

**SYMPATRIC NESTING EASTERN PRAIRIE POPULATION CANADA GEESE
AND LESSER SNOW GEESE ON THE HUDSON BAY LOWLANDS:
NEST SURVIVAL AND SPATIAL DISTRIBUTION**

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DEDICATION

I dedicate this dissertation to Carlie, Mamane, Mom, Dad, and the nesting Canada geese
of Cape Churchill

Five great sources of inspiration

ABSTRACT

The distribution and abundance of breeding lesser snow geese (*Chen caerulescens caerulescens*) in northern Manitoba, Canada have expanded considerably during the last 30 years, and snow geese now use areas where they did not previously occur and were traditionally used solely by breeding Eastern Prairie Population (EPP) Canada geese (*Branta canadensis interior*). Breeding and migrating snow and Ross's geese (*Chen rossii*) have dramatically altered sub-arctic vegetation along Hudson Bay, but the direct or indirect effects of these growing populations on other species, particularly sympatric nesting EPP Canada geese, is not well documented. To better understand relationships between snow geese and EPP Canada geese, I evaluated factors influencing survival and spatial distribution of Canada goose nests across a range of spatial and temporal scales. I employed nest distribution data, 2001 – 2007, and spatial point-pattern analyses to assess (1) whether nesting Canada geese exhibited territoriality, (2) whether current spatial patterns of Canada goose nest distribution were evolutionarily stable, and (3) whether spatial patterns of Canada goose nest fate were associated with the density of nesting snow geese. In addition, I employed logistic-exposure models to evaluate factors influencing within- and among-year variation in the probability of nest survival for Canada goose nests from 2005 – 2007 in areas with different histories and densities of snow goose nesting. Specifically, I tested the apparent-competition hypothesis and the nesting-association hypothesis as mechanisms to describe interactions between nesting Canada geese and snow geese. I examined factors influencing the spatial distribution of nesting EPP Canada geese in a coastal tundra landscape between 1976 and 2007, and assessed whether associations with these factors have changed in light of changes to the

coastal salt marsh vegetation from snow goose herbivory. Lastly, I modeled Canada goose nest count data collected during range-wide aerial breeding population surveys conducted annually for EPP Canada geese in northern Manitoba, Canada, 1987 – 2008. I employed mixed-effects Poisson regression to (1) quantify spatial relationships between nesting lesser snow geese and Canada geese; (2) assess factors influencing the distribution of nesting Canada geese at a range-wide spatial scale (101,500 km²); and (3) evaluate how well local (i.e., nest or study area) spatial-scale associations predict range-wide distribution patterns.

Point-pattern analyses indicated territoriality among nesting Canada geese and that changes in snow goose nest proximity and density may influence Canada goose nest fate. However, logistic-exposure models did not support the apparent-competition or nesting-association hypotheses as mechanisms governing associations among Canada goose nest survival and nesting snow geese; particularly relative to the strong effects of collared lemming (*Dicrostonyx richardsoni*) and arctic fox (*Alopex lagopus*) population dynamics. Canada goose nest density was negatively associated with increasing distance to coastal salt marsh brood-rearing habitat; however, from 1976 to 2007, this relationship appeared to be changing to where in more recent years increased distance to salt marsh was positively associated with density of nesting Canada geese. Three models of Canada goose nest counts from range-wide aerial surveys—all containing factors related to previous Canada goose nest density (representing recruitment), distance to Hudson Bay, general habitat type, and lesser snow goose nest density—had the lowest mean-squared error among all models considered and were unbiased. The relationship between Canada goose nests and snow goose nest density suggested that the abundance of nesting Canada

geese and snow geese varied similarly across habitats throughout the entire EPP breeding range (e.g., both abundant near the coast), but that very high snow goose abundance may have negative impacts on Canada goose nest density.

My analyses of data from multiple spatial and temporal scales suggested that associations between the distribution of Canada goose nests and nesting snow geese was likely related to alteration of coastal salt marshes from snow goose foraging, and subsequent changes in the distribution of Canada goose brood-rearing habitat use; rather than influences related to Canada goose nest survival. My analyses highlight that a continuing shift in the spatial distribution of nesting snow geese along western Hudson Bay will have implications for the spatial distribution of sympatric nesting Canada geese.

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CHAPTER 1

EVIDENCE FROM SPATIAL POINT-PATTERN ANALYSES OF TERRITORIALITY AND INTER-SPECIFIC INTERACTIONS AMONG SYMPATRIC NESTING CANADA GEESE AND LESSER SNOW GEESE

INTRODUCTION

The spatial distribution of nesting birds is likely influenced by multiple factors that vary in their importance among spatial scales (i.e., spatial resolution and spatial extent) and exhibit potentially complex interactions (Johnson 1980, Wiens et al. 1987, Wiens 1989). At a local spatial scale (e.g., nest level [high resolution, small extent]), habitat attributes and access to resources (e.g., food, water, cover), inter- and intra-specific interactions or associations, and predator pressure likely influence spatial patterns of nesting birds (Lack 1968, Burger 1984, Brown and Bomberger Brown 1996, Tremblay et al. 1997, Rolland et al. 1998) while at a regional spatial scale (i.e., low resolution, large extent), climate and geomorphology are also likely to be important (Wiens 1989). The magnitude of the effect of these factors is directly related to the amount they influence the vital rates of nesting birds; primarily the survival of the nest or the survival of the nesting bird (Clark and Shutler 1999, Richardson and Bolen 1999). Although changes in climate or geomorphology may affect range-wide reproductive performance leading to shifts in nesting distribution across the entire species' range, these interactions likely occur over a long temporal extent, and subsequently are difficult to predict or manage (Wiens 1989). Changes in the spatial distribution of nests over a shorter temporal extent are likely driven by local spatial-scale interactions. If nest-level interactions result in reduced nesting success and low recruitment, the distribution of nests will likely change over time to favor use of available nest sites that produce the highest possible nest success and recruitment (Burger 1984, Clark and Shutler 1999). Describing the distributions of nests, quantifying spatial variation in vital rates (e.g., nest success), and identifying short-term changes in nesting patterns at the local spatial scale can provide

insight into processes influencing a species' distribution (Martin 1993, Clark and Shutler 1999, Diggle 2003, Baddeley and Turner 2005).

Long-term monitoring (>30 years) of breeding Eastern Prairie Population (EPP) Canada geese (*Branta canadensis interior*) at Cape Churchill, Manitoba, Canada has documented a decline in nest density (Walter 1999, D.E. Andersen, Minnesota Cooperative Fish and Wildlife Research Unit, unpublished data); however, across the EPP nesting range, the breeding population has remained relatively stable or increased (Raedeke et al. 2007). This suggests there may have been a shift in the spatial distribution of nesting Canada geese in this region. However, the spatial extent or cause of this shift is unknown. Currently, there is concern about the influence of the increasing abundance of lesser snow goose (hereafter, snow goose; *Chen caerulescens caerulescens*) and Ross's goose (*Chen rossii*) populations on breeding EPP Canada geese (Ankney 1996; Batt 1997; Walter 1999; Nack and Andersen 2004, 2006; Gleason et al. 2004).

Nesting snow and Ross's geese have expanded their spatial distribution along western Hudson Bay during the last 20 years (Ankney 1996, Abraham and Jefferies 1997, Batt 1997, Jefferies et al. 2006), moving into areas that were traditionally used solely by nesting EPP Canada geese (Walter 1999). At a range-wide spatial scale, EPP Canada geese and snow geese utilize similar coastal tundra nest habitat and occur in high densities across this habitat (Malecki et al. 1980, Cooke et al. 1995, Humburg et al. 2000, Mowbray et al. 2000, Jefferies et al. 2006). However, at a more local spatial scale, snow geese are colony nesters (spatial aggregation) and Canada geese typically exhibit dispersed (spatial inhibition; i.e., maximize distance between nests) nesting ecology

(Cooke et al. 1995; Walter 1999; Mowbray et al. 2000, 2002), although have also been considered “semi-colonial” (see Mowbray et al. 2002).

Evolution of colonialism in nesting snow geese was likely driven by decreased risk of depredation on an individual nest when in larger groups, compensating for their smaller size and reduced individual defensive capabilities (Findlay and Cooke 1982; Samelius and Alisauskas 2000, 2001) relative to Canada geese. Under the predator-protection hypothesis, nests occurring in large aggregations experience increased nest survival due to reduced probability of nest depredation, a benefit that outweighs the potential costs of nesting in high densities (e.g., competition for resources, attraction of predators), which ultimately drives the evolution of coloniality (Wittenberger and Hunt 1985, Martin 1995, Richardson and Bolen 1999). A slightly more general yet related hypothesis, the protective-association hypothesis, predicts the evolution of aggregation between two species as the result of increased nest survival for one or both species through predator protection or possibly some other mechanism (Burger 1984, Baldwin 2006). The evolution of dispersed nesting behavior in northern-nesting Canada geese is thought to be influenced by nest defense in that a single adult Canada goose is capable of deterring an arctic fox (*Alopex lagopus*; Bahr 1989), the most important nest predator (Walter 1999). Thus, in the absence of a highly aggregated resource, or benefits from aggregation in addition to group defense (e.g., “information center”; Ward and Zahavi 1974), Canada geese likely optimize their reproductive performance by selecting nesting habitat or nest sites that increases their probability of nest survival while also maximizing their access to resources (e.g., food, water, cover). Theoretically, and assuming homogenous spatial distribution of resources, this pattern of selection results in dispersed nesting and

territoriality, thus maximizing the distance to a nearest conspecific (spatial inhibition). Whether the dispersed, territorial reproductive strategy of Canada geese remains evolutionarily stable (i.e., the probability of successfully reproducing is higher compared to alternative strategies [e.g., protective-association with snow geese]; Maynard Smith and Price 1973) when occurring sympatrically with colonial nesting snow geese is not known.

Spatial statistics for point patterns provide a rigorous format for quantifying spatial distributions, testing simple hypotheses, and examining potential interactions between points (Diggle 1983, 2003; Manly 2001). I employed spatial point-pattern analyses to quantify patterns of EPP Canada goose nests, EPP Canada goose nest fate, and snow goose nests at two study areas in northern Manitoba, Canada with different temporal durations (5 – 6 years and 10 – 15 years) of sympatric nesting Canada and snow geese. Specifically, I assessed two components of Canada goose nest ecology. First, I tested the hypothesis that EPP Canada geese exhibit dispersed nesting ecology and territoriality. I then assessed whether the observed spatial patterns of Canada goose nest fate supported dispersed nesting ecology and territoriality as an evolutionarily stable nesting strategy. I predicted (1) that if EPP Canada goose nests were dispersed, consistent with territoriality, EPP Canada geese would maximize their distance to neighboring nests thus exhibiting regularity or inhibition in their nesting patterns, and (2) if this strategy was stable then successful nests should also exhibit regularity or inhibition in their distribution. Second, by examining two study areas with differences in the temporal extent of sympatric nesting Canada geese and snow geese, I tested the protective-association hypothesis as a driving mechanism behind the observed spatial

distribution of Canada goose nests relative to snow goose nests after >10 years of nesting sympatrically. I predicted that (1) if EPP Canada geese benefited from snow goose aggregations in the form of reduced probability of nest failure (i.e., the protective-association hypothesis) in areas with recent sympatric nesting, I would observe positive spatial correlation or aggregation with snow geese where both species have been nesting for >10 years. Conversely, (2) if Canada geese experience increased probability of nest failure when nesting among snow geese, over time they would tend towards a negative correlation with snow goose nests.

STUDY AREA

The EPP Canada goose breeding range includes ~101,500 km² of northern Manitoba, Canada (Malecki et al. 1980). The highest density of breeding EPP Canada geese is found along a strip of coastal tundra habitat bordering western Hudson Bay (Humburg et al. 2000). The Nestor One study area (~ 48 km²; 58° 34' N, 93° 11' W) was south of Cape Churchill and approximately 60 km east-southeast of the town of Churchill, Manitoba, Canada. Nesting snow geese (>5 nests) have been present at Nestor One beginning in 2001. My second study area, Broad River (~10 km²; 58° 07' N, 92° 51' W), was located ~60 km south of Nestor One along the Hudson Bay coast. Annual aerial breeding-ground surveys documented a >200% increase in the number of snow goose nests near the mouth of the Broad River since 2000 (Raedeke et al. 2007). Nestor One and Broad River were located inside of Wapusk National Park (11,475 km²) within the broader ecosystem of the Hudson Bay Lowlands. Coastal salt marshes, beach ridges, sedge meadows, and interior sedge-meadow complexes composed the major habitat types at both study areas (Didiuk and Rusch 1979, Walter 1999). More detailed information

about the vegetation community composition and abundance throughout Wapusk National Park was presented in Brook (2001).

METHODS

NEST SEARCHING AND NEST FATE

Systematic ground surveys for nesting EPP Canada geese followed standardized protocols outlined in Walter (1999) and have been conducted annually at Nestor One since 1976 (Walter 1999, Reiter 2006). Beginning in 1998, nest observers carried global positioning system (GPS) units to record the Universal Transverse Mercator (UTM) coordinates of Canada goose and snow goose nests at Nestor One. In 2005 and 2006, I systematically searched the Broad River study area with 3 additional observers following the same protocols used at Nestor One and recorded the coordinate locations for all Canada and snow goose nests discovered. At Nestor One and Broad River, observers estimated the hatch date for all nests using egg flotation and egg candling (Westerkov 1950, Weller 1956, Walter and Rusch 1997a, Reiter and Andersen 2008a) and returned to nests at or subsequent to the estimated hatch date to determine nest fate. Canada goose nests were classified as successful (e.g., large intact egg membranes) or failed (e.g., small shell fragments, predator sign; Didiuk and Rusch 1979, Walter 1999) at final nest visits.

DATA PREPARATION

UTM coordinates for EPP Canada goose nests at Nestor One were available for 1998 – 2007; however, in 1998 and 1999 many nests were missing coordinates, and in 2000 and 2004 there were very few Canada goose nests. Furthermore at Nestor One, snow goose nests have only been present at levels >5 nests in 2001 – 2003 and 2005 –

2007. I used nest data from only these 6 years in analyses of point patterns at Nestor One, and data from 2005 – 2006 from the Broad River.

Irregular study area boundaries and highly heterogeneous distribution of habitats can confound analysis of spatial point patterns (Diggle 2003, Haase 1995). I imported EPP Canada goose and snow goose nest data into R v.2.5.1 (© 2007 The R Foundation for Statistical Computing) and used the SPATSTAT package for point-pattern analysis (Baddley and Turner 2005). This software permitted increased flexibility and reality in the analysis of point patterns, allowing for irregular study area borders as well as incorporating areas within a study region $[A]$ where no events can occur (e.g., unsuitable cover types). Both Nestor One and Broad River are irregularly shaped and at Nestor One, habitat that is not used by nesting geese (e.g., water and large beach ridges) divides the area. I used ArcMAP 9.0 (© 1998 – 2004 ESRI) and the vegetation classification layer of Brook (2001) to delineate water and beach ridges at Nestor One and Broad River. I considered water bodies and inland beach ridges >1 ha in size as patches of non-habitat. I coded non-habitat patches into the image I created in R representing Nestor One (Fig. 1). The Broad River was highly homogenous with only small bodies of water. I did not code any non-habitat patches for the Broad River (Fig. 1) study area. The Nestor One and Broad River study areas derived from GIS and implemented in R were 30.52 km^2 and 9.61 km^2 , respectively.

ANALYSES OF POINT PATTERNS

Analyses of spatial point patterns primarily utilize inter-point distances over a selected region, A (Diggle 2003). These distances are compared to those simulated using an underlying Poisson process. Nearest-neighbor analysis incorporates the distance from

each point to its nearest-neighbor point (Clark and Evans 1954) and provides information about local-scale or first-order spatial patterns (Liu 2001). Ripley's K -function quantifies spatial patterns across multiple spatial scales and incorporates information about the expected count of all points at different distances from each point of interest to assess second-order patterns (Ripley 1976, Haase 1995). First-order and second-order bivariate analyses can also test for independence in the spatial point patterns of two or more types (e.g., 2 species, successful versus failed nests; Andersen 1992, Diggle 2003).

For each species in each year at each study area, I conducted a first-order nearest-neighbor analysis and a second-order Ripley's- K analysis. The calculation of the empirical nearest-neighbor G -estimate was:

$$G_{ij}(r) = n_i^{-1} \sum I(r_{ij} \leq r)$$

Where, $G_{ij}(r)$ was the probability a nest of type i has a nearest neighbor of type j at distance, r ; n_i was the total number of nests of type i ; I was an indicator variable assigned a value of 1 if $r_{ij} \leq r$ and 0 otherwise; and r_{ij} was the distance from nest of type i to its nearest neighbor of type j (Diggle 2003, Baddeley and Turner 2005).

The calculation of the Ripley's- K estimate $K_{ij}(r)$ was:

$$K_{ij}(r) = n_i^{-1} n_j^{-1} A \sum I(r_{ij} \leq r)$$

Where, n_j was the total events of type j , and A was the area (m^2) of the study region. All remaining variables were the same as defined for $G_{ij}(r)$. Both equations (G -estimate and Ripley's K -estimate) were employed for both univariate (type $i = type j$) and bivariate (type $i \neq type j$) analysis.

I compared the observed test statistic, $K_{ij}(r)$ or $G_{ij}(r)$, against the distribution of $K_{ij}(r)$ or $G_{ij}(r)$ from 199 permutations of point patterns based on a Poisson-process model with the same density as the observed nests (Diggle 2003). The 5th and 195th ranked values of the simulated statistic at each distance evaluated formed the 95% critical envelope (95% CE). I constructed 95% CE to test for significant deviations from complete spatial randomness in each of my analyses. At each distance, observed $K_{ij}(r)$ or $G_{ij}(r)$ below the 95% CE indicated significant deviations from complete spatial randomness towards regularity or spatial inhibition at the $\alpha = 0.05$ significance level, whereas observed $K_{ij}(r)$ or $G_{ij}(r)$ above the 95% CE identified significant aggregation. The 95% CE was based on:

$$\text{exact significance level} = 2 * nrank / (1 + nsim).$$

Where, $nrank$ was the n^{th} ranked largest and n^{th} ranked smallest value for the calculated test statistic from the simulated patterns at each distance evaluated, and $nsim$ was the total number of simulations (Baddeley and Turner 2005). For my analysis, $nrank = 5$ and $nsim = 199$.

For analyses of the distribution of successful versus failed Canada goose nests, I employed a random labeling simulation (Diggle 2003). This technique assumed the spatial distribution of all Canada goose nests whether they eventually failed or succeeded was generated by the same underlying process. I tested whether, given this underlying distribution of nests, the marks (e.g., successful or failed) were distributed randomly in space. I constructed the 95% CE by simulating 199 permutations of the point pattern when I assigned marks randomly.

Finally, I utilized multi-type (i.e., bivariate) analysis, which assumed nests of each type came from their own underlying spatial process, to evaluate whether EPP Canada goose nest fate was correlated with its spatial positioning relative to snow goose nests. I evaluated successful and failed EPP Canada goose nests separately, relative to all snow goose nests.

HYPOTHESES AND PREDICTIONS

I framed my analysis in terms of three questions regarding Canada goose nesting distribution and ecology in two broad categories.

EPP Canada goose nest patterns

Question 1: Do EPP Canada geese exhibit dispersed nesting and territoriality?

I predicted that if Canada geese exhibited dispersed nesting and territoriality then first- and second-order patterns of Canada goose nest distribution should reveal spatial inhibition. However, a mixed strategy of first-order inhibition and second-order aggregation might suggest local-scale territoriality coupled with selection of habitat or other factors influencing broader-scale patterns.

Question 2: Does the observed spatial pattern of EPP Canada goose nest distribution represent an evolutionarily stable nesting strategy?

If a pattern of spatial inhibition was evolutionarily stable, random labeling should identify successful nests as having both first- and second-order inhibition, and failed nests as first- and second-order aggregated. Conversely, patterns of aggregation in first- and second-order analysis of all nests as well as of successful nests would suggest stable aggregation in Canada goose nesting patterns. Evidence of first-order inhibition and

second-order aggregation in successful nests, and first-order aggregation and second-order inhibition of failed nests would support the mixed-strategy as evolutionarily stable.

EPP Canada goose and snow goose interactions

Question 3: Does the protective-association hypothesis provide a mechanism explaining the fate of Canada goose nests where Canada geese nest sympatrically with lesser snow geese?

I considered first- and second-order aggregation of successful Canada goose nests with snow goose nests and first- and second-order inhibition between failed Canada goose nests and snow goose nests as evidence in support of the protective-association hypothesis. This hypothesis would be further supported if short-term spatial patterns of Canada goose nest fate and snow geese nests at Nestor One suggested aggregation between successful Canada goose nests and snow goose nests, coupled with data from longer-term sympatric nesting at Broad River that identified a positive association between Canada goose nests and snow goose nests. Alternatively, Baldwin (2006) identified patterns of interactions between nesting cackling geese (*Branta hutchinsii*) and Ross's geese that would likely result in first-order aggregation of failed Canada goose nests with snow goose nests but second-order aggregation between successful Canada goose nests and snow goose nests. This would suggest that at a local scale (e.g., nearest neighbor) Canada geese do not benefit from a nearby nesting snow goose; however, at a broader scale, when incorporating information about the overall density of nesting snow geese, Canada goose nests are more likely to succeed if aggregated with snow geese than if located away from snow goose aggregations.

ASSUMPTION

Because not all nests are found during nest searching, I considered the observed number of nests per m^2 (λ_j) to be a measure of relative nest density among years and species. For summary statistics, I converted λ_j from nests per m^2 (used in point-pattern analysis calculations) to nests per km^2 to facilitate interpretation. Because the detection probabilities of a Canada goose nest and snow goose nest are likely different, I did not directly compare the relative nest density between species.

Analyses of spatial point patterns typically assumes all events (e.g., nests) were detected within a selected region (probability of detection = 1). However, the theoretical calculation of Ripley's- K estimate ($K_{ij}(r) = \lambda_j^{-1} E[N_{ij}(r)]$) is the ratio of the expected count of points in an area defined by a circle of radius, r ($E[N_{ij}(r)]$) under complete spatial randomness, and the mean nest density (λ_j). Therefore, if a random sample of the pattern is removed, the resulting K -estimate is proportional to the K -estimate of the entire spatial pattern. Essentially, "random thinning" (Diggle 2003) multiplies both values in the ratio by the probability (p) that one event is kept. Walter and Rusch (1997b) reported the probability of discovering an EPP Canada goose nest was 0.72, and importantly, that there was no spatial variation in this probability at Nestor One. For my analyses, I assumed 0.72 was equivalent to p and thus the observed spatial sample of nests represented a random and spatially unbiased subset of the full point pattern. A similar argument applies in nearest-neighbor analysis in which the theoretical distribution function of G_{ij} [$G_{ij}(r) = 1 - \exp(-\lambda_j \pi r^2)$], under complete spatial randomness, is defined by λ_j . Therefore, removing a random selection of proportion p of the nests does not change the shape of the distribution of G_{ij} .

RESULTS

NEST SUMMARY

Between 2000 and 2007, EPP Canada goose relative nest density was substantially lower (4.27 nests per km², $SE = 0.66$, $n = 8$) at Nestor One than in 2005 and 2006 at Broad River (42.45 nests per km², $SE = 0.45$, $n = 2$; Table 1). Snow goose relative nest density was also much greater at Broad River (22.35 nest per km², $SE = 6.35$, $n = 2$) than Nestor One (0.98 nests per km²; $SE = 0.39$, $n = 8$; Table 1). Apparent nest success (successful nests ÷ total number of nests) averaged 0.49 ($SE = 0.10$, $n = 8$) for Canada geese at Nestor One between 2000 and 2007 and 0.71 ($SE = 0.02$, $n = 2$) at Broad River in 2005 and 2006. Snow goose nests experienced substantially lower nest success at Nestor One (0.23, $SE = 0.09$, $n = 5$) between 2002 and 2007 than at Broad River (0.63, $SE = 0.03$, $n = 2$) in 2005 and 2006 (Table 1).

INTRA-SPECIFIC SPATIAL PATTERNS OF NESTS

At Nestor One, in 3 (2001, 2003, 2006) of 6 years evaluated, Canada goose nests exhibited significant deviations from complete spatial randomness towards inhibition based on the distribution of nearest neighbors between 75 and 200 m (see x-axis of Fig. 2). However, in second-order analyses, the $K_{ij}(r)$ for all Canada goose nests fell above the 95% CE, tending toward aggregation, across many distances in 5 of 6 years (Fig. 3). At Broad River in 2005 and 2006, Canada goose nests exhibited significant inhibition at ~20 – 60 m in first-order analysis and significant aggregation at all distances evaluated in second-order analysis (Fig. 4).

Question 1: Do EPP Canada geese exhibit dispersed nesting and territoriality?

Significant inhibition in nearest-neighbor analyses for Canada goose nests supported the hypothesis that Canada geese exhibited territoriality in nesting patterns. However, second-order patterns [$K_{ij}(r)$] suggested the overall distribution of nesting Canada geese within my study areas was aggregated. These combined results indicate there may be multiple factors, which vary among spatial scales and in their effect on nest distributions, driving the spatial patterns of Canada goose nests.

Given the underlying spatial distribution of Canada goose nests at Nestor One, the spatial pattern of successful Canada goose nests did not deviate from random labeling in any year evaluated at either spatial scale. At Broad River in 2005 and 2006, successful Canada goose nests exhibited spatial inhibition at local (~20 – 50 m) scales, and significant aggregation at all distances in second-order analyses (Fig. 5). Although failed Canada goose nests at Nestor One exhibited few trends in first-order analysis, second-order analysis indicated significant deviations from random labeling towards aggregation for at least some distances in 5 of 6 years (Fig. 6). Within the second order analysis at Nestor One, I observed significant aggregation of failed nests at scales of 400 – 600 m in 2002 and 2006; and at broader scales of 800 – 1,200 m in 2003, 2005, and 2007. At Broad River in 2005 and 2006, failed Canada goose nests were aggregated at ~100 – 200 m in first-order analysis and at all distances in second-order analyses in both years (Fig. 7).

Question 2: Does the observed spatial pattern of EPP Canada goose nest distribution represent an evolutionarily stable nesting strategy?

Results from Broad River identified local-scale territoriality as a stable nesting strategy with successful nests inhibited and failed nests aggregated in first-order analysis.

Second-order results from Nestor One suggested that there was aggregation of failed nests within the current spatial pattern of nests, yet successful nests were distributed randomly. Although there may be clusters of failed nests, successful nests were still located randomly within the current pattern suggesting the current second-order pattern of aggregation should persist.

Snow goose nests at Nestor One tended significantly toward aggregation in 4 of 6 years evaluated based on first-order analyses (Fig. 8), in 5 of 6 years based on the second order *K*-estimate (Fig. 9), and across nearly all distances. At the Broad River, snow goose nests were significantly aggregated across nearly all distances in all analyses (Fig. 10). Thus, at all spatial scales in almost all years and in both study areas, snow geese exhibited aggregated nesting.

INTER-SPECIFIC SPATIAL PATTERNS OF NESTS

At Nestor One, I observed few significant deviations (1 of 6 years) from complete spatial randomness in the relationship between successful Canada goose nests and snow goose nests in first-order analysis. Second-order deviations from complete spatial randomness occurred in 2003, 2005, and 2006 (Fig. 11). In 2003, there was significant aggregation between successful Canada goose nests and snow goose nests at all distances. In 2005, nests exhibited significant inhibition at 1,000 – 1,200 m, whereas 2006 nests exhibited significant aggregation at shorter distances (~150 – 250). At Broad River, successful Canada goose nests were significantly aggregated with snow goose nests across nearly all distances in both first- and second-order analyses in 2005 and 2006 (Fig. 12).

At Nestor One, failed Canada goose nests and snow goose nests exhibited significant, albeit variable, interactions at some distances in all 6 years based on first-order analysis (Fig. 13). Between 2005 and 2007, there was significant aggregation between failed Canada goose nests and snow goose nests; however, in 2003, there was significant inhibition between failed Canada goose nests and snow goose nests. In second-order analyses for Nestor One, the observed pattern between failed Canada goose nests and snow goose nests deviated substantially from complete spatial randomness across many distances in 4 of 6 years (Fig. 14). From 2005 to 2007 there was significant aggregation, however, in 2003 the relationship was exactly opposite with significant inhibition between failed Canada goose nests and snow goose nests. At Broad River, failed Canada goose nests were aggregated with snow goose nests at all distances in both first- and second-order analyses in 2005 and 2006 (Fig. 15).

Question 3: Does the protective-association hypothesis provide a mechanism explaining spatial variation in the fate of Canada goose nests where Canada geese nest sympatrically with lesser snow geese?

I observed aggregation between failed Canada goose nests and snow goose nests at Nestor One in first- and second-order analysis, and inhibition between successful Canada goose nests and snow goose nests in second-order analysis when density of snow geese was low (2005 – 2007). When density of snow goose nests was high (2003) successful Canada goose nests were aggregated with snow geese. Combined, these results suggest the effect of snow goose nests on Canada goose nest fate may change depending on overall snow goose nest density. Similarly, at Broad River (where snow goose nest density was much higher than at Nestor One), successful Canada goose nests

tended to be aggregated strongly with snow goose nests in both first- and second-order analysis.

DISCUSSION

The relative spatial positioning and changes in the distribution of two species can offer evidence concerning inter-specific interactions (Andersen 1992, Tilman and Lehman 1997). My quantification of the spatial distribution of EPP Canada goose nests, Canada goose nest fates, and snow goose nests near Cape Churchill, Manitoba identified several strong non-random patterns in nest distribution and fate, and partially confirmed the protective-association hypothesis as a mechanism influencing interactions between nesting Canada geese and snow geese over the last 10 – 15 years. The probability of nest failure in Canada geese nesting sympatrically with snow geese was conditional on snow goose nest density. This pattern supported the protective-association hypothesis as it applies to interactions between nesting Canada geese and nesting snow geese in northern Manitoba.

Although spatial patterns of northern-nesting Canada geese have been described as “highly territorial” (Mowbray et al. 2002), few studies have directly addressed the scale at which the territorial pattern was realized and whether this pattern was dependent upon the spatial scale of the observations. My results provide some of the first quantitative evidence that spatial patterns of Canada goose nests may differ depending on the spatial scale of the observations. The spatial distribution of EPP Canada goose nests varied from dispersed to aggregated across spatial scales between 2001 and 2007, often exhibiting nearest-neighbor (~20 – 50 m) intra-specific inhibition, while significantly aggregating with con-specifics at broader spatial scales (>1,000 m). This local-scale

inhibition may identify the spatial extent of territories in densely nesting Canada geese in a tundra landscape, and supports the hypothesis that Canada geese will exhibit local-scale territoriality. The cause(s) of broader scale aggregation was less clear but may include distribution of available habitat, access to resources, distribution of predators, or associations with conspecifics as well as other species.

Patterns of Canada goose nest fate I observed in northern Manitoba indicated that territoriality among Canada goose nests was likely an evolutionarily stable nesting strategy. At both Nestor One (short-term sympatric nesting) and Broad River (longer-term sympatric nesting), failed Canada goose nests tended to be aggregated within the underlying pattern of all Canada goose nests, while at the nearest-neighbor scale successful nests exhibited inhibition or randomness. The stability of second-order aggregation of nesting Canada geese was not as clear. However, second-order spatial patterns of Canada goose nests have remained consistent over 6 years at Nestor One, and the density of nesting Canada geese at Broad River has been increasing in the areas where the highest densities were observed in the late 1980s and early 1990s, suggesting further aggregation. Recent studies by Reiter (2006) and Miller et al. (2007) identified con-specific nest density to be positively associated with Canada goose nest survival. Together these observations support the continued persistence of second-order aggregation in Canada goose nesting patterns.

If Canada goose nests experienced increased nest success when associated with aggregations of snow geese, the protective-association hypothesis predicts that over time nests would tend toward further aggregation. This prediction was partially confirmed by the strong aggregations of Canada goose and snow goose nests at Broad River where

Canada geese and snow geese have been nesting sympatrically for ≥ 10 years. The nest densities of both species have increased during this time (Walter 1999, Raedeke et al. 2007) with now some of the highest densities of Canada goose nests recorded in arctic and subarctic regions occurring at Broad River. The current (2005 – 2007) pattern of aggregation between failed Canada goose nests and snow goose nests at Nestor One contrasted with observations from the Broad River. However, in 2003, successful Canada goose nests were significantly aggregated with snow goose nests at Nestor One. This reversal in the relationship between Canada goose nest fate and snow goose nests at Nestor One was accompanied by declining numbers of nesting snow geese. In 2003, there were 91 snow goose nests at Nestor One, and from 2005 – 2007 this number declined from 69 to 13 (Table 1). Large numbers of nesting birds are often necessary to successfully establish a new colony when group defense and predator protection play an important role in nesting ecology (Findlay and Cooke 1982). In Alaska, nests of black brant (*Branta bernicla*) experienced lower rates of depredation in colonies with >100 nests (Raveling 1989). Cooke et al. (1995) documented high nest success and low depredation rates in snow geese at the La Pèrouse Bay colony ($>20,000$ nesting pairs) near Churchill, Manitoba. In my study, snow geese experienced substantially lower apparent nest success when nesting at low densities at Nestor One compared to higher densities at Broad River (Table 1). It may be that Canada geese and snow geese only begin to benefit from associations when aggregations of snow goose nests reach a level that results in the benefits of group defense from predators. Aggregations beneath this threshold may attract predators and increase the likelihood of nest failure.

However, in 2003, lemming densities were very high at Nestor One and 8 snowy owls (*Nyctea scandiaca*) nested on the study area. Previous studies have reported a protective-association between nesting geese and nesting snowy owls in tundra landscapes (Tremblay et al. 1997, Bêty et al. 2001). In this relationship, geese benefit from reduced predator pressure from arctic foxes and other nest predators as the result of nesting near an aggressive nest defender (e.g., snowy owls). While defending their own nests, snowy owls increase the probability of survival for nests of other species nearby. In 2003 at Nestor One, the average nearest-neighbor distance of successful and failed Canada goose nests to snowy owl nests was 300 m and 543 m, respectively. However, average nearest-neighbor distance of successful and failed Canada goose nests to snow goose nests was 255 m and 557 m, respectively, and average nearest-neighbor distance of snow goose nests to snowy owl nests was only 149 m. Successful Canada goose nests were aggregated with both snowy owl nests and snow goose nests in 2003, suggesting a potential protective-association among Canada geese, snowy owls, and snow geese. Whether Canada goose nests benefited more from their proximity to snow goose nests or proximity to snowy owl nests in 2003 at Nestor One is not clear.

Baldwin (2006) reported that the probability of nest survival in cackling geese was positively associated with a nest being located within a Ross's goose colony but negatively associated with the number of Ross's goose nests within 30 m. My first- and second-order analysis of successful Canada goose nests relative to snow goose nests at Broad River identified aggregation at both scales. The difference in results between these studies may simply be the considerably lower snow goose nest densities in my analysis, thus limiting the number of snow goose nests within short distances of Canada goose

nests, than that of Ross's goose nests in Baldwin's study. If the density of nesting snow geese continues to increase at Broad River to nest densities of Ross's geese observed by Baldwin (2006) or of snow geese at La Pèrouse Bay (Cooke et al. 1995), the relationship between Canada goose nest fate and nearest-neighboring snow goose nest may shift from positive and aggregation to negative and inhibition.

Snow geese nested in aggregations (Mowbray et al. 2000) at both Nestor One and Broad River, and aggregation of snow goose nests occurred across all densities of nests I evaluated. Furthermore, I identified different trends in snow goose nest abundance between Nestor One and Broad River. At Nestor One, snow goose nest density increased dramatically in the early 2000s but seems to have steadily declined in recent years. Factors limiting the expansion of the Nestor One snow goose nest aggregations are not known, however, the importance of adequate coastal salt marsh vegetation for snow geese has been well documented (Gadallah and Jefferies 1995). Recent declines in snow goose nest density at La Pèrouse Bay, ~20 km west of Nestor One, coincided with the loss of salt marsh vegetation (Cooke et al. 1995, Jefferies et al. 2006). At Nestor One, the majority of salt marsh habitat has been altered by snow geese over the last 30 years, suggesting that this area may be unable to support high densities of nesting snow geese. Conversely, the density of snow goose nests at Broad River, which was much greater than at Nestor One but substantially less than observed elsewhere in the Arctic (Lepage et al. 1996, Didiuk et al. 2001, Samelius et al. 2007), appears to have grown substantially since 1995 when few snow goose nests were located in ground searches at Broad River (Walter 1999, D.E. Andersen, unpublished data). Currently, the status of coastal salt marshes near Broad River is not well known, limiting comparisons between study areas.

Increases in the number of snow geese along western Hudson Bay have had “catastrophic” impacts on coastal tundra vegetation (Jefferies et al. 2006). However, little attention has been dedicated to their potential impacts on other vertebrate species. Analyses of spatial point patterns provided a rigorous framework to test hypotheses regarding spatial patterns of nesting Canada geese and snow geese, and processes influencing these patterns. My results suggested the probability of Canada goose nest failure was influenced by the size and distribution of snow goose nest aggregations. Spatial variation in this probability was related to the overall density of snow goose nests, and perhaps snowy owl nests in 2003, and thus may also vary with time. Whether this variation will ultimately influence the evolution of nesting strategies in Canada geese (i.e., dispersed vs. aggregated) was unclear, despite evidence from Broad River that Canada geese and snow geese may nest successfully in the same dense aggregations. Managers should continue to quantify the relative spatial distributions of Canada goose nests and snow goose nests and the spatial distribution of Canada goose nest survival through annual breeding-ground surveys in this region. Temporal trends in the relative spatial distribution of these two tundra-nesting species provide critical insights into the long-term implications of snow goose population expansions on EPP Canada geese and potential management strategies in a spatially integrated framework.

TABLE 1. Summary of number of nests (n), nest fates (S = successful; F = failed), and relative nest density (λ_j) for Eastern Prairie Population Canada goose (*Branta canadensis interior*) nests and lesser snow goose (*Chen caerulescens caerulescens*) nests at two study areas near Cape Churchill, in northern Manitoba, Canada between 2000 and 2007.

AREA	YEAR	<u>Canada geese</u>				<u>Lesser snow geese</u>			
		n	λ_j	S	F	n	λ_j	S	F
Nestor One	2000	67	2.20	4	63	0	0	-	-
	2001	160	5.24	132	28	42	1.38	-	-
	2002	118	3.87	39	79	6	0.20	0	6
	2003	152	4.98	92	60	91	2.98	46	45
	2004	23	0.75	3	20	0	0	-	-
	2005	173	5.67	128	45	68	2.23	1	17
	2006	177	5.80	127	50	18	0.59	18	50
	2007	173	5.67	93	80	13	0.43	4	9
Broad River	2005	403	41.90	291	104	154	16.00	87	60
	2006	413	43.00	284	129	276	28.70	182	94

FIGURE 1. The (A) Nestor One (~30 km²) and (B) Broad River (~10 km²) study areas generated using R statistical software and the SPATSTAT package. Polygons within Nestor One identify water and beach ridge patches that were >1 ha in size and classified as habitat not suitable for goose nesting. Inset map identifies general location of study areas.

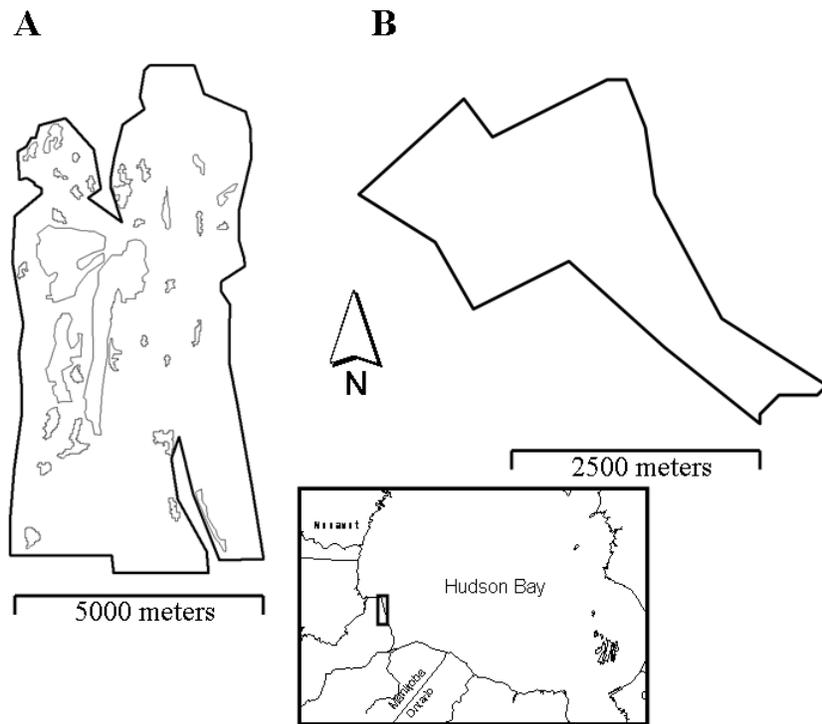


FIGURE 2. First-order nearest-neighbor G -estimate of all Eastern Prairie Population Canada goose (*Branta canadensis interior*) nests at Nestor One, 2001 - 2003, 2005 – 2007. The dashed line represents the theoretical distribution under complete spatial randomness, the dotted lines are the upper and lower 95% critical envelope (CE), and the solid black line is the observed distribution of $G_{ij}(r)$. Observed distribution above the 95% CE indicated aggregation while below the 95% CE indicated inhibition.

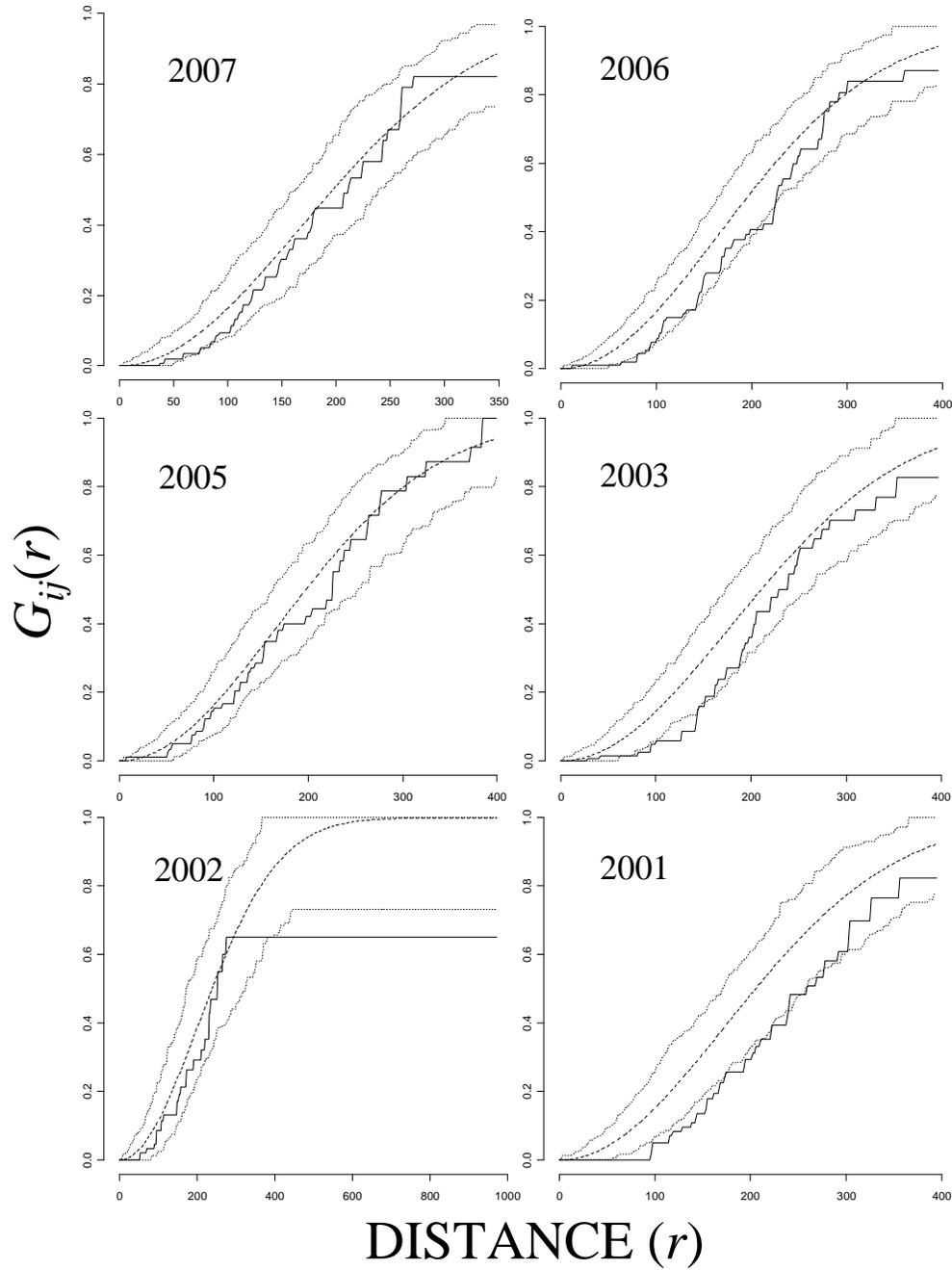


FIGURE 3. The second-order Ripley's K -estimate of all Eastern Prairie Population Canada goose (*Branta canadensis interior*) nests at Nestor One, 2001 - 2003, 2005 - 2007. The dashed line represents the theoretical distribution under complete spatial randomness, the dotted lines are the upper and lower 95% critical envelope (CE), and the solid black line is the observed distribution of $K_{ij}(r)$. Observed distribution above the 95% CE indicated aggregation while below the 95% CE indicated inhibition.

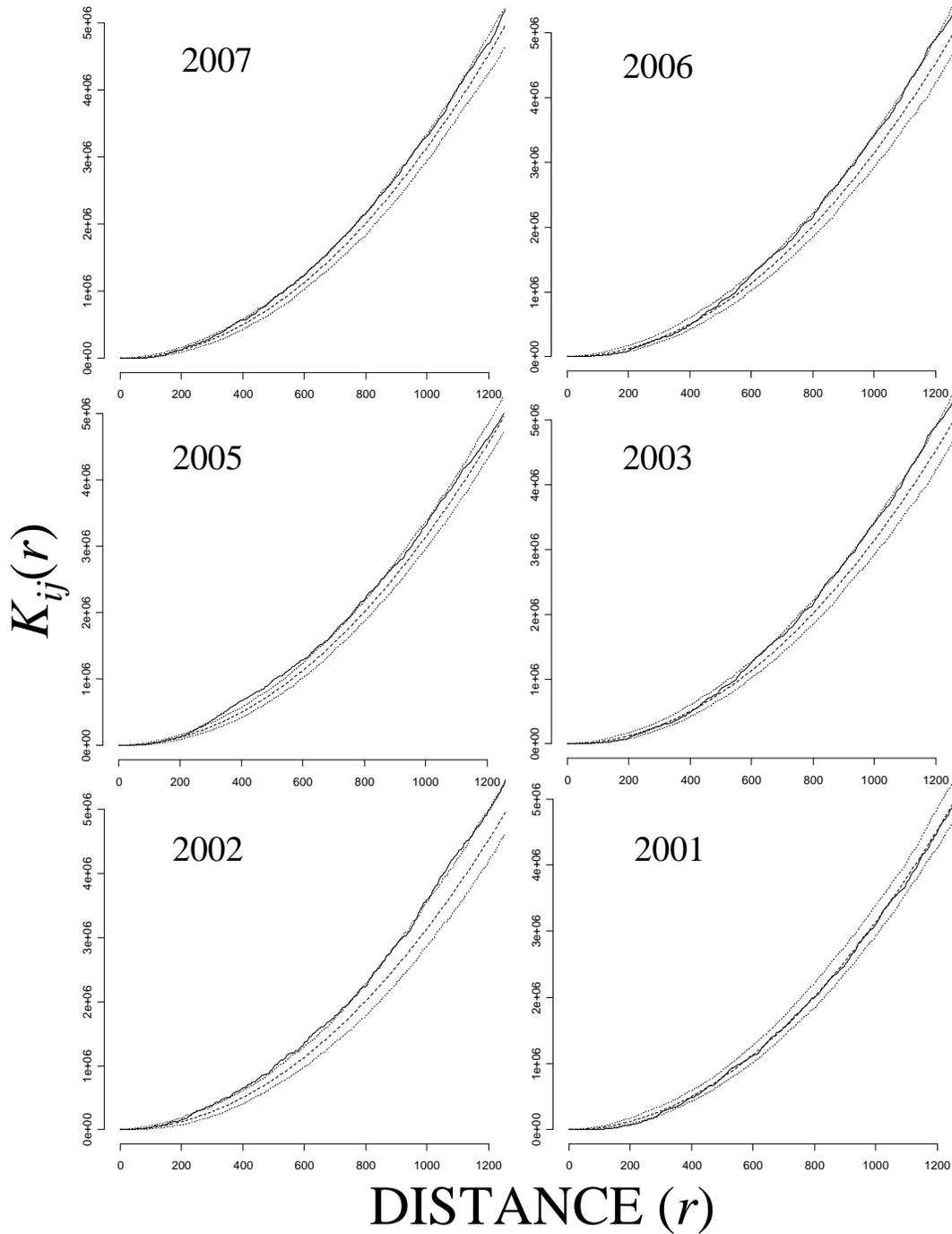


FIGURE 4. First-order nearest-neighbor G -estimate (left column), and the second-order Ripley's K -estimate (right column) of all Eastern Prairie Population Canada goose (*Branta canadensis interior*) nests at Broad River, 2005 – 2006. The dashed line represents the theoretical distribution under complete spatial randomness, the dotted lines are the upper and lower 95% critical envelope (CE), and the solid black line is the observed distribution of $G_{ij}(r)$ or $K_{ij}(r)$. Observed distribution above the 95% CE indicated aggregation while below the 95% CE indicated inhibition.

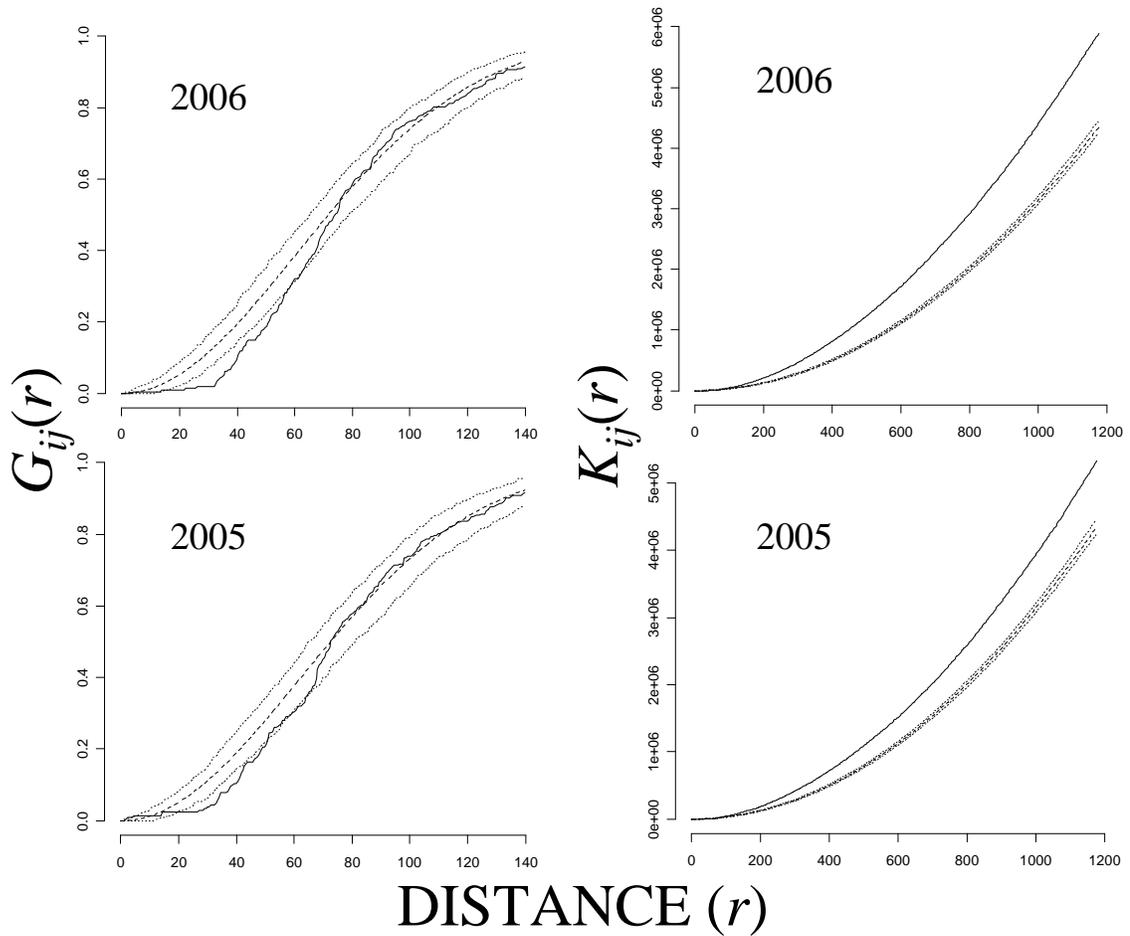


FIGURE 5. First-order nearest-neighbor G -estimate (left column) and the second-order Ripley's K -estimate (right column) of successful Eastern Prairie Population Canada goose (*Branta canadensis interior*) nests at Broad River, 2005 – 2006. The dashed line represents the theoretical distribution under complete spatial randomness, the dotted lines are the upper and lower 95% critical envelope (CE), and the solid black line is the observed distribution of $G_{ij}(r)$ or $K_{ij}(r)$. Observed distribution above the 95% CE indicated aggregation while below the 95% CE indicated inhibition.

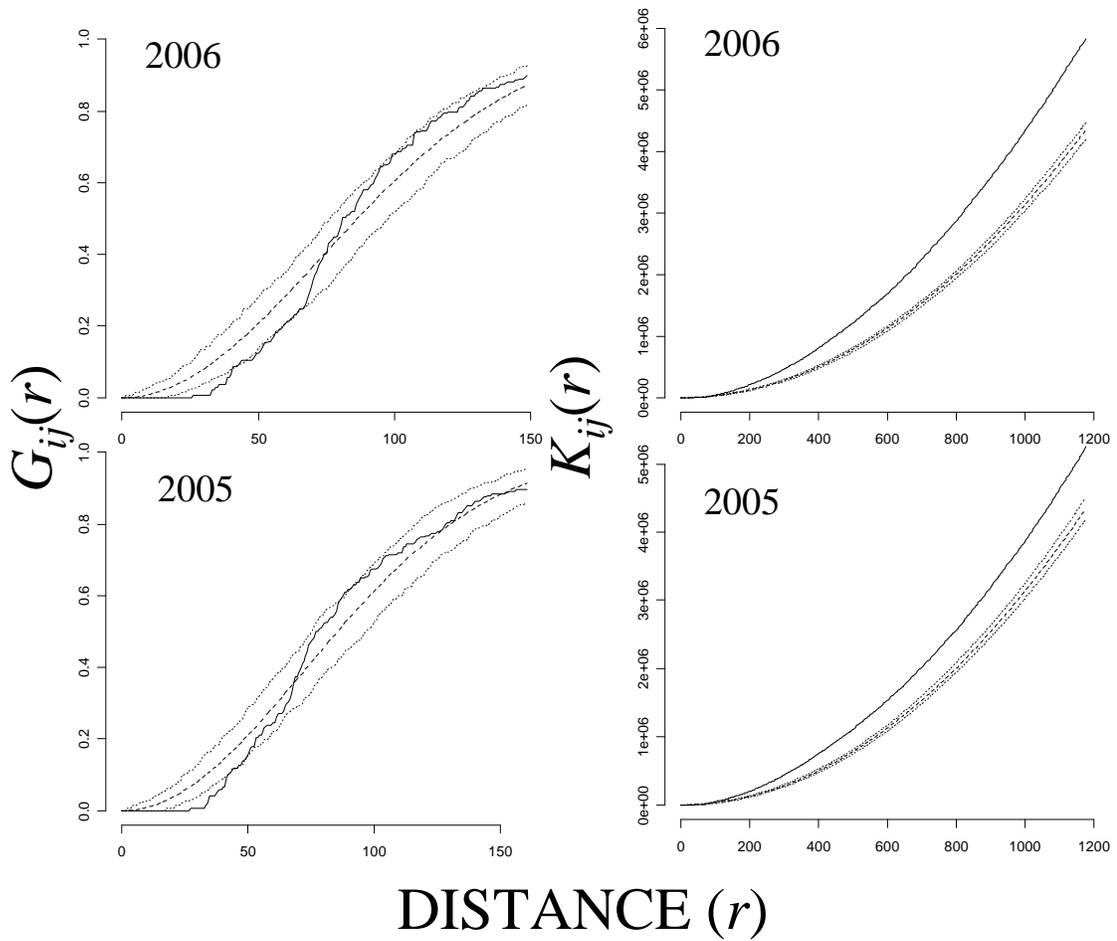


FIGURE 6. Second-order Ripley's K -estimate of failed Eastern Prairie Population Canada goose (*Branta canadensis interior*) nests at Nestor One, 2001- 2003, 2005 – 2007. The dashed line represents the theoretical distribution under complete spatial randomness, the dotted lines are the upper and lower 95% critical envelope (CE), and the solid black line is the observed distribution of $K_{ij}(r)$. Observed distribution above the 95% CE indicated aggregation while below the 95% CE indicated inhibition.

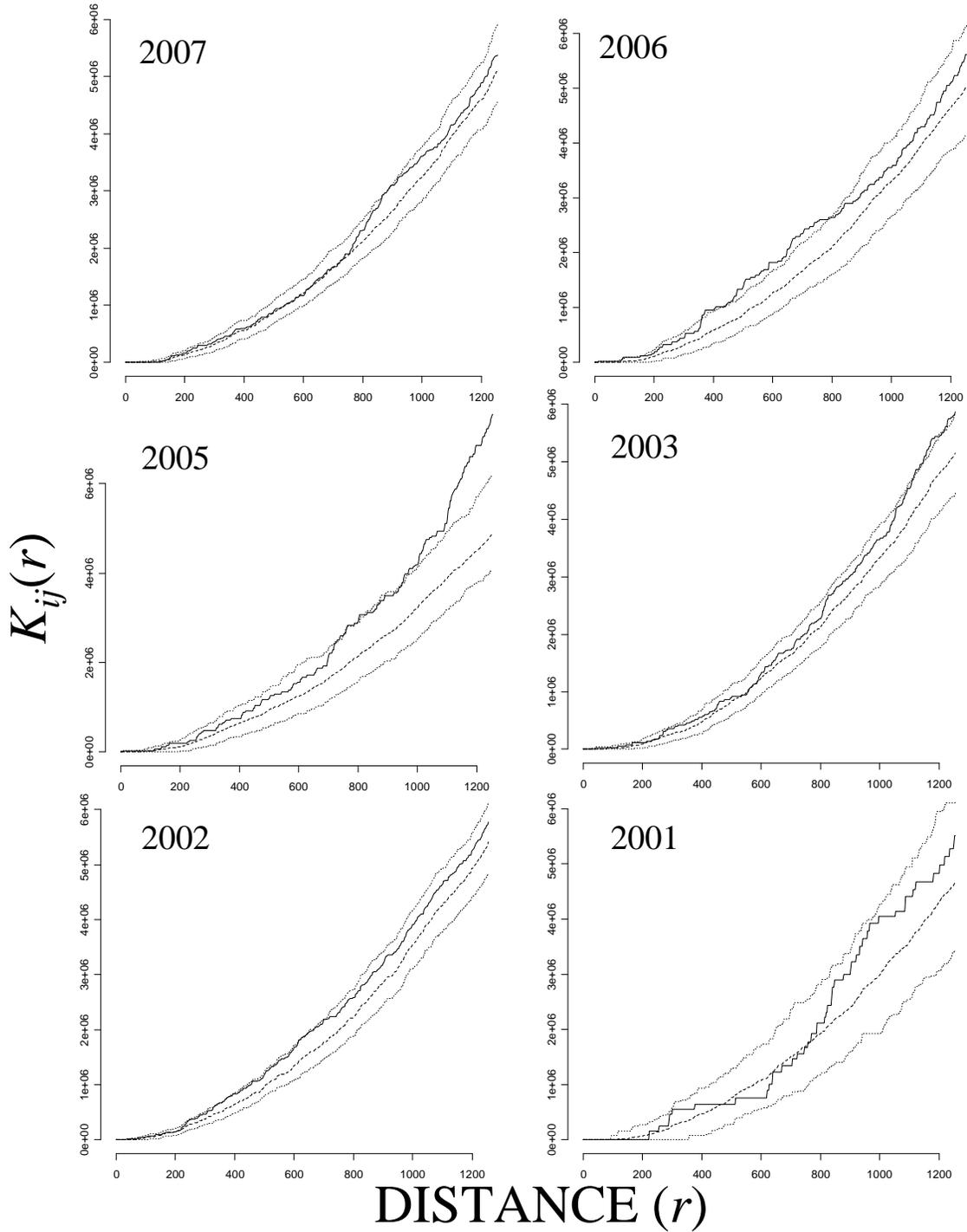


FIGURE 7. First-order nearest-neighbor G-estimate (left column) and the second-order Ripley's K -estimate (right column) of failed Eastern Prairie Population Canada goose (*Branta canadensis interior*) nests at Broad River, 2005 – 2006. The dashed line represents the theoretical distribution under complete spatial randomness, the dotted lines are the upper and lower 95% critical envelope (CE), and the solid black line is the observed distribution of $G_{ij}(r)$ or $K_{ij}(r)$. Observed distribution above the 95% CE indicated aggregation while below the 95% CE indicated inhibition.

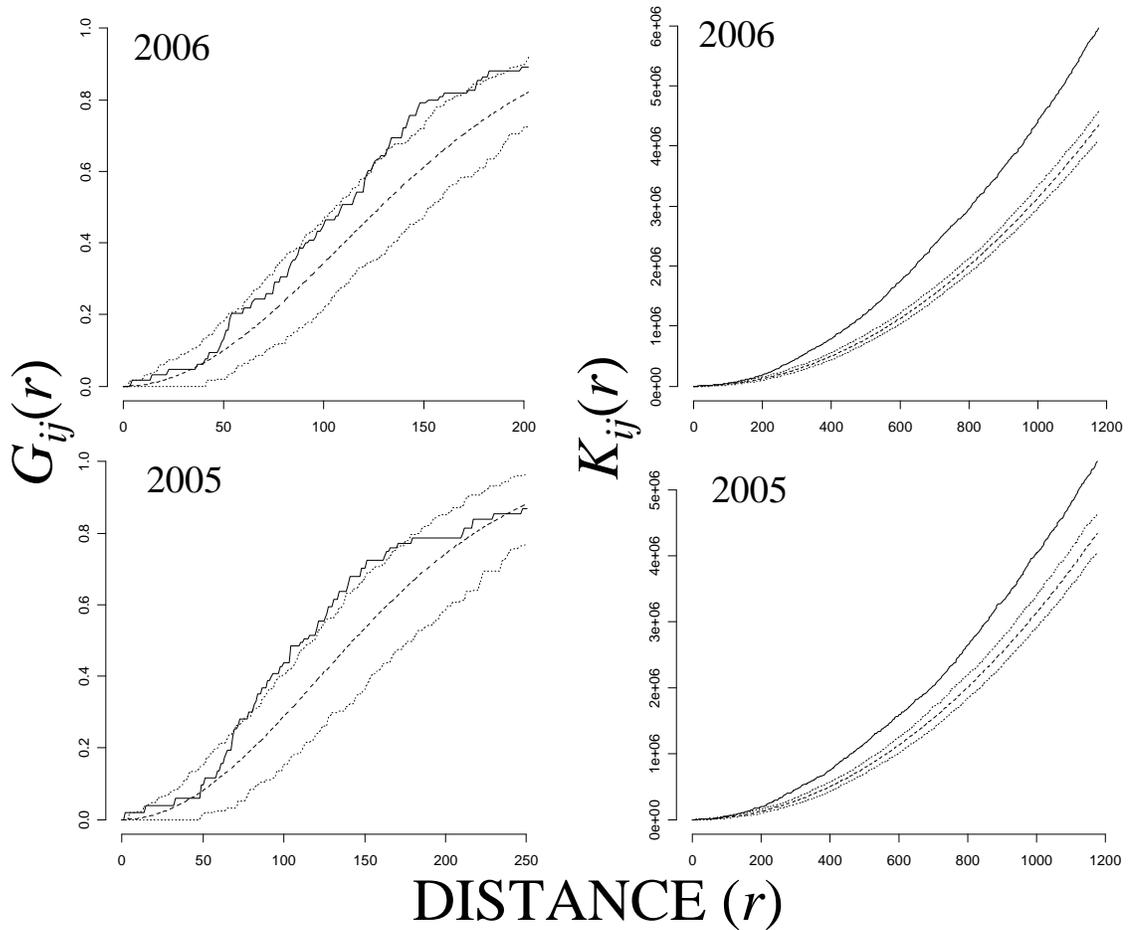


FIGURE 8. First-order nearest-neighbor G -estimate of all lesser snow goose (*Chen caerulescens caerulescens*) nests at Nestor One, 2001 – 2003, 2005 - 2007. The dashed line represents the theoretical distribution under complete spatial randomness, the dotted lines are the upper and lower 95% critical envelope (CE), and the solid black line is the observed distribution of $G_{ij}(r)$. Observed distribution above the 95% CE indicated aggregation while below the 95% CE indicated inhibition.

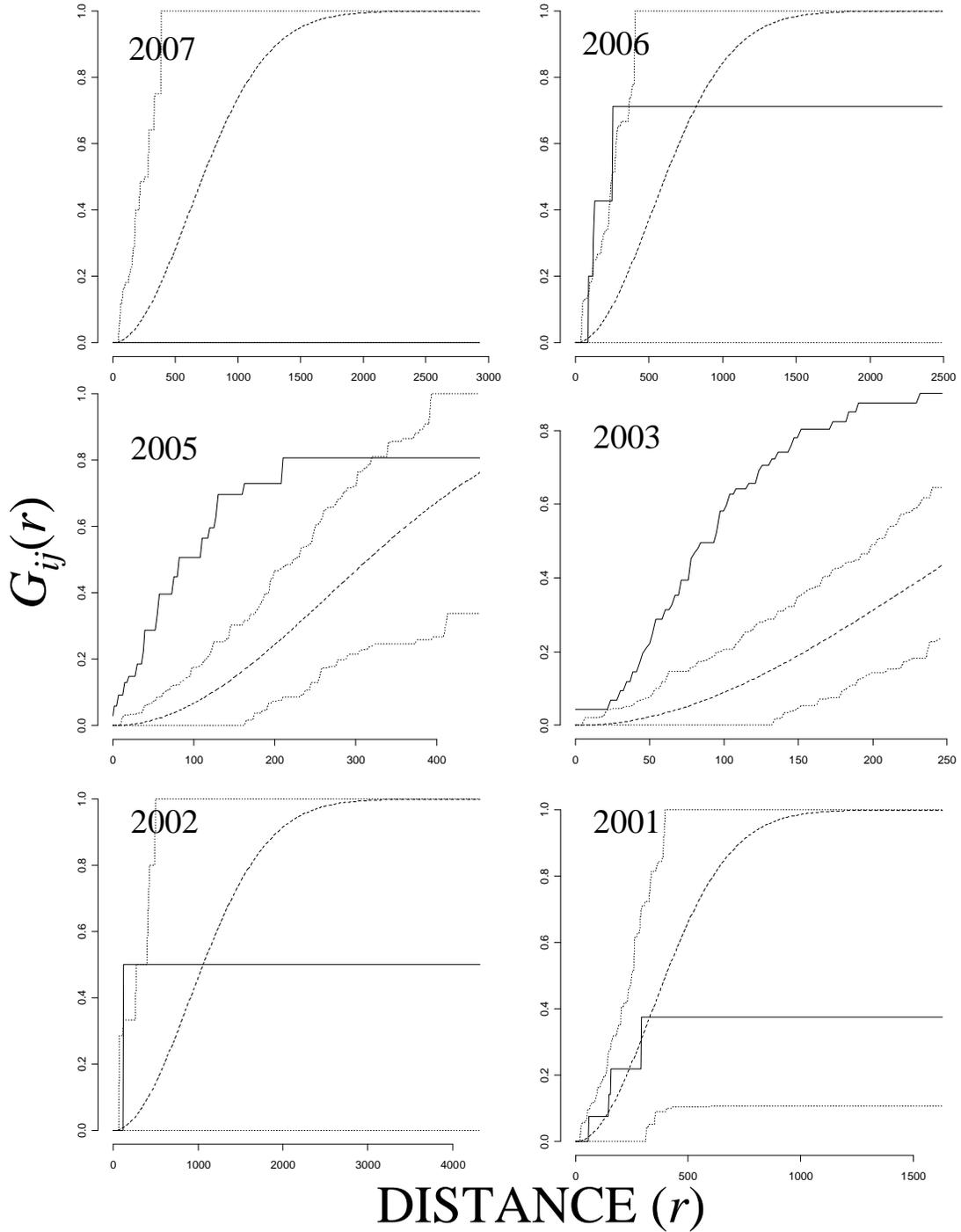


FIGURE 9. Second-order Ripley's K -estimate of all lesser snow goose (*Chen caerulescens caerulescens*) nests at Nestor One, 2001 – 2003, 2005 – 2007. The dashed line represents the theoretical distribution under complete spatial randomness, the dotted lines are the upper and lower 95% critical envelope (CE), and the solid black line is the observed distribution of $K_{ij}(r)$. Observed distribution above the 95% CE indicated aggregation while below the 95% CE indicated inhibition.

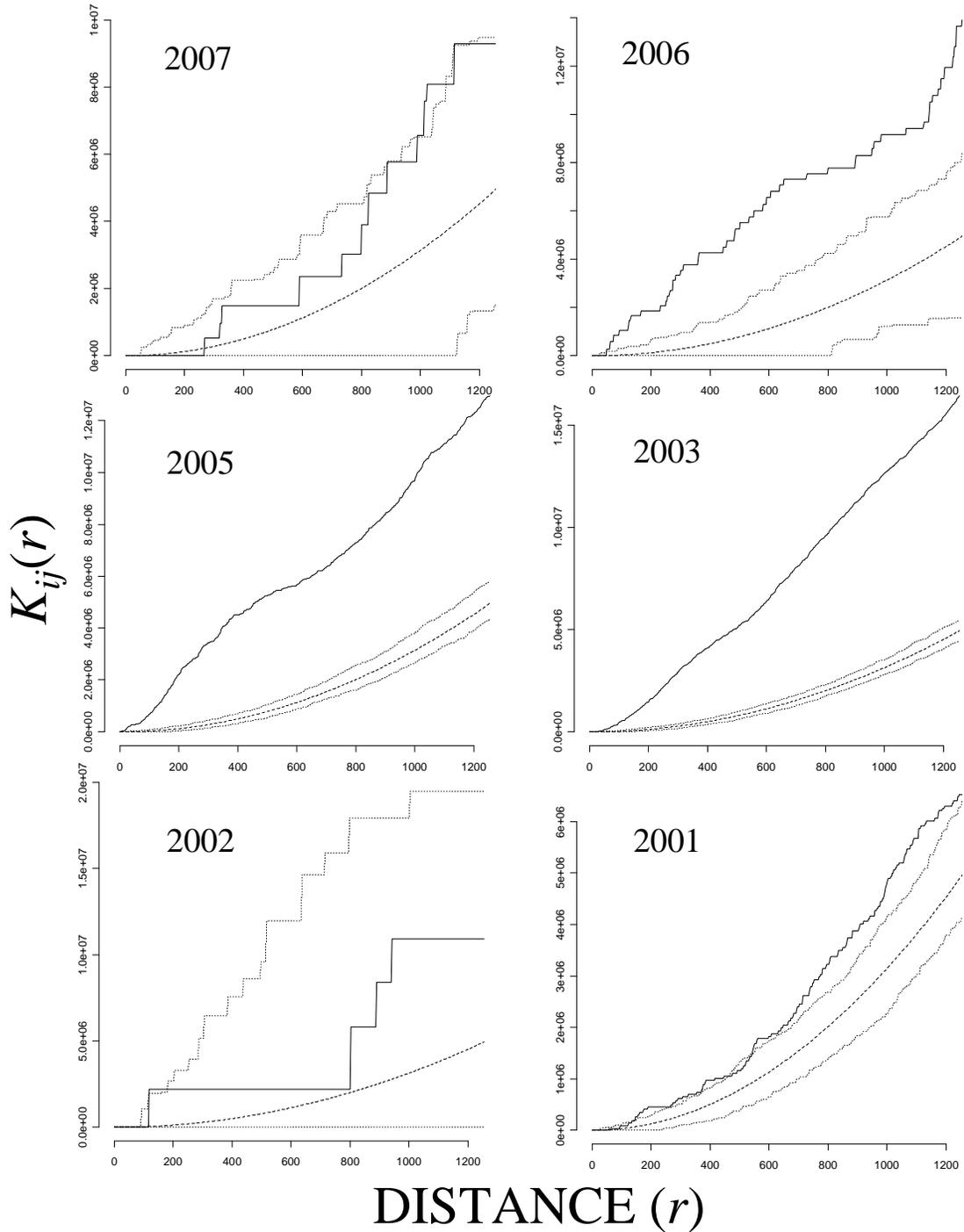


FIGURE 10. First-order nearest-neighbor G -estimate and the second-order Ripley's K -estimate of all lesser snow goose (*Chen caerulescens caerulescens*) nests at Broad River, 2005 – 2006. The dashed line represents the theoretical distribution under complete spatial randomness, the dotted lines are the upper and lower 95% critical envelope (CE), and the solid black line is the observed distribution of $G_{ij}(r)$ or $K_{ij}(r)$. Observed distribution above the 95% CE indicated aggregation while below the 95% CE indicated inhibition.

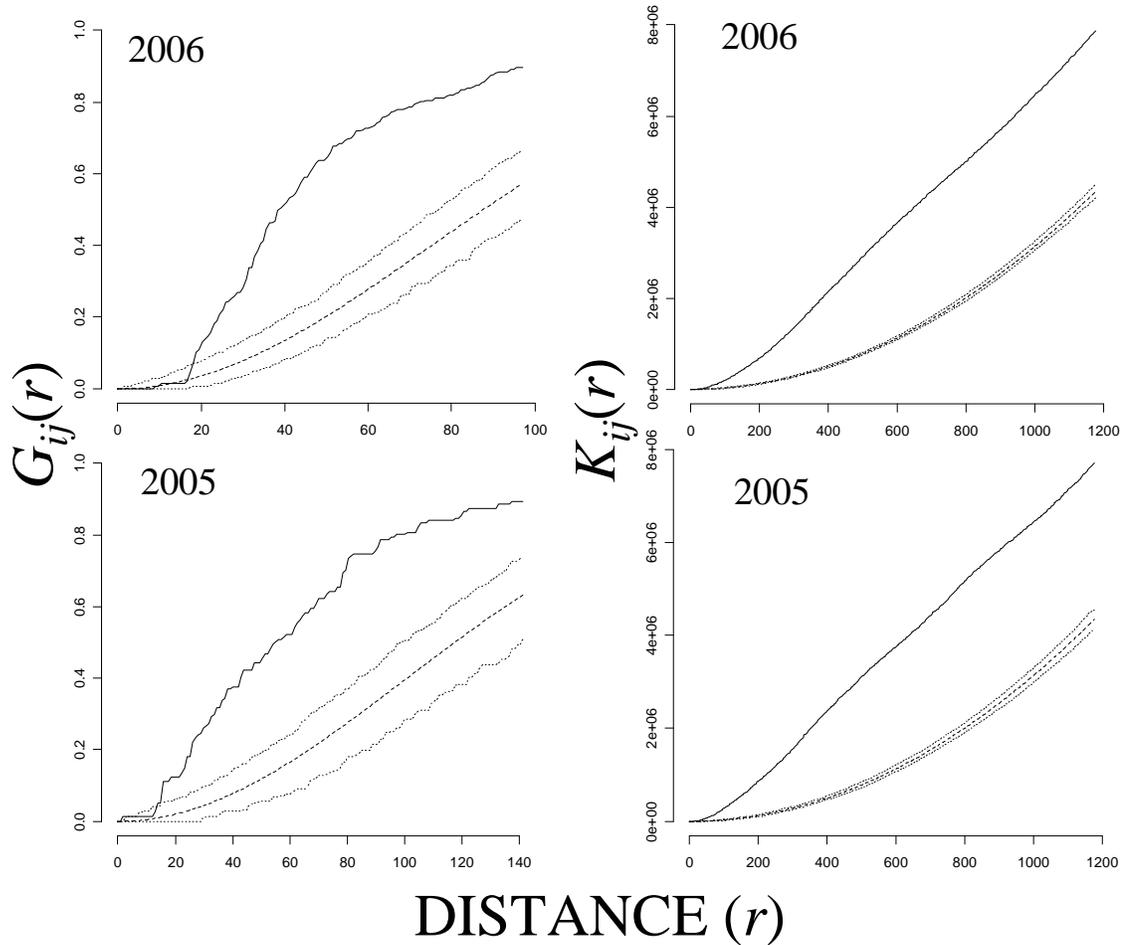


FIGURE 11. Second-order multi-type Ripley's K -estimate of successful Eastern Prairie Population Canada goose (*Branta canadensis interior*) nests relative to all lesser snow goose (*Chen caerulescens caerulescens*) nests at Broad River, 2005 – 2006. The dashed line represents the theoretical distribution under complete spatial randomness, the dotted lines are the upper and lower 95% critical envelope (CE), and the solid black line is the observed distribution of $K_{ij}(r)$. Observed distribution above the 95% CE indicated aggregation while below the 95% CE indicated inhibition.

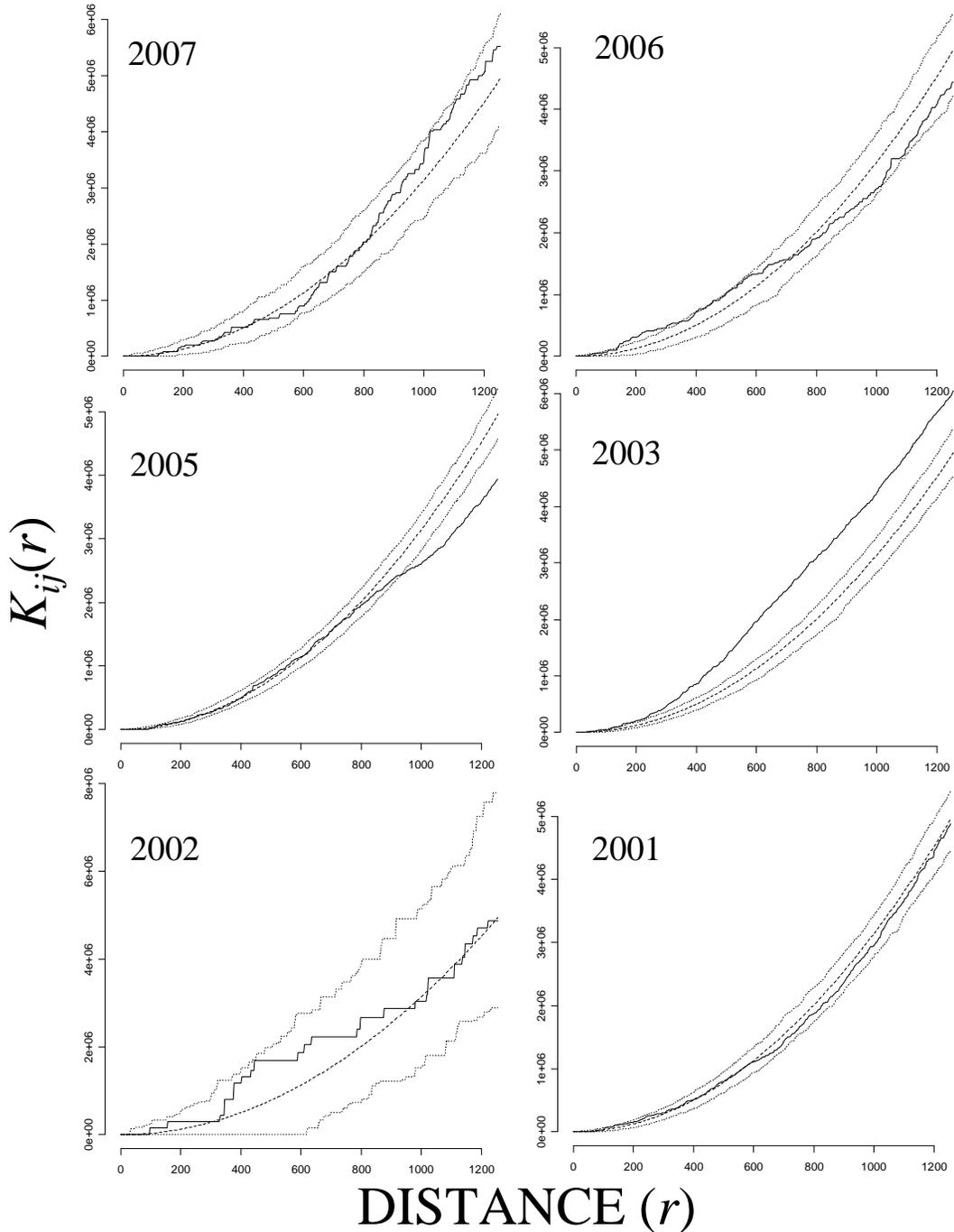


FIGURE 12. First-order nearest-neighbor multi-type G -estimate (left column) and the second-order multi-type Ripley's K -estimate (right column) of successful Eastern Prairie Population Canada goose (*Branta canadensis interior*) nests relative to all lesser snow goose (*Chen caerulescens caerulescens*) nests at Broad River, 2005 – 2006. The dashed line represents the theoretical distribution under complete spatial randomness, the dotted lines are the upper and lower 95% critical envelope (CE), and the solid black line is the observed distribution of $G_{ij}(r)$ or $K_{ij}(r)$. Observed distribution above the 95% CE indicated aggregation while below the 95% CE indicated inhibition.

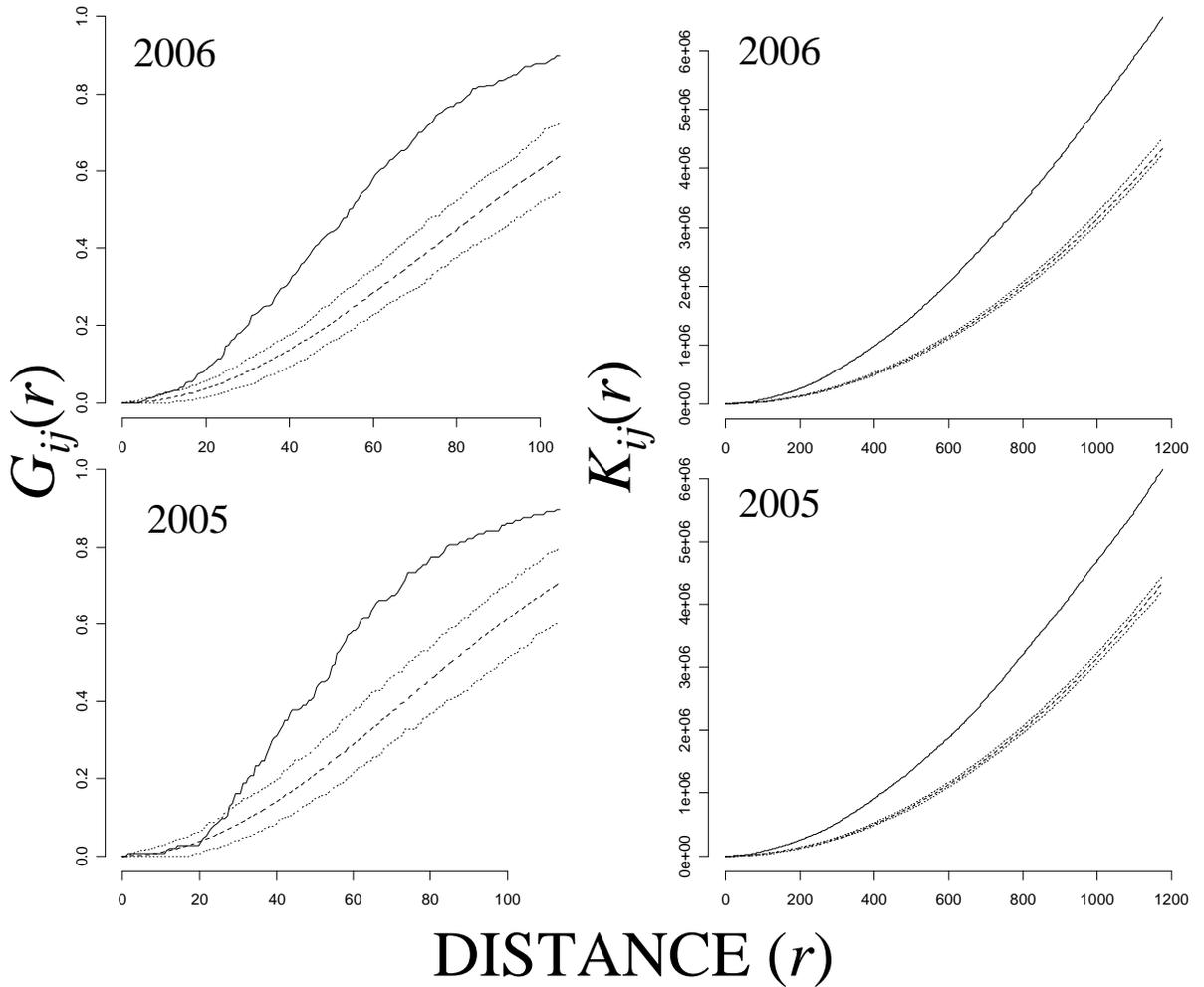


FIGURE 13. First-order nearest-neighbor multi-type G -estimate of failed Eastern Prairie Population Canada goose (*Branta canadensis interior*) nests relative to all lesser snow goose (*Chen caerulescens caerulescens*) nests at Nestor One, 2001 – 2003, 2005 – 2007. The dashed line represents the theoretical distribution under complete spatial randomness, the dotted lines are the upper and lower 95% critical envelope (CE), and the solid black line is the observed distribution of $G_{ij}(r)$. Observed distribution above the 95% CE indicated aggregation while below the 95% CE indicated inhibition.

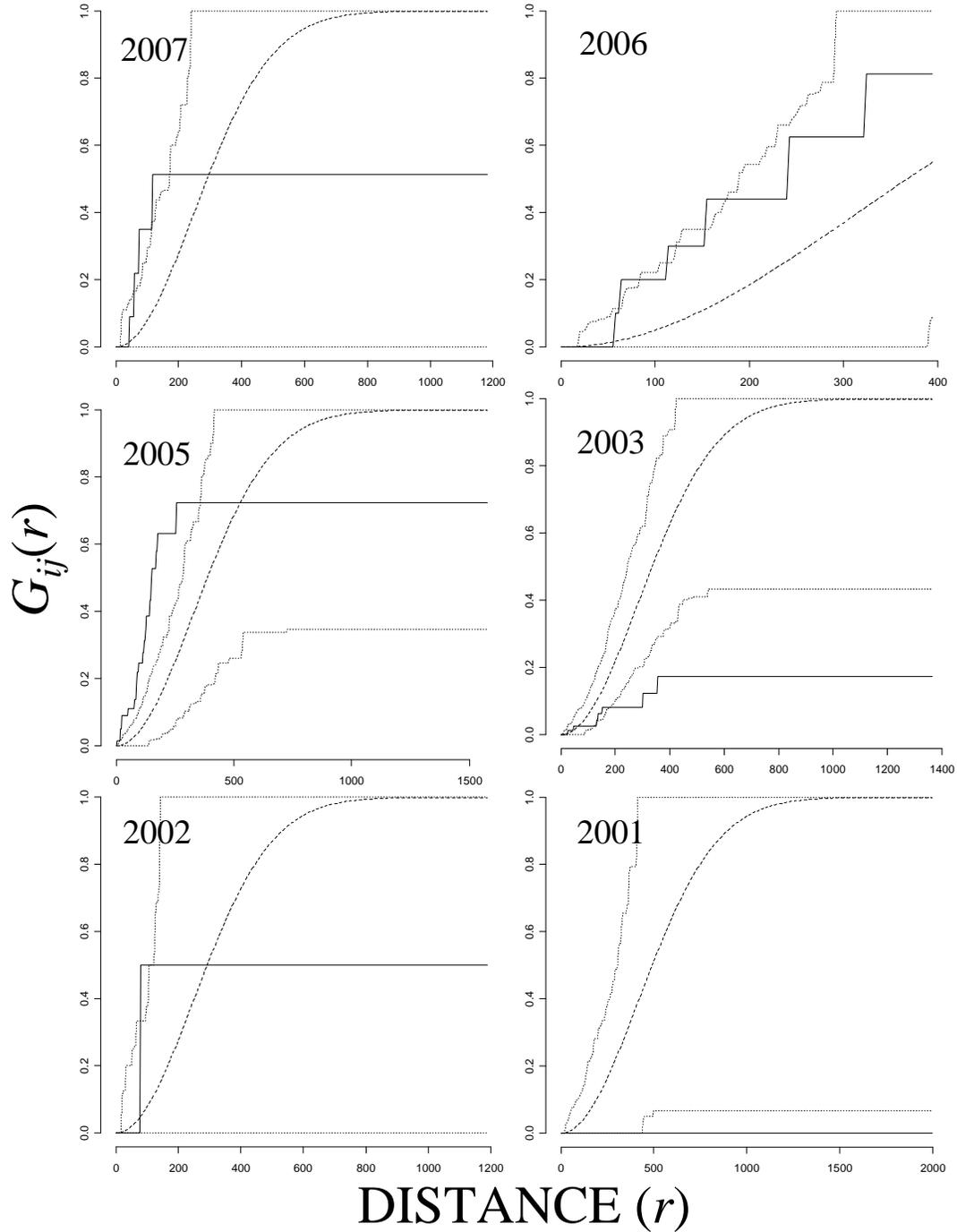


FIGURE 14. Second-order multi-type Ripley's K -estimate of failed Eastern Prairie Population Canada goose (*Branta canadensis interior*) nests relative to all lesser snow goose (*Chen caerulescens caerulescens*) nests at Nestor One, 2001 – 2003, 2005 – 2007. The dashed line represents the theoretical distribution under complete spatial randomness, the dotted lines are the upper and lower 95% critical envelope (CE), and the solid black line is the observed distribution of $K_{ij}(r)$. Observed distribution above the 95% CE indicated aggregation while below the 95% CE indicated inhibition.

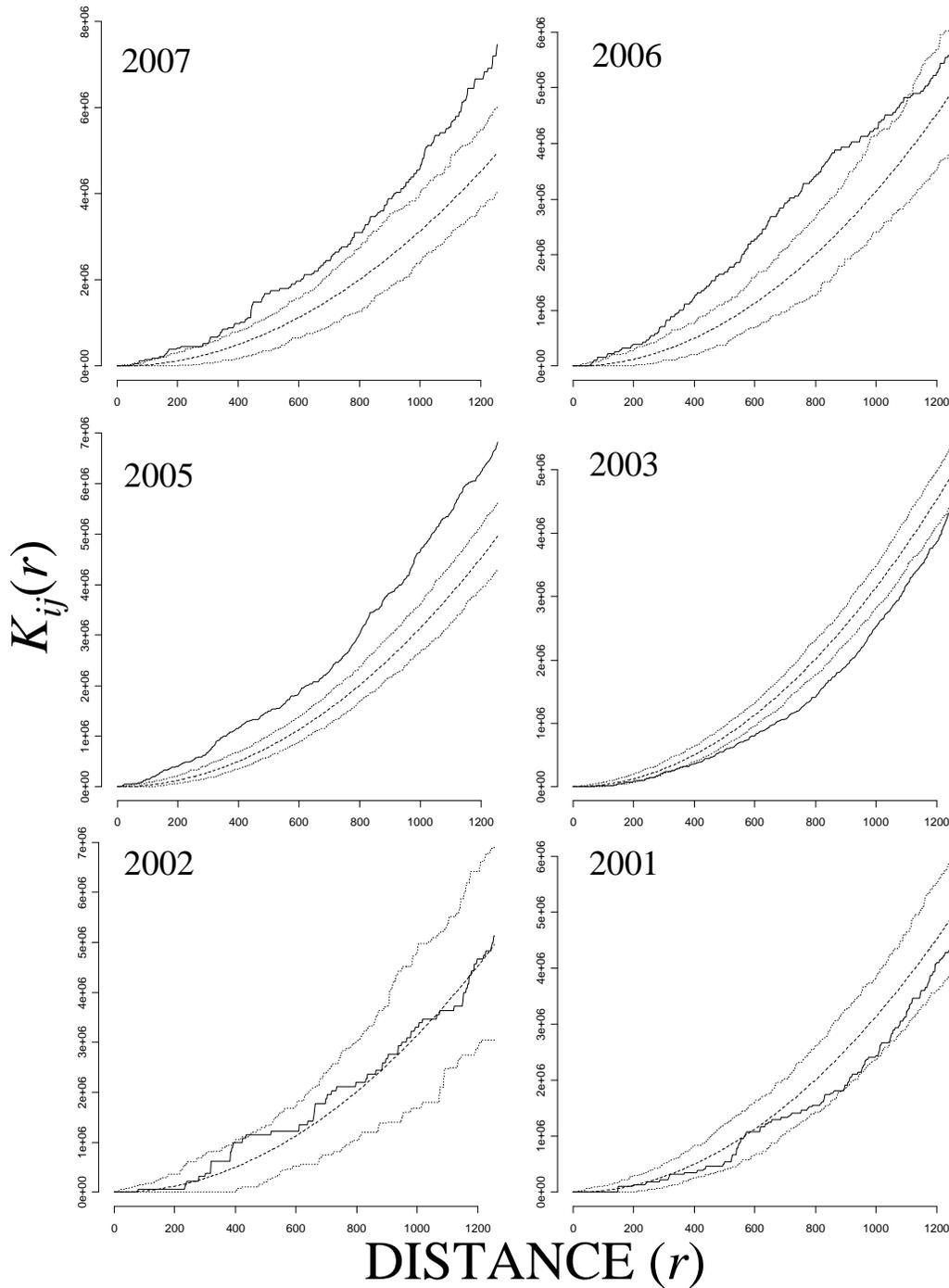
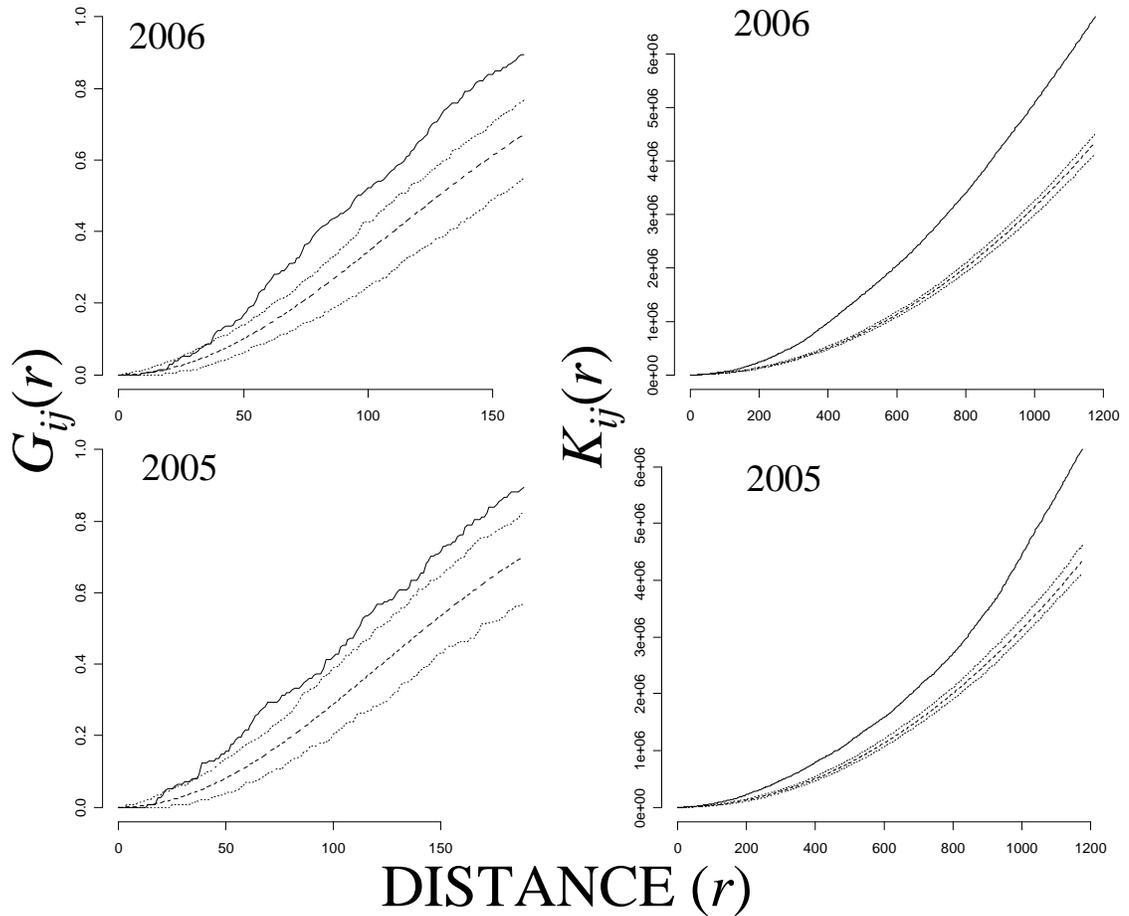


FIGURE 15. First-order nearest-neighbor multi-type G -estimate (left column) and the second-order multi-type Ripley's K -estimate (right column) of failed Eastern Prairie Population Canada goose (*Branta canadensis interior*) nests relative to all lesser snow goose (*Chen caerulescens caerulescens*) nests at Broad River, 2005 – 2006. The dashed line represents the theoretical distribution under complete spatial randomness, the dotted lines are the upper and lower 95% critical envelope (CE), and the solid black line is the observed distribution of $G_{ij}(r)$ or $K_{ij}(r)$. Observed distribution above the 95% CE indicated aggregation while below the 95% CE indicated inhibition.



CHAPTER 2
THE INFLUENCE OF LESSER SNOW GOOSE NESTS ON SURVIVAL OF
EASTERN PRAIRIE POPULATION (EPP) CANADA GOOSE NESTS IN
NORTHERN MANITOBA

INTRODUCTION

Interactions among species are a fundamental component of ecosystems. Changes in the distribution and abundance of species can have direct and indirect impacts on co-occurring species and ecosystems (Sinclair and Byrom 2006). In northern Manitoba, Canada, nesting lesser snow geese (*Chen caerulescens caerulescens*) have expanded their distribution and increased in abundance considerably during the last 25 years (Ankney 1996, Batt 1997, Jefferies et al. 2006). They have expanded into areas where they did not previously occur and that were traditionally used allopatrically by nesting Eastern Prairie Population (EPP) Canada geese (*Branta canadensis interior*; Walter 1999). The impact that large populations of snow geese have on sub-arctic vegetation communities, including the complete removal of above- and below-ground plant biomass and subsequent hypersalination of soils in coastal salt marshes, is well documented (Kerbes et al. 1990, Srivastava and Jefferies 1996, Jano et al. 1998, Jefferies and Rockwell 2002). Considerably less information exists on the direct or indirect effects of this growing population on other avian species (however see Gleason et al. 2004, Baldwin 2006, Sammler et al. 2008), particularly co-occurring EPP Canada geese.

Direct interactions between species often are realized as a resource-consumer relationship where a newly colonizing species is an overly efficient consumer of a resource (e.g., snow geese and salt marsh vegetation), or as inter-specific competition where a newly colonizing species is a superior competitor for limited resources (Tilman and Kareiva 1997). More specifically, direct interactions among nesting birds include nest parasitism and territoriality, which are often realized through physical confrontations. Nesting Canada geese and snow geese in northern Manitoba do not likely

compete for limited nesting space or local food resources as typically, along Hudson Bay, Canada geese initiate their nests before snow geese (M.E. Reiter, unpublished data) and food availability on the nesting grounds prior to and during incubation is not thought to be related to nest success or nest-site selection in sub-arctic nesting geese (Ryder 1970, 1975; Moser and Rusch 1998). Furthermore, there is no evidence of nest parasitism of Canada goose nests by snow geese in this population (D.E. Andersen, unpublished data).

Indirectly, the arrival of new species or changes in abundance and distribution of existing species may influence local predator-prey dynamics (Schmitz et al. 2003). Large aggregations of nesting snow geese may increase the abundance of shared nest predators (e.g., arctic fox [*Alopex lagopus*]; Walter 1999), potentially increasing the probability of Canada goose nest depredation. Holt (1977) termed negative, indirect interactions through shared predators as “apparent competition”. Alternatively, nesting associations have been observed between many species and typically involve increased nest survival through reduced nest depredation for a species when nesting among aggregations of another species (Burger 1984, Post and Seals 1993, Baldwin 2006). How nesting aggregations of lesser snow geese affect nest survival of sympatric nesting Canada geese in northern Manitoba is not known, however predator, prey, and alternative prey dynamics among arctic fox, lemmings (*Dicrostonyx richardsoni*) and nesting Canada geese are important in this system (Reiter 2006).

Factors influencing annual survival of Canada goose nests in northern Manitoba include weather conditions on the breeding grounds and annual fluctuations in arctic fox abundance (Reiter 2006). However, factors influencing variation in the probability of survival of individual Canada goose nests within a nesting season are potentially more

complex and include inter- and intra-specific density dependence and interactions, predator pressure (e.g., arctic fox predation), nest-predator behavior, the defensive capabilities of nesting geese, and the abundance of alternative prey (e.g., collared lemmings) for potential nest predators (Walter 1996, Walter 1999, Reiter 2006). To assess the relative importance of these factors, I developed a conceptual model representing multiple factors potentially influencing within- and among-year variation in nest survival of EPP Canada goose nests in northern Manitoba (Fig. 1), and identified the potential mechanisms of influence of increasing density and expanding distribution of nesting lesser snow geese. I assessed evidence in support of this model by evaluating multiple competing hypotheses within 6 distinct categories of Canada goose nest survival using logistic-exposure models (Shaffer 2004). Specifically, I tested the apparent-competition hypothesis and the nesting-association hypothesis as mechanisms to describe interactions between nesting Canada geese and snow geese in this ecosystem.

STUDY AREA

The EPP breeding range includes ~101,500 km² in northern Manitoba (Malecki et al. 1980) with the highest density of breeding Canada geese found along a strip of coastal tundra bordering western Hudson Bay (Humburg et al. 2000; Chapter 4, this volume). I studied nesting Canada geese and lesser snow geese at 2 study areas located in this strip of coastal tundra. The Nestor One study area was situated just south of Cape Churchill and approximately 60 km east-southeast of the town of Churchill, and was characterized by low relief, continuous permafrost, and poor drainage (Fig. 2; Wellein and Lumsden 1964, Didiuk and Rusch 1979). Sedge-dominated meadows, elevated beach ridges, coastal salt marshes, and willow (*Salix* spp.) – birch (*Betula* spp.) scrub composed the

major vegetation zones (Brook 2001). The core study area was ~48 km², consisted of ~30 km² of nesting habitat (i.e., non-water), and was located within Wapusk National Park (11,475 km²). Ground surveys for nesting EPP Canada geese have been completed annually at Nestor One since 1976; however, nesting snow geese have only occurred at Nestor One in considerable numbers (>5 nests) since 2000. Brood-rearing snow geese have altered the coastal salt marsh habitat near Nestor One considerably since the late 1970s (Jano et al. 1998, Sammler et al. 2008).

The Broad River study area was located ~60 km south of Nestor One along the Hudson Bay coast (Fig. 2). The core study area, just north of the river mouth, was ~10 km², and consisted of the same general vegetation zones as Nestor One (Brook 2001). Annual aerial breeding-ground surveys have documented an approximately 200% increase in the number of snow goose nests near the mouth of the Broad River since 2000 (Raedeke et al. 2008). Ground surveys for nesting Canada geese 1987 – 1989 and 1994 – 1995 found few snow goose nests at the Broad River study area (G. Ball, personal communication), suggesting that nesting snow geese have only recently colonized this area.

METHODS

NEST SEARCHING, NEST OBSERVATIONS, AND NEST FATE

I systematically searched for Canada goose and lesser snow goose nests at Nestor One and Broad River with 3 – 5 additional observers as part of annual EPP Canada goose nesting-ground surveys (Walter 1999) from 2005 to 2007. At all nests encountered, observers flushed females and recorded goose species, number of eggs present, presence and abundance of nest predators (herring gull [*Larus argentatus*], parasitic jaeger

[*Stercorarius parasiticus*], arctic fox, polar bear [*Ursus maritimus*], arctic wolf [*Canus lupus*]), and nest-site type (wetland, upland, or shore-island). I determined the incubation day (i.e., the number of days since initiating egg incubation; AGE) of nests using egg flotation or egg candling if egg flotation data were not recorded (Westerkov 1956, Walter and Rusch 1997a, Reiter and Andersen 2008a). Observers recorded Universal Transverse Mercator (UTM; North American Datum 1927, Zone 15) coordinates of the nest location using a Global Positioning System (GPS) unit and marked nest locations with a 7.5 cm x 12.5 cm plastic orange flag placed 10 m north of the nest bowl (Didiuk and Rusch 1979, Walter 1999).

I observed Canada goose nests regularly (~ 3 – 5 day intervals) from a distance of >200 m, so as not to flush females with each nest check, throughout the incubation period following initial nest discovery at Nestor One. Due to logistical constraints, I only observed nests at Broad River during the initial nest discovery and then to determine nest fate post-hatch. At each nest observation following initial discovery, if a female was present, I assumed that ≥ 1 egg was still intact and thus considered the nest active. If the female and male were not present, I visited the nest to determine its fate. I categorized each nest as: (1) successful, if ≥ 1 egg hatched, identified by the presence of goslings or eggshells and intact membranes; (2) depredated, if few or no eggshell fragments were present; or (3) still active, if intact eggs were found in the nest. I monitored all nests until a final fate (i.e., eggs hatched or the nest was depredated) could be assigned. I revisited all snow goose nests post-hatch to determine the fate of the nest, but did not make regular nest observations.

ARCTIC FOX DEN OCCUPANCY

Variation in arctic fox den activity is strongly related to Canada goose nest survival (Reiter 2006). Arctic fox dens along the Hudson Bay Lowlands are primarily constructed on elevated beach ridges and are conspicuous because of increased vegetative growth as the result of soil enrichment and disturbance (Bahr 1989; Roth 1998, 2003). Intensive aerial and ground searches of the area between Cape Churchill and the Broad River in the 1990s identified 88 dens across the region and documented a preference of beach ridge habitat for den building (Roth 1998). At Nestor One and Broad River, I visited known arctic fox dens and searched for additional dens along beach ridges. In each year between 2005 and 2007, I made ≥ 2 visits to all dens. At each visit, I evaluated den occupancy by the presence of fox or fresh fox sign (fresh scat, prey remains, and/or digging) indicative of an active den (Macpherson 1969). I used a small plastic rake to clear den entrances of fox tracks and digging at each den visit. I classified a den as occupied if fresh fox sign was evident at >1 visit.

ABUNDANCE OF LEMMINGS

Variation in the primary food of arctic fox (i.e., collared lemmings) may affect fox reproductive behavior and thus predation pressure on nesting Canada geese (Reiter 2006). I collected fox scat when encountered during nest searching and at fox dens between 2005 and 2007. I autoclaved all scat and washed samples with light detergent and water through size 20 and 40 mesh sieves until all component materials were separated. I dried residual material in a drying oven at $\sim 60^{\circ}\text{C}$ and examined each sample with a binocular microscope to determine the presence or absence of lemming remains and other prey items (Macpherson 1969, Garrott et al. 1983). I assumed that arctic fox consumed lemmings proportional to their availability and quantified relative lemming

abundance (LEMMING) in each year as the proportion of arctic fox scat that contained lemming remains (Garrott et al. 1983). Because Reiter and Andersen (2008b) identified strong synchrony in lemming abundance at Nestor One and Broad River between 1991 and 2004, I pooled scat data from the 2 study areas to assign a common measure of the relative abundance of lemmings for both study areas in each year.

DATA ANALYSIS AND HYPOTHESES

Nest Survival

I modeled the daily probability of Canada goose nest survival using logistic-exposure models (Shaffer 2004) and PROC GENMOD in SAS v.9.1 (© 2007 The SAS Institute.). This approach allowed the daily probability of nest survival to vary through the incubation period and multiple covariates to be included. The logistic-exposure model used nest observation intervals as the sampling unit during which a nest either survived or failed. The daily probability of nest survival (DSR_i) was assumed to be constant during each nest observation interval, i . DSR_i was related to model covariates as:

$$DSR_i = \frac{\exp(\beta_0 + \sum_{j=1}^n \beta_j * X_j)}{1 + \exp(\beta_0 + \sum_{j=1}^n \beta_j * X_j)}$$

Where, β_0 was an intercept term, and $\sum_{j=1}^n \beta_j * X_j$ was the sum of the effect of n covariates, j . Similar to logistic regression, the logistic exposure model assumed that covariates were linearly related to nest survival via a link function. The standard logit-link function was modified to account for differing nest observation interval lengths:

$$g(\theta) = \log_e \left(\frac{\theta^{\frac{1}{t}}}{1 - \theta^{\frac{1}{t}}} \right)$$

Where $g(\theta)$ was the linear combination of the intercept and covariates terms $(\beta_0 + \sum_{j=1}^n \beta_j * X_j)$, θ was the probability of nest survival, and t was the number of days in an interval between nest observations.

I considered my analysis within the context of a large conceptual model of Canada goose nest survival that contained 6 general categories (Fig. 1) and a seventh category representing nuisance effects. Within each category, I evaluated competing hypotheses about processes influencing nest survival given the variables within that category (Tables 1 & 2). Of specific interest for my analyses were covariates within categories that quantified the effect of increasing numbers of nesting snow geese on nesting Canada geese (indicated in Figure 1 by the bold arrows). I evaluated a total of 19 variables in model development, not including interactions among variables and quadratic terms, from the following general categories (Table 1).

I. Inter- and Intra-specific Density Dependence

I considered 2 general hypotheses within the density-dependence category. First, I evaluated nearest-neighbor distances because behavioral interactions between nesting geese would likely be realized at the nearest-neighbor spatial scale. I considered the distance (m) from each Canada goose nest to the nearest-neighboring Canada goose nest (nnCAGO) and snow goose nest (nnLSGO) in my analysis as a measure of the effect of behavioral interactions between nesting geese. Because nesting Canada geese can be highly territorial (see Chapter 1, this volume), when nests are closer together more time

may be spent defending a territory against other nesting geese, thus reducing energy reserves that could be employed to defend against nest predators (Ryder 1975). I predicted that both nnCAGO and nnLSGO would be positively related to nest survival.

Second, I examined whether competition as indicated by the overall proximity to all other nesting geese affected nest survival. Preferably, the precise mechanism of influence between nesting geese could be identified (e.g., increased competition for local resources or increased abundance of local predators); however, these are often difficult to estimate and may not represent the full suite of inter- or intra-specific effects as the result of close spatial proximity. The nearest-neighbor distance only provides information from a very local spatial scale. Pacala and Levin (1997) quantified the effect of individuals of species 2 on individuals of species 1 with a negative exponential function that weighted the effect of species' 2 density decreasingly with distance from species 1. A proposed calculation (D.H. Johnson, personal communication) that may provide a more complete measure of possible effects across a broader spatial extent, and is similar to the approach of Pacala and Levin (1997) is a proximity index. This was calculated as:

$$PI_j = \sum_{i=1, i \neq j}^n \frac{1}{dist_{i,j}}$$

Where, $dist_{i,j}$ was the Euclidian distance from nest j to nest i . The reciprocal of this value was summed for all nests i , to derive the PI for nest j (PI_j). Because the value of a proximity index was a function of the total number of nests and the total distance to nests, which are both associated with the total area (e.g., km^2) being considered, nests from different study areas of different sizes may inherently have different PI_j . To standardize for my 2 study areas, I divided all PI_j s by the total area searched for nests at

Nestor One or Broad River. I considered a separate proximity index for Canada goose nests (piCAGO) and snow goose nests (piLSGO).

I predicted increased piCAGO would increase nest survival, as several studies (see Reiter 2006, Miller et al. 2007) have identified conspecific nest density as having a positive effect on Canada goose nest survival. I considered multiple competing hypotheses regarding the effects of snow goose nests on nesting Canada geese. (1) The indirect-competition hypothesis: increased snow goose nest density provides a concentrated food resource that attracts nest predators resulting in higher predator pressure and lower nest survival for Canada geese nesting nearby; therefore, piLSGO should be negatively related to nest survival. (2) The nest-association hypothesis: increased snow goose nest density attracts nest predators resulting in higher predator pressure, but also provides the benefits of group defense; therefore piLSGO should be positively related to nest survival. (3) The combined non-linear hypothesis: increased snow goose nests attract predators when there are few snow goose nests but provide no group defense, attract predators and provide the benefits of group defense when there are moderate numbers of snow geese, and become too dense for co-occurring species (particularly dispersed nesting Canada geese) when there many snow goose nests; therefore, Canada goose nest survival varies nonlinearly. Canada geese experience low nest survival when piLSGO is small or large but relatively higher nest survival when piLSGO is at moderate levels. I predicted that a quadratic piLSGO term would be included in the best-supported model over a linear form of piLSGO if this hypothesis best described the effects of changes in the abundance of nesting snow geese on nesting Canada geese.

One possible bias in spatial indices (e.g., nearest-neighbor distance) is edge effects (Diggle 2003). Edge effect bias occurs because often a study area is a small fraction of the total area occupied by a species. Thus, nests occurring near the edges of a study area may have a biased estimate of nearest-neighbor distance or PI_j because nests outside of the study area boundary are not observed and thus not incorporated into the calculation. To correct nearest-neighbor distances for edge effect bias, I assigned a “corrected” nearest-neighbor value at random to each of the potentially biased nearest-neighbor distances (i.e., nearest-neighbor distance farther than the nearest edge). The random value was bounded on the low side by the nearest edge and the high side by the nearest-neighbor observed for each potentially biased nest within each study area, and was drawn from the distribution of nearest-neighbor distances for all unbiased nests within each study area within each year (i.e., nests with a nearest-neighbor distance closer than the nearest edge). I used a mirror-based edge correction for my proximity-index calculations, which simulated additional nests outside of the observed study area based on a mirror of the observed nests within the study area. Spatial simulations suggested that these *ad hoc* edge corrections reduced edge effect bias (M.E. Reiter, unpublished data).

II. Nest Predators

I quantified avian predator pressure (AVIAN) as whether ≥ 1 predator (herring gull or parasitic jaeger) was observed within 250 m of the nest during the first nest observation of an interval. I quantified mammalian predator pressure (MAMMAL) as whether ≥ 1 mammalian predator (arctic fox, wolf, or polar bear) was within 250 m of the

nest or mammalian predator sign (scat or urine scent) was observed at the nest during the first nest observation of an interval.

The presence of occupied arctic fox or wolf dens provided another measure of potential predator pressure that likely varies with a den's proximity to a nest. I included this measure of predation pressure in the models, quantified as the distance (m) from the nest to the nearest occupied fox or wolf den (DEN). I predicted that nests with avian or mammalian predator presence and nests that were closer to occupied fox or wolf dens would have a lower probability of nest survival; thus, AVIAN and MAMMAL should be negatively associated with nest survival, and DEN should be positively associated with nest survival.

III. Snow Goose – Predator Interactions

Of particular interest in this study was quantifying potential interactions between snow goose nests, Canada goose nests, and their shared nest predators. I considered interactions between the proximity index of snow goose nests (piLSGO) and the occurrence of nest predators, both AVIAN and MAMMAL, and interactions between nnLSGO and the occurrence of nest predators. Support for the nesting-association hypothesis would be realized as a positive association between nest survival and piLSGO or negative association between nest survival and nnLSGO when an avian or mammalian nest predator was observed. A negative association between nest survival and piLSGO or positive association between nest survival and nnLSGO when an avian or mammalian nest predator was observed would support the apparent-competition hypothesis. I also considered 2 additive models (nnLSGO + DEN and piLSGO + DEN), which provided a

measure of the combined effects of spatial proximity to snow geese and spatial proximity to occupied fox or wolf dens on Canada goose nest survival.

IV. Predator Behavior

Predators, particularly arctic fox, often hunt opportunistically (Macpherson 1969, Bahr 1989, Roth 1998, Samelius and Alisauskas 2000). The proximity of one Canada goose nest (n_1) to another depredated goose nest (n_2) may influence n_1 's probability of survival. I evaluated differences in predator behavior, and more generally, spatial heterogeneity in nest survival using 4 variables. By incorporating the nearest depredated Canada goose nest (nfCAGO) and the nearest depredated lesser snow goose nest (nfLSGO) in nest survival models, I assessed whether spatial patterns of nest failures and thus predator hunting behavior in this system were species specific. If arctic fox exhibit no feeding preference between Canada goose nests and snow goose nests the relationship between nfCAGO and nfLSGO and nest survival should be the same. I hypothesized the relationship would be positive, where increased nfCAGO or increased nfLSGO would result in increased nest survival. Furthermore, if the positive association of nfLSGO with Canada goose nest survival was greater than the positive association of nfCAGO and nest survival, then being farther from depredated snow goose nests is more beneficial than being farther from other Canada geese, lending support for the apparent-competition hypothesis. However, if the association of nfLSGO with Canada goose nest survival were less than (i.e., less positive or negative) the association of nfCAGO and nest survival, then snow goose nests buffer Canada goose nests and thus nests close to failed snow goose nests have a higher probability of survival, whereas nests close to failed Canada goose nests would suffer relatively lower nest survival. I also incorporated the

nearest failed nest of either species that failed prior to a nest's discovery (nfEARLY), and the nearest failed nest of either species that was active when a nest was discovered but subsequently failed (nfACTIVE) in nest survival models. I assessed whether (1) predators consistently used the same areas, which would result in a positive association between nest survival and nfEARLY, or (2) predators hunt opportunistically and thus there are often clusters of depredated nests, inducing a positive association with nest survival and nfACTIVE.

V. Indirect Trophic System Effects

In years with abundant lemmings, arctic fox increase their reproductive output and occupy a higher proportion of available den territories (Roth 2003). Therefore, if years with abundant lemmings attract nest predators to the study area to occupy available dens, then LEMMING should be negatively associated with nest survival (Reiter 2006). However, if abundant lemmings serve as a buffer for nesting birds (as is predicted by the bird-lemming hypothesis; Angelstam et al. 1984), then a positive association should be observed between nest survival and LEMMING. I also considered interaction terms LEMMING*MAMMAL and LEMMING* AVIAN, which quantified whether the effect of predators near a nest on nest survival changed in some years depending on lemming abundance.

VI. Defensive Capabilities and Study Effects

Different nest types may experience different probabilities of nest survival (MacInnes and Misra 1972, Didiuk and Rusch 1979). Nest types determined at nest discovery were set as a 3-level factor in models (TYPE: upland, wetland, or shore-

island). I predicted nests occurring along uplands, which are used as travel corridors by arctic fox and wolves, should have lower nest survival, while nests located on shorelines or islands should be more easily defended (Bahr 1989) and thus should have relatively higher nest survival.

I predicted incubation day would affect the ability or willingness of a goose to defend its nest. During incubation Canada geese lose up to 31% of their body weight, rarely leaving the nest to feed (Moser and Rusch 1998). Often nest survival is low early in incubation because those nests that are most vulnerable to be depredated fail early (Grand et al. 2006). Such a relationship would be positive between incubation day and nest survival. However, an incubating female Canada goose and gander that have defended the territory throughout incubation may be more likely to leave the nest or territory to feed near the end of incubation (after nearly 28 days of limited consumption), and therefore would be absent from the nest or less able to defend against nest predators, resulting in a negative relationship between incubation day and nest survival. Ryder (1975) hypothesized that territorial nesting geese would attempt to optimize their territory size between a larger territory that provided more food and limited the time having to leave the area to feed during incubation, and a smaller territory that was less energetically costly to defend. A third competing hypothesis would predict a combination of effects where nest survival is low early in incubation however, geese in the later part of incubation still may be away from the nest more feeding, and physically incapable of aggressive nest defense (Ryder 1975). I included a quadratic effect of incubation day to assess this hypothesis and tested whether nest survival varied non-linearly as a function of incubation day.

Because the timing of snow melt and spring phenology can play an important role in Canada goose nest survival (Reiter 2006), I considered the average Julian date of an interval to be the phenology covariate (DATE) in nest-survival models. In years of late snow melt, fewer Canada geese initiate nests and those that do may be more likely to fail due to reduced body condition and thus reduced defensive capabilities (Ryder 1975). I predicted that observation intervals when DATE was large would have lower nest survival than observation intervals when DATE was small.

Because a female goose that is flushed may subsequently be less likely to defend a nest against an approaching predator, I included whether a goose was flushed during the first observation of an interval (FLUSH) in models to quantify the potential effect of flushing geese from nests during nest searching. I attempted not to flush geese during all observations following the initial nest discovery. I predicted flushing a goose would result in either abandonment of the nest and thus low probability of nest survival, or a reduction in the ability to defend the nest due to being away from the nest resulting in lower probability of nest survival. To evaluate the potential mechanism by which flushing a nesting Canada goose by observers may influence nest survival, I considered models with interaction terms FLUSH*AVIAN or FLUSH*MAMMAL. I predicted females flushed when predators were present would have a lower probability of nest survival for the subsequent observation interval.

VII. Nuisance effects

To evaluate the magnitude of spatial variation in addition to spatially varying covariates included above, I considered the UTM coordinate divided by 1,000 for the easting (X) and northing (Y) of the nest location. Because nests were identified at 2

spatially distinct study areas and there may be correlation among nest fates within areas not accounted for by other covariates, I considered a 2-level factor representing study area effects (SA). Lastly, I evaluated a 3-level factor representing each year of the study (2005, 2006, and 2007) to quantify potentially large year-to-year variation in nest survival (Reiter 2006).

MODEL DEVELOPMENT

The large number of variables considered in this analysis, the possibility of complex interactions among covariates, and the multiple competing hypotheses being evaluated within each category made developing a moderate-sized (<100) set of *a priori* models implausible, unless I assumed that variables within each general category were not additive across categories. I combined an information-theoretic competing model framework (Burnham and Anderson 2002) with cross-validation (Snee 1977) to (1) reduce the total number of variables and possible interactions in models using an *a priori* model set; (2) develop a reduced model set, which considered composite models where covariates from separate categories were included together in models; and (3) assess the goodness-of-fit of each of my models of Canada goose nest survival prior to making inferences.

First, I developed a set of 32 simple models *a priori* (Table 2) to evaluate factors influencing the probability of Canada goose nest survival within 6 general categories related to major components of Canada goose nest survival and a seventh category representing a set of nuisance variables (Table 2). I randomly split my dataset into training and testing subsets, which consisted of 904 nests and 1,031 observation intervals

and 914 nests and 1,044 observation intervals, respectively. I split data by nests so all observation intervals of an individual nest would be in the same random subset.

I used the training dataset to evaluate my 32 *a priori* models with logistic-exposure in an information-theoretic model-selection framework (Burnham and Anderson 2002) and ranked fitted models using Akaike's Information Criterion (AIC_c). I evaluated the relative support for each model within each of the model categories by calculating the difference between the AIC_c of each model, i , within-category model set, j , and the AIC_c of the best model (i.e., lowest AIC_c) within-category model set, j (ΔAIC_{cij}). I also calculated ΔAIC_c values for the combined set of all models from all categories to assess which categories best described variation in Canada goose nest survival. I assessed support for individual covariates in each model based on a Type III analysis (Hosmer and Lemeshow 2000). This likelihood approach evaluated covariates by comparing the likelihood of a model when the covariate value was set to 0 and when it was estimated. The importance of the covariate as quantified by Type III analysis was not conditional on the order it was specified in the model (Hosmer and Lemeshow 2000).

I developed composite models composed of variables included in *a priori* models with $\Delta AIC_{cij} < 2.0$ in within-category analysis or that were supported by a Type III P -value < 0.1 . Second, I considered stricter criteria and developed models consisting of variables included in *a priori* models with $\Delta AIC_{cij} < 2.0$ in within-category analysis and that were also supported by a Type III P -value < 0.05 . To avoid including related variables in the same model, I excluded covariates that had a Spearman correlation coefficient $> |0.7|$ from the same composite models. Along with composite models, I evaluated *a priori* models with cross-validation if their ΔAIC_c was < 10 when compared

among all 32 *a priori* models. I used the training dataset to estimate parameters for this reduced model set (i.e., composite models and best *a priori* models). I employed these parameter estimates and the test dataset to predict the probability of surviving an observation interval for each observation interval in the test data.

The logistic-exposure model predicts continuous probability values between 0 and 1 for each observation interval, which are compared to binary observed values representing nest success or nest failure in cross-validation. Threshold probability cut-offs have been used to assign success-failure or presence-absence to predicted probabilities in wildlife studies (Pearce and Ferrier 2000). Most commonly, observations with a predicted probability of >0.5 are considered a success and those with a predicted probability <0.5 a failure. Although these values provide a measure of predictive accuracy, they are dependent on both the threshold probability cut-off value and the relative frequency of success and failure in the population (Pearce and Ferrier 2000). The receiver operating characteristic (ROC) curve and the associated area-under-the-curve (AUC) index provide a measure of accuracy that is independent of threshold probability cut-off values and the relative frequency of events (Metz 1978, 1986; Pearce and Ferrier 2000). I used the ROCR package (Sing et al. 2005) for R v.2.5.1 (© 2007 The R Foundation for Statistical Computing) to calculate ROC curves and the AUC for each composite model and each of the best-supported *a priori* models. The AUC calculated in ROCR was based on the non-parametric Mann-Whitney statistic, which compared the rank of predicted values associated with success with the rank of predicted values associated with failures. This test of model accuracy and discrimination capacity evaluated the hypothesis that predicted probabilities were assigned at random, $AUC = 0.5$

versus non-random, $AUC > 0.5$. I calculated 95% CI for the AUC of each model using 200-bootstrap resamples of the data and the percentile method (Manly 2001). I considered a model with a 95% CI for AUC that did not overlap 0.5 to predict better than random; however, only models with an $AUC > 0.7$ were considered a good fit. I developed a top model set based on models where the 95% CI of their AUC score overlapped the 95% CI of the model with the top AUC score.

Although AUC discriminates well among good-fitting and poor-fitting models providing a measure of goodness-of-fit, it often does not perform as well when discriminating among multiple-competing “good” models (Pearce and Ferrier 2000). Thus, often selecting a “best” model for inference is difficult and ignoring model selection uncertainty may result in biased inferences (Buckland et al. 1997). Model-averaging parameter estimates provides a framework to incorporate model selection uncertainty into model inference (Buckland et al. 1997, Burnham and Anderson 2002). However, model-averaging requires each model to receive a weight and the sum of the weights of all models being averaged sum to 1. The cross-validation methodology does not provide the weights necessary to allow for multi-model inference. Thus to evaluate the magnitude and direction of influence of parameters and to draw inferences about factors influencing the survival of Canada goose nests, I evaluated models from my top model set, based on cross-validation and AUC, using the entire (i.e., training + test) dataset. I ranked the fitted models using AIC_c and calculated model averaged parameter estimates using Akaike weights (w_i) and the following equation:

$$\hat{\beta}_j = \sum w_i \hat{\beta}_{ij}$$

Where, $\hat{\beta}_j$ was the weighted-average parameter estimate of covariate j , and $\hat{\beta}_{ij}$ was the parameter estimate for covariate j in model i . I followed Burnham and Anderson (2002) and estimated the unconditional variance [$\hat{\text{var}}(\hat{\beta}_j)$] for the weighted-average parameter estimates as:

$$\hat{\text{var}}(\hat{\beta}_j) = \left[\sum_{i=1}^R w_i \sqrt{\hat{\text{var}}(\hat{\beta}_{ij} | g_i) + (\hat{\beta}_{ij} - \hat{\beta}_j)^2} \right]^2$$

Where, R equaled the number of models being averaged, and $\hat{\text{var}}(\hat{\beta}_{ij} | g_i)$ was the predicted variance of $\hat{\beta}_{ij}$ given that it was in model, g_i . To correct for possible model-selection bias, I assumed that models where a specific covariate j did not occur had a $\beta_{ij} = 0$ (Burnham and Anderson 2002). I constructed 95% CI for $\hat{\beta}_j$ as:

$$\hat{\beta}_j \pm 2 * \sqrt{\hat{\text{var}}(\hat{\beta}_j)}$$

I used model-averaged survival estimates to graphically display variation in nest survival.

RESULTS

CANADA GOOSE NESTS, NEST OBSERVATIONS, INCUBATION DAY, AND DATE

I searched for Canada goose nests at Nestor One, 2005 – 2007, and at Broad River, 2005 – 2006. The earliest date I discovered nests was 24 May and the latest was 26 June (Table 3). I discovered a total of 1,160 active nests at Nestor One (2005 – 2007) and Broad River (2005 – 2006). I found 65 and 86 nests that had already failed at the

time nest-searching was conducted at Nestor One and Broad River, respectively. The average density of active Canada goose nests at Broad River (43.02 nests per km²) was 8 times higher than at Nestor One (5.14 nests per km²; Table 3). When corrected for the probability of detecting an active nest based on estimates of Walter and Rusch (1997b), I estimated the average density of active nests to be 55.87 nests per km² and 6.68 nests per km² at Broad River and Nestor One, respectively. Incubation day of nests at discovery was similar between study areas in each year with nests slightly older at Nestor One than Broad River in 2005, but older at Broad River than at Nestor One in 2006 (Table 3). I made 1,855 observations of 468 nests at Nestor One from 2005 – 2007 with an average of 5.0 [standard deviation (SD) = 3.72] days between observations, resulting in 1,381 observation intervals. At Broad River, I made 1,387 observations of 692 nests, resulting in 694 observation intervals. The average observation interval was 16.8 (SD = 4.15) days at Broad River. Despite the possibility of highly variable onset of snow melt and spring phenology in this region of Canada, 2005 – 2007 consisted of one later-than-average year and 2 earlier-than-average years based on the estimated median hatch date, which varied at Nestor One (2005 = 28 June, 2006 and 2007 = 17 June) and at the Broad River (2005 = 24 June and 2006 = 11 June). The proportion of each nest type was similar among years at Nestor One and Broad River, but Broad River had substantially more wetland nests than Nestor One (Fig. 3). The nest type with the highest proportion of nests was wetland-sedge meadow at both study areas.

LESSER SNOW GOOSE NESTS

I discovered 69 snow goose nests in 2005, 19 in 2006, and 14 in 2007 at Nestor One, and 156 and 269 in 2005 and 2006, respectively, at Broad River. Fifty-five nests

were active at discovery and 48 were already failed at discovery at Nestor One, while 370 nests were active and 55 were already failed at discovery at Broad River.

PROXIMITY INDEX, NEAREST NEIGHBORS, AND NEAREST FAILED NEIGHBORS

Due to the high density of Canada goose nests and snow goose nests, Broad River had larger mean values for the proximity index to other Canada goose nests and snow goose nests, as well as smaller mean distances to nearest neighbors and nearest failed neighbors than observed at Nestor One (Table 4).

PREDATORS, ARCTIC FOX DEN OCCUPANCY, AND DISTANCE TO NEAREST DEN

Mammalian predators (arctic fox and wolf) were observed at or near a Canada goose nest in 1.3% of observation intervals. This was consistent among years and among study areas (Table 5). Avian predators were observed at or near a Canada goose nest in 32% of observation intervals. This was more variable among years than among study areas (Table 5).

I evaluated 26 arctic fox dens in 2005 and 29 in 2006 at Nestor One and Broad River, and 18 in 2007 at Nestor One only, for evidence of occupancy. Only 2 dens ($p = 0.08$) were occupied in 2005, 10 dens ($p = 0.34$) were occupied in 2006, and 5 dens ($p = 0.28$) were occupied in 2007. At Nestor One between 2005 and 2007, Canada goose nests averaged 2,587 m (SD = 1,690) to the nearest occupied fox den, while at Broad River the average distance to the nearest occupied arctic fox or wolf den was 2,086 m (SD = 674; Table 4). At both study areas there was substantial variation among years in the mean distance to the nearest occupied arctic fox den, which followed year-to-year variation in fox den occupancy, with on average shorter distances to active dens in years with high den occupancy.

ABUNDANCE OF LEMMINGS

The proportion of arctic fox scat containing lemming remains varied among years, from 0.48 (23 of 48, SE = 0.07) in 2005, to 0.54 (33 of 61, SE = 0.06) in 2006, and 0.77 (27 of 35, SE = 0.07) in 2007.

NEST SURVIVAL MODELING

Within-category *a priori* model set

Within the density-dependence category, only models consisting of nearest-neighbor distances received substantial support based on ΔAIC_{cij} (Table 6). Parameter estimates from the top 2 models suggested that increasing nearest-neighbor distances to either other Canada goose nests or snow goose nests had a negative influence on nest survival (Table 6). These covariates were also supported by Type III analysis ($P \leq 0.05$). The third- and fourth-ranked models within this category included piCAGO and a piCAGO*piCAGO interaction term, were $<5 \Delta AIC_{cij}$ units from the top-ranked model, and piCAGO had a $P < 0.1$ in Type III analysis when the quadratic term was included (Table 6). Based on these results, I included nnLSGO, nnCAGO, and the quadratic form of piCAGO in composite models.

Only the distance to the nearest active fox den received support within predator-category models based on AIC_c and Type III analysis, with increasing distance to an active arctic fox den associated with increased probability of nest survival (Table 6). This was consistent with my *a priori* hypotheses and was further supported in the snow goose – predator category with the additive model including nnLSGO and DEN performing far better than the other models in this category (based on AIC_c). Type III analyses indicated that both nnLSGO and DEN were strongly related ($P < 0.05$) to nest

survival. Models containing interactions between avian presence and snow geese received little support based on AIC_c ($\Delta AIC_{cij} > 2.0$) or Type III analysis ($P > 0.1$), while models with mammal presence and snow geese would not converge (DNC) due to the low frequency of mammal occurrence in the data and were therefore removed from further analyses (Table 6).

Within the predator-behavior category, models were all closely ranked based on ΔAIC_{cij} (1.61 – 3.81), although only nfACTIVE from the top-ranked model based on AIC_c was supported by Type III analysis ($P < 0.1$; Table 6). Parameter estimates for all models within this category were similar and suggested that as the distance to the nearest failed nest increased, the probability of a Canada goose nest surviving increased. Because the 4 nearest-failed nest covariates were highly correlated ($|r| > 0.7$), I considered only nfACTIVE when developing composite models.

Within-year temporal variation was evident as both DATE and AGE effects appeared in top-ranked models within the nest-defense category (Table 6). Although the effect of DATE received the most support based on AIC_{cij} , and Type III analysis ($P < 0.05$), there was relatively weaker support for the effect of AGE and the quadratic effect of incubation day (AGE*AGE). Effects of flushing a goose and nest type were not indicated as important based on AIC_{cij} or Type III analysis (Table 6).

Within the indirect-effects category, the effect of year-to-year variation in lemming abundance (LEMMING) on nest survival received the most support based on AIC_{cij} . Furthermore, when compared among all 32 *a priori* models evaluated, the LEMMING-only model had the lowest AIC_c and received over 50% of the Akaike weight ($w_i = 0.51$). LEMMING had a strong negative association with nest survival and

a highly significant ($P < 0.0001$) Type III analysis (Table 6). Strong among-year variation was also supported in the nuisance category, as a model with a categorical YEAR effect received all of the Akaike weight ($w_{ij} = 1.00$), while strong spatial variability received limited support from AIC_{cij} or Type III analysis. Study area effects, although not supported within-category by AIC_{cij} , received some support based on Type III analysis ($P = 0.07$).

Composite Models and Cross-Validation

I developed 5 composite models based on the analysis of 32 *a priori* models with the training dataset (Table 7). Due to strong correlations ($r > |0.7|$) among some covariates appearing in composite models (nnLSGO, nnCAGO, nfACTIVE, and piCAGO), I considered 3 separate composite models using variables from models with $\Delta AIC_{cij} < 2.0$ in within-category analysis or that were supported by a less conservative Type III analysis (P -value < 0.1). The last 2 composite models were developed with stricter criteria, again using variables from within-category models with $\Delta AIC_{cij} < 2.0$ but with more conservative (P -value < 0.05) Type III analysis results (Table 7). I included 3 additional models selected from the 32 *a priori* models evaluated with the training dataset along with the composite models in cross validation. These included a LEMMING model, a LEMMING*AVIAN model, and a YEAR model; which were the top model (LEMMING only) or $< 4 AIC_c$ units of the top model when compared among all 32 *a priori* models. Combined, these 3 models received 100% of the Akaike weight (w_i) when compared among all 32 *a priori* models. I also included an intercept-only model to represent constant survival resulting in a total of 9 models I evaluated with cross validation to assess goodness-of-fit.

All composite and best *a priori* models except the intercept-only (AUC = 0.53) model indicated good model fit (AUC > 0.7; Table 8). The 95% CI for the intercept-only model overlapped 0.5 suggesting using a constant-survival model predicting survival in the test data was equivalent to flipping a coin. The 95% CI of AUC for all models, except the intercept-only model, overlapped the AUC 95% CI of the model with the largest AUC value (Table 8), suggesting ROC analysis did not distinguish among these models, but that all 8 fit the data well.

Parameter Estimates and Multi-Model Inference

I estimated parameters from which to make inference using the full data set (i.e., training + test) and 8 models where the AUC 95% CI overlapped the AUC 95% CI of the model with the largest AUC value. I then ranked these 8 models fitted to the full data set using AIC_c and generated Akaike weights (w_i) to use when calculating model-averaged parameter estimates. The relative rank of the 8 models when compared via AIC_c using the full dataset were similar to ranks of the same 8 models based on AUC scores from cross-validation, except for composite model II, which ranked much higher based on AIC_c than AUC (Table 8). However, AIC_c discriminated more distinctly among the 8 models in the model set with 4 of the composite models combined receiving nearly all of the Akaike weight ($\sum w_i = 0.96$; Table 8). Model-averaged parameter estimates with unconditional standard errors suggested LEMMING, AGE, and AGE*AGE to be variables strongly associated with Canada goose nest survival (Table 9). In years with large LEMMING, nest survival was relatively lower than years with small LEMMING (Fig. 4). While within years as incubation day increased, nest survival initially increased however decreased late in incubation (Fig. 4).

DISCUSSION

Despite substantial research on the impacts of increasing density and expanding distribution of lesser snow geese on the tundra and coastal salt marsh vegetation along Hudson Bay in northern Manitoba, much less information exists on their potential impact on co-occurring species; particularly sympatric nesting Canada geese (however see Gleason et al. 2004, Baldwin 2006, Sammler et al. 2008). Factors influencing nest survival in northern nesting Canada geese are likely complex and difficult to observe directly (Walter 1999, Reiter 2006). To quantify the magnitude of influence of increasing nesting snow geese among multiple factors likely to influence within- and among-year variation in nest survival, I constructed a conceptual model representing multiple factors potentially influencing the survival of Eastern Prairie Population Canada goose nests in northern Manitoba (Fig. 1). I assessed evidence in support of this model by evaluating multiple competing hypotheses within 6 distinct components of Canada goose nest survival, and evaluated the influence of increasing density and expanding distribution of lesser snow geese. By incorporating data on both within- and among-year variation in nest survival, I quantified temporal variability in nest survival at 2 resolutions. Among-year variability in lemming abundance and within-year changes in incubation day (i.e., nest age) were significantly related to the probability of Canada goose nest survival. I found no support for the apparent-competition or nesting-association hypotheses as mechanisms describing interactions among nesting Canada geese and snow geese.

Strong year-to-year variation in nest survival of Canada geese has been well documented (Walter 1999, Gleason et al. 2004, Reiter 2006). In this system, arctic fox

establish breeding territories and reproduce in years with high lemming abundance while dispersing or becoming nomadic in years when lemmings are scarce (Bahr 1989, Roth 2003). Reiter (2006) found the relative abundance of arctic fox as indexed by activity at dens to be negatively associated with nest survival of Canada geese at Nestor One between 1992 and 2004; in years with high fox activity, nest survival was low. My analysis of data from 2 study areas, presented here, suggested that the proportion of arctic fox scat containing lemming remains varied substantially between 2005 and 2007, presumably as a result of changes in lemming abundance, and was negatively related to Canada goose nest survival. Furthermore, both den occupancy and the average distance to the nearest den varied among years between 2005 and 2007, and paralleled variation in lemming abundance as inferred from arctic fox scat analysis. When relative lemming abundance was high, den occupancy was high, the average distance of a nest to an active fox den was small, and subsequently Canada goose nest survival was low. The opposite was true in years of relatively low lemming abundance. My results supported the importance of year-to-year variation in Canada goose nest survival observed in previous studies, and further emphasized the important role of arctic fox and lemmings in this coastal tundra ecosystem (Reiter 2006).

My analysis provides the first evaluation of within-year variation in nest survival of EPP Canada geese. Daily survival rates varied non-linearly with incubation day, increasing until ~18 days of incubation and then declining. My results supported one of my *a priori* hypotheses, and were consistent with Grand et al. (2006), that variability in nest survival as a function of incubation day may be non-linear if nests that are more likely fail are depredated early in incubation, while the ability to defend against predators

ultimately declines with incubation day due to reduced energy reserves and increasing time away from the nest. Ryder (1972, 1975) first predicted the importance of arctic goose condition to nest defense, and the potential for reduced nest survival late in incubation in nests with suboptimal clutch sizes and territories. These hypotheses suggested that female arctic-nesting geese would optimize their clutch size, by maximizing the number of eggs laid while also maintaining reserves to remain on the nest throughout incubation and maximize nest survival. Furthermore, the gander selects an optimal territory size; small enough for adequate defense while large enough to provide food for the gander late in incubation in order to maintain body condition for continued territorial defense. In theory, pairs with territories too small to provide adequate forage late in incubation would have to leave to feed, resulting in decreased nest survival. My analysis supported the importance of late-incubation condition as a potential mechanism influencing nesting EPP Canada geese.

Ultimately, I found little support for an influence of nesting snow geese on nest survival of EPP Canada geese. These results differ from Gleason et al. (2004) who reported higher nest survival for Canada geese nesting away from snow goose aggregations, and from Baldwin (2006) who found increased nest survival in cackling geese (*Branta hutchinsii*) nesting within a Ross's goose (*Chen rossii*) colony versus outside of a Ross's goose colony. Point-pattern analyses from 2001 – 2007 at Nestor One (Chapter 1, this volume) suggested that failed Canada goose nests tended to aggregate with low snow goose nest density while successful nests aggregated with relatively higher snow goose nest density. However, logistic-exposure models evaluated here suggested that neither the overall intensity of nesting snow geese (i.e., the proximity

index, piLSGO) nor the nearest-nesting snow goose (nnLSGO) strongly influenced, either directly or indirectly through interactions with shared predators, nest survival of Canada geese, when considered in light of all factors potentially influencing Canada goose nest survival (Fig. 1). Furthermore, my data suggested that there were no differences in overall predator pressure, avian or mammal, between Nestor One, where Canada goose and snow goose densities were both relatively low, and Broad River, which had much higher nest densities. This is different than both Gleason et al. (2004) and Baldwin (2006) who report higher incidences of avian predators in areas with high snow goose or Ross' goose nest density; however, neither study formally collected avian-predator data. Comparatively, however, even the highest densities of snow goose nests observed in this study (~ 33 nest per km^2) were substantially lower than densities of Ross' goose nests observed by Baldwin (2006; $>1,000$ nests per km^2). The large difference in the density of nesting snow geese between this and other studies may have contributed to the observed difference in results.

My approach to data analysis was unique and provided a conceptual hybrid between (1) the information-theoretic approach (e.g., Burnham and Anderson 2002), which was largely driven by *a priori* model development and identifying the most parsimonious model; and (2) cross-validation, which provided a framework for reducing the number of parameters and the size of the model set, and evaluating the goodness-of-fit of nest-survival models (Snee 1977, Shaffer and Thompson 2007). This approach was valuable for analysis of a large dataset that addressed a complex ecological model with multiple categories and multiple competing hypotheses. Development of *a priori* models in the information-theoretic approach was critical to generating scientifically-based

hypotheses, but was complicated by the large number of covariates. Therefore, developing a model set of reasonable size was impractical and may have ignored additive effects and important interactions between covariates from different categories within the general nest-survival model (Hilborn and Mangel 1997). Furthermore, ensuring adequate model fit is important for unbiased model inference (Burnham and Anderson 2002). I considered my approach as 3 distinct steps: (1) a preliminary study that addressed simple hypotheses and considered covariate interactions and potentially additive effects (training data and 32 *a priori* models); (2) data collected to test the initial results from the preliminary study and to evaluate model fit; and (3) a combination of the 2 datasets to draw inference about the population of nests based on the most parsimonious of the models with adequate goodness-of-fit. Overall, I reduced the number of covariates considered in my final model set by nearly half based on empirical evidence, limited the total number of models being evaluated to a set well-supported by data, and reduced the likelihood of spurious results.

Understanding the mechanisms affecting vital rates (e.g., births, deaths) of a population of animals is critical for their management. It is particularly important when evaluating the effects of changes to the local ecosystem through changes in the distribution of co-occurring species. Nesting lesser snow geese have increased in density and expanded in distribution substantially along western Hudson Bay in the last 30 years, and appear to have influenced brood-habitat use by Canada geese (Nack and Andersen 2004, 2006) and subsequently the local and range-wide distribution of nesting Canada geese (Chapters 2 & 4, this volume). However, I did not find strong evidence that snow geese nesting at the densities observed in this study have influenced local predator, prey,

and alternative-prey dynamics that drive much of the variation in Canada goose nest survival in this region (Reiter 2006). Despite the complexities of the conceptual model of Canada goose nest survival I evaluated (i.e., multiple categories, with multiple covariates and interactions), my analysis lends further support for the importance of annual fluctuations in arctic fox and lemming populations in the population dynamics of Canada geese in this region, and provides the first evidence of strong temporal variation in the probability of nest survival during incubation.

TABLE 1. Variables included in models of Eastern Prairie Population (EPP) Canada goose (*Branta canadensis interior*) nest survival at Nestor One (2005 – 2007) and the Broad River (2005 – 2006) study areas in northern Manitoba, Canada.

VARIABLE	DEFINITION
piLSGO	Proximity index of snow goose nests ^a
piCAGO	Proximity index of Canada goose nests ^a
nnLSGO	Distance (m) to nearest snow goose nest ^a
nnCAGO	Distance (m) to nearest Canada goose nest ^a
AVIAN	Presence (1) or absence (0) of avian predators during first nest observation of interval ^b
MAMM	Presence (1) or absence (0) of mammalian predators during first nest observation of interval ^b
TYPE	Type of nest: wetland, upland, or shoreline-island ^a
FLUSH	Female goose being flushed or not flushed during the first nest observation of interval ^b
nfACTIVE	Distance (m) to nearest failed nest based on nests that were active when discovered ^a
nfEARLY	Distance (m) to nearest failed nest based on nests that were failed when discovered ^a
nfCAGO	Distance (m) to the nearest failed Canada goose nest ^a
nfLSGO	Distance (m) to the nearest failed snow goose nest ^a
AGE	Average incubation day of nests during interval ^b
DATE	Average Julian date during interval ^b
LEMMING	Proportion of arctic fox scat that contained lemming remains in each year ^c
YEAR	Three-level factor representing each year of the study: 2005, 2006, 2007 ^c
SA	Two-level factor representing each study area: Broad River and Nestor One
X Y	The easting (X) and northing (Y) UTM coordinate for each nest location ^a

^avariable estimated uniquely for each nest but remained the same for each observation interval on the same nest

^bvariable estimated uniquely for each nest but changed for each nest for each observation interval

^cvariable estimated uniquely for each year but was the same for all nests and all observation intervals within each year

TABLE 2. Set of 32 models developed *a priori* to evaluate factors influencing nest survival of Eastern Prairie Population (EPP) Canada geese (*Branta canadensis interior*) nesting near Cape Churchill in northern Manitoba, Canada. Models were classified under several competing hypothesis categories. All quadratic and interaction models contained both the interaction or squared term and the individual covariates.

HYPOTHESIS CATEGORY	MODEL^a
DENSITY DEPENDENCE	piLSGO piCAGO nnLSGO nnCAGO piLSGO*piLSGO piCAGO*piCAGO
PREDATOR EFFECTS	AVIAN MAMM DEN
SNOW GOOSE – PREDATOR INTERACTIONS	piLSGO*AVIAN piLSGO*MAMM piLSGO + DEN nnLSGO*AVIAN nnLSGO*MAMM nnLSGO + DEN
PREDATOR BEHAVIOR	nfACTIVE nfEARLY nfLSGO nfCAGO
INDIRECT EFFECTS	LEMMING LEMMING*MAMM LEMMING*AVIAN
DEFENSIVE CAPABILITIES & STUDY EFFECTS	AGE AGE*AGE DATE FLUSH TYPE FLUSH*AVIAN FLUSH*MAMM
NUISANCE EFFECTS	YEAR SA X + Y

^asee Table 1 for covariate definitions

TABLE 3. Summary of Eastern Prairie Population (EPP) Canada goose (*Branta canadensis interior*) nests that were active when discovered at Nestor One (2005 – 2007) and Broad River (2005 – 2006) study areas in northern Manitoba, Canada.

Year	NESTOR ONE				BROAD RIVER			
	Search dates	No. nests ^a	Nest density ^b	Mean incubation day at discovery ^c (standard deviation)	Search dates	No. nests ^a	Nest density ^b	Mean incubation day at discovery ^c (standard deviation)
2005	2 June – 26 June	163	5.37	9.75 (SD = 4.81)	1 June – 5 June	340	42.34	8.97 (SD = 2.91)
2006	24 May – 11 June	165	5.43	10.48 (SD = 4.31)	22 May – 28 May	352	43.70	13.28 (SD = 3.92)
2007	29 May – 10 June	140	4.61	16.51 (SD = 5.98)	- ^d	-	-	-
TOTAL	24 May – 26 June	468	5.14	12.02 (SD = 5.82)	22 May – 5 June	692	43.02	11.16 (SD = 4.07)

^atotal number of nests found active

^bnests per km² based on 30.35 km² at Nestor One and 8.05 km² at Broad River; not corrected for probability of detection

^cMean incubation day based on egg flotation and egg candling

^dBroad River study area was not searched in 2007

TABLE 4. Mean and standard deviation (SD) of observed nearest-neighbor Canada goose (*Branta canadensis interior*) and lesser snow goose (*Chen caerulescens caerulescens*) nest distances (m; nnCAGO, nnLSGO), proximity indices (piCAGO, piLSGO), nearest-failed nests (m; nfEARLY, nfACTIVE, nfCAGO, nfLSGO), and nearest occupied arctic fox (*Alopex lagopus*) or wolf (*Canis lupus*) den (DEN) for all Eastern Prairie Population (EPP) Canada goose nests at Broad River (2005 – 2006) and Nestor One (2005 – 2007) in northern Manitoba, Canada.

Variable ^a	Broad River			Nestor One		
	Mean	SD	<i>n</i> ^b	Mean	SD	<i>n</i> ^b
nnCAGO	86.27	39.73	692	241.89	123.92	468
nnLSGO	260.55	443.53	692	1413.45	1207.84	468
piCAGO	0.0222	0.0049	692	0.0014	0.0002	468
piLSGO	0.0140	0.0074	692	0.0003	0.0003	468
nfEARLY	188.57	129.49	692	763.54	550.47	468
nfACTIVE	150.29	120.26	692	516.06	360.27	468
nfCAGO	141.27	89.25	692	470.85	328.83	468
nfLSGO	277.83	328.86	692	1107.77	831.00	468
DEN	2085.68	673.59	692	2587.30	1689.90	468

^a see Table 1 for covariate definitions

^b sample sizes were based on the total number of nests, not observation intervals because these variables did not change during the incubation period

TABLE 5. Summary of avian (AVIAN) and mammalian (MAMMAL) nest predators observed within 250 m of Eastern Prairie Population (EPP) Canada goose (*Branta canadensis interior*) nests during nest observations at the Nestor One (NO; 2005 – 2007) and Broad River (BR; 2005 – 2006) study areas in northern Manitoba, Canada.

Study Area	Year	No. intervals	No. AVIAN ^a	PA ^b	No. MAMMAL ^c	PM ^d
NO	2005	615	201	0.32	1	0.002
	2006	616	165	0.27	14	0.02
	2007	156	71	0.46	4	0.03
BR	2005	340	99	0.29	9	0.03
	2006	354	131	0.37	0	0.00

^atotal number of nest observation intervals where ≥ 1 avian predator was observed ≤ 250 m from the nest during the first visit of the interval

^bproportion of nest observation intervals where an avian predator was observed

^ctotal number of nest observation intervals where ≥ 1 mammalian predator was observed ≤ 250 m from the nest during the first visit of the interval

^dproportion of nest observation intervals where a mammalian predator was observed

TABLE 6. Summary of 32 *a priori* models analyzed using logistic-exposure models and a random subset of Eastern Prairie Population (EPP) Canada goose (*Branta canadensis interior*) nest observation data from the Broad River (2005 – 2006) and Nestor One (2005 – 2007) study areas in northern Manitoba, Canada. All interaction models included the interaction term and the individual covariates.

CATEGORY	MODEL ^a	AIC _c	ΔAIC_{cij} ^b	w_{ij} ^c	ΔAIC_c ^d	w_i ^e	PARAMETER ESTIMATE (TYPE III P-VALUE)	K ^f
DENSITY DEPENDENCE	nnCAGO	725.18	0.00	0.51	23.12	0.00	$\beta_{nnCAGO} = -0.002$ (0.02)	2
	nnLSGO	726.52	1.34	0.26	24.46	0.00	$\beta_{nnLSGO} = -0.0002$ (0.05)	2
	piCAGO* piCAGO	728.88	3.70	0.08	26.82	0.00	$\beta_{piCAGO} = 0.33$ (0.07) $\beta_{piCAGO}^2 = -0.24$ (0.16)	3
	piCAGO	728.89	3.71	0.08	26.83	0.00	$\beta_{piCAGO} = 0.10$ (0.22)	2
	piLSGO	730.37	5.19	0.04	28.31	0.00	$\beta_{piLSGO} = 0.02$ (0.84)	2
	piLSGO* piLSGO	730.86	5.68	0.03	28.80	0.00	$\beta_{piLSGO} = 0.15$ (0.26) $\beta_{piLSGO}^2 = -0.07$ (0.22)	3
PREDATOR	DEN	722.77	0.00	0.94	20.71	0.00	$\beta_{DEN} = 0.0002$ (0.006)	2
	AVIAN	729.31	6.54	0.04	27.25	0.00	$\beta_{AVIAN} = 0.1938$ (0.29)	2
	MAMMAL	729.91	7.14	0.03	27.85	0.00	$\beta_{MAMMAL} = -0.64$ (0.48)	2
SNOW GOOSE - PREDATOR	nnLSGO + DEN	719.63	0.00	1.00	17.58	0.00	$\beta_{nnLSGO} = -0.0002$ (0.02) $\beta_{DEN} = 0.0002$ (0.002)	3
	piLSGO + DEN	724.49	22.43	0.00	22.43	0.00	$\beta_{piLSGO} = 0.04$ (0.59) $\beta_{DEN} = 0.0002$ (0.005)	3
	nnLSGO*AVIAN	727.96	25.90	0.00	25.90	0.00	$\beta_{nnLSGO} = -0.0001$ (0.10) $\beta_{AVIAN} = 0.37$ (0.11) $\beta_{nnLSGO*AVIAN} = -0.0002$ (0.25)	4
	piLSGO*AVIAN	733.21	31.15	0.00	31.15	0.00	$\beta_{piLSGO} = -0.001$ (0.84) $\beta_{AVIAN} = 0.18$ (0.37) $\beta_{piLSGO*AVIAN} = 0.04$ (0.83)	4
	nnLSGO*MAMMAL	DNC ^g						
	piLSGO*MAMMAL	DNC ^g						
PREDATOR BEHAVIOR	nfACTIVE	726.61	0.00	0.55	24.55	0.00	$\beta_{nfACTIVE} = 0.0006$ (0.05)	2
	nfCAGO	728.21	1.61	0.25	26.16	0.00	$\beta_{nfCAGO} = 0.0005$ (0.14)	2

TABLE 6. continued

INDIRECT EFFECTS	nfEARLY	729.55	2.94	0.13	27.49	0.00	$\beta_{\text{nfEARLY}} = 0.0002 (0.35)$	2
	nfLSGO	730.41	3.81	0.08	28.35	0.00	$\beta_{\text{nfLSGO}} = 0.0000 (0.99)$	2
	LEMMING	702.06	0.00	0.82	0.00	0.51	$\beta_{\text{LEMMING}} = -4.89 (<0.0001)$ $\beta_{\text{LEMMING}} = -5.43 (<0.0001)$	2
	LEMMING*AVIAN	705.13	3.07	0.18	3.07	0.11	$\beta_{\text{AVIAN}} = -0.50 (0.59)$ $\beta_{\text{LEMMING*AVIAN}} = 1.12 (0.50)$	4
	LEMMING*MAMMAL	DNC ^c						
NEST DEFENSE	DATE	726.48	0.00	0.38	24.42	0.00	$\beta_{\text{DATE}} = 0.03 (0.05)$	2
	AGE*AGE	727.15	0.67	0.27	25.09	0.00	$\beta_{\text{AGE}} = 0.20 (0.12)$ $\beta_{\text{AGE}^2} = -0.006 (0.06)$	3
	AGE	728.56	2.08	0.13	26.50	0.00	$\beta_{\text{AGE}} = -0.03 (0.17)$	2
	FLUSH	728.89	2.41	0.11	26.83	0.00	$\beta_{\text{FLUSH}} = -0.26 (0.22)$ $\beta_{\text{FLUSH}} = 21.64 (0.27)$	2
	FLUSH*MAMMAL	730.80	4.33	0.04	28.74	0.00	$\beta_{\text{MAMMAL}} = 0.03 (0.22)$ $\beta_{\text{FLUSH*MAMMAL}} = -21.93 (0.23)$ $\beta_{\text{FLUSH}} = -0.17 (0.27)$	4
NUISANCE	FLUSH*AVIAN	731.24	4.77	0.03	29.18	0.00	$\beta_{\text{AVIAN}} = 0.27 (0.43)$ $\beta_{\text{FLUSH*AVIAN}} = -0.18 (0.69)$	4
	TYPE	731.85	5.37	0.03	29.79	0.00	$\beta_{\text{WETLAND}} = -0.22 (0.75)$ $\beta_{\text{UPLAND}} = -0.16 (0.75)$	3
	YEAR	702.64	0.00	1.00	0.58	0.38	$\beta_{2005} = 1.51 (<0.001)$ $\beta_{2006} = 0.94 (<0.001)$	3
	X + Y	726.79	24.15	0.00	24.73	0.00	$\beta_{\text{X}} = 0.12 (0.11)$ $\beta_{\text{Y}} = 0.03 (0.18)$	3
	STUDY AREA	727.17	24.53	0.00	25.11	0.00	$\beta_{\text{Broad River}} = 0.33 (0.07)$	2

^asee Table 1 for covariate definitions

^b ΔAIC_{ij} = difference between AIC_c of each model, i , within each category, j , and the model with the lowest AIC_c within category, j .

^c w_{ij} = Akaike weight for each model, i , when evaluated against other models within the same category, j

^d ΔAIC_c = difference between AIC_c of each model, i , and the model with the lowest AIC_c of all models from all categories

^e w_j = Akaike weight for each model, i , when evaluated against all models from all categories

^f K = number of parameters in the model

^gDNC = models that did not converge when fitting logistic-exposure models

TABLE 7. Set of 5 composite models developed to evaluate factors influencing nest survival of Eastern Prairie Population (EPP) Canada geese (*Branta canadensis interior*) nesting near Cape Churchill in northern Manitoba, Canada.

MODEL	FORM^a
COMPOSITE I	nnCAGO + nnLSGO + DEN + AGE + AGE*AGE + DATE + LEMMING + SA
COMPOSITE II	piCAGO + piCAGO*piCAGO + DEN + AGE + AGE*AGE + DATE + LEMMING + SA
COMPOSITE III	nfACTIVE + DEN + AGE + AGE*AGE + DATE + LEMMING + SA
COMPOSITE IV	nnCAGO + nnLSGO + DEN + LEMMING
COMPOSITE V	nfACTIVE + DEN + DATE + LEMMING

^asee Table 1 for covariate definitions

TABLE 8. Summary of area-under-curve (AUC) estimates based on cross-validation of models developed using ~50% of the Eastern Prairie Population (EPP) Canada goose (*Branta canadensis interior*) nest data and applied to predict survival for the remaining ~50% of the data from northern Manitoba, Canada (2005 – 2007). Akaike’s Information Criterion (AIC_c) values were based on logistic-exposure models fitted, using the full dataset, to the set of 8 models best-supported by AUC.

MODEL ^a	AUC [95% CI]	AIC _c	ΔAIC _c ^b	w _i ^c
COMPOSITE I	0.7415 [0.6954 - 0.7853]	1402.06	7.33	0.02
COMPOSITE V	0.7413 [0.6916 - 0.7808]	1402.70	7.97	0.02
COMPOSITE III	0.7396 [0.6916 - 0.7834]	1394.73	0.00	0.83
LEMMING*AVIAN	0.7375 [0.6875 - 0.7808]	1413.00	18.27	0.00
LEMMING	0.7369 [0.6902 - 0.7954]	1409.25	14.52	0.00
COMPOSITE IV	0.7367 [0.6780 - 0.7856]	1411.83	17.10	0.00
YEAR	0.7357 [0.6842 - 0.7819]	1411.00	16.27	0.00
COMPOSITE II	0.7283 [0.6806 - 0.7716]	1398.43	3.70	0.13
CONSTANT	0.5296 [0.4547 - 0.5461]	-	-	- ^d

^aSee Tables 2 & 3 for variables included in each model.

^bΔAIC_c = difference between AIC_c of each model and the model with the lowest AIC_c

^cAkaike weight

^dModel was not included in generating Akaike weights and model-averaged parameter estimates

TABLE 9. Model-averaged parameter estimates for 8 models of Eastern Prairie Population (EPP) Canada goose (*Branta canadensis interior*) nest survival in northern Manitoba, Canada. Models were developed using a cross-validation framework and parameters were averaged using the entire dataset of nest observations and Akaike weights (w_i).

VARIABLE ^a	$\hat{\beta}_j$ ^b	LOWER 95% CI	UPPER 95% CI
INTERCEPT	7.43	2.85	12.00
DENSITY DEPENDENCE			
mnCAGO	0.00	0.00	0.00
nnLSGO	0.00	0.00	0.00
piCAGO	-0.18	-0.89	0.53
piCAGO*piCAGO	0.06	-0.19	0.32
PREDATORS			
AVIAN	0.00	-0.0002	0.0002
DEN	0.0001	-0.00003	0.0002
PREDATOR BEHAVIOR			
nfACTIVE	0.0006	-0.0002	0.001
INDIRECT TROPHIC EFFECTS			
LEMMING	-5.12	-6.89	-3.34
LEMMING*AVIAN	0.0001	-0.0003	0.0004
NEST DEFENSE			
AGE	0.36	0.15	0.57
AGE*AGE	-0.01	-0.02	-0.005
DATE	-0.02	-0.05	0.003
NUISANCE			
STUDY AREA			
Broad River	-0.09	-1.18	1.01
YEAR - 2005	0.0003	-0.001	0.002
YEAR - 2006	0.0002	-0.001	0.001

^asee Table 1 for covariate definitions

^b $\hat{\beta}_j$ was the model averaged parameter estimate for covariate j

FIGURE 2. Location of the Nestor One and Broad River study areas used to study Eastern Prairie Population (EPP) Canada goose (*Branta canadensis interior*) nest survival along the Hudson Bay Lowlands near Cape Churchill in northern Manitoba, Canada, 2005 – 2007.

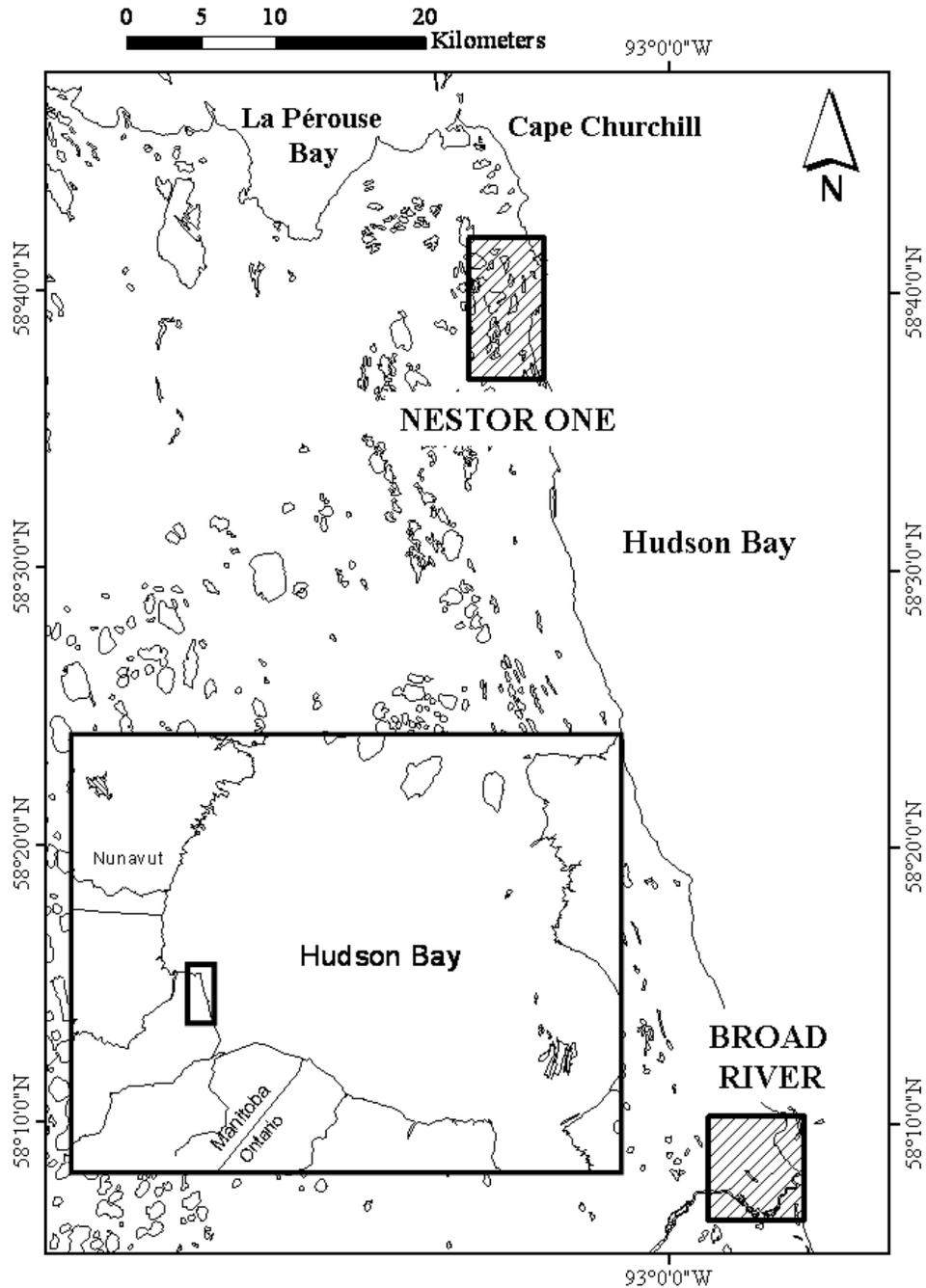


FIGURE 3. Proportion of Eastern Prairie Population (EPP) Canada goose (*Branta canadensis interior*) nests of each type (wetland, upland, shore-island) at (A) Broad River 2005 – 2006, and (B) Nestor One 2005 – 2007 near Cape Churchill in northern Manitoba Canada.

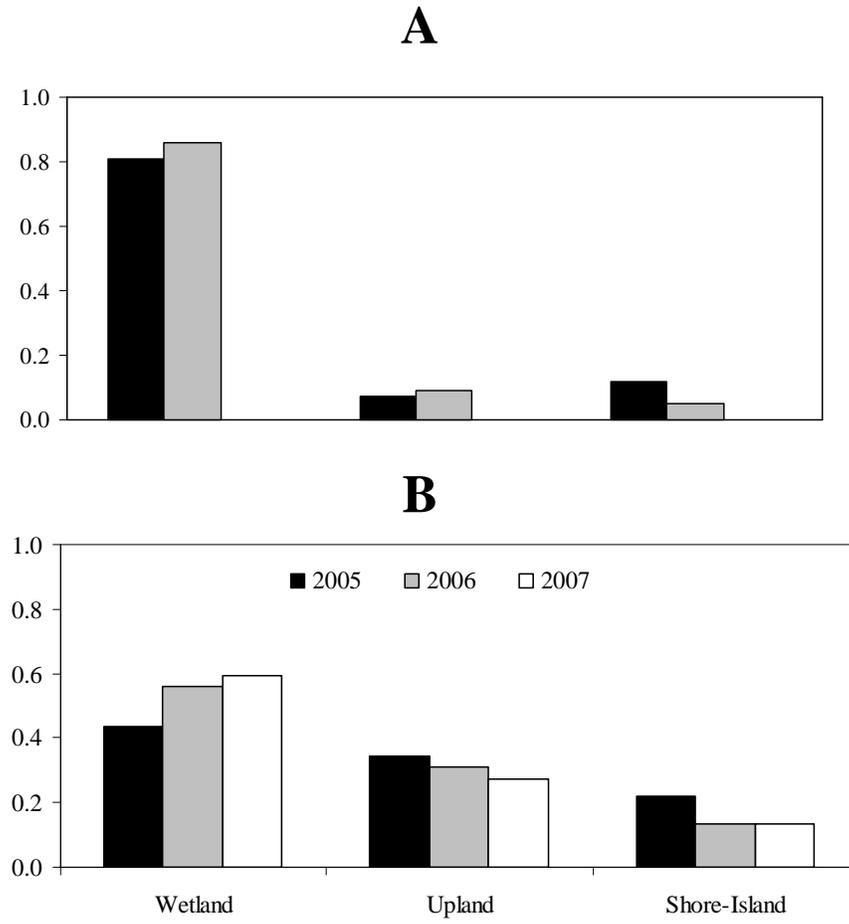
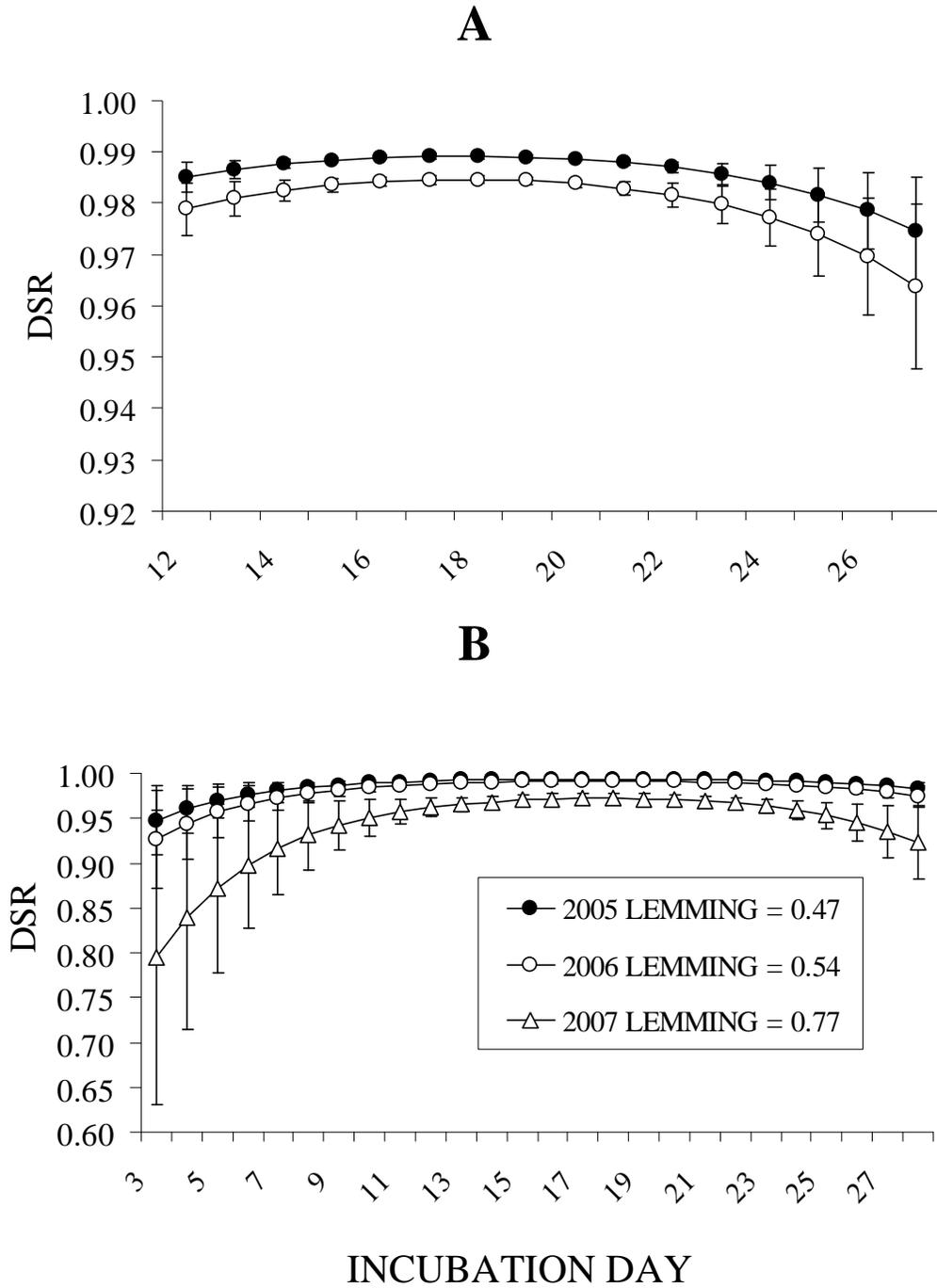


FIGURE 4. Effects of incubation day and lemming abundance (LEMMING) on the daily survival rate (DSR) of Eastern Prairie Population (EPP) Canada goose (*Branta canadensis interior*) nests at (A) Broad River, 2005 – 2006; and (B) Nestor One; 2005 – 2007, in northern Manitoba. DSRs were based on model-averaged estimates and were predicted only for the range of nest ages observed at each study area. Error bars represent 95% confidence intervals.



CHAPTER 3
POTENTIAL IMPACTS OF LESSER SNOW GOOSE-MEDIATED HABITAT
ALTERATION ON CANADA GOOSE NEST DENSITY
1976 – 2007

INTRODUCTION

Understanding factors influencing habitat use by breeding birds is important for their conservation and management. This is increasingly true in light of global changes in the distribution and abundance of many species (Chapin et al. 2000), and the predictions of global climate change models, which suggest the possibility of additional changes in the spatial distribution of avian populations (Hitch and Leberg 2007, Root and Schneider 2007). How changes in the distribution and abundance of breeding bird species will affect habitat use of other breeding birds is not well understood but, at a minimum, requires an understanding of the current breeding-habitat use of each species (Root and Schneider 2007).

The Eastern Prairie Population (EPP) Canada goose (*Branta canadensis interior*) breeding range extends across nearly 101,500 km² of predominantly tundra and boreal forest along the western coast of Hudson Bay in northern Manitoba, Canada (Malecki et al. 1980). Within their range, nesting EPP geese are found at the highest densities close to the Hudson Bay coastline (Humburg et al. 2000). Declines in EPP Canada goose nest density at some locations during the last 20 years coupled with increasing nest density elsewhere (Walter 1999), suggest there may be a shift in the spatial distribution of nesting EPP geese. Whether this shift in nest density has resulted in changes of habitat use by nesting Canada geese in this region is unknown.

Concurrently, nesting lesser snow geese (hereafter, snow geese; *Chen caerulescens caerulescens*) have expanded their distribution and increased in abundance along western Hudson Bay (Ankney 1996, Abraham and Jefferies 1997, Batt 1997) and throughout most of the central North American Arctic. They have begun breeding in

areas where they are not known to have previously nested and that were traditionally used by one nesting goose species, EPP Canada geese (Walter 1999). In addition, large numbers of snow geese and Ross's geese (*Chen rossii*) that breed farther north, forage along the western Hudson Bay coastline during migration. The impact that large populations of snow geese have on subarctic vegetation communities is well documented (Kerbes et al. 1990, Jano et al. 1998, Jefferies et al. 2006). Less information exists regarding how snow goose-mediated change to vegetation communities might affect co-occurring species, particularly nesting EPP Canada geese (Ankney 1996, Abraham and Jefferies 1997, Batt 1997).

Nack and Andersen (2006) suggested that brood-rearing habitat use by EPP Canada geese near Cape Churchill, Manitoba has changed over the last 25 years to where broods currently use interior sedge meadows with greater frequency than coastal salt marshes. This distinct shift was thought to be influenced by the alteration of coastal salt marshes from foraging by geese. Furthermore, recent climate change models predict increasing temperature, alteration of sea-level dynamics and precipitation regimes, and decreases in the depth and extent of permafrost in arctic and subarctic regions along Hudson Bay (Gough 1998, Gagnon and Gough 2005). Such broad-scale climatic change will have implications for vegetation communities. To quantify the effect changes to vegetation communities as the result of snow goose grazing (short-term) and potentially climate change (long-term) might have on nesting EPP Canada geese, it is important to understand the factors influencing current variation in the intensity of use of the coastal tundra landscape by nesting EPP Canada geese.

I used a geographic information system (GIS) to model long-term data on the distribution of EPP Canada goose nests relative to the distribution of selected vegetation communities. I examined EPP Canada goose nest density over both space and time at 3 study areas along western Hudson Bay in northern Manitoba, Canada. Specifically, my objectives were to: (1) model factors (particularly proximity and abundance of selected vegetation communities) influencing variation in density of nesting EPP Canada geese across a coastal tundra landscape between 1976 and 2007, and (2) assess whether associations with factors have changed over the last 30 years in light of changes to the coastal salt marsh vegetation resulting from goose foraging.

STUDY AREA

I considered 3 distinct study areas, each consisting of multiple subunits searched for nests. The Nestor One study area (~ 32-km²; 58° 34' N, 93° 11' W) was just south of Cape Churchill and approximately 60 km east-southeast of the town of Churchill, Manitoba (Fig. 1). The Broad River study area (~29-km²; 58° 07' N, 92° 51' W) was 60-km south-southeast of Nestor One along the Hudson Bay coastline, and the Churchill study area (~13-km²; 58°45' N, 94°00' W) was located 45 km west of Nestor One and 15 km east of the town of Churchill. Both Nestor One and Broad River were within Wapusk National Park (11,475 km²), and their eastern boundaries were Hudson Bay. The Churchill study area was west of Wapusk National Park, and its northern boundary was Hudson Bay. All three study areas were within a narrow strip of coastal tundra, characterized by low relief, continuous permafrost, poor drainage, beach ridges, coastal marshes, and coastal tundra vegetation (Wellein and Lumsden 1964, Didiuk and Rusch 1979), and were contained within the larger Hudson Bay Lowlands ecosystem. Across

all 3 study areas, the coastal tundra vegetation was dominated by shrubs (*Betula glandulosa*, *Salix* spp., *Myrica gale*), sedges (*Carex* spp.), herbaceous plants (*Scirpus caespitosus*, *Dryas interfolia*, *Salicornia borealis*), mosses (*Sphagnum* spp.), and lichens. Brook (2001) identified 7 vegetation classes occurring at all 3 study areas, generalized as: salt marsh, sedge meadow, willow (*Salix* spp.) - birch (*Betula* spp.) shrub, uplands, unvegetated ridge, unvegetated shore, and water (Fig. 2). Only these 7 vegetation classes occurred at Nestor One and Broad River, and in similar proportions (Fig. 2). The Churchill study area was dominated (>75% of the total area) by the 7 vegetation classes in common with Nestor One and Broad River, but also contained an additional 5 vegetation classes. These additional classes were predominately lichen-spruce bogs, and comprised <25% of the total area (Fig. 2). Overall, these 3 study areas had similar proportions of each vegetation class as that occurring across the entire region, and were a good representation of the coastal tundra vegetation within ~ 8 km of the Hudson Bay coast (Fig. 2). All study areas supported a diversity of breeding waterfowl (Anseriformes), shorebirds (Charadriiformes), and passerines (Passeriformes), and occurred within areas of the highest density of breeding EPP Canada geese within their range (Humburg et al. 2000).

METHODS

NEST DISCOVERY

Beginning in 1976, systematic ground surveys for EPP Canada goose nests have been conducted annually near Cape Churchill, Manitoba. These surveys followed standard protocols after Didiuk and Rusch (1979), Walter (1999), and Nack and Andersen (2006). Subunits within Nestor One (Fig. 3), Broad River (Fig. 4), and

Churchill (Fig. 5) study areas ranged from 0.46 to 4.77 km² ($\bar{x} = 1.38$ km²) in size, and were systematically searched using 4 – 6 observers spaced at 50 – 250 m intervals, depending upon terrain and visibility. At Nestor One, subunits were searched for nests in each year between 1976 and 2007. Subunits of the Broad River study area were searched during 1987 – 1989, 1994 – 1995, and 2005 – 2006, and subunits of the Churchill study area were searched during 1993, 1994, and 2005. Nest-searching subunits were delineated primarily on the basis of prominent land features (e.g., beach ridges, lakes) to allow for consistent navigation of the subunits prior to use of global positioning systems (GPS). Although subunits in each study area were somewhat arbitrarily defined, they were representative of the available coastal tundra in this region, based on a comparison (see Fig. 2) of the proportion of area composed of each vegetation class in each study area with the proportion of area composed of each vegetation class across the entire coastal tundra region (< 8 km from the Hudson Bay Coast, extending from south of Broad River to Churchill). Using ArcMap 9.0 (© 1998 – 2004 ESRI) and the Brook (2001) vegetation classification, I digitized subunit boundaries for each study area based on aerial photos used during nest searching.

DATA PREPARATION

I summarized data from annual nesting ground surveys for each subunit (*i*) in each study area (*j*) in each year (*k*). In all, I included 23 subunits at Nestor One, 8 at Broad River, and 6 at the Churchill study area in my analysis. The mean area per subunit at Nestor One was 1.49 km² (SE = 0.24), 2.45 km² (SE = 0.38) at Broad River, and 2.32 km² (SE = 0.26) at Churchill. Because the probability of discovering an active nest ($P = 0.77$) was different than the probability of discovering an already failed nest ($P = 0.39$),

and both probabilities were < 1 (Walter and Rusch 1997b), I multiplied the number of active nests discovered in each subunit at each study area in each year by 1.30 (a_{ijk}) and the number of failed nests discovered by 2.56 (f_{ijk}). The sum of a_{ijk} and f_{ijk} was the visibility bias-corrected estimate of the number of nests in each subunit in each study area in each year (n_{ijk}). I estimated nest density (nests per km²) in each subunit, study area, and year (\hat{D}_{ijk}) as:

$$\hat{D}_{ijk} = \frac{a_{ijk} + f_{ijk}}{A_{ij}} = \frac{n_{ijk}}{A_{ij}}$$

where, A_{ij} was the area (km²) of each subunit, i , in each study area, j . In using density as measure of abundance, I assumed that density was not area dependent. I checked this assumption by modeling the natural logarithm of nest count against the natural logarithm of area with a linear mixed-model (Pinheiro and Bates 2000). The 95% confidence interval (95% CI) of the regression coefficient for the natural logarithm of area overlapped 1 suggesting there was a consistent relationship between an area and count, and thus no relationship between area and density.

VARIABLES FOR MODELING DENSITY AND HYPOTHESES

I employed ArcMap 9.0 and a vegetation classification layer derived from Landsat TM imagery (Brook 2001) to obtain variables used to test hypotheses of factors influencing the density of nesting EPP Canada geese (Table 1). I considered the following variables, each within one of four general categories, in a competing-model framework (Burnham and Anderson 2002).

Predator Avoidance

In this region of Canada, terrestrial mammals, primarily arctic foxes (*Alopex lagopus*) and wolves (*Canis lupus*), are predators of goose nests and utilize beach ridges as travel corridors and den locations (Bahr 1989; Roth 1998, 2003). I calculated the proportion of total area of upland beach ridges and unvegetated ridges in each subunit (UPLAND). If nest density was strongly influenced by terrestrial predator distribution then subunits with high values of UPLAND should have low nest density. Additional predator avoidance in areas frequented by terrestrial predators, especially for Canada goose broods, includes access to water. I calculated the availability of water as the proportion of subunit area composed of water (WATER).

Avian predators (e.g., herring gulls [*Larus argentatus*], jaegers [*Stercorarius* spp.]) may also influence the distribution and density of nests. This region of coastal tundra has little protective-vegetation cover from avian predators. However, nesting among or near low-lying willow and birch shrubs can provide cover from avian predators for both eggs and broods immediately following hatch. I calculated the proportion of subunit area composed of shrub willow and birch (COVER). If avoidance of avian predators influenced nest density, high values of COVER should be associated with high nest density.

Food and Brood-Rearing Habitat

Sedge meadows, with abundant *Carex aquatilis*, are a food resource for nesting and brood-rearing Canada geese in this region (Didiuk and Rusch 1979, Nack and Andersen 2006). I calculated the proportion of area composed of sedge meadow for each subunit at each study area (SEDGE). If food availability or brood-rearing habitat was

important in influencing nest density, abundance of sedge meadow should be positively associated with nest density.

Historically, brood-rearing habitat for EPP Canada geese nesting in this region was coastal salt marsh (Didiuk and Rusch 1979). I calculated the proximity to salt marsh as the distance (m) from the centroid of each subunit to the nearest patch (1 pixel [30 x 30 m] from Brook [2001]) of salt marsh (DISTSALT). Because the proportion of subunit area composed of coastal salt marsh was very low across all subunits, I considered whether salt marsh vegetation occurred (1 = occurred, 0 = did not occur) in the subunit (SALT) an alternative measure of salt marsh availability. If proximity to traditional brood-rearing areas was important, then subunits close to coastal salt marshes or that contained salt marsh should have higher nest density.

Temporal Change and Habitat

Recent changes in brood-rearing habitat use by Canada geese were likely a function of declines in salt marsh vegetation abundance resulting from foraging by abundant populations of snow geese (Nack and Andersen 2006), Ross's geese, and perhaps Canada geese and cackling geese (*Branta hutchinsii*). The decline in salt marshes and shift in brood-rearing habitat use has occurred over the same time period during which data were collected for this study. However, the available vegetation classification (Brook 2001) was based on images of the region taken in July 1996 and thus represented a fixed-point in time. Alternative annual measures of salt marsh abundance do not exist. Nevertheless, if (1) alteration of salt marsh has occurred over time as the result of foraging by geese; (2) Canada goose broods have shifted habitat use toward more interior sedge meadows (Nack and Andersen 2006); and (3) the proximity to

brood-rearing habitat is important to habitat use by nesting EPP Canada geese; there may be an interaction between time, which I considered a continuous covariate in all models (standardized to 1976 = year 1 [YEAR]), and distance to salt marsh (DISTSALT) or presence of salt marsh (SALT). In addition, there may also be an interaction between time (YEAR) and abundance of sedge meadows (SEDGE), representing the change in use of brood-rearing habitat. For all interactions considered in my models, I included the individual terms in the interaction and the interaction term.

Spring Phenology

Between years, EPP nest density varies considerably as a function of spring nesting-ground conditions. Years with very high nest density typically occur when spring phenology is early, characterized by warm spring conditions, early snow melt, and early nest initiation (Walter 1999). These years are also associated with high nest success (Reiter 2006). The opposite was true in years with late spring phenology and late Canada goose nest initiation. Variation in nest-initiation dates occurs between study areas but not substantially within study areas (Walter 1999). Because I estimated hatch date directly, based on a fixed 28-day incubation period, and extrapolated nest-initiation dates, I calculated the median hatch date for each study area in each year (HATCH) as a surrogate for nest-initiation date and standardized hatch date to 1 May (i.e., 1 May = day 1).

Temporal and Spatial Correlation

Accounting for temporal and spatial autocorrelation is necessary to accurately estimate sample variance (Manly 2001). I evaluated temporal correlation in my time-

series data using autocorrelation functions (Box and Jenkins 1978) both prior to model fitting and again with model residuals.

Because subunit boundaries were arbitrarily delineated within each study area, there was likely spatial autocorrelation associated with the spatial configuration of subunits. I assessed spatial autocorrelation in my data using Moran's *I* (Moran 1950). Because many of my covariates likely varied spatially, their inclusion in a model(s) accounted for some spatial autocorrelation in the data. However, I examined the residuals of the best-supported model(s) with Moran's *I* to test for unexplained spatial autocorrelation.

DATA ANALYSES

Because my data included repeated measurements of the same subunits, which likely resulted in correlation among observations, I employed linear mixed-model regression (Pinheiro and Bates 2000) to evaluate factors influencing the density of Canada goose nests in each subunit at each study area in each year. Because the distribution of the density of goose nests was skewed, I used the natural logarithm transformed nest density (LNDENSITY) in my analyses. The mixed-effects model took the general form:

$$LNDENSITY_{ijk} = \beta_i + \sum \beta_n + SUBUNIT_i + \varepsilon_{ijk}$$

Where, $LNDENSITY_{ijk}$ was the natural-log density of Canada goose nests in subunit, i , at study area, j , in year, k ; β_i was the intercept term for each subunit, i ; $\sum \beta_n$ was the set of n fixed-effect parameters; $SUBUNIT_i$ was the random effect of subunit, accounting for between-subunit variance, and ε_{ijk} was the residual variance

associated with each subunit, i , at each study area, j , in each year, k . Both $SUBUNIT_i$ and ε_{ijk} were the variance components of random variables from an assumed normal distribution with mean equal to zero. I included the random effect $SUBUNIT_i$ in all models I evaluated.

I had *a priori* information that there were different temporal trends in nest density among study areas, and that HATCH would strongly influence any model of Canada goose nest density in this region (Walter 1999). Furthermore, of primary interest in this analysis were habitat factors associated with Canada goose nest density. I therefore conducted my analysis in 2 stages. First, I considered a set of 5 *a priori* base models (Table 2) to account for long-term temporal trends and year-to-year variation in nest density as the result of variation in spring phenology. I ranked these 5 models using Akaike's Information Criterion (AIC) and considered the model with the lowest AIC to be the best-supported model (Burnham and Anderson 2002). I calculated Akaike weights (w_i), defined as the probability that the i^{th} model was the best of the i models evaluated given the data, to further compare among models in my model set. I used the best-supported model as the base model for all additional model analyses.

I considered a set of 20 additional *a priori* models, including an intercept-only and a global model (Table 2) in a competing model framework, to test hypotheses regarding factors influencing the density of Canada goose nests. To prevent colinearity and model instability, I did not include variables that were highly correlated ($|r| > 0.60$) based on Pearson's correlation coefficient in the same model. I again ranked models using AIC and considered models $< 2 \Delta AIC$ ($\Delta AIC = AIC$ of the i^{th} model - lowest AIC

in the model set) units of the best-supported model to be a competing model. I assessed the relative importance of variables by calculating the average w_i of the models in which they were included. I did not use the cumulative w_i because all variables were not included in an equal number of models. I further assessed the relative importance of all variables in the best-supported model and the precision of the model parameter estimates based on their estimated 95% CI. I considered a 95% CI of a parameter estimate that overlapped zero to indicate that the parameter was unimportant in the model.

Post hoc, I considered 3 additional models, all variations of the best-supported model (Table 2), to test whether my *a priori* assumption about the importance of YEAR, SITE, and HATCH in all models was reasonable: (1) HATCH was removed; (2) YEAR*SITE was removed; and (3) both HATCH and YEAR*SITE were removed. I considered large ΔAIC values (>10) between these models and the best-supported model to be evidence supporting the inclusion of the base-model variables. I further examined the goodness of fit of my best-supported model by estimating the percent of variance explained by fixed-effects in the model as $100 \times (1 - (\text{residual variance of top ranked model} / \text{residual variance of intercept only model}))$ (Verbeke and Molenberghs 2000). I considered this a measure of overall model fit, with 0 indicating poor fit and 100 indicating a perfect fit.

RESULTS

NEST DISCOVERY

I estimated Canada goose nest density in each subunit at each of 3 study areas in each year using data from 631 subunit searches among 37 units between 1976 and 2007. In each year at a given study area, not all subunits were searched for Canada goose nests.

At Nestor One, 14 subunits were searched in every year of the survey (1976 – 2007) and 9 additional subunits were searched at Nestor One from 1993 – 2007 (Fig. 3). Across all subunits in all years at Nestor One, Canada goose nest density averaged 8.99 (SE = 0.33) nests per km². At Broad River, 4 subunits were searched 1987 – 1989, 8 subunits 1994 – 1995, and 4 subunits 2005 – 2006 (Fig. 4). Nest density averaged 29.75 (SE = 4.67) nests per km² at Broad River. At Churchill, 6 subunits were searched in 1993, and 3 subunits in 1994 and 2005 (Fig. 5), with an average of 17.97 nests per km² (SE = 2.27).

MODEL SELECTION

My best-supported base model included an intercept, SITE, YEAR, YEAR*SITE, HATCH, and the random effect, SUBUNIT, and received 100% of the Akaike weight (w_i ; Table 3). I used this model for all subsequent analyses.

In my best-supported model evaluating specific hypotheses regarding nest density and habitat use, LNDENSITY was associated with DISTSAULT and DISTSAULT*YEAR, in addition to variables in the base model. One other model was <2 Δ AIC units from the best-supported model and included 2 additional variables, YEAR*SEDGE and SEDGE (Table 3). Combined, the top 2 models received >85% of the Akaike weight (w_i), however the best-supported model ($w_i = 0.62$) received 2.5 times more Akaike weight, given the data and the set of models evaluated, than the second best-supported model ($w_i = 0.25$).

The relative strength of influence, based on the average Akaike weight (\bar{w}_i) of each variable given all models in which it was included, identified overwhelming support for DISTSAULT*YEAR ($\bar{w}_i = 0.30$) and DISTSAULT ($\bar{w}_i = 0.14$). There was less Akaike weight associated with SEDGE*YEAR ($\bar{w}_i = 0.07$) and SEDGE ($\bar{w}_i = 0.04$), and

practically no Akaike weight associated with any other variables, outside of those included in the base model.

Based on the best-supported model, there was strong positive association of YEAR and DISTSALT*YEAR with LNDENSITY (Table 4). Conversely, HATCH and DISTSALT had a strong negative association with LNDENSITY. At Nestor One, there was a strong negative temporal trend ($\beta_{\text{NestorOne*YEAR}} = -0.12$) relative to Broad River. However, there was no trend in LNDENSITY over time at Churchill relative to Broad River (Table 4). The 95% CI for the between-subunit variance of the random effect, SUBUNIT_{*i*}, and for the within-subunit variance (ε_{ijk}) did not overlap zero, indicating the relatively large amount of residual variance.

Overall, fixed effects in my best-supported model accounted for 38.5% of the residual variance in LNDENSITY relative to the intercept-only model. All 3 of my *post-hoc* models were a substantially worse fit ($\Delta\text{AIC} > 10$) to the data given the set of models evaluated, suggesting my inclusion of the base model variables was appropriate. Furthermore, my intercept-only model was ranked last indicating that all the models I considered were improvements over a no-variable model.

TEMPORAL AND SPATIAL CORRELATION

The autocorrelation function for LNDENSITY revealed significant temporal autocorrelation and Moran's *I* identified significant spatial autocorrelation ($I = 0.01$, $z = 6.04$, $P < 0.01$). However, the residuals of the best-supported model were not correlated temporally or spatially ($I = -0.001$, $z = 0.55$, $P > 0.05$).

DISCUSSION

There have been dramatic alterations to vegetation communities across western Hudson Bay in subarctic Canada as the result of goose foraging (Jefferies et al. 2006). Furthermore, arctic and subarctic regions around Hudson Bay are predicted to experience changes in climate (Gagnon and Gough 2005) leading to longer-term changes to the coastal tundra ecosystem. These events will likely have both direct and indirect impacts on animals that inhabit these regions, although these impacts are not well documented or understood. Quantifying how species currently use the coastal tundra landscape will allow comparison with future conditions, and inform predictions of long-term impacts of snow goose population growth and climate change. Overall, my analysis identified the importance of proximity to traditional coastal salt marsh brood-rearing habitat to nesting habitat use by EPP Canada geese. As the distance to salt marshes increased the density of nesting Canada geese decreased. In contrast, Canada goose nest density was not associated with the amount of upland area used most frequently by terrestrial nest predators, the availability of cover from avian predators, or access to water.

I also documented a temporal trend in the relationship between nest density and the distance to historical brood-rearing salt marsh habitat where through time, as distance to salt marsh increased, nest density increased. Over this same period, intact salt marsh habitat has declined along western Hudson Bay (Jefferies et al. 2006) and EPP Canada goose broods have switched to using interior freshwater sedge meadows (Nack and Andersen 2006). My data suggest the distribution of nesting EPP Canada geese may have changed as a result of changes in brood-rearing habitat use. Similar shifts in nest distribution of snow geese accompanied the decline of salt marsh at nearby La Pérouse Bay (Cooke et al. 1995). Changes in the association of proximity to salt marsh habitat

with Canada goose nest density over time provided evidence that as brood-rearing habitat changes occur the distribution of nesting geese may also change.

In many precocial avian species, the incubation of eggs until hatch and the raising of broods to fledge occur in distinct areas. My results suggest that for Canada geese breeding in subarctic northern Manitoba, use of nesting habitat is closely related to proximity and availability of brood-rearing habitat. The evolution of habitat use by breeding birds is largely considered to be influenced by factors directly associated with the survival of the nest, the survival of young to fledging, or the survival of the nesting bird (Martin 1995). Canada goose nest distribution and density in this landscape are likely influenced by both the probability of nest survival and proximity to brood-rearing habitat that provides high rates of survival of young to fledge. Although Nack and Andersen (2006) documented a change in brood-rearing habitat use over 30 years near Cape Churchill, they did not assess the impacts of this change on brood survival. Understanding factors influencing both nest and brood survival may be needed to fully understand the spatial patterns of use of coastal tundra habitat by breeding EPP Canada geese over time at this spatial scale.

Overall, my analyses suggested that EPP Canada goose nest density along the western Hudson Bay coast has increased through time, although there were substantial differences in this trend among my study areas. The temporal trend observed in this analysis supports data from aerial surveys of the entire EPP breeding range that suggest the population has remained relatively stable or increased over the last 30 years (Raedeke et al. 2007). Therefore, declines in salt marsh habitat over this same period do not seem to have had an appreciable affect on EPP Canada geese at a range-wide population level.

This suggests that declines in nest density of Canada geese at Nestor One represent a shift in the spatial distribution of nesting EPP Canada geese and not a decline in their overall abundance. The substantial increase in density of nesting EPP Canada geese at Broad River, to levels greater than observed at Nestor One in the late 1970s (Walter 1999), likely offsets declines in nest density at other locations. Our understanding of EPP Canada goose nest density would benefit from ground surveys at multiple study areas to reduce bias in nesting data as the result of landscape-level variation in temporal trends of nest density. Furthermore, although several studies have quantified the extent of salt marsh alteration at locations along a nearly 2,000 km stretch of Hudson Bay coastline (Jano et al. 1998, Jefferies et al. 2006), long-term time-series of changes to salt marsh do not exist for the entire EPP Canada goose nesting range. Acquiring time-series data on salt marsh quality and level of alteration by goose foraging in areas with different densities of nesting Canada geese and snow geese would provide additional insights into the importance of proximity to salt marshes and the effect of goose grazing on breeding EPP geese.

I observed strong year-to-year variation in the nest density of EPP Canada geese related to year-to-year variation in the estimated median hatch date. This was consistent with observations of Walter (1999), who also reported low nest density in years with late spring snow melt and late nest initiation. Reiter (2006) documented a strong influence of spring phenology, reporting that in years of early spring phenology and relatively high nest density, EPP Canada geese experienced higher nest success.

The use of remotely sensed vegetation data and GIS has greatly increased the flexibility of habitat use analyses (Wiens 2002). However, often the spatial scale at

which habitat use is assessed is limited due to the resolution of GIS data (van Horne 2002). I evaluated habitat use by nesting Canada geese and sought to attribute underlying mechanisms to the observed patterns using GIS data with a resolution of 30 x 30 m. This level of resolution seemed appropriate for assessing habitat relations, but may not be suitable for assessing factors that affect nest predation. In this region, predation is a primary factor influencing Canada goose nest survival (Walter 1999, Reiter 2006). However, vegetation classes associated with predation pressure (e.g., uplands that serve as travel corridors for primary nest predators) were not included in my best-supported model, and received very little Akaike weight. Although, broad spatial-scale habitat use may influence the nature of interactions between breeding geese and nest predators, it may be finer spatial scale (e.g., <30 x 30m resolution) nest attributes (e.g., height of vegetation, nest type) that influence nest survival. Because nesting Canada geese will move broods several km to brood-rearing habitat (Nack and Andersen 2006), the coarser resolution habitat data I used was probably more appropriate for evaluating access to brood-rearing habitat than finer-scale habitat characteristics that influence nest depredation.

Jefferies et al. (2006) suggested the “catastrophic” effects of snow goose grazing on coastal salt marshes of western Hudson Bay may take 100s of years to recover. Recent climate models predicting changing sea level dynamics in Hudson Bay suggest climate change will have implications for vegetation communities (e.g., salt marsh) and successional dynamics in coastal areas (Gough 1998). Furthermore, warming temperatures and loss of permafrost will also likely result in changes in vegetation communities along Hudson Bay (Gough and Wolfe 2001, Gagnon and Gough 2005) over

long time periods. Although the implications of goose-mediated or climate-induced changes to these salt marsh habitats for EPP Canada geese are not yet fully understood, my data suggest that long-term and widespread changes in the distribution and abundance of vegetation communities used by Canada geese may result in changes in the distribution of nesting geese. My analyses suggested proximity to traditional brood-rearing habitat influenced the distribution of EPP Canada goose nests along (within approximately 8 km) the Hudson Bay coast; however, the importance of these areas may be declining over time. Continued goose-mediated or climate-induced loss of salt marsh habitat will further change the spatial distribution of nesting Canada geese in this region in the future. However, it is not yet clear how changes in the spatial distribution of nesting geese may influence EPP Canada goose population dynamics. As habitat quality in coastal areas decreases as salt marsh habitats decline, other portions of the EPP Canada goose breeding range may experience increases in breeding density. If higher breeding densities develop in poorer quality habitats as a result of alterations of historically used habitats, there may be implications for nest and brood survival, and subsequently productivity and recruitment of EPP Canada geese.

TABLE 1. Variables included in linear mixed-models used to evaluate factors influencing the density (nests per km²) of Eastern Prairie Population (EPP) Canada goose (*Branta canadensis interior*) nests on the Hudson Bay Lowlands in northern Manitoba, Canada.

VARIABLE	DEFINITION
Fixed Effects	
SEDGE	Proportion of total subunit area composed of sedge meadow
UPLAND	Proportion of total subunit area composed of upland-beach ridge
COVER	Proportion of total subunit area composed of willow-birch vegetation
WATER	Proportion of total subunit area composed of water
DISTSALT	Distance (m) from subunit centroid to the nearest patch (30 x 30 m pixel) of salt marsh
SALT	Categorical variable indicating the presence of salt marsh in subunit
HATCH	Median hatch date for nests at each study area; standardized to 1 May = 1.
SITE	Categorical variable representing each study site; Nestor One, Broad River, and Churchill
YEAR	Year of observation; standardized to 1976 = 1
Random Effects	
SUBUNIT	Between-subunit variance
ε_{ijk}	Within-subunit variance
Response	
LN DENSITY	Natural log-transformed nest density (nests per km ²)

TABLE 2. Models considered in a 3-part linear mixed-model analysis to evaluate factors associated with the density of Eastern Prairie Population (EPP) Canada goose (*Branta canadensis interior*) nests on the Hudson Bay Lowlands in northern Manitoba, Canada. Part I compared 5 *a priori* models of temporal variation in nest density. Part II compared 20 *a priori* models of hypotheses related to habitat factors influencing nest density. Part III examined the importance of the temporal variation in the best-supported model. All model comparisons were based on Akaike's Information Criterion (AIC).

I. BASE MODEL	MODEL
Temporal Trend and Variation	
YEAR	1
SITE	2
YEAR*SITE	3
Annual Variation and Spring Phenology	
HATCH	4
YEAR*SITE + HATCH	5
II. HYPOTHESES^a	
Predator Avoidance	
<i>Terrestrial</i>	
UPLAND	6
WATER	7
<i>Avian</i>	
COVER	8
<i>Combined</i>	
UPLAND + WATER + COVER	9
Brood Habitat	
DISTSALT	10
SALT	11
SEDGE	12
DISTSALT + SEDGE	13
SALT + SEDGE	14
Combined	
DISTSALT + WATER + SEDGE + COVER	15
DISTSALT + WATER + COVER + UPLAND	16
SALT + WATER + SEDGE + COVER	17
SALT + WATER + COVER + UPLAND	18
Brood Habitat Temporal Interactions^b	
YEAR*DISTSALT	19
YEAR*SEDGE	20
YEAR*SALT	21
YEAR*DISTSALT + YEAR*SEDGE	22
YEAR*SALT + YEAR*SEDGE	23
Global	
YEAR*SITE + HATCH + YEAR*DISTSALT + YEAR*SEDGE + UPLAND + COVER + WATER + SALT	24

TABLE 2. continued	
INTERCEPT only	25
III. <i>Post-Hoc</i>	
Best-supported model – HATCH	26
Best-supported model - TIME*SITE	27
Best-supported model - HATCH - TIME*SITE	28

^aAll models under Part II. Hypotheses included the best-supported base model terms in addition to those listed.

^bAll models with interaction terms include the individual variables and the interaction term.

TABLE 3. Summary of model selection results for the base model, hypotheses, and *post-hoc* analysis of factors associated with the density of Eastern Prairie Population (EPP) Canada goose (*Branta canadensis interior*) nests on the Hudson Bay Lowlands in northern Manitoba, Canada.

MODEL	SPECIFICATIONS	AIC	Δ AIC	w_i
BASE MODEL^a				
5	SITE*YEAR + HATCH	1255.56	0.00	1.00
3	SITE*YEAR	1316.03	60.48	0.00
1	YEAR	1380.07	124.51	0.00
4	HATCH	1469.33	213.78	0.00
2	SITE	1497.11	241.55	0.00
HYPOTHESES^b				
19	DISTSALT*YEAR	1241.03	0.00	0.62
22	DISTSALT*YEAR + SEDGE*YEAR	1242.83	1.80	0.25
10	DISTSALT	1246.43	5.40	0.04
24	DISTSALT * YEAR + SEDGE * YEAR + SALT*YEAR+ COVER + UPLAND + WATER	1246.67	5.64	0.04
13	DISTSALT + SEDGE	1248.42	7.39	0.02
16	DISTSALT + WATER + COVER + UPLAND	1248.97	7.94	0.01
15	DISTSALT + WATER + SEDGE + COVER	1249.67	8.64	0.01
14	SALT + SEDGE	1251.06	10.03	0.00
8	COVER	1251.82	10.79	0.00
17	SALT + WATER + SEDGE + COVER	1253.82	12.79	0.00
18	SALT + WATER + UPLAND + COVER	1253.90	12.87	0.00
11	SALTFACT	1253.94	12.91	0.00

TABLE 3. continued

12	SEDGE	1254.27	13.24	0.00
9	UPLAND + COVER + WATER	1254.89	13.86	0.00
23	SALT * YEAR + SEDGE * YEAR	1254.97	13.94	0.00
21	SALFACT * YEAR	1255.07	14.04	0.00
20	SEDGE * YEAR	1256.24	15.21	0.00
7	WATER	1257.15	16.12	0.00
6	UPLAND	1257.46	16.43	0.00
25	INTERCEPT	1529.37	288.34	0.00
<i>POST-HOC^c</i>				
19	SITE*YEAR + HATCH + DISTSALT*YEAR	1241.03	0.00	1.00
26	SITE*YEAR + DISTSALT*YEAR	1301.55	60.52	0.00
27	HATCH + DISTSALT*YEAR	1310.07	69.04	0.00
28	DISTSALT*YEAR	1373.74	132.71	0.00

^athe best-supported Base Model was used in all models addressing specific hypotheses

^ball models included the best-supported Base Model; SITE*YEAR + HATCH

^cthree *post-hoc* models compared to the best-supported Hypotheses model

TABLE 4. Summary of parameter estimates from best-supported model examining factors associated with the density of Eastern Prairie Population (EPP) Canada goose (*Branta canadensis interior*) nests on the Hudson Bay Lowlands in northern Manitoba, Canada.

VARIABLE	B	SE	95% CI
Intercept	3.64	0.43	2.81, 4.47
YEAR	0.06	0.02	0.02, 0.09
SITE – Nestor One	1.30	0.38	0.52, 2.06
SITE - Churchill	0.05	0.88	-1.72, 1.82
Nestor One*YEAR	-0.12	0.02	-0.15, -0.08
Churchill*YEAR	-0.03	0.04	-0.12, 0.05
HATCH	-0.03	0.003	-0.03, -0.02
DISTSALT	-0.0003	0.00007	-0.0005, -0.0002
DISTSALT*YEAR	0.00001	0.000003	0.000002, 0.00001
SUBUNIT	0.18		0.12, 0.28
ϵ_{ijk}	0.62		0.59, 0.66

FIGURE 1. The location of three study areas (Broad River, Churchill, and Nestor One) along western Hudson Bay in northern Manitoba, Canada, used to evaluate factors influencing the density of nesting Eastern Prairie Population (EPP) Canada geese (*Branta canadensis interior*). Hatched areas indicate location of the higher resolution maps (Figs. 3 – 5).

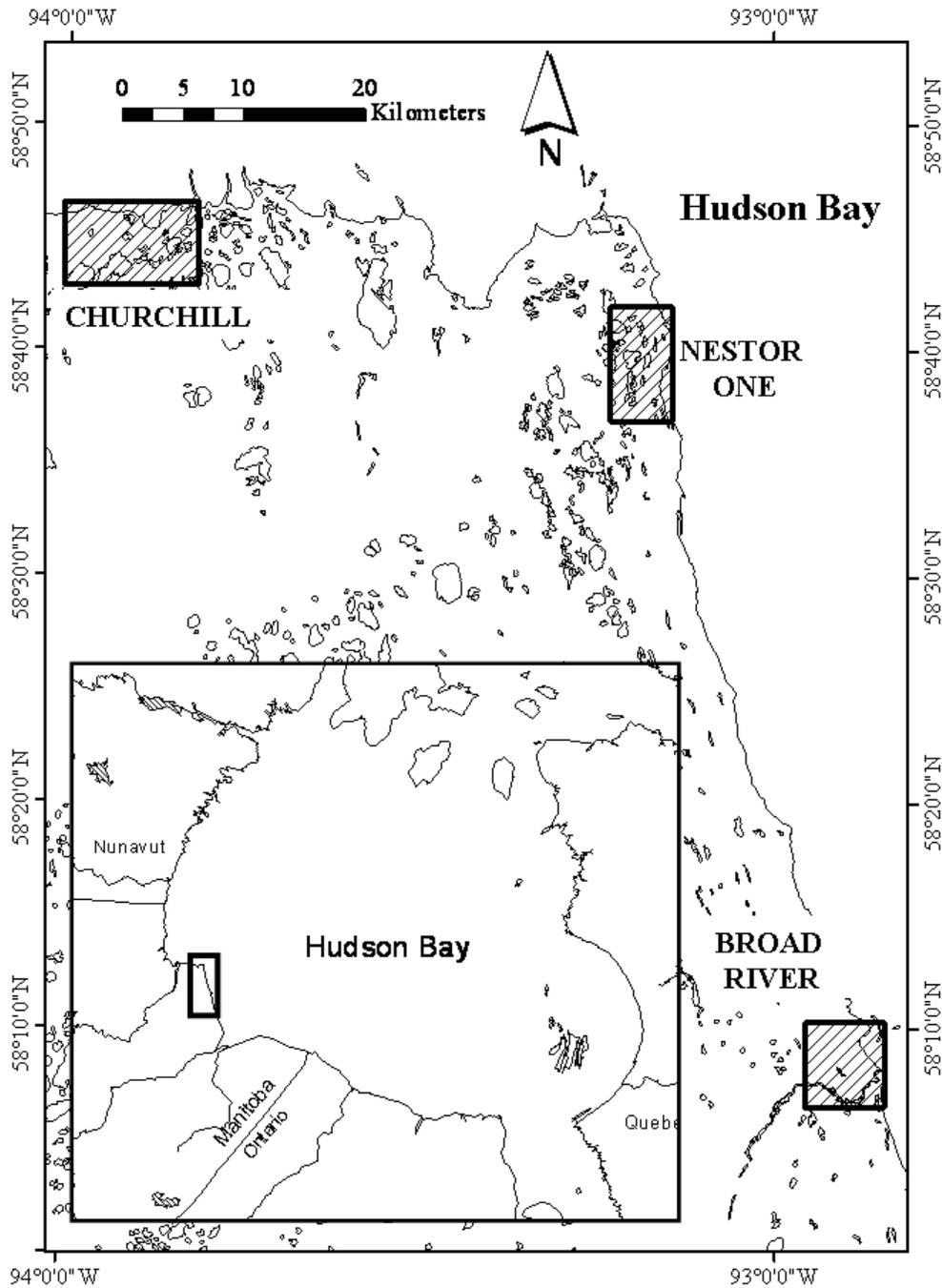


FIGURE 2. Proportion of total area of each vegetation classification (from Brook 2001) for each study area (Broad River, Churchill, and Nestor One) and generally along the Hudson Bay Coast (Coastal Tundra; <8 km from the coast) in northern Manitoba, Canada.

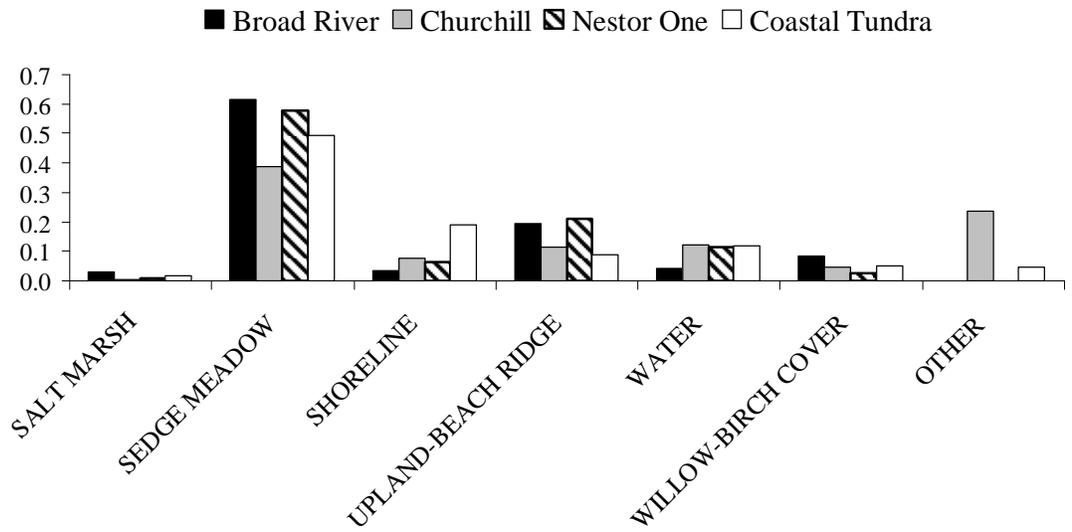


FIGURE 3. Configuration of Eastern Prairie Population (EPP) Canada goose (*Branta canadensis interior*) nest searching subunits at the Nestor One study area in northern Manitoba, Canada. I estimated annual EPP nest density (nests per km²) in 14 subunits searched annually 1976 – 2007, and in 9 additional subunits 1993 – 2007. Lakes and large beach ridges indicated on the map were not searched for nests.

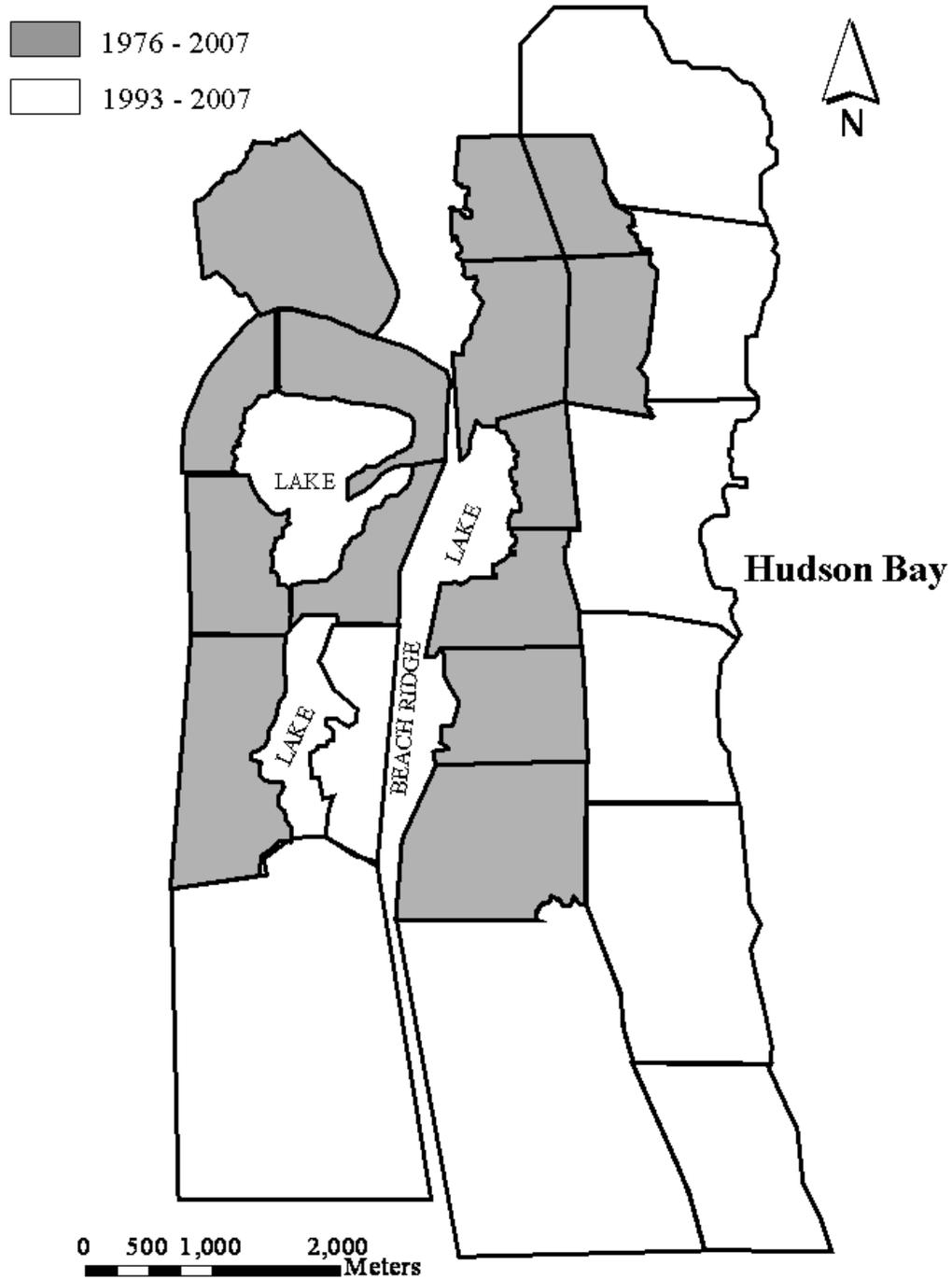


FIGURE 4. Configuration of Eastern Prairie Population (EPP) Canada goose (*Branta canadensis interior*) nest searching subunits at the Broad River study area in northern Manitoba, Canada. I estimated annual EPP nest density (nests per km²) for 1987 – 1989, 1994 – 1995, and 2005 – 2006.

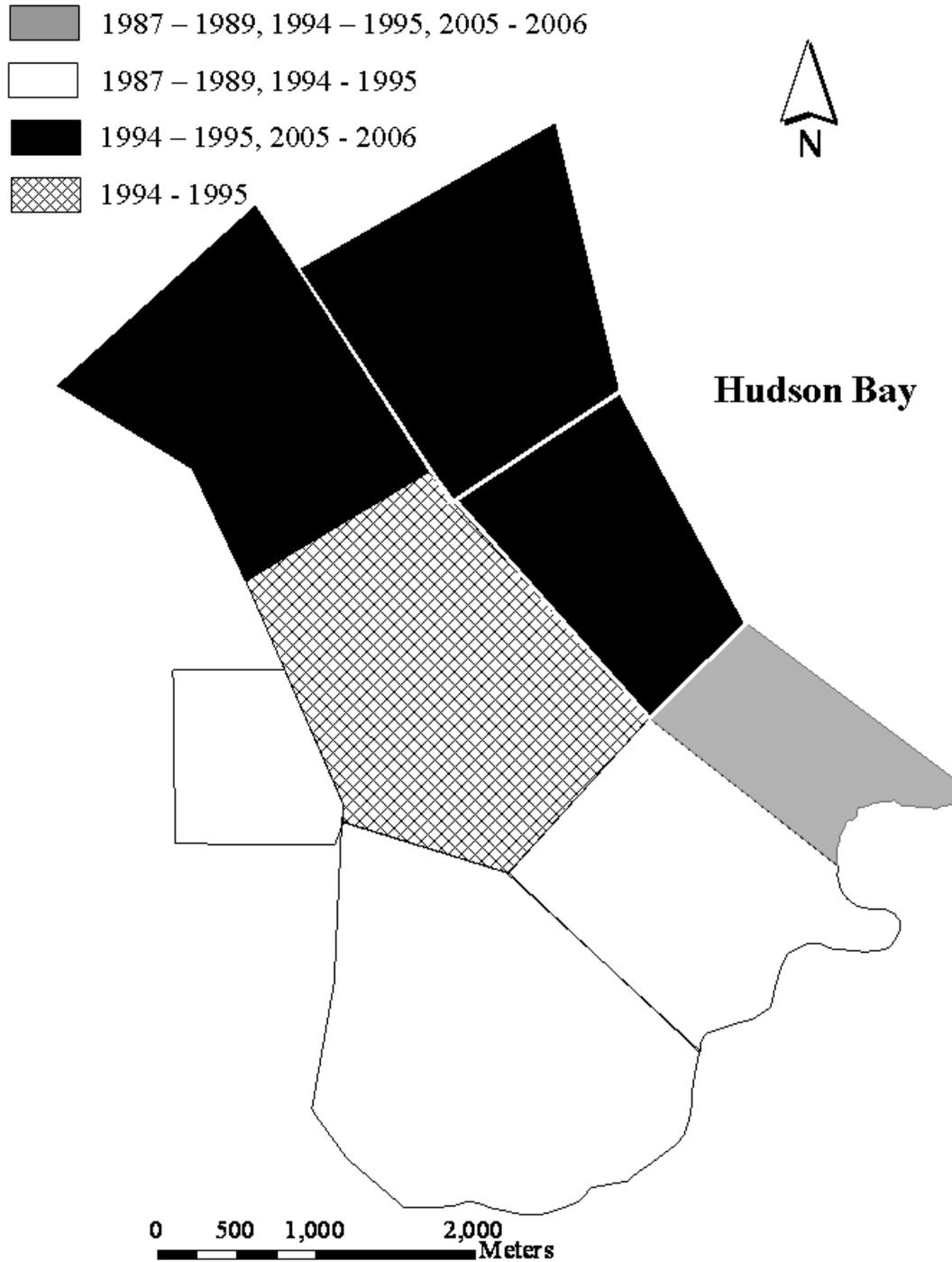
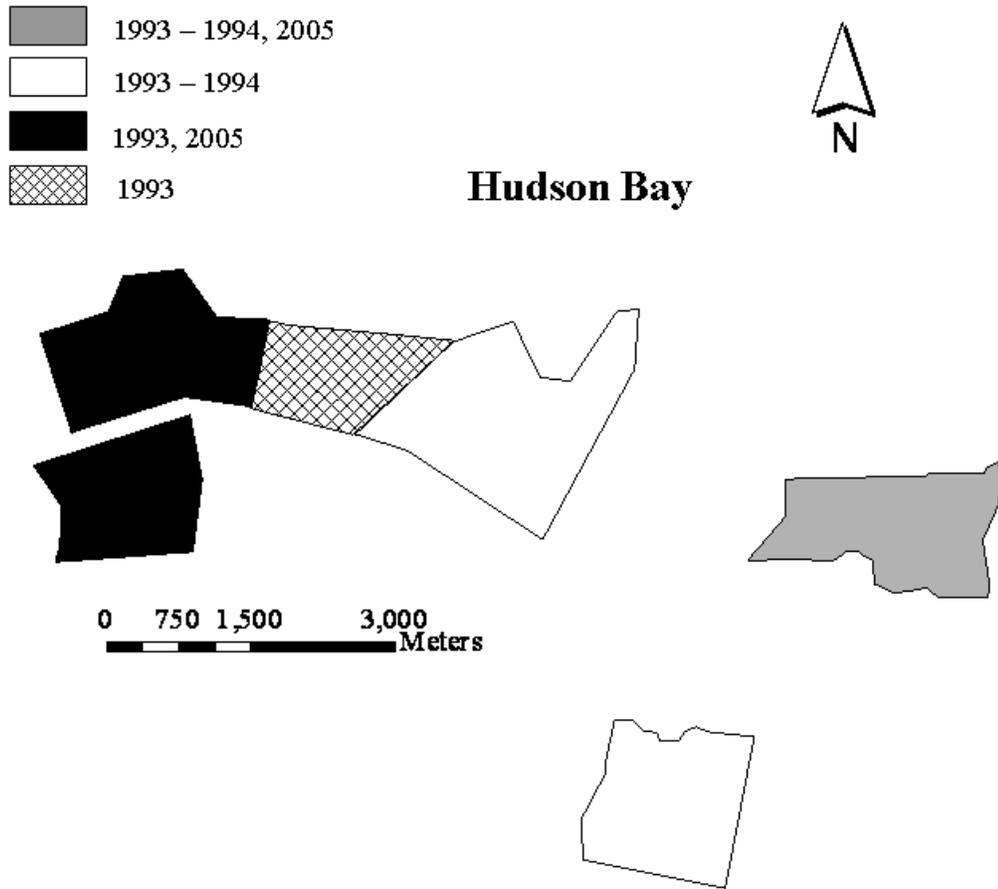


FIGURE 5. Configuration of Eastern Prairie Population (EPP) Canada goose (*Branta canadensis interior*) nest searching subunits at the Churchill study area in northern Manitoba, Canada. I estimated annual EPP nest density (nests per km²) for 1993 – 1994, and 2005.



CHAPTER 4
THE INFLUENCE OF SPECIES INTERACTIONS AND HABITAT ON THE
RANGE-WIDE DISTRIBUTION OF BREEDING EASTERN PRAIRIE
POPULATION CANADA GEESE IN NORTHERN MANITOBA

INTRODUCTION

Inter- and intra-specific interactions are potentially important factors influencing the distribution of populations (Tilman and Kareiva 1997). The spatial scale at which species interactions occur is often at the resolution of individuals (i.e., grain) and within smaller subsets of the entire population (i.e., extent). These local spatial interactions can often be observed over a relatively short temporal scale; thus, studies evaluating the potential impacts of changes in species distribution and composition frequently examine local (e.g., high resolution, small spatial extent) spatial scales and limited temporal scales (Levin 1992, Kneitel and Chase 2004, Sinclair and Byrom 2006). However, the impact of local-scale interactions may be realized at broader spatial scales as changes to the spatial distribution of a particular species or population that likely manifest themselves over a much longer temporal scale. Although frequently hypotheses have been made regarding the broad-scale implications of local-scale interactions, often data do not exist to corroborate spatially and temporally scaled-up predictions (Wootton 2001). Currently in northern Manitoba, Canada, data recorded at a fine spatial resolution ($\sim 1\text{-km}^2$) across a broad spatial ($\sim 101,500\text{ km}^2$) and temporal (22 years) extent exist to assess the spatial and temporal patterns of 2 goose species.

Eastern Prairie Population (EPP) Canada geese (*Branta canadensis interior*) nest throughout $\sim 101,500\text{ km}^2$ of coastal tundra, lowlands, and boreal forest along western Hudson Bay in northern Manitoba, Canada (Malecki et al. 1980, 1981), although the highest nest densities have historically been found close to Hudson Bay (Humburg et al. 2000). Localized ground surveys (1976 – 2008) near Cape Churchill, Manitoba documented a decline in nest density (Walter 1999, D. Andersen, Minnesota Cooperative

Fish and Wildlife Research Unit, unpublished data), however a second area farther south (~60 km) has experienced increased nest density since 1987 (see Chapter 3, this volume). In addition, the EPP of Canada geese has remained stationary or increased across its range since 1976 (Raedeke et al. 2008). This suggests the distribution of nesting EPP Canada geese may be changing at a spatial scale larger than the current ground monitoring area (~48-km²).

Concurrently, nesting lesser snow geese (*Chen caerulescens caerulescens*) have expanded their distribution considerably along western Hudson Bay (Ankney 1996, Abraham and Jefferies 1997, Batt 1997). Intensive foraging by large populations of migrating and breeding snow geese can dramatically alter sub-arctic vegetation (Kerbes et al. 1990, Srivastava and Jefferies 1996, Jano et al. 1998, Jefferies and Rockwell 2002); however, less is known about the direct or indirect effects of this growing breeding population on other species, particularly sympatrically nesting Canada geese (however see, Nack and Andersen 2004, 2006; Sammler et al. 2008; Chapters 1, 2, and 3, this volume).

Range-wide breeding population aerial surveys have been conducted annually for EPP Canada geese beginning in 1972 (Malecki et al. 1981, Humburg et al. 2000). Nesting snow geese have been recorded on these aerial transects in northern Manitoba since 1987. With increasing numbers of lesser snow geese across the EPP Canada goose breeding range, these data provide landscape-level information regarding their inter-specific relationship. Employing the aerial survey data, I (1) modeled the effects of inter- (snow goose) and intra-specific nest density, habitat type, spring phenology, and time on EPP Canada goose nesting distributions throughout the survey region from 1992 – 2008;

(2) developed hypotheses derived from interactions observed at a local-scale (i.e., nest or study area; see Chapters 1, 2, and 3, this volume) to evaluate their importance when considering a range-wide spatial extent; and (3) used the best-supported model(s) based on cross-validation to predict overall EPP reproductive effort across the entire breeding range in each year, and generate predictive maps using a geographic information system (GIS).

STUDY AREA

The EPP Canada goose breeding range along the western shores of Hudson Bay (56 – 60°N, 92 – 97°W; Fig. 1) is defined by the transition from the boreal forest in the south to arctic tundra in the north (Malecki et al. 1980). Two primary physiographic regions define the EPP range: the Precambrian Canadian shield, consisting of hills, glacial eskers, glacial moraines, and drumlins; and the Hudson Bay Lowlands, characterized by low relief and poor drainage (Ritchie 1962, Malecki et al. 1981). Lakes, rivers, and streams compose the majority of water in the Canadian Shield areas, whereas shallow permanent, semi-permanent, and ephemeral ponds are common in the Hudson Bay Lowlands. Primary vegetation zones within these 2 regions are tundra, forest-tundra, lowlands, and open- and closed-coniferous forest (Ritchie 1962, Malecki et al. 1981). Grasses, sedges (*Carex* spp.), willow (*Salix* spp.), birch (*Betula* spp.), and black and white spruce (*Picea mariana*, *P. glauca*), compose the major vegetation types, and a high diversity of lichens and mosses are common across all vegetation zones (Brook 2001). Over the previous 30 years, as snow geese have expanded their nesting range along the coastal tundra of western Hudson Bay (Abraham and Jefferies 1997), coastal salt marshes, composed of primarily *Carex* spp., *Puccinellia* spp., *Salicornia borealis*, and

Salix spp., have been altered substantially by intense grazing and grubbing (Jefferies et al. 2006). These salt marshes were historically the primary brood-rearing habitat for EPP Canada geese, although recent data suggest this may be changing in the Cape Churchill region (Nack and Andersen 2004, 2006).

METHODS

AERIAL SURVEYS

Operational aerial surveys to estimate population size and reproductive effort of EPP Canada geese have been conducted annually on the EPP breeding grounds since 1976; with the exception of 1980. However, nesting snow geese were only recorded beginning in 1987. Aerial surveys consisted of 28 transects (Fig. 1) averaging 81.43 km (SD = 31.21, Range: 22.6, 139.7), allocated based on stratified-random sampling across 6 strata defined by vegetation zones and variable densities of geese (see Malecki et al. 1981 for details of survey development). The 6 habitat strata (see Fig. 2A – C) included: (1) tundra (strata 2 [7,946 km²], 4 [4,332 km²], and 5 [8,023 km²]); (2) lowlands (strata 3 [14,210 km²] and 6 [18,236 km²]); and (3) open - and closed-coniferous forest and forest tundra (stratum 1 [48,641 km²]).

Transects were flown 40 – 60 m above ground level (Malecki et al. 1981, Humburg et al. 2000) using a fixed-wing aircraft, and geese observed within 200 m were recorded on 1-minute observation intervals by one observer on each side of the aircraft. Canada geese were identified as singles, singles with a nest, pairs, pairs with a nest, and in groups. Observers also recorded singles that flushed and were later joined by another goose, and singles that were flushed from a nest and later joined by another goose as distinct categories. I followed Humburg et al. (2000) and considered all singles that

flushed and were later joined by another goose to indicate reproductive pairs.

Subsequently, I estimated the number of nesting EPP goose pairs (i.e., Canada goose nests) for each observation interval, along each transect in each year as the sum of singles, pairs with nest, and flushed singles that were joined by a second goose. I employed this count as the response variable for all model analyses.

Malecki et al. (1981) estimated that ~70% of Canada geese were detected during these aerial surveys and suggested the observed values of singles and pairs should be multiplied by 1.42 to account for geese that were unobserved. Because this correction is assumed to be constant across all strata, transects, and years, I did not apply it to the raw counts of Canada goose nests but employed it to estimate total nests in each year by multiplying the estimated number of nests from the best-supported model by 1.42 (see Model Development and Data Analysis below).

I used the total flight time for each transect in each year and transect length to calculate the average 1-minute observation interval (average distance [km] flown per 1-minute of flight time). I used information about flight direction, Universal Transverse Mercator (UTM) coordinates of transect endpoints, and ArcMap 9.1 (© 1999 – 2004 ESRI, Inc., Redlands, CA) to assign UTM coordinates to the midpoint of each observation interval on each transect in each year. I considered the mid-point of each observation interval to be the location where geese were counted.

MODEL COVARIATES

I considered covariates under 7 general categories when developing models of EPP Canada goose nest counts (Table 1).

Intra-specific Interactions

Moser and Rusch (1989) estimated that 15% of 3-year old, 40% of 4-year old, and 100% of 5-year of EPP Canada geese reproduce. Under the assumption that female EPP Canada geese exhibit natal philopatry (Allen 1996), I hypothesized *a priori* that the count of Canada goose nests in year, $t - 5$ ($CAGO_{t-5}$), would be positively correlated with the count of Canada goose nests in year, t . My prediction suggested observation intervals with high nest counts in year, $t - 5$, should have high or higher nest counts in year, t . Because flight times varied among years and subsequently the exact spatial location of 1-minute observation intervals varied among years, I estimated the number of Canada goose nests in year, $t - 5$, for each 1-minute observation interval in the current year, t , using an inverse-distance-weighted mean of the observed data in year, $t - 5$. I estimated the count of Canada goose nests in year, $t - 5$, for all 1-minute observation intervals on all transects and in all years (1992 – 2008) using data from 1987 – 2003. I used the ArcMap 9.1 and the Geostatistical Analyst extension to complete these calculations.

It was unclear from the literature whether Canada goose nest counts in year, $t - 5$, would influence the expected nest counts over the area of the average 1-minute observation interval ($\sim 1 \text{ km}^2$) in year, t , in a density-independent or density-dependent manner. A modeled linear relationship would test the hypothesis that changes in nesting Canada geese are density independent over the densities of Canada goose nests observed and at this spatial scale in this region. However, spatial point-pattern analyses indicated intra-specific territoriality among nesting Canada geese (see Chapter 1, this volume). Density-dependent growth, likely driven by territoriality, could be modeled with a logistic form. I evaluated a linear and logistic form of the association of Canada goose nest counts from year, $t - 5$, with Canada goose nest counts in year, t , to assess (1)

whether Canada goose nest counts experienced time lags in growth, and (2) whether nest counts in year, t , were density dependent or independent Canada goose nest counts from year, $t - 5$. The logistic form was:

$$\beta_1 * CAGO_{t-5} \left(1 - \frac{CAGO_{t-5}}{\beta_2}\right)$$

Where β_1 and β_2 were parameters to be estimated, and $CAGO_{t-5}$ was the variable representing Canada goose counts from year, $t - 5$. To facilitate model convergence, I standardized estimated Canada goose nest counts from year, $t - 5$, by dividing by 100.

Inter-specific Interactions

The effect of the increasing number of nesting lesser snow geese on the distribution of nesting EPP Canada geese was of primary interest in this analysis. I calculated snow goose nest density on each observation interval, i , in year, t , as the count of snow goose nests in year, t , divided by the area surveyed during observation interval, i . I included a density (standardized to density of snow goose nests on observation interval /100) of snow goose nests in the current year, t , to account for possible inter-specific effects ($LSGO_t$). Under the assumption of natal philopatry (Allen 1996) and the estimate of 100% of 5-year old birds reproducing (Moser and Rusch 1989), if nesting snow geese influence the survival of Canada goose nests when nesting sympatrically, then Canada goose recruitment into the area would likely also be affected at a 5 year time-lag. To assess time-lag effects of snow goose nests on Canada goose nest density, I estimated snow goose nests in year, $t - 5$ ($LSGO_{t-5}$), for each observation interval in year, t , as an inverse-distance-weighted average of observation intervals from year, $t - 5$. Lastly, I

evaluated cumulative time-lag effects of snow geese by calculating the average estimated density of snow goose nests for the previous 5-years for each observation interval, i , in year, t , based on an inverse-distance-weighted average of observation intervals from the previous 5 years (AUTOLSGO).

Analyses of local interactions and spatial patterns among nesting Canada geese and snow geese in this region (Chapters 1 – 3, this volume) identified fairly weak associations. However, spatial point-pattern analyses suggested that increased density of snow goose nests may result in increased nest survival for Canada goose nests and subsequently aggregation with nesting snow geese. This was supported by observations of high densities of nesting Canada geese in areas with moderately dense aggregations of snow geese. However, long-term data (1976 – 2007) on Canada goose nest distribution and brood-rearing habitat use near the Hudson Bay coast (<8 km) suggested that nest density was increasing away from traditional coastal brood-rearing habitat (see Chapter 3, this volume), and concurrently, that Canada goose broods near Cape Churchill have switched from salt marsh to sedge meadows as primary brood-rearing habitat (Nack and Andersen 2006). Employing this finer scale information, I predicted that at the spatial extent considered in this analysis, Canada goose nest counts would vary non-linearly (e.g., quadratically) with snow goose nest counts from the current and previous years. My hypothesis predicted that where there were few snow goose nests, there were likely to be few nesting Canada geese as historically they both nest close to Hudson Bay near coastal salt marshes. However, as snow goose nest numbers increase, Canada goose nests increase either from use of similar habitat (e.g., coastal tundra) or as the result of buffering from shared nest-predators and thus increased nest survival when nesting

sympatrically with snow geese (however see Chapter 2, this volume). At very high snow goose nest densities, my hypothesis predicted reduced Canada goose nests either as the result of locally altered salt marshes and thus loss of brood-rearing habitat, and a subsequent spatial shift in Canada goose nests, or declines in nest survival, and thus reduced recruitment to the area. I considered linear and quadratic forms of snow goose variables to test this hypothesis.

Habitat Strata

Nesting birds likely select habitat at multiple spatial scales (Johnson 1980). I evaluated 4 habitat-strata classifications (Table 1) representing different grains of spatial resolution. I compared among each measure of habitat association data based on the magnitude of the effect on the observed nest count and the ability to predict Canada goose nest counts in cross-validation. First, I included a 6-level factor representing each of the originally defined strata (Table 1; Fig. 2A). The original 6 strata were then aggregated into a 3-level factor based on general vegetation classifications that included: (1) tundra (20,300 km²); (2) lowlands (32,450 km²); and (3) closed- and open-coniferous forest and forest-tundra (48,640 km²; Fig. 2B). These were further aggregated into the 2-level factor with coastal (20,300 km²) and interior strata (81,100 km²; Fig. 2C). I also employed a land-cover layer derived from the Advanced Very High Resolution Radiometer (AVHRR) sensor operating on board United States National Oceanic and Atmospheric Administration (NOAA) satellites (<http://geogratia.cgdi.gc.ca.html>). Three vegetation classes, (1) tundra, (2) transitional forest, and (3) coniferous forest, were defined across the EPP range with these data (Fig. 2D), and were set as second 3-level

factor. I assigned each observation interval along each transect in each year to 1 stratum from each of the 4 habitat-strata classifications.

EPP Canada geese historically used the coastal salt marshes along Hudson Bay for brood-rearing and sedge meadows just inland from of the coast for nesting (Didiuk and Rusch 1979, Walter 1999). Furthermore, Humburg et al. (2000) suggested that, range-wide, EPP Canada goose nest density was highest near the Hudson Bay coastline. I hypothesized that coastal areas (e.g., tundra or coastal strata) would have a stronger positive effect on Canada goose nest counts than the interior strata (e.g., coniferous forest or interior strata). Also, because each of the 4 habitat-strata classifications represented a different grain of spatial resolution (e.g., 6-level strata was finer resolution than 2-level strata), models with different habitat-strata classification covariates represented competing hypotheses about the best spatial resolution for predicting the count of Canada goose nests across their breeding range.

Brood-Rearing Habitat

Previous data suggested that EPP Canada goose nest density declines as a function of increasing distance to coastal salt marsh brood-rearing habitat (Humburg et al. 2000; Chapter 3, this volume) and proximity to brood-rearing habitat has been important to the distribution of temperate-nesting Canada geese (Anderson and Combs 2004). Spatial data on coastal salt-marsh distributions did not exist from the entire EPP breeding range, however where data were available, the distribution of coastal salt marsh was highly correlated (Pearson's correlation coefficient, $r > 0.9$) with the location of the Hudson Bay coastline. I examined variation in Canada goose nest counts as a function of the distance to the Hudson Bay coast to evaluate the effect of proximity to traditional

brood-rearing habitat. For each observation interval, I assigned the distance (km; standardized by dividing by 100) from the mid-point of the observation interval to the nearest shore of Hudson Bay. Again following Humburg et al. (2000), I predicted that distance to Hudson Bay would be negatively associated with Canada goose nest abundance, and tested this hypothesis by examining the direction of influence (i.e., positive or negative) of the parameter estimate. A negative linear-parameter estimate would be concordant with a decline in nest density as the distance to the coast increased. It would also be consistent with analyses from a more limited spatial extent; <8 km from the Hudson Bay coast (see Chapter 3, this volume).

However, given the spatial extent of these data and previous research that identified aggregation of Canada goose nests near Hudson Bay (Humburg et al. 2000), I predicted declining nest counts as a function of the distance to the Hudson Bay shore might occur less rapidly as the distance to the coast became large. To test this hypothesis I also modeled the relationship between nest density and the distance to Hudson Bay as a half-normal function (Williams et al. 2002) taking the form:

$$\exp(-HUDSONBAY^2 / 2 * \beta_1^2)$$

Where, *HUDSONBAY* was the distance to Hudson Bay and β_1 was a parameter to be estimated.

Spring Phenology

Previous analyses of nesting EPP Canada geese along the Hudson Bay Coast documented a strong effect of spring phenology and the timing of snow melt on nest density (Reiter 2006; Chapter 3, this volume). In coastal tundra areas, years with late snow melt are associated with low nest density. I quantified variation of spring

phenology among years using the Julian day of the median hatch date of nesting EPP Canada geese near Cape Churchill, Manitoba in each year. I predicted that years with late median hatch dates would have lower nest counts.

Temporal Trend

I considered a continuous covariate of year in my analysis to quantify long-term temporal trends in nest counts. Based on historical estimates (Raedeke et al. 2008), I predicted that there likely would be no significant temporal trend.

Spatial-Temporal Interactions

Nack and Andersen (2006) identified a shift in brood-rearing habitat use by EPP Canada geese from coastal salt marshes to interior sedge meadows. In addition, changes in nesting habitat associations (see Chapter 3, this volume) have occurred in this region, with density of nesting Canada geese farther from the Hudson Bay coastline experiencing increases in recent years. Thus, the strength of the positive relationship between nesting Canada geese and coastal brood-rearing areas may be decreasing through time. I examined interactions between habitat strata from each of the 4 habitat-strata classifications and year to assess differences in temporal trends among strata. I also evaluated a continuous interaction between year and distance to the Hudson Bay coast to evaluate whether observations from aerial surveys were consistent with finer-scale nest density analysis (Chapter 3, this volume), which suggested areas farther from traditional coastal brood-rearing areas were associated with higher nest densities in more recent years.

MODEL DEVELOPMENT AND DATA ANALYSIS

I used mixed-effects Poisson regression (Littel et al. 1996) to model the observed count of Canada goose nests for each observation interval along each survey transect in each year. However, the direction of travel along an individual transect varied among years, and the time to fly each transect varied depending on plane speed, plane direction, wind speed, and wind direction. Thus, different distances were surveyed along each observation interval on each transect in different years, and on different transects within the same year; thus the observed count would partially be a function of the distance flown during the observation interval. I incorporated an offset term, equal to the natural logarithm of the area (km²) surveyed per observation interval, into my Poisson regression models to account for variable flight speeds (Littel et al. 1996).

Each observation interval on an individual transect likely was spatially correlated. Although model covariates accounted for some of the correlation along each transect in each year, there was likely to be correlated residual error associated with factors influencing the count of goose nests along an individual transect in each year (e.g., time of day of the survey, direction of flight, visibility). I considered each transect in each year to represent a random sample from the population of transects (transect*year), and modeled among-transect*year variation using a random effect. My mixed-effects Poisson regression model took the following general form:

$$\ln(C_{ijk}) = \beta_{jk} + offset_{ijk} + \sum \beta_{ijk} + tran_j * year_k + \varepsilon_{ijk}$$

Where C_{ijk} was the count of goose nests at the i^{th} observational interval, on the j^{th} transect, in the k^{th} year (C_{ijk} was assumed to be Poisson distributed with mean, λ); β_{jk} was a unique intercept term for each transect*year ($tran_j * year_k$); $offset_{ijk}$ was an offset

term equal to the natural log of the total area (km²) surveyed on observation intervals with $\beta_{offset_{ijk}} = 1$; $\sum \beta_{ijk}$ was the sum of fixed effect covariates measured for each observation interval on each transect in each year; $tran_j*year_k$ was the random effect of each transect, j , in each year, k ; and ε_{ijk} was the residual error. The random effect of transect*year was assumed to be normally distributed with mean equal to 0 and variance = $transect_j*year_k$.

The goals of my data analysis were two-fold: (1) to quantify factors influencing the range-wide distribution of Canada goose nests as part of testing hypotheses about the impacts of increasing snow goose nest aggregations, and scaling-up hypotheses from finer spatial-scale analyses; and (2) to develop models that could be used to accurately predict the spatial distribution and overall abundance of EPP Canada goose nests throughout their breeding range. Because of the duality of goals in my analysis, I used a cross-validation framework to develop and evaluate a competing model set (e.g., how well each model predicted compared to other models evaluated), while also evaluating the goodness of fit (e.g., are any of the models good at prediction).

I randomly split my data into 2 approximately equal parts; a model-training subset and a model-testing subset. Before analyzing these data, I selected 12 variables *a priori* representing hypotheses under 7 categories of factors influencing the distribution of nesting Canada geese (Table 1). I examined the training dataset using summary statistics, scatter plots, interaction plots, and simple Poisson regressions with Proc GENMOD and NLMIXED in SAS v.9.1 (The SAS Institute, Inc. ©2008) to quantify the influence of variables and interactions among variables selected *a priori*. I used Akaike's Information Criterion (AIC) to guide the evaluation of simple *a priori* models within each of the more

general covariate categories (Burnham and Anderson 2002). I removed covariates with an AIC value greater than or equal to the AIC value for an intercept-only model from further analysis, and developed a set of composite models to evaluate using cross-validation. Each composite model consisted of several covariates from the general categories, and incorporated hypotheses about the importance of these categories for prediction.

I estimated parameters for each composite model using Proc NLMIXED. I combined parameter estimates derived from the training dataset and covariate values from the testing dataset to predict Canada goose nest counts for each observation interval in the test dataset. I compared among models using, (1) the mean error of prediction of Canada goose nest counts on each observation interval as a measure of bias; and (2) mean squared error (MSE) of prediction of Canada goose nest counts as a measure of overall accuracy (i.e., $\text{bias}^2 + \text{variance}$). I considered a model with a 95% confidence interval (95% CI) for the mean error that overlapped 0 to be unbiased and the model with the lowest MSE the best-predictive model. I considered a model with just the 6 habitat strata and random effect of transect*year to be a model-based approach to the current prediction method of estimating Canada goose nest abundance from aerial surveys using a weighted nest-density average from each stratum. I also considered an intercept-only model with and without the random-effect term, to quantify the changes in prediction as a function of model covariates. I examined the direction of influence of parameter estimates (i.e., their sign) from the top model(s) and their 95% CI as a measure of the overall effect of each covariate.

Spatial and Temporal Correlation

These aerial survey data contained observation intervals that were close together in both space and time along transects, and thus there was likely spatial and temporal correlation among intervals. Although species interactions and habitat-association covariates, as well as the random-effect, transect*year, accounted for some lack of independence among observation intervals, residual spatial and temporal autocorrelation can result in underestimates of variance and thus erroneous inference. I evaluated spatial autocorrelation in goose nest counts prior to modeling fitting and in the residuals of each model fit using Moran's I (Moran 1950) calculated using the program Geoda 0.9.5.i5 (©1998 – 2004 Luc Anselin and the Regents of the University of Illinois). I employed autocorrelation functions to quantify temporal correlation and variability in Canada goose nest counts, and to evaluate temporal autocorrelation in the residuals following model fitting (Box and Jenkins 1978).

SPATIAL PREDICTIONS OF TOTAL NESTS

I employed the top model(s) based on cross-validation and MSE, GIS layers representing parameter estimates, and GIS layers representing variable values in ArcMap 9.1 to predict Canada goose nest distributions across the entire breeding range in each year. I resampled all GIS layers so that each pixel represented a 1-km² area; approximately the average area surveyed per observation interval. Layers were combined using the form of the top model(s) and map algebra commands in the Model Builder module in ArcMap 9.1. I further evaluated the top model(s) by comparing the estimated number of productive geese from the model(s) with traditional estimates of productive geese. I estimated the total abundance of productive Canada geese across the range for each year of the survey using the sum of predicted nest counts in each map multiplied by

a probability of detection correction of 1.42 (Malecki et al. 1981) and then multiplied by 2 to represent the goose pair at each nest. I estimated point-wise 95% confidence tubes for the predicted number of productive geese by estimating productive geese using all lower 95% confidence interval (95% CI) parameter estimates in the model and then using all upper 95% CI of parameter estimates (Einmahl and McKeague 1999). The traditional estimate of productive geese was derived from strata-specific nest densities (count of goose nests on transects within each strata divided by the total area surveyed in each strata), and densities were based on observation intervals of 2.59 km² (converted from 1 square mile). I calculated a weighted average of nest density using the density estimates from each strata, weighted by the area of each strata. I multiplied the weighted-average density by the total area of the EPP range and then by 2.84 (to account for probability of detection, 1.42, and 2 productive geese per nest) to estimate total number of productive geese range-wide. I generated 95% CI of the estimated number of productive geese based on the traditional method using strata-specific variances (Manly 2001).

Because my model-based estimates of productive geese appeared to capture the long-term trend but not the year-to-year variation observed in the traditional calculations of productive geese (see Results), I considered 3 *post-hoc* models. These 3 *post-hoc* models attempted to capture among-year variation by including the spring phenology effect into the top 3 composite models based on cross-validation and MSE, despite it not being included originally in composite models due to limited support (AIC of the spring phenology model = AIC for the intercept-only model; see Table 2) in analysis of the training dataset.

Lastly, I estimated the cumulative change in the number of Canada goose nests in each 1-km² block across the entire EPP range using the predicted nest count GIS layers for each year and map algebra commands in ArcMap 9.1. I estimated the annual change in each 1-km² block as the predicted number of nests in the block in year, t , minus the predicted number of nests in the same block in year, $t - 1$. I summed the annual changes across all years, 1992 – 2008, to estimate the cumulative change for each 1-km² block.

RESULTS

TRANSECT SUMMARY

Between 1987 and 2008, the earliest date to initiate aerial surveys was 21 May (2006) while the latest date to begin the surveys was 16 June (2004). On average it took 4 survey days (SD = 1.7 days) to complete a survey of all 28 transects in each year between 1987 and 2008. All transects were surveyed at least 1 time in each compass direction (east and west or north and south) between 1987 and 2008. Based on a 200 m strip on either side of the plane, representing the area over which each observer surveyed, a total of 1,123 km² was surveyed each year from 1987 – 2008; approximately 1% of the EPP Canada goose nesting range.

Between 1987 and 2008, 37,132 observation intervals were recorded by 6 different observers. I assumed no “observer effect” and combined the number of Canada geese recorded by each observer over the same observation interval on each transect in each year as the total count for each observation interval. This resulted in a total of 18,566 observation intervals used in my analysis. Due to variation in plane speed, wind direction, and wind speed, the distance surveyed over each full 1-minute interval (some observation intervals were <1-minute at the end of transects) varied from 1.71 km to 3.55

km and averaged 2.71 (SD = 0.4) km. On average each 1-minute observation interval counted the number of geese over 1-km².

NESTING CANADA GEESE

The raw total count of singles, pairs observed with nests, and flushed singles that were later joined by another goose (i.e., Canada goose nests) varied moderately among years between 1987 and 2008 (Fig. 3). The sum of these 3 categories exhibited significant variation among transects, suggesting spatial variability in nest counts within the EPP nesting range (Fig. 4).

NESTING SNOW GEESE

Overall, the total annual count of nesting lesser snow geese increased on transects from <100 in 1987 to >500 in 2008, but was highly variable between 1999 and 2005 (Fig. 3). Snow goose nests were more spatially aggregated than Canada goose nests with >98% of snow geese recorded between 1987 and 2008 occurring on only 10 (36%) of 28 transects. In comparison, total counts from 82% (23 of 28) of transects need to be combined to include 98% of the observed Canada goose nests over the same time period.

MODEL RESULTS

There were 7,590 observation intervals made on 251 transect*year combinations in my training subset of the data, and 6,661 observation intervals in the testing subset of the data in my analysis; comprising 53% and 47% of the full data set, respectively, for 1992 – 2008. The years 1987 – 1991 were employed to provide estimates for time-lag covariates of up to 5 years before the current year.

Analysis of the model training dataset suggested that the logistic form of Canada goose nest density in year, $t - 5$, was a better fit than the linear form based on AIC (Δ AIC

= 290); however, both forms were a substantial improvement over intercept-only models (Table 2). The linear effects of snow geese either in the current year, or as the result of a previous year's abundance, accounted for no variability in Canada goose nest counts, indicated by the equality of AIC values for these models compared with the AIC value of the intercept-only model (Table 2). However, models considering the quadratic effect of snow goose nest variables (i.e., $LSGO_t$, $LSGO_{t-5}$, and $AUTOLSGO$) on Canada goose counts were considerably better than intercept-only models based on AIC values, and the 95% CI of parameter estimates in these models did not overlap 0.

The influence of distance to Hudson Bay was negative, as suggested by the negative linear-parameter estimate; however, the half-normal form received a considerably lower AIC score (Table 2). The half-normal form of the distance to Hudson Bay received the lowest AIC value of all *a priori* models evaluated with the training dataset and the linear form of the distance to Hudson Bay received the second lowest AIC value. All habitat-strata classifications were an improvement over an intercept-only model (Table 2). However, the original classification of 6 strata received the most support relative to the other classifications based on AIC.

Both my measure of spring phenology (i.e., Julian median hatch date at Cape Churchill) and the continuous-time covariate of year received no support in initial analyses based on AIC, and the 95% CI of parameter estimates overlapped 0. I removed these covariates from consideration in composite models (Table 2). Although spatio-temporal interaction models received some support over an intercept-only model based on AIC, there was little or no improvement over models containing the habitat-strata

classification only (Table 2), which suggested the addition of the temporal trend interaction did little to improve model fit.

Based on the training dataset results, I developed 27 models to evaluate with cross-validation (Table 3). I considered variables and model forms from the same general category (Table 1) in separate models. Overall, 11 (41%) of the 27 models, including 3 models with the lowest MSE, yielded unbiased predictions, with the 95% CI of their mean prediction error including zero (Table 3). A model containing the logistic form of $CAGO_{t-5}$, the half-normal form of the distance to Hudson Bay, the 6-level habitat-strata classification, and the quadratic form of $LSGO_{t-5}$, in addition to an offset term, intercept, and the random effect, $\text{transect} \times \text{year}$, had the lowest MSE. However, models with different snow goose nests covariates (i.e., $LSGO_t$, $LSGO_{t-5}$, or $AUTOLSGO$) but the same quadratic form of this covariate had nearly identical MSE (Table 3). These 3 best-predicting models improved overall prediction accuracy (MSE) by 45% compared to an intercept-only model. Overall, the best-supported models reduced spatial and temporal autocorrelation substantially (Fig. 5).

I estimated parameters for the top 3 models using the entire dataset (training + testing). Overall, $CAGO_{t-5}$ had a positive effect on nest counts in year, t (Table 4); however, a high level of support for models with the logistic form of this covariate (Table 3) indicated a reduction in the positive association when $CAGO_{t-5}$ was large. My results suggested Canada goose nest counts in year, t , would be negatively associated with Canada goose densities in year, $t-5$, when there was $>15-20$ nests per km^2 . Inter-specific effects of nesting snow geese were also non-linear. Parameter estimates for $LSGO_{t-5}$ and $AUTOLSGO$ were consistent with a relationship in which Canada goose

nest counts were positively associated with snow goose nest density; however, very high snow goose nest densities resulted in lower Canada goose nest counts (Table 4).

Parameter estimates for $LSGO_t$ suggested an opposite relationship in which increasing snow goose nests in the current year initially resulted in lower Canada goose nest counts but as snow goose nest density became large, Canada goose nest counts also increased.

However, only the average density of snow goose nests for the previous 5 years ($AUTOLSGO$) had 95% CI of parameter estimates that did not overlap zero suggesting I was better able to estimate this effect.

The habitat-strata classification based on 6 strata was included in all 3 of the best-predicting models and overall, models with the 6 strata were the most unbiased (Table 3). Coastal tundra (strata 4 and 5) had the highest expected counts relative to the lowlands of stratum 6. Stratum 2 (tundra) and stratum 3 (lowlands) also had higher expected counts relative to stratum 6. However, the effect of stratum 1 (forest) was close to 0 suggesting only a small increase in the expected count in this stratum compared to stratum 6. The negative, linear effect of the distance to Hudson Bay suggested decreasing expected counts at longer distances from the coast; however, the improved fit of the half-normal form relative to the linear model suggested the decline in expected counts as a function of distance to Hudson Bay became less farther from the coast. The random effect of $transect*year$ was >0 and its 95% CI did not include zero, suggesting that there was remaining correlated error associated with the survey of an individual transect in a given year (Table 4).

SPATIAL PREDICTIONS OF TOTAL NESTS

Because the top 3 models had very similar MSE, I averaged the predicted values from each model for each 1-km² block using GIS, and then summed the average value to estimate the uncorrected number of Canada goose nests across the range. I corrected predicted Canada goose nest counts for visibility (x 1.42) and multiplied by 2 to represent a nesting pair. The estimated number of breeding EPP geese averaged 56,604 between 1992 and 2008 based on these models. This was lower than the average over the same period based on the traditional stratified random sample calculation (68,522 productive geese; Fig. 6). The model-based predictions suggested a stationary population of reproductive geese between 1992 and 2008; however, the traditional calculations indicated high annual variability in reproductive effort. I considered 3 *post-hoc* models that included all effects included in the top 3 models based on MSE, but added the phenology effect (i.e., median Julian hatch date of EPP Canada goose nests near Cape Churchill, Manitoba) to try to incorporate observed annual variation in estimated breeding population size. These 3 *post-hoc* models fit the data well based on cross-validation (MSE = 0.7180 – 0.7275), and the direction of influence and magnitude of the effect of covariates based on parameter estimates, except for the intercept term, did not change (Table 5) compared with the 3 best-supported models based on MSE in the original model set (Table 4). The variance of the intercept term became large in the 3 *post-hoc* models; however, the phenology effect, which received little support in model development (Table 2), had a strong negative effect on nest counts and the 95% CI of the parameter estimate did not overlap 0. However, despite the inclusion of a phenology effect, the estimated number of reproductive geese based on *post-hoc* models remained fairly stable and predicted only modest year-to-year variation (Fig. 6). Furthermore, 95%

confidence tubes estimated using the *post-hoc* models were large, reflecting the increased variance in the intercept term.

The predicted cumulative change in Canada goose nests (1992 – 2008) in 1-km² blocks throughout the breeding range based on the average of the top 3 models identified one large area of increase (1 – 4 nests per km²) in EPP Canada goose nests, occurring along the Hudson Bay coast from White Whale River (93 5' 00" W; 58 27' 00" N) south to the mouth of the Broad River (92 50' 00" W; 58 0' 00" N); and areas of decline in nests (1 – 3.5 nests per km²) along the east side of La Pérouse Bay and near Cape Churchill (Fig. 7). The remaining portions of the range varied almost equally between a cumulative increase of 1 nest per km² to a cumulative decline of 1 nest per km². The spatial location of these predicted cumulative changes were similar to data from ground surveys in these areas (see Chapter 3, this volume).

DISCUSSION

Processes influencing the distribution of species across a broad spatial extent (e.g., range-wide) are likely complex and may involve factors from several spatial resolutions (Johnson 1980). My analysis suggested the range-wide distribution of nesting EPP Canada geese in northern Manitoba was associated with multiple factors measured at different spatial resolutions including intra-specific density-dependent effects, snow goose nest density, proximity to traditional brood-rearing habitat, and habitat strata. My study confirmed long-term population monitoring summaries (Raedeke et al. 2008) that indicate the total range-wide breeding population of EPP Canada geese has remained stationary. However, my spatial prediction maps identified localized spatio-temporal variation in nest density along the Hudson Bay coast that was consistent with long-term

trends in EPP nest density within ~8 km of the Hudson Bay coast (Chapter 3, this volume), and with the observed long-term changes in the spatial distribution of brood-rearing Canada geese in this region (Nack and Andersen 2004). Both the changes in nest distributions and brood-rearing habitat use have occurred concurrently with increased abundance and expanded distributions of nesting lesser snow geese, and alteration of coastal salt marshes.

However, my analysis identified only a moderate effect of lesser snow goose nest density on the expected count of nesting Canada geese. Canada goose nest counts were associated non-linearly (i.e., quadratically) with snow goose nest density, and low Canada goose nest counts were typically associated with very low and very high snow goose nest densities. These data confirmed my *a priori* hypothesis that at the spatial extent considered by the aerial surveys, high Canada goose nests counts are likely associated with snow geese due to shared nesting habitat along the Hudson Bay coast, but ultimately Canada geese do not nest at high densities in the presence of very high densities of nesting snow geese. A previous study suggested that Canada geese experience reduced nest survival when nesting among snow geese (Gleason et al. 2004). However, nest survival analyses of sympatric nesting snow geese and Canada geese from 2 areas near Cape Churchill (Chapter 2, this volume) suggested that the spatial proximity and abundance of nesting snow geese did not significantly influence Canada goose nest survival. Alternatively to impacts of nest survival, high densities of nesting snow geese may contribute to alteration of local coastal-brood rearing habitat, resulting in changes to brood-rearing habitat use (Nack and Andersen 2004, 2006), and subsequently a shift in the spatial distribution of Canada goose nests (Chapter 3, this volume).

My study documented density-dependent time-lag associations of nesting Canada geese with Canada goose nest density in subsequent years. The strong positive association between Canada geese in year, $t - 5$, and the current density of Canada geese in the same location provided support for natal philopatry; which suggests female geese born in a specific location return to that location to breed. It was unlikely that the time-lag association with nest density was driven by non-related geese (i.e., geese that do not share some common ancestors) moving into the area to nest, as typically adult nesting Canada geese show high site fidelity (Allen 1996). Strong support for the logistic form of the relationship between nest counts and the Canada goose time-lag covariate suggested that at the spatial resolution considered in this study ($\sim 1 \text{ km}^2$; the average area surveyed per observation interval), the time-lag effect of nesting Canada geese was density dependent. It was unclear what specific mechanism(s) drove the apparent density dependence. Nesting Canada geese often exhibit strong territoriality (Mowbray et al. 2002; Chapter 1, this volume), which might limit nest density, and failed Canada goose nests in an area of high nest density near Cape Churchill were found to be more aggregated than successful Canada goose nests in spatial point-pattern analyses (see Chapter 1, this volume). However, other studies have identified a positive association between Canada goose nest density and nest survival (Reiter 2006, Miller et al. 2007). Thus, as the density of nesting Canada geese becomes very high, optimal breeding areas (e.g., high nest survival) may ultimately occur where nest densities are relatively lower.

At a range-wide scale these analyses supported the importance of proximity to coastal salt marsh habitat (i.e., brood-rearing habitat) on the distribution of nesting Canada geese. The association of the Hudson Bay coast with Canada goose nests was the

same as their association across a small spatial extent within 8 km of the coast (see Chapter 3, this volume). This provided support for spatial scaling of this covariate (i.e., the effect of the covariate remains the same when considered in analyses of different spatial scales). However the lack of importance of an interaction between the distance to Hudson Bay and year at a range-wide spatial extent suggested that the importance of this covariate has not changed over time; which was different than observed in analyses across a smaller spatial extent (see Chapter 3, this volume). Furthermore, the association of Canada goose nest counts with the distance to Hudson Bay, when considered at the spatial extent of the EPP breeding range, was better modeled non-linearly (i.e., half-normal) compared to the linear relationship used to model changes over a smaller spatial extent close to Hudson Bay (see Chapter 3, this volume). These results suggested that although a factor associated with nest density of Canada geese locally can be scaled up to predict nest distribution across a larger spatial extent, the form of the association may not remain the same, and the importance of interactions may also change.

To estimate breeding abundance across a species' or population's range, data from the full extent of the range are needed; however, the appropriate resolution of these data necessary to gain insight into species ecology is not always clear and often is limited by logistics (van Horne 2002). Therefore, simple models with easy-to-measure covariates can provide reasonable population estimates, but result in little mechanistic insight (Nichols 2001). Despite efforts to consider more habitat-specific strata (e.g., lowlands, tundra, coast etc.), the finest resolution (i.e., 6-level habitat-strata classification) received the most support and was included in my best-supported models based on cross-validation. However, predictions using a model containing only the 6-

level habitat-strata classification were less accurate than the best-predicting models based on MSE, which included additional covariates; identifying the limited predictive strength of the habitat strata only. Ultimately, finer resolution habitat data (e.g., Brook 2001) may be needed to fully understand the specific characteristics of habitat within each strata in this region that promote high Canada goose nest densities (however see, Chapter 3, this volume).

The annual, range-wide predictions of productive geese based on the models I developed exhibited less among-year variance than estimates generated using the traditional stratified-random sample method. The *post-hoc* inclusion of a phenology effect did not substantially change the total range-wide predictions based on the best-supported models. My point-wise model estimates of productive Canada geese were also, on average, lower than the traditional estimates. However, cross-validation suggested my best-supported models were unbiased when predicting at the resolution of a 1-km² block, and thus the range-wide model predictions were also likely unbiased. Therefore, traditional estimates may include positive bias in the estimated number of reproductive geese. By including additional covariates in my models (e.g., distance to Hudson Bay, snow goose density), I accounted for within-strata variation in nest counts that the traditional approach does not. Excluding finer resolution data may lead to biased estimates, particularly when there is aggregation of counts (e.g., nests) as observed close to the Hudson Bay coast. However, the within-year variance of productive goose estimates was higher in the model-based approach than in the traditional estimate. So, although my models generated predictions with lower bias, the increased number of parameters resulted in increased variance in my predictions. The trade-off between

reduced bias and increased variance is common when developing models (Burnham and Anderson 2002) and must be considered in light of the goals of the model analyses.

These models predicted the distribution of Canada goose nests with little bias (i.e., low mean error) and with reasonable accuracy (i.e., low MSE). Furthermore, these models defined mechanisms influencing the abundance of nesting EPP Canada geese throughout a broad spatial extent along western Hudson Bay in northern Manitoba using data recorded at a relatively high spatial-resolution (~1-km² observation areas). My analyses suggested that although processes observed at high-resolution across a small spatial extent, relative to a species' range, may have similar effects (i.e., sign of the association) on the species' distribution across a broader spatial extent, the form of the effect is often better related non-linearly when considering scaling up to range-wide spatial scales, and the importance of interactions among covariates may change. My data provided the first empirical evidence that, over time, high snow goose nest densities are associated with lower Canada goose nest density, and that nesting EPP Canada geese experience local-scale density dependence; providing evidence of the potential effects of intra-specific territoriality. Overall, changes in the distribution of nesting Canada geese along the coast of western Hudson Bay have occurred concurrently with and over the same spatial areas as changes in brood-rearing habitat use and alteration of coastal salt marshes. Together, these results suggest that as nesting snow geese increase and as coastal salt marshes continue to be altered, the breeding ecology and spatial distribution of Canada geese will also likely change.

TABLE 1. Summary of covariates considered in mixed-effects Poisson regression models of counts of Eastern Prairie Population (EPP) Canada goose (*Branta canadensis interior*) nests from aerial surveys 1987 – 2008 in northern Manitoba, Canada.

CATEGORY	MODEL DESCRIPTION
INTRA-SPECIFIC EFFECTS	
^a CAGO _{<i>t</i>-5}	Estimate of Canada goose nest density on an observation interval, 5 years before current observation in year, <i>t</i> .
INTER-SPECIFIC EFFECTS	
^b LSGO	Observed density of lesser snow goose (<i>Chen caerulescens caerulescens</i>) nests on an observation interval in year, <i>t</i>
^b LSGO _{<i>t</i>-5}	Estimate of lesser snow goose nest density on an observation interval, 5 years before current observation in year, <i>t</i> .
^b AUTOLSGO	Average estimated density of lesser snow goose nests on an observation interval, for 5 years before current observation in year, <i>t</i> .
HABITAT	
Strata 6	The original 6 strata used to define the stratified random sample of transects (see Malecki et al. 1981)
Strata 3	The aggregation of the original 6 strata into: (1) Tundra, (2) Lowlands, and (3) Forest.
Strata 2	The aggregation of the original 6 strata into: (1) Coast, and (2) Interior.
Strata 3 GIS	Strata from Canadian National Land Cover data: (1) Tundra, (2) Transitional forest, and (3) Coniferous forest.
^c Hudson Bay	The distance (km) to Hudson Bay.
PHENOLOGY	
JHATCH	Julian day of the median hatch date at Cape Churchill
TEMPORAL TREND	
YEAR	Year as a continuous variable
SPATIO-TEMPORAL TRENDS	
Hudson Bay*YEAR	Interaction term to model spatial changes in Canada goose nest counts over time as the result of degraded salt marsh brood habitat by lesser snow geese.
Strata 3*YEAR	Interaction to assess differences in temporal trend by strata
Strata 2* YEAR	Interaction to assess differences in temporal trend by strata
Strata 3 GIS*YEAR	Interaction to assess differences in temporal trend by strata

^aCovariate was considered in linear and logistic forms

^bCovariate was considered in linear and quadratic forms

^cCovariate was considered in linear and half-normal forms

TABLE 2. Summary of *a priori* models fit with maximum likelihood using a model-training dataset (53% of data) to evaluate hypotheses of factors influencing the count of Eastern Prairie Population (EPP) Canada geese (*Branta canadensis interior*) on range-wide aerial surveys in Manitoba, Canada, 1992 – 2008. All models were evaluated included the random effect of each transect in each year (transect-year). The model form was linear unless indicated otherwise in parentheses; log = logistic, quad = quadratic; half = half-normal. Models were ranked within general categories based on Akaike's Information Criterion (AIC). AIC scores in **bold** were equal to or larger than the AIC score for the intercept-only models.

CATEGORY	AIC	Δ AIC ^a	BETA [95% CI]
INTRA-SPECIFIC			
CAGO _{t-5} (log)	12615	0	$\beta_1 = 72.92$ [67.48, 78.35] $\beta_2 = 0.13$ [0.12, 0.14]
CAGO _{t-5}	12905	290	$\beta_1 = 32.49$ [30.58, 34.40]
INTER-SPECIFIC			
AUTOLSGO (quad)	13743	0	$\beta_1 = 8.97$ [6.99, 10.95] $\beta_2 = -15.42$ [-20.32, -10.52]
LSGO (quad)	13756	13	$\beta_1 = 6.36$ [4.99, 7.74] $\beta_2 = -7.80$ [-10.03, -5.57]
LSGO _{t-5} (quad)	13826	84	$\beta_1 = 3.65$ [1.80, 5.51] $\beta_2 = -3.93$ [-6.60, -1.25]
AUTOLSGO	13844	101	$\beta_1 = 0.181$ [-0.30, 0.66]
LSGO	13844	101	$\beta_1 = 0.14$ [-0.22, 0.50]
LSGO _{t-5}	13845	102	$\beta_1 = 0.06$ [-0.44, 0.57]
BROOD HABITAT			
Hudson Bay (half)	12473	0	$\beta_1 = 0.13$ [0.12, 0.14]
Hudson Bay	12523	50	$\beta_1 = -2.71$ [-2.88, -2.55]
HABITAT STRATA			
Strata 6	13278	0	$\beta_{strata1} = 0.06$ [-0.20, 0.31]; $\beta_{strata2} = 1.21$ [0.92, 1.50]; $\beta_{strata3} = 1.18$ [0.90, 1.47]; $\beta_{strata4} = 2.54$ [2.30, 2.77]; $\beta_{strata5} = 2.05$ [1.81, 2.30]
Strata 3	13447	169	$\beta_{lowlands} = -1.61$ [-1.82, -1.40] $\beta_{forest} = -2.71$ [-2.40, -2.02]
Strata 2	13474	196	$\beta_{coast} = 1.98$ [1.82, 2.13]
Strata 3 GIS	13721	443	$\beta_{transition} = -1.15$ [-1.35, -0.95] $\beta_{conifer} = -1.11$ [-1.62, -0.60]
PHENOLOGY			
JHATCH	13844		$\beta_1 = -0.70$ [-2.62, 1.22]
TEMPORAL			
YEAR	13844		$\beta_1 = -0.03$ [-0.06, 0.005]
SPATIO-TEMPORAL			
Hudson Bay*YEAR	12523	0	
Strata 3*YEAR	13441	918	
Intercept	13843		

^a Δ AIC = AIC for model *i* - minimum AIC; compared within categories when applicable.

TABLE 3. Summary of cross-validation (MSE = mean squared-error; 95% CI Error = 95% confidence interval for mean error of prediction) results from 27 models used to predict counts of Eastern Prairie population (EPP) Canada goose (*Branta canadensis interior*) nests using aerial survey data from Manitoba, Canada 1992 – 2008. Terms in italics indicated a covariate form that differed from linear. In addition to covariates listed below, all models (except the 2 indicated) included an intercept term, an offset term (equal to the natural logarithm of the area [km²] surveyed), the half-normal form for the distance (km) to Hudson Bay, and the random effect of transect-year.

MODEL	MSE	95% CI Error
<i>logistic</i> CAGO _{t-5} + STRATA 6 + <i>quadratic</i> LSGO _{t-5}	0.7213	-0.03, 0.01
<i>logistic</i> CAGO _{t-5} + STRATA 6 + <i>quadratic</i> LSGO	0.7214	-0.03, 0.01
<i>logistic</i> CAGO _{t-5} + STRATA 6 + <i>quadratic</i> AUTOLSGO	0.7291	-0.03, 0.01
<i>logistic</i> CAGO _{t-5} + STRATA 2 + <i>quadratic</i> LSGO _{t-5}	0.7445	-0.07, -0.02
<i>logistic</i> CAGO _{t-5} + STRATA 3 + <i>quadratic</i> LSGO	0.7445	-0.06, -0.02
<i>logistic</i> CAGO _{t-5} + STRATA 3 + <i>quadratic</i> LSGO _{t-5}	0.7445	-0.06, -0.02
<i>logistic</i> CAGO _{t-5} + STRATA 2 + <i>quadratic</i> LSGO	0.7446	-0.07, -0.02
<i>logistic</i> CAGO _{t-5} + STRATA 3 + <i>quadratic</i> AUTOLSGO	0.7474	-0.06, -0.02
<i>logistic</i> CAGO _{t-5} + STRATA 2 + <i>quadratic</i> AUTOLSGO	0.7474	-0.06, -0.02
<i>logistic</i> CAGO _{t-5} + STRATA 3 GIS + <i>quadratic</i> LSGO _{t-5}	0.8157	-0.12, -0.08
<i>logistic</i> CAGO _{t-5} + STRATA 3 GIS + <i>quadratic</i> LSGO	0.8159	-0.12, -0.08
<i>logistic</i> CAGO _{t-5} + STRATA 3 GIS + <i>quadratic</i> AUTOLSGO	0.8179	-0.12, -0.08
STRATA 6	1.0727	-0.01, 0.04
CAGO _{t-5} + STRATA 3 GIS + <i>quadratic</i> AUTOLSGO	1.1812	-0.12, -0.07
CAGO _{t-5} + STRATA 3 + <i>quadratic</i> AUTOLSGO	1.1955	-0.05, 0.0001
CAGO _{t-5} + STRATA 3 GIS + <i>quadratic</i> LSGO	1.1969	-0.12, -0.07
CAGO _{t-5} + STRATA 2 + <i>quadratic</i> AUTOLSGO	1.2059	-0.06, -0.003
CAGO _{t-5} + STRATA 6 + <i>quadratic</i> AUTOLSGO	1.2122	-0.01, 0.04
CAGO _{t-5} + STRATA 3 + <i>quadratic</i> LSGO	1.2161	-0.05, 0.0001
CAGO _{t-5} + STRATA 2 + <i>quadratic</i> LSGO	1.2271	-0.06, -0.002
CAGO _{t-5} + STRATA 6 + <i>quadratic</i> LSGO	1.2344	-0.01, 0.04
CAGO _{t-5} + STRATA 3 GIS + <i>quadratic</i> LSGO _{t-5}	1.2354	-0.12, -0.07
CAGO _{t-5} + STRATA 3 + <i>quadratic</i> LSGO _{t-5}	1.2637	-0.06, 0.001
^a OFFSET + INTERCEPT	1.2723	-0.04, 0.001
CAGO _{t-5} + STRATA 2 + <i>quadratic</i> LSGO _{t-5}	1.2762	-0.06, -0.001
CAGO _{t-5} + STRATA 6 + <i>quadratic</i> LSGO _{t-5}	1.2815	-0.01, 0.04
^a OFFSET + INTERCEPT + TRANSECT*YEAR	1.3129	-0.23, -0.17

^aModel included only terms listed in table

TABLE 4. Estimates (β_i) and 95% confidence intervals (CI) of parameters from the top 3 models, based on mean squared error (MSE), of factors influencing the count of Eastern Prairie Population (EPP) Canada goose (*Branta canadensis interior*) nests on range-wide aerial surveys in Manitoba, Canada, 1992 – 2008.

COVARIATE ^a	β_i	95% CI	COVARIATE ^a	β_i	95% CI	COVARIATE ^a	β_i	95% CI
Intercept	-2.64	-2.80, -2.48	Intercept	-2.64	-2.80, -2.48	Intercept	-2.64	-2.80, -2.48
^b CAGO _{t-5}	40.27	37.05, 43.50	^b CAGO _{t-5}	40.00	36.80, 43.20	^b CAGO _{t-5}	40.13	36.88, 43.37
^c CAGO _{t-5}	0.14	0.13, 0.15	^c CAGO _{t-5}	0.14	0.13, 0.15	^c CAGO _{t-5}	0.14	0.13, 0.15
^d Hudson Bay	0.13	0.12, 0.14	^d Hudson Bay	0.13	0.12, 0.14	^d Hudson Bay	0.13	0.12, 0.14
strata1	0.27	0.08, 0.46	strata1	0.27	0.07, 0.46	strata1	0.27	0.08, 0.46
strata2	1.00	0.78, 1.22	strata2	1.00	0.78, 1.22	strata2	1.00	0.78, 1.22
strata3	1.20	0.99, 1.41	strata3	1.20	0.99, 1.41	strata3	1.20	1.00, 1.41
strata4	1.81	1.64, 1.99	strata4	1.83	1.65, 2.00	strata4	1.81	1.64, 1.99
strata5	1.64	1.46, 1.82	strata5	1.64	1.46, 1.82	strata5	1.64	1.46, 1.82
LSGO _{t-5}	0.44	-0.50, 1.39	LSGO	-0.52	-1.10, 0.06	AUTOLSGO	1.77	0.41, 3.13
LSGO _{t-5} *	-0.33	-1.10, 0.44	LSGO*	0.13	-0.19, 0.46	AUTOLSGO*	-4.38	-7.15, -1.60
LSGO _{t-5}			LSGO			AUTOLSGO		
transect-year	0.29	0.25, 0.32	transect-year	0.28	0.25, 0.32	transect-year	0.29	0.25, 0.32

^aSee Table 1 for covariate definitions

^bFirst term of logistic form

^cSecond term of logistic form

^dTerm from half-normal form

TABLE 5. Estimates (β_i) and 95% confidence intervals (CI) for parameters from 3 *post-hoc* models of factors influencing the count of Eastern Prairie Population (EPP) Canada goose (*Branta canadensis interior*) nests on range-wide aerial surveys in Manitoba, Canada, 1992 – 2008.

COVARIATE ^a	β_i	95% CI	COVARIATE ^a	β_i	95% CI	COVARIATE ^a	β_i	95% CI
Intercept	-1.26	-2.12, -0.39	Intercept	-1.24	-2.10, -0.38	Intercept	-1.25	-2.11, -0.39
^b CAGO _{t-5}	40.15	36.92, 43.37	^b CAGO _{t-5}	40.50	37.28, 43.72	^b CAGO _{t-5}	39.98	36.74, 43.22
^c CAGO _{t-5}	0.14	0.13, 0.15	^c CAGO _{t-5}	0.14	0.13, 0.15	^c CAGO _{t-5}	0.14	0.13, 0.15
^d Hudson Bay	0.13	0.12, 0.14	^d Hudson Bay	0.13	0.12, 0.14	^d Hudson Bay	0.13	0.12, 0.14
strata1	0.27	0.08, 0.46	strata1	0.27	0.07, 0.46	strata1	0.27	0.08, 0.46
strata2	1.00	0.78, 1.22	strata2	1.00	0.78, 1.22	strata2	1.00	0.78, 1.22
strata3	1.20	0.99, 1.41	strata3	1.20	0.99, 1.41	strata3	1.20	0.99, 1.41
strata4	1.82	1.64, 1.99	strata4	1.82	1.65, 2.00	strata4	1.82	1.64, 1.99
strata5	1.64	1.46, 1.82	strata5	1.64	1.46, 1.82	strata5	1.65	1.46, 1.82
LSGO _{t-5}	0.43	-0.51, 1.39	LSGO	-0.54	-1.12, 0.03	AUTOLSGO	1.71	0.36, 3.07
LSGO _{t-5} *	-0.33	-1.09, 0.45	LSGO*	0.14	-0.18, 0.47	AUTOLSGO*	-4.26	-6.99, -1.53
LSGO _{t-5}	-0.33	-1.09, 0.45	LSGO	0.14	-0.18, 0.47	AUTOLSGO	-4.26	-6.99, -1.53
JHATCH	-0.79	-1.28, -0.31	JHATCH	-0.80	-1.28, -0.32	JHATCH	-0.79	-1.28, -0.31
transect- year	0.28	0.24, 0.32	transect-year	0.28	0.24, 0.32	transect- year	0.29	0.24, 0.32

^aSee Table 1 for covariate definitions

^bFirst term of logistic form

^cSecond term of logistic form

^dTerm from half-normal form

FIGURE 1. Location of range-wide aerial transects surveyed for nesting Eastern Prairie Population (EPP) Canada geese (*Branta canadensis interior*) and nesting lesser snow geese (*Chen caerulescens caerulescens*) 1987 – 2008 in northern Manitoba, Canada.

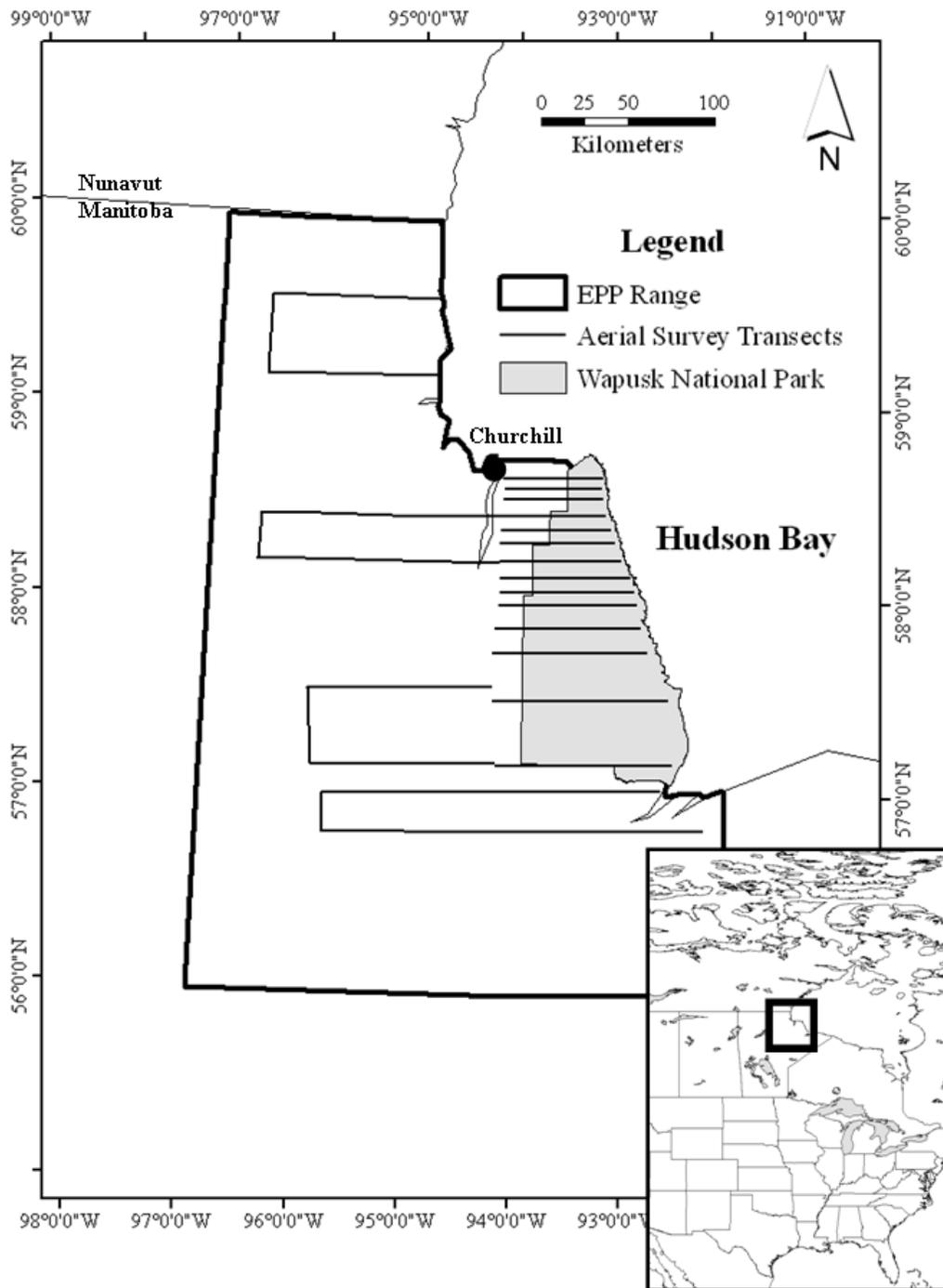


FIGURE 2. Habitat-strata classifications located within the Eastern Prairie Population (EPP) Canada goose (*Branta canadensis interior*) nesting range in northern Manitoba, Canada: (A) original 6 strata defined by Malecki et al. (1981); and (B) aggregation of original 6 strata to 3 vegetation classes; (C) aggregation of original 6 strata to 2 general classes; and (D) 3 strata defined by Advanced Very High Resolution Radiometer (AVHRR) sensors operating on board United States National Oceanic and Atmospheric Administration (NOAA) satellites.

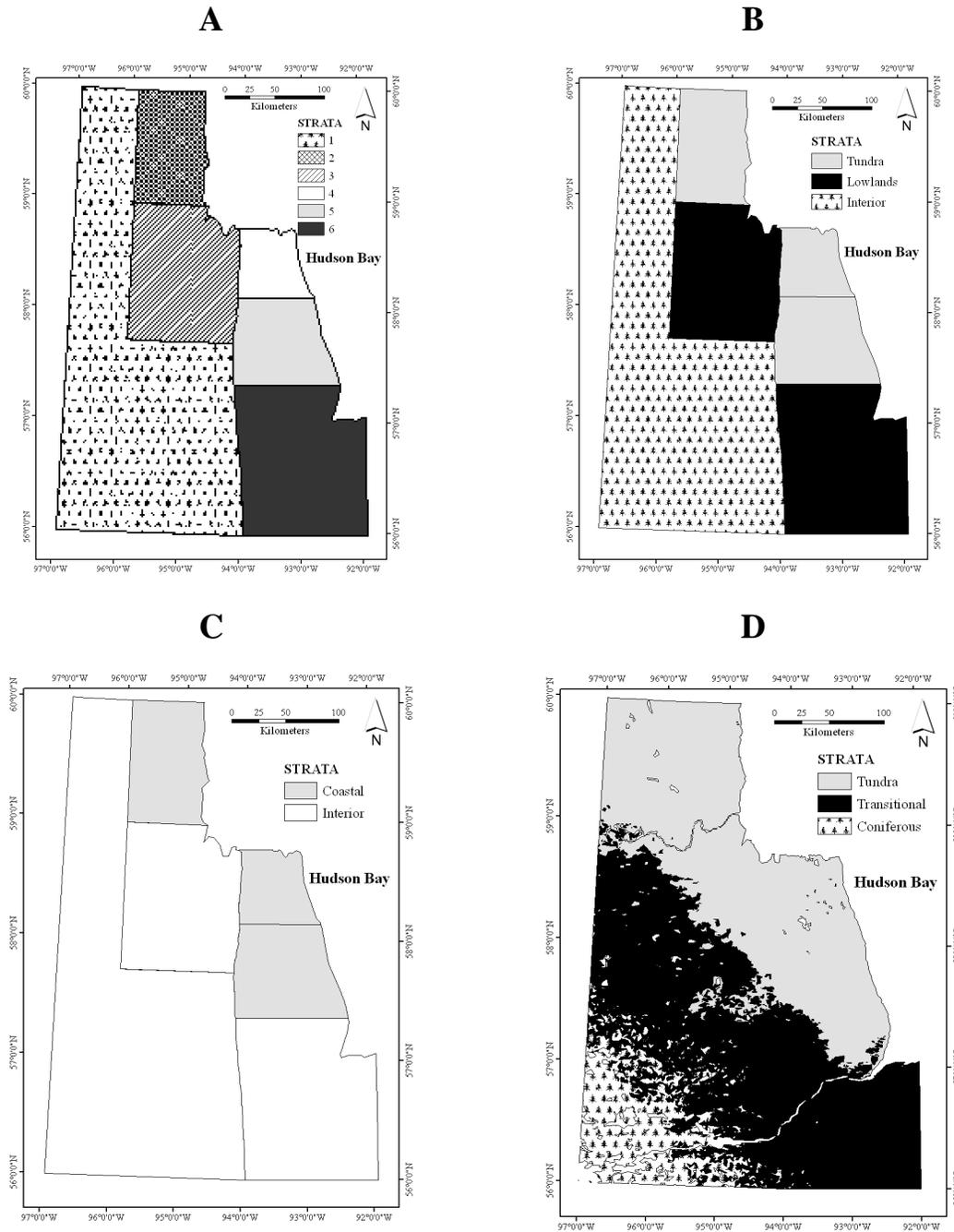


FIGURE 3. Total observed count (not corrected for visibility) of Eastern Prairie Population (EPP) Canada goose (*Branta canadensis interior*) nests and lesser snow goose (*Chen caerulescens caerulescens*) nests along all aerial transects in northern Manitoba, Canada 1987 – 2008.

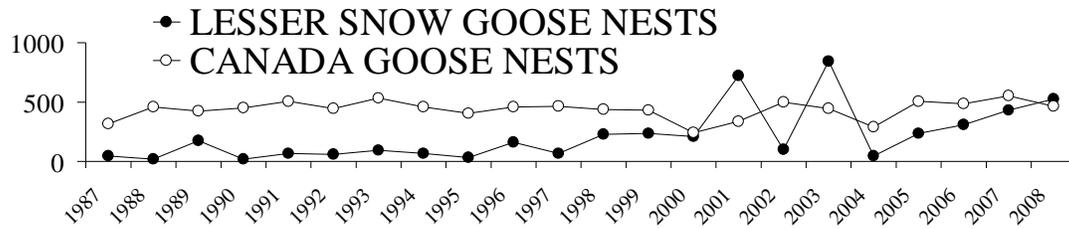


FIGURE 4. Estimated mean density (nests per km²) \pm 2 standard errors, of Eastern Prairie Population (EPP) Canada goose (*Branta canadensis interior*) nests on 28 aerial transects in northern Manitoba, Canada 1987 – 2008; organized below by stratum.

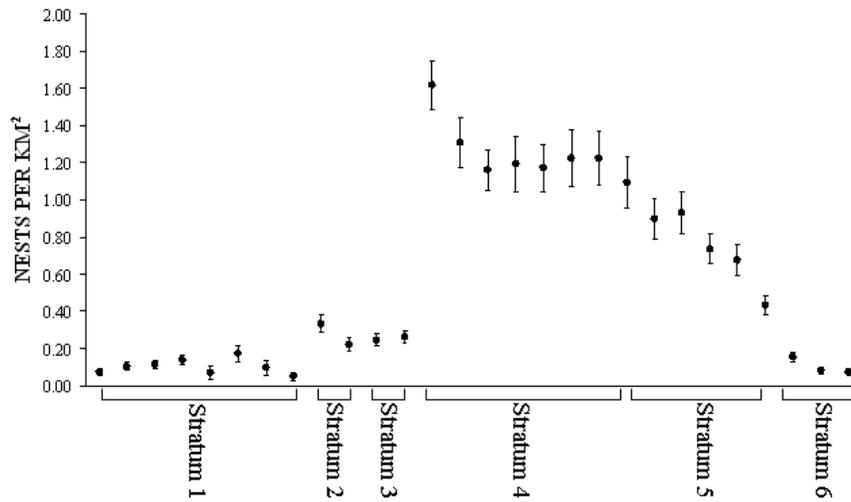


FIGURE 5. Temporal (Spearman's rho; top) and spatial (Moran's I; bottom) correlograms for observed counts (OBSERVED) of Eastern Prairie Population (EPP) Canada goose (*Branta canadensis interior*) nests in Manitoba, Canada, 1992 – 2008, and the residuals of the best predicting model (TOP MODEL).

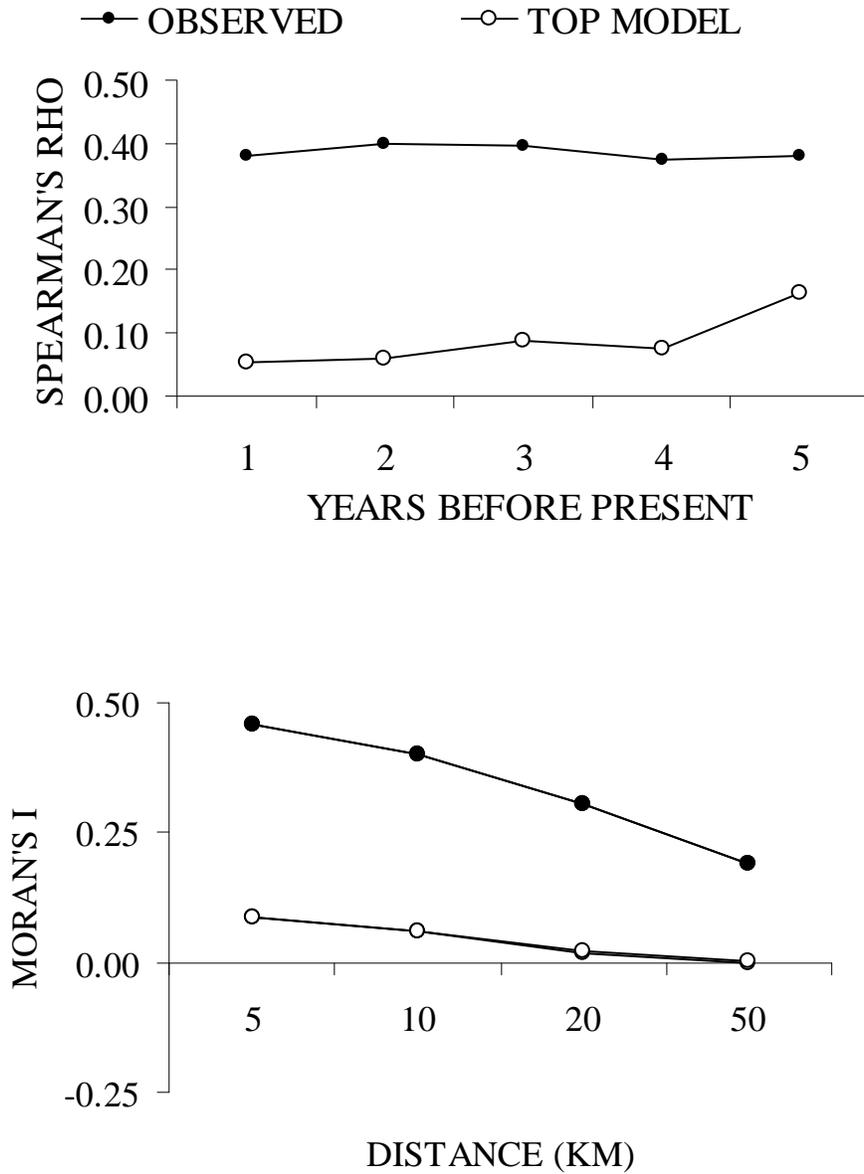


FIGURE 6. Estimated number of reproductive Eastern Prairie Population (EPP) Canada geese (*Branta canadensis interior*) in northern Manitoba, 1992 – 2008. Estimates were based on the average point-wise estimates of the 3 best-supported models based on cross-validation (MODEL); the traditional method of calculating a unique nest density estimate for each strata, multiplying by strata area, and summing across all strata (TRADITIONAL); and the average point-wise estimates of the 3 *post-hoc* models (POSTHOC). Predicted nest counts were corrected for visibility ($\times 1.42$) and the presence of 2 geese at each nest ($\times 2$; goose and gander) to predict the total number of productive geese. The upper and lower lines represent 95% confidence tubes for each point-wise estimate from the 3 best-supported models based on 95% confidence intervals of parameters in those models (95% CT MODEL).

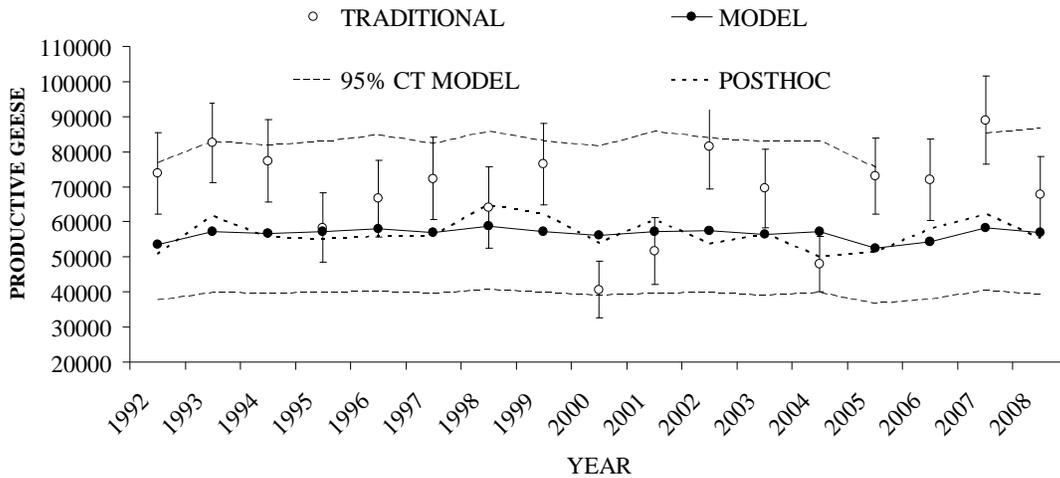
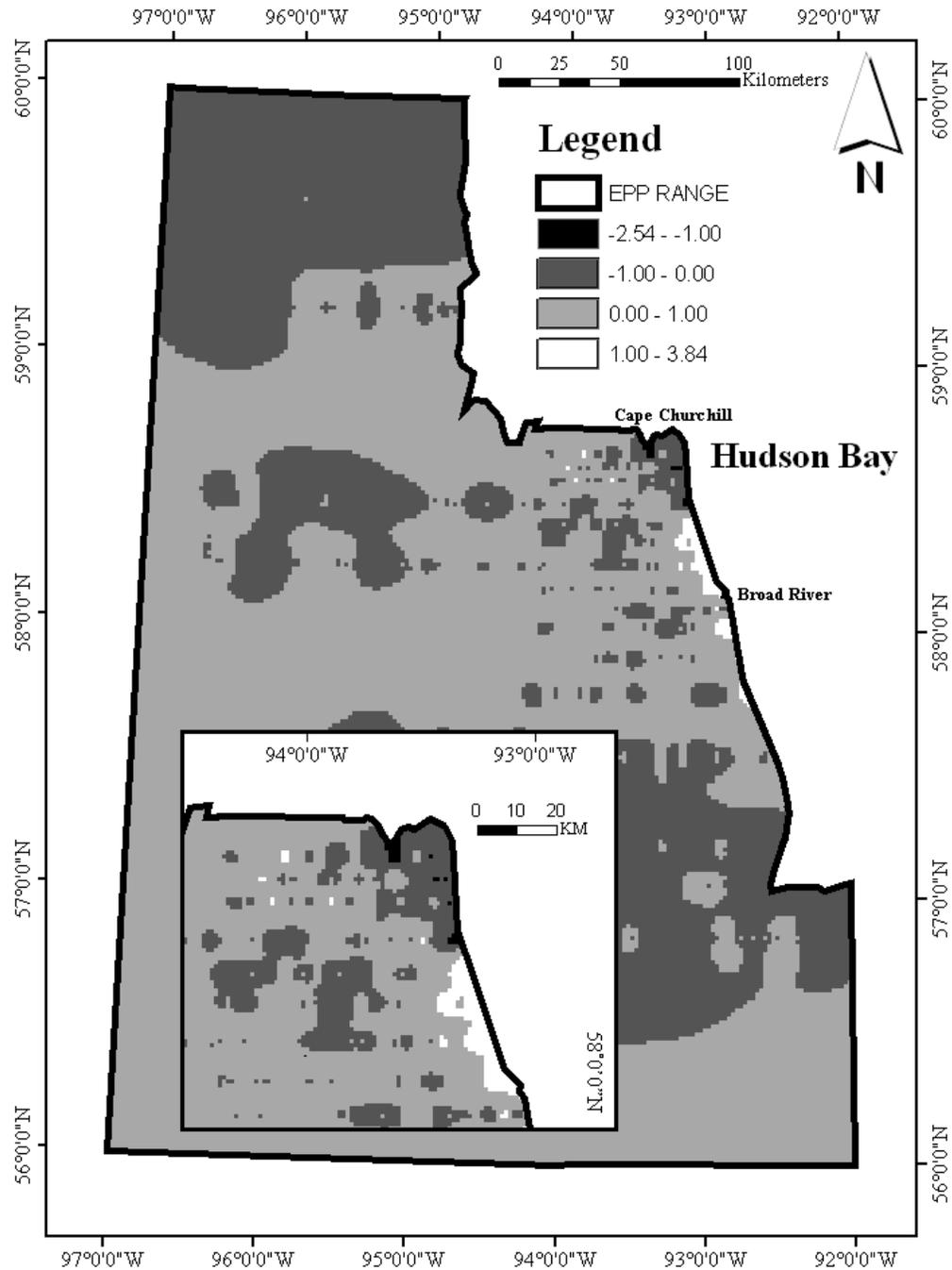


FIGURE 7. Predicted cumulative change in the number of Eastern Prairie Population (EPP) Canada goose (*Branta canadensis interior*) nests per 1-km² pixel across a ~101,500 km² range in northern Manitoba, Canada between 1992 and 2008. Goose nests were estimated for each 1-km² pixel in each year using the 3 top models based on cross-validation. Annual change was estimated by subtracting estimates of goose nests in year, $t - 1$, from estimates in year, t , for each 1-km² pixel. The inset map is an enlargement of an area near Cape Churchill where the largest cumulative changes in Canada goose nests have occurred.



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