savannah Sparrow, but will also negatively affect functionally similar species that are less adaptable and more sensitive to changes in habitat conditions (Dornak et al. 2013). Short-eared Owls (*Asio flammeus*), Yellow Rails (*Coturnicops noveboracensis*), and Semipalmated Sandpipers (*Calidris pusilla*) are also negatively affected by the loss of habitat (see Rockwell et al. 2009), and even sympatrically nesting sea ducks suffer from apparent competition with Snow Geese (Iles et al. 2013). The trophic cascade induced by Snow Geese could thus result in irreversible losses of avian species richness and biodiversity along the Hudson Bay lowlands if the Snow Goose population continues to grow. Although Snow Geese may not affect regional populations of bird species with extensive ranges (e.g., see BBS results for Savannah Sparrows above), reduced avian biodiversity within the Hudson Bay lowlands will lead to the loss of important ecosystem functions such as insect consumption and seed dispersal, further exacerbating the cascading effects of Snow Geese. These issues are of utmost concern to the international agencies that manage migratory birds (Leafloor et al. 2012).

Our data suggest that climate extremes (warm and wet) can actually benefit Savannah Sparrows at the northern extent of their range, but the subtle effects are swamped out by destruction of habitat ultimately caused by an overabundance of Snow Geese. To prevent a collapse of the Hudson Bay lowland ecosystem, managers will need to meet their mandate of reducing Snow Goose abundance to a level at which habitat can recover (Abraham et al. 2012). Unfortunately, liberalization of sport harvest in an attempt to achieve this goal has not worked, and additional actions will need to be considered (Alisauskas et al. 2011, Koons et al. 2014). We recommend incorporating our frameworks for modeling habitat (Peterson et al. 2013) and avian breeding occurrence (present study) into local and regional monitoring efforts of Arctic and sub-Arctic avian communities that live in proximity to Snow Goose colonies. This will allow managers to detect trends and, hopefully, the recovery of passerine breeding numbers in response to management actions aimed at reducing Snow Goose abundance to sustainable levels (Rumpff et al. 2011).

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