Sympatric Nesting Eastern Prairie Population (EPP) Canada Geese and Lesser Snow

Geese on the Hudson Bay Lowlands:

Nest Depredation and Spatial Distribution

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INTRODUCTION

Long-term monitoring (>25 years) of breeding Eastern Prairie Population (EPP) Canada geese (*Branta canadensis interior*) at Cape Churchill has documented a decline in nest density (Walter 1999, D. Andersen, Minnesota Cooperative Fish and Wildlife Research Unit, unpublished data). Walter (1999) identified nest depredation, particularly by arctic fox (*Alopex lagopus*), as the most consistent factor affecting EPP reproductive success and subsequent recruitment over 20 years (1976 – 1996). Currently, there is concern about the influence of increasing nesting light goose populations (lesser snow goose [*Chen caerulescens caerulescens*] and Ross's goose [*Chen rossii*]) on breeding Canada geese (Ankney 1996, Batt 1997, Walter 1999, Nack 2003, Nack and Andersen 2004, Gleason et al. 2004), and the potential interacting effects of predators and light goose abundance on Canada goose population dynamics in northern Manitoba.

Nesting lesser snow geese have expanded their distribution considerably during the last 20 years (Ankney 1996, Abraham and Jefferies 1997, Batt 1997) moving into areas where they did not previously occur, and that were traditionally used solely by nesting EPP Canada geese (Walter 1999, Nack and Andersen 2004). The detrimental impact that large populations of snow geese have on sub-arctic vegetation communities is well documented (Kerbes et al. 1990, Srivatava 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 species, particularly sympatrically nesting Canada geese (Ankney 1996, Abraham and Jefferies 1997, Batt 1997). On Akimski Island in southern James Bay, Canada goose reproductive performance was reduced in the presence of sympatrically nesting lesser snow geese compared with when snow and Canada geese nested allopatrically (Gleason et al. 2004), yet the mechanisms contributing to the observed difference are not clear. Large groups of snow geese may alter local predator-prey dynamics (Walter 1999), potentially influencing nest depredation of Canada geese. However, how dense nesting aggregations of lesser snow geese affect nest depredation on sympatrically nesting species is not known.

Herein, we report on research activities conducted in 2004 to further assess the potential impact of increased snow goose nesting aggregations on EPP Canada geese. We address the following questions:

1. How do nesting aggregations of lesser snow geese affect the probability of depredation of sympatric EPP Canada goose nests at 2 sites with different histories of snow goose nest presence?

2. How are sympatrically nesting Canada and snow geese arranged spatially relative to each other?

3. How are nesting EPP Canada geese distributed across the landscape and what factors influence the observed distribution?

Factors influencing the probability of depredation of a goose nest are potentially complex and involve interactions between local nest density, predator abundance, alternative prey abundance, and the defensive capabilities of adult geese (Bahr 1989, Walter 1996, Walter 1999). In 2004, we began to collect and assess data relative to Canada goose nest depredation at Nestor One, and have begun to assess patterns in Canada goose nest distribution derived from annual

breeding ground surveys. To address the first objective, we collected data to model the probability of nest depredation and estimate the effect of multiple biological covariates (see Table 1). To address the second objective, we continued nest searching near Cape Churchill, and will use these and historical data to assess the spatial pattern of nest distribution and depredation. The spatial distribution of Canada goose nests relative to aggregations of snow geese has not been assessed, yet may provide important clues about the influence of rapidly increasing local snow goose nest densities. If Canada geese benefit from these aggregations in the form of reduced probability of nest depredation, we predict, over time, they would tend towards positive spatial correlation or aggregation with snow geese. Conversely, if Canada geese experience increased probability of nest depredation when nesting densely with snow geese, then we predict a negative correlation in spatial nest patterns. To address the third objective, we will use existing breeding survey data. Breeding population surveys have been conducted annually for EPP Canada geese beginning in 1972 and continuing through 2004 (Malecki et al. 1981, Humburg et al. 2000, Raedeke et al. 2004). Nesting snow geese have been recorded on these aerial transects since 1981. These annual surveys summarize population trends used for long-term monitoring and harvest management (Malecki et al. 1981, Humburg et al. 1998, Humburg et al. 2000, Raedeke et al. 2003) but have not been used to quantify shifts in spatial distribution and density. With increasing numbers of lesser snow geese across the EPP Canada goose range (Abraham and Jefferies 1997), these data provide additional landscape-level information regarding their inter-specific relationship.

STUDY AREA

The EPP breeding range includes nearly 54,000 km^2 in northern Manitoba (Malecki et al. 1980). The highest density of breeding Canada geese is found along a strip of coastal habitat bordering Hudson Bay. The Nestor One study area (NO), just south of Cape Churchill and approximately 60 km east-southeast of the town of Churchill, Manitoba, Canada (Fig. 1), lies within this narrow strip of coastal tundra nesting habitat, characterized by low relief, continuous permafrost, poor drainage, beach ridges, coastal marshes, and coastal tundra vegetation (Wellein and Lumsden 1964, Didiuk and Rusch 1979). The core study area is ~ 48 km^2 and is located inside of Wapusk National Park (11,475 km^2). Coastal salt marsh, beach ridge/sedge meadow, and interior sedge meadow compose the major habitat types outlined by Didiuk and Rusch (1979). More recently, Brook (2001) detailed the vegetation community composition and abundance throughout Wapusk National Park. Prior to 2001, 0-2 snow goose nests were located annually during nest searching on the study area. However, from 2001 to 2003 there were 55, 6, and 94 snow goose nests, respectively.

The Broad River study area (BR) is located ~55 km south of NO in Wapusk National Park along Hudson Bay (Fig. 1). The core study area, just north of the river mouth, is ~20 km^2, and consists of the same general habitat types as NO (Brook 2001). Eight units have been searched for nesting Canada geese sporadically over the last 20 years. Annual aerial breeding ground surveys document a roughly 200% increase in the number of snow goose nests near the mouth of the Broad River since 2000 (Raedeke et al. 2004).

METHODS
Nest Depredation

Nest searching at NO was conducted 16-21 June 2004. At all nests encountered, females were flushed and nest number, goose species, number of eggs present, incubation stage [(using

candling and flotation methods) (Westerkov 1950, Weller 1956)], presence of predators, flush distance, nest site type (Type 1 = in sheet H_2O, saturated ground, sedge/H_2O; Type 2 = shore, point, island; Type 3 = beach ridge, upland, pressure ridge), and general nest condition were recorded on nest cards. Universal Transverse Mercator (UTM) coordinates of the nest location were determined with a Global Positioning System (GPS) unit (recording +/- [m] error values) and imported to a digital field map (Nack 2003). Nest locations were marked with a 3" x 5" plastic orange flag placed 10 m north of the nest bowl (Didiuk and Rusch 1979, Walter 1999). Based on a 28-day incubation period, nests were revisited at or subsequent to the predicted hatch date to determine outcome (Didiuk and Rusch 1979). Nests were categorized as successful if at least 1 egg successfully hatched, identified by the presence of goslings or eggshells and intact membranes, depredated if few or no eggshell fragments were found in the nest, abandoned if found with intact cold eggs, or unknown. All depredated nests were assessed to identify the predator responsible. Holes in eggs or presence of eggshells are indicators of avian predation while missing eggs indicate mammalian predation (Walter 1999, Anthony et al. 2004). Identification of mammalian nest predators was made by the presence of key species-specific signs: scat, urine smell, or visual identification of individual.

We conducted ground-based arctic fox den surveys along beach ridges within NO and visited all known den locations. Dens were marked with a GPS and evaluated for occupancy by the presence of fox or fresh fox sign indicative of an active den (Macpherson 1969). The presence of prey items (lemming carcasses, goose carcasses, etc.) around the site was recorded. The proportion of den sites with fox activity can be compared to previous years as a rough index of relative annual arctic fox abundance near Cape Churchill. Because potential predator pressure likely varies with the proximity of an active fox den to a nest, it was measured as a separate variable, quantified as the distance (m) from each nest to the nearest active fox den.

Two methods were used to quantify local abundance of collared-lemmings (*Dircrostonyx richardsoni*); willow (*Salix* spp.) scar analysis and arctic fox scat-analysis. At Cape Churchill, collared-lemming*s* feed primarily on willow (*Salix* spp.). Surveys for scarring on willows provide a measure of local cycles of lemming abundance (Danell et al. 1981, Danell et al. 1999, Predavec et al. 2001). We collected scars from 300 random plots within the Nestor One study area and used a dissecting microscope to age scars based on the number of growth rings since the scarring event (Danell et al. 1981, Danell et al. 1999; see Appendix I for a more thorough treatment of these methods and analysis). Arctic fox scat analysis can also provide an index of annual collared lemming abundance. We collected fox scat when encountered during nest searching and at fox dens. At the time of collection each scat was aged according to criteria in Macpherson (1969) and allowed to air dry until analyzed in the lab. Samples were autoclaved, washed with light detergent and water, and passed through standard size (no. 5, 20 and 40) mesh sieves, until all component materials were separated. Samples were dried at 55°C for 2 hours. Materials from each sample were examined for 10 minutes to determine the presence or absence of lemming remains and other prey items (Macpherson 1969, Stickney 1991). If no lemming remains were identified after initial search a more intensive hair analysis was conducted using both dissecting and compound microscopes for comparative analysis (see Day 1966). The annual lemming abundance index for the study area is simply the proportion of scats containing lemmings.

Investigator visits to nests can increase the probability of goose nest depredation (MacInnes and Misra 1972). A random subset of nests was revisited once each day for 5 days post-discovery. During repeated visits, the nest was observed using a spotting scope or binoculars

from > 250m and the female was not flushed. The presence or absence of the male, female, or both geese was noted, and all observed predators were recorded. If adult geese were not present for 2 consecutive days, we visited the nest to determine its status as active, depredated, or abandoned. We compare the Mayfield estimate of Daily Survival Rate (DSR) from prior to discovery with that for the 5 days post-discovery as a measure of potential influence of visitation on nest survival. To account for potential effects of nest visitation, the number of times a female was flushed from the nest was also calculated for each nest.

Variables for all nests (Table 1) were tabulated and prepared for use in nest survival model development. Nest density (km^{-2}) of both Canada goose and snow goose nests within 250m of each Canada goose nest and the distance (m) of each Canada goose nest to the nearest depredated nest were calculated using Arc View 3.3.

Spatial Distribution

Point pattern analysis utilizes inter-event (inter-point) distances over a given area to quantify spatial patterns and associations (Diggle 1983, Bailey and Gatrell 1995). These distances are compared to those generated by a Poisson process, to test the null hypothesis that points are distributed randomly in 2-dimensional space. Deviations from a random distribution indicate either regularity or clustering of the observed pattern. Nearest-neighbor analysis incorporates the mean distance from each point to its nearest neighbor (Clark and Evans 1954). A *z*-statistic can be calculated for the observed mean nearest neighbor distance by comparing it to the mean distance to nearest neighbor expected in a large random distribution of the observed density. We used 1-tailed (lesser snow geese) and 2-tailed (Canada geese) z-tests to evaluate nest aggregation.

Nearest neighbor analysis provides information about local scale or first-order spatial patterns; however spatial organization at even slightly greater scales is ignored (Bailey and Gatrell 1995). Ripley's K-function addresses spatial patterns at multiple scales and is based on the variance of the distances between points (Ripley 1976, Haase 1995). Ripley's K also evaluates bivariate point patterns, testing for independence in the spatial pattern of 2 groups of events (Andersen 1992). The spatial pattern of depredated nests, for example, can be evaluated against the distribution of successful nests to assess spatial variations in nest fate (i.e., independence, positive association, negative association).

In 2004, we completed (1) a statistical-based description of spatial patterns of Canada and lesser snow goose nests at NO using nearest-neighbor analysis and Ripley's K, (2) a bivariate analysis to test for spatial independence of Canada goose and lesser snow goose nests, and (3) univariate and bivariate analyses to explore spatial trends and patterns in Canada goose nest depredation. Nest location coordinates for EPP geese at NO were available for 1998, 1999, 2001, 2002, and 2003. Lesser snow goose nests were only present at notable levels (i.e., > 5 nests total) in 2001 and 2003. Only 2001 and 2003 were used for bivariate analysis to test for independence between Canada goose and snow goose nests.

Landscape Distribution

In 2004, beginning and endpoints of flight transects during EPP breeding ground surveys were recorded by survey observers. These data were digitized and mapped using Arc View 3.3. Based upon endpoints, transects lines were constructed and a 200m buffer established on either

side, representing the area over which geese are counted (Malecki et al. 1981, Humburg et al. 2000).

RESULTS
Nest Depredation

Late winter storms and relatively cold temperatures resulted in high snow pack and very late spring phenology. The late year resulted in the lowest EPP nest density recorded over the previous 28 years, 0.82 nests per 100 ha at Cape Churchill. A total of 24 nests was discovered. Nest success for EPP in 2004 was the second lowest over this same period (Andersen et al. 2004). We made 79 nests visits. Most nests were visited only 2 times ($n = 17$), however some were visited 3 ($n = 1$), 6 ($n = 1$), 7 ($n = 4$) or 8 ($n = 1$) times. Of the 24 nest types, 37.5% were Type 1 ($n = 9$), 33.3% were Type 2 ($n = 8$), and 29.2% were Type 3 ($n = 7$). Mean ($\pm$ SE) distance from each Canada goose nest to the nearest depredated nest was 700 ($\pm$ 88.5) m. Canada goose nest density within 250m of each nest averaged 0.598 ($\pm$0.04) nests per km^2. No snow goose nests were located at NO in 2004.

On 15 June 2004, we conducted a survey flight to BR (Note: flight provided by U.S. Fish and Wildlife Service, Brian Lubinski). We observed very few nesting Canada geese and snow geese nesting near the mouth of the Broad River. These observations were confirmed with staff of Wapusk National Park working on the ground in the area at this time. Thus, nest searching at BR was not conducted in 2004.

We surveyed 17 arctic fox dens within and surrounding NO. Dens were visited at least once and as many as 3 times. Fourteen dens had sign of fresh fox activity during at least 1 visit ($p = 0.82$). This is above the 12-year average (0.653 $\pm$ 0.06) and not captured in the 95% confidence interval for the long-term mean (0.523, 0.783). However, only 5 (29%) of 17 dens surveyed appeared to sustain activity throughout the goose breeding period. The median distance of goose nests to the nearest active fox den was 1189 m, ranging from 178 m to 3337 m.

Willow stem scar ages ($n = 794$) ranged from 0 to 13 years. A non-linear model was fit to the observed scar-age frequency for analysis (see Appendix I). Based on the distribution of scar age,, 2004 was a period of declining lemming populations at Cape Churchill and 2003 a peak lemming year. This is consistent with field observations during 2003 and 2004 (D. Andersen, pers. comm., S. Maxson, pers. comm.). These data were used to evaluate the "bird-lemming" hypothesis at Cape Churchill (Appendix I).

We collected arctic fox scats ($n = 89$) at NO from 11 June 11 2004 to 10 July 10 2004. Based upon the crude scat aging classification of Macpherson (1969), the oldest sample was from late April and the most recent from early July. Eighty-four (94.4%) of the 89 arctic fox scats analyzed contained evidence of lemming remains. Scat was also collected at BR, 15-18 June 2004 and 29 June to 4 July 2004 by Wapusk National Park personnel. All scat from BR ($n = 7$) contained lemming remains.

The Mayfield estimate of daily nest survival prior to discovery was 0.96 for all Canada goose nests at NO. Based upon 5 nests monitored for 5 days post-initial discovery, daily survival rate was 1.0. Due to the small sample size, robust inference regarding the influence of nest visits cannot be made with these data.

Spatial Distribution

EPP nests appeared to be distributed randomly across NO based upon both nearest-neighbor and Ripley's K analysis. There was some evidence to support a trend towards

aggregation in some years, however, based upon 19 Monte Carlo simulations of Ripley's K, it was not significant at $\alpha = 0.05$ (Haase 1995). There was also no evidence of a strong temporal shift in observed distribution patterns of EPP from 1998 – 2003. Lesser snow goose aggregations provided a clearer overall trend. First order analysis in 2001 and 2003 suggested a marginally ($z = 1.59$, $P \approx 0.06$) to highly ($z = 7.87$, $P < 0.0002$) significant trend towards clumping. Spatial analyses based on Ripley's K also indicated aggregation for snow goose nests.

Bivariate analysis between successful and depredated Canada goose nests did not reveal deviations from independence for any year. Data were sufficient to conduct bivariate analysis of depredated Canada goose and all snow goose nests in 2001 and 2003. In 2001, there was a significant trend towards negative association. This result provides some evidence that depredated Canada goose nests tend to be further away from snow goose aggregations then expected randomly. Bivariate analyses between successful Canada goose and all snow goose nests were completed for 2001 and 2003 and results suggested significant deviations from independence towards positive spatial association.

Landscape Distribution

During 2004 aerial surveys, coordinates were recorded for 19 of the 24 transect lines. Coordinates were converted into decimal degrees and UTM format for use in Arc View 3.3. Transect lines were drawn between endpoints with a 200m buffer placed around each line to estimate survey area.

DISCUSSION and 2005 RESEARCH PLAN
Nest Depredation

Although we were able summarize and record variables of interest for each nest found in 2004, the limited sample size ($n = 24$) prevented rigorous model development. Furthermore, the lack of nesting lesser snow geese, a key variable of interest, confounded analysis efforts. Beginning in 2005, we will conduct nest searches at both NO and BR. Resulting data will be used to model the influence of lesser snow geese on Canada goose nest survival. We hope to improve our estimates of daily nest survival and subsequently the daily probability of failure by observing nests at a distance, to determine if they are still active, at regular intervals (every 3 to 7 days). A number of recent papers outline improved methods for modeling daily nest survival (Dinsmore et al. 2002, Shaffer 2004, Hazler 2004, Rotella et al. 2004) and measuring the influence of numerous biological covariates. We will utilize these methods for future analysis. Also, we hope to better evaluate the influence of nest visits by remotely monitoring more nests in the days post discovery.

Spatial Analysis

These analyses describe the spatial patterns and potential interactions of Canada and snow goose nests near Cape Churchill. Although the data are preliminary, there is some evidence to suggest that Canada geese nesting near snow goose nest aggregations and those further away suffer different probabilities of nest depredation. We will use these methods to quantitatively describe the nest distributions of Canada geese and lesser snow geese at Nestor One and the Broad River in 2005 and perhaps in 2006. Results of this work provide insight as to the degree of spatial correlation in the probability of depredation between both inter- and intra-specific nests. Accounting for potential spatial correlation will improve models examining the probability of nest depredation and the influence of lesser snow goose nesting aggregations.

Because changes in nest distribution may be the long-term effect of either positive of negative nest associations, data collected at BR, where Canada geese and snow geese have nested sympatrically for nearly 15 years, will provide additional insight into this relationship.

Landscape Analysis

In 2005, we will coordinate with the aerial survey crew to record the endpoint coordinates for remaining transects. We also plan to digitize the results of the annual surveys in Arc View 3.3 and begin to develop models assessing long-term changes in nesting distribution at the landscape scale.

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Figure 1: Cape Churchill Region: Nestor One (NO) and Broad River (BR) Study Areas
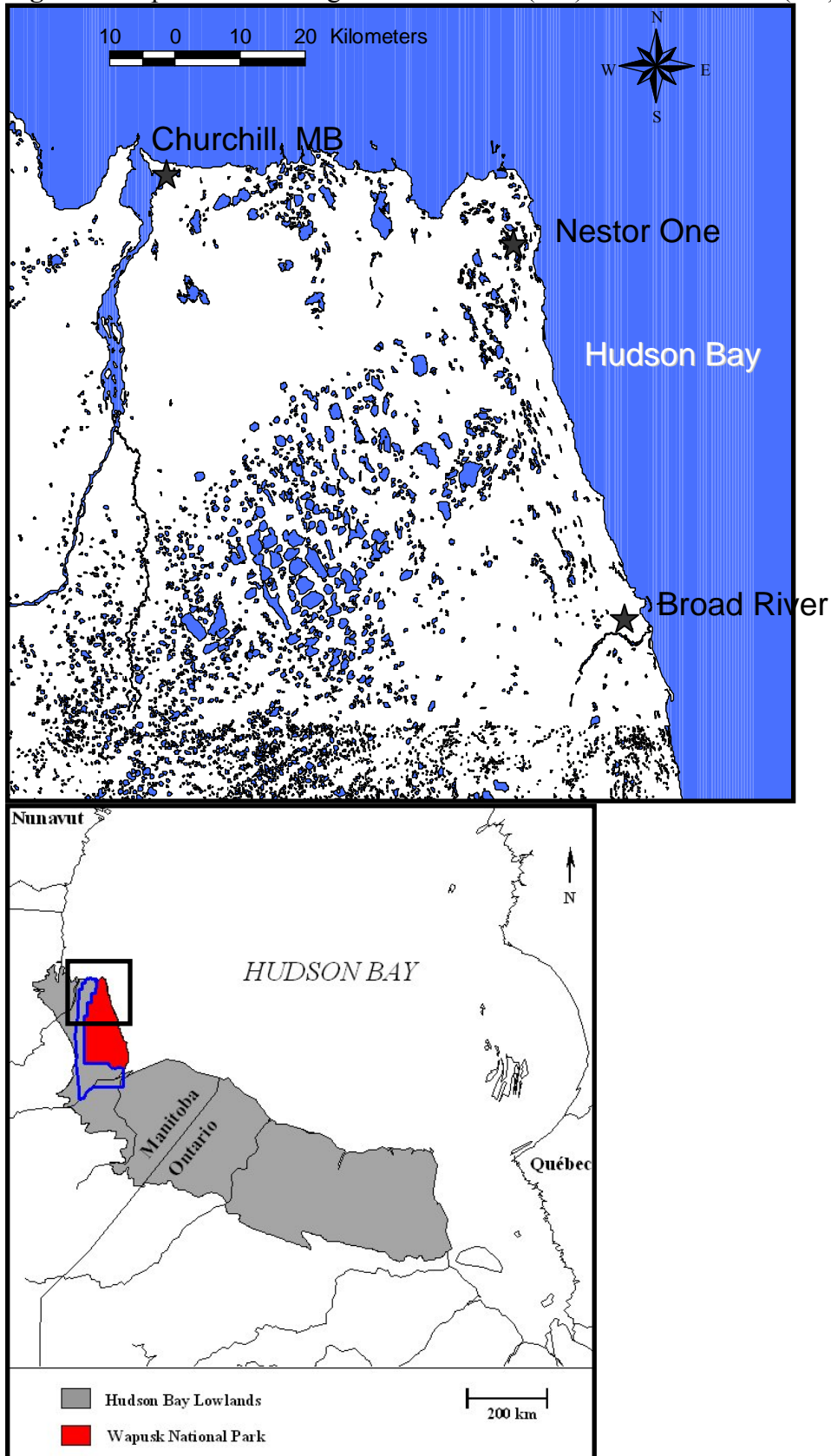
Table 1: Variables estimated from the data and included in model development and selection

Variable	Method of Estimation	Description
NEST EFFECTS CAGO density	Density of Canada goose nests (km-2) within a 250m buffer around each nest	Index of competition and local prey abundance Measure of intra-specific effects
LSGO density	Density of lesser snow goose nests (km-2) within a 250m buffer around each nest	Index of competition and local prey abundance Measure of inter-specific effects
Avian	Proportion of nest visits where an avian predator was observed	Index of predator pressure Specific predator effects
Mammal	Proportion of nest visits where mammal sign/ individual was observed	Index of predator pressure Specific predator effects
Fox	Distance (m) to nearest active fox den	Index of predator pressure Effect of local active fox dens
Proximity	Distance (m) to nearest depredated Canada goose or snow goose nest	Index of predator pressure Effect of opportunistic hunting
Nest type	One of 3 broad nest site characteristics (see Methods and Didiuk and Rusch 1979)	Index of defensive capability Measure of influence of nest type on nest depredation
Nest visitation	The number of times the female is flushed from the nest	Measure of effects of nest visitation
SITE EFFECTS Lemming	Proportion of arctic fox scat with lemming remains	Index of alternative prey abundance Effect of periodically abundant food resource on local predator pressure

Appendix 1.

Historical trends in lemming abundance and nest success of Canada geese: examining the "bird-lemming" hypothesis at Cape Churchill, Manitoba

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ABSTRACT
The "bird-lemming" hypothesis describes the dynamic interaction of predator, prey, and alternative prey in determining reproductive success in arctic-nesting birds. Data collected during annual Eastern Prairie Population (EPP) Canada goose (*Branta canadensis interior*) breeding ground surveys over the last 15 years at Cape Churchill, Manitoba provide adequate estimates of 2 of 3 parameters typically used in the analysis of this cyclic pattern; nest success and the proportion of locally active arctic fox (*Alopex lagopus*) dens. A detailed assessment of the third parameter, the annual abundance of lemmings, is lacking. In 2004, we collected and aged 794 willow (*Salix* spp.) stem scars, caused by the gnawing of collared lemmings (*Dicrostonyx richardsoni*), over 300 random points throughout a 48-km^2 study area near Cape Churchill. Scar ages ranged from 0 to 13 years. We used Poisson regression with identity kernel mean function to develop models relating ecological factors to Canada goose nesting success, and models were ranked using Akaike's Information Criterion (AIC). Model parameters included were fox abundance in the current and previous years, lemming abundance in the current and previous years, and goose nest density. We included 14 models that incorporated first order combinations of parameters. The 4 models with the most empirical support all included nest density and lemming abundance in the current year. Adding additional parameters did not improve models substantially. These data do not support the "bird-lemming" hypothesis for Cape Churchill. However, they do suggest the importance of local prey abundance in influencing predator dynamics, and subsequently Canada goose nest success.

Keywords: "bird-lemming" hypothesis, EPP Canada geese, nest success

The dynamic interaction of predator, prey, and alternative prey in determining reproductive success in arctic-nesting birds has been detailed in Russia and northern Canada (Summers 1986, Underhill et al. 1993, Bety et al. 2002). Parameters used in the analysis of this

cyclic pattern, or the "bird-lemming" hypothesis include; the proportion of nests depredated, the proportion of locally active fox dens, and the annual abundance of lemmings. Data collected during annual Eastern Prairie Population (EPP) Canada goose (*Branta canadensis interior*) breeding ground surveys over the last 10 to15 years at the Nestor One study area near Cape Churchill, Manitoba, provide estimates of the first 2 parameters, but there have been no data available on lemming abundance through the same time period. Lemming abundance has been reported to be cyclic in this region (Shelford 1943, Scott 1993, Roth 1998), yet data on recent trends in lemming abundance are unavailable.

Techniques to monitor lemming populations traditionally include intensive grid snap-trapping or live-trap mark-recapture (e.g., Roth 1998). Although these methodologies provide annual abundance estimates, they are time intensive and only provide data for sampled years. An alternative technique, originally used for voles (Danell et al. 1981) but later extended to lemmings (Danell et al. 1999, Predavec et al. 2001), involves collecting scars on the outer layers of the shrubs utilized as a food resource by small mammals. Scars result when small mammals gnaw plant stems, and depending upon local growing conditions, scars can remain visible for up to 30 years (Danell et al. 1981). Following collection of scars, dendrochronological techniques can be used to identify both the age of the scar and the age of the stem. Frequency distributions of the scar-ages provide a relative lemming abundance index for up to the previous 30 years (Danell et al. 1999, Predavec et al. 2001). At Cape Churchill, collared-lemming (*Dicrostonyx richardsoni)* populations feed primarily on willow (*Salix* spp.). Surveys for scarring on these plant species can provide evidence of local cycles of lemming abundance.

Herein, we document (1) using willow scar-age distributions to determine relative annual abundance of lemmings from 1991 to 2004 at Nestor One, and (2) examine the "bird-lemming" hypothesis as a mechanism influencing year-to-year variation in EPP Canada goose reproductive performance over the last 114 years, by modeling the relationship of lemming and fox abundance with Canada goose nest success.

STUDY AREA

The EPP breeding range includes nearly 54,000 km^2 in northern Manitoba (Malecki et al. 1980). The highest density of breeding Canada geese is found along a strip of coastal tundra habitat bordering Hudson Bay. The Nestor One study area, just south of Cape Churchill and approximately 60 km east-southeast of the town of Churchill, Manitoba, Canada (Figure 1), lies within this narrow strip of coastal tundra nesting habitat, characterized by low relief, continuous permafrost, poor drainage, beach ridges, coastal marshes, and coastal tundra vegetation (Wellein and Lumsden 1964, Didiuk and Rusch 1979). The core study area is ~ 48 km^2 and is located inside of Wapusk National Park (11,475 km^2). Coastal salt marsh, beach ridge/sedge meadow, and interior sedge meadow compose the major habitat types as outlined by Didiuk and Rusch (1979). More recently, Brook (2001) detailed the vegetation community composition and abundance throughout Wapusk National Park.

METHODS

Lemming Abundance

In 2004, 300 plots were established at random throughout Nestor One using ArcView 3.3 (ESRI®). Plots were defined based on a random coordinate and a 5-m radius around that point. At each plot, we collected 3 willow scars. Because fresh scars may be more readily detected than older scars, samples were collected based upon a random selection of the first 5 visually identified scars to reduce visibility bias. Samples were placed into a breathable brown envelope, and labeled according to plot and order of collection within the plot. If all 3 samples could not be located within a plot, we selected a random compass bearing and walked a transect in that direction for 100m. The observer continued to search within 5m of either side of the transect. If 3 samples were not collected after the first 100m, we selected another random compass bearing and walked a transect in that direction for 100m. We recorded coordinates for locations where scars were collected outside of the original plot and noted missing samples (those not found after both transects). For each scar, we identified the species of willow. All willow samples were air dried at the field site until they were brought back to the lab (4-6 weeks).

In the lab, we reexamined scars for the presence of teeth marks to determine if they were caused by lemmings. Scars that were not the result of lemming gnawing were discarded. We cut a cross-section of the stem at the scar using plant clippers and resulting willow stems were

soaked in warm water to soften. We cleaned the surface of the softened "rounds" with a scalpel, and placed them into a drying oven at 50-60°C for ≥48 hours.

We subsequently examined cross-sections using a standard dissecting microscope, measured stem diameter (mm), and counted the total number of growth rings in the stem and the number of growth rings occurring since the scarring event. Stems that could not be read clearly were removed from further analysis.

Nest Success

Since 1976, systematic breeding ground surveys have been conducted at Nestor One. Survey results are used to estimate the number of goose nests present, success rate, and cause of failure (Walter 1999, Andersen et al. 2004). We used these data to calculate annual nest success for Canada geese. We calculated the probability of daily nest survival during incubation prior to nest discovery and corrected for visibility bias based on Walter and Rusch (1997). We extended this daily survival rate to the entire 28-day incubation period, assuming that daily nest survival was constant across incubation. Because this approach uses the daily survival rate prior to nest discovery, any influence of visitation on nest survival is excluded. Annual nest success was calculated as follows:

$$(1) \qquad \text{Nest success} = (\frac{ED - fn}{ED})^{28} \; ,$$

where ED = total exposure days for all nests from incubation to discovery and fn = the number of failed nests at discovery corrected for visibility bias:

$$(2) \qquad ED = \frac{\sum d_i}{ca} + \frac{0.5 * \sum d_f}{cf} \; ,$$

where d_i is the number of days from incubation to discovery for each i, active nests; d_f is the number of days from incubation to discovery for each f, the number of already failed nests (days for failed nests are multiplied by 0.5, because it cannot be known when the failure occurred in the interval since last visit); ca is a visibility correction factor of 0.77 for active nests; and cf is a visibility correction factor of 0.39 for failed nests (Walter and Rusch 1997), where:

$$(3) \qquad fn = \frac{f}{cf}$$

Fox Abundance

As part of the annual breeding ground research activities, known arctic fox (*Alopex lagopus*) dens are visited on and near the study area. Dens are designated as active or not-active by the presence of fox or fresh fox sign indicative of an active den (Macpherson 1969). The proportion of active dens provides an estimate of annual fox abundance. Data on fox den activity were available for 1992 to 2004.

Data Analysis

Willow Scars:--We constructed frequency distributions based upon willow scar age. To correct for reduced visibility of older scars because of plant growth and plant death, we fit a non-linear model to the observed data using Poisson regression in the program Arc (© 1994-1999 D. Cook and S. Weisberg). We used this model to predict scar frequencies back in time and decay-corrected scar frequencies served as an index of lemming abundance in analyses for all years.

"Bird-Lemming" Hypothesis:--We used Poisson regression with an identity kernel mean function to evaluate the relationship of 5 factors with annual nest success. We developed a *priori* models based upon previously published descriptions of predator-prey dynamics under the "bird-lemming" hypothesis and ranked these models using Akaike's Information Criterion (AIC) (Burnham and Anderson 2002). Included parameters were:

θ_{lt} : *abundance of lemmings at time, t*

The abundance of lemmings may indirectly influence nest success by providing a primary food resource for potential nest predators, especially arctic fox. Under the "bird-lemming" hypothesis, lemming abundance should be positively correlated with nest success.

θ_{lt-1}: *abundance of lemmings at time, t - 1*

Foxes respond numerically to a peak lemming year with high den occupancy and increase in local fox population size. Lemming populations generally crash in a year following a peak, creating a food shortage. Foxes then switch to feeding on nesting birds and their eggs. Foxes are assumed not to immediately depart the area in a low lemming year.

θ_{ft}: *proportion of active fox dens at time, t*

High fox den activity is typically indicative of a peak lemming year. Under the "bird-lemming" hypothesis, foxes feed primarily on lemmings, and thus fox den activity should

be positively correlated with nest success. However, high den activity also suggests large numbers of foxes in the area, and thus may result in lower nest success.

θ_{ft-1}: *proportion of active fox dens at time, t - 1*

If den activity was high in the previous year then there should be an increase in the local fox population, assuming they remain in the area after lemmings crash or return the following year to locations with high lemming abundance in previous years. Foxes may then switch to goose nests, thus reducing nest success at time, *t*.

θ_{nd}: *nest density at time, t*

High nest densities would indicate early spring phenology, nesting females likely in better condition, and thus higher nest success (Walter 1999). The opposite may be true for late nesting years. Although median hatch date may also be indicative of annual nesting conditions, this parameter was significantly correlated with θ_{nd} (Spearman's rho = 0.69, *P* < 0.05) and thus not used in models.

RESULTS

Willow Data

A total of 844 scars was collected at Nestor One in 2004. Fifty willow samples were discarded from the analysis because they were not scars or appeared to have come from a dead plant. Because the age of a dead plant cannot be known at the time of collection, the age of a scar on a dead plant cannot be determined. We aged 794 willow stem scars and scar ages ranged from 0 to 13 years. The frequency distribution of scar ages appeared cyclic and we fit the following model to the observed data:

$$Scars = exp(-0.34*age)*(218.41+161.99*sin(2*\pi*(age+2.79)*0.36))$$

The first factor in the model accounted for the decrease in detectability of scars as a function of age (older scars were more difficult to detect and disappeared as a result of plant death or lower visibility with time). By removing this term, we predicted scar-age frequency in the absence of decreasing detectability with age. The frequency distributions of scar ages (Fig. 2) represent both the observed scar-age frequency and the model-predicted scar-age frequency. These projections are comparable to trap data in the region from 1994 to 1997 (Roth 1998).

Model Development

Fourteen models were used in analysis (single-factor $n = 5$, two-factor $n = 6$, three-factor $n = 3$). All of the top 4 models included θ_{nd} and θ_{lt} (Table 1). Parameter estimates (±SE) were 5.14 (±0.92) and -0.07 (±0.02) for θ_{nd} and θ_{lt}, respectively. Adding a third parameter (θ_{lt-1}, θ_{ft}, or θ_{ft-1}) did not significantly change estimated values of nest density and lemming abundance parameters, and all 3 additional parameters had a similar relationship with nest success (-0.02 to -0.09). In addition, AIC weights suggested nearly 1.5 times more support for the 2-parameter model, compared to any 3-parameter model.

DISCUSSION

Data presented here identify a lemming population at Cape Churchill with regular 3-year cycles. Furthermore, the implementation of the willow-scar ageing technique has allowed us to track these cycles over the past 14 years. Independent verification from trap data (Scott 1993, Roth 1998) supports observations of a cyclic lemming population and this technique as a measure of relative lemming abundance in this region.

Canada goose nest success appears primarily related to goose nest density and lemming abundance. Increased nest density, and likely early nesting phenology, is related to higher nest success, consistent with our *a priori* hypothesis. In years of low nest density, increased nest depredation, despite high lemming abundance, may be the result of a higher proportion of total nests being encountered by foxes. Female geese also may lack adequate endogenous reserves in late years, leading to increased time away from the nest, resulting in more time when nests are not adequately defended and potentially increased propensity for nest abandonment when attacked by a predator. However, the negative relationship of current lemming abundance and nest success is opposite of that predicted by the "bird-lemming" hypothesis. We propose that this may be indicative of a numerical response by predator communities to changes in lemming abundance. In years when lemmings are abundant, both arctic foxes and other predators (jeagers, owls, hawks, gulls, etc.) will be more abundant on the study area, feeding on both lemmings and on eggs of geese and other birds. In years with low lemming abundance, the number of predators on the study area drops, and foxes, opportunistic predators with potentially large home-ranges, may move to areas with higher food availability. Expanding nesting

aggregations of lesser snow geese (*Chen caerulescens caerulescens*) and Ross' geese (*C. rossii*) in this region may serve to locally support fox populations in years of low lemming abundance.

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Table 1. Ranking of 14 *a priori* models developed to describe patterns of nest success in Eastern Prairie Population Canada geese at Cape Churchill, Manitoba from 1992-2004..

Model	Δ_{AIC}	w
$\theta_{nd} + \theta_{lt}$	0.00	0.376
$\theta_{nd} + \theta_{lt} + \theta_{lt-1}$	0.87	0.244
$\theta_{nd} + \theta_{lt} + \theta_{ft}$	1.23	0.204
$\theta_{nd} + \theta_{lt} + \theta_{ft-1}$	1.62	0.168
θ_{nd}	9.30	0.003
$\theta_{nd} + \theta_{lt-1}$	10.43	0.002
$\theta_{nd} + \theta_{ft-1}$	11.09	0.001
$\theta_{nd} + \theta_{ft}$	11.24	0.001
$\theta_{ft-1} + \theta_{lt}$	18.86	3.07E-05
θ_{lt}	22.73	4.44E-06
$\theta_{lt} + \theta_{lt-1}$	23.15	3.6E-06
θ_{ft-1}	23.22	3.48E-06
θ_{ft}	28.37	2.66E-07
θ_{lt-1}	28.40	2.62E-07

θ_{lt} : abundance of lemmings at time, t

θ_{lt-1}: abundance of lemmings at time, t - 1

θ_{ft}: proportion of active fox dens at time, t

θ_{ft-1}: proportion of active fox dens at time, t - 1

θ_{nd}: nest density at time, t

Figure 1. Hudson Bay Lowlands and Nestor One Study Area near Cape Churchill, MB
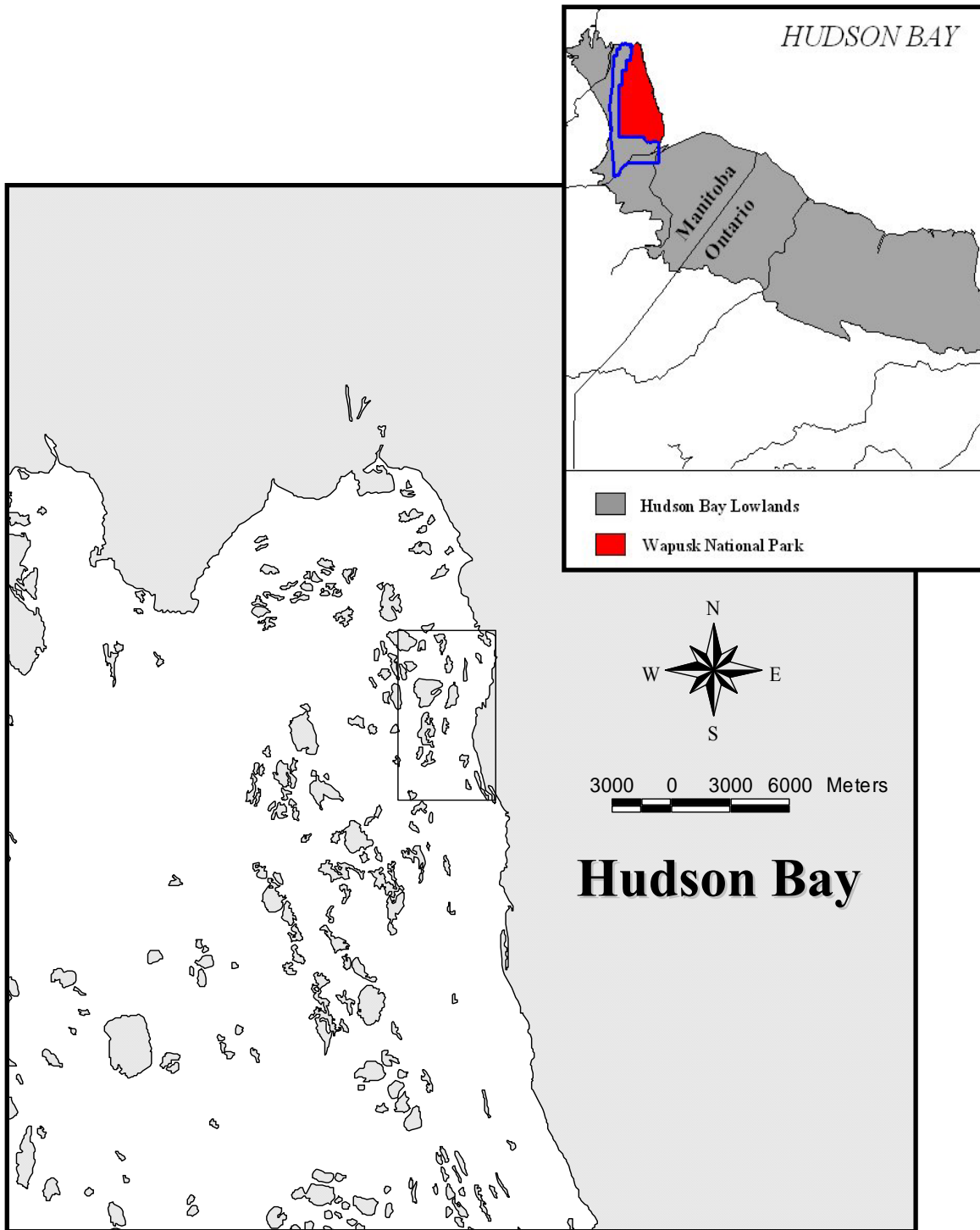
Figure 2. Observed and model-predicted willow scar age frequency from Cape Churchill, Manitoba: 1991 – 2004.
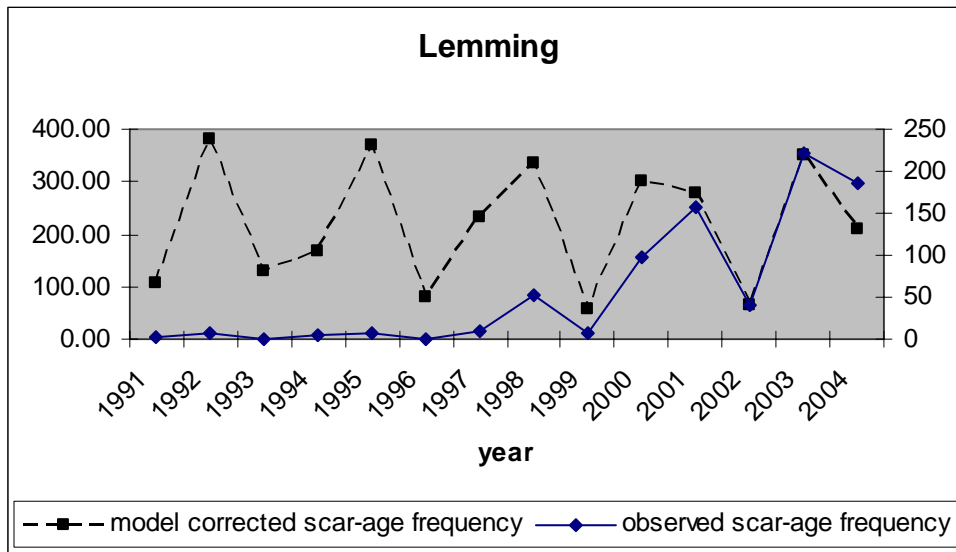
Figure 3. Lemming abundance index and annual Eastern Prairie Population Canada goose nest success at Cape Churchill, Manitoba: 1991 – 2004.