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David E. Andersen

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Name of Faculty Advisor

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Signature of Faculty Advisor

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Date

GRADUATE SCHOOL

**HISTORICAL TRENDS IN COLLARED LEMMING (*DICROSTONYX  
RICHARDSONI*) ABUNDANCE AND NEST SUCCESS OF EASTERN PRAIRIE  
POPULATION (EPP) CANADA GEESE (*BRANTA CANADENSIS INTERIOR*) IN  
NORTHERN MANITOBA: EVALUATING THE “BIRD-LEMMING”  
HYPOTHESIS**

A THESIS  
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**CHAPTER 1:  
HISTORICAL TRENDS IN COLLARED LEMMING ABUNDANCE NEAR  
CAPE CHURCHILL, MANITOBA, CANADA**

## ABSTRACT

Regular, multi-annual cycles observed in the population abundance of small mammals in arctic and sub-arctic ecosystems across many regions has stimulated substantial research, particularly among population ecologists. Hypotheses addressing the cause of regular cycles include mechanisms such as predator-prey interactions, limitation of food resources, and migration or dispersal, as well as abiotic factors such as cyclic climatic variation and environmental stochasticity. However, long-term time-series of population data for small mammals in North America are generally lacking. Small rodent abundance is typically quantified by trapping grids and capture-mark-recapture techniques. These methods are time-consuming and provide data only for the time period during which trapping occurred. Alternative approaches may provide useful information regarding population trends, especially in remote areas where logistics make intensive trapping and marking of individual small mammals impractical. In 2004 and 2005, we used indirect methods to estimate trends in population size of collared lemmings (*Dicrostonyx richardsoni*), and evaluated the extent of synchrony between lemming populations at 2 coastal tundra study areas separated by ~ 60 km near Cape Churchill, Manitoba, Canada. We collected scars on willow plants (*Salix* spp.) resulting from lemming feeding. Scar-ages ranged from 0 to 13 years at both study areas. Scar-age frequency appeared cyclic and we used Poisson regression to model the observed scar-age frequency. Lemming populations cycled with 2.83 year periodicity and the phase of the cycle was synchronous between the 2 study areas. Modeling scar-age frequency data resulted in estimates of relative lemming abundance at broad spatial and temporal scales, and allowed us to evaluate synchrony between study areas.

## INTRODUCTION

The population dynamics of small mammals in arctic and sub-arctic ecosystems have been well documented (Elton 1942, Shelford 1943, Stenseth and Ims 1993, Scott 1993, Danell et al. 1999). Lemmings (*Dicrostonyx* spp.; *Lemmus* spp.) and voles (*Microtus* spp.; *Clethrionomys* spp.) in Europe, Asia, and North America exhibit both regular cyclic and non-cyclic trends in abundance over time (Stenseth and Ims 1993, Erlinge et al. 1999, Predavec et al. 2001). Regular, multi-annual cycles observed in the abundance of populations across many regions has stimulated substantial research, particularly in population ecology (see reviews in Kendall et al. 1999, Stenseth 1999). Hypotheses addressing the cause of regular cycles (reviewed in Stenseth and Ims 1993), include mechanisms such as predator-prey interactions (Erlinge et al. 1983, Steen et al. 1990), limitation of food resources (Pitelka 1964, Laine and Henttonen 1983), and migration or dispersal (Krebs 1978), as well as abiotic factors such as cyclic climatic variation and environmental stochasticity (Scott 1993). Studies in Fennoscandia suggest that the intensity of multi-annual cycles may follow a latitudinal gradient with more northern populations (> 60°N Latitude) having multi-annual cycles and southern populations exhibiting only seasonal variation in population size (Henttonen et al. 1985, Stenseth 1999). Despite the causes of multi-annual fluctuations, variation in availability of a potential food resource for arctic and sub-arctic predators likely has implications for regional trophic dynamics (Angelstam et al. 1984, Summers 1986, Underhill et al. 1993, Bêty et al. 2002, Kjellander and Nordstom 2003). However, to rigorously evaluate hypotheses regarding the causes of observed cyclic population dynamics and potential trophic interactions that may result, long-term time-series of microtine abundance are

needed. In Europe, long-term data sets for voles and other small mammals exist (Stenseth 1999), yet extensive data sets for small mammals in North America are lacking (however see, Shelford 1943, Scott 1993).

Small rodent abundance is typically quantified using trapping grids and capture-mark-recapture techniques (Framstad et al. 1993, Pitelka and Batzli 1993, Roth 2003). These methods are time-consuming and provide data only for the time period in which the trapping occurred. Data from a small number of years may not reveal the extent of population variation or long-term trends in abundance (Berryman 2002). In addition, trapping is frequently conducted at only small spatial scales due to logistical constraints. This limits the extent to which inference can be made regarding population abundance and synchrony of population dynamics at broader spatial scales. As asynchrony in microtine population cycles may occur at scales as small as 50 – 100 km (Predavec et al. 2001), extending conclusions based on population data from 1 location to a landscape or regional level may not be warranted. Also, to evaluate the influence of small mammal population variation on predator species dynamics, especially those with large home-ranges such as arctic fox (*Alopex lagopus*), or that may be nomadic [e.g. snowy owl (*Nyctea scandiaca*), rough-legged hawk (*Buteo lagopus*)], data are needed on relative small mammal abundance at a broader spatial scale than typically provided by trapping data.

An alternative technique to trapping, 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 food by small mammals. Scars are created by gnawing of the plant by the animal. Depending upon local growing

conditions, scars can remain visible for up to 30 years (Danell et al. 1981, Danell et al. 1999). By collecting a random sample of scars from an area and determining scar ages, it is possible to estimate the relative abundance of small mammals for previous years. Although collecting samples can be time intensive, lab analysis is efficient, and ultimately this technique provides a method for evaluating relative small mammal abundance at both broad spatial and temporal scales. Previous analysis of these datasets has been limited to identifying peaks in the plotted scar-age distribution as evidence of peaks in mammal abundance (Danell et al. 1999, Predavec et al. 2001). In addition, the probability of detecting a scar is higher for more recent scars because older scars can be harder to identify due to plant growth, and there are likely fewer old scars available to be collected because of natural plant death. Therefore, the observed scar-age frequency distribution typically decays as a function of time. So, although generally useful at identifying phases of population cycles, previously these data have not lent themselves to extensive analysis. More sophisticated statistical techniques are needed that correct for the effects of visibility bias and plant death to make these data more useful (Predavec et al. 2001).

Along the low-lying coastal tundra regions of the Hudson Bay Lowlands near Cape Churchill, Manitoba, Canada, the collared-lemming (*Dicrostonyx richardsoni*) is the primary small mammal. Multi-annual population cycles have been observed near the town of Churchill, Manitoba and may be influenced by fall and winter weather conditions (Shelford 1942, Scott 1993). However, the magnitude of population cycles and synchrony across tundra areas of the Hudson Bay Lowlands is unknown. Collared lemmings feed primarily on willow (*Salix* spp.; Batzli 1993) and surveys for scarring on

these plant species could provide long-term time series of local relative lemming abundance.

Herein we report on (1) the collection of willow scars from 2 distinct areas of coastal tundra near Cape Churchill, Manitoba, Canada, (2) modeling observed scar-age distributions and correcting for visibility bias to provide an estimate of historical relative lemming abundance, and (3) examining the extent of synchrony between 2 disjunct survey locations. Specifically, our objectives were to assess (1) the utility of scar-age frequency to modeling past lemming abundance, and (2) the spatial synchrony of lemming population fluctuations.

## **STUDY AREA**

The Hudson Bay Lowlands in Manitoba, Canada are comprised of an area of low-lying tundra and boreal forest ecosystems along the western shores of Hudson Bay (Fig. 1). The region extends from Southern James Bay in Ontario (52° 54' N, 82° 10' W) northwest to just north of the town of Churchill, Manitoba (59° 27' N, 94° 53' W). The Nestor One study area (hereafter, NO; 58° 34' N, 93° 11' W) is just south of Cape Churchill and approximately 60 km east-southeast of the town of Churchill. The core study area is ~ 48 km<sup>2</sup> and is located inside of Wapusk National Park (11,475 km<sup>2</sup>). It lies within a narrow strip of coastal tundra 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). Coastal salt marsh, beach ridge/sedge meadow, and interior sedge meadow compose the major habitat types (Didiuk and Rusch 1979, Brook 2001). Seven species of willow can be found at NO including, *Salix lanata*, *S. reticulata*, *S. brachycarpa*, *S. candida*, *S. pedicellaris*, *S.*

*arctophila*, and *S. planifolia* (Brook 2001). The climate in this area is influenced strongly by Hudson Bay, which can remain frozen for up to 9 months of the year. Previously, small mammal trap data from this location suggested that collared lemmings were the only small mammals that occurred on the study area (Roth 2003).

The Broad River study area (hereafter, BR; 58° 07' N, 92° 51' W) is located ~ 60 km south of NO along the Hudson Bay coast and also lies within Wapusk National Park. The core study area, just north of the river mouth, is ~ 20 km<sup>2</sup> and consists of the same general habitat types as NO (Brook 2001). All willow species found at NO occur at BR. However, BR is much closer to the boreal forest edge than NO and this may influence the small mammal species composition at BR. No trap data or other small mammal survey data currently exist for BR.

## **METHODS**

In 2004, we established 300 plots at random throughout NO using ArcView 3.3 (Environmental Systems Research Institute, Inc © 2002). Each plot consisted of the Universal Transverse Mercator (UTM) coordinate point and a 5 m radius buffer around that point. At each plot, we collected 3 willow scars. Because fresh scars may be easier to identify than older scars, we collected samples based upon a random selection of the first 5 visually identified scars to reduce visibility bias. If we could not locate all 3 samples within a plot, we selected a random compass heading and traversed a transect in that direction for 100 m. We continued to search 5 m either side of the transect and stopped to collect samples when detected. If we did not collect all 3 samples after the first 100 m, we selected another random compass heading, which we followed for 100 m. We recorded the UTM coordinates for locations where scars were collected outside of the

original plot and missing samples (locations where we did not find scars on either transect). In 2005, we collected willow scars along 10 randomly established transects and opportunistically during other research activities at BR. As at NO, we used a 5 m radius buffer around each transect or collection point and collected a random sample of scars. In 2004 and 2005, we determined if scars were caused by lemming gnawing based on the presence of teeth marks. If possible, we identified the willow species for each scar collected. We placed samples into individual breathable brown paper envelopes, and labeled each according to plot and order of collection within the plot. We air dried all willow samples until we brought them to the lab for analyses.

In the lab, we reexamined scars for the presence of teeth marks to determine if they were caused by lemmings. Scars not the result of lemming gnawing or that were collected from a dead plant were discarded from further analysis. The age of a dead plant cannot be known because growth has stopped, thus the age of a scar on a dead plant cannot be determined. We cut a cross-section of the scar using plant clippers and soaked it in warm water for 5 minutes. We cleaned the surface of the softened “round” with a scalpel, and placed the samples into a drying oven at 50-60°C for  $\geq 48$  hours (Predavec et al. 2001).

We examined all willow cross-sections using a dissecting microscope. We measured the stem diameter (mm), determined the total number of growth rings on the stem (stem age), and those occurring since the scarring event (scar age). We removed from further analysis stems that could not be read clearly. We calculated the age of the stem when it was scarred as the stem age minus the scar age. We report mean (SE) values for stem diameter, stem age, and stem age when scarred for NO and BR. We used

2-tailed  $t$ -tests to compare these values between study areas. To evaluate the extent of visibility bias, we used analysis of variance (ANOVA) to examine variation in scar ages based on the order in which the scars were visually identified in the field.

We used generalized Poisson regression with a non-linear kernel mean function to fit a statistical model to the raw scar-age frequency data. Because older scars may be harder to see due to plant growth and older scars may be less abundant due to plant death, we included an exponential decay term in the model of the observed scar-age frequency. By removing this term, we could predict scar-age frequency in the absence of reduced visibility and plant death. The predicted scar abundance provides a measure of relative collared lemming abundance. We initially fit a model to the combined data for both locations. Then, we fit a model with common decay functions between the sites but different trend parameter estimates. Next, we split the data by study areas and fit separate regression models. Using these 3 model forms, we examined whether the trend in lemmings cycles was the same for NO and BR. We predicted that if lemming population trends were synchronous between the 2 study areas the model that pooled data from both locations would perform at least as well as separate models for each location or the model with a common decay but separate trends. Lastly, we evaluated to what extent the reduction in scar detection differed between NO and BR by fitting a model with common trend functions but different decay terms. We compared all models using Akaike's Information Criterion corrected for small sample sizes (hereafter  $AIC_c$ ; Burnham and Anderson 2002).

We used the predicted frequency of scar ages from the best-supported model as a measure of relative lemming abundance for each year. We examined the parameter

estimates from the model with the most support to evaluate both the decay rate of scars and indirectly, the periodicity and amplitude of the lemming population. We calculated 95% confidence intervals (hereafter C.I.) using standard Wald estimates for linear parameters estimates. However, because Wald estimates may lead to over-confidence when assessing non-linear parameter estimates, we followed the procedures described in Cook and Weisberg (1990) to estimate 95% C.I. for non-linear parameters. We generated 95% C.I. of the predicted scar-age frequency for each model using the delta method (Cramér 1946, Oehlert 1992). We used SAS v.9.1 (SAS Institute, Inc. © 2003) and Arc (D. Cook and S. Weisberg © 2004) for statistical analyses.

## **RESULTS**

In 2004, we collected 844 scars at NO. After inspection in the lab, we discarded 50 samples from the analysis because they were not scars caused by lemmings, appeared to have come from a dead plant, or the scar age could not be accurately determined. We aged 794 willow stem scars, with  $\geq 1$  from each of the 7 willow species that occur at NO (Table 1). Scar ages ranged from 0 to 13 years with a mean of 2.29 (SE = 0.08). Stem diameter averaged 4.25 (SE = 0.06) mm and the mean stem age when collected was 7.74 (SE = 0.13) years. The average stem age when the scarring event occurred was 5.46 (SE = 0.11) years.

In 2005, we collected 253 scars at BR along 10 random transects ( $n = 110$ ) and opportunistically during other research activities ( $n = 143$ ). After inspection in the lab, we removed 14 samples from further analysis. We aged 239 willow scars and there was  $\geq 1$  scar from each of the 7 local willow species. Scar ages ranged from 0 to 13 years with a mean of 2.98 (SE = 0.15) years. The stem diameter ( $n = 238$ ) averaged 4.78 (SE =

0.10) mm and the mean age of stems ( $n = 238$ ) collected was 8.35 (SE = 0.20) years. The mean stem age when scarred ( $n = 238$ ) was 5.34 (SE = 0.18) years. Both the mean age when collected ( $t = 2.35$ ,  $df = 1,022$ ,  $P < 0.02$ ) and the mean stem diameter ( $t = 4.51$ ,  $df = 1,027$ ,  $P < 0.0001$ ) were larger when compared to scars collected at NO (Table 1). However, we detected no significant difference ( $t = 0.49$ ,  $df = 1,022$ ,  $P > 0.62$ ; Table 1) in the mean stem age when scarred between NO and BR. Based on ANOVA, mean scar ages were not strongly associated with the order in which they were visually identified ( $F_{4,763} = 1.24$ ,  $P = 0.29$ ).

The observed frequency distribution of scar ages appeared cyclic at both locations (Fig. 2) and we fit the following general model (hereafter, Common) to the observed data:

$$E(Y|X) = N * \exp(\ln(0.5) * X / \alpha_0) * (\alpha_1 + \alpha_2 * \sin(2 * \pi * (X - \alpha_3) / \alpha_4))$$

where,  $Y$  is the count of scars of age  $X$ ,  $N$  is the total number of scars in the sample,  $X$  is the scar age in number of years before present,  $\alpha_0$  is the half-life for scars (i.e., on average, half of the scars will become undetectable every  $\alpha_0$  years),  $\alpha_1$  and  $\alpha_2$  are tuning parameters for the amplitude of the curve,  $\alpha_3$  is a another tuning parameter that shifts the period to match the data, and  $\alpha_4$  is the period corresponding to scar age and indirectly to the lemming population. We fit 3 variations of the Common model structure. The first allowed for separate trend functions for each study area but a common decay term (hereafter, Trend):

$$E(Y|X) = G * N * \exp(\ln(0.5) * X / \alpha_0) * (\alpha_1 + \alpha_2 * \sin(2\pi(X - \alpha_3) / \alpha_4)) + (1 - G) * N * \exp(\ln(0.5) * X / \alpha_0) * (\alpha_{11} + \alpha_{21} * \sin(2\pi(X - \alpha_{31}) / \alpha_{41}))$$

All parameters are the same as the Common model however, here  $G$  represents study area and equals 1 for NO and 0 for BR. The second variation of the Common model fit a unique model to each of the study areas (hereafter, Separate):

$$E(Y|X) = G * N * \exp(\ln(0.5) * X / \alpha_0) * (\alpha_1 + \alpha_2 * \sin(2\pi(X - \alpha_3) / \alpha_4)) + (1 - G) * N * \exp(\ln(0.5) * X / \alpha_{01}) * (\alpha_{11} + \alpha_{21} * \sin(2\pi(X - \alpha_{31}) / \alpha_{41}))$$

Lastly, to evaluate the degree to which the reduction in willow scar detection rates as a function of age varied between the 2 study areas, we allowed for a common trend function but different decay terms. Such variation may, for example, occur as the result of differing local growing conditions. This model with unique decay terms for each study area (hereafter, Decay) took the following form:

$$E(Y|X) = G * N * \exp(\ln(0.5) * X / \alpha_0) * (\alpha_1 + \alpha_2 * \sin(2\pi(X - \alpha_3) / \alpha_4)) + (1 - G) * N * \exp(\ln(0.5) * X / \alpha_{01}) * (\alpha_1 + \alpha_2 * \sin(2\pi(X - \alpha_3) / \alpha_4))$$

Overall, the Common model had the lowest AIC<sub>c</sub> value, indicating it was likely the best fit of the 4 models evaluated (Table 2). None of the other models were within 2 AIC<sub>c</sub> units of the Common model, which had a 92% probability of being the best model based on AIC<sub>c</sub> weights ( $w_i$ ). All other models received substantially less support (Table 2). The predicted scar-age frequency values for the Common model compared well with those observed at both NO and BR (Fig. 2).

The first term in the models evaluated [ $\exp(\ln(0.5) * X / \alpha_0)$ ] accounted for the exponential decay in detection of scars as a function of age (older scars are more difficult to detect and disappear as a result of plant death). By removing this term, we predicted scar-age frequency in the absence of bias as the result of scar age. Using the Common model and the point estimates of parameter values for the Common model, we removed

the exponential decay term and plotted the predicted scar-age distribution in the absence of reduced visibility as a function of scar-age separately for NO and BR (Fig. 3). The 95% C.I. for the predicted scar-age frequencies in the absence of decay were typically larger for older scars (Fig. 3).

As with the observed scar-age distributions at the 2 study areas, qualitatively the predicted distributions of willow scar-ages were nearly identical between the 2 study areas. Model selection results suggested that the frequency distribution of willow scar-ages could be modeled adequately using the same parameter estimates (Common model) for both NO and BR. There was strong synchrony in scar-age frequency and subsequently relative lemming abundance between study areas.

The parameter estimates for the Common model indicated a regular period ( $\alpha_4$ ) of 2.832 (SE = 0.024) years for lemming cycles over the last 14 years in this region (Table 3). We forced amplitude to remain constant due to small sample size ( $n = 15$  years), however, there appears to have been a trend shift over the last 2 cycles; from a pattern of low, mid, high and then a crash back to low in the 1990s to a pattern of low, high, mid, and then low again. This change is apparent at both study areas (Fig. 3). The parameter estimate for  $\alpha_0$  represents the half-life of willow scars. Based on the Common model estimates, half life of scars was 2.131 (SE = 0.077) years (Table 3).

## **DISCUSSION**

Using the scar-sampling techniques first described by Danell et al. (1981), herein we present a new method of analysis of lemming abundance in the Hudson Bay Lowlands of northern Manitoba. Such analyses allow for assessment of spatial synchrony of lemming population trends and provide estimates of historical relative

lemming abundance. The collared lemming populations at Nestor One and Broad River appear strongly cyclic with approximately 3-year periods. Although we have no ability to compare directly across other locations, as we are unaware of concurrent studies examining lemming abundance in this region, previous studies have identified 3- to 4-year cycles in collared lemming abundance at the town of Churchill (Shelford and Twomey 1941, Shelford 1943, Scott 1993). Recent trapping that occurred at Cape Churchill (1994 – 1997; Roth 2003) was temporally limited but suggested a 4-year period in lemming abundance in this area. Based on our data, the lemming cycles appear to be synchronous between Nestor One and the Broad River. If lemming populations were asynchronous between Nestor One and Broad River, we would expect that either the Separate or Trend models would have been the best-supported model of those evaluated. Although synchrony in microtine populations can occur across a broad spatial scale (Predavec et al. 2001), Wrigley (1974) suggested that lemmings were asynchronous between the town of Churchill and the Seal River to the north, a distance of only 56 km, and that further north (208 km) the phase of the lemming population was again different than the other 2 locations. However, Shelford and Twomey (1941) asserted that peaks in lemming abundance near Cape Churchill roughly coincided with peaks in abundance near Churchill Town. These observations are somewhat unexpected in that near the town of Churchill tundra patches are inter-mixed with patches of boreal forest. At Cape Churchill and the Seal River, low-lying coastal tundra predominates and the boreal forest edge is >10 km from these locations. Therefore, one might expect synchrony between the Seal River and Cape Churchill based on general habitat and climatic conditions, rather than

the latter and the town of Churchill. Our data clearly identify synchrony in the collared lemming populations at 2 coastal tundra locations separated by 60 km.

Although the cause of landscape-level synchrony in populations is not known, one hypothesis suggests wide-ranging nomadic avian predators may influence synchrony of rodent populations (Ydenberg 1987). Under Ydenberg's (1987) hypothesis, if populations were asynchronous, nomadic predators would over-exploit certain populations that may be at peak abundance when others are at a population low. This potential for exploitation ultimately makes synchrony more advantageous to all local prey populations. It has been documented that potential avian predators of lemmings are more abundant in years with high lemming abundance in this region (Shelford 1943, Smith and Foster 1957), however, any causal link between their presence and regional synchrony in lemming populations is not known.

Our results also provide insight on the detection probability of scars. Our data suggest that scar identification is not biased by differences in visibility between old and young scars. Therefore, it may be reasonable to collect all scars identified during a survey without randomizing the order in which they are collected. This would increase the efficiency of scar collection. Furthermore, although the decay rates between our 2 study areas were similar, we envision that this may not always occur, particularly if study areas are located far apart. Similar to the analysis presented here, future studies should consider a model(s) that allows for separate decay rate parameters for each study area.

Although snap-trapping and capture-mark-recapture techniques provide direct estimates of local lemming abundance, data are often spatially and temporally limited. Our study provides a method of estimating lemming abundance indirectly. Although

using dendrochronology is not unique to this study (Danell et al. 1980, Danell et al. 1999, Predavec et al. 2001), our application of generalized Poisson regression with a non-linear kernel mean function to generate visibility bias-corrected scar-age frequencies is new. By accounting for reduced visibility of older scars and plant death, we generated a measure of late fall to early summer relative lemming abundance that can be used in additional studies. Furthermore, time-series data for up to 14 years, and longer in other studies (see Danell et al. 1999, Predavec et al. 2001), can be acquired through 1 or 2 field season(s) of data collection. The ease of willow-scar collection also makes this technique appealing to studying lemming dynamics over a broad spatial scale.

Our estimates of the lemming cycles and relative abundance using the willow scars and subsequent non-linear modeling efforts at Nestor One agreed well with limited trap data and anecdotal evidence from this study area. Previous studies that applied both willow-scar analysis and local trapping concurrently support the use of dendrochronology to accurately estimate local relative lemming abundance (Danell et al. 1999, Predavec et al. 2001). We are limited in our comparisons, but it appears that our application of this technique along the Hudson Bay Lowlands, at least at Nestor One, has yielded results corroborated by limited independent data on lemming abundance and population cycles. Since 1976, annual Canada goose (*Branta canadensis interior*) breeding ground surveys have been conducted near Cape Churchill. During surveys, observers have informally assessed lemming abundance by recording the presence of lemmings and lemming sign (e.g., nests, burrows, scat). These observations of relative lemming abundance have been reported in annual reports to the Mississippi Flyway Council Technical Section. These informal data corroborated our estimated relative abundance in nearly all years (1991 to

2005). However, in some years (e.g., 2002 and 1995) observational data suggested moderate lemming densities whereas our model identified these years as low and high, respectively. Roth (2003) conducted small mammal trapping at Nestor One between 1994 and 1997. Only in 1995 did these data differ from ours, which suggested that lemmings were at a population peak in the winter and spring of 1995. However, trap data collected in late-June to August of 1995 identified a significant decline in lemming abundance from 1994 population levels. This suggests that the lemming population was in a period of decline between late winter 1995 and late summer 1995, and that the peak in population may have occurred sometime during the summer of 1994. Our estimates of relative lemming abundance in 1994 and 1995 are limited by small samples sizes with only 6 scars aged to 1995 and 5 scars aged to 1994. The paucity of scars from these years results in low precision of the estimated relative lemming abundance for these years at Nestor One (Fig. 3a). At a minimum, our model estimates capture the overall phase of the lemming population cycle over all years evaluated when compared to limited independent data.

Our modeling techniques incorporated a few simplifying assumptions. First, we assumed that feeding on willow stems does not drastically influence the overall availability of willow in an area. Therefore, the number of scars represented the relative abundance of lemmings directly and current lemming abundance did not influence future willow availability. Although arctic plant growth may cycle, such cycles have not been shown to occur as the result of lemming browsing (Laine and Henttonen 1983). Furthermore, it is unclear whether a change in plant growth would influence lemming gnawing rates and subsequently the number of observed scars. It may be more likely that

the cycles occurring in the plant growth would cause a decline in food resource for the lemmings, and thus lemming populations would crash.

Second, because this dendrochronological technique quantifies the amount of growth that has occurred since the scarring event, estimates of relative lemming abundance covered the entire time period since the previous growing season ended until the time of collection. Plant growth ends in early to mid-fall in arctic and sub-arctic ecosystems. Therefore, our analyses provide a measure of relative lemming abundance for a rather long interval within each year. If a lemming population crash occurred within that time period, extrapolating estimated relative lemming abundance to the following late-spring and early-summer may be inappropriate. However, previous studies (e.g. Erlinge et al. 1999, Predavec et al. 2001) have demonstrated agreement between willow scar data and summer trapping data. Intra-annual variation in lemming abundance, however, cannot be accounted for using this technique.

Third, we assumed all small mammals within the study area that may create scars are cycling with some degree of synchrony. Previous studies near the town of Churchill suggested that lemmings may lag behind voles by 1 year in the peak population phase, but that both populations would likely experience a crash in the same year (Shelford 1943). Trapping conducted at Nestor One in the 1990s (Roth 2003) did not result in the capture of any other small mammal species, but such data for Broad River are lacking. However, the synchrony in lemming population cycles between Broad River and Nestor One indicated in this study suggested that even if species were present at Broad River that do not occur at Nestor One, they likely exhibit similar population fluctuations as the local collared lemming population.

We have evaluated the population trends of collared lemmings within the tundra ecosystem of the Hudson Bay Lowlands near Cape Churchill, Manitoba. Our ability to explicitly model the observed scar-age frequencies allowed for an analysis of lemming population synchrony across 2 study areas and generated estimates of relative lemming abundance for the previous 14 years in this region. Although further studies using scar collection and concurrent small mammal trapping may lend additional support to this technique, we feel the analysis presented here is a potentially useful approach to estimating past lemming abundance. Direct estimates of wildlife population abundance are time intensive and spatially and temporally limited. Continued efforts, similar to those presented here, should be made to increase the rigor of indirect methods of population quantification. These may ultimately provide the most efficient way to gather data on species across both space and time in a variety of arctic and sub-arctic landscapes.

#### **LITERATURE CITED**

- Angelstam, P., E. Lindstrom, and P. Widen. 1984. Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. *Oecologia* 62:199-208.
- Batzli, G.O. 1993. Food selection by lemmings. Pages 281-301 *in* N.C. Stenseth and R.A. Ims, editors. *The biology of lemmings*. Academic Press, London, U.K.
- Bêty, J., G. Gauthier, E. Korpimäki, and J.F. Giroux. 2002. Shared predators and indirect trophic interactions: lemming cycles and arctic nesting geese. *Journal of Animal Ecology* 71:88-98.
- Berryman, A.A. 2002. Population cycles: causes and analysis. Pages 3-28 *in* A.A. Berryman, editor. *Population cycles: the case for trophic interactions*. Oxford University Press. Oxford, U.K.
- Brook, R.K. 2001. Structure and dynamics of the vegetation in Wapusk National Park and the Cape Churchill Wildlife Management Area of Manitoba: community and

- landscape scales. Thesis, Natural Resources Institute, University of Manitoba, Winnipeg, Manitoba, Canada. 290pp.
- Burnham, K.P. and D.R. Anderson. 2002. Model selection and inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA. 488pp.
- Cook, R.D. and S. Weisberg. 1990. Confidence curves in nonlinear regression. *Journal of the American Statistical Association* 85:544–551.
- Cramér, H. 1946. *Mathematical methods of statistics*. Princeton University Press. Princeton, New Jersey, USA.
- Danell, K., L. Ericson, and K. Jakobsson. 1981. A method for describing former fluctuations of voles. *Journal of Wildlife Management* 45:1018-1021.
- \_\_\_\_\_, S. Erlinge, G. Högstedt, D. Hasselquist, E.B. Olofsson, T. Seldal, and M. Svensson. 1999. Tracking past and ongoing lemming cycles on the Eurasian tundra. *Ambio* 28:225-229.
- Didiuk, A.B. and D.H. Rusch. 1979. Ecology of broods of Canada geese in northern Manitoba. Final Research Report, Wisconsin Cooperative Wildlife Research Unit, Madison, Wisconsin, USA. 216pp.
- Elton, D.S. 1942. *Voles, mice, and lemmings*. Oxford Press. Oxford, UK. 496pp.
- Erlinge, S., K. Danell, P. Frodin, D. Hasselquist, E. Olofsson, T. Seldal, and M. Svensson. 1999. Asynchronous population dynamics of Siberian lemmings across the Palearctic tundra. *Oecologia* 119:493-500.
- \_\_\_\_\_, G. Göransson, L. Hansson, G. Högstedt, O. Liberg, I.N. Nilsson, T. Nilsson, T. von Schantz, and M. Sylven. 1983. Predation as a regulation factor on small rodent populations in southern Sweden. *Oikos* 40:36-52.
- Framstad, E., N.C. Stenseth, and E. Ostbye. 1993. Time series analysis of population fluctuations of *Lemmus lemmus*. Pages 97-155 in N.C. Stenseth and R.A. Ims, editors. *The biology of lemmings*. Academic Press, London, U.K.
- Henttonen, H., A.D. McGuire, and L. Hansson. 1985. Comparisons of amplitudes and frequencies (spectral analyses) of density variation in long term data sets of *Clethrionomys* species. *Annales Zoologici Fennici* 6:221-228.
- Kendall, B.E., C.J. Briggs, W.W. Murdoch, P. Turchin, S.P. Ellner, E. McCauley, R.M. Nisbet, and S.N. Wood. 1999. Why do populations cycle? A synthesis of statistical and mechanistic modeling approaches. *Ecology* 80:1789-1805.

- Kjellander, P. and J. Nordström. 2003. Cyclic voles, prey switching in red fox, and roe deer dynamics – a test of the alternative prey hypothesis. *Oikos* 101:338-344.
- Krebs, C.J. 1978. A review of the Chitty hypothesis of population regulation. *Canadian Journal of Zoology* 56:2463-2480.
- Laine, K. and H. Henttonen. 1983. The role of plant production in microtine cycles in northern Fennoscandia. *Oikos* 40:407-418.
- Oehlert, G.W. 1992. A note on the delta method. *The American Statistician* 46:27-29.
- Pitelka, F.A. 1964. The nutrient recovery hypothesis for arctic microtine cycles. I. Introduction. Pages 55-56 in D. Crisp, editor. *Grazing in terrestrial and marine environments*. Blackwell Scientific Press, Oxford, U.K.
- \_\_\_\_\_ and G.O. Batzli. 1993. Distribution, abundance and habitat use by lemmings on the north slope of Alaska. Pages 213-236 in N.C. Stenseth and R.A. Ims, editors. *The biology of lemmings*. Academic Press, London, U.K.
- Predavec, M., C.J. Krebs, K. Danell, and R. Hyndman. 2001. Cycles and synchrony in the collared lemming (*Dicrostonyx groenlandicus*) in arctic North America. *Oecologia* 126:216-224.
- Roth, J.D. 2003. Variability in marine resources affects arctic fox population dynamics. *Journal of Animal Ecology* 72:668-676.
- Scott, P.A. 1993. Relationship between onset of winter and collared lemming abundance at Churchill, Manitoba, Canada: 1932 – 1990. *Arctic* 46:293-296.
- Shelford, V.E. 1943. The abundance of collared lemming (*Dicrostonyx groenlandicus* (Tr.) var. *richardsoni* Mer.) in the Churchill area, 1929 to 1940. *Ecology* 24:472-484.
- \_\_\_\_\_ and A.C. Twomey. 1941. Tundra animal communities in the vicinity of Churchill, Manitoba. *Ecology* 22:47-69.
- Smith, D.A. and J.B. Foster. 1957. Notes on the small mammals of Churchill, Manitoba. *Journal of Mammalogy* 38:98-114.
- Steen, H., N.G. Yoccoz, and R.A. Ims. 1990. Predators and small mammal cycles: an analysis of a 79-year time series of small rodent population fluctuations. *Oikos* 59:115-120.

- Stenseth, N.C. 1999. Population cycles in voles and lemmings: density dependence and phase dependence in a stochastic world. *Oikos* 87:427-461.
- Stenseth, N.C. and R.A. Ims. 1993. Population dynamics of lemmings: temporal and spatial variation – an introduction. Pages 61-96 in N.C. Stenseth and R.A. Ims, editors. *The biology of lemmings*. Academic Press, London, U.K.
- Summers, R.W. 1986. Breeding production of dark-bellied brent geese *Branta bernicla bernicla* in relation to lemming cycles. *Bird Study* 33:105-108.
- Underhill, L.G., R.P. Prys-Jones, E.E. Syroechkovski, N.M. Groen, V. Karpov, H.G. Lappo, M.W.J van Roomen, A. Rybkin, H. Schekkerman, H. Siekman, and R.W. Summers. 1993. Breeding of waders (Charadrii) and brent geese *Branta bernicla bernicla* at Prochishcheva Lake, northeastern Taimyr, Russia, in a peak and a decreasing lemming year. *Ibis* 135:277-292.
- Wellein, E.G. and H.G. Lumsden. 1964. Northern forests and tundra. Pages 67-76 in J.P. Lunduska, editor. *Waterfowl tomorrow*. United States Government Printing Office, Washington, D.C., USA.
- Wrigley, R.E. 1974. Ecological notes on animals of the Churchill Region of Hudson Bay. *Arctic* 27:201-213.
- Ydenberg, R.C. 1987. Nomadic predators and geographical synchrony in microtine population cycles. *Oikos* 50:270-272.

Table 1. Summary of the sample size ( $n$ ), mean ( $\bar{x}$ ), standard error (SE), and 95% confidence intervals for willow (*Salix* spp.) scar sample measurements including stem diameter (mm), stem age (years), scar age (years), and stem age when scarred (years) for Nestor One (NO) and Broad River (BR), near Cape Churchill, Manitoba.

	<i>NO</i>				<i>BR</i>			
	$n$	$\bar{x}$	SE	95% C.I.	$n$	$\bar{x}$	SE	95% C.I.
Stem diameter (mm)	791	4.25	0.06	4.13, 4.36	238	4.78	0.10	4.59, 4.98
Stem age (years)	786	7.74	0.13	7.49, 7.99	238	8.34	0.20	7.94, 8.73
Scar age (years)	794	2.29	0.08	2.13, 2.45	239	2.98	0.15	2.68, 3.28
Stem age when scarred (years)	786	5.46	0.11	5.24, 5.67	238	5.34	0.18	4.98, 5.71

Table 2. Model deviance, number of parameters ( $K$ ), Akaike's Information Criterion corrected for small sample size ( $AIC_c$ ), and model weights ( $w_i$ ) for models of the scar-age frequency of willows (*Salix* spp.) scarred by lemmings at 2 study sites near Cape Churchill, Manitoba.  $AIC_c$  is calculated as the  $Deviance + 2K + (2K(K+1)/n - K - 1)$ , where  $n$  is the sample size.

Model <sup>a</sup>	Deviance	$K$	$AIC_c$	$\Delta AIC_c$	$w_i$
Common	123.735	5	140.402	0.000	0.923
Decay	122.867	6	145.367	4.965	0.077
Trend	119.628	9	173.628	33.226	0.000
Separate	119.079	10	194.079	53.677	0.000

<sup>a</sup>Common = common trend and decay terms fit to both Nestor One (NO) and Broad River (BR) study areas

Decay = common trend but separate decay terms fit to NO and BR

Trend = separate trend but common decay terms fit to NO and BR

Separate = separate trend and separate decay terms fit to NO and BR

Table 3. Parameters in the best-support (Common) model [ $E(Y|X) = N * \exp(\ln(0.5) * X / \alpha_0) * (\alpha_1 + \alpha_2 * \sin(2 * \pi * (X - \alpha_3) / \alpha_4))$ ] of willow (*Salix* spp.) scar-age frequency at 2 study areas near Cape Churchill, Manitoba.  $\alpha_0$  is the half life of scars in years,  $\alpha_1$  and  $\alpha_2$  are tuning parameters corresponding to the amplitude,  $\alpha_3$  is a tuning parameter that shifts the period to match the data, and  $\alpha_4$  is the period of scar-ages and indirectly lemmings.

Parameter	Definition	Estimate [SE]	95% C.I. (Lower, Upper)
$\alpha_0$	Half-life of scars	2.131 [0.077]	1.972, 2.290
$\alpha_1$	Amplitude	0.357 [0.18]	0.320, 0.394
$\alpha_2$	Amplitude	-0.268 [0.019]	-0.307, -0.229
$\alpha_3$	Period Shift	-3.263 [0.059]	-3.398, -3.140
$\alpha_4$	Period	2.832 [0.024]	2.781, 2.887

Figure 1. Location of Nestor One and Broad River willow collection sites within Wapusk National Park on the Hudson Bay Lowlands, Manitoba, Canada.

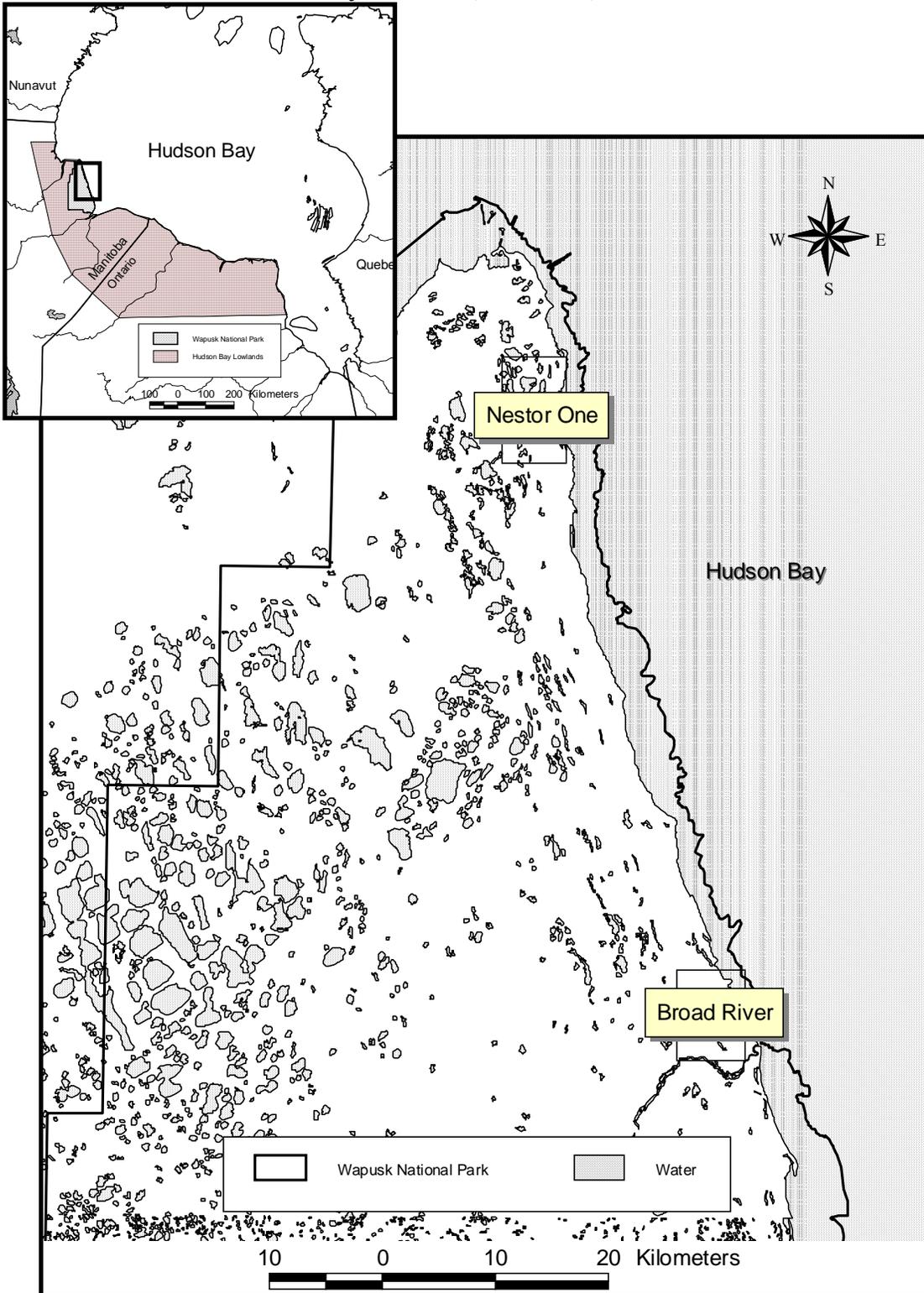
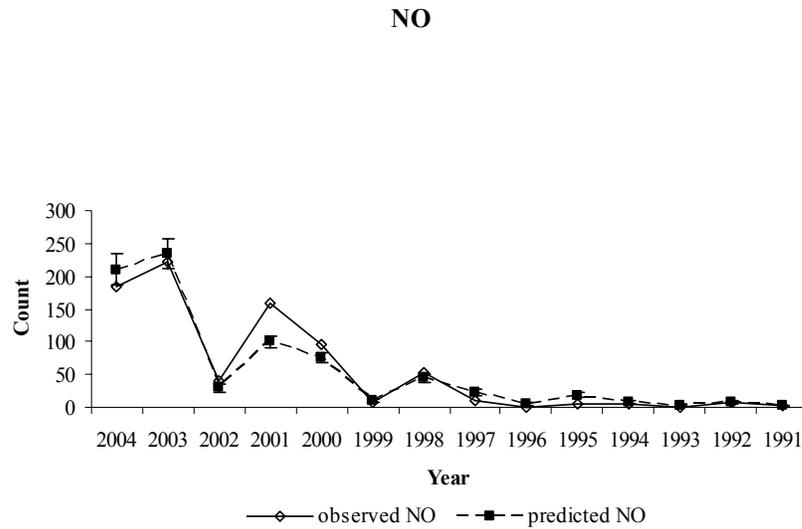


Figure 2. Observed willow (*Salix* spp.) scar-age frequency for (a) Nestor One (NO) and (b) Broad River (BR) and predicted scar-age frequency using the Common model  $[E(Y|X) = N * \exp(\ln(0.5) * X / \alpha_0) * (\alpha_1 + \alpha_2 * \sin(2 * \pi * (X - \alpha_3) / \alpha_4))]$  for NO and BR. Error bars represent 95% confidence intervals for predicted counts using the delta method and Common model.

(a)



(b)

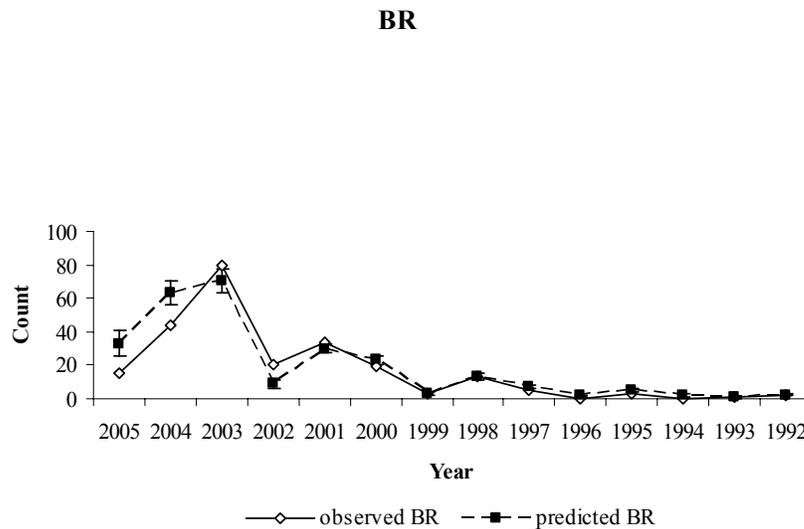
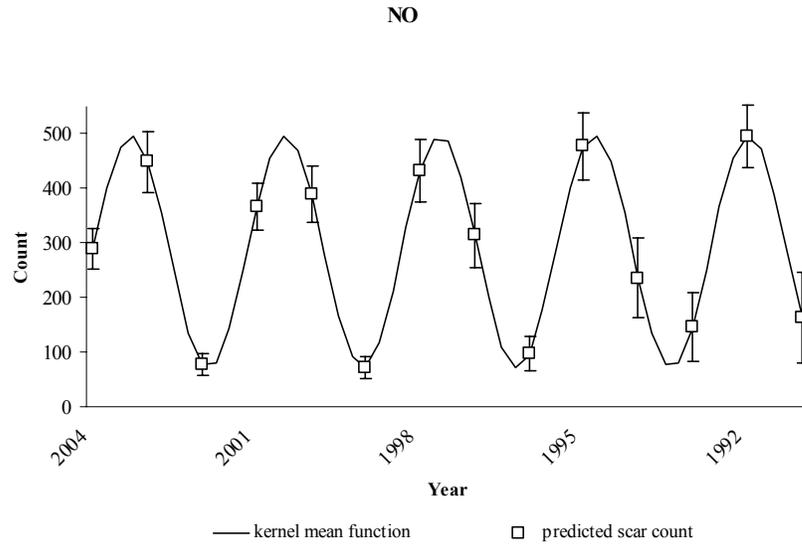
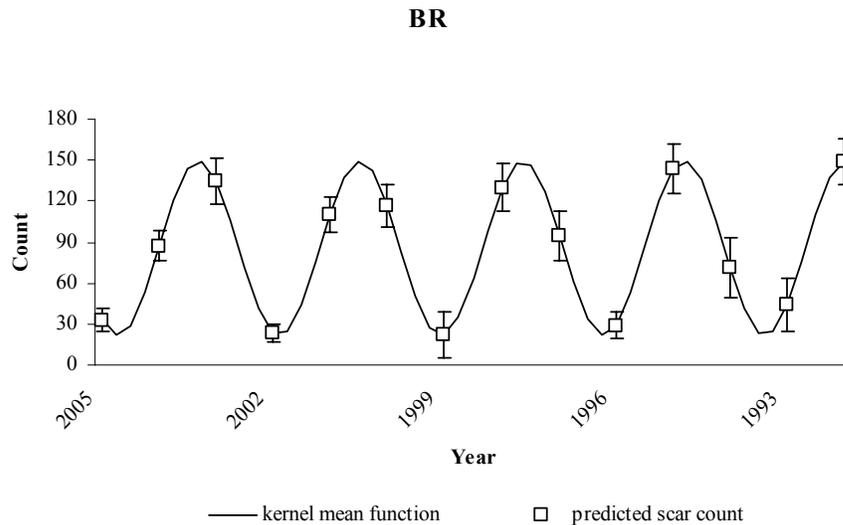


Figure 3. Fitted kernel mean function for the Common model when the exponential decay term is removed [ $E(Y|X) = N * (\alpha_1 + \alpha_2 * \sin(2 * \pi * (X - \alpha_3) / \alpha_4))$ ] and predicted willow (*Salix* spp.) scar-age counts for years 1991 – 2004 for Nestor One (a) and years 1992 – 2005 for Broad River (b). Error bars represent 95% confidence intervals for predicted counts using the delta method and Common model.

(a)



(b)



**CHAPTER 2:  
TRENDS IN NEST SUCCESS OF EASTERN PRAIRIE POPULATION CANADA  
GEESE 1993 - 2004: EXAMINING THE “BIRD-LEMMING” HYPOTHESIS AT  
CAPE CHURCHILL, MANITOBA**

## ABSTRACT

The bird-lemming hypothesis, a specific form of the alternative prey hypothesis, describes the dynamic interaction of predator, prey, and alternative prey in determining reproductive success in arctic-nesting birds. We assessed this hypothesis using data collected during annual Eastern Prairie Population (EPP) Canada goose (*Branta canadensis interior*) breeding ground surveys at Cape Churchill, Manitoba, and measures of relative abundance of collared lemmings (*Dicrostonyx richardsoni*) based on analysis of willow (*Salix* spp.) scar-age frequency distribution. We assessed nest success prior to and post-discovery of nests, and included the following variables in regression models of annual nest success; arctic fox (*Alopex lagopus*) abundance in the current and previous year, lemming abundance in the current and previous year, and nest density. We analyzed 2 separate time periods, 1993 – 2004 and 1998 – 2004, because fox removal occurred on our study area from 1994 - 1996. We developed models *a priori* and ranked them using Akaike's Information Criterion corrected for small sample sizes (AIC<sub>c</sub>). Our results were not consistent with predictions of the bird-lemming hypothesis, but suggested that nest density, arctic fox relative abundance, and lemming relative abundance from the previous year influenced predator-prey dynamics and subsequently, nest success. Furthermore, local fox trapping and nest-discovery may also impact nest success. Our results also suggest that predators may respond more quickly and across a broader spatial scale to declines in primary prey (e.g., lemmings) than previously considered under the bird-lemming hypothesis.

## INTRODUCTION

Substantial inter-annual variation occurs in the reproductive performance of many arctic and sub-arctic nesting geese (Bruggink et al. 1994, Walter 1999, Gleason et al. 2004). Factors influencing this variation may include annual weather fluctuations (Ryder 1970, Raveling and Lumsden 1977, MacInnes and Dunn 1988, Bruggink et al. 1994, Walter 1999) and changes in predator pressure (Raveling and Lumsden 1977, Angelstam et al. 1984, Summers 1986, Bêty et al. 2002). Weather variation typically takes the form of delayed spring phenology and the late onset of snow melt. In years with late snow melt, many geese forego nesting, presumably because they use endogenous energy resources for maintenance and are unable to invest adequate resources in reproduction. Geese nesting in late years experience an abbreviated season and short gosling fledgling period, which generally results in poor recruitment. Under such conditions, nesting geese may spend more time off the nest feeding and be more likely to abandon their nests (Ryder 1970, Moser and Rusch 1998).

Variation in nest success from changes in predator pressure is likely more complex and involves the dynamic interaction of predator, prey, and alternative prey (Angelstam et al. 1984, Summers 1986, Summers and Underhill 1987, Underhill et al. 1993, Wilson and Bromley 2001, Bêty et al. 2002, Blomqvist et al. 2002, Korpimäki et al. 2005). The alternative prey hypothesis (APH) generally refers to predator-prey relationships in which predators specialize on primary prey until that prey population declines below a threshold density, at which point they functionally respond and consume alternative prey (Angelstam et al. 1984, Small et al. 1993). Typically, this interaction occurs when the predator is highly specialized and experiences reduced fitness when the

primary prey becomes less abundant (Angelstam et al. 1984, Norrdahl and Korpimäki 2000).

The bird-lemming hypothesis is a particular example of the APH. Annual variation in nest success of arctic-nesting birds and the relationship with microtine rodents has been recognized in northern Russia and Europe (Angelstam et al. 1984, Summers 1986, Underhill et al. 1993, Blomqvist et al. 2002) and in North America (Wilson and Bromley 2001, Bêty et al. 2002). Under this hypothesis, arctic fox (*Alopex lagopus*) or other predators specialize in feeding on primary prey, lemmings (*Dicrostonyx* spp.; *Lemmus* spp.), and increase reproduction when lemmings are abundant. In years when lemming abundance is low, particularly following a peak year, predators functionally respond and switch to feeding on alternative prey such as ground-nesting birds and bird eggs. Loss of their primary food resource is predicted to increase arctic fox mortality rates and result in a delayed numerical decline in the arctic fox population. Lemmings increase in abundance as predator pressure declines. Ground-nesting birds are predicted to experience reduced reproductive performance in the year following a lemming peak, but likely recover in subsequent years as predator populations decline (Angelstam et al. 1984, Summers 1986). To examine the bird-lemming hypothesis and evaluate associated predictions of predator-prey dynamics, long-term data on multiple species are needed.

At Cape Churchill, Manitoba, Eastern Prairie Population (EPP) Canada geese (*Branta canadensis interior*) have exhibited substantial inter-annual variation in nest success over 30 years (1976 – 2005). Arctic fox depredation accounts for over 80% of nest failures in some years (Walter 1996, 1999) and local arctic fox dens have been

monitored regularly for activity. Near the town of Churchill (Shelford 1943, Shelford and Twomey 1941, Scott 1993) and more recently at Cape Churchill (Roth 2003, Reiter 2006 ), strong multi-annual cycles have been documented in collared lemming (*Dicrostonyx richardsoni*) populations, a primary prey of arctic fox in this area (Bahr 1989). However, the extent to which annual fluctuations in local goose nest success coincides with variation in lemming and arctic fox abundance in this region is unknown. We used these existing data to evaluate the bird-lemming hypothesis as a mechanism influencing inter-annual nest success variation in EPP Canada geese. Specifically, we (1) present time-series data summaries of annual EPP Canada goose nest success, nest density, median hatch date, annual arctic fox den activity, and relative annual lemming abundance from Cape Churchill, Manitoba between 1993 and 2004, and (2) use linear regression to model nest success as a function of arctic fox and lemming abundance in the current and previous year, median hatch date, and nest density. We interpret our results in the context of predictions from the bird-lemming hypothesis, and assess assumptions of that hypothesis in light of our results.

## **STUDY AREA**

The EPP Canada goose breeding range includes nearly 54,000 km<sup>2</sup> in northern Manitoba (Malecki et al. 1980). The highest density of breeding Canada geese is found along a narrow strip of coastal tundra habitat on the west side of Hudson Bay within the broader ecosystem of the Hudson Bay Lowlands. The Nestor One study area (58° 34' N, 93° 11' W) is located just south of Cape Churchill and approximately 60 km east-southeast of the town of Churchill, Manitoba, Canada (Fig. 1). Nester One lies within a narrow strip of coastal tundra nesting habitat, characterized by low relief, continuous

permafrost, poor drainage, shallow lakes, ephemeral ponds, and coastal tundra vegetation (Wellein and Lumsden 1964, Didiuk and Rusch 1979). The study area, established in 1976 and located inside of Wapusk National Park (11,475 km<sup>2</sup>), is ~ 48 km<sup>2</sup>. Coastal salt marshes, beach ridges, sedge meadows, and interior sedge meadow complexes comprise the major habitat types (Didiuk and Rusch 1979). The northern boreal forest ecosystem begins ~ 10 km inland from Nestor One and the Hudson Bay coastline (Brook 2001).

Arctic foxes breed in relatively high densities on the coastal tundra in this region, utilizing established dens along large, elevated beach ridges (Garrott et al. 1983, Bahr 1989, Roth 2003). Nomadic avian predators such as snowy owls (*Nyctea scandiaca*) and rough-legged hawks (*Buteo lagopus*) often nest in this area, particularly during years of abundant small-mammal populations (Shelford 1945). In addition to nesting Canada geese, potential prey for avian and mammalian predators include nesting waterfowl (Anseriformes), shorebirds (Charadriiformes), and collared lemmings. A breeding colony of >20,000 nesting light geese (lesser snow geese [*Chen caerulescens* *caerulescens*] and Ross' geese [*C. rossii*]) occurs <20 km from Nestor One at La Pérouse Bay (Fig. 1; Cooke et al. 1995).

## **METHODS**

### **Nest Success**

Since 1976, systematic ground surveys for Canada goose nests and nest monitoring were completed annually at Nestor One. Standardized protocols follow methods described in Didiuk and Rusch (1979) and Walter (1999). Nest-searching crews (4-5 people) spaced at regular intervals systematically searched previously established study units (Walter 1999). At all nests encountered, females were flushed and the

number of eggs present, incubation stage (determined using candling and flotation methods; Westerkov 1950, Weller 1956, Walter and Rusch 1997a), presence of predators (herring gull [*Larus argentatus*], parasitic jaeger [*Stercorarius parasiticus*], arctic fox, polar bear [*Ursus maritimus*], wolf [*Canis lupus*]), and general nest condition were recorded on nest cards. Beginning in 1998, Universal Transverse Mercator (UTM) coordinates of the nest location, determined with a Global Positioning System (GPS) unit, have been recorded and imported to a digital field map (DNRGarmin program, Minnesota Department of Natural Resources © 2001; Nack and Andersen 2004). In all years, nest locations were marked with a 7.5 x 12.5 cm 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 predicted hatch date to determine outcome (Didiuk and Rusch 1979, Walter 1999). We categorized nests as (1) successful if  $\geq 1$  egg hatched, indicated by the presence of goslings or eggshells and intact membranes, (2) depredated if few or no eggshell fragments were found in the nest, (3) abandoned if found with intact, cold eggs, or (4) unknown. We assessed depredated nests to determine the predator responsible and considered holes in eggs or presence of small eggshells indicators of avian depredation while missing eggs indicated mammalian nest depredation (Walter 1999, Anthony et al. 2004). We identified mammalian nest predators by the presence of key species-specific signs: scat, urine smell, or visual identification of an individual.

We calculated annual nest success using daily survival rates (DSR) after initial discovery (Mayfield 1975). We followed methods described by Johnson (1979) to establish 95% confidence intervals (hereafter, 95% C.I.). By assuming a constant DSR

and only using daily survival probabilities for the period post-discovery, the Mayfield method does not account for potential observer effects on survival rate (e.g., nest survival may be altered following discovery) or changes in DSR through incubation. To evaluate if this biased our estimates of Canada goose nest success, we also calculated an *ad hoc* measure of nest DSR for the period prior to discovery (Allen 1996). We estimated the DSR for the period prior to nest discovery based on exposure days from the start of incubation to discovery. We calculated exposure days for active nests at discovery as the number of days between the estimated start of incubation (based on floating and candling) and the discovery date. We considered exposure days for already-failed nests at discovery to be half the number of days between median start of incubation date, based on all active nests, and the date the failed nest was discovered. Because detection probabilities for failed nests and active nests are different, we divided exposure days for active and failed nests by 0.77 and 0.39, respectively, to correct for visibility bias (Allen 1996, Walter and Rusch 1997b). We used the DSR prior to discovery to calculate nest success for the entire 28-day incubation period of Canada geese in this region. We assumed constant daily nest survival through the nesting period for this calculation. Formally, we calculated annual nest success for the period prior to discovery as follows:

$$(1) \quad Nest\ success = \left( \frac{ED - fn}{ED} \right)^{28},$$

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.

$$(2) \quad ED = \frac{\sum d_a}{ca} + \frac{0.5 * \sum d_f}{cf},$$

where  $d_a$  is the number of days from incubation to discovery for each  $a$ , active nests;  $d_f$  is the number of days from incubation to discovery for each  $f$ , already failed nests (days for failed nests are multiplied by 0.5, because it cannot be known when exactly the failure occurred in the interval);  $ca$  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 1997b).

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

We used this method because (1) we could correct for the discrepancy in nest visibility between active and already-failed nests (failed nests typically are more difficult to find), so failed nests are not underrepresented in the data; (2) we could estimate the day of incubation accurately using candling and egg floating techniques (Walter and Rusch 1997a); and (3) because Canada goose nest initiation in this region is highly synchronous (Walter 1999), we could assume that nests that have already failed, on average, were initiated near the median initiation date for nests that were still active.

### **Nest Density**

We calculated nest density for each year of nest surveys from 1993 to 2004 as the number of Canada goose nests per 100 ha of wetland nest habitat. We divided the number of nests active when discovered by 0.77 and nests already failed at discovery by 0.39 to account for differences in detection probabilities between active nests and failed nests (Walter and Rusch 1997b). We used the 95% C.I. of estimates for the visibility correction values to generate a 95% C.I. for nest density in each year.

### **Median Hatch Date**

We used egg floating and candling to estimate the number of days eggs had been incubated when each nest was discovered and, based on a 28-day incubation period, we estimated the hatch date for each nest (Westerkov 1950, Weller 1956, Walter and Rusch 1997a, Walter 1999). We summarized median hatch dates for nesting Canada geese in each year from 1993 to 2004 and considered hatch date to be a continuous variable. We standardized all median hatch dates relative to June 1, such that, for example, a year with a median hatch date of July 2 was assigned a value of 32 for median hatch date.

### **Lemming Abundance**

We used lemming relative abundance estimated in Reiter (2006) to assign relative lemming abundance at Nestor One between 1992 and 2004. Reiter (2006) adapted methods described by Danell et al. (1981) and Danell et al. (1999) to generate a relative measure of lemming abundance. Relative lemming abundance was determined by collecting a random sample of willow (*Salix* spp.) plant scars ( $n = 794$ ) caused by lemming feeding at the Nestor One study area and determining the distribution of scar ages using dendrochronological techniques. Older scars are typically underrepresented in such a sample due to plant growth (e.g., reduced visibility of older scars) and plant death (e.g., reduced numbers of older scars still alive). Reiter (2006) used non-linear Poisson regression to model the distribution of scar ages and correct for the reduced detection of older scars. Values of relative lemming abundance represented the expected number of willow plant scars caused by lemming feeding in each year, in the absence of reduced visibility of scars as the result of scar age. This method estimated relative lemming abundance from the end of the previous plant growing season to the following spring in each year. Previous studies found that small mammal captures in the summer months

were similar to relative small mammal population estimates for the previous winter to spring using scar analysis (Erlinge et al. 1999, Predavec et al. 2001).

### **Fox Abundance**

We visited known arctic fox dens on and near the study area as part of annual EPP Canada goose research activities. We designated dens as active or not-active based on the presence of fox or fresh fox sign (digging, scent, prey remains, or scat) indicative of an active den (Macpherson 1969). We calculated the proportion of active dens as an estimate of annual relative fox abundance. Data were available for 1992 to 2004. We calculated 95% C.I. for the proportion of active dens in each year using the percentile method and the distribution of 1,000 bootstrapped estimates of fox den occupancy (Efron and Tibshirani 1993).

### **Data Analysis**

We calculated general summary statistics for all variables and report means (SE). Because the bird-lemming hypothesis assumes some degree of cycling in predator and prey populations and nest success, we used autocorrelation functions (ACF; Box and Jenkins 1976, Turchin 1990) and the  $s$ -statistic (Henttonen et al. 1985) as preliminary assessments of cycling and broad population patterns for all variables. All ACF were evaluated at the  $\alpha = 0.05$  significance level. The  $s$ -statistic is the standard deviation of the log (base<sub>10</sub>) values of the data. Typically, values of  $s > 0.5$  indicate a cycling population and  $s < 0.5$  a non-cycling population (Henttonen et al. 1985).

We used linear regression to assess factors related to annual nest success and to specifically evaluate the bird-lemming hypothesis. We developed *a priori* models based upon previously published descriptions of predator-prey dynamics under the bird-

lemming hypothesis (Summers 1986, Summers and Underhill 1987). We ranked models using Akaike's Information Criterion corrected for small sample sizes ( $AIC_c$ ; Akaike 1973, Burnham and Anderson 2002) and evaluated the fit of top models based on overall  $F$ -tests and  $R^2$  values for each model (Cook and Weisberg 1999). We considered the following variables in model development:

$L_t$ : abundance of lemmings in year,  $t$

The abundance of lemmings in the current year may indirectly influence nest success by providing a primary food resource for potential nest predators, especially arctic fox. If lemmings are abundant, then predators will specialize on them; however, if lemmings are not abundant, predators will switch to depredating nests. Under the bird-lemming hypothesis, lemming abundance in the current year should be positively correlated with nest success (Table 1).

$L_{t-1}$ : abundance of lemmings in year,  $t - 1$

Foxes may respond to a peak lemming year with high den occupancy, large litters, and subsequently a numerical increase in the local fox population size (Macpherson 1969, Eberhardt et al. 1983, Strand et al. 2000, Wilson and Bromley 2001). Lemming populations generally crash in a year following a peak, creating a food shortage. Under the bird-lemming hypothesis, foxes are assumed not to depart the area in a low lemming year and are predicted to functionally respond and switch to feeding on nesting birds and their eggs. Thus, under the bird-lemming hypothesis, lemming abundance from the previous year is predicted to have a negative relationship with nest success in the current year (Table 1).

$FD_t$ : proportion of active fox dens in year,  $t$

High fox den activity is typically indicative of a peak lemming year (Macpherson 1969, Eberhardt et al. 1983, Angerbjörn et al. 1999). Under the bird-lemming hypothesis, fox specialize on lemmings, and thus fox den activity should be positively correlated with nest success (Table 1). An alternative hypothesis would suggest that high den activity also indicates fox are in the area, and thus may result in increased predator pressure and lower nest success.

*FD<sub>t-1</sub>: proportion of active fox dens in year, t - 1*

If den activity was high in the previous year then, under the bird-lemming hypothesis, there is predicted to be a numerical increase in the local fox population in the current year. This assumes that fox remain in the area, or at least return to the area in the following spring and summer even if lemmings decline. Foxes are predicted to functionally respond and switch to depredating goose nests, reducing nest success in the current year, *t*. Thus, den activity from the previous year should be negatively associated with nest success in the current year under the bird-lemming hypothesis (Table 1).

*D: nest density in year, t*

High nest densities are typically found during years with early spring phenology (Bruggink et al. 1994, Walter 1999). In years of early or average snow melt nesting females are in better condition and experience higher nest success (Ryder 1970, Raveling and Lumsden 1977, Moser and Rusch 1998, Walter 1999). The opposite may be true for late nesting years. Nest density should be positively associated with nest success (Table 1). Nest density may also influence local predator abundance.

*HD: median hatch date in year, t*

Median hatch date is indicative of spring phenology and annual nesting conditions (MacInnes and Dunn 1988, Bruggink et al. 1994, Walter 1999, Leafloor et al. 2000). We considered median hatch date as a variable that may influence annual nest success and predicted a negative relationship between median hatch date and nest success (Table 1).

Because arctic fox trapping occurred at Nestor One between 1994 and 1996 (Walter 1996) and likely affected local predator-prey dynamics, we analyzed data from 1993 to 2004 and 1998 to 2004 separately. If fox trapping did not influence trophic dynamics, we predicted the top models would be similar for both sets of years. We also analyzed all models in each set of years separately using the estimate of nest success post-discovery and nest success estimates for the period prior to discovery (Allen 1996) as response variables. We used Spearman rank correlation tests to further evaluate assumed associations among covariates under the bird-lemming hypothesis and to consider additional hypotheses (Hollander and Wolfe 1999). We compared means using *t*-tests (Moore and McCabe 2003) and used programs SAS v.9.1 (The SAS Institute, Inc. © 2001) and R v.2.2 (The R foundation for Statistical Computing © 2005) for statistical analyses.

## **RESULTS**

### **Nest Success**

Estimates of Canada goose nest success post-discovery ranged from 0.01 to 0.85 with a mean of 0.48 (SE = 0.08) between 1993 and 2004 and ranged from 0.01 to 0.71 with a mean of 0.38 (SE = 0.09) between 1998 and 2004 (Table 2). Nest success estimates prior to discovery ranged from 0.27 to 0.81 with a mean of 0.57 (SE = 0.05) between 1993 and 2004 and ranged from 0.27 to 0.81 with a mean of 0.56 (SE = 0.08)

between 1998 and 2004. Although the estimates for nest success prior to discovery were higher than the post-discovery estimates in most years, the 95% C.I. of the means overlapped for both sets of years (Table 2).

Both estimates of nest success exhibited substantial year to year variation (Fig. 2). Autocorrelation functions indicated positive correlations at a 4-year lag for the post-discovery estimates of nest success between 1993 and 2004 (Fig. 3a) and a negative correlation at 1- and 3-year lags and a positive correlation at 4 years between 1998 and 2004 (Fig. 3b). None of the correlations was statistically significant. The *s*-statistic for nest success post-discovery was 0.53 between 1993 and 2004 and 0.64 between 1998 and 2004. Autocorrelation functions for nest success prior to discovery between 1993 and 2004 indicated weak negative correlations at all lags from 1 to 3 years and a positive correlation for lags of 4 and 5 years (Fig. 3c). Between 1998 and 2004, the ACF for nest success prior to discovery indicated a negative correlation at 2-year lags and a positive correlation at 4-year lags (Fig. 3d). None of the correlations was significant. The *s*-statistic for nest success prior to discovery was 0.16 and 0.18 between 1993 and 2004 and 1998 and 2004, respectively.

### **Nest Density**

Nest density at Nestor One ranged from 1.23 to 12.22 nests per 100 ha of wetland nesting habitat with a mean of 7.92 (SE = 0.85) between 1993 and 2004. Between 1998 and 2004 nest density averaged 7.48 (SE = 1.44) nests per 100 ha of wetland (Table 2). Qualitatively, nest density was stable in the mid-1990s, but has become more variable in recent years (Fig. 4). The ACF provides little evidence of regular cycles for 1993 – 2004

(Fig. 5a) or 1998 – 2004 (Fig. 5b) and the  $s$ -statistic for nest density during these periods was 0.26 and 0.34, respectively.

### **Median Hatch Date**

Median hatch date ranged from 13 June (13) to 11 July (41), with a mean of 25 June (25.25, SE = 2.30) between 1993 and 2004 and a mean of 25 June (25.00, SE = 3.92) within the same range of dates between 1998 and 2004 (Table 2). The ACF for median hatch date had no correlations at any lag times for either 1993 - 2004 (Fig. 5c) or 1998 - 2004 (Fig. 5d), and the  $s$ -statistics supported these results with  $s = 0.16$  for 1993 - 2004 and  $s = 0.19$  for 1998 - 2004. Median hatch date was significantly correlated with nest density ( $r = -0.49$ ,  $P \approx 0.05$ ). Because the density of a prey item, such as nests, may influence the abundance of predators and the probability of being depredated, we included only nest density in regression analysis as a predictor of annual variation in nest success to account for fluctuations in spring phenology.

### **Lemming Abundance**

Between 1993 and 2004, relative lemming abundance (i.e., predicted scar-age counts) ranged from 72.21 to 476.50 with a mean of 278.99 (SE = 43.48) per year. Relative abundances were similar between 1998 and 2004 with a mean of 296.60 (SE = 13.33; Table 2, Fig. 6). Based on data from Reiter (2006), relative lemming abundance cycled with a period of 2.8 years at Nestor One over the period from 1991 – 2004. The ACF supports this periodicity estimate with a significant positive correlation between lemming abundance at 3-year lags between 1993 and 2004 (Fig. 7a). There were also significant negative correlations at 1- and 4-year lags during this time period. The ACF trend was similar for 1998 to 2004 but with no significant correlations (Fig. 7b).

However, the  $s$ -statistic was 0.31 and 0.35 between 1993 and 2004 and 1998 and 2004, respectively.

### **Arctic Fox Abundance**

The proportion of active fox dens ranged from 0.13 to 0.91 between 1993 and 2004 with a mean of 0.61 (SE = 0.07). However, the total number of dens surveyed in each year ranged from 4 to 17, and resulted in substantial variation in the width of the estimated 95% C.I. for the proportion of active fox dens (Fig. 8). Between 1998 and 2004, the proportion of arctic fox dens with activity ranged from 0.50 to 0.91 with a mean of 0.74 (SE = 0.05; Table 2). The ACF indicated no strong correlations when using the 1993 to 2004 data (Fig. 7c); however, we observed a positive correlation at 1-year lags and a negative correlation at 2- and 3-year lags in the 1998 to 2004 data (Fig. 7d). None of the correlations was statistically significant. The  $s$ -statistic for fox dens also provided little evidence of cycling with  $s = 0.26$  between 1992 and 2004 and  $s = 0.09$  between 1998 and 2004.

### **Model Summary**

#### 1993 to 2004

We used 15 *a priori* models in analysis (5 single-factor, 7 2-factor, and 3 3-factor models, Table 3). When we used estimated nest success post-discovery as the response variable, 1 model received substantial support as the best model among those evaluated for the 1993 - 2004 data set (Table 3). This model contained both  $D$  and  $FD_t$ , and an intercept term ( $\beta_0$ ). None of the other models were  $\leq 2$  AIC<sub>c</sub> units from the top model. Furthermore, the top model received 0.61 of the AIC<sub>c</sub> weight, indicating over 5 times more support as the best model evaluated than the next closest model (Table 3). Both the

overall  $F$ -test ( $F_{3,8} = 4.72, P = 0.03$ ), and the  $R^2$  value (0.64) suggested a good fit of the model to the data. Parameter estimates from the top model indicated a positive relationship between  $D$  and nest success ( $\beta_D = 0.06$ ), whereas the proportion of active fox dens was negatively related to nest success ( $\beta_{FDt} = -0.64$ ). 95% C.I. for both parameters did not overlap zero (Table 4).

For models based on estimates of nest success prior to discovery for 1993 - 2004, none received substantial support, and all 5 single-factor models were  $\leq 2$  AIC<sub>c</sub> units from the top model (Table 5). Even the best of the top models, which included only  $D$ , fit the data poorly ( $F_{2,9} = 1.62, P = 0.23; R^2 = 0.14$ ).

#### 1998 to 2004

Estimated nest success post-discovery between 1998 and 2004 was best modeled using  $D, L_{t-1}$ , and an intercept term ( $\beta_0$ ). This model was substantially better than others evaluated receiving nearly all of the AIC<sub>c</sub> weight ( $w_i = 0.97$ ; Table 6). The next closest model was separated by  $>7$  AIC<sub>c</sub> units. Overall, the model fit was good ( $F_{3,3} = 116.72, P = 0.0003$ ), and accounted for substantial variation in nest success ( $R^2 = 0.98$ ; Table 5). Parameter estimates indicated that both nest density ( $\beta_D = 0.07$ ) and relative lemming abundance from the previous year ( $\beta_{Lt-1} = 0.001$ ) were positively related to nest success. 95% C.I. for both parameters did not overlap zero (Table 4).

When we evaluated estimated nest success prior to discovery for 1998 – 2004, 1 model received nearly 3 times more support than the next closest model based on AIC<sub>c</sub> weights ( $w_i = 0.41$  vs.  $w_i = 0.15$ , respectively), and  $>2$  AIC<sub>c</sub> units separated the top model from the next competing model. The top model contained only  $D$  and an intercept term ( $\beta_0$ ; Table 7). This model, however, fit the data poorly ( $F_{2,4} = 2.73, P = 0.16$ ) and

accounted for only 35% of variation in nest success ( $R^2 = 0.35$ ; Table 7). Although the parameter estimate for density was positive ( $\beta_D = 0.03$ ), the 95% C.I. overlapped zero (Table 4).

## **DISCUSSION**

### **Nest Success**

Nest success of EPP Canada geese near Cape Churchill, Manitoba exhibited substantial year-to-year variation in the 1990s and early 2000s. Our data identified regular multi-annual cycles in nest success rates over this time with roughly 4-year periodicity. These fluctuations over the previous 12 years contrast to nest success trends from the 1980s at Nestor One (Walter 1999), when nest success rates remained consistently low and never were >30%. The causal mechanism of this observed depression in nest success is thought to be increased nest depredation by arctic fox (Walter 1999). Interestingly, average nest success for 1998 - 2004, which does not include the years when arctic fox removal occurred on our study area, is lower than that for 1993 - 2004 when using both post-discovery and prior to discovery estimates of nest success.

We compared the 1994 - 1996 data (years when arctic foxes were trapped and removed from the study area) to the 1998 - 2004 estimates of nest success post-discovery. This comparison indicated a difference in nest success between these time periods ( $t = -1.41$ ,  $df = 8$ ,  $P = 0.09$ ), with mean nest success during trapping years higher than mean nest success for 1998 - 2004. This may indicate a positive effect of arctic fox trapping on nest success of EPP Canada geese between 1994 and 1996. Fox removal has positively influenced nesting geese elsewhere in the Arctic (Anthony et al. 1991).

On average, estimates of nest success prior to discovery were higher than nest success post-discovery between 1993 and 2004. Although 95% C.I. for the 2 estimates overlapped, these results suggest that daily survival rates decreased during incubation. However, previous studies of Canada goose nest success found that daily survival rates increase during the incubation period (MacInnes and Misra 1972, Bruggink et al. 1994). Alternatively, there may be a negative effect of discovery on nest success, which resulted in lower nest success post-discovery. Previous studies in this region are confounding in that Allen (1996) observed differences in nest success prior to discovery and post-discovery, using the same techniques applied here, yet Didiuk and Rusch (1979) and Walter (1999) found nest mortality to vary little through incubation and suggested that nest discovery had little effect on the probability of nest success. We acknowledge that our estimate of nest success prior to discovery, and also used by Allen (1996), is *ad hoc* and relies heavily on visibility bias-correction values. If values used to correct for the difference in visibility of active versus already-failed nests are inaccurate or vary through time, our estimates of nest success prior to discovery may be biased. Without further statistical evaluation of this method of estimating nest success prior to discovery or additional data on inter-annual variation in visibility bias, we cannot rigorously test for the presence of an observer effect.

### **Lemming Abundance**

The lemming population at Cape Churchill fluctuates with regular 3-year cycles. Although the estimate of relative lemming abundance determined from willow-scar analysis is primarily for the period after the end of the previous growing season to the beginning of the next season (the late fall to spring), previous studies demonstrated a

correlation between scar-age-based predictions of lemming abundance and trap-based estimates of relative lemming abundance in the following summer (Erlinge et al. 1999, Predavec et al. 2001). However, intra-annual variation in relative abundance cannot be evaluated using this method and the exact timing of lemming population “crashes” cannot be determined. The timing of a lemming decline may influence fox survival and behavior (Summers and Underhill 1987, Angerbjörn et al. 1991, Roth 2003). A decline occurring just before winter may result in increased mortality, whereas less mortality may result if the decline occurs just prior to the summer and the return of alternative prey (e.g., bird nests).

### **Fox Den Occupancy**

Activity at arctic fox dens varied considerably between 1992 and 2004. Although the trends were not strongly cyclic, we observed substantial year to year changes in den activity. Such strong variation in den activity rates has been observed elsewhere (Macpherson 1969, Elmhagen et al. 2000, Strand et al. 2000) and is typically attributed to fluctuations in primary food resources. However, studies conducted near concentrated, abundant arctic fox food resources identify much less inter-annual variation in fox den activity (Eberhardt et al. 1983, Prestrud 1992). Decisions about whether to den are usually made during early spring (Angerbjörn et al. 1991, Strand et al. 2000) and likely before the presence of nesting geese in the area. Arctic fox pairs will often forego breeding and maintaining a den territory in years when food resources are less abundant (Landa et al. 1998, Strand et al. 2000). At Cape Churchill, we found that fox den activity was positively correlated ( $r = 0.49$ ,  $P \approx 0.13$ ) with estimates of relative lemming abundance from the previous winter and spring. Although the positive relationship

between lemmings and fox den activity was not statistically significant, it represents the tendency of arctic foxes to occur at dens at greater rates when food resources, particularly lemmings, are abundant.

Den activity rates were higher between 1998 and 2004 versus between 1993 and 2004. We found a lower ( $\chi^2 = 13.10$ ,  $df = 1$ ,  $P < 0.0005$ ) proportion of active fox dens when comparing 1994 - 1996 to 1998 - 2004. This provides further evidence that arctic fox removal between 1994 and 1996 may have temporarily improved nesting performance of EPP Canada geese near Cape Churchill.

### **Bird-Lemming Hypothesis**

Our selected models were not consistent with predictions of the bird-lemming hypothesis as a mechanism influencing year-to-year variation in Canada goose nest success near Cape Churchill, Manitoba under any of the 4 regression analyses. However, our analyses reflected the importance of arctic fox and lemming abundance in this trophic system. Our model analyses using the 1993 - 2004 data were likely influenced by the arctic fox removal program between 1994 and 1996. Nest density was positively related to nest success when we used either nest success prior to discovery or nest success post-discovery as the response variable. Fox den activity in the current year, however, had a significantly negative relationship only with nest success post-discovery. This was opposite of the relationship predicted under the bird-lemming hypothesis (Table 1). The inclusion of fox den activity in the current year in models of nest success post-discovery suggested the impact of arctic fox den activity may increase during the nesting period. If den activity is high, arctic fox reproduction is also likely high (Macpherson 1969, Strand et al. 2000). Although lemmings may be abundant, by midway through goose nest

incubation, growing juvenile foxes will require more resources (Tannerfeldt et al. 1994). As the demand for food resources increases, predator pressure may also increase and could lead to higher nest depredation during late incubation (Bahr 1989). Allen (1996) found considerable differences between estimates of nest success prior to discovery and post-discovery, particularly in a high fox year. His data also suggested that nest success was lower post-discovery.

There also may be an effect of nest discovery that is magnified by arctic fox den activity. Previous studies identified a possible negative impact of discovery on nest success (MacInnes and Misra 1972, Raveling and Lumsden 1977, Raveling 1989). However, whether or how nest searching and discovery might interact with fox den activity is unclear. It may be that following the initial nest visit, fox follow visual or scent cues to find nests. Although previous studies have found that orange marker flags (used here and in other studies), a potential visual cue for predators, do not increase the probability of nest depredation (Vacca and Handel 1988, Armstrong 1996), no studies have evaluated the possibility of human scent attracting foraging foxes to goose nests.

Between 1998 and 2004, Canada goose nest success post-discovery was primarily related to nest density and relative lemming abundance in the previous year. During the same years, nest success prior to discovery was influenced only by nest density. The strong effect of density in the 1998 - 2004 models was consistent with the 1993 - 2004 model analyses. Increased nest density, and likely early nesting phenology, was related to higher nest success, consistent with our *a priori* hypothesis. However, whether the effect of nest density is solely an indicator of spring phenology and the condition of nesting geese, or if there is also some interaction with predator abundance, is not known.

We found a weak positive association ( $r = 0.40$ ,  $P \approx 0.40$ ) between fox den activity and Canada goose nest density between 1998 and 2004, suggesting that nest density likely does not influence the intensity of fox activity. However, in years of low nest density, female geese may experience reduced endogenous reserves resulting in increased time away from the nest and potentially increased likelihood of nest abandonment when attacked by a predator (Ryder 1970, Moser and Rusch 1998).

Lemming abundance from the previous year was only included in models with nest success post-discovery as the response variable. The positive relationship of lemming abundance from the previous year and nest success in the current year was opposite that predicted by the bird-lemming hypothesis (Table 1). The negative correlation between nest success in the current year and lemming abundance from the previous year predicted by the bird-lemming hypothesis follows this model: If lemmings were abundant in the previous year, then there will be high reproduction among arctic foxes in the previous year. This increases the number of predators in the area. Although there may be some mortality among arctic foxes, there will be greater numbers of individuals in the following year that functionally respond to the decline of lemmings by switching to depredating goose nests, leading to reduced nest success. On the contrary, if lemmings were not abundant in the previous year, arctic foxes will not reproduce, and there will be little or no numerical increase in predator abundance. Therefore, nest success should be high in the current year. Furthermore, if lemmings were low in the previous year and experience regular multi-annual population cycles, then we would expect that lemmings would increase in the current year. The increase of primary prey should buffer potential depredation of goose nests, also resulting in high nest success.

We reconsidered some of the assumptions of predator-prey relationships underlying the bird-lemming hypothesis to evaluate this discrepancy between the prediction of the bird-lemming hypothesis and our data.

First, under the bird-lemming hypothesis, fox den activity should be positively correlated with relative lemming abundance. Typically, the number of reproductive arctic fox is higher when lemmings are abundant, and declines in years of low lemming abundance (Macpherson 1969, Bahr 1989, Angerbjörn et al. 1991, Tannerfeldt and Angerbjörn 1998, Angerbjörn et al. 1999). However, studies near large goose colonies in northern Canada and Alaska suggest goose eggs are the primary prey item during the summer months rather than small mammals for many foxes inhabiting these areas (Stickney 1991, Samelius and Alisauskas 2000). Thus, this first assumption of the bird-lemming hypothesis may be invalid in some arctic regions, particularly if ground-nesting birds are abundant. However, our data were consistent with this assumption, exhibiting a strong positive association between lemming abundance and fox den activity.

Second, the lemming population should cycle regularly and thus relative lemming abundance should be negatively correlated between successive years. Lemmings and voles (*Microtus* spp.; *Clethrionomys* spp.) in arctic and sub-arctic ecosystems exhibit both cyclic and non-cyclic population fluctuations (Stenseth and Ims 1993, Erlinge et al. 1999, Predavec et al. 2001). In regions where small mammal populations do not fluctuate considerably, the bird-lemming hypothesis may not apply to the local predator, prey, and alternative prey dynamics (Oksanen et al. 2001, Klemola et al. 2002). Our data indicate that lemmings cycled on our study area as relative lemming abundance in the current year had a significantly negative association with relative lemming abundance for

the previous year ( $r = -0.71$ ,  $P \approx 0.04$ ) and the ACF for relative lemming abundance indicated cycling.

Finally, the bird-lemming hypothesis assumes that the fox population experiences increased mortality when lemmings decline and only births and deaths influence the overall number of predators and subsequent predator pressure. This, in theory, results in all surviving predators remaining in the area to depredate goose nests even when the lemming population has crashed. However, if we consider the biology of the arctic fox and other potential nest predators more carefully and the spatial scale of our study, this final assumption is likely invalid, and may have contributed to the discrepancy between the observed data and the predictions of the bird-lemming hypothesis.

The extent of increased arctic fox mortality, and subsequently the magnitude of the numerical decline likely depends on the timing of the lemming population crash (Tannerfeldt et al. 1994, Angerbjörn et al. 1999), the abundance of alternative food resources (natural [Roth 2003] or man-made [Eberhardt et al. 1982, 1983]), and the prevalence of disease (Kaplan 1985, Ballard et al. 2001). If alternative prey, particularly nesting birds, is not abundant, foxes may become nomadic and increase their home ranges substantially (Chesemore 1968, Macpherson 1969, Wrigley and Hatch 1976, Eberhardt et al. 1983, Landa et al. 1998). Long-distance dispersal and migration is common among arctic foxes especially when confronted with dramatic changes in the availability of food resources (Chesemore 1968, Wrigley and Hatch 1976, Eberhardt and Hanson 1978). Juvenile arctic foxes may disperse up to 70 km from their natal den in the first year in search of food or territories (Strand et al. 2000). Adults, particularly males, undergo long-range migrations mainly in search of food (Chesemore 1968, Macpherson

1969, Wrigley and Hatch 1976). Arctic foxes will return to den sites in the spring; however, they will enlarge their home ranges in search of food and even forego reproduction, rarely returning to the den site in years of low food resources (Macpherson 1969, Landa et al. 1998, Strand et al. 2000, Eide et al. 2004). Furthermore, the spatial organization of foraging foxes may change within a season in response to fluctuations in the distribution of food resources (Jepsen et al. 2002, Eide et al. 2004). These movements may contribute to rapid fluctuations in the abundance of arctic foxes in some areas.

There also may be incentives for arctic foxes to disperse or migrate from den territories when primary prey declines if more abundant populations of alternative food resources exist nearby (Tannerfeldt and Angerbjörn 1998). Studies near large goose nesting colonies have reported increased arctic fox presence when small mammal populations are low (Samelius and Alisauskas 2000, Wilson and Bromley 2001, Bêty et al. 2002). Nomadic avian goose-nest predators also disperse when small mammal populations decline (Shelford 1945, Ydenberg 1987, Korpimäki 1994) and typically return as prey increases. Korpimäki (1994) found no time lag in the decline of avian predators when voles declined. It may be a combination of increased mortality and dispersal that influences the local predator population when primary prey declines. The magnitude and timing of change in predator pressure on alternative prey (e.g., goose nests) may be different depending on whether the functional response of predators is to remain in the area, switching to bird nests, or to disperse following a decline of primary prey. Together, this implies that predator dynamics are both temporally and spatially complex and involve movements across broad spatial scales.

At the scale of our study ( $\sim 48\text{-km}^2$ ), we would observe this movement response of predators to changes in prey availability or abundance as a change in predator pressure (e.g., reduced den activity); however, it is a functional response at a broader spatial scale. Predators switch to an alternative prey resource, but that resource may occur outside of our study area. Less than 20 km from Nestor One is the La Pérouse Bay lesser snow goose and Ross' goose colony with >20,000 nesting pairs of light geese. This is a much higher density of potential food for predators than Canada geese at Nestor One, which average 7.5 nests per 100 ha of wetland nesting habitat. Cooke et al. (1995) reported that “abnormally large” numbers of arctic foxes occurred near the La Pérouse Bay snow goose colony in some years. Whether these years coincide with low lemming years following a lemming peak, as has been documented in other goose colonies (Samelius and Alisauskas 2000, Wilson and Bromley 2001, Bêty et al. 2002), is not known. Human habitation sites may also attract foxes during low primary prey years (Eberhardt et al. 1982, 1983). The town of Churchill, Manitoba, <60 km from the Nestor One study area, has a waste disposal site and other human-associated food resources that provide a reliable concentrated food resource, possibly attracting arctic foxes.

Unfortunately, our data on relative fox abundance are limited. Our data contain substantial variation and imprecision due to the few dens monitored in some years. Furthermore, they provide only a crude estimate of fox presence at a den and not of actual fox abundance. In years when prey is scarce, little activity may occur at dens. Whether there are few arctic foxes in the area, as the result of death and dispersal, or simply reduced reproductive activity cannot be determined using these data.

The nest success of EPP Canada geese near Cape Churchill exhibits strong annual variation. Our data demonstrate the importance of predator-prey dynamics in this annual variation; however, we are unable to unequivocally identify the ultimate causal mechanism. Changes in lemming abundance affect the predator population, yet whether this results in fewer predators when lemmings decline due to increased mortality or predator dispersal and migration remains unclear. We propose the response by predator communities to changes in lemming abundance at Nestor One occurs more rapidly and across a broader spatial scale than assumed under the bird-lemming hypothesis. In years when lemmings are abundant, both arctic foxes and other predators (jaegers, owls, hawks, etc.) are more abundant on the study area, feeding on both lemmings and goose nests. In years with low lemming abundance, the number of predators on the study area drops, and foxes, opportunistic predators with potentially large home ranges (Macpherson 1969, Chesemore 1968, Wrigley and Hatch 1976, Eberhardt and Hanson 1978, Anthony 1997) may move to areas with higher food availability (e.g., goose colony or Churchill) reducing depredation of Canada goose nests near Nestor One.

Our study evaluates the bird-lemming hypothesis as it pertains to geese with dispersed nesting ecology in North America. Previous studies conducted near large goose nesting colonies supported the predictions of the bird-lemming hypothesis (Wilson and Bromley 2001, Bêty et al. 2002) as more foxes arrived near the colony when lemmings declined and geese experienced reduced nest survival. Data collected at a broader spatial scale than evaluated here are necessary to more thoroughly evaluate the bird-lemming hypothesis in dispersed-nesting geese. Ultimately, the bird-lemming

hypothesis may serve as a model of the mechanism influencing annual nest success of birds on a landscape scale in this region.

## LITERATURE CITED

- Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. Pages 267-281 in B.N. Petroc and F. Csaki, editors. Second International Symposium on Information Theory, Akademiai Kiado, Budapest, Hungary.
- Allen, B.W. 1996. Movements and nest success of Canada geese in northern Manitoba. Thesis, University of Wisconsin, Madison, Wisconsin, USA. 47pp.
- Angelstam, P., E. Lindstrom, and P. Widen. 1984. Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. *Oecologia* 62:199-208.
- Angerbjörn, A., B. Arvidson, E. Noren, and L. Stromgren. 1991. The effect of winter food on reproduction in the arctic fox, *Alopex lagopus*: a field experiment. *Journal of Animal Ecology* 60:705-714.
- \_\_\_\_\_, M. Tannerfeldt, and S. Erlinge. 1999. Predator – prey relations: arctic foxes and lemmings. *Journal of Animal Ecology* 68:34-49.
- Anthony, R.M. 1997. Home ranges and movements of arctic fox (*Alopex lagopus*) in western Alaska. *Arctic* 50:147-157.
- \_\_\_\_\_, P.L. Flint, and J.S. Sedinger. 1991. Arctic fox removal improved nest success of black brant. *Wildlife Society Bulletin* 19:176-184.
- \_\_\_\_\_, J.B. Grand, T.F. Fondell, and B.F.J. Manly. 2004. A quantitative approach to identifying predators from nest remains. *Journal of Field Ornithology* 75:40-48.
- Armstrong, T. 1996. Effects of research activities on nest predation in arctic-nesting geese. *Journal of Wildlife Management* 60:265-269.
- Bahr, J. 1989. The hunting ecology of arctic foxes (*Alopex lagopus*) near Cape Churchill, Manitoba. Thesis, University of Manitoba, Winnipeg, Manitoba, Canada. 129pp.
- Ballard, W.B., E.H. Follmann, D.G. Ritter, M.D. Robards, and M.A. Cronin. 2001. Rabies and canine distemper in an arctic fox population in Alaska. *Journal of Wildlife Diseases* 37:133-137.

- Bêty, J., G. Gauthier, E. Korpimäki, and J.F. Giroux. 2002. Shared predators and indirect trophic interactions: lemming cycles and arctic nesting geese. *Journal of Animal Ecology* 71:88-98.
- Blomqvist, S., N. Holmgren, S. Åkesson, A. Hedenström, and J. Pattersson. 2002. Indirect effects of lemmings on sandpiper dynamics: 50 years of counts from southern Sweden. *Oecologia* 133:146-158.
- Box, G.E.P. and G.M. Jenkins. 1976. *Time series analysis, forecasting and control*. Holden Day, Oakland, California, USA.
- Brook, R.K. 2001. *Structure and dynamics of the vegetation Wapusk National Park and the Cape Churchill Wildlife Management Area of Manitoba: community and landscape scales*. Thesis, Natural Resources Institute, University of Manitoba, Winnipeg, Manitoba, Canada. 290pp.
- Bruggink, J.G., T.C. Tacha, J.C. Davies, and K.F. Abraham. 1994. Nesting and brood-rearing ecology of Mississippi Valley Population Canada geese. *Wildlife Monographs* 58:1-39.
- Burnham, K.P. and D.R. Anderson. 2002. *Model selection and inference: a practical information-theoretic approach*. Second edition. Springer-Verlag, New York, New York, USA. 488pp.
- Chesemore, D.L. 1968. Distribution and movements of white foxes in northern and western Alaska. *Canadian Journal of Zoology* 46:849-854.
- Cook, R.D. and S. Weisberg. 1999. *Applied regression including computing and graphics*. John Wiley and Sons, Inc. New York, New York, USA. 593pp.
- Cooke, R., R.F. Rockwell, and D.B. Lank. 1995. *The snow geese of La Pérouse Bay: natural selection in the wild*. Oxford University Press. Oxford, U.K. 297pp.
- Didiuk, A.B. and D.H. Rusch. 1979. *Ecology of broods of Canada geese in northern Manitoba*. Final Research Report, Wisconsin Cooperative Wildlife Research Unit, Madison, Wisconsin, USA. 216pp.
- Danell, K., L. Ericson, and K. Jakobsson. 1981. A method for describing former fluctuations of voles. *Journal of Wildlife Management* 45: 1018-1021.
- \_\_\_\_\_, S. Erlinge, G. Högstedt, D. Hasselquist, E.B. Olofsson, T. Seldal, and M. Svensson. 1999. Tracking past and ongoing lemming cycles on the Eurasian tundra. *Ambio* 28:225-229.

- Eberhardt, L.E., R.A. Garrott., and W.C. Hanson. 1983. Den use by arctic foxes in northern Alaska. *Journal of Mammalogy* 64:97-102.
- \_\_\_\_\_ and W.C. Hanson. 1978. Long-distance movements of arctic foxes tagged in northern Alaska. *Canadian Field-Naturalist* 92:386-389.
- \_\_\_\_\_, W.C. Hanson, J.L. Bengtson, R.A. Garrott, and E.E. Hanson. 1982. Arctic fox home range characteristics in an oil development area. *Journal of Wildlife Management*. 46:183-190.
- Efron, B. and R.J. Tibshirani. 1993. *An introduction to the bootstrap*. Chapman and Hall, New York, New York, USA. 436pp.
- Eide, N.E., J.U. Jepsen, and P. Prestrud. 2004. Spatial organization of reproductive arctic foxes, *Alopex lagopus*: responses to changes in spatial and temporal availability of prey. *Journal of Animal Ecology* 75:1056-1068.
- Elmhagen, B., M. Tannerfeldt, P. Verucci, and A. Angerbjörn. 2000. The arctic fox (*Alopex lagopus*): an opportunistic specialist. *Journal of Zoology* 251:139-149.
- Erlinge, S.G., K. Danell, P. Frodin, D. Hasselquist, E. Olofsson, T. Seldal, and M. Svensson. 1999. Asynchronous population dynamics of Siberian lemmings across the Palearctic tundra. *Oecologia* 119:493-500.
- Garrott, R.A., L.E. Eberhardt, and W.C. Hanson. 1983. Arctic fox den identification and characteristics in northern Alaska. *Canadian Journal of Zoology* 61:423-426.
- Gleason, J.S., K.F. Abraham, C.D. Ankney, and J.O. Leafloor. 2004. Variation in reproductive performance of Canada geese in the presence and absence of lesser-snow geese. Pages 75-83 in T.J. Moser, R.D. Lien, K.C. VerCauteren, K.F. Abraham, D.E. Andersen, J.G. Bruggink, J.M. Colucey, D.A. Graber, J.O. Leafloor, D.R. Luukkonen, and R.R. Trost, editors. *Proceedings of the 2003 International Canada Goose Symposium*. Madison, Wisconsin, USA.
- Henttonen, H., A.D. McGuire, and L. Hansson. 1985. Comparisons of amplitudes and frequencies (spectral analyses) of density variation in long term data sets of *Clethrionomys* species. *Annales Zoologici Fennici*. 26:221-228.
- Hollander, M. and D.A. Wolfe. 1999. *Nonparametric statistical methods*. Second edition. John Wiley and Sons, Inc. New York, New York, USA. 787pp.
- Jepsen, J.U., N.E. Eide, Prestrud, P., and L.B. Jacobsen. 2002. The importance of prey distribution in habitat use by arctic foxes (*Alopex lagopus*). *Canadian Journal of Zoology* 80:419-429.

- Johnson, D.H. 1979. Estimating nest success: the Mayfield method and an alternative. *Auk* 96:651-661.
- Kaplan, C. 1985. Rabies: a worldwide disease. Pages 1-21 *in* P.J. Bacon, editor. Population dynamics of rabies in wildlife. Academic Press. New York, New York, USA.
- Klemola, T., M. Tanhuanpää, E. Korpimäki, and K. Ruohomäki. 2002. Specialist and generalist natural enemies as an explanation for geographical gradients in population cycles of northern herbivores. *Oikos* 99:83-94.
- Korpimäki, E. 1994. Rapid or delayed tracking of multi-annual vole cycles by avian predators? *Journal of Animal Ecology* 63:619-628.
- \_\_\_\_\_, L. Oksanen, T. Oksanen, T. Klemola, K. Norrdahl, and P.B. Banks. 2005. Vole cycles and predation in temperate and boreal zones of Europe. *Journal of Animal Ecology* 74:1150-1159.
- Landa, A., O. Strand, J.D.C. Linnell, and T. Skogland. 1998. Home-range sizes and altitude selection for arctic foxes and wolverines in an alpine environment. *Canadian Journal of Zoology* 76:448-457.
- Leafloor, J.O., M.R.J. Hill, D.H. Rusch, K.F. Abraham, and R.K. Ross. 2000. Nesting ecology and gosling survival of Canada geese on Akimiski Island, Nunavut, Canada. Pages 109 – 116 *in* K.M. Dickson, editor. Towards conservation of the diversity of Canada geese (*Branta canadensis*). Canadian Wildlife Service Occasional Paper Number 103.
- MacInnes, C.D. and R.K. Misra. 1972. Predation on Canada goose nests at McConnell River, Northwest Territories. *Journal of Wildlife Management* 36:414-422.
- \_\_\_\_\_ and E.H. Dunn. 1988. Components of clutch size variation in arctic-nesting Canada geese. *Condor* 90:83-89.
- Macpherson, A.H. 1969. The dynamics of Canadian arctic fox populations. Canadian Wildlife Service Report Series 8:1-52.
- Malecki, R.A., F.D. Caswell, K.M. Babcock, R.A. Bishop, and R.K. Brace. 1980. Major nesting range of the Eastern Prairie Population of Canada geese. *Journal of Wildlife Management* 44: 229-232.
- Mayfield, H. 1975. Suggestions for calculating nest success. *Wilson Bulletin* 87:456-466.
- Moore, D.S. and G.P. McCabe. 2003. Introduction to the practice of statistics. Fourth edition. W.H. Freeman and Company. New York, New York, USA. 828pp.

- Moser, T.J. and D.H. Rusch. 1998. Body condition dynamics of interior Canada geese in northern Manitoba. Pages 347-354 in D.H. Rusch, M.D. Samuel, D.D. Humburg and B.D. Sullivan, editors. *Biology and management of Canada Geese. Proceedings of the International Canada Goose Symposium, Milwaukee, Wisconsin, USA.*
- Nack, R.R. and D.E. Andersen. 2004. Distribution of Eastern Prairie Population Canada goose broods, 1977-2002: potential influence of snow geese. Pages 130-136 in T.J. Moser, R.D. Lien, K.C. VerCauteren, K.F. Abraham, D.E. Andersen, J.G. Bruggink, J.M. Colucey, D.A. Graber, J.O. Leafloor, D.R. Luukkonen, and R.R. Trost, editors. *Proceedings of the 2003 International Canada Goose Symposium. Madison, WI, USA.*
- Norrdahl, K. and E. Korpimäki. 2000. Do predators limit the abundance of alternative prey? Experiments with vole-eating avian and mammalian predators. *Oikos* 91:528-540.
- Oksanen, T., L. Oksanen, M. Schneider, and M. Aunapuu. 2001. Regulation, cycles, and stability in northern carnivore-herbivore systems: back to first principles. *Oikos* 94:101-117.
- Predavec, M., C.J. Krebs, K. Danell, and R. Hyndman. 2001. Cycles and synchrony in the collared lemming (*Dicrostonyx groenlandicus*) in arctic North America. *Oecologia* 126:216-224.
- Prestrud, P. 1992. Denning and home-range characteristics of breeding arctic foxes in Svalbard. *Canadian Journal of Zoology* 70:1276-1283.
- Raveling, D.G. 1989. Nest-predation rates in relation to colony size of black brant. *Journal of Wildlife Management* 53:87-90.
- \_\_\_\_\_ and H.G. Lumsden. 1977. Nesting ecology of Canada geese in the Hudson Bay Lowlands of Ontario: evolution and population regulation. *Fish and Wildlife Research Report No. 98. Ministry of Natural Resources. Ontario, Canada.*
- Reiter, M.E. 2006. Historical trends in collared lemming (*Dicrostonyx richardsoni*) abundance and nest success of Eastern Prairie Population Canada geese (*Branta canadensis interior*) in northern Manitoba: evaluating the "bird-lemming" hypothesis. Thesis, University of Minnesota, St. Paul, Minnesota, USA. 80pp.
- Roth, J.D. 2003. Variability in marine resources affects arctic fox population dynamics. *Journal of Animal Ecology* 72:668-676.

- Ryder, J.P. 1970. A possible factor in the evolution of clutch size in Ross' goose. *Wilson Bulletin* 82:5-13.
- Samelius, G. and R.T. Alisauskas. 2000. Foraging patterns of arctic foxes at a large arctic goose colony. *Arctic* 53: 279-288.
- Scott, P.A. 1993. Relationship between the onset of winter and collared lemming abundance at Churchill, Manitoba, Canada: 1932 – 1990. *Arctic* 46:293-296.
- Shelford, V.E. 1943. The abundance of the collared lemming (*Dicrostonyx groenlandicus* (tr.) var. *richardsoni* mer.) in the Churchill Area, 1929 to 1940. *Ecology* 24:472-484.
- \_\_\_\_\_. 1945. The relation of snowy owl migration to the abundance of collared lemming. *Auk*. 62:592-596.
- \_\_\_\_\_ and A.C. Twomey. 1941. Tundra animal communities in the vicinity of Churchill, Manitoba. *Ecology* 22:47-69.
- Small, R.J., V. Marcstrom, and T. Willebrand. 1993. Synchronous and nonsynchronous population fluctuations of some predators and their prey in central Sweden. *Ecography* 16:360-364.
- Stenseth, N.C. and R.A. Ims. 1993. Population dynamics of lemmings: temporal and spatial variation – an introduction. Pages 61-96 in N.C. Stenseth and R.A. Ims, editors. *The biology of lemmings*. Academic Press, London, U.K.
- Stickney, A. 1991. Seasonal patterns of prey availability and the foraging behavior of arctic foxes (*Alopex lagopus*) in a waterfowl nesting area. *Canadian Journal of Zoology* 69:2853-2859.
- Strand, O., A. Landa, J.D.C. Linnell, B. Zimmerman, and T. Skogland. 2000. Social organization and parental behavior in the arctic fox. *Journal of Mammalogy* 81:223-233.
- Summers, R.W. 1986. Breeding production of dark-bellied brent geese *Branta bernicla bernicla* in relation to lemming cycles. *Bird Study* 33:105-108.
- \_\_\_\_\_ and L.G. Underhill. 1987. Factors related to breeding production of brent geese *Branta b. bernicla* and waders (Charadrii) on the Taimyr Peninsula. *Bird Study* 34:161-171.
- Tannerfeldt, M. and A. Angerbjörn. 1998. Fluctuating resources and evolution of litter size in arctic fox. *Oikos*. 83:545-559.

- \_\_\_\_\_, A. Angerbjörn, and B. Arvidson. 1994. The effect of summer feeding on juvenile arctic fox survival: a field experiment. *Ecography* 17:88-96.
- Turchin, P. 1990. Rarity of density dependence or population regulation with lags? *Nature* 344:660-663.
- Underhill, L.G., R.P. Prys-Jones, E.E. Syroechkovski, N.M. Groen, V. Karpov, H.G. Lappo, M.W.J van Roomen, A. Rybkin, H. Schekkerman, H. Siekman, and R.W. Summers. 1993. Breeding of waders (Charadrii) and brent geese *Branta bernicla bernicla* at Prochishcheva Lake, northeastern Taimyr, Russia, in a peak and a decreasing lemming year. *Ibis* 135:277-292.
- Vacca, M.M. and C.M. Handel. 1988. Factors influencing predation associated with visits to artificial goose nests. *Journal of Field Ornithology* 59:215-223.
- Walter, S.E. 1996. Aspects of Canada goose nesting ecology in northern Manitoba: age, visibility, and arctic fox predation. Thesis, University of Wisconsin, Madison, Wisconsin, USA. 62pp.
- \_\_\_\_\_. 1999. Nesting ecology of Eastern Prairie Population Canada geese. Dissertation, University of Wisconsin, Madison, Wisconsin, USA. 204pp.
- \_\_\_\_\_ and D.H. Rusch. 1997a. Accuracy of egg flotation in determining age of Canada goose nests. *Wildlife Society Bulletin* 25:854-857.
- \_\_\_\_\_ and D.H. Rusch. 1997b. Visibility bias on counts of nesting Canada geese. *Journal of Wildlife Management* 61:768-772.
- Wellein, E.G. and H.G. Lumsden. 1964. Northern forests and tundra. Pages 67-76 in J.P. Lunduska, editor. *Waterfowl tomorrow*. United States Government Printing Office, Washington, D.C., USA.
- Weller, M.W. 1956. A simple field candler for waterfowl eggs. *Journal of Wildlife Management* 20:111-113.
- Westerkov, K. 1950. Methods for determining the age of game bird eggs. *Journal of Wildlife Management* 14:56-57.
- Wilson, D.J. and R.G. Bromley. 2001. Functional and numerical responses of predators to cyclic lemming abundance: effects on loss of goose nests. *Canadian Journal of Zoology* 79:525-532.
- Wrigley, R.E. and D.R.M. Hatch. 1976. Arctic fox migrations in Manitoba. *Arctic* 29:147-158.

Ydenberg, R.C. 1987. Nomadic predators and geographical synchrony in microtine population cycles. *Oikos* 50:270-272.

Table 1. Summary of explanatory variables considered in regression analyses and their predicted association with nest success of Eastern Prairie Population Canada geese (*Branta canadensis interior*) under the “bird-lemming” hypothesis. The predicted association for *D* and *HD* with nest success is based on previous studies of factors influencing nesting Canada geese.

Variable	Description	Predicted association w/ nest success
$L_t$	Relative lemming abundance in year, $t$	Positive
$L_{t-1}$	Relative lemming abundance in year, $t - 1$	Negative
$FD_t$	Proportion active fox dens in year, $t$	Positive
$FD_{t-1}$	Proportion active fox dens in year, $t - 1$	Negative
$D$	Density of goose nests per 100 ha of wetland in year, $t$	Positive
$HD$	Median hatch date of Canada goose nests in year, $t$	Negative

Table 2. Summary statistics for all variables considered in analysis of Eastern Prairie Population Canada goose (*Branta canadensis interior*) nest success near Cape Churchill, Manitoba for 1993 - 2004 and 1998 - 2004.  $L_{t-1}$  and  $FD_{t-1}$  were calculated based on  $L_t$  and  $FD_t$  from 1992 - 2003.

Variable <sup>a</sup>	1993 – 2004			1998 – 2004		
	Mean	SE	95% C.I.	Mean	SE	95% C.I.
<i>Mayfield</i>	0.48	0.08	0.30, 0.65	0.38	0.09	0.14, 0.61
<i>Prior</i>	0.57	0.05	0.45, 0.69	0.56	0.08	0.38, 0.75
$L_t$	278.99	43.48	374.69, 183.29	296.56	60.48	148.57, 444.54
$L_{t-1}$	296.18	47.10	192.50, 399.86	300.44	60.53	152.34, 448.55
$FD_t$	0.61	0.07	0.45, 0.77	0.74	0.05	0.60, 0.87
$FD_{t-1}$	0.60	0.07	0.44, 0.75	0.64	0.10	0.39, 0.88
$D$	7.92	0.85	6.05, 9.79	7.48	1.44	3.96, 10.99
$HD$	25.25	2.30	30.31, 20.19	25.00	3.92	15.40, 34.59

<sup>a</sup> *Mayfield* = nest success post-discovery  
*Prior* = nest success prior to discovery  
See Table 1 for definition of all other variables

Table 3. Summary of regression analysis for 1993 – 2004 when estimates of Eastern Prairie Population Canada goose (*Branta canadensis interior*) nest success post-discovery were used as the response for all models. Models were ranked using Akaike’s Information Criterion corrected for small sample size ( $AIC_c$ ) and evaluated based on  $AIC_c$  weights ( $w_i$ ).  $K$  is the number of model parameters and  $n$  is the sample size.

Model <sup>a</sup>	$AIC_c$	$\Delta AIC_c$	$w_i$	$K$	$n$	$R^2$
D + $FD_t$	-32.61	0.00	0.61	4	12	0.64
$FD_t$	-29.27	3.34	0.12	3	12	0.29
D	-29.27	3.35	0.12	3	12	0.29
D + $L_t$ + $FD_t$	-26.35	6.27	0.03	5	12	0.64
$L_{t-1}$	-26.26	6.35	0.03	3	12	0.09
$FD_{t-1}$	-25.95	6.66	0.02	3	12	0.07
$L_t$	-25.84	6.77	0.02	3	12	0.06
D + $L_{t-1}$	-25.20	7.42	0.02	4	12	0.33
$L_t$ + $FD_t$	-25.14	7.47	0.01	4	12	0.33
D + $L_t$	-24.73	7.88	0.01	4	12	0.30
D + $FD_{t-1}$	-24.62	8.00	0.01	4	12	0.30
$L_t$ + $L_{t-1}$	-21.62	10.99	0.00	4	12	0.10
$FD_{t-1}$ + $L_t$	-21.56	11.06	0.00	4	12	0.09
D + $L_t$ + $L_{t-1}$	-18.91	13.70	0.00	5	12	0.33
D + $L_t$ + $FD_{t-1}$	-18.47	14.15	0.00	5	12	0.30

<sup>a</sup>see Table 1 for variable definition

Table 4. Summary of coefficient estimates and 95% confidence intervals for models of Eastern Prairie Population Canada goose (*Branta canadensis interior*) nest success that received the most support (lowest  $AIC_c$ ) in regression analyses. If the 95% confidence interval for the estimate did not overlap zero, the effect of the variable was considered significantly different from zero at the  $\alpha = 0.05$  significance level.

Years	Response	Model	Parameter	Est.	95% C.I.
1993 - 2004	Post-discovery	$\beta_0 + D + FD_t$	$\beta_0$	0.44	-0.01, 0.88
			$\beta_D$	0.06	0.01, 0.10
			$\beta_{FD_t}$	-0.64	-1.14, -0.15
1998 - 2004	Post-discovery	$\beta_0 + D + L_{t-1}$	$\beta_0$	-0.47	-0.64, -0.30
			$\beta_D$	0.07	0.06, 0.09
			$\beta_{L_{t-1}}$	0.001	0.0007, 0.001
1998 - 2004	Prior-discovery	$\beta_0 + D$	$\beta_0$	0.33	-0.08, 0.73
			$\beta_D$	0.03	-0.02, 0.08

Table 5. Summary of regression analysis for 1993 – 2004 when the estimates of Eastern Prairie Population Canada goose (*Branta canadensis interior*) nest success prior to discovery were used as the response for all models. Models were ranked using Akaike’s Information Criterion corrected for small sample size ( $AIC_c$ ) and evaluated based on  $AIC_c$  weights ( $w_i$ ).  $K$  is the number of model parameters and  $n$  is the sample size.

Model <sup>a</sup>	$AIC_c$	$\Delta AIC_c$	$w_i$	$K$	$n$	$R^2$
D	-36.23	0.00	0.26	3	12	0.14
$L_t$	-35.29	0.94	0.16	3	12	0.07
$FD_t$	-34.98	1.24	0.14	3	12	0.05
$FD_{t-1}$	-34.43	1.80	0.10	3	12	0.00
$L_{t-1}$	-34.43	1.80	0.10	3	12	0.00
D + $L_t$	-33.65	2.58	0.07	4	12	0.28
D + $FD_t$	-32.65	3.58	0.04	4	12	0.20
D + $FD_{t-1}$	-31.73	4.50	0.03	4	12	0.09
D + $L_{t-1}$	-31.56	4.67	0.02	4	12	0.14
$FD_t$ + $L_t$	-31.37	4.86	0.02	4	12	0.13
$L_t$ + $L_{t-1}$	-31.29	4.94	0.02	4	12	0.12
$FD_{t-1}$ + $L_t$	-30.80	5.43	0.02	4	12	0.09
D + $L_t$ + $FD_t$	-28.96	7.27	0.01	5	12	0.37
D + $L_t$ + $L_{t-1}$	-28.06	8.16	0.00	5	12	0.32
D + $L_t$ + $FD_{t-1}$	-27.37	8.86	0.00	5	12	0.28

<sup>a</sup>see Table 1 for variable definition

Table 6. Summary of regression analysis for 1998 – 2004 when the estimates of Eastern Prairie Population Canada goose (*Branta canadensis interior*) nest success post-discovery were used as the response for all models. Models were ranked using Akaike’s Information Criterion corrected for small sample size ( $AIC_c$ ) and evaluated based on  $AIC_c$  weights ( $w_i$ ).  $K$  is the number of model parameters and  $n$  is the sample size.

Model <sup>a</sup>	$AIC_c$	$\Delta AIC_c$	$w_i$	$K$	$n$	$R^2$
D + L <sub>t-1</sub>	-23.05	0.00	0.97	4	7	0.98
D	-15.49	7.56	0.02	3	7	0.63
FD <sub>t-1</sub>	-9.76	13.29	0.00	3	7	0.17
FD <sub>t</sub>	-9.29	13.75	0.00	3	7	0.11
L <sub>t-1</sub>	-8.68	14.37	0.00	3	7	0.03
L <sub>t</sub>	-8.50	14.55	0.00	3	7	0.01
D + L <sub>t</sub>	-4.15	18.90	0.00	4	7	0.75
FD <sub>t</sub> + D	-1.93	21.11	0.00	4	7	0.66
FD <sub>t-1</sub> + D	-1.50	21.55	0.00	4	7	0.63
FD <sub>t-1</sub> + L <sub>t</sub>	4.17	27.22	0.00	4	7	0.18
FD <sub>t</sub> + L <sub>t</sub>	4.70	27.74	0.00	4	7	0.11
L <sub>t</sub> + L <sub>t-1</sub>	4.95	28.00	0.00	4	7	0.08
L <sub>t</sub> + L <sub>t-1</sub> + D	17.38	40.43	0.00	5	7	0.99
D + L <sub>t</sub> + FD <sub>t</sub>	37.14	60.19	0.00	5	7	0.77
D + FD <sub>t-1</sub> + L <sub>t</sub>	37.58	60.63	0.00	5	7	0.76

<sup>a</sup>see Table 1 for variable definition

Table 7. Summary of regression analysis for 1998 – 2004 when the estimates of Eastern Prairie Population Canada goose (*Branta canadensis interior*) nest success prior to discovery was used as the response for all models. Models were ranked using Akaike’s Information Criterion corrected for small sample size ( $AIC_c$ ) and evaluated based on  $AIC_c$  weights ( $w_i$ ).  $K$  is the number of model parameters and  $n$  is the sample size.

Model <sup>a</sup>	$AIC_c$	$\Delta AIC_c$	$w_i$	$K$	$n$	$R^2$
D	-14.62	0.00	0.41	3	7	0.35
$L_{t-1}$	-12.56	2.06	0.15	3	7	0.13
$L_t$	-12.26	2.36	0.13	3	7	0.09
$FD_{t-1}$	-12.11	2.51	0.12	3	7	0.07
$FD_t$	-12.00	2.62	0.11	3	7	0.06
$D + L_{t-1}$	-10.73	3.89	0.06	4	7	0.85
$D + L_t$	-8.71	5.91	0.02	4	7	0.80
$FD_t + D$	-0.74	13.88	0.00	4	7	0.36
$FD_{t-1} + D$	-0.63	13.99	0.00	4	7	0.35
$FD_{t-1} + L_t$	0.18	14.80	0.00	4	7	0.28
$L_t + FD_t$	1.09	15.71	0.00	4	7	0.17
$L_t + L_{t-1}$	1.34	15.96	0.00	4	7	0.14
$L_t + L_{t-1} + D$	15.86	30.48	0.00	5	7	0.98
$D + FD_{t-1} + L_t$	32.79	47.41	0.00	5	7	0.81
$D + L_t + FD_t$	32.82	47.44	0.00	5	7	0.81

<sup>a</sup>see Table 1 for variable definition

Figure 1. The Cape Churchill region of Manitoba, Canada and the location of the Nestor One study area.

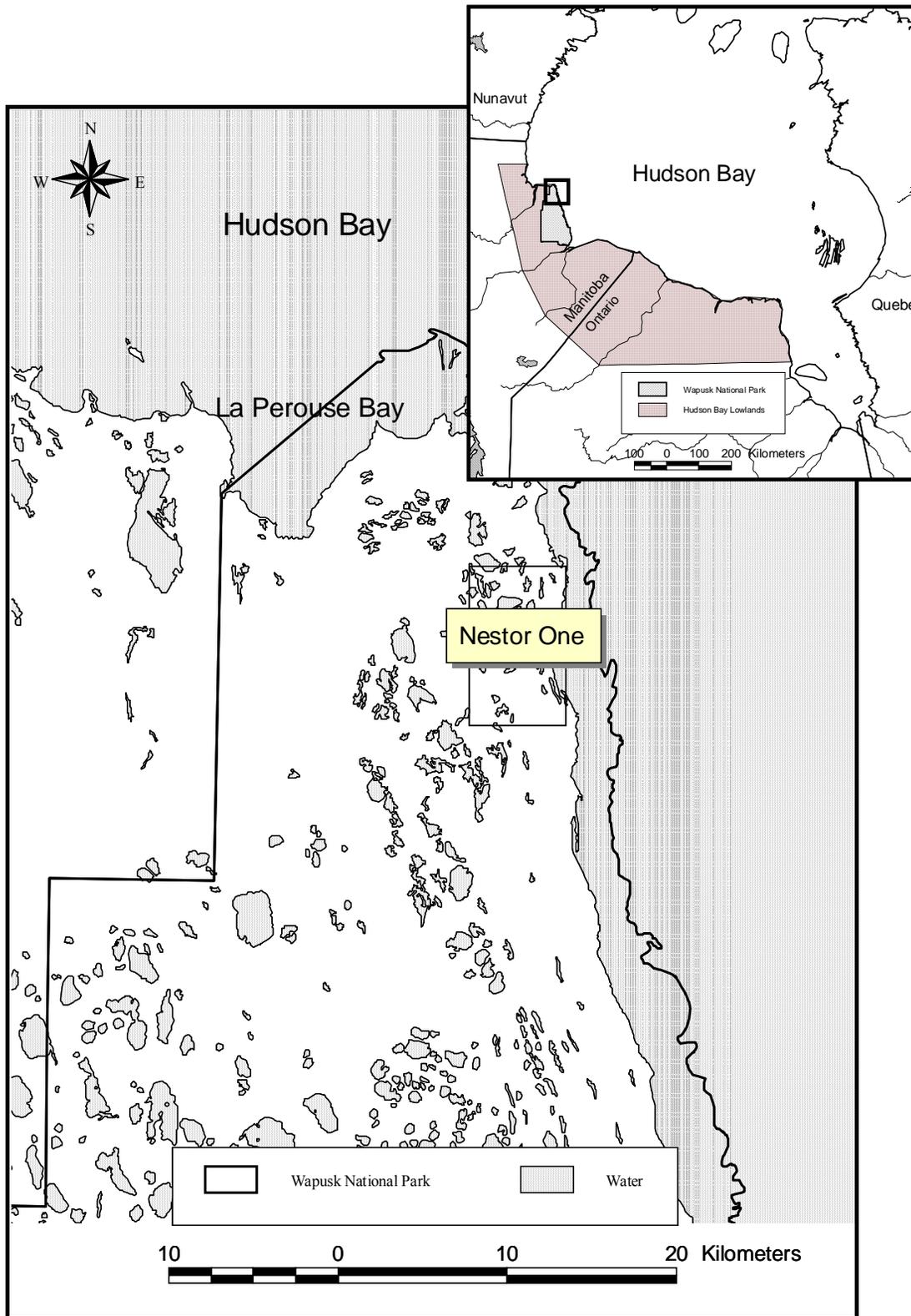


Figure 2. Estimated Eastern Prairie Population Canada goose (*Branta canadensis interior*) nest success for the period post-discovery and prior to discovery between 1993 and 2004. Mayfield nest success estimates averaged 0.48 (SE = 0.08) and nest success prior to discovery averaged 0.57 (SE = 0.05). Error bars represent 95% confidence intervals..

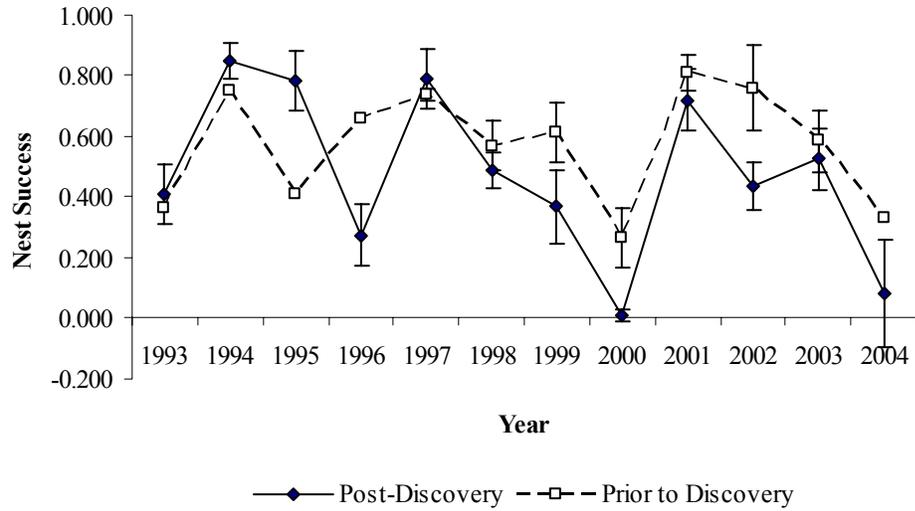


Figure 3. Autocorrelation function (ACF) plots for: (a) the estimate of nest success post-discovery 1993 – 2004, (b) the estimate of nest success post-discovery 1998 – 2004, (c) the estimate of nest success prior to discovery 1993 – 2004, and (d) the estimate of nest success prior to discovery 1998 – 2004. Lag values are in years. Dashed lines represent the  $\alpha = 0.05$  significance level.

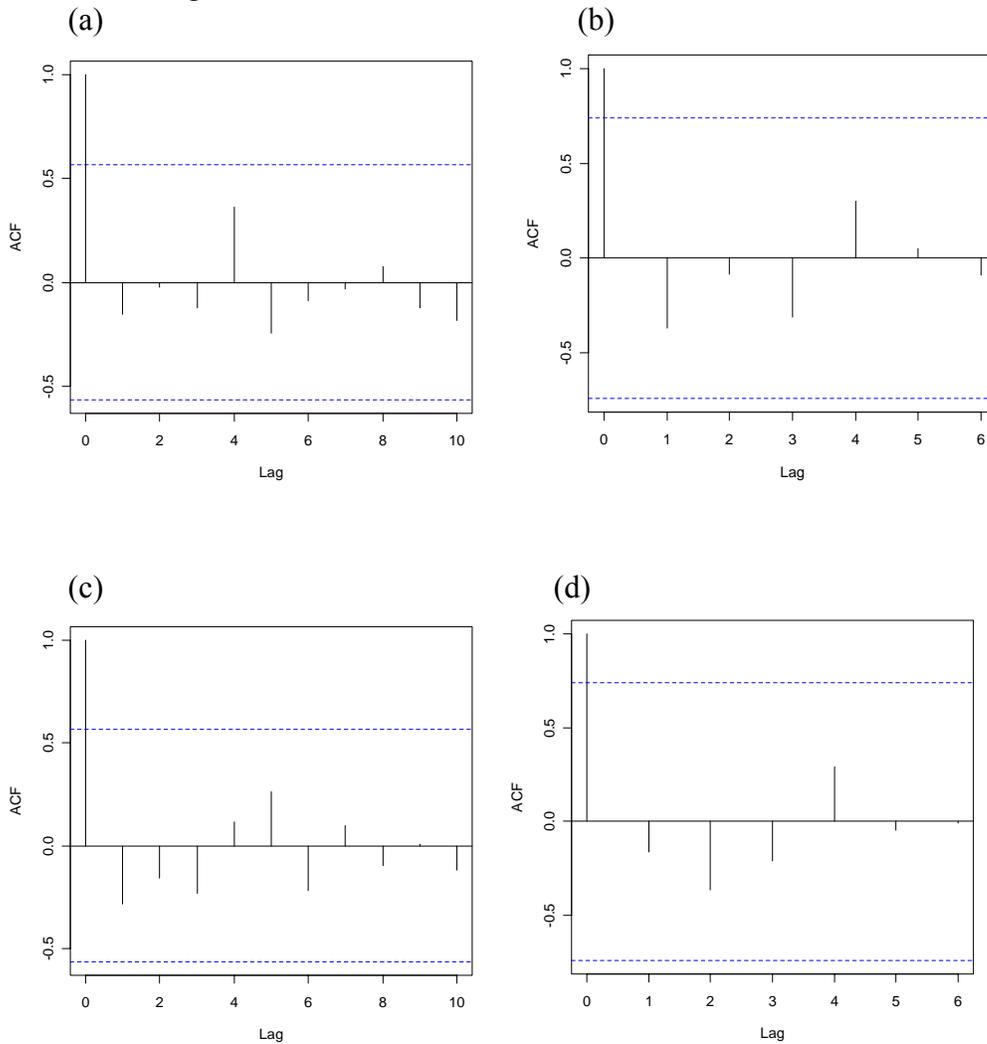


Figure 4. Eastern Prairie Population Canada goose (*Branta canadensis interior*) nest density (nests per 100 ha wetland nest habitat) on the Nestor One study area near Cape Churchill, Manitoba between 1993 and 2004. Error bars represent 95% confidence intervals. Mean nest density was 7.92 (SE = 0.85) nests per 100 ha of wetland.

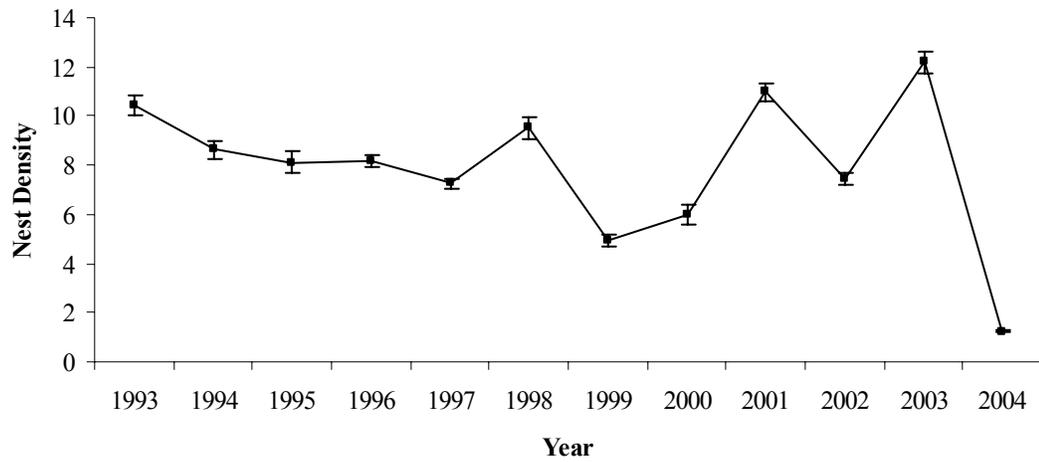


Figure 5. Autocorrelation function (ACF) plots for: (a) Canada goose nest density for 1993 – 2004, (b) Canada goose nest density for 1998 – 2004, (c) median hatch date 1993 - 2004, and (d) median hatch date 1998 – 2004. Lag values are in years. Dashed lines represent the  $\alpha = 0.05$  significance level.

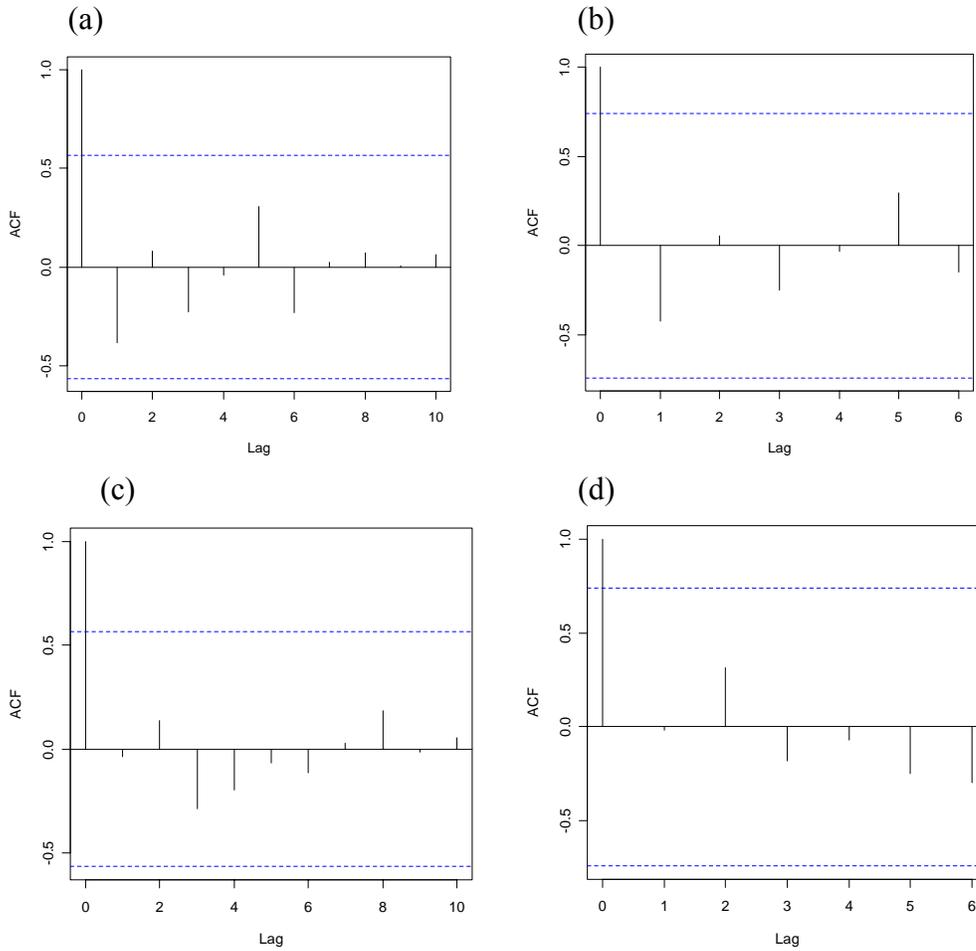


Figure 6. Predicted relative collared lemming (*Dicrostonyx richardsoni*) abundance based on willow (*Salix* spp.) scar analysis. Fitted kernel mean function when the exponential decay term is removed [ $E(Y|X) = N*(0.36 - 0.27*\sin(2*\pi*(X + 3.263)/2.83))$  where  $Y$  is the count of scars of age  $X$ ,  $N$  is the sample size] and predicted scar age counts for years 1992 – 2004 near Cape Churchill, Manitoba. Error bars represent 95% confidence intervals for predicted counts.

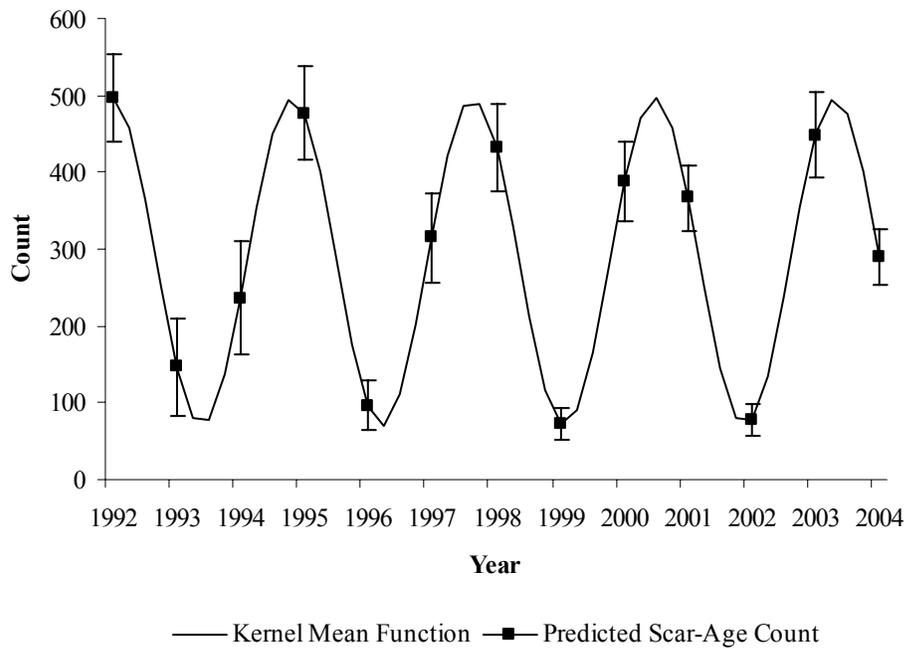


Figure 7. Autocorrelation function (ACF) plots for: (a) the relative abundance of collared lemmings 1992 - 2004, (b) relative abundance of collared lemmings 1998 – 2004, (c) the proportion of active arctic fox dens 1992 -2004, and (d) the proportion of active arctic fox dens 1998 -2004. Lag values are in years. Dashed lines represent the  $\alpha = 0.05$  significance level.

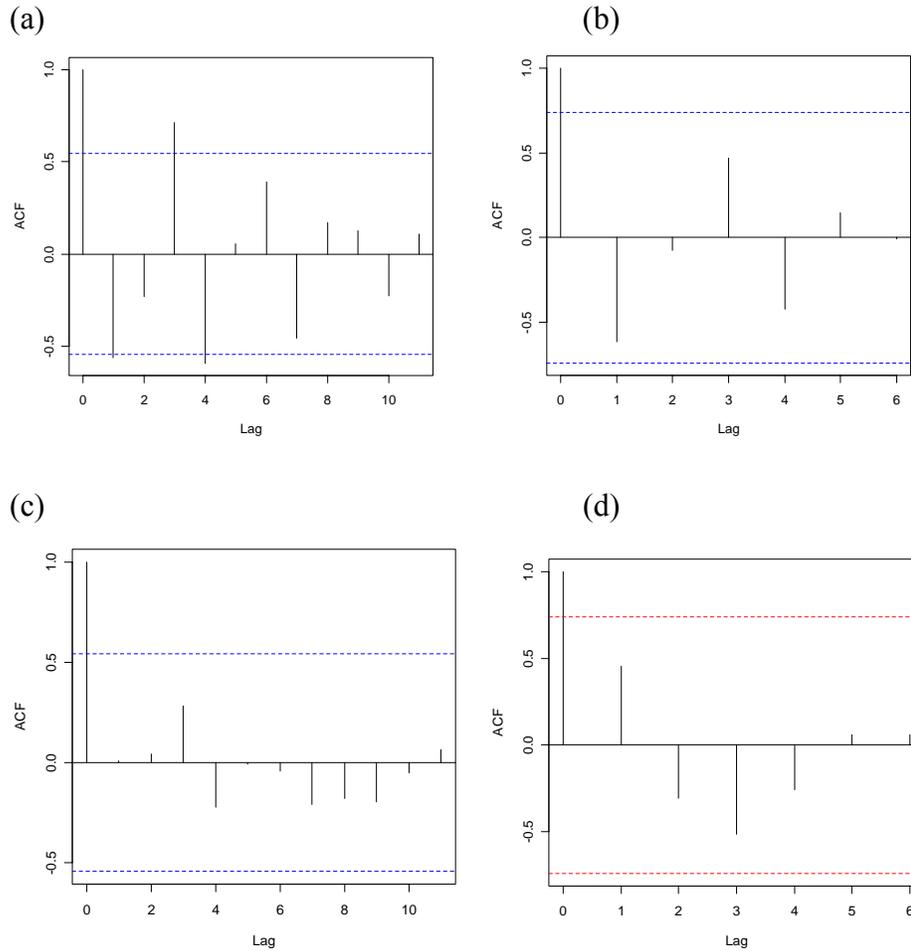


Figure 8. The proportion of arctic fox (*Alopex lagopus*) dens active near Cape Churchill, Manitoba between 1992 and 2004. Error bars represent 95% confidence intervals generated using the distribution of 1,000 bootstrap resamples. Mean proportion of active dens was 0.61 (SE = 0.07).

