THE ROLE OF DISPERSAL IN POPULATION DYNAMICS OF BREEDING ROSS'S GEESE

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GENERAL ABSTRACT

Spatial variation in density of organisms can lead to challenges in estimation of population size. Associated vital rates responsible for this variation also may vary geographically and in response to local ecological conditions, with the result that subunits of a metapopulation may have different trajectories. Both temporal and spatial variation in population size occurs not only as a result of additions through birth and deletions through death, but also from gains and losses arising from immigration and emigration, respectively. Although virtually all organisms have evolved mechanisms for dispersal, the role of movement in population dynamics has received far less attention than have contributions from recruitment and losses to mortality. I used mark-recapture techniques to make inferences about the role of movement in local population dynamics of Ross's Goose (*Chen rossii*) colonies by estimating rates of movement between breeding subpopulations in the Queen Maud Gulf metapopulation. I also assessed decision-based philopatry (i.e., the role of previous nesting outcome; *sensu* Hoover 2003) and a potential cost of reproduction to female geese through experimental manipulation of nesting success.

Previous nest fate influenced intra-colony dispersal as failed nesters moved further between consecutive nest sites, but inter-colony movement was not affected by previous nest fate. Regardless of previous nest fate, Ross's Geese did not exhibit philopatry to nest sites, or to breeding territories, suggesting that philopatry occurs at a larger spatial scale. Breeding success accounted for a detectable, but only small amount of variation (<11%) in dispersal distance within colonies. I suggest that temporal variation in habitat availability favors flexibility in settling patterns by geese in a changing matrix of habitat availability, governed largely by receding snow cover. Such flexibility is necessary for nesting as early as possible, because recruitment is strongly linked to timing of breeding by arctic-nesting geese. Colonial philopatry may be important not only for favorable nesting but also for access to high-quality feeding areas adjacent to colonies. Such feeding areas represent a predictable food resource important not only to growing goslings, but also adult survival regardless of the outcome of their breeding attempt.

I concluded from experimental manipulation that successful reproduction was encumbered with a cost to survival of females. I argue that such a cost of breeding is more likely to be incurred when climatic conditions during incubation are harsh, and when the breeding population is larger.

I did not find evidence for geographic variation in survival, but rates of philopatry varied markedly among colonies. The substantial exchange of females among breeding colonies (1) underscores the potential for dispersal to alter breeding distribution, (2) demonstrates that the influence of immigration on colony-specific rates of population growth was nontrivial, and (3) provides behavioral evidence for extensive gene flow resulting from female dispersal. Estimates of emigration and survival from my studies were used in combination with those for fecundity parameters and colony-specific population growth rates (λ) to interpolate the role of immigration from a simple balance equation. During years for which rates of movement were estimated, immigration constituted 9-20% of λ at the Karrak Lake colony, suggesting that movement was an important contribution to population growth.

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CHAPTER 1. THE ROLE OF DISPERSAL IN POPULATION DYNAMICS: A GENERAL INTRODUCTION

1.1 THE ROLE OF DISPERSAL IN POPULATION DYNAMICS

The primary variable of interest in population ecology is population size (Williams et al. 2002), which can be defined as the number of organisms of a given species distributed across some defined area (Krebs 1972). On the broadest spatial scale (i.e., the entire population of a species throughout its distribution), temporal variation in population size occurs as a result of additions through birth and deletions through death. However, viewing population process on the broadest spatial scale oversimplifies the spatial aspect of population ecology (Andrewartha and Birch 1954) because organisms usually are not distributed evenly throughout their range. Moreover, spatial variation can lead to challenges in estimation of population size, and relevant vital rates responsible for its variation. Recognition of spatial variation in abundance and associated vital rates often requires stratification of a population into spatially distinct subpopulations whose dynamics may behave independently from one another and in response to local ecological conditions. As well, conservation concerns and prescribed management efforts may best be focused on local populations of a species rather than over its global distribution. However, virtually all organisms have evolved mechanisms for dispersal. Such ability to move can be adaptive by allowing individuals to escape unfavorable environmental conditions, or to sample habitats and permit selection of new habitats in which likelihood of survival or successful reproduction may improve. If present, movement must also be considered for a complete understanding of local population processes. Immigration and emigration serve as vehicles for addition and deletion of individuals from local populations, and complement those from births and death, respectively. Thus, if ignored, movement of individuals may confound inferences

about local population dynamics, and requires that movement should be estimated for a full understanding of its role in population growth.

Movement has long been recognized as an important process from both ecological and evolutionary perspectives. However, until recently, methodological limitations curtailed our ability to derive robust inference about the process of dispersal and its influence on population dynamics. Consequently, the role of dispersal in structuring populations remains one of the largest gaps in our knowledge of ecological dynamics.

Much of our current understanding of dispersal behavior and life history evolution in birds is based on return rates (i.e., the proportion of marked individuals released in one year that are recaptured in the following year). Return rates are the product of (1) surviving, (2) returning to the study area if alive, and (3) being resighted/recaptured if alive and on the study area (Brownie et al. 1993, Nichols and Kendall 1995); thus, any difference in return rate can be attributed to a difference in recapture, survival, or presence (Clobert 1995, Martin et al. 1995). Many recent methodological advances for estimating parameters associated with dispersal are cast within a capture-recapture framework (reviews by Nichols 1996, Nichols and Kaiser 1999, Bennetts et al. 2002), which accounts for resighting probability (Lebreton et al. 1992, Clobert 1995, Martin et al. 1995) and allows distinguishing between mortality and dispersal (Clobert and Lebreton 1991, Nichols and Kendall 1995, Spendelow et al. 1995). I used marked individuals to address questions pertaining primarily to spatial aspects of Ross's Goose (*Chen rossii*) population ecology. Recent population trends propound several questions regarding Ross's Goose movement, and several life history characteristics of Ross's Geese render them amenable for investigating movement.

1.2 CHANGES IN DISTRIBUTION AND ABUNDANCE OF LIGHT GEESE

Populations of Ross's Geese and Lesser Snow Geese (*C. caerulescens*, hereafter Snow Geese, collectively referred to as 'light geese') breeding in the Canadian Arctic have increased exponentially over the past 30 years (Boyd et al. 1982, Kerbes et al. 1983, Alisauskas et al. 1998). Agricultural practices have changed the North American landscape and brought about improved foraging conditions for light geese, which

combined with management efforts, have created conditions favorable to survival and recruitment. By adapting to agricultural habitats, light geese have greatly expanded their migration and winter ranges, and the nutrient and energy subsidy garnered from using croplands during these periods (Alisauskas et al. 1988, Bateman et al. 1988, Alisauskas and Ankney 1992) has effectively released the birds from a continental carrying capacity that previously limited populations to much lower levels. Consequently, light goose populations are now considered 'overabundant' (Ankney 1996, Batt 1997, Moser 2001). This range expansion draws attention to dispersal as a factor influencing population dynamics; for one thing, dispersal facilitated the pioneering of agricultural habitats thought to have led ultimately to unprecedented increases in light goose abundance.

Knowledge of dispersal behavior in light geese is primarily limited to descriptive accounts of changes in breeding, migration, or winter distribution of Ross's Geese and documentation of female-biased natal and breeding philopatry in Snow Geese. For example, as the continental population of Ross's Geese increased, it expanded eastward from its historic winter range in California, to the midcontinent region (Dzubin 1965, McLandress 1979, Ryder and Alisauskas 1995, Moser 2001, Alisauskas et al. 2006a) where they occurred only rarely before the 1970s (Bellrose 1976). Today, Ross's Geese are commonly sighted in the midcontinent region (see Alisauskas 1998) and appear to be continuing their eastward shift in distribution (Alisauskas et al. 2006a). On breeding areas, new breeding colonies of light geese have formed (Alisauskas and Boyd 1994, Alisauskas unpublished data) and existing colonies have enlarged (MacInnes and Kerbes 1987, Alisauskas and Boyd 1994, Cooke et al. 1995). Further, Snow Geese have expanded their breeding range in the central Arctic (Alisauskas and Boyd 1994, Kerbes 1994) and Ross's Geese have expanded their breeding range into the eastern arctic and subarctic (Didiuk et al. 2001, J. Leafloor personal communication).

Knowledge about philopatry (and complementary dispersal) in light geese is limited to information from studies on Snow Geese nesting at the southern edge of their breeding range at La Pérouse Bay (LPB), Manitoba. Descriptions of higher return rates by female Snow Geese compared to males provided evidence for female-biased natal

and breeding philopatry (Cooke et al. 1975, Cooke et al. 1995). Most gene flow in Snow Geese was thought to be through male dispersal (Cooke et al. 1975, Rockwell and Cooke 1977, Rockwell and Barrowclough 1987). However, genetic studies provide evidence supporting extensive gene flow involving females (Avise et al. 1992, Quinn 1992), and expansion of breeding distribution by light geese confirms female dispersal.

Philopatry is usually considered an adaptive strategy that confers some benefit to the individual because of previous experience and familiarity with the environment. However, there is evidence from Snow Geese nesting at LPB that philopatry can be maladaptive. Increased Snow Goose abundance has dramatically impacted coastal areas of Hudson and James Bays where goose herbivory (Cargill and Jefferies 1984, Hik and Jefferies 1990, Zellmer et al. 1993, Abraham and Jefferies 1997) has resulted in habitat degradation at breeding colonies and brood-rearing areas (Kerbes et al. 1990). These changes in habitat quality, in turn, are thought to have caused long-term declines in fecundity on local (Cooch et al. 1989) and continental scales (Alisauskas 2002), and in reductions in gosling growth rates (and subsequent adult body size, Alisauskas 2002) and gosling survival (Cooch et al. 1991a,b, Williams et al. 1993). Although females that continue to return to breed in such highly degraded habitats, such as at LPB, may suffer reduced fecundity, some geese have responded to this habitat degradation by emigrating to new breeding areas. Rates of permanent emigration from LPB appear to have increased (Francis and Cooke 1993), presumably this emigration includes some movement to other breeding colonies; and local dispersal to less impacted areas near traditional nesting (Ganter and Cooke 1998) and brood-rearing areas (Cooch et al. 2001) has been documented. Thus, it appears that female emigration has occurred, but we lack insight into the proportion that chose to emigrate.

Observations of range expansion, genetic evidence for extensive dispersal, and findings from long-term studies at LBP suggest that dispersal is an important process in population dynamics of light geese. Nonetheless, we lack complete understanding of the process of dispersal, its consequences, potential factors invoking the behavior, and its influence on population process. Dispersal has enormous potential to influence light goose population dynamics during all phases of the life cycle. The objectives of my research were to:

1. Estimate rates of between-colony breeding dispersal (and its complement, philopatry) within the Queen Maud Gulf metapopulation of Ross's Geese to gain insight into its role in influencing species distribution, colony-specific population growth rates, and rates of gene flow.
2. Evaluate the role of breeding experience as a factor influencing breeding dispersal using an experimental manipulation of nesting success.
3. Test the hypothesis that a trade-off exists between current reproduction and future survival by comparing survival of females that hatched young to those that did not.
4. Evaluate the potential for geographic heterogeneity in Ross's Goose survival rates. If strong philopatry is exhibited throughout the annual cycle, limited exchange of individuals among subpopulations may result in subpopulation-specific rates of survival as mortality risks are likely to vary on a continental scale.
5. Evaluate the potential influence of breeding dispersal on colony-specific population growth rates within the Queen Maud Gulf metapopulation.

I have organized my thesis into four data chapters and a synthesis. The data chapters are formatted as journal articles and each includes an Abstract and Introduction section. All of my research questions relied upon having a sample of marked individuals, so to reduce redundancy in the Methods sections of subsequent data chapters I have include a general methods section where I describe the study area, capture and marking of geese, and protocol for surveys for marked individuals. Methodologies specific to each chapter are found therein.

1.3 GENERAL METHODS

1.3.1 Study Area

Most fieldwork took place at Colony 3 (hereafter, Karrak Lake; Fig. 1.1), site of the Karrak Lake Research Station where investigations of Ross's Goose breeding ecology have occurred continuously since 1991. Karrak Lake ($67^o14'$ N, $100^o15'$ W) is located in the Queen Maud Gulf Migratory Bird Sanctuary (QMGMBS), Nunavut, Canada, ~60 km from the coast. The QMGMBS was established in 1961 primarily to protect the nesting grounds of what was then a markedly reduced continental population
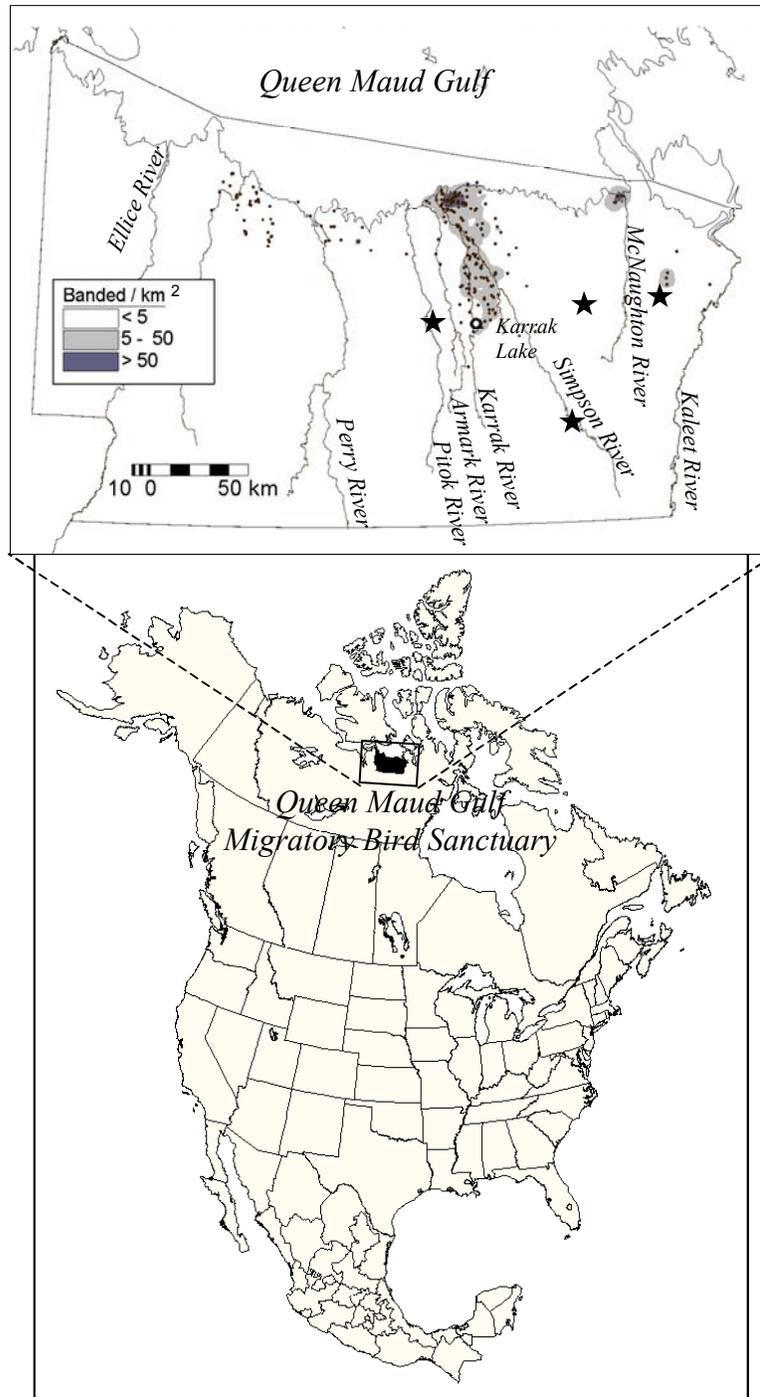
Figure 1.1. Location of the Karrak Lake Research Station, focal breeding colonies, and Ross's Goose banding efforts (1991-2003) within brood rearing areas in the Queen Maud Gulf Migratory Bird Sanctuary, Nunavut, Canada. An open circle delineates Karrak Lake, while stars delineate locations of other breeding colonies where fieldwork occurred (1999-2003). Banding drive locations are shown as dots, while shaded areas depict density of geese banded.

of Ross's Geese. Most (~95%) Ross's Geese breed on the mainland just south of Queen Maud Gulf (QMG) in colonies of the central arctic lowland within the Sanctuary (Kerbes 1994, Ryder and Alisauskas 1995; Fig. 1.2). Breeding colonies are generally composed of Ross's Geese and congeneric Lesser Snow Geese. Karrak Lake is one of the largest known colonies in the Sanctuary and has grown rapidly in both numbers of nesting geese (from 426,000 in 1993 to 960,000 in 2003) and terrestrial area occupied by nesting geese (from ~63 km^2 in 1993 to ~176 km^2 in 2003, Alisauskas unpublished data). Ryder and Alisauskas (1995) provide detailed descriptions of typical landscapes and habitat characteristics of QMG breeding colonies.

In addition to work at Karrak Lake, surveys for marked individuals were conducted annually (1999-2003) at four other colonies (9, 10, 46 and 81; Fig. 1.2). I selected these colonies because they represent some of the largest known colonies within QMGMBS and collectively account for ~90% of the known continental breeding population of Ross's Geese (Ryder and Alisauskas 1995, Alisauskas et al. 1998).

1.3.2 Capture and Marking of Geese

Several years of marking efforts before 1999 provided the sample of marked geese that made my research possible. Flightless Ross's Geese were captured within brood-rearing habitats during adult remigial molt (10 July-15 August 1991-2003) by driving them into portable corral traps using a helicopter (Timm and Bromley 1976). After hatch, most geese move northward (Slattery 1994) and tend to be homogenously distributed in brood-rearing areas located between their breeding colony and the coast (Slattery 2000). Capture efforts were focused along the Simpson (1991-2003) and McNaughton (1999-2003) river drainages, brood-rearing areas located north of the two largest known colonies (Karrak Lake and Colony 10, respectively) in the Sanctuary, and to a lesser extent, in the Perry River region (1991-2003; Fig. 1.1). Age-class (adult, or after-hatch-year [AHY] vs. juvenile, or hatch-year [HY]) was determined using plumage characteristics and sex was determined by cloacal examination. Following methods used by Alisauskas and Lindberg (2002), all birds were marked with a metal legband and a portion was also marked with a plastic neckband engraved with a unique
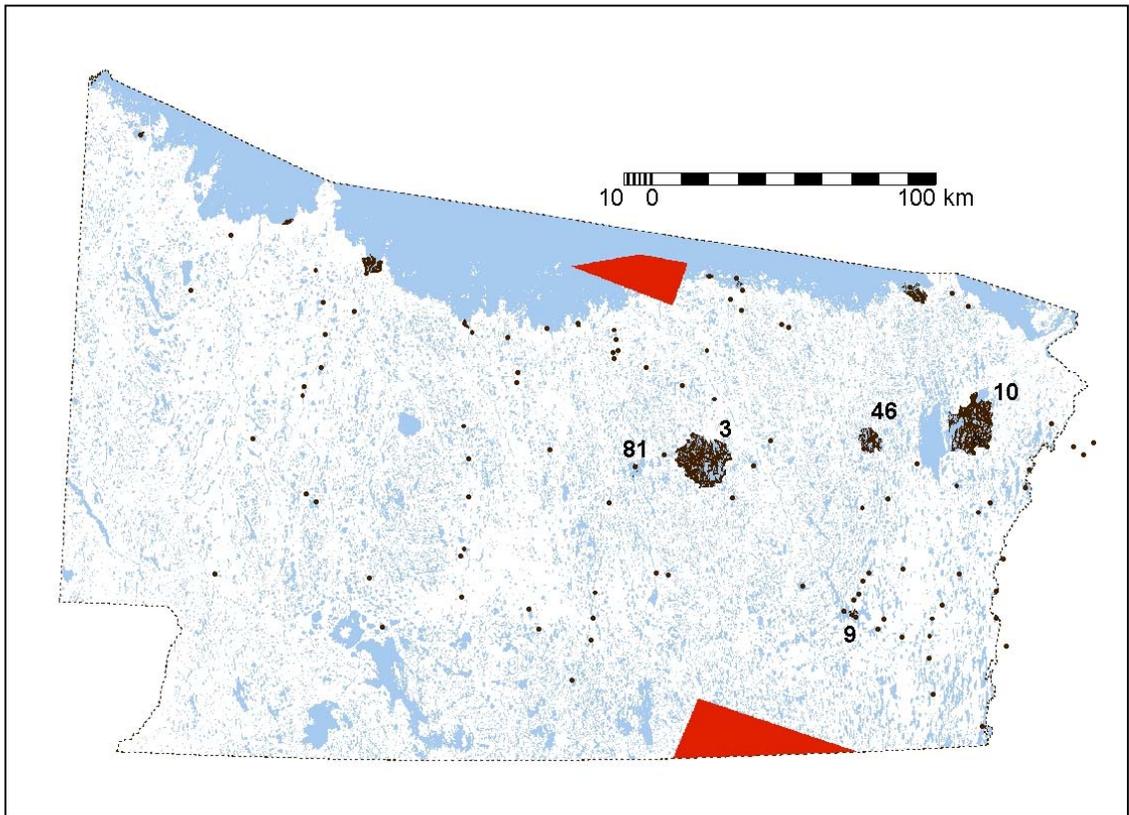
Figure 1.2. Distribution of known breeding colonies of Ross's and Lesser Snow Geese within the Queen Maud Gulf Migratory Bird Sanctuary, Nunavut, Canada. Light grey areas indicate water, dark grey areas indicate missing satellite imagery, black dots indicate colony locations, and black areas depict spatial extent of larger colonies. Numbers correspond to colony identification where surveys for neckbanded geese were conducted, 1999-2003: Colonies 3 (Karrak Lake), 9 (Simpson River, 66°46' N, 99°08' W), 10 (East McNaughton, 67°21' N, 98°04' W), 46 (West McNaughton, 67°18' N, 98°57' W), and 81 (Reference Lake, 67°15' N, 100°50' W).

alphanumeric code. Geese were released *en masse* after banding to facilitate reformation and cohesion of family units.

1.3.3 Surveys for Marked Geese

I restricted surveys for neckbanded geese to their 23-day incubation period (Ryder 1972) because of my interest in estimating dispersal between breeding attempts. Observations strictly during incubation reduced potential for bias caused by sampling non-breeding adults, as territorial breeders displace most non-breeders from colonies by the onset of incubation (Ryder and Alisauskas 1995). Extent of breeding distribution at each colony was mapped each year during early incubation from a helicopter. Data were digitized and imported into SPANS GIS (PCI Geomatics 1999) study area with Albers equal area projection. Layers showing colony extent were overlaid with a layer showing land and water (30 m resolution from LandSat imagery) to calculate the area of terrestrial habitat at each colony occupied by nesting geese. Spatial extent of breeding colonies can encompass large areas; for example, in 2002 terrestrial habitat occupied by nesting geese was 164.9 km^2 at Colony 3, 10.3 km^2 at Colony 9, 151.2 km^2 at Colony 10, 39.8 km^2 at Colony 46, and 1.9 km^2 at Colony 81. Due to this vast area in which neckbands could only be searched for on foot, it was impossible to survey colonies in their entirety with the manpower at my disposal. Instead, I selected a contiguous area within each colony thought to have the highest nesting densities, so that efficiency of detecting neckbands was maximized. Consistency of sampling was maintained by searching for neckbands within these same areas each year. Within colonies and years, I assumed that the ratio of neckbanded to unmarked birds was relatively uniform and unrelated to variation in nesting density. Observers documented any broken neckbands found on the ground during neckband surveys.

CHAPTER 2. BREEDING DISPERSAL BY ROSS'S GEESE IN THE QUEEN MAUD GULF METAPOPULATION

2.1 ABSTRACT

I estimated rates of breeding philopatry and complementary dispersal within the Queen Maud Gulf metapopulation of Ross's Geese (*Chen rossii*) using multistate modeling of neckband observations at five breeding colonies, 1999-2003. Probability of philopatry was female-biased, but varied among colonies. Probabilities of annual movement among breeding colonies ranged 0.02 to 0.14 for females and 0.12 to 0.38 for males, and was substantially higher than expected. These estimates (1) underscore the potential for dispersal to alter breeding distribution, (2) demonstrate substantial potential exists for movement to influence colony-specific rates of population growth, and (3) provide behavioral evidence for extensive gene flow. Sex differences in apparent survival, estimated from multistate models, likely resulted from a combination of higher rates of neckband loss by males compared to females, and higher rates of permanent emigration by males from my study area, rather than arising from actual differences in true survival.

2.2 INTRODUCTION

Species distributions often encompass broad geographic ranges that include great spatial variability in landscape characteristics. Corresponding variability in ecological conditions leads to uneven distributions of density throughout a species' range, because animals congregate in areas where habitats are most suitable. Such subpopulations are often geographically separated from each other by areas of less suitable habitats (Wiens 1997). Nevertheless, almost all species have evolved mechanisms that allow dispersal across unsuitable or less than optimal habitats.

Consequently, disjunct conspecific populations are potentially interconnected through migration networks or dispersal to new breeding areas. Such potential for movement among subpopulations is key to the concept of metapopulations (Hanski and Simberloff 1991), where persistence is a function of not only survival and recruitment of individuals but also of immigration and emigration between component subpopulations (Levins 1969, 1970).

In North America, breeding and wintering distributions of continental populations of the closely-related Ross's Goose (*Chen rossii*) and Lesser Snow Goose (*Chen caerulescens*, hereafter Snow Goose, collectively referred to as 'light geese') are such that they fall within the conceptual domain of a metapopulation. Both species breed at spatially discrete colonies in arctic and subarctic habitats and winter in allopatric subpopulations across a broad range in southern North America (Ryder and Alisauskas 1995, Mowbray et al. 2000). Despite spatial segregation of breeding subpopulations, there is tremendous potential for exchange of light geese because of mixing during migration when long-term pair bonds begin to form during late winter and continue through spring migration (Ryder and Alisauskas 1995, Mowbray et al. 2000).

Much attention in North America has focused on the exponential population increase of light geese and their potential to damage breeding habitats (Batt 1997, Moser 2001). Regardless of causes resulting in unchecked population growth, light goose populations are markedly larger and occur over much broader winter ranges than they did 50 years ago. Winter range expansion highlights the ability of Snow Geese and Ross's Geese to adapt to changing landscape conditions (Alisauskas et al. 1988, Alisauskas 1998). Despite these species' apparently adaptive movement during the nonbreeding period, female Snow Geese were thought to be generally philopatric to breeding colonies (Cooke et al. 1995), even when the consequences of philopatry appeared to be maladaptive such as when population densities exceed carrying capacity (Cooch et al. 1989, Cooch et al. 1991a, but see Cooch et al. 2001). No information about vagility of Ross's Geese was available.

I estimated rates of movement among breeding colonies by Ross's Geese to gain insight about the potential for breeding dispersal to influence species distribution and

gene flow in light geese. I focused the current analysis on Ross's Geese because of uninterrupted marking within the Queen Maud Gulf Migratory Bird Sanctuary (QMGMBS) since 1989 that resulted in a substantial marked population at the outset of this study. Efforts to neckband Snow Geese in the QMGMBS, and to obtain subsequent resightings, have recently increased (Drake and Alisauskas unpublished data), but there remain insufficient data to include them in the current analysis. Nonetheless, Ross's Geese and Snow Geese associate throughout their annual cycles (Alisauskas 2002), and the extent of such associations during breeding likely has increased recently with the growth in number of Snow Geese in the QMGMBS where >95% of the continental population of Ross's Geese breeds (Kerbes 1994).

2.3 METHODS

2.3.1 Assigning Individual to Geographic Strata

Because I could not assign with certainty Ross's Geese captured on brood-rearing areas in August to colonies in which they nested the previous June, I included only those birds that were resighted at breeding colonies in June 1999-2003. Only 501 goslings were neckbanded during 1999-2002, so I excluded these from consideration; I further judged that their inclusion would have doubled the number of parameters to be estimated while increasing the sample size only by ~ 15%. Hence, this analysis included adult birds ($n = 3,233$) sighted at least once at one of the sampled colonies during 1999-2003, regardless of year of marking.

2.3.2 Analysis

I used multistate modeling (Arnason 1973, Hestbeck et al. 1991, Brownie et al. 1993, Schwarz et al. 1993) in Program MARK to analyze resight data of neckbanded Ross's Geese for estimation of dispersal and complementary philopatry probabilities. Multistate models allow estimation of probabilities for apparent survival, $(\hat{\phi})$, detection, $(\hat{p})$, and movement among states (i.e., colonies), $(\hat{\psi})$. I considered variation by colony, sex, and year for each of these estimates, subscripted as $\{\phi_c, p_c, \psi_c\}$, $\{\phi_x, p_x, \psi_x\}$, or $\{\phi_t, p_t, \psi_t\}$, respectively. As such, the fully parameterized global model $\{\phi_{c \cdot x \cdot t}, p_{c \cdot x \cdot t}, \psi_{c \cdot x \cdot t}\}$ had 240 potentially estimable parameters. The iterative routine used during the

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maximization of the likelihood function failed to converge numerically for this model, so I re-examined input data and found that movement was not detected in 99 of the 160 possible colony-, sex-, and time-specific movements. I obtained convergence after fixing these parameters to zero, but was warned by Program MARK that convergence was suspect. Numerical estimation for a few models from the candidate set resulted in inconsistent deviances relative to the number of parameters being estimated. Inconsistency in changes of deviance confirmed that the global model failed to converge properly even after fixing parameters (G. W. White personal communication). Consequently, I reduced the number of strata from five to three, thus reducing the number of parameters being estimated while maintaining biologically relevant models, as follows.

I constrained movement to occur among three strata only: Karrak Lake, Colony 10, and other colonies combined (9, 46, and 81; hereafter, other colonies). Strata were redefined based on colony sizes (Fig. 1.2) and sampling effort. Karrak Lake and Colony 10 represent the two largest colonies within the QMGMBS (~433,000 and ~386,000 breeding Ross's Geese in 1998, respectively; Alisauskas et al. 1998), and Colonies 9, 46, and 81 are substantially smaller (ranging between ~30,000 and ~95,000 in 1998; Alisauskas et al. 1998). Sampling effort varied somewhat among years at different colonies from the interplay between spring phenology and availability of aircraft with which to visit study colonies. Sampling effort was highest at Karrak Lake, where unlike other colonies, it could be accessed entirely by foot or by boat from a permanent research facility. All other colonies were accessed by helicopter, and so neckband observations there ranged from one to four days. Relative sampling effort among colonies was consistent such that Karrak Lake > Colony 10 > other colonies, for all years of the study. Numerical convergence was attained after reducing the number of geographic strata from five to three in the global model.

My reduced global model $\{\phi_{c \cdot x \cdot t}, p_{c \cdot x \cdot t}, \psi_{c \cdot x \cdot t}\}$ had 96 potentially estimable parameters, including all sources of variation and all possible interactions. My modeling approach was to test fit of the global model to the data and then, based upon biological knowledge of the study organism and differences in sampling effort, compare a set of candidate models with reduced numbers of parameters to assess parsimony and fit of

models to the data using AICc (Burnham and Anderson 1998). Program MARK does not provide goodness-of-fit tests specifically for multistate data sets, so I parameterized the data as a single-stratum (i.e., all colonies combined) Cormack-Jolly-Seber (CJS) data set and tested for goodness-of-fit of model ϕ_{s*t}, p_{s*t} (Lebreton and Pradel 2002) using 1000 iterations of the parametric bootstrap available for such global models in Program MARK. Deviance of the global model was less than 85% of the simulated deviance indicating that the data were not overdispersed so a variance inflation factor ($\hat{c}$) was not used (Burnham and Anderson 1998).

I considered 15 models in the candidate set. Movement probability was the primary parameter of interest, so my approach to hypothesis testing and parameter estimation was to reduce sources of variation in probabilities of resighting and then survival, while retaining full-structured variation in movement probabilities. First, I reduced sources of variation in p. I retained effects of colony and time in all parameterizations of p because sampling effort varied among colonies, and because I suspected temporary emigration as the size of breeding populations at colonies varies annually (Alisauskas and Rockwell 2001). I considered four additional parameterizations of p including (1) a multiplicative interaction between colony and additive effects of sex and time, $p_{c*[x+t]}$, (2) a completely additive model, p_{c+x+t}, and (3) additive, p_{c+t}, and (4) multiplicative, p_{c*t}, models without sex effects. I used the parameterization of p from the best of these models in all subsequent modeling of survival and movement probabilities.

Including the structure within the global model, I considered six parameterizations of ϕ. Breeding colonies represent subpopulations where the potential for colony-specific differences in ϕ has implications for colony-specific growth rates as well as potential fitness costs to individuals. There is considerable clinal variation in winter ground and migration route affinities of Ross's Geese marked in QMG over a narrow range of ~200 km of longitude (Alisauskas et al. 2006a); thus it is likely that different segments of the QMG metapopulation are subject to geographically variable harvest pressure (Moser and Duncan 2001), so I tested for colony specific rates of survival by comparing model ϕ_{c*x*t} to ϕ_{x*t}. Most evidence suggests that true survival, S, does not vary between sexes in most species of geese (Melinchuk and Ryder 1980,

Alisauskas and Lindberg 2002, but see Francis and Cooke 1992b and Chapter 5).
However, sex differences in philopatry to breeding colonies may still result in sex-
specific ϕ, because ϕ is the product of survival and fidelity; so, I considered ϕ_{c*x*t} vs.
ϕ_{c*t}. After testing for colony and sex effects, I considered models with additive effects
of sex and time ϕ_{x+t}, a linear time trend ϕ_{x+T}, and a model that included only the effect
of sex ϕ_x.

I proceeded to estimate ψ starting with models optimally structured for p and ϕ.
I retained colony structure in ψ in all models because of my interest in stratum-specific
estimates. These included fully multiplicative effects of colony, sex and year ψ_{c*x*t},
additive effects of sex and time specific to each colony $\psi_{c*[x+t]}$, complete additivity
ψ_{c+x+t}, a multiplicative model excluding the effect of sex ψ_{c*t}, and an additive model
with colony and sex effects ψ_{c+x}. All manipulations of model structure were done with
the design matrix in Program MARK, and all models were fit using the logit link
function (White and Burnham 1999).

2.4 RESULTS

Model $\{\phi_{x+t}, p_{c+t}, \hat{\psi}_{c+x}\}$ was clearly best supported by the data ($w_{AICc} = 0.993$, Table
2.1); thus, all estimates were based on this model. In this model apparent survival varied
over time in parallel between sexes, but was equal among colonies. Predictably,
recapture probabilities varied among colonies, but differences were consistent for all
years of study. Movement probability was constant over time but varied among colonies
in parallel between sexes. Estimates of apparent survival ranged between 0.631 ± 0.038
(SE) and 0.682 ± 0.033 for females, and between 0.489 ± 0.034 and 0.546 ± 0.044 for
males (Table 2.2). Recapture probabilities varied in an additive fashion among colonies
and years, but were as low as 0.069 ± 0.025 for Colonies 9, 46 and 81, and as high as
0.612 ± 0.037 at Karrak Lake (Fig. 2.1). Colony- and sex-specific dispersal probabilities
ranged from 0.023 ± 0.024 to 0.344 ± 0.085 for females and from 0.122 ± 0.063 to
0.376 ± 0.074 for males (Fig. 2.2a); these probabilities represent movement of
thousands of individuals among subpopulations (Fig. 2.2b, see DISCUSSION).

Of the 56 broken neckbands found on the ground during surveys, 44 had fallen off male Ross's Geese but only 12 were from females. Compared to 7,904 males and 7,718 females that had been marked with neckbands, this represents a strong male bias in apparent rates of neckband loss (likelihood ratio $\chi^2 = 17.53$, df $= 1$, $P < 0.001$).

Table 2.1. Model structure, AIC$_c$, ΔAIC$_c$, model weight (w_{AICc}), number of parameters (K), and model deviance, for multistate modeling of survival (ϕ), recapture (p), and dispersal (ψ) probabilities of neckbanded Ross's Geese within the Queen Maud Gulf metapopulation, 1999-2003. Asterisks indicate multiplicative interactions between colony (c), sex (x), and time (t). Plus signs indicate an additive model. 'Global' denotes the most parameterized model.

Model			AIC$_c$	ΔAIC$_c$	w_{AICc}	K	Model Deviance
ϕ_{x+t}	p_{x+t}	ψ_{c*x}	7045.07	0.00	0.99	22	471.50
ϕ_{x+t}	p_{x+t}	ψ_{c+x}	7055.23	10.16	0.01	15	495.81
ϕ_{x+t}	p_{x+t}	$\psi_{c*(x+t)}$	7059.02	13.95	0.00	39	450.85
ϕ_{x+t}	p_{x+t}	ψ_{c*x*t}	7069.92	24.85	0.00	51	437.14
ϕ_{x+t}	p_{x+t}	ψ_{c+x+t}	7071.52	26.45	0.00	17	508.06
ϕ_{x*t}	p_{c+t}	ψ_{c*x*t}	7072.85	27.78	0.00	54	433.88
ϕ_{c*x*t}	p_{c+t}	ψ_{c*x*t}	7073.95	28.88	0.00	66	410.15
ϕ_{x}	p_{c+t}	ψ_{c*x*t}	7075.55	30.48	0.00	50	444.82
ϕ_{x+T}	p_{c+t}	ψ_{c*x*t}	7077.50	32.43	0.00	51	444.72
ϕ_{c*x*t}	p_{c+x+t}	ψ_{c*x*t}	7078.21	33.14	0.00	70	406.10
ϕ_{c*x*t}	$p_{c*(x+t)}$	ψ_{c*x*t}	7078.46	33.39	0.00	74	398.02
ϕ_{c*x*t}	p_{c*t}	ψ_{c*x*t}	7081.36	36.29	0.00	72	405.08
ϕ_{c*x*t}	p_{c*x*t}	ψ_{c*x*t} global	7081.86	36.79	0.00	72	405.58
ϕ_{c*t}	p_{x+t}	ψ_{c*x*t}	7094.46	49.39	0.00	60	443.10
ϕ_{x+t}	p_{x+t}	ψ_{c*t}	7127.93	82.86	0.00	33	532.02

Table 2.2. Apparent survival estimates from multistate modeling of neckbanded adult Ross's Geese breeding within the Queen Maud Gulf metapopulation, 1999-2003. Survival was best modelled by including sex and time effects, but was equal among sampled colonies. Probabilities are given ± SE.

Year	Apparent Survival probability	
	Female	Male
1999	0.682 ± 0.038	0.546 ± 0.044
2000	0.657 ± 0.035	0.516 ± 0.040
2001	0.653 ± 0.033	0.489 ± 0.035
2002	not estimated	not estimated
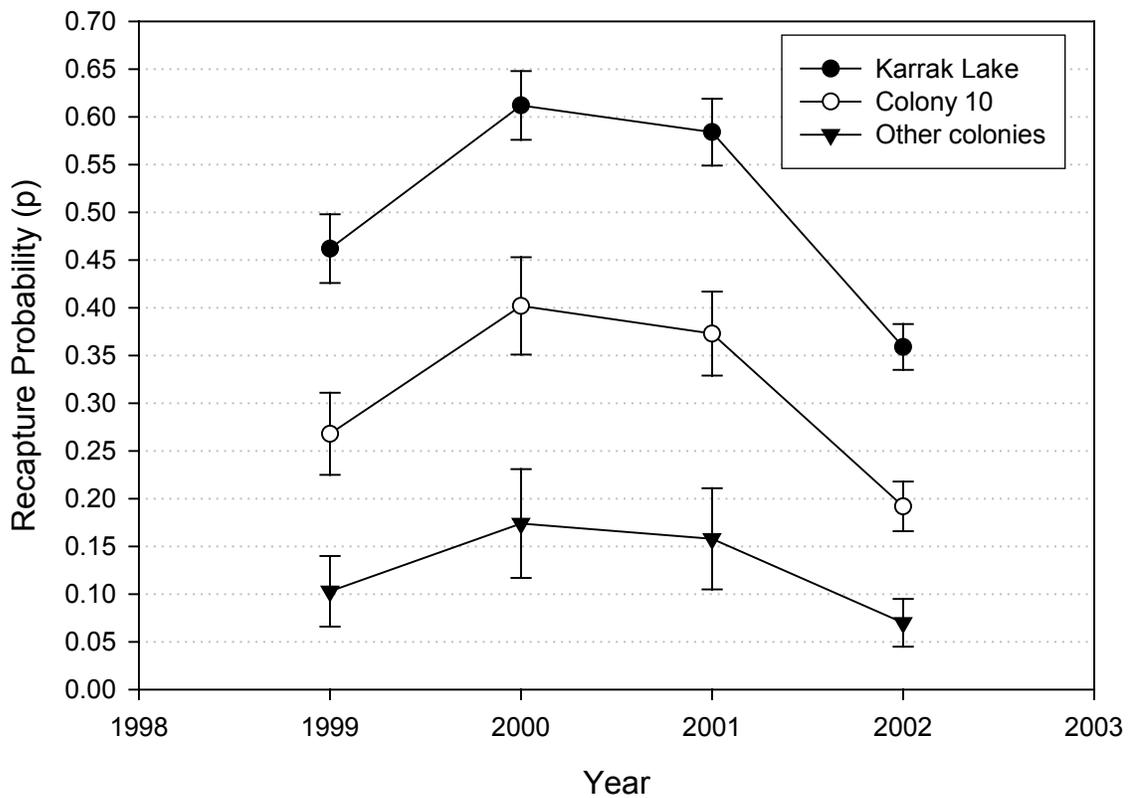
Figure 2.1. Colony-specific detection probabilities from multistate modeling of neckbanded adult Ross's Geese resighted at breeding colonies within the Queen Maud Gulf metapopulation, 1999-2003. Bars represent standard error of the estimate.
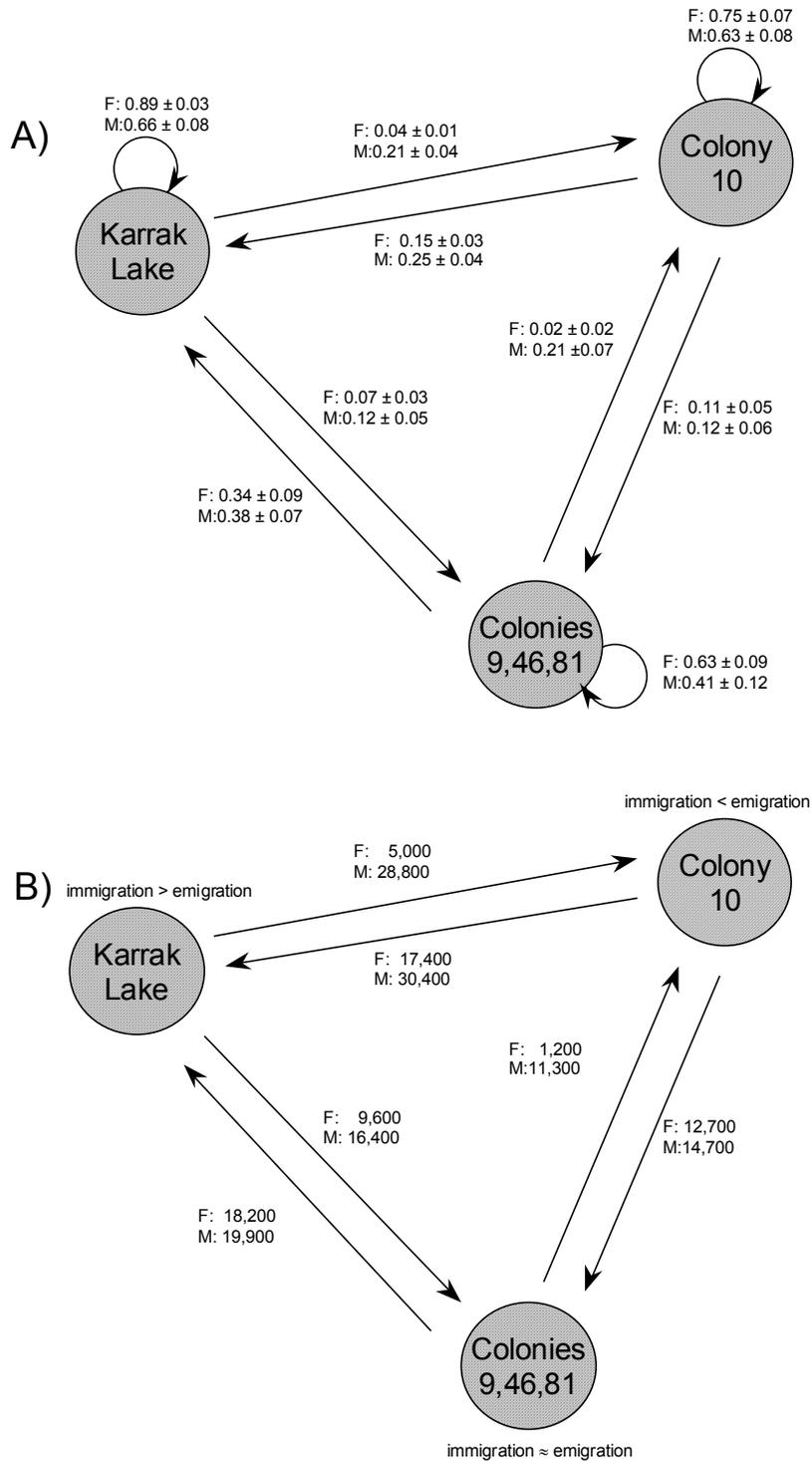
Figure 2.2. Breeding philopatry and dispersal of female (F) and male (M) Ross's Geese from multistate modeling of neckband resightings at breeding colonies within the Queen Maud Gulf metapopulation, 1999-2003. (A) Dispersal probabilities ± SE and (B) calculated numbers combining movement probabilities with estimates of population size for each colony.

2.5 DISCUSSION

2.5.1 Movement Probability

Results of this study were consistent with the general prediction of the mating-system hypothesis (Greenwood 1980, Rohwer and Anderson 1988); Ross's Goose breeding philopatry is female-biased. This result is qualitatively consistent with the pattern of female-biased philopatry that has emanated from studies that primarily employed return rates to gain inference on philopatry in waterfowl (Geramita and Cooke 1982, Anderson et al. 1992: Table 11-3). However, similar to other investigations that have used mark-recapture methods (Lindberg et al. 1998, Doherty et al. 2002, Blums et al. 2003), sex-specific estimates of philopatry in this study were substantially higher than return rates reported for waterfowl (Anderson et al. 1992: Table 11-3). More notable was that female philopatry was highly variable among colonies and was less than absolute in all cases. In any given year, a substantial portion of the Queen Maud Gulf (QMG) Ross's Goose breeding population consists of dispersers. This finding underscores the importance of dispersal in colony-specific population dynamics of Ross's Geese in the QMG region, and its potential to influence breeding distribution and gene flow.

I applied estimates of female dispersal probabilities to estimated sizes of breeding subpopulations and found that they represent large numbers of birds that switch colonies annually. I used breeding population estimates of light geese at Karrak Lake (~866,000) from Alisauskas et al. (1998) and assumed that about 50% are Ross's Geese, half of which are females (216,500). Assume that 216,500 females nest at Karrak Lake during year i, survive at a rate of 0.83 (i.e., the most recent published survival rate of adults that were not marked with neckbands; Alisauskas et al. 2006a), and breed during $i + 1$ at a hypothetical rate of 0.75. Thus, at $i + 1$ there are ~179,700 (216,500 x 0.83) surviving individuals of which 134,800 (179,700 x 0.75) will breed. Of those breeders, ~14,600 (134,800 x 0.108) will disperse from Karrak Lake and breed at another colony. Accordingly, assuming that average nesting density is equal among colonies, then based on colony area (km^2; Alisauskas et al. 1998), colony 10 had ~772,000 geese (~193,000 female Ross's Geese) and colonies 9, 46 and 81 combined represented ~339,000 geese (~84,800 female Ross's Geese). Assuming the same rates of survival and breeding probability, I applied stratum-specific estimates of dispersal

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from the other colonies to Karrak Lake and found that ~17,400 (193,000 x 0.83 x 0.75 x 0.145) females emigrate from Colony 10, and ~18,200 (84,800 x 0.83 x 0.75 x 0.344) females emigrate from the other combined colonies to Karrak Lake. Such calculations suggest a net increase of ~21,000 (35,600 – 14,600) females to Karrak Lake within a given year due to breeding dispersal alone (Fig. 2.2b).

Based upon limited information about movements of geese to and from La Pérouse Bay (LPB), and overwhelming female-bias in re-encounters at the colony, Cooke et al. (1995) argued that gene flow was male-mediated among breeding subpopulations of Snow Geese, while acknowledging that females showed some dispersal (Geramita and Cooke 1982). More recently, Cooch et al. (2001) used a retrospective analysis to analyze life table response of the LPB colony and showed that emigration of adults had increased over time. Their results suggested that philopatry to brood rearing areas may be more flexible than philopatry to nesting areas. My results suggest that breeding philopatry is also a flexible trait in closely-related Ross's Geese. Given similarities in life histories of these congeners and their sympatry throughout the annual cycle, dispersal by female Snow Geese may be more common than previously thought.

Although my analysis was focused on Ross's Goose movement between breeding colonies within the QMG metapopulation, 21% (680/3233) of the Ross's Geese used in this analysis were immigrants to the QMG region that were banded along the West Coast of Hudson Bay (WHB); 8.5% (58/680) of these were females. Movement of WHB geese into the QMG region represent breeding dispersal of distances ranging 500-800 km depending upon colony of settling. There exists substantial additional movement of geese, but because observations of marked geese at WHB breeding colonies did not begin until 2002, I could not estimate rates of dispersal between these regions.

Estimates of annual dispersal among breeding colonies by Ross's Geese provide strong behavioral evidence for extensive gene flow among breeding subpopulations. This behavioral finding for Ross's Geese is consistent with genetic studies of Snow Geese, which suggested little or no phylogeographic structure in frequency of mtDNA haplotypes detected in Snow Geese from different breeding areas across North America

(Avise et al. 1992, Quinn 1992). Additionally, based on recoveries from each of the Pacific, Central and Mississippi Flyways (Alisauskas et al. 2006a), there is great overlap in winter range used by Ross's Geese marked in different brood-rearing areas used by the QMG metapopulation. Overall, Ross's Geese from QMG now have one of the most extensive winter ranges of any arctic-nesting goose species from a single arctic region. Shared winter areas of Ross's Geese with different breeding locations, high rates of movement by both sexes of Ross's Geese among colonies in QMGMBS, and the fact that 21% of the geese included in this analysis had originated from another breeding region, hint at considerable potential for dispersal to influence gene flow in Ross's Geese. I suggest that subpopulations of light geese are extensively interconnected by broadly overlapping migration networks, which likely enhances gene flow. Such widespread movement patterns would be consistent with the genetic evidence for "considerable population connectedness" inferred by Avise et al. (1992).

Studies of other colonial geese have shown that dispersal increases with increasing population density (Lindberg et al. 1998), and that emigration can be an adaptive response to habitat degradation (Cooch et al. 1993, Cooch et al. 2001). I was unable to estimate population density at breeding colonies within the QMGMBS, other than for Karrak Lake, and so was precluded from directly assessing breeding dispersal as a function of breeding density. Nevertheless, I found an asymmetry favoring movement toward Karrak Lake despite it being the most expansive colony of the ones studied. Density dependent effects on gosling growth and survival on brood-rearing areas north of Karrak Lake have been detected (Slattery and Alisauskas 2002), so other factors may override a connection to dispersal probability. For example, there is a strong cline in chronology of snowmelt with that in the west of QMGMBS consistently far in advance (e.g., ~5% snow cover in 2003) compared to that 300 km to east (>75% snow cover in 2003, R. Alisauskas personal observation). Early nesting by arctic-breeding geese has strong fitness benefits (Cooke et al. 1984) because of the short time available for goslings to attain flight before freeze-up (Raveling 1978). Hence, geese at Karrak Lake consistently may enjoy more favorable snow-free nesting conditions compared to most other colonies to the east. Consistent with this idea is that female

emigration from colony 10, the most eastward colony examined, exceeds female immigration to colony 10 for both Karrak and other colonies.

2.5.2 Apparent Survival Rates

Sex differences in apparent survival provide insights to potential sources of bias when interpreting my results, given what is known about true survival estimates. My estimates of apparent survival for neckbanded Ross's Goose females generally corresponded with estimates for true survival rates of neckbanded females from band recovery models (Alisauskas et al. 2006a); however, male apparent survival ranged 0.11-0.22 lower than estimates for true survival of neckbanded males. Accordingly, I suggest that at least in part, the differences in apparent survival between males and females resulted from violation of model assumptions rather than arising solely from differences in true survival between sexes. Multistate models will produce survival estimates that are biased low if movement of individuals to an unobserved state occurs (i.e., permanent emigration from the sampled areas and/or marker loss). I suggest that the sex differences in estimates of apparent survival resulted in part from a combination of (1) higher rates of permanent emigration by males, from surveyed areas, than by females and (2) higher rates of neckband loss by males. A higher rate of permanent emigration by males from my study area is consistent with the finding of greater vagility within my study area by male than by female geese. Additionally, rates of neckband loss are generally higher for males in numerous other goose species (Alisauskas and Lindberg 2002 and references therein). Low recapture probability of Ross's Geese during annual banding efforts precluded direct estimation of neckband loss as done by Alisauskas and Lindberg (2002). Nevertheless, discovery of nearly four times as many broken neckbands from males than from females, despite similar numbers marked, is in agreement with the general pattern of higher neckband loss by males. Most of these neckbands were lost probably during aggressive behaviour by males on breeding territories. The general correspondence between estimates of survival for neckbanded females from multistate modeling to those for neckbanded females from band recovery models (Alisauskas et al. 2006a, Chapter 5) suggests that permanent

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emigration by females, from the areas I sampled, was close to zero during the course of this study.

CHAPTER 3. AN EXPERIMENTAL ASSESSMENT OF DECISION RULES: PHILOPATRY IN A CAPITAL BREEDER

3.1 ABSTRACT

I studied female Ross's Geese (*Chen rossii*) nesting in a colony at Karrak Lake, Nunavut, Canada, from 2000 to 2003, to evaluate the prior experience hypothesis (PEH) as an explanation for breeding site philopatry in migratory birds. I experimentally manipulated nesting success of randomly-chosen females and determined subsequent dispersal distances for successful and failed breeders. Previous nest fate influenced dispersal distance; successful nesters generally dispersed shorter distances than failed nesters. Although observed differences in dispersal distances were consistent with predictions from the PEH, estimated dispersal distance for both groups exceeded 1500 m suggesting that philopatry occurs at a scale larger than that of the nest site or territory. Regardless of previous nest success, some breeding dispersal within the colony constituted asymmetrical movement toward areas of higher nesting density. Contrary to the prediction of the PEH, successful nesters generally returned at lower rates than failed nesters, but this difference was detectable during only one year. I suggest that geese showed flexible selection of nest sites to ensure earliest possible nest initiation; I propose that early nesting in general is adaptive because it minimizes depletion of stored nutrients for maintenance, and allows earlier allocation of such nutrients toward eggs and energetic requirements of incubation.

3.2 INTRODUCTION

Dispersal represents individual decisions that determine settling patterns responsible for population-level changes in distribution and abundance. Despite recognition of movement as an important evolutionary force (Clobert et al. 2001), our

understanding of mechanisms that govern decisions by individuals to disperse, or to return to specific breeding locations, is not well understood. Many migratory bird species exhibit breeding philopatry (Greenwood 1980, Greenwood and Harvey 1982), representing species that have different nest types (e.g. cavity, cup, ground), mating systems (mate-defense *vs*. resource-defense), and which produce young that require variable levels of parental care (precocial *vs*. altricial young; e.g. Newton and Marquis 1982, Dow and Fredga 1983, Gavin and Bollinger 1988, Pärt and Gustafsson 1989, Paton and Edwards 1996, Lindberg and Sedinger 1997). Estimation of philopatry is scale-dependent and subject to bias (Koenig et al. 1996, Lambrechts et al. 1999, Cilimburg et al. 2002), but the widespread occurrence of philopatry suggests that such behavior is adaptive.

Decisions about movement between sequential breeding sites likely involve complex interactions among numerous influences including mate or site competitors, predator presence, food resources, or availability and suitability of nest sites. Nevertheless, previous reproductive output may serve as a logical and tractable metric of overall suitability of a previous breeding site. Thus, prior breeding experience likely influences decisions about where to breed in future [i.e., Prior Experience Hypothesis (PEH)].

The degree to which individuals use previous reproductive performance to assess where to make subsequent attempt to breed is expected to vary among species; nest sites, and adjacent resources, are likely to show high interspecific variation in the contribution and importance to successful production of offspring. A causal link between reproductive performance and breeding philopatry has been demonstrated using experimental manipulation in songbirds (Haas 1998, Hoover 2003), but support for the generality of this phenomenon requires further study among other taxa. For example, most songbirds are income breeders because they use local food resources for egg production (Meijer and Drent 1999) and produce altricial young that are brooded in nests until fledging. So, nest site selection probably is influenced by perceptions and decisions about both (1) security from predation, and (2) availability of food near nest sites. In contrast, capital breeders rely largely on endogenous reserves for egg production and incubation, and often produce precocial young that may be brooded

several kilometers from the nest site (e.g. arctic-nesting geese). Thus, such species are more likely to base decisions about nest site fidelity solely on security of sites from predation because food resources near the nest have little consequence on egg production, incubation cost, or growth of newly-hatched young.

I manipulated nesting success of female Ross's Geese (*Chen rossii*) to test whether there is a response in breeding philopatry by a capital breeder with precocial young. Several studies have demonstrated correlations between nest success and subsequent site fidelity of female waterfowl (Dow and Fredga 1983, Hepp et al. 1989, Lindberg and Sedinger 1997), but I am unaware of studies wherein the effect of nest success through experimental manipulation on subsequent site fidelity was estimated directly. Arctic-nesting geese are ideally suited for testing the prediction that reproductive failure reduces breeding philopatry. Natal and breeding philopatry is female-biased (Anderson et al. 1992) and pair formation by arctic-nesting geese occurs on wintering and spring staging areas, so site and mate fidelity are separate (Greenwood and Harvey 1982, but see Hoover 2003). Use of nutrient reserves to meet metabolic costs of egg production and incubation varies among species (Ankney and MacInnes 1978, Budeau et al. 1991, Alisauskas and Ankney 1992, Gauthier et al. 2003), but endogenous reserves are generally an important determinant of reproductive success in geese (Alisauskas 2002). In this study, I used traditional measures of site fidelity (i.e. dispersal distance and return rates) to test the prediction of the PEH. I also considered other ecological covariates that I thought were likely to influence philopatry, but that were beyond my ability to control. The PEH predicts that individuals that experience nesting failure are more likely to disperse to another breeding site, whereas those that produce young are more likely to breed again in the same location.

3.3 METHODS

3.3.1 Relevant Life History Aspects of the Study Organism

Ross's Geese are highly gregarious throughout the annual cycle, and, like Lesser Snow Geese (*C. caerulescens*; Mowbray et al. 2000), establish monogamous breeding pairs on wintering and spring staging areas. Pair bonds can last several years (Alisauskas and Drake unpublished data). Timing of arrival at nesting colonies

generally begins after snow cover is <70% (K. Drake and R. Alisauskas personal observation), but in some years nesting can be delayed, presumably by events farther south. Upon arrival, pairs establish a territory in which the female builds a nest on a snow-free patch of ground. Ross's Geese nest at densities of up to 272 nests/ha (Alisauskas unpublished data). Geese begin laying eggs within 2-3 days of arrival when there is little or no green vegetation available. In addition, breeding geese provided with supplemental food did not differ from control birds in body condition at the end of incubation, which suggests that geese breeding at Karrak Lake subsisted independently of local food resources (Gloutney et al. 1999). Last, Ross's Goose goslings are self feeding and able to walk (nidifugous) within 1 day of hatch (Ryder and Alisauskas 1995); goslings and parents disperse from nest sites to brood-rearing areas within 48 hr. Hence, I suggest that, if breeding philopatry by Ross's Geese is decision-based on previous experience, then the decision is simplified to perceived security of nest sites, and does not involve assessment of local food resources.

3.3.2 Nest Searching

This study was conducted at the Karrak Lake breeding colony (Fig. 1.2). Nesting geese with neckbands were observed from distances of up to 500 m with spotting scopes during incubation (late-May to early-July, 2000-2003). At times, high-density of nesting geese can confuse identification by observers of nests produced by neckbanded individuals. In such instances, fixing cross hairs in spotting scopes as a reference, and then walking to them confirmed nest locations of focal animals. Global position systems were used to determine Universal Transverse Mercator (UTM Zone 13) grid coordinates of nest locations. To facilitate location and verification of nest identity during subsequent visits, wooden stakes marked with neckband codes were placed beneath nest bowls and eggs were marked with indelible ink. I recorded clutch size (CS) and estimated incubation stage (days) by candling eggs (Weller 1956) to permit calculation of nest initiation date. CS was multiplied by 1.2 days, the interval between eggs (Ryder 1969a), and added to incubation stage to calculate nest initiation date.

I did not manipulate nest fate in 2000, but determined fate of 142 nests of neckbanded geese found that year. In 2001 and 2002, I found nests of 292 and 294

neckbanded females, respectively, and randomly assigned half to treatment (eggs removed during the last week of incubation) or control (eggs not removed) groups. Control nests were revisited after hatch and were considered successful if at least one egg hatched, judging from the presence of eggshell caps and/or egg membranes. Nests that failed from abandonment or depredation were assigned to a third group of natural failures. Due to unusually high rates of nest abandonment in 2001, natural nest failures represented the largest group in that year.

3.3.3 Snow Cover

Habitat availability is known to influence settling patterns of nesting geese (Abraham 1980, Lepage et al. 1996, Reed et al. 2004), so I estimated snow cover using data collected from 100 m snow survey transects ($n = 12$, Alisauskas unpublished data). Transects were visited every 3-4 days from arrival by personnel at the study area in each year (18-22 May) to the end of snowmelt (usually mid- to late-June). Snow depth was measured at 5 m intervals, beginning at 0 m and ending at 100 m. For my purpose, I calculated average daily snow cover by dividing the total number of points along the transect that had snow cover (regardless of depth) by the total sampling points ($n = 252$). To calculate daily snow cover for days between successive surveys, I assumed that snowmelt was linear and used predicted values between days when snow surveys were done. Figure 3.1 displays graphically the annual (2001-2003) interplay between snowmelt and percent of nests initiated within the colony (see Section 3.3.4 for an explanation of percent of nests initiated).

3.3.4 Effect of Nest Failure on Dispersal Distance

All measures of dispersal involved nests initiated in consecutive years. Dispersal distance was calculated as the length of a straight line between nest locations. Dispersal distance and nest fate were known for 22 females found in three consecutive years of the manipulation study (2001-2003). To avoid pseudoreplication, I randomly-selected one observed dispersal distance from each such female to include in analyses. I used

2001

2002
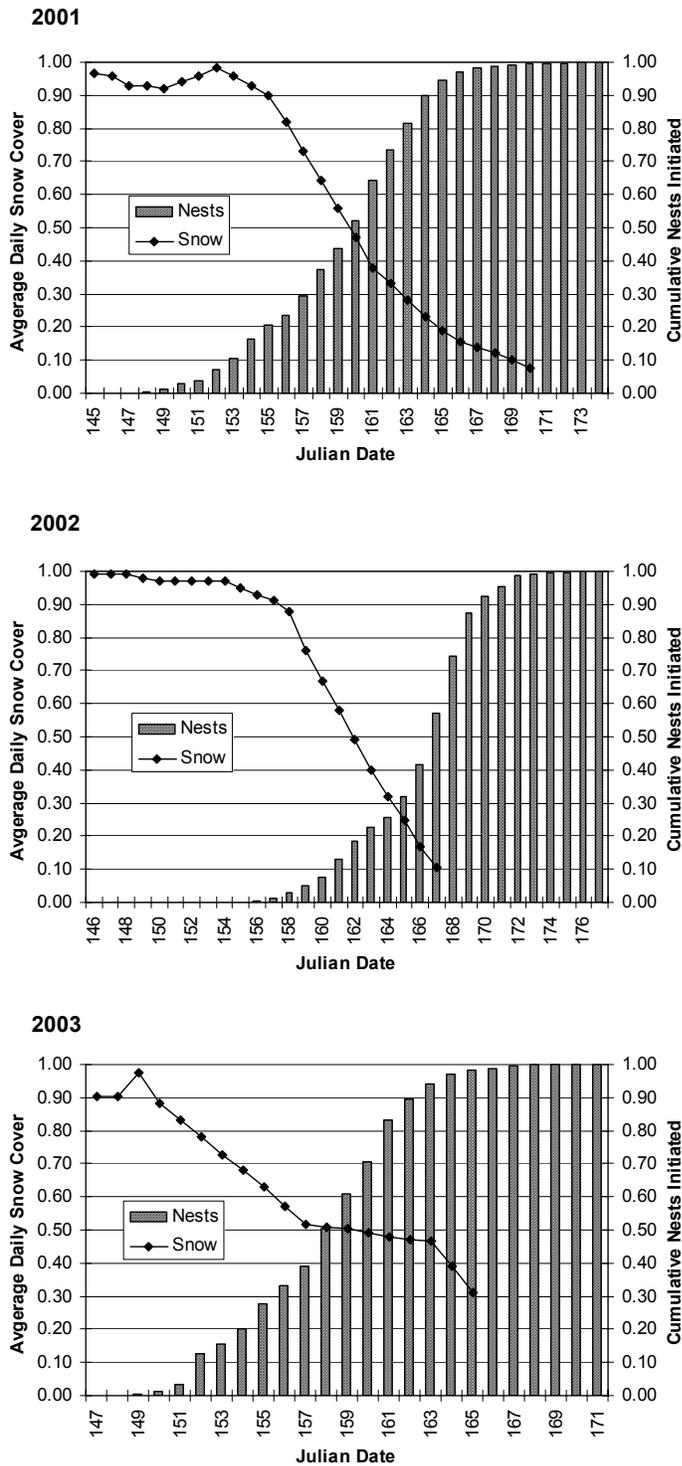
2003

Figure 3.1. Chronology of snowmelt and nest initiation by Ross's Geese at the Karrak Lake breeding colony, Queen Maud Gulf Migratory Bird Sanctuary, Nunavut, Canada (2001-2003).

data from years during manipulations, to compared dispersal distances by marked females with induced failures ($n = 57$) with those of females with natural nest failures ($n = 39$) (t-test, unequal variation, PROC TTEST, SAS 1996) and found no difference in distances dispersed ($p = 0.43$). Thus, I combined data from induced failures and natural failures ($n = 96$) in subsequent analyses for comparison with dispersal distance of successful nesters ($n = 36$).

I believed that factors other than induced nest fate could influence dispersal, and so included several covariates in my *a priori* candidate set of 14 models. There are advantages of earlier nest initiation on production of young (Cooch et al. 1991a, Sedinger and Flint 1991), and because nests are initiated only in snow-free habitat, I considered snow cover at time of nest initiation as an individual covariate of dispersal distance. Nesting Ross's Geese are territorial (Ryder and Alisauskas 1995), so individuals that arrive later are likely to face greater competition for nest sites (Fig. 3.1) and may settle in less preferred sites. Hence, as an index of competition for available nesting habitat, I included percent of nests initiated within the colony at time of nest initiation as another individual covariate. Percent of nests initiated was determined from a data set collected at systematically placed 30 m radius plots located throughout the colony (Alisauskas unpublished data). Number of sampled plots containing Ross's Goose nests varied annually and ranged from 58 to 113, and the combined total of Ross's Goose nests within these plots each year ranged from 690 to 866. I hypothesized that timing of arrival might also influence dispersal distance; however, I could not reliably determine how long an individual was present on the colony before initiating a nest. Thus, I calculated a relative nest initiation date (NID) for each bird by subtracting the annual colony mean nest initiation date for Ross's Geese (calculated from nest plot data) from the NID of each individual. Arriving birds commonly have ovulated follicles (Alisauskas unpublished data) and eggs dumped outside of nest bowls are common throughout the colony, suggesting that there is likely a strong advantage for selecting a nest site and preparing a nest bowl before egg-laying begins; so, relative NID should serve as a suitable index for timing of arrival. I considered interaction effects between snow cover and relative NID, and between snow cover and percent of nests initiated. Finally, nesting densities vary spatially and temporally throughout the colony, so some

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areas are undoubtedly preferred over others. In general, nesting density was lowest at the colony perimeter and increased towards the center; but the transition from low to high nesting densities is neither smooth nor continuous (Fig. 3.2). To account for such edge effects, I included two variables to account for the location of nests within the colony: distance from the Karrak Lake shoreline (to serve as an index of the centrality of the nest location within the colony), and whether a nest was located in an area with above-, or below-average nesting density (see below). I used general linear models for analysis (PROC GLM, SAS Institute 1996) and Akaike Information Criteria adjusted for small sample size (AIC_c) for model selection (Burnham and Anderson 2002).

3.3.5. Return Rates

I computed return rates to the colony for each group by dividing the number of marked birds that were detected as breeders on the study area in year $t + 1$ by the total number of marked birds composing that group in year t. I recognize that return rates offer limited inference on philopatry because detection probability is not accounted for, and non-returning individuals could have either dispersed or died (Martin et al. 1995), but due to limitations of the data, it was not possible to include in a capture-recapture analysis the combination of nesting outcome and geographic location. Accordingly, I provide return rates to allow comparison with other studies that have used them. Assuming equal survival and resighting probabilities between successful and failed breeders, the PEH predicts lower return rates for failed breeders if nesting failure leads to dispersal from the study area. I compared proportions of returning birds in each category using 2 x 3 contingency tables.

3.3.6. Paired Observations

I performed a paired *t*-test on data for 16 females for which I calculated dispersal distances in two years (i.e., between three consecutive nest attempts), but nest fate differed preceding each dispersal event. I used these data to test the one-tailed hypothesis that dispersal distance is greater following nest failure than after a successful nesting attempt.

32
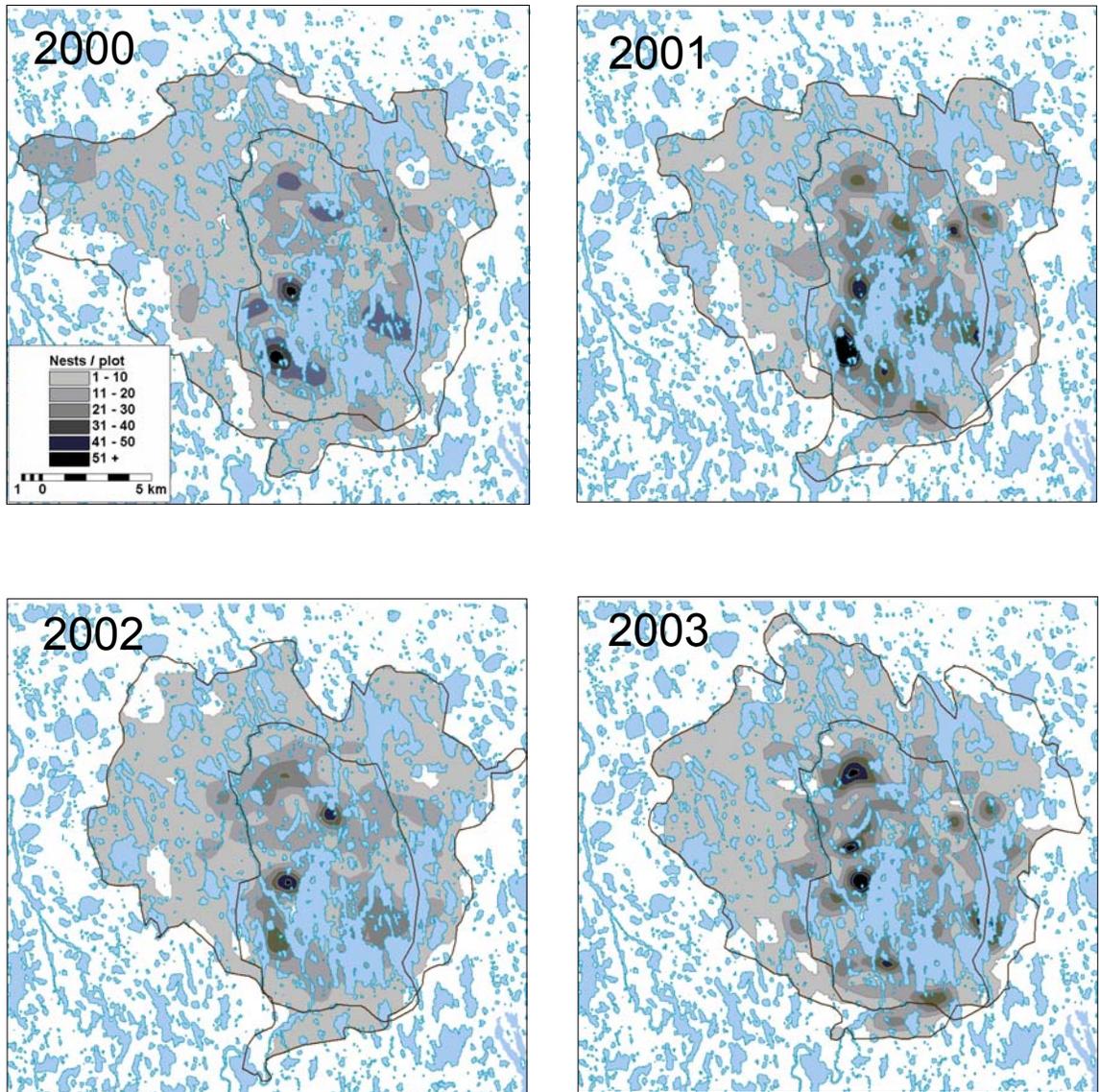
Fig. 3.2. Colony boundary (outer line), study area boundary (inner line), and spatial variability in density of nesting geese at the Karrak Lake breeding colony, Nunavut, Canada, 2000-2003.

3.3.7 Movement Between Low-, and High-density Nesting Strata

I used multistate modeling (Arnason 1973, Hestbeck et al. 1991, Brownie et al. 1993, Schwartz et al. 1993) to estimate probability of movement between landscapes of below-average and above-average nesting density during 2000-2003. I compared annual estimates of state-specific transition probabilities, for intervals i to $i + 1$, to the proportion of the study area represented by each density stratum in year $i + 1$. If movement probabilities and proportions of the study area in each stratum were the same, I inferred random movement; if movement probabilities were different from proportions of the study area represented by high- and low-density strata, I inferred that movement was nonrandom or selective. Using the extent of colony area and nest plot data, I calculated annual average nesting densities for years 2000-2003 (Fig. 3.2). Nest locations of neckbanded females were imported into SPANS GIS (PCI Geomatics 1999) to determine whether their nests were located in areas above or below the year-specific average of nesting density. In some instances I was unable to determine the current nest location of females for which I had determined the location of their previous nest. Occasionally, neckbanded birds were detected after they stepped off of nests, and identity of nests could not be determined with certainty because of high densities of neighboring nests. If so, I recorded location of such females assuming reasonably that she was <10 m from her nest. These were not included in the analysis of nest fate effect on dispersal distance, but were included in this capture-recapture analysis because the scale of precision likely would have been sufficient to ensure inclusion of such nests in correct strata of nest density. From these data, I created encounter histories coded by density strata and conducted the analysis using Program MARK (White and Burnham 1999).

The number of parameters in multistate models can be very large if all potential sources of variation are considered for all parameters. My primary interest was in estimating transition probabilities between areas of above- and below-average nesting density, so I parameterized the global model to include both time and stratum effects on movement, while assuming that apparent survival and resighting probabilities were equal between strata, but allowed to vary with time. Thus, I began with global model $\{\phi_t, p_t, \psi_{s*t}\}$ where ϕ, p, and ψ represent apparent survival (hereafter survival),

resighting, and movement probabilities, respectively; subscripts 's' and 't' indicate stratum and time effects, respectively. I assessed goodness-of-fit of the global model to data using Program U-CARE (Choquet et al. 2003, Pradel et al. 2003), and, based on results of the Arnason-Schwartz test ($\chi^2 = 20.716$, $p = 0.055$, df = 12), applied a variance inflation factor ($\hat{c}$) calculated as the χ^2 statistic divided by the degrees of freedom ($\hat{c} = 1.726$). I considered seven models, including the global, in the candidate set. Three models maintained full structure in movement with constant survival and time-dependent resighting probability $\{\phi_., p_t, \psi_{s*t}\}$, time-dependent survival and constant resighting probability $\{\phi_t, p_., \psi_{s*t}\}$, and no time effect on either survival or resighting probabilities $\{\phi_., p_., \psi_{s*t}\}$. Three other models included different parameterizations of ϕ and p listed above, while considering only stratum effects on movement $\{\psi_s\}$. I modified the design matrix for all manipulations of model structure, using the logit link function (White and Burnham 1999). Model selection was based on QAIC$_c$. Finally, to ensure that the stratum effect was not trivial, I assessed the fit of two *a posteriori* models where ϕ and p were constant (the best structure of these parameters based on the above model selection), while considering two alternate parameterizations with stratum effects on movement deleted: time dependent movement $\{\psi_t\}$, and neither time nor stratum effects on movement $\{\psi_.\}$.

3.4 RESULTS

3.4.1 Dispersal Distance

Observed dispersal distances between nest sites in consecutive years ranged from 4 to 6,666 m for successful nesters ($n = 36$) and from 0 to 9,781 m for failed nesters ($n = 96$). The most parsimonious model with dispersal distance as a response variable included only nest fate as the predictor variable (Table 3.1). Model-averaged parameter estimates demonstrated that successful nesters generally dispersed shorter distances [95% CI ($\bar{x}$) = 1,526 ± 2,143 m] than failed nesters (2,564 ± 1,621 m) with an effect size of 1,037 ± 931 m. Confidence intervals for slope estimates of all other parameters included zero.

Table 3.1. RSS (residual sum of squares), ΔAIC_c, AIC weight (ω_{AICc}), and number of parameters (K) of all candidate models considered explaining breeding dispersal distance of individual female Ross's Geese at the Karrak Lake breeding colony, Nunavut, Canada, 2001-2003. Models were based on general linear models in which dispersal distance was the response variable.

Model	RSS	ΔAIC_c	ω_{AICc}	K	r^2
F	696883527	0.00	0.283	3	0.032
F, P	692461399	1.29	0.149	4	0.039
F, SC, P, N, K	671078777	1.50	0.133	6	0.068
F, SC	696188482	2.00	0.104	4	0.033
intercept	720265540	2.26	0.091	2	0.000
F, SC, P	691487113	3.26	0.055	5	0.040
P	718966191	4.12	0.036	3	0.000
SC	720265540	4.36	0.032	3	0.000
F, SC, P, N, K, D	664708491	4.74	0.026	8	0.077
F, SC, P, N, K, D, SC*N	653952727	4.89	0.025	9	0.092
F, SC, P, N, K, D, SC*N, SC*P	642818415	4.97	0.024	10	0.107
F, SC, P, SC*P	690707583	5.31	0.020	6	0.041
F, SC, P, N	690729313	5.31	0.020	6	0.041
SC, P, N. K, D, SC*N, SC*P	676999626	9.47	0.009	9	0.060

Abbreviations: nest fate = F; snow cover = SC; percent of nests initiated = P; nest initiation date = N; distance of nest location from the Karrak Lake shoreline = K; nesting density class = D.

3.4.2 Return Rates

Return rates did not support predictions of the PEH. Successful nesters generally returned at lower rates than failed nesters (Table 3.2), but an effect of nesting success was detectable only in the first year ($\chi^2 = 6.05$, df = 2, $p = 0.048$), and not the second ($\chi^2 = 2.84$, df = 2, $p = 0.242$). Combining induced and natural failures in the analysis produced similar results for the first (Fisher's exact test, $p = 0.010$) and second year (Fisher's exact test, $p = 0.144$).

3.4.3 Paired Observations

Twelve of 16 females moved farther after a failed nesting attempt ($\overline{d}_{Fail} \pm SE = 2,629 \pm 657$ m) than after a successful one ($\overline{d}_{Success} = 1,430 \pm 358$ m). On average, females moved 1,199 m farther ($n = 16$, $SE = 300$, $P = 0.08$) following nest failure.

3.4.4 Movement in Relation to Nesting Density

I made 952 resightings of 673 neckbanded females either on or near their nests. Models with only stratum effects in the parameterization of movement were most supported by data (Table 3.3), but there was some support for temporal variability in movement probabilities, so I model-averaged parameter estimates. Female Ross's Geese were more apt to move to areas with above-average nesting density than to areas with below-average nesting density during all years of the study (Table 3.4). Ross's Geese moved nonrandomly (i.e., at rates higher than expected relative to the proportional size of density strata within the study area) to areas of above-average density in 2001-2002; probabilities of inter-stratum movement in 2003 were in proportion to size of density strata that year. My *a posteriori* check confirmed that data did not support models that excluded stratum effects of nest density in the parameterization of movement {i.e., ψ_t and $\psi_.$}.

3.4.5 Supplementary Data from Chapter 2

At least 15 females (6 successful: 9 failed) from this study at Karrak Lake were known to have dispersed 23-97 km to other colonies within the Queen Maud Gulf

Table 3.2. Return rates relative to nesting outcome in the previous year for female Ross's Geese nesting at the Karrak Lake colony, Nunavut, Canada, 2001-2003. Values in parentheses are the number of birds that returned/total number.

Year	Successful	Induced failure	Natural failure
2001-2002	20% (18/88)	36% (35/97)	33% (38/114)
2002-2003	21% (26/124)	30% (36/122)	21% (10/48)

Table 3.3. Model structure, quasi-deviance, $\Delta QAIC_c$, model weight (ω_{AICc}), and number of parameters (K) for all candidate models considered for multistate modeling of transition probabilities for female Ross's Geese breeding at the Karrak Lake colony, Nunavut, Canada, 2000-2003. Transition probabilities represent interannual movement from areas (strata) with below average nesting density to areas with above average nesting density, and vice versa. Model parameters include: apparent survival (ϕ), recapture (p), and transition (ψ) probabilities. Asterisks indicate multiplicative interactions between density stratum (s) and time (t), whereas a '.' denotes exclusion of these effects. 'Global' denotes the most parameterized model.

Model			QDeviance	$\Delta QAIC_c$	ω_{AICc}	K
$\phi_.$	$p_.$	ψ_s	50.01	0.00	0.32	4
ϕ_t	$p_.$	ψ_s	46.28	0.32	0.27	6
$\phi_.$	p_t	ψ_s	47.68	1.73	0.13	6
ϕ_t	p_t	ψ_{s*t} global	38.13	2.42	0.09	11
$\phi_.$	$p_.$	ψ_{s*t}	44.50	2.63	0.08	8
ϕ_t	$p_.$	ψ_{s*t}	40.77	3.00	0.07	10
$\phi_.$	p_t	ψ_{s*t}	42.17	4.40	0.03	10
[a] $\phi_.$	$p_.$	$\psi_.$	72.70	20.67	0.00	3
[a] $\phi_.$	$p_.$	ψ_t	71.93	23.95	0.00	5

$\hat{c} = 1.726$
[a] *a posteriori* models that excluded stratum effects of nest density on movement

Table 3.4. Probabilities of movement by nesting female Ross's Geese between areas with above-, and below-average nesting density within the Karrak Lake breeding colony, Nunavut, Canada, 2000-2003. Also shown are proportions of the study area with above- and below-average nesting density. Movement probabilities are state-specific transitions for the interval i to $i + 1$, whereas proportion of the study area represented by each density stratum are for year $i + 1$. Model-averaged transition probabilities are presented ± 1 SE.

Year	Below to Above	Above to Below	Above	Below
2000-2001	0.60 ± 0.08	0.33 ± 0.11	42%	58%
2001-2002	0.63 ± 0.06	0.29 ± 0.06	44%	56%
2002-2003	0.65 ± 0.07	0.24 ± 0.07	68%	32%

region, suggesting that movement between colonies is not influenced by previous reproductive outcome (likelihood ratio $\chi^2 = 0.06$, df $= 1$, $P > 0.75$).

3.5 DISCUSSION

3.5.1 The Effect of Prior Experience on Breeding Philopatry

Movement by Ross's Geese both within and among colonies seems pervasive in the Queen Maud Gulf metapopulation (Chapter 2, Drake and Alisauskas 2004, this study). Previous nest fate was the best predictor, among those considered, of dispersal distance and induced movement by females of ~1 km within the colony between years. Although detectable, breeding success accounts for a small amount (<11%; Table 3.1) of variation in dispersal distance within colonies, and it does not appear to influence movements among colonies. Judging from the small proportion of variation explained by the candidate models and estimated dispersal distances exceeding 1500 m regardless of previous nest fate, >89% of nest site selection is also influenced by factors other than those that I considered.

My results suggest that support for the PEH depends highly on the scale at which dispersal is measured. If I were to base inference solely on differences in dispersal distance, my results support the prediction that failed birds should disperse farther if prior experience is used to determine location of subsequent breeding attempts. Despite the fact that greater dispersal distance by failed nesters should have lead to them having a higher risk of leaving the study area, this did not result in them having lower return rates, so processes other than dispersal are likely to have caused differences in return rates (discussed below). Lack of consistency in support for predictions of the PEH suggests that the decision process of habitat selection that ultimately determines dispersal patterns, likely involves many factors occurring at several spatial scales. How previous information is applied, and the degree to which the application of this information overlaps on different spatial scales, is apt to vary with life history strategy and environmental stability.

Annual migration of birds generally involves transit between areas where food supply is abundant for a limited time. If philopatry depends on reproductive success as a metric of site quality, then temporal and spatial acquisition of resources for reproduction

in turn may influence settling patterns. The breeding period of arctic-nesting geese can be divided into two important phases of nesting and brood-rearing. Nesting begins with arrival of geese each spring to an environment in breeding colonies where food resources are generally unavailable or offer poor nutritive value (Gloutney et al. 1999, 2001), and the timing and extent of snow-free nesting habitat are unpredictable. Females arrive in advanced stages of rapid follicular development (Bon 1996) and lay eggs shortly after arriving at the colony. Although females generally have ample endogenous reserves to meet energy requirements of nesting (average nest success over a 14-year period is 82%; Alisauskas unpublished data), short delays in nesting can have negative impacts on reproductive output because clutch size is smaller in later nests (Findlay and Cooke 1982, Lepage et al. 2000), producing smaller goslings with slower growth rates (Cooch et al. 1991a,b, Sedinger and Flint 1991), and lower rates of recruitment (Cooke et al. 1984, Sedinger et al. 1995, 2004). Although breeding geese forage throughout the nesting period at Karrak Lake, little food is ingested; in fact, most available vegetation is of poor digestibility (Gloutney et al. 2001) and is used primarily as material with which to construct nests. Because nesting habitat does not offer much food for parents or goslings, geese probably do not become attached to specific nest sites.

Including non-manipulation and manipulation years, I recorded locations of 216 nesting females in consecutive years. Of these, only one bird returned exactly to its previous nest bowl, although it had failed the previous year. Even if the definition of philopatry is relaxed to include return to a previous nesting territory, only four birds (2 successful and 2 failed) returned ≤10 m of their previous nest site; based on limited information about nesting territory size of Ross's Geese (Ryder and Alisauskas 1995), territory overlap would have occurred for two of these birds (1 successful; 1 failed). Like Lindberg and Sedinger (1997), I suspect that selection pressures which favor early arrival and nest initiation (Slattery and Alisauskas 2002) render timing of nesting to be a greater influence of reproductive success than would nest location. Some movement between nest sites may result simply from behavioral flexibility required for early nesting that ultimately results in offspring emergence coinciding with peak food availability on brood-rearing areas (Raveling 1978).

Breeding philopatry likely is resource driven, but brood-rearing areas probably represent the resource to which philopatry by Ross's Geese occurs. Precocial goslings disperse up to 70 km from natal colonies with their parents after hatch (Slattery 2000) to vast areas of sedge (*Carex* spp.) meadows. Such meadows represent a predictable food supply consistently available in most years. This is a critical time for goslings because they must attain sufficient size and functional maturity to migrate south to fall staging areas, while adults undergo molt and also must store sufficient reserves for the migration. As in other regions where recruitment of Snow Geese has been negatively influenced by declines in food abundance (Cooch et al. 2001), spatial variation in food resources on brood-rearing areas north of Karrak Lake appear to influence recruitment by Ross's Geese (Slattery 2000, Slattery and Alisauskas 2002); however, this limitation has been insufficient as yet to cause local population decline (Alisauskas and Rockwell 2002). Although goslings are subject to several selection pressures (i.e., predation, disease, parasites, weather, and food availability), productivity by most populations of arctic-nesting geese is under strong environmental control (Ankney and MacInnes 1978, Cooke et al. 1995, Bon 1996, Alisauskas 2002); even when distribution of food is predictable, weather, the principle determinant of productivity in arctic-nesting geese, is highly unpredictable for the duration of the arctic summer. Geese tend to nest when conditions are still uncertain, but hatch seems to be timed to the coincidence of abundant foods on brood-rearing areas; there is far less likelihood of snow covering up brood-rearing areas than there is of snow covering exposed ground a month earlier. Considering that arctic-nesting geese exhibit philopatry to brood-rearing areas (Cooke and Abraham 1980, Lindberg and Sedinger 1998), philopatry to nesting areas may occur (~90% adult female fidelity to Karrak Lake; Chapter 2, Drake and Alisauskas 2004) in part because adjacent brood-rearing areas represent a predictable food resource important to adult survival regardless of the outcome of their breeding attempt.

An evolutionary history of breeding in an unpredictable environment may favor flexibility in fine-scale fidelity to breeding sites. Switzer's (1993) models predict that philopatry should vary inversely with heterogeneity in habitat quality and longevity of the organism, and vary directly with cost of switching territories and with age. He also assessed two decision rules strategies: 'always-stay' and 'win-stay: lose-switch'. The

'always-stay' strategy performed well in unpredictable environments, whereas the 'win-stay: lose-switch' strategy did well in predictable environments. Compared to terrestrial habitats in other ecosystems, the habitat of arctic-nesting geese is relatively homogenous, but availability is highly unpredictable. My results generally support Switzer's predictions taking scale into context. On a landscape scale, Ross's Geese generally stay at Karrak Lake regardless of previous nest fate (Chapter 2), but almost always switch to a new nest site probably because territory quality is similar among sites, and time is of essence. The general applicability of Switzer's (1993) models is appealing, but predictions regarding breeding site fidelity need to consider the temporal and spatial scales at which resources critical for successful reproduction are acquired. Capital breeders rely on endogenous reserves for successful reproduction, so the suite of characteristics used to assess site suitability may be much simpler than those used by income breeders.

In two of three years, rates of movement by Ross's Geese towards areas of above-average nesting density were higher than those expected by random chance. In the final year of this study, rates of movement were consistent with the availability of each density-class within the study area; although probability of movement toward areas of higher nest densities remained consistent with previous years, area of above-average nesting density increased markedly (Table 3.4). While there was substantial annual variation in the spatial distribution of nest density, certain regions of the colony consistently contained nest densities 4-6 times greater than the colony average. In general, such high-density areas were near the center of the colony (Fig. 3.2) where geese have nested for several decades (Alisauskas et al. 2006b). Plant communities within the colony have been altered as a direct result of vegetation removal by nesting geese. Consequently, amount and diversity of vegetation is markedly reduced in areas with a longer history of nesting geese (Alisauskas et al. 2006b). Devegetation likely results in decreased snow depth, thereby advancing dates of snow clearance and availability of nesting habitat. In addition, directional movement toward areas of higher nesting density may also be related to advancing social status with increasing age as older geese tend to nest earlier (Finney and Cooke 1978, Flint and Sedinger 1992). I

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was unable to test for this effect because I did not know the age of marked individuals as most neckbanded geese were marked as sexually mature adults.

Alternatively, movement toward areas of higher nesting density may be motivated by anti-predator benefits associated with improved communal vigilance, effects of predator swamping, and mobbing behavior (Slattery et al. 1998). Historically, Ross's Geese nested on islands in shallow lakes perhaps to avoid nest predation by Arctic Fox (*Alopex lagopus*; Ryder 1969b). Concurrent with Ross's Goose population increase, terrestrial area occupied by nesting geese expanded into previously unused island and mainland habitats (Kerbes et al. 1983, McLandress 1983, Kerbes 1994). At Karrak Lake, this expansion by nesting Ross's Goose into mainland habitats occurred sometime between 1969 and 1975, but densities of nesting Ross's Geese remained highest on islands that had been used for nesting in the late 1960's (McLandress 1983). Terrestrial area of the colony has increased more than sixty-fold since McLandress' study, and most nests (> 97%), and the highest nesting densities, are now found on mainland habitats (Alisauskas unpublished data). *Per capita* rates of nest predation are lower in larger colonies (Raveling 1989); thus, areas of mainland habitats with high nesting densities may function as ecological equivalents to islands. If so, reproductive parameters may differ between areas of above-average densities compared to below-average nesting densities. However, based on nest plot data, clutch size and nest success were similar between areas of below-average and above-average nesting density, which suggests that neither partial nor full clutch loss varies with density. In two years nest initiation date was 1.3 and 2.5 days earlier in above-average areas (Alisauskas unpublished data) suggesting that these areas are either preferred or available at an earlier date. In addition, Samelius and Alisauskas (2000) estimated that foxes took 4-8% of eggs from the Banks Island colony of Lesser Snow Geese; a colony that is about half the size of the Karrak Lake nesting population. Based on knowledge about fox population size and rates of egg removal by foxes at Karrak Lake, foxes could be expected to remove a maximum of ~11% of the eggs laid at Karrak Lake (Samelius personal communication); a number substantially below the long-term rate of 18% complete nest failure. Perhaps the Karrak Lake colony has exceeded a size threshold at which a functional response in predation rate would make the *per capita* rate of egg or

clutch loss very low. Historically, movement toward existing areas of high nest density may have been adaptive when colony size was smaller and *per capita* risk of predation may have been greater. However, the similarity between recent rates of Ross's Goose nest success and those during 1966-1968 (Ryder 1972) suggests that predation pressure has remained similar, at least during the past 40 years.

3.5.2 Can Anything Be Gained from Return Rates?

The shortcomings of using return rates to gain insight into demographic process have been previously discussed (Martin et al. 1995); nevertheless, return rates are commonly relied upon to 'test' hypotheses set forth to explain difference in site fidelity and/or 'survival' between successful and unsuccessful nesting birds. The PEH states that differential philopatry occurs as an outcome of experienced-based choices by individuals and thus, difference in return rates arise from differential philopatry (or site fidelity), and not simply as a result of differential mortality (Bollinger and Gavin 1989, Haas 1998). Two other common explanations for differential return rates include the renesting stress hypothesis (Haas 1998) and the low quality hypothesis (Pugesek and Diem 1990). The first states that stress associated with renesting results in higher annual mortality; thus, renesting individuals are less likely to return to their previous breeding site because they have died. The low quality hypothesis states that low reproductive success is associated with birds in poor condition that are also more likely to die, which causes them to have lower rates of return. I did not consider the latter two hypotheses because arctic-nesting geese do not renest, and the random assignment of individuals to experimental manipulation should have resulted in equal proportions of high- and low-quality individuals in each group. Nonetheless, these hypotheses all predict lower return rates of failed breeders, but return rates do not allow differentiating between the underlying processes (dispersal and mortality) producing the observed pattern.

For example, as it pertains to my study system, the PEH predicts that nest failure will result in an increase in the probability of dispersal. This prediction was supported by the fact that dispersal distance was greater for female Ross's Geese that experienced nesting failure; yet, observed return rates were in a direction opposite to that predicted by the PEH, successful breeders returned at lower rates than failed breeders. Given

presence in the study area, it is reasonable to assume that detection probability is independent of previous nest fate; thus, explanations for differential return rates can be 'narrowed down' to a difference in survival and/or emigration probability. My results from capture-recapture analysis (Chapter 4) suggest that successful nesters survive at lower rates and that a difference in mortality may be responsible for lower return rates of successful females. But even after accounting for known mortalities, return rates were still lower for successful nesters. Confounding things further, I found differences in annual resighting probabilities between successful and failed nesters (Chapter 4). Failed nesting resulted in increased dispersal distance, which should have increased the risk of these birds leaving the study area, but detection of failed breeders was lower only during the last year of my study (Fig. 4.2). Finally, there exists the potential for differences in future breeding probability between successful and failed nesters. For example, if greater incidence of nonbreeding results from successful reproduction in the previous year (i.e., a cost of reproduction), this may lead to a lower rate of return by successful breeders that is unrelated to differential dispersal or mortality. Given that absence from the sample population can arise from several processes, return rates likely will never permit identification of the biological process(es) responsible for patterns observed in wild populations of birds.

3.5.3 Summary

It clearly is important to consider the scale at which dispersal is measured because estimates of dispersal depend explicitly on the spatial configuration of the study area itself, and discontinuities in distribution of study animals. It is intractable to define dispersal as a binary response (i.e., stay vs. move) in a landscape with contiguous occupancy, as is the case for intracolonial movements of Ross's Geese. Instead, distance moved is an appropriate metric of dispersal at such a scale. However, movement probability among insular colonies comprising a metapopulation is easily treated as a binary response, and lends itself to estimation of movement probability using multistate methods. Each approach was necessary because decisions by Ross's Geese about where to attempt to nest appear to be at least a two-stage process occurring primarily at the

metapopulation level between colonies, and secondarily at a more localized scale involving landscape variability within colonies.

My impressions about predictability, quality, and abundance of nesting habitat across landscapes in which Ross's Geese nest, suggest to me that decisions about breeding philopatry occur primarily at the metapopulation level. I believe that there are two important determinants for the geographic location of Ross's Goose colonies. Most colonies of Ross's Geese in QMGMBS are associated with islands in shallow lakes that become ice-free earliest, and so historically they were probably the best sites to avoid mammalian predation. However, as critical to fitness as successful nesting is the survival of goslings to adulthood. While nesting success may provide a direct metric for colony quality, an indirect metric that is pertinent to settling patterns by prenesting adults may be proximity of colonies to high-quality brood-rearing areas. Aspects of brood ecology of geese, such as gosling growth during movement from natal colonies to brood-rearing areas, can have large effects on gosling survival (Slattery 2000, Slattery and Alisauskas 2002). Lack of philopatry to nest sites and my previous finding of ~90% fidelity to Karrak Lake (Chapter 2, Drake and Alisauskas 2004) lead me to suggest that philopatry occurs as a result of an affinity to broader landscape features rather than to nest sites or even territories. I propose that philopatry to the colony may be driven by a predictable supply of food on adjacent brood-rearing areas that ensures high survival of adults regardless of the outcome of their reproductive attempt.

At the finer scale, nest success and gosling survival may be relevant to intracolonial movements as well, but in different ways. Nevertheless, intracolonial movements appear to be governed by additional, less predictable events that limit nesting habitat. When nests sites are limited, when breeding territories contain resources used to meet metabolic costs of reproduction, and/or when predation pressure is such that safe sites are difficult to find (e.g., Hoover 2003), site fidelity is more likely to be exhibited at a finer scale. Each of these situations should lead to increased spatial heterogeneity in probability of successful nesting. Temporally predictable heterogeneity in site quality should increase the importance of previous reproductive experience on philopatry (Switzer 1993). Reliance by Ross's Geese on nutrient reserves, and spatially random nest success diminish the importance of where geese nest; nesting is conditional

on ground being snow free. Nest site availability can be highly variable from year to year due to timing and pattern of snow melt, and I suspect that this is the most important determinant of intracolonial movement between sequential nest sites.

If a difference in dispersal distance was the only criterion for evaluating the PEH, my results support the PEH by demonstrating a causal relationship between previous nesting outcome and subsequent dispersal distance. However, estimated dispersal distances exceeded 1500 m regardless of previous nest fate, and homing to nest sites or territories was exceedingly rare. Ross's Geese showed ~90% fidelity to Karrak Lake (Drake and Alisauskas 2004), but <11% of finer-scale adjustments to settlement patterns within the Karrak Lake colony, although statistically detectable, appeared to be overshadowed by random or unmeasured effects. There is strong selection for arctic-nesting geese to nest early. While reliance on nutrient reserves emancipates females from a dependency on local food resources during nesting (Ryder 1970, Ankney and MacInnes 1978), long delays in snowmelt and nesting after arrival to a nesting colony can deplete nutrient reserves. Furthermore, a strong relationship between gosling mortality and lateness of nesting is pervasive in arctic-nesting geese (Cooch et al. 1991b, Sedinger and Flint 1991, Lepage et al. 1999) and is an additional selection pressure favoring early nesting. Thus, the adaptiveness of early nesting from these two causes alone likely favors decisions that advance nesting at the expense of philopatry. I suggest that there is great advantage to females that can quickly exploit snow free habitat in which to nest as gaps in snow cover emerge with more rapid snow melt. Acquisition of nest sites and surrounding territories undoubtedly would be hastened by flexibility in movement after arrival to a colony by allowing continuous prospecting, rather than homing directly to previous nest sites.

CHAPTER 4. IS THERE A SURVIVAL COST TO SUCCESSFUL NESTING BY FEMALE ROSS'S GEESE?

4.1 ABSTRACT

Life history theory assumes a trade-off between current reproduction and survival. Most bird studies have focused on costs of rearing nidicolous young, as these costs are assumed to be low in species with nidifugous young. I investigated costs of reproduction in a breeding population of Ross's Geese (*Chen rossii*), a species having self-feeding nidifugous young. I experimentally tested for a trade-off between current and future reproduction using modern methods of estimation that permit unbiased inference about true survival. I estimated survival and resighting probabilities of female geese using multistate capture-resighting analysis that incorporates recoveries of dead birds. I found that annual survival estimates of successful nesting birds were consistently lower than those of failed breeders. There was evidence that a cost of breeding is more likely incurred when conditions during incubation are harsh, and when the breeding population is larger. I also found differences in annual resighting probabilities of successful and failed nesters, but interacting group and time effects and multiple forms of temporary emigration prevent using differential resighting rates to draw further inference about the biological process responsible for such detection differences. Failed nesters had a larger proportion of total mortality associated with hunting; thus, a cost of breeding likely resulted from an increase in vulnerability of successful nesters to mortality factors other than hunting.

4.2 INTRODUCTION

Fundamental to life-history theory is the notion that the evolution of life history characteristics is constrained by trade-offs that link life history traits (Roff 1992, Stearns

1992). In the context of life-history theory, reproduction and survival are viewed as competing processes because individuals must balance the allocation of limited resources between these activities. Thus, individuals may incur a cost of reproduction (Williams et al. 1966) whereby current reproductive effort (1) reduces survival probability, or (2) impedes or prevents future reproductive investment, breeding success, or breeding probability, without affecting survival.

There are clear examples of costs of current breeding effort at the expense of future breeding performance in birds (reviews in Nur 1988, Lindén and Møller 1989), but evidence for trade-offs between breeding investment and survival probability remains inconclusive to date. Studies that have tested hypotheses involving breeding costs in birds frequently manipulate numbers of offspring that parents are induced to rear, and then compare return rates as a function of offspring number (e.g., Reid 1987, Jacobsen et al. 1995, Golet et al. 1998, but see Golet et al. 2004). However, because return rates are the product of the probabilities of (1) surviving, (2) returning to the study area if alive, and (3) being resighted/recaptured if alive and on the study area (Brownie et al. 1993, Nichols and Kendall 1995), group-specific differences in return rate may result from differences in any or all of these separate probabilities (Clobert 1995, Martin et al. 1995). Additionally, most studies have focused on variation in family size, conditional on offspring presence, rather than comparing breeders that raise young to breeders that do not rear young.

Using proper methods of estimation, Golet et al. (2004) detected a survival cost to reproduction in Black-legged Kittiwakes (*Rissa tridactyla*) by comparing survival of adults that raised young to those whose clutch was removed late in incubation. Their findings demonstrated that demands of provisioning nidicolous young compromised future reproductive potential by reducing apparent survival of adult birds. Relative to nidicolous species, costs of chick rearing in precocial birds with nidifugous young are assumed to be low (Winkler and Waters 1983, Rohwer 1992) because they avoid costs of food provisioning directly to offspring after hatch as nutrient transfer to young is done *in ovo*. Despite the fact that metabolic costs of caring for growing young are likely much lower for nidifugous birds with self-feeding offspring, parenting may still carry costs. For example, in ducks and geese, parents that care for young have less time for

self-maintenance (i.e., feeding) than do parents without young (Lessells 1987, Seddon and Nudds 1992, Ruusila and Pöysä 1998); thus, brood rearing may inhibit the ability of female parents to restore body condition, which in turn, may compromise future reproductive efforts or survival. In addition, parents will often put themselves at risk while defending young (Afton and Paulus 1992). Although there is potential for precocial species to incur costs from brood rearing, this topic has received less attention than in altricial species.

Recent studies that examined costs of brood rearing in waterfowl have demonstrated costs to future reproduction (Milonoff et al. 2004) and survival (Hartke et al. 2006). These findings were reported for female ducks in which pair bonds dissolve after egg laying and females solely provide parental care. Although ducks and geese share many life history characteristics, geese have long-term pair bonds and exhibit bi-parental care (Prevett and MacInnes 1980), so costs associated with brood rearing may be less for female geese.

Evidence for costs associated with brood rearing in geese is equivocal. Williams et al. (1994) found no evidence of negative effects to fitness in relation to offspring number (over the natural range of brood sizes) in adult female Lesser Snow Geese (*Chen caerulescens*). Whereas, using brood size manipulation, Lessells (1986) found that demands of parenthood rendered female Canada Geese (*Branta canadensis*) less efficient at recouping body condition, and they bred later in the following year. Considering that parenting may inhibit the recouping of body condition, and that survival of adult female geese increases with body condition (Schmutz and Ely 1999), successful reproduction may come at a cost to survival of female geese.

Herein, I experimentally tested whether nest success by Ross's Geese (*C. rossii*) resulting in offspring that accompany adults after hatch constituted a cost, a benefit or was a neutral influence on adult female survival probability. In addition to comparing group-specific survival rates, I estimated the effect of three ecological covariates on survival probability: a year-specific index of timing of breeding, temperature during the nesting interval, and prefledging age-ratios during capture efforts. I used multistate capture-recapture analysis that incorporates information from recoveries of dead birds (Kendall et al. 2006) sampled over their entire distribution so that estimates were of true

survival, i.e., unconfounded by emigration probability (Brownie et al. 1985). To my knowledge, this is the first study to investigate costs to true survival as a result of successful nesting.

4.3 METHODS

4.3.1 Data

Data used for this analysis were collected at Karrak Lake during surveys for neckbanded geese, described in Chapters 1 and 3.

4.3.2 Analysis

I used multistate models (Arnason 1973, Hestbeck et al. 1991, Brownie et al. 1993, Schwarz et al. 1993), as implemented in Program MARK, that combine information from resightings of unique marks on live birds during nesting with information from marks recovered from dead birds killed and reported by hunters for years 2000-2003 (hereafter recoveries; Kendall et al. 2006). Such multistate models permit estimation of true survival probability (S), resighting probability (p), state-specific transition probability (ψ), and reporting probability (r). Reporting probability is distinct from band reporting rate, λ, which is the probability that a hunter will report the band given that (s)he has killed and retrieved a banded bird (Brownie et al. 1985). Yet, both reporting probability and band reporting rate have an association with recovery probability, f, which is the probability that a marked bird is killed and retrieved by a hunter, and its band reported (Brownie et al. 1985). Reporting probability is $r = \dfrac{f}{(1-S)}$, or the proportion of mortality, $M = (1 - S)$, composed of birds shot, retrieved and reported. My main interest was to compare survival of adult females from two experimental groups or states: (1) those in a control group that hatched at least one gosling (state 'S'), and (2) those in a treatment group whose eggs were removed from their nests, thereby inducing total nest failure (state 'F'). I also was interested in comparing state-specific reporting probabilities because they can provide insight into the fraction of total mortality associated with harvest. It is reasonable to assume that the reporting component of r would not depend upon previous nest fate; thus, support for

group-specific differences in r would suggest differential vulnerability to hunting mortality. In my study, state-specific resighting probability was confounded with probability of permanent emigration from the study area on the nesting grounds. However given presence on the study area, I could think of no biological or methodological reason why detection should have been related to previous nest fate *per se*. So, differences in resighting probability in relation to nest fate could only result from differences in emigration probability. The transition of many individuals from successful to failed state was induced as part of the experimental design, and was of no direct ecological interest, so reductions in model structure of ψ do not represent tests of biological hypotheses.

I began with a candidate set of models that excluded covariate effects ($M = 16$). The global model included all potential sources of variation and interactions $\{S_{g*t}, p_{g*t}, \psi_{g*t}, r_{g*t},\}$. Subscripts 'g' and 't' represent group (i.e., nest fate) and time effects, respectively; whereas, absence of group, time, or covariate effects is denoted by a period (e.g. $\psi_.$). I reduced the structure of transition probability while maintaining full structure in other parameters because transitions between nest fates did not always represent ecological processes, but instead resulted from manipulations of nest fate. I maintained the best structure of transition (i.e., $\psi_.$) when testing for group differences and temporal variability in survival, resighting, and reporting probabilities. When evaluating temporal variation in survival, I also considered two time trend models (denoted by 'T' e.g., S_{g*T}), because Ross's Goose survival has recently declined with increased harvest (Alisauskas et al. 2006a).

Using the structure of the best-approximating model, I further considered 10 additional models in which survival was constrained to be a function of single or combinations of year-specific covariates. Arctic-nesting geese incur significant physiological costs during reproduction, which are likely to be greater when environmental conditions are harsh or when nesting is delayed. Thus, I hypothesized that in years of later mean nest initiation, or when colder temperatures persist during nesting, females are more likely to finish nesting in poorer condition; such reduced condition may impinge on survival probability. I predicted a negative relationship between survival and an early-late index (ELI) of timing of nest initiation (calculated as

the difference between annual mean nest initiation and the long-term average for 1991-2003, Julian date), and a positive relationship between survival and average relative temperature during nesting (calculated as mean wind chill during nest initiation and incubation; WC, °C). I further considered that harvest of Ross's Goose adults may increase in years when there is high production of goslings; this is because juvenile geese are twice as vulnerable as adults to hunting (Alisauskas et al. 2006a) and adults closely associate with young. I tested this prediction by constructing models in which adult survival was constrained as a function of annual juvenile/adult age ratios (JAR) determined from banding data. Lastly, birds that experienced natural nest failure may have represented individuals of low quality; so, I considered a model wherein the parameter structure was similar to that of the best approximating model, using three groups instead of two.

I used AIC$_c$ for model selection and modified the design matrix for all manipulations of model structure using the logit link function. The relative plausibility of each model was assessed by comparing differences between the AIC$_c$ value for the best model and values for all other models (ΔAIC$_c$), and by comparing Akaike model weights (Burnham and Anderson 2002). Akaike weights (w_i) sum to 1, and w_i provides a measure of the support for model i given the data and the set of models. I based inference and model averaged parameter estimates on a confidence set of models for which the evidence ratio $\dfrac{\mathcal{L}(g_i \mid x)}{\mathcal{L}(g_{\min} \mid x)} \approx 0.125$ (Burnham and Anderson 2002) where $\mathcal{L}$ is the likelihood of model g_i, given the data x, and g_{min} is the best-supported model. I could not assess goodness-of-fit of these data because methods have not been developed for multistate models with recoveries. However, I was reassured by the fit of data to multistate models where states represented nesting densities (Chapter 3) and thus, considered the data robust for analysis using multistate models that incorporate recoveries.

4.4 RESULTS

There were 894 resightings of 665 neckbanded females for which nest fate was known. Forty-two of these females were reported as shot and recovered by hunters.

Table 4.1. Results of model selection for multistate models incorporating dead recoveries for female Ross's Geese breeding at the Karrak Lake colony, Nunavut, Canada, 2000-2003. Model parameters include: true survival (S), recapture (p), transition (ψ), and reporting (r) probabilities. Asterisks indicate interactions between group effects (g: successful and failed nesting attempt, or 3g: successful, natural failure and experimental failure) and temporal variability (t); whereas, '+' denote additive effects in model structure. Year-specific covariates are wind chill (WC), early-late index (ELI), and juvenile/adult age ratio (JAR). Absence of group, time, or covariate effects is denoted by a period within parentheses. 'Global' denotes the most parameterized model.

Model	Deviance	ΔAIC_c	ω_{AICc}	K
$S_{(g+WC)} p_{(g*t)} \psi_{(.)} r_{(g)}$	1643.65	0.00	0.150	12
$S_{(g*WC)} p_{(g*t)} \psi_{(.)} r_{(g)}$	1642.06	0.47	0.119	13
$S_{(g+WC+JAR)} p_{(g*t)} \psi_{(.)} r_{(g)}$	1642.22	0.63	0.110	13
$S_{(g+ELI)} p_{(g*t)} \psi_{(.)} r_{(g)}$	1644.50	0.85	0.098	12
$S_{(g+WC+ELI)} p_{(g*t)} \psi_{(.)} r_{(g)}$	1642.69	1.10	0.087	13
$S_{(g*t)} p_{(g*t)} \psi_{(.)} r_{(g)}$	1636.58	1.19	0.083	16
$S_{(g*ELI)} p_{(g*t)} \psi_{(.)} r_{(g)}$	1642.86	1.27	0.080	13
$S_{(g+t)} p_{(g*t)} \psi_{(.)} r_{(g)}$	1640.88	1.35	0.076	14
$S_{(g+WC+ELI+JAR)} p_{(g*t)} \psi_{(.)} r_{(g)}$	1640.88	1.35	0.076	14
$S_{(g+ELI+JAR)} p_{(g*t)} \psi_{(.)} r_{(g)}$	1643.89	2.30	0.048	13
$S_{(g*t)} p_{(g*t)} \psi_{(.)} r_{(.)}$	1641.21	3.75	0.023	15
$S_{(g*t)} p_{(g*t)} \psi_{(.)} r_{(g+t)}$	1635.19	3.96	0.021	18
$S_{(g*t)} p_{(g*t)} \psi_{(.)} r_{(t)}$	1638.43	5.13	0.012	17
$S_{(g*t)} p_{(g*t)} \psi_{(.)} r_{(g*t)}$	1635.12	5.99	0.007	19
$S_{(g*t)} p_{(g*t)} \psi_{(g*t)} r_{(g*t)}$ global	1630.89	8.04	0.003	22
$S_{(g*t)} p_{(g*t)} \psi_{(g)} r_{(g*t)}$	1635.11	8.07	0.003	20
$S_{(g*t)} p_{(g*t)} \psi_{(t)} r_{(g*t)}$	1633.15	8.20	0.002	21
$S_{(t)} p_{(g*t)} \psi_{(.)} r_{(g)}$	1650.52	8.93	0.002	13
$S_{(g*JAR)} p_{(g*t)} \psi_{(.)} r_{(g)}$	1652.31	10.72	0.001	13
$S_{(g+T)} p_{(g*t)} \psi_{(.)} r_{(g)}$	1656.74	11.03	0.000	11
$S_{(g+JAR)} p_{(g*t)} \psi_{(.)} r_{(g)}$	1656.47	12.83	0.000	12
$S_{(g*T)} p_{(g*t)} \psi_{(.)} r_{(g)}$	1656.64	12.99	0.000	12
$S_{(g)} p_{(g*t)} \psi_{(.)} r_{(g)}$	1662.31	16.60	0.000	11
$S_{(g*t)} p_{(g+t)} \psi_{(.)} r_{(g)}$	1676.58	39.12	0.000	15
$S_{(g*t)} p_{(t)} \psi_{(.)} r_{(g)}$	1682.73	41.13	0.000	13
$S_{(g*t)} p_{(g)} \psi_{(.)} r_{(g)}$	1693.37	49.72	0.000	12
$S_{(3g*t)} p_{(g*t)} \psi_{(.)} r_{(g)}$	1770.90	137.59	0.000	17

There was no support for models in which the effects of group or time were eliminated from the parameterization of S or p, thus indicating that group and temporal structure existed. Similarly, there was no support for stratification of nest fate into three groups described in METHODS (Table 4.1; model $\{S_{(3g*t)} \, p_{(g*t)} \, \psi_{(.)} \, r_{(g)}\}$). My results support the hypothesis that successful reproductive comes with cost to survival; in general, survival was best parameterized with additive effects between group and ecological covariates or time, but there was some support for models with interactions between these terms (Table 4.1). Estimated survival probability of successful nesters was consistently lower than that of failed nesters, but 95% confidence intervals overlapped considerably in three of four years (Fig. 4.1). Nevertheless, the model-averaged effect size of breeding success (where success = 1 and failure = 0) on survival over all years was $\hat{\beta} = -0.87$ (-1.94, 0.21 unconditional 95% CI). The unconditional 90% confidence interval for overall effect size was $-1.77, 0.04$). Examination of model-specific estimates for the effect of breeding success on survival revealed that when survival was parameterized as $S_{(g*t)}$, standard errors of effect size were much larger than other models included in the confidence set. If these two models are removed from the confidence set (remaining models $\Sigma\omega_{\text{AICc}} = 0.84$), the effect size is $\hat{\beta} = -0.73$ (-1.41, -0.04, unconditional 95% CI). Models in which survival was constrained to be a function of covariates were generally better supported than models without constraints. I model-averaged slope estimates of environmental covariates over the subset of models in which these effects were included. Models with wind chill as a covariate for survival received the most support ($\Sigma\omega_{\text{AICc}} = 0.54$, $\hat{\beta} = 2.99$, -1.23, 7.20, unconditional 95% CI), followed by those with nest initiation date ($\Sigma\omega_{\text{AICc}} = 0.39$, $\hat{\beta} = 0.46$, -5.05, 5.98) and age ratio ($\Sigma\omega_{\text{AICc}} = 0.23$, $\hat{\beta} = 3.77$, -2.91, 10.47). The slope coefficient was in the direction predicted by my hypotheses about respective influence of wind chill on survival, but not for lateness of nesting or age ratio during marking. Although confidence intervals around model-averaged slope estimates for wind chill included zero, slope coefficients for effects of wind chill were in the predicted direction in all models that included these constraints, and confidence intervals excluded zero in three of these models. Resighting probability was best parameterized as time dependent that

differed between groups; detection of failed nesters was greater than of successful nesters in the first two years, but greater for successful nesters in the last (Fig. 4.2). Reporting probability was best parameterized without temporal variability but differed between birds that were successful (r_s = 0.049, 0.028, 0.086 unconditional 95% CI) and unsuccessful (r_f = 0.119, 0.075, 0.184) at their nesting attempt. Assuming equal band-reporting rate between treatment groups, this result suggests that the fraction of total mortality associated with harvest was greater for failed nesters.
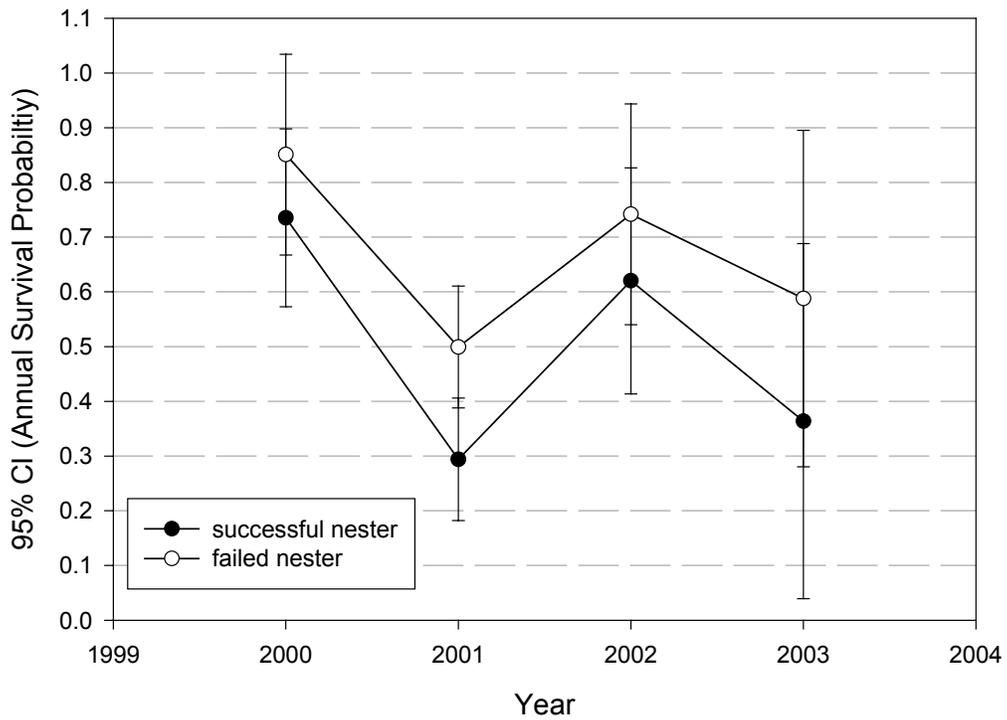
Fig. 4.1. Model-averaged estimates of annual survival probabilities, 95% CI($\hat{S}_i$), of adult female Ross's Geese that hatched and failed to hatch eggs at the Karrak Lake colony, Queen Maud Gulf Migratory Bird Sanctuary, Nunavut, Canada, 2000-2003. Estimates are based on multistate models incorporating recoveries of dead birds.
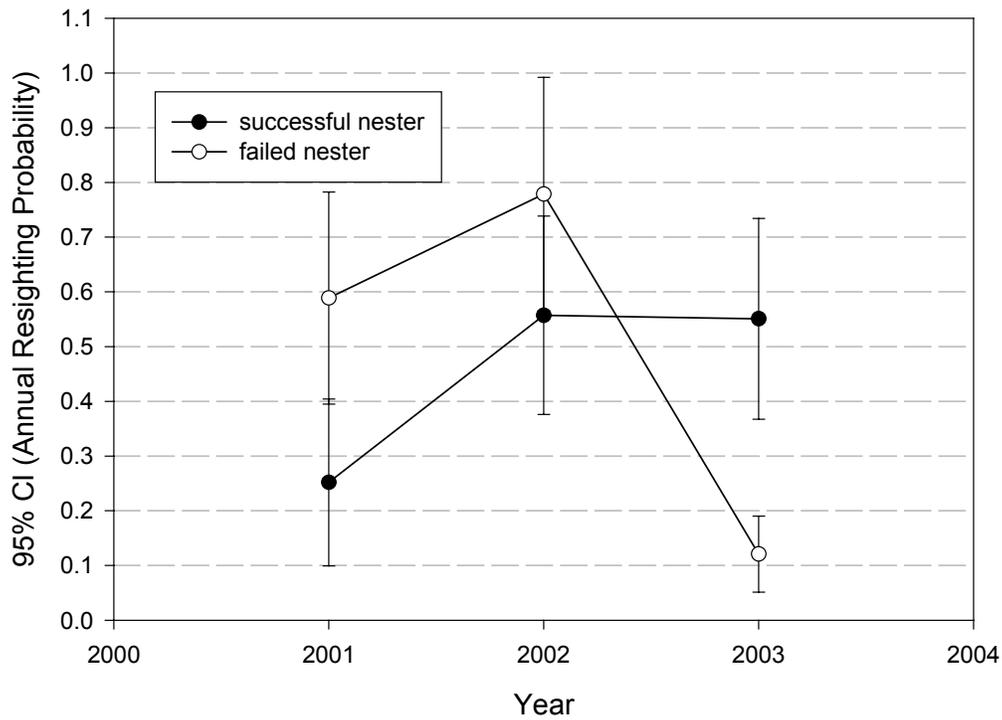
Fig. 4.2. Estimates of annual resighting probability, 95%CI($\hat{p}_i$), of female Ross's Geese following successful and failed nesting attempts at the Karrak Lake colony, Queen Maud Gulf Migratory Bird Sanctuary, Nunavut, Canada, 2000-2003. Results are from multistate models incorporating dead recoveries. Model-averaged parameter estimates are presented with 95% CI.

4.5 DISCUSSION

Although the costs of rearing precocial young have often been considered low (Winkler and Waters 1983, Rohwer 1992) and most evidence suggests that trade-offs are absent between current reproduction and future reproduction or survival in precocial species (Savard and Eadie 1989, Williams et al. 1994, Loonen et al. 1999, but see Milonoff et al. 2004, and Hartke et al. 2006), my results demonstrate a cost of reproduction to future survival of female Ross's Geese. In my comparison, successful and unsuccessful females should have had similar costs of egg laying, so the cost of reproduction likely arises from differences in terms of energetic costs of late incubation (~1 week) and brood rearing. I suggest that environmental conditions during nesting, and composition of individuals within the breeding population, are the most plausible factors responsible for annual variation in the magnitude of reproductive costs in female Ross's Geese.

Estimates of survival for successful nesting female Ross's Geese were consistently lower than those of failed nesters. Confidence in this inferred effect of breeding on survival was strengthened because I combined direct experimentation with modern methods of estimation that permit unbiased inference about survival. I also found weak support for a relationship between temperature during nesting and survival probability in the year following breeding in both successful and failed breeders. The difference in survival was more likely to be greater between groups when conditions were colder during incubation; thus any effects of temperature on survival were greater, i.e., during cooler years, on breeders than on failed nesters (Fig. 4.1). I found no relationship of survival to group-level covariates for timing of breeding or post-breeding age ratio prior to departing the arctic for fall migration. Contrary to my prediction, the observed pattern of survival suggested that survival declined in years of earlier nest initiation and increased when breeding was delayed. This pattern underscores a potential sampling limitation (discussed below), but considering that the number of geese nesting at Karrak Lake increases with earlier breeding (Alisauskas unpublished data), probably due to increased likelihood of breeding, then a cost of breeding to survival may more likely appear when incidence of breeding is greater. Survival of both groups was lower in years with earlier nest initiation (2001 and 2003), and the distance between point estimates of group-specific survival was greater in these years (Fig. 4.1).

These findings are consistent with the hypothesis that reproduction poses a trade-off that is expressed physiologically by increased mortality, and complemented my finding of a cost of reproduction on survival to adults that were not relieved of parental duty by means of experimental manipulation.

Detection of trade-offs between fitness components in wild populations can be difficult because environmental interactions can lead to positive correlation between life history traits (van Noordwijk and de Jong 1986). Furthermore, free-ranging populations often are composed of individuals that differ in quality, where 'good' individuals may outperform 'poor' individuals in several life history traits (Cam et al. 2002). Consequently, the ability to detect trade-offs is influenced by the degree to which the sampled population reflects true variation in individual quality found within the real population.

The extent to which a population of interest is sampled in proportion to its actual composition can be confounded by temporary emigration. For example, snow conditions on breeding areas can cause marked annual variation in probability of breeding by arctic-nesting geese (Reed et al. 2004). Considering that reproductive decisions are adjusted to body condition and migratory behavior in Greater Snow Geese (Bêty et al. 2004), it is likely that incidence of breeding increases as favorable nesting conditions develop earlier, as individuals are probably more apt to assume the risks of breeding. Reduced variation in individual quality within the sampled population would impede my ability to detect consistently annual evidence for a cost of breeding to survival if in some years the population of breeders consists primarily of good quality individuals. This is particularly pertinent when there is positive covariation between survival and breeding probability (Cam et al. 2002). In my study, sampling was restricted to the breeding population, as nonbreeders remained outside the colony in which my study area was located (Figure 3.2). I was unable to directly estimate breeding probability due to sampling limitations, but considering that survival alone cannot be responsible for the observed annual changes in population size of nesting geese at Karrak Lake (R. Alisauskas unpublished data), breeding probability of Ross's Geese likely varies markedly from year to year, as in other species of arctic-nesting geese (Reed et al. 2004, Sedinger et al. 2006). In years of lower breeding probability it

was possible that the sample was composed of better quality individuals representing a smaller range of individual quality than in a year when a larger fraction of the population bred. Thus, the cost of breeding may be more acute in years when breeding phenology is earlier because it seems reasonable that when conditions favorable to breeding develop earlier, the proportion of low quality individuals composing the breeding cohort will increase.

Reproductive costs may not necessarily involve a direct reduction in survival probability following reproduction, but instead could be expressed as reductions in breeding probability in the following year. In my capture-recapture study, nonbreeding represents a form of temporary emigration because nonbreeders do not remain at breeding colonies. Such temporary emigration from the study area without death is confounded with detection probability, and so would predictably result in reduced resighting probabilities. Thus, if successful nesting results in lower breeding probability relative to failed nesters in the following year, resighting probabilities may provide insight into biological processes. Viallefont et al. (1995) used such differences in recapture rates of Lesser Snow Geese to infer that age of first breeding directly affected the likelihood of nesting the following year, i.e., the cost of breeding was much more acute in younger birds.

In my study, lower resighting probability of successful nesting Ross's Geese in 2001 and the qualitatively similar result in 2002 (Fig. 4.2), is consistent with the prediction that successful nesting comes at a cost by lowering breeding probability in the following year. This pattern, however, did not persist in 2003 as resighting probability declined markedly for failed breeders. I could think of no methodological or biological reason why previous nest fate should influence detectability of marked Ross's Geese, given presence at Karrak Lake; hence, differences in group-specific resighting probabilities should have reflected differences in rates of emigration (or absence from the sample population). However, given that an animal is alive, emigration from my study area could result from nonbreeding, or from breeding outside the study area. I detected no difference in probability of moving to another breeding colony in a small sample of females for which I knew the fate of their previous breeding attempt (Chapter 3), but failed nesting increased distance of dispersal before Ross's

Geese nested in the same colony the following year (Chapter 3). Such increased propensity to move farther by failed nesters also may predispose failed nesters to leave the sample population at a greater rate than successful nesters, especially if the magnitude of the dispersal response to failed breeding increases with the number of failed breeding attempts an individual experiences. Because emigration from the sample population can result from nonbreeding or breeding dispersal, both resulting in lower resighting probability, I am precluded from making inference into biological process based on comparisons of group-specific resighting probabilities

   To my knowledge, this is the first study to detect reduced survival probability following successful production of offspring in geese. Successfully nesting females incurred a cost to survival, but contrary to my prediction, this cost did not appear to be related to increased vulnerability to hunting mortality. Failed nesters had a larger proportion of total mortality associated with hunting, and thus were more vulnerable to this mortality factor. Hence, the cost of breeding incurred by female Ross's Geese in this study, likely resulted from increased vulnerability to mortality factors other than hunting. This is an interesting result considering the benefits of social structure in geese. Goose families remain together at least until the beginning of reproduction the following year (Prevett and MacInnes 1980), and these social bonds result in a dominance hierarchy such that large goose families dominate smaller families, which in turn, dominate pairs and single geese (Boyd 1953, Hanson 1953, Raveling 1970, Gregoire and Ankney 1990). Dominance leads to acquisition and defense of food patches (Gregoire and Ankney 1990) and so presumably affords nutritional benefits to parents with young compared to adults without young. Results of my study suggest that the benefit of increased social dominance to females that have families may be offset, in part, by an increase in mortality to adult females.

CHAPTER 5. SURVIVAL OF ROSS'S GEESE: SEX DIFFERENCES, BREEDING CHRONOLOGY AND BREEDING LONGITUDE

5.1 ABSTRACT

I investigated sex differences, and the effects of timing of breeding, and longitude of capture on survival of Ross's Geese (*Chen rossii*), marked between 1991-2003, in the Queen Maud Gulf Migratory Bird Sanctuary, Nunavut, Canada. Based on (1) earlier evidence for apparent differences in affinity to winter areas by different breeding subpopulations, and (2) far higher limits to daily harvest by hunters in midcontinent flyways than in the Pacific flyway, I predicted that survival probability of Ross's Geese would decline from western to eastern breeding longitude. Contrary to my prediction, I could detect no such relationship. Overall, survival of adult females was 0.02 lower than that of adult males; thus, average longevity of adult females was only 80-89% that of adult males. Models that included timing of breeding in the parameterization of adult survival were better supported over those without, suggesting that timing of breeding has some influence on survival of adult geese. Consistent with other studies, I also found a strong negative relationship between timing of breeding and survival of juvenile Ross's Geese. In years when breeding was delayed, usually by late snowmelt, survival for corresponding cohorts of juvenile Ross's Geese was reduced. I estimated that annual survival of juveniles declined by ~0.02 each day that hatch was delayed.

5.2 INTRODUCTION

Anthropogenic influences can impose pressures on the life history of organisms different from those under which such species evolved. Human activity can induce continental or global changes in the distribution of habitats and associated resources. In turn, this can have large-scale effects on the distribution and abundance of free-ranging

wildlife populations. Additionally, direct exploitation of such populations by humans can affect vital rates whose dynamics over the annual cycle or geographic range of an animal may be vastly altered. To properly manage and conserve such exploited wildlife populations, a broad understanding of the geographic and temporal variation in vital rates should be a goal of applied wildlife biology. An excellent North American example of anthropogenic effects on free-ranging wildlife populations involves midcontinent Lesser Snow Geese (*Chen caerulescens caerulescens*, hereafter Snow Geese; Ankney 1996, Batt 1997, Jefferies et al. 2004a,b). Although a highly sought-after species by humans, numbers of snow geese have grown far above historic levels (Batt 1997). This unprecedented population growth has resulted in severe environmental degradation in some breeding areas (Batt 1997). The review by Batt (1997) led to recommendations for increased harvest with the objective of reducing population density on arctic breeding areas (Rockwell et al. 1997).

Major changes in management have been implemented to reduce the population of mid-continent Snow Geese. The main approach has been to encourage increased annual harvest. For example, season lengths and daily limits to harvest by individual hunters increased incrementally in the U.S. Central and Mississippi Flyways (hereafter midcontinent flyways) and Canadian Prairie Provinces during the 1990s. Hunting regulation were further liberalized in February 1999 under a special conservation order allowing harvest of light geese in U.S. midcontinent flyways between 10 March and 1 September, and special regulations in Canada permitted harvest of Snow Geese during spring and summer in Manitoba (beginning 1999) and Saskatchewan and Nunavut (beginning 2001). Although directed primarily at Snow Geese, these regulatory changes have potential to affect Ross's Goose (*C. rossii*, referred to collectively with Snow Geese as 'light geese') populations because harvest management of Ross's Geese is done in aggregate with Snow Geese (Moser and Duncan 2001), and Ross's Geese are now common in midcontinent flyways, where they overlap with the midcontinent Snow Goose population.

The continental population of Ross's Geese has increased dramatically in abundance, and expanded its distribution eastward (Dzubin 1965, McLandress 1979, Ryder and Alisauskas 1995, Moser 2001, Alisauskas et al. 2006a). Historically, Ross's

Geese wintered largely in California and occurred only rarely in the midcontinent before the 1970s (Bellrose 1976). Ross's Geese are now commonly sighted (Alisauskas 1998) and hunted (Alisauskas et al. 2006a) in the midcontinent region, far outside of their previous winter range. The affinity of Ross's Geese to eastern vs. western portions of this broadened winter range also corresponds somewhat with the longitude at which they are found during summer. For example, Ross's Geese marked in the western portion of the Queen Maud Gulf Migratory Bird Sanctuary (QMGMBS) are more likely to be recovered in the Pacific Flyway (71%) than those marked in the central (52%) or eastern (21%) parts of the Sanctuary (Alisauskas et al. 2006a). Hunting mortality of adult geese is largely additive to natural mortality (Francis et al. 1992, Gauthier et al. 2001, Alisauskas et al. 2006a), so the recent liberalization of opportunities for hunting light geese in midcontinent flyways that far exceeds those on traditional Ross's Goose winter areas in the Pacific Flyway may have resulted in geographic heterogeneity in survival rates. Spatial and temporal variation in adult survival can affect population dynamics, especially in long-lived organisms, such as Ross's Geese, where change in population size is usually most sensitive to adult survival (Lebreton and Clobert 1991, Rockwell et al. 1997, Alisauskas and Rockwell 2001). Such longitudinal clines in breeding distributions, winter distributions, and hunting pressure lead to a prediction of clinal variation in survival probability in Ross's Geese. Geese are highly mobile, however, and the strength of this prediction would be undermined by the frequency with which Ross's Geese change winter areas.

Knowledge about sex differences in energy demand and predation risk in arctic-nesting geese suggests the possibility of sex differences in survival. Metabolic costs are substantially greater for female geese than for males during the breeding season resulting in poorer female condition at the end of nesting relative to males (Ankney 1977, Ankney and MacInnes 1978, Ankney 1982). Recently, Samelius and Alisauskas (2006) estimated sex-specific probabilities of Snow Goose depredation by Arctic Fox and found that females faced a far greater probability of physical contact with these predators. Sex differences in energetics, behavior, and predation risk associated with reproduction predict reduced survival of female Ross's Geese compared to males. Resulting differences could have important consequences on population models of

Ross's Geese, which are important for proper conservation and management. Although sex differences in survival of adult ducks are obvious (Johnson et al. 1992), most previous studies of geese have reported similar probabilities of annual survival for both sexes (Samuel et al. 1990, Francis and Cooke 1992b, Ward et al. 1997, Menu et al. 2002). In Chapter 4, I provided evidence that successful nesters survived at lower rates than did failed nesters, and that the strength of this effect varied annually. Herein, I was interested to test the prediction of diminished survival of female Ross's Geese in relation to males.

In addition to a prediction of lower survival among females compared to males, several lines of evidence suggest that sex difference in mortality of arctic-nesting geese should be greater when breeding is delayed. Survival of adult females is related to body condition (Schmutz and Ely 1999), and ability to restore condition is likely influenced by the time available between hatch and southward migration (Raveling et al. 1992, Schmutz et al. 1994, Schmutz and Ely 1999); thus, in addition to sex differences, survival probability may be compromised by delays in annual breeding schedules. Previous research on breeding chronology in arctic-nesting geese focused on its influence on recruitment (e.g., Cooch 2002, Slattery and Alisauskas 2002, Alisauskas 2002) through combined effects of timing of fledging, breeding propensity, clutch size, nest success and gosling survival. Instead, I was interested in the role that delays in reproduction, brought on largely by delayed arctic snowmelt, might play as an influence on adult survival in arctic-nesting geese. I reasoned that further stratification by sex of heterogeneity in adult survival could lead to (1) increased precision of estimates and improved ability to offer management prescriptions, while also (2) contributing to our general understanding of population dynamics in arctic-nesting geese.

I tested whether the location where geese were captured on the breeding grounds played a role in heterogeneity of annual survival rate in Ross's Geese. Survival of adult geese declines as harvest increases (Francis et al. 1992, Gauthier et al. 2001, Alisauskas et al. 2006a); thus, I predicted that survival probability of Ross's Geese would decline with longitude of banding (i.e., from west to east) in response to a presumed cline in harvest pressure. I also examined whether survival differed between sexes; such a difference has relevance to (1) lifetime reproductive success, and thus (2) proper

construction of population models for Ross's Geese. Lastly, I tested the hypothesis that adult survival declines when breeding is delayed.

5.3 METHODS

5.3.1 Data

I used data from goose banding efforts 1991-2003. Juvenile geese were not marked with neckbands during 1991-1993 or 2002. Ross's Geese were captured on brood-rearing areas about 4 weeks after they dispersed from highly insular breeding colonies, so I did not know with certainty the breeding colony occupied that year. Nevertheless, Ross's Geese generally moved north, within days of hatch, to brood-rearing areas adjacent to nesting colonies (Slattery 2000). So, for example, it is reasonable to assume that geese captured in the region north of Karrak Lake originated from a colony in the vicinity of Karrak Lake (i.e. within 30 km; Slattery 1994) in the year of marking, and not from the other two sampled regions (i.e., Perry River 85 km to the west, or McNaughton River 100 km to the east). A longitudinal correspondence between summer banding locations and migration and wintering locations suggests that the probability of a Ross's Goose using a midcontinent flyway increases as longitude of banding location declines (Alisauskas et al. 2006a). Thus, I used longitude at which geese were first captured as a continuous individual covariate.

5.3.2 Analysis

I obtained recovery information from the Bird Banding Laboratory and considered only geese that were shot by hunters or researchers. Data were formatted into individual encounter histories so that longitude of banding could be included as an individual covariate. I used the band recovery models of Brownie et al. (1985) as implemented in Program MARK to estimate annual survival, S_i, and recovery, f_i, probabilities. I used age-structured models to accommodate the transition of juvenile birds (or hatch-year [HY]) to adult birds (or after hatch-year [AHY]) during the interval following banding. One-year intervals begin at the midpoint of banding in year t until the midpoint of banding in year $t + 1$. I constrained Program MARK to not estimate S_i or f_i of neckbanded goslings for years when none were marked. Thus, the global model

{S $_{A\ (LB[s*t]\ *\ NB[s*t])\ *\ J\ (LB[s*t]\ *\ NB[s*t])}$ f $_{A\ (LB[s*t]\ *\ NB[s*t])\ *\ J\ (LB[s*t]\ *\ NB[s*t])}$} had 184 estimable

parameters instead of 200, where 'A' and 'J' represent AHY and HY age-classes,

respectively, 'LB' and 'NB' refer to marker type (legband only vs. neckband plus

legband), 's' represents sex, and 't' represents time (year). I assessed goodness-of-fit of

the global model using the median $\hat{c}$ test in Program MARK and applied a variance

inflation factor ($\hat{c} = 1.198 \pm 0.043$ SE) to correct for possible overdispersion and to

adjust variance estimates of $\hat{S}_i$ and $\hat{f}_i$.

Model selection was based on minimization of AIC$_c$ after adjusting values for

overdispersion (QAIC$_c$; Burnham and Anderson 2002). I assessed the relative

plausibility of each model by comparing differences between the QAIC$_c$ value for the

best model and values for all other models (ΔQAIC$_c$), and by comparing Akaike model

weights (Burnham and Anderson 2002). Akaike weights (w_i) sum to 1, and w_i provides

a measure of the support for model i given the data and the set of models. Models with

ΔQAIC$_c$ ≤2 were included in the confidence set of best models (Burnham and Anderson

2002). I considered models where survival and recovery rate parameters were

constrained to be equal over potential sources of variation such as sex and time, but I

maintained marker and age structure in all models because neckbands are known to

influence survival (Schmutz and Morse 2000, Alisauskas and Lindberg 2002,

Alisauskas et al. 2006a), and because survival and recovery probabilities commonly

vary by age-class in geese and most other vertebrates. As alternatives to interacting

main effects on both S_i and f_i, I considered additive models with parallelism in effects

on S_i and f_i over time. Because my interest was primarily in survival, I sequentially

constrained parameters in a hierarchy of models by first testing time and sex effects as

sources of variation in recovery rates, and then used the best parameterization of

recovery when testing for effects on survival. An earlier analysis based in part on the

same banded sample of Ross's Geese (Alisauskas et al. 2006a) found strong support for

models that considered temporal variation in age-specific S_i as either linear time trends,

S_T, or as a function of age-specific annual harvest as a group covariate, S_H; thus, I

included models with these parameterizations when evaluating temporal variation in S_i

and f_i. I followed the approach used by Alisauskas et al. (2006a) for estimating total

annual harvest of Ross's Geese for each age class. I investigated the effect of timing of

breeding on survival by including mean nest initiation date at Karrak Lake (Alisauskas unpublished data), denoted as 'NID' in model notation, as a year-specific covariate to explain temporal variability in S_i. I predicted that survival of HY geese would decline with later nest initiation because timing of hatch is a major source of variation in gosling growth and development (Cooch et al. 1991b, Sedinger and Flint 1991, Lepage et al. 1999), and first-year survival of Snow Goose goslings hatched in late years is lower than those hatched in early years (Francis et al. 1992). The predicted relationship between survival of adult geese and NID is less clear. On one hand, I might expect a negative relationship if later NID results in adult geese completing the nesting period in poorer condition relative to earlier years and this leads to increased vulnerability to mortality factors (i.e., a cost of breeding). Alternatively, environmental conditions that bring about delayed nesting may also reduce breeding probability, and reduce the proportion of the population incurring physiological costs of breeding. I used the structure of the best approximating model when assessing longitude of banding (BLON) as an individual covariate explaining variation in survival probability. Hence, I assessed fit of three models wherein (1) slopes between the covariate BLON and various combinations of age and marker type were different, (2) slopes were parallel between marker types but not ages, or (3) slopes were parallel between all 4 combinations of age and marker type.

5.4 RESULTS

Numbers of geese captured and marked during 1991-2003 were: 10,412 adults with legbands, 12,996 adults with neckbands, 11,452 goslings with legbands, and 3,370 goslings with neckbands of which 661, 1,074, 718, and 319, respectively, were shot and reported to the Bird Banding Laboratory until the end of the 2002/2003 hunting season. Although the adult sample included some subadults and adult nonbreeders, most of the adults in this sample had attempted to breed in the year of their capture (i.e., ~95% of AHY females captured during 1999-2003 had a visible brood patch). I considered 75 models with survival and recovery probabilities structured by age, marker type, sex, and time. Before assessing the effect of BLON on $\hat{S}_i$, Akaike weight of the best model {S $_A$ (LB[s+NID+H] * NB[s+NID+H]) * J (LB[NID] * NB[NID]) f $_A$ (LB[s+t] + NB[t]) * J (LB[s+t] + NB[t])} was 0.912, and

support for this model was ~33.5 times (0.912/0.027) that of the next best model; thus, I used the structure of this model when testing the effect of the individual covariate BLON. Cumulative weight of the top three models was 0.977, and aside from the presence of BLON in two of these, parameterization of all other effects on survival and recovery was the same (Table 5.1). There was sufficient difference in model quality between the best two models (ΔQAIC$_c$ = 3.20), so estimates of survival and recovery were based on the best model.

Recovery probability varied in an additive manner between marker types within the age-classes and generally increased over the course of the study (Fig. 5.1). There was considerable uncertainty about how to proceed with the inclusion of sex effects on recovery, but when sex effects on recovery were removed from all combinations of age and marker types, model quality declined substantially (ΔQAIC$_c$ = 117.98). There was equal support for seven models (i.e., within <1 ΔQAIC$_c$ unit) that included a sex effect on f_i, albeit in different combinations of age and marker types; thus, I based the inclusion of sex effects within each age-class and marker type on the relative support from these models. Sex effects on f_i were most supported for legbanded adults ($\Sigma\omega_{QAICc}$ = 0.740) and juveniles ($\Sigma\omega_{QAICc}$ = 0.738), and less so for neckbanded adults ($\Sigma\omega_{QAICc}$ = 0.161) and juveniles ($\Sigma\omega_{QAICc}$ = 0.536); therefore, I retained sex effects on f_i of legbanded birds only, and then used this parameterization of recovery {i.e., f $_{A\ (LB[s+t]\ +\ NB[t])\ *\ J\ (LB[s+t]\ +\ NB[t])}$} in subsequent models when evaluating effects on survival. Although inclusion of sex effects on f_i^{LB} improved model fit, confidence intervals around the slope estimate for sex effect included both positive and negative values (95%CI($\hat{\beta}_{SEX}$) = -0.061 ± 0.119 on a logit scale). There were no differences in annual recovery rates between males and females (Fig. 5.1). There was no support for models for which recovery probability of adults or juveniles was constrained to be a function of harvest or longitude of banding.

Annual variation in S_i^{AHY} was best parameterized with combined effects of annual harvest and nest initiation date, whereas annual variation in S_i^{HY} was modeled best as a function of nest initiation date only. Within marker type, survival of adults

Table 5.1. Model selection results for effects of age (after hatch year vs. hatch year), sex, marker (legband [LB] or neckband with legband [NB]), and year, on survival (S) and recovery (f) probabilities of Ross's Geese marked as either adults (A) or juveniles (J) within the Queen Maud Gulf Migratory Bird Sanctuary, Nunavut, Canada, 1991-2003. Only shown are models having a model weight > 0 and the most general model from a candidate set of 75 models (variance inflation factor, $\hat{c} = 1.198$). Shown for each model are: deviance, quasi-AIC difference corrected for small sample size (ΔQAIC$_c$), model weight (*w*), and number of parameters (*K*). Model notation represents estimates stratified by age (S_A or S_J) and marker (LB or NB), with effects of sex (s), annual harvest (H), nest initiation date (NID), linear time trend (T), temporal variation by time (t), and an individual covariate longitude of banding (BLON). Asterisks denote multiplicative interactions among specified effects, whereas a plus sign denotes parallelism between effects. 'Global' denotes the most parameterized model.

Model	Quasi-Deviance	ΔQAIC$_c$	*w*	*K*
S_A (LB [s+H+NID] * NB [s+H+NID]) * J (LB [NID] * NB [NID]) f_A (LB [s+t] + NB [t]) * J (LB [s+t] + NB [t])	22293.59	0.00	0.729	27
S_A ((LB [s+H+NID] * NB [s+H+NID])+BLON) * J ((LB [NID] * NB [NID])+BLON) f_A (LB [s+t] + NB [t]) * J (LB [s+t] + NB [t])	22292.79	3.20	0.147	29
S_A (LB [s+H+NID+BLON] * NB [s+H+NID+BLON]) * J (LB [NID+BLON] * NB [NID+BLON]) f_A (LB [s+t] + NB [t]) * J (LB [s+t] + NB [t])	22291.52	3.94	0.102	30
S_A (LB [s+NID] * NB [s+NID]) * J (LB [NID] * NB [NID]) f_A (LB [s+t] + NB [t]) * J (LB [s+t] + [NB+t])	22300.61	7.02	0.022	27
S_A (LB [s+H] * NB [s+NID] * J (LB [T] * NB [T]) f_A (LB [s+t] + NB [t]) * J (LB [s+t] + NB [t])	22297.17	13.59	0.001	32
S_A (LB [s*t] * NB [s*t]) * J (LB [s*t] * NB [s*t]) f_A (LB [s*t] * NB [s*t]) * J (LB [s*t] * NB [s*t]) Global	22364.03	329.68	0.000	156

Fig. 5.1. Estimates of annual recovery probabilities, 95% CI($\hat{f}_i$), of Ross's Geese marked in the Queen Maud Gulf Migratory Bird Sanctuary, Nunavut, Canada, 1991-2003, as adults (AHY) or goslings (HY), with either legbands only (LB) or also with neckbands (NB). Sex effects on recovery probability were not supported for neckbanded birds. Estimates derive from the most parsimonious model based on QAIC$_c$ model selection.

varied in parallel between the sexes, but there was no parallelism between age-classes or marker types over time (Fig. 5.2). Inclusion of sex as an effect on S_i^{AHY} improved model fit, and overall adult females survived at a lower rate than males (95%CI($\hat{\beta}_{SEX}^{AHY}$) = -0.257 ± 0.157 on a logit scale). There were no annual differences in survival estimates of males and females as confidence intervals overlapped considerably for annual estimates, but the reciprocal of the logit transformation,

$$\left(\frac{e^{-3.882}}{\left(1 + e^{-3.882}\right)} \right), \qquad\qquad \text{Equation 5.1}$$

showed that, overall, adult females survive at a rate 0.020 ± 0.019 lower than that of adult males. Sex effects on S_i^{HY} were not supported by the data. Inclusion of NID as an effect on survival improved model fit, but the effect of NID on survival was equivocal for adults having either marker type (95%CI($\hat{\beta}_{NID}^{LB}$) = -0.047 ± 0.203 and ($\hat{\beta}_{NID}^{NB}$) = 0.035 ± 0.051), and for HY birds marked with neckbands (95%CI($\hat{\beta}_{NID}^{NB}$) = 0.018 ± 0.140), as estimated coefficients were imprecise and confidence intervals included both positive and negative values. As expected, survival declined with later NID in HY birds marked with legbands (95%CL($\hat{\beta}_{NID}^{LB}$) = -0.069 ± 0.066); the reciprocal of the logit transformation, $\left(\frac{e^{-3.695}}{\left(1 + e^{-3.695}\right)} \right)$, provided an estimate of a daily decline in HY survival of ~0.021 per day for every day that hatch was delayed. Annual survival of adults was negatively related to adult harvest, but this relationship was weaker for adults marked with legbands compared to those marked with neckbands (95%CI($\hat{\beta}_{H}^{LB}$) = -1.728 ± 2.902 and ($\hat{\beta}_{H}^{NB}$) = -1.682 ± 1.272). Although longitude of banding, was included in two of the top three models, its effect on survival was equivocal; estimates for slopes of survival in relation to longitude were (95%CI($\hat{\beta}_{BLON}^{AHY}$) = 0.059 ± 0.133 and ($\hat{\beta}_{BLON}^{HY}$) = -0.039 ± 0.248).
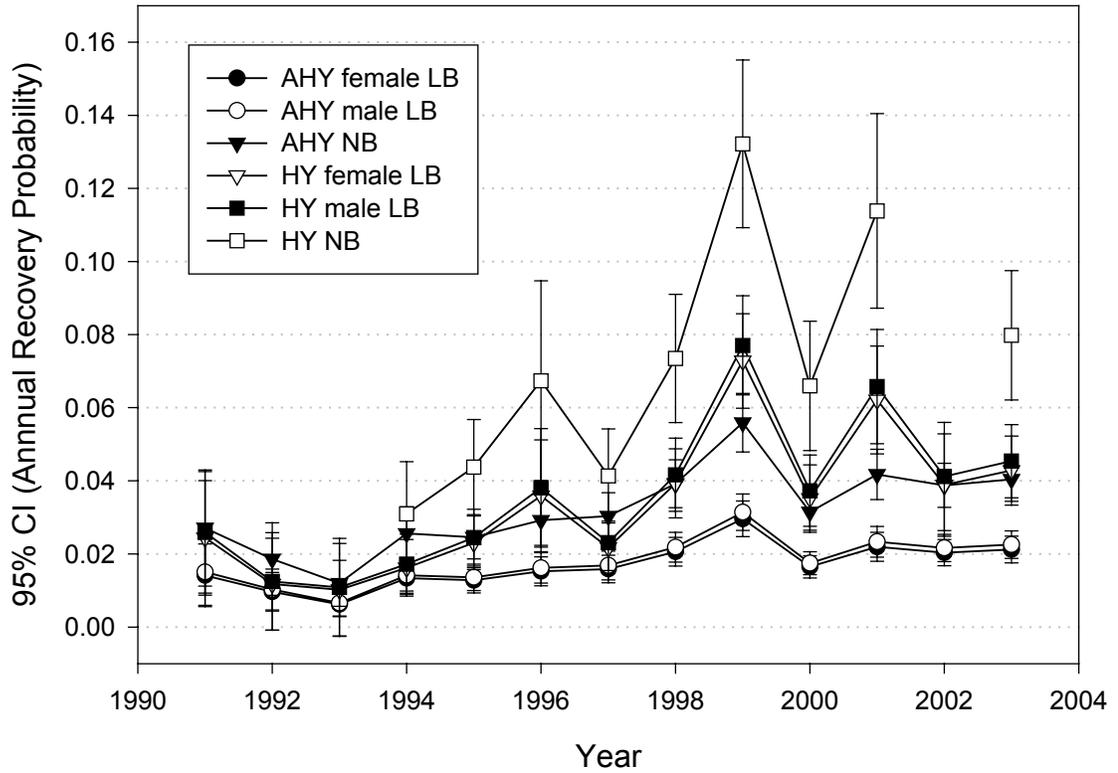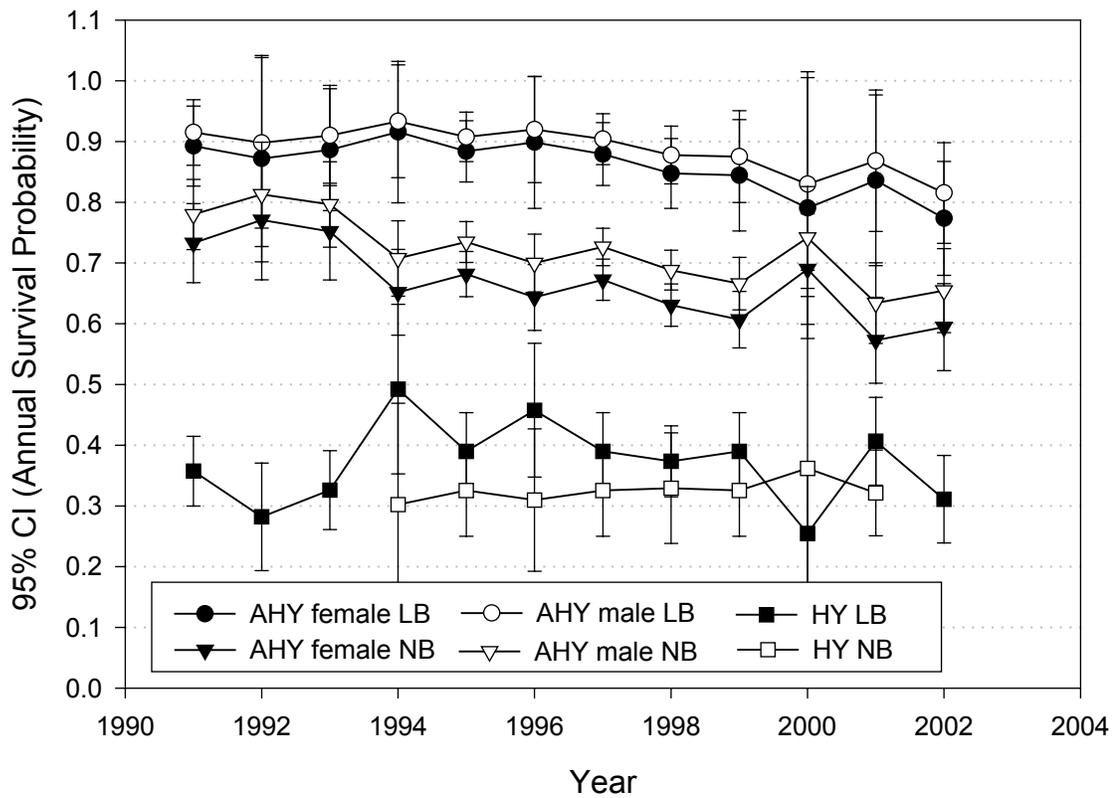
Fig. 5.2. Estimates of annual survival probabilities, 95% CI($\hat{S}_i$), of Ross's Geese marked in the Queen Maud Gulf Migratory Bird Sanctuary, Nunavut, Canada, 1991-2003, as adults (AHY) or goslings (HY), with either legbands only (LB) or also with neckbands (NB). Estimates derive from the most parsimonious model based on QAIC$_c$ model selection.

5.5 DISCUSSION

  I predicted that survival probability of Ross's Geese should decline from western to eastern longitudes of banding within QMGMBS because (1) Ross's Geese marked in the eastern QMGMBS tend to be recovered at a much higher proportion in the midcontinent than those marked in the western part of the sanctuary (Alisauskas et al. 2006a), (2) harvest has increased in the midcontinent such that, for the past several years, ≥75% of the U.S. harvest of Ross's Geese has occurred in the midcontinent region (Kruse et al. 2005), and (3) harvest mortality generally is additive to natural mortality in adult geese (Francis et al. 1992, Gauthier et al. 2001, Alisauskas et al. 2006a). Nonetheless, longitude at which Ross's Geese were banded in the QMGMBS did not influence survival probability, so increased harvest in midcontinent flyways does not appear to have resulted in differential survival among major colonies of Ross's Geese in the QMGMBS. This result is consistent with findings of equal rates of apparent survival among breeding populations (Chapter 2, Drake and Alisauskas 2004).

  Although estimates of harvest rate (i.e., the proportion of birds alive at the beginning of the hunting season that are shot and retrieved during that same hunting season) for North American geese are absent (but see Gauthier et al. 2001), hunting regulations represent an attempt to produce a desired rate of harvest, or at least change the harvest rate in a specified direction. Indeed, increases in bag and possession limits within midcontinent flyways have resulted in greater harvest of Ross's Geese, and of light geese in general (Kruse et al. 2005). Correspondingly, survival of adult Ross's Geese has declined with increased harvest (Alisauskas et al. 2006a), although results herein suggest that this relationship exists only for neckbanded adults. Yet, consistent with Alisauskas et al. (2006a), survival in Ross's Geese overall appears to have continued to decline. Despite increased harvest (H), harvest rate $\hat{h} = \dfrac{\hat{H}}{\hat{N}}$, may not have changed, or even may have declined, because the continental population of Ross's Geese has continued to increase at the same time. Additionally, co-occurrence of Ross's Geese in the midcontinent with far more numerous Snow Geese may dilute harvest pressure on midcontinent Ross's Geese compared to those that migrate and winter in the Pacific Flyway. Estimates of harvest rates of arctic-breeding geese are unavailable, but

if reporting rate (λ) is constant, then recovery rate (f) should reflect harvest rate because $f = h\lambda$. Assuming constant reporting rates, the slight increase in recovery rates of Ross's Geese during this study could be interpreted as evidence for a continental increase in harvest rate. But this interpretation of recovery rate should be viewed with caution because reporting rate can vary geographically (Henny and Burnham 1976, Nichols et al. 1995), and the implementation of 1-800 legbands in 1995 likely has had the intended result of increasing reporting rates. Hence, proportional differences in recoveries of Ross's Geese in each flyway (Alisauskas et al. 2006a) may have arisen from differences in harvest rate and/or changes in reporting rate. If reporting rate changed with implementation of 1-800 legbands, this could easily have confounded any relationship between f and H. A study aimed at estimating band reporting rates of arctic-nesting geese is currently underway and preliminary evidence suggests that band reporting rate is higher in the Mississippi Flyway than elsewhere for migrant Canada Geese (*Branta canadensis*) (T. Moser personal communication). If this preliminary finding applies to Ross's Geese, then the east-west gradient in proportions of recoveries in migratory flyways may not reflect differences in harvest rate among flyways.

I think that longitude of capture in the Arctic is a reasonable indicator of breeding subpopulation in the year of marking. However, its long-term utility may be compromised by the frequent exchange of Ross's Geese among breeding populations and perhaps between winter areas. At the two largest colonies that serve as the major source of birds in the sampled areas, probability of breeding dispersal by females was > 0.11 (Drake and Alisauskas 2004); some individual Ross's Geese were known to have switched nesting colonies in three consecutive breeding attempts (Drake unpublished data). Thus, capture location is not necessarily a reliable indicator of previous or future breeding location. Good estimates of winter philopatry in geese are generally absent (Robertson and Cooke 1999), but in the case where it has been adequately addressed, Canada Geese exhibited considerable movement between large geographic regions (Hestbeck et al. 1991). Considering the adaptive nature of light geese, illustrated by their proclivity to expand range and exploit new habitats (Alisauskas et al. 1988, Alisauskas 1998), and the continual increase in numbers of Ross's Geese found in midcontinent flyways (Alisauskas 1998), I suspect that there is substantial movement of

individuals among winter areas in the same flyways, and potentially among different flyways. Such movement was responsible for the large-scale eastward expansion in winter range into the midcontinent by Ross's Geese (Alisauskas et al. 2006a). Although there exists a geographic pattern of recoveries of migrating and wintering Ross's Geese related to their longitude of capture in the Arctic, there is probably sufficient movement among subpopulations to confound the ability to detect differences in survival. As well, mate loss followed by remating, both of which very likely have increased more recently with increased harvest of Ross's Geese across North America (Alisauskas et al. 2006a), may contribute to additional movement. Variation among colonies in migration routes (Francis and Cooke 1992a) has potential to result in subpopulation survival differences if risk of mortality varies spatially and philopatry persists; however, considering overlap in migration routes (Alisauskas et al. 2006a) and the current level of mixing among breeding colonies (Chapter 2, Drake and Alisauskas 2004) by geese that winter in different flyways, movement may have been sufficiently high to confound detection of heterogeneity in survival among breeding subpopulations.

Bi-parental care and maintenance of long-term pair bonds throughout the annual cycle are life history characteristics of geese that expose both sexes to similar mortality risks. Consequently, some mortality factors (especially hunting) probably do not act independently on each member of a pair (Prevett and MacInnes 1980). Hence, even if survival differs between sexes in adult geese, the difference is likely to be small, difficult to detect on an annual basis, and probably confined to certain periods of the annual cycle (Schmutz et. 1994, Schmutz and Ely 1999). Using composite Z-statistics, Francis and Cooke (1992b) found sexual differences in survival and recovery rates in 5 of 10 data sets for adult Snow Geese; there was some suggestion that female Snow Geese had slightly lower survival than males, but because this difference was small relative to total adult mortality, they concluded that mortality was mainly due to factors independent of sex. My data supported models that included a sex effect in the parameterization of survival of adult Ross's Geese, and my findings were similar to those of Francis and Cooke's (1992b) in that the sexual difference that we found is small relative to total mortality. I was unable to detect annual differences in sex-specific survival (Fig. 5.2), but overall, adult females survived at a lower rate than adult males.

For long-lived waterfowl such as Ross's Geese, even small differences in survival can project to marked differences in average lifespan. For example, using the lowest estimate (0.815) for survival of legbanded adult males I calculate an average lifespan of

$$\left(\frac{1}{-\ln(0.815)}\right) = 4.89 \text{ years.} \hspace{3cm} \text{Equation 5.2}$$

Subtracting 0.02 from the survival rate of legbanded males and recalculating an average lifespan for adult females shows that their longevity is expected to be 4.36 years, or only ~89% of the mean lifespan of adult males. The same calculations with the highest estimate (0.915) for survival of legbanded adult males lead to a difference in adult lifespan of 2.24 years between sexes; adult females in this case would live only 80% as long as adult males, on average. The effect of such apparently small sex differences in survival of 0.02 resulting in a 0.11 to 0.20 difference in longevity has potential to greatly alter sex-specific expectations of lifetime reproductive success, especially when survival rates are high (>0.90). A sex difference in lifetime reproductive success could attenuate somewhat because geese are monogamous, and members of the surplus sex that result from sex differences in adult survival would have a higher probability of nonbreeding; nevertheless, this should result in an unequal sex ratio favoring males.

I speculate that sexual differences in physiological costs associated with reproduction, and increased mortality suffered by nesting females are the most likely causes of differential survival between the sexes. Nutritional ecology during winter and migration is similar between sexes of Snow Geese (Alisauskas et al. 1988, Alisauskas and Ankney 1992), but metabolic costs are substantially greater for females during the breeding period resulting in poorer condition at the end of the nesting period relative to males (Ankney 1977, Ankney and MacInnes 1978, Ankney 1982). Incubating females can even deplete nutrient reserves to the point of starvation (Harvey 1971, Ankney 1975, 1976). The sex difference in body condition after breeding likely varies annually because environmental conditions during breeding can fluctuate markedly from year to year. For example, cold and windy conditions increase energy expenditure. In addition, during years when breeding is delayed and/or freeze-up occurs early, time available for restoring body condition will be shortened before conditions on breeding areas motivate southward migration. Other than my results in Chapter 4, I am unaware of any studies

that demonstrate a direct negative effect of breeding on survival of adult female geese; nevertheless, (1) survival of adult females increases with body condition (Schmutz and Ely 1999), and (2) females appear to be most vulnerable during the period following reproduction (Raveling et al. 1992, Schmutz et al. 1994, Schmutz and Ely 1999). So, I suggest that costs related to breeding provide the most plausible explanation for the overall sex difference in survival of Ross's Geese.

I did not find unequivocal evidence for a relationship between survival of adults and NID, but models that included NID in the parameterization of survival were favored over those without NID, suggesting that annual variation in mean NID accounts for some of the annual variation in survival of adult Ross's Geese. Ideally, an investigation of the potential for timing of breeding to influence variability in survival should be based on marked individuals for whom this variable is known; for most investigations of arctic-nesting geese, this is not feasible. As such, I used NID as a year-specific covariate to assess the potential for timing of breeding to explain annual variability in survival at the aggregate level. I used estimates of NID that were calculated from data collected at one of the two largest colonies in the Sanctuary (located in the western portion of the sanctuary), so they serve only as an index for breeding chronology for the greater metapopulation. This is because I included individuals from different colonies in my analysis, and mean NID may have varied among colonies due to a longitudinal cline in chronology of snowmelt; such a cline is consistently present each spring, and occurs earlier in the western portion of the Sanctuary compared to that 300 km to east (R. Alisauskas personal observation). Inclusion of an undetermined number of nonbreeders in the capture data likely further confounded my ability to detect an effect of timing of breeding on survival. Capture efforts generally focused on brood-rearing flocks, but such flocks could have included nonbreeders. Although I was unable to quantify the number of nonbreeders captured for each year included in this study, >95% of AHY females captured during 1999-2003 had a brood patch and the protocol for capture efforts has remained consistent for the duration of the study; thus, most of the adult birds included in this analysis had made an attempt to breed in the year of their marking.

Most (~95%) Ross's Geese breed within the QMGMBS (Kerbes 1994, Ryder and Alisauskas 1995), so my aggregate level analysis permits inference about the effect

of breeding chronology on gosling survival at the metapopulation level. Breeding seasons of the Queen Maud Gulf (QMG) metapopulation that were delayed, usually by late snowmelt, clearly reduced survival for corresponding cohorts of juvenile Ross's Geese. This result is consistent with findings that late-hatching goslings are structurally smaller and lighter for a given age than earlier-hatching gosling (Cooch et al. 1991b, Sedinger and Flint 1991, Lepage et al. 1999), and show lower rates of survival than earlier hatching goslings from the same cohort (Sedinger et al. 1995, Slattery 2000, Cooch 2002, Slattery and Alisauskas 2002, Hill et al. 2003). I estimate that survival of juvenile Ross's Geese declined ~0.021 per day, so that a mere 5-day delay in mean nest initiation results in a cohort-level decline of ~0.10 (i.e., 0.979^5) in offspring survival. Reduced offspring survival may act as a strong selection pressure favoring flexible nest site selection, especially if flexibility results in earlier breeding. Landscape level dispersal by adult Ross's Geese is not related to previous breeding experience (Chapter 3), but instead may be motivated by habitat availability as influenced by rates of snowmelt. A west-east cline in snowmelt exists within the QMG region, and so NID is likely to vary geographically, with earlier breeding in the western portions of the Sanctuary. Within the QMG region, this may favor westward adult dispersal, and would be consistent with my earlier finding of asymmetrical (i.e. westward) movement among QMG colonies of Ross's Geese (Chapter 2, Drake and Alisauskas 2004).

I suspect that my inability to detect an effect of mean NID on annual survival of juvenile birds marked with neckbands may have been related to non-random sampling of goslings in late years. Juvenile geese must be large enough at capture to ensure that neckbands of constant size cannot slip over the head. However, the proportion of goslings with heads large enough to prevent neckband loss declines dramatically in years when nesting is delayed, resulting in a sample representative of only the largest goslings in such years. Furthermore, even in early or average years, neckbanded goslings represent a biased sample of larger goslings that do not include the full range in gosling size present in the population.

CHAPTER 6. THE ROLE OF MOVEMENT: A SYNTHESIS

Movement of individuals among populations has the potential to affect the distribution and size of populations; thus, estimation of dispersal probability is necessary to understand its influence on local and metapopulation dynamics. A portion of my research involved estimating rates of movement and survival to further our understanding of the potential for movement to influence population dynamics of breeding Ross's Geese (*Chen rossii*), and to account for movement in future population modeling efforts. I also investigated the potential for breeding dispersal to result from decision rules by conducting an experimental manipulation of nest success, and I examined a potential trade-off between current reproduction and future survival.

6.1 BREEDING DISPERSAL

My results demonstrated that the movement of Ross's Geese among Queen Maud Gulf (QMG) breeding colonies involved tens of thousands of birds moving each year from one breeding colony to another. Quantitative inference from my study is restricted to the QMG colonies that I sampled, but there existed substantial immigration into my QMG study area: a fifth of the geese in my sample were known immigrants that were marked along the West Coast of Hudson Bay (WHB). Immigration from WHB was male-biased, but a nontrivial proportion of breeding females also moved to new colonies. Rates of exchange of light geese between the QMG region and other breeding areas in the eastern arctic currently are unknown. But during 1999-2004, sightings of neckbanded Lesser Snow Geese (*C. caerulescens caerulescens*) from the eastern arctic also increased within the QMG region (Drake unpublished data), partly because of increased efforts to mark Snow Geese. Most eastern arctic Snow Geese sighted in the QMG region were males, but female immigration to the QMG also occurred. I speculate

that the exchange of females among breeding subpopulations encompasses the entire breeding region of Ross's Geese; this might also be the case for the midcontinent population of Lesser Snow Geese.

Breeding failure appeared to influence breeding dispersal of Ross's Geese, but only on a local scale (Chapter 3); breeding failure did not appear to influence long distance dispersal in a small sample of females ($n = 15$) whose nest fate, and subsequent dispersal to another colony, were known. It is unknown to what extent multiple experiences factor into dispersal decisions (or decisions about other life history characteristics) by individuals, but long-lived species are likely to rely upon an accumulation of information from several years of experience.

The motivation for long distance (between colony) dispersal in Ross's Geese remains unknown, but it might be linked to knowledge about other locations with suitable breeding habitat. In their review of family structure in Snow Geese, Prevett and MacInnes (1980) suggested that goslings learn migration and winter locations from parents. Breeding pairs often are accompanied to breeding areas by their surviving offspring from the previous year, but as egg-laying begins, families break up (Prevett and MacInnes 1980). By incubation, yearlings generally join flocks of other nonbreeders or failed breeders, these birds undergo molt prior to southward migration to wintering areas. In many species of waterfowl, segments of the population migrate northward from their breeding grounds to undergo summer molt (Salomonsen 1968, Davis et al. 1985, Abraham et al. 1999). Abraham (1980) recognized that molt migration by nonbreeding geese might function as prospecting behavior, whereby new areas of suitable breeding habitat are encountered; Abraham speculated that molt migration rarely resulted in permanent emigration by females. Ross's Geese breeding in the QMG region are at the terminus of their breeding range, so further northward migration related to molt is not likely to occur. Rather, nonbreeding flocks of light geese (which presumably also include failed breeders) probably remain in the QMG region; during transit of personnel to sampled breeding colonies (K. Drake) and during aerial transects that covered a larger portion of the Sanctuary (R. Alisauskas personal observation) flocks ranging from <10 to several hundred birds were commonly observed. Most Ross's Geese probably do not make their first breeding attempt until ≥3

years old (Drake unpublished data), which ensures that most reproductively mature adults will have spent at least two summer on the breeding grounds without being attached to a nest. Delayed sexual maturity, breeding failure, or opting out of breeding in one year presents an opportunity to gather information that might be used at some point in the future. These birds are free to move about, and while they search for food, they likely discover the locations of other breeding colonies and suitable brood-rearing areas. It is unknown the extent to which geese gather and use information obtained while on the breeding grounds as a nonbreeder (or failed breeder), but the proclivity to disperse to another breeding colony might increase with knowledge of alternative breeding sites.

The interplay between variation in habitat availability, stage of follicular development by females, and social status of pairs ensures that some degree of dispersal occurs between successive nesting attempts by arctic-nesting geese. Lindberg and Sedinger (1997) found little evidence that fidelity to nest sites by Black Brant (*Branta bernicla nigricans*) was adaptive and concluded that geese were not likely to delay breeding to maintain fidelity to the nest site they had used in the previous year. Similarly, dispersal distance of Snow Geese at La Pérouse Bay was not correlated with age, status of pair bond, or timing of nest initiation; rather, Snow Geese dispersal was most influenced by available nesting area, i.e., exposed ground (Abraham 1980). Abraham did not find an effect of previous reproductive experience on dispersal distance, but his inference was limited by very small sample size. I found that failed nesters moved greater distances before nesting in the following year than did successful nesters. Dispersal distance in both groups of female Ross's Geese was >1,500 m on average (Chapter 3). Although arctic-nesting geese that fail in their previous reproductive attempt tend to disperse further than successful breeders (Lindberg and Sedinger 1997, Chapter 3), within-colony dispersal by arctic-nesting geese appears to be an inherent trait that is mostly influenced by habitat availability. This availability, in turn, is governed by depth, distribution and disappearance rate of melting snow all of which can be highly variable from year to year. Some within-colony movement of Ross's Geese appeared to result from movement towards areas of higher nesting densities, and in some years nest initiation dates were earlier in above-average areas

(Alisauskas unpublished data) suggesting that these areas are either preferred or available at an earlier date. Finally, although breeding philopatry is female-biased (Chapter 2), the role of male geese in determining settling patterns has not been studied. Males are the primary defenders of breeding territories (Ryder 1975) and deterrents to foraging predators (Samelius and Alisauskas 2006); thus, dominance status of the male is apt to influence a pair's ability to compete for, secure, and retain a nesting territory until goslings hatch.

6.2 REPRODUCTIVE COSTS

Although life history theory predicts that longer-lived species preserve survival at the expense of reproduction, reproduction may come at a cost to individuals that attempt to breed. In general, Ross's Goose females that nested successfully survived at lower rates than failed nesters. I found that breeding had a deleterious effect on future survival: the effect was largest in 2001 - a year in which the onset of breeding was early (Alisauskas unpublished data) and with one of the largest estimated breeding populations for Karrak Lake. Spring conditions on breeding grounds have a large role on breeding probability of arctic-nesting geese and incidence of breeding increases when conditions permit earlier breeding (Reed et al. 2004). Nesting densities provide a good index of annual variation in breeding probability of Greater Snow Geese (*C. caerulescens atlantica*; Reed et al. 2004); thus, it is likely that annual variation in breeding probability factors large in annual changes in population size at Karrak Lake. Recent evidence suggests that premigration condition influences laying date and clutch size in Greater Snow Geese (Bêty et al. 2003), and given that variation in individual quality (e.g., condition) is a ubiquitous characteristic of wild populations, it seems reasonable that when conditions favorable to breeding develop earlier, the proportion of low quality individuals composing the breeding cohort will increase. I did not directly assess the relationship between survival and population size, but survival varied in parallel between successful and failed breeders; increasing in years when the nesting population was smaller, and vice versa. The ability to detect a cost of breeding likely varies from year to year because of variation in climatic conditions. Climatic conditions influence the timing and probability of breeding (i.e., who is in the sample); they also

determine the rate of energy expenditure during incubation and, thus, the condition of females at end of incubation.

An understanding of life history evolution often requires estimation of the relationship between survival and other life history traits. To my knowledge, this is the first study to demonstrate a cost of reproduction based on estimation of true survival, although Golet et al. (2004) did find a tradeoff between reproduction and apparent survival. Several previous studies of life history evolution in birds have examined the relationship between reproduction and survival by comparing return rates. When detection is imperfect, return rates will provide biased survival estimates (Lebreton et al. 1992, Clobert 1995); the potential for bias and invalid inference drawn from return rates has been discussed previously (Martin et al. 1995).

In many cases, previous reproductive experience influences the magnitude of the dispersal response (Greenwood and Harvey 1982, Chapter 3), and long-distance breeding dispersal may occur regardless of the outcome of a previous nesting attempt (Chapter 3). In any case, emigration from the study area is likely to result in group-differences in availability for capture which will be confounded with other forms of emigration (i.e., non-breeding). Cilimburg et al. (2002) cautioned against the use of return rates in light of the potential for spatial and temporal variation in the extent of emigration. I add that in most studies of wild populations, multiple forms of emigration are likely to exist; dispersal must be accounted for, as it can influence the sampling process and is likely to be linked to other life history characteristics. Inference into biological process may be gained from comparing group-specific sampling probabilities (Nichols 1992, Nichols et al. 1994), but only if absence from the sample results from a single cause, or when additional information regarding absence exists.

6.3 SPATIAL HETEROGENEITY IN SURVIVAL

Considering the diversity of biomes and climatic conditions encountered by light geese during their annual cycle, it is probable that mortality risks vary geographically. Thus, if philopatry is exhibited throughout the annual cycle and the exchange of individuals among subpopulations is infrequent, then rates of survival may differ among subpopulations. I did not detect spatial heterogeneity in survival when comparing rates

of apparent survival among breeding colonies 1999-2003 (Chapter 2), or when assessing the relationship between location of capture and true survival probability, 1991-2003 (Chapter 5). I suspect that any potential for differential survival resulting from spatial heterogeneity in mortality is homogenized by the substantial exchange of individuals among breeding colonies (Chapter 2), and possibly between wintering subpopulations. Absence of spatial heterogeneity in survival simplifies population modeling.

6.4 THE ROLE OF MOVEMENT IN SUBPOPULATION GROWTH

I had insufficient data to estimate directly the role of movement in population growth rate using a reverse-time capture-recapture approach because I could not determine the capture probability of goslings (Nichols et al. 2000). Similarly, I chose not to use a matrix metapopulation model to determine the role of movement in population growth (Caswell 2001), because of insufficient information on age-specific, and colony-specific breeding parameters, and estimates of natal philopatry. Nevertheless, temporal changes in population size result from four primary population processes; thus, population growth rate can be expressed as a balance equation that incorporates gains and losses:

$$\lambda = F + S - E + I \hspace{2cm} \text{(Equation 6.1)}.$$

where population growth rate (λ) is written as a function of *per capita* female recruitment (F), survival rate (S), emigration rate (E), and immigration rate (I). The long-term study of reproductive biology of Ross's Geese at Karrak Lake provides reproductive information specific to this colony; thus, I use Karrak Lake as a case study to get an idea of the contribution of movement to subpopulation growth rate. Although recruitment is apt to vary spatially, for illustrative purposes, I assume equal rates of *per capita* female recruitment between Karrak Lake and Colony 10 to compare potential contributions of movement to colony-specific population growth rates.

The annual number of breeding light geese at Karrak Lake ($\hat{N}_t$) has been estimated for 1993-2005 using stratified sampling of nests at 30 m radius plots systematically placed throughout the colony (Alisauskas unpublished data). Following

Eberhardt and Simmons (1992), log-linear regression of Log($\hat{N}_t$) on t, where $t_0 =$ 1993, gives the intrinsic rate of increase (*r*), and the population growth rate is calculated by:

$$\hat{\lambda} = 1 + r \qquad\qquad\qquad \text{(Equation 6.2).}$$

Karrak Lake is the only colony for which population size can be calculated from ground-based sampling, but periodic estimates of light geese obtained from aerial photography (Kerbes et al. 2006, see Table 6.1) provide another means to estimate population growth rate at Karrak Lake, and also for some of the same colonies that I surveyed for neckbanded geese. However, estimates of λ deriving from aerial photography are limited to pre-1999; thus, ground sampling at Karrak Lake provides more current estimates of λ than those available for other colonies. Nonetheless, the general agreement of estimates from different methods (Table 6.1) lends confidence to the assertion that, based on personal observations during surveys (K. Drake) and mapping of annual change in colony perimeter (R. Alisauskas unpublished data), Colony 10 has grown at a faster rate than Karrak Lake.

Data gathered during a long-term study (1991-2005) of the reproductive biology of Ross's Geese at Karrak Lake provide estimates of many of the necessary reproductive parameters for calculation of *per capita* female recruitment (Table 6.2). Survival of Ross's Goose goslings from hatch to fledge is an area requiring more data, so I assume that this rate is similar to those of Lesser Snow Geese goslings reported by Rockwell et al. (1997) and use the value 0.64 (sensu Alisauskas and Rockwell 1997). Using White's (2000) method, I averaged annual estimates (1991-2002) of post-fledge gosling survival and adult female survival from legbanded birds. Because adult survival declines with increased harvest (Alisauskas et al. 2006a) and also has declined in recent years (Alisauskas et al. 2006a, Chapter 5), I averaged adult female survival over years of conservation order harvest for which I had estimates (i.e., 1999-2002; Table 6.2). I calculated $\hat{F}$ as the product of the reproductive and juvenile survival parameters listed in Table 6.2. Estimates of colony-specific rates of emigration (Chapter 2) for Karrak Lake and Colony 10 are presented in Table 6.3.

Table 6.1. Estimated population growth rates ($\hat{\lambda}$) for mixed species breeding colonies of Ross's and Lesser Snow Geese (collectively referred to as light geese) at Karrak Lake and Colony 10 (McNaughton), Queen Maud Gulf Migratory Bird Sanctuary, Nunavut, Canada.

Colony	Species	$\hat{\lambda}$	Source of data
$\hat{\lambda}$ Karrak (1993-2005)	Light geese	1.087	1993-2005 nest plots, Alisauskas unpublished data
$\hat{\lambda}$ Karrak (1999-2005)	Light geese	1.072	1999-2005 nest plots, Alisauskas unpublished data
$\hat{\lambda}$ Karrak (1967-1998)	Light geese	1.110	Kerbes et al. 2006
$\hat{\lambda}$ Karrak (1967-1998)	Ross's Geese	1.097	Kerbes et al. 2006
$\hat{\lambda}$ Karrak (1988-1998)	Light geese	1.075	Kerbes et al. 2006
$\hat{\lambda}$ Karrak (1988-1998)	Ross's Geese	1.098	Kerbes et al. 2006
$\hat{\lambda}$ McNaughton (1967-1998)	Light geese	1.154	Kerbes et al. 2006
$\hat{\lambda}$ McNaughton (1967-1998)	Ross's Geese	1.135	Kerbes et al. 2006
$\hat{\lambda}$ McNaughton (1988-1998)	Light geese	1.157	Kerbes et al. 2006
$\hat{\lambda}$ McNaughton (1988-1998)	Ross's Geese	1.131	Kerbes et al. 2006

Table 6.2. Survival and reproductive parameters for Ross's Geese.

	Parameter	Estimate	Source of data
Reproduction	Clutch size	3.290	1991-2005 nest plots, Alisauskas unpublished data
	Breeding Probability	0.820	Alisauskas and Rockwell 2001
	Nest Success	0.820	1991-2005 nest plots, Alisauskas unpublished data
	Hatch Success	0.820	1995-1998 nest plots, *in* Alisauskas and Rockwell 2001
	Sex ratio of offspring	0.500	assumed
	F (*per capita* female reproduction)	0.214	Product of juvenile survival and recruitment parameters
Survival	Hatch to fledge	0.640	Alisauskas and Rockwell 2001
	Post-fledge$^{1991-2002}$	0.369[a]	Chapter 5 (averaged over all years)
	Adult$^{1999-2002}$	0.811[a]	Chapter 5 (averaged over years during conservation order harvest)
	Adult$^{1991-2002}$	0.859[a]	Chapter 5 (averaged over all years)

[a] Average survival calculated using White's (2000) method.

Table 6.3. Estimates of Ross's Goose permanent emigration from the Karrak Lake and McNaughton (Colony 10) breeding colonies, 1999-2003, Queen Maud Gulf Migratory Bird Sanctuary, Nunavut, Canada. Model selection resulted in a model with constant rates of movement receiving virtually all of the support from the data, so there is only one estimate of emigration per colony that applies to all years of the study. Estimates are presented with lower (LCL) and upper (UCL) 95% confidence limits.

	Emigration		
Colony	LCL	Point Estimate	UCL
Karrak Lake	0.05	0.11	0.17
McNaughton	0.11	0.25	0.39

I calculated the contribution of movement, both immigration and emigration, toward λ by using $\hat{\lambda}$, $\hat{F}$, $\hat{S}$, and $\hat{E}$ in Equation 6.1 to solve for $\hat{I}$. I did this for each estimate of population growth rate at Karrak Lake and Colony 10 (Table 6.4). These calculations suggest that population size of geese at these colonies would decline without immigration. Population growth rate at Karrak Lake is likely augmented by (1) the general westward movement of Ross's Geese among larger breeding colonies within the QMG region (Chapter 2), and (2) contributions from other smaller QMG colonies that were not sampled. In recent years, it appears that nesting populations at some of the smaller colonies within the QMG region have declined, and some of the smallest colonies had disappeared by 2005 (R. Alisauskas personal communication); thus, a general movement of geese from smaller colonies to the largest colonies may have occurred. Given the general westward movement of Ross's Geese within the QMG region, it seems unlikely that the population growth rate of Colony 10 would be maintained solely by contributions from other QMG breeding colonies. I sampled the largest known colonies in the Sanctuary, and among these, there was a net loss of birds from Colony 10 (Figure 2.2B). There is substantial immigration from WHB given the numbers of marked geese in my sample that originated from this region. It seems probable that the contribution of birds from WHB to Colony 10 is greater than contributions to more western QMG colonies considering that 32.0-43.5% of the marked birds sighted at Colony 10 had originated from WHB, whereas at Karrak Lake, WHB geese represented 10.1-15.9% of neckbands read.

Additional research on colony-specific recruitment and rates of natal philopatry is needed in order to better understanding the role of movement in population dynamics of arctic nesting geese. Nonetheless, results presented in this section demonstrate that the role of movement in population dynamics of breeding Ross's Geese is nontrivial. Even if the higher estimate of average adult survival (0.859) were assumed in Equation 6.1, immigration from Karrak Lake still would have ranged 0.049-0.207 and 0.168-0.479 for Colony 10. The assumption of equal recruitment rate among colonies is not likely to be met because known spatial variability in snowmelt and geographic variability in climatic conditions over broad arctic regions influences breeding success (Boyd et al. 1982, Alisauskas 2002). A higher rate of *in situ* recruitment at Colony 10

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Table 6.4. Potential *per capita* contribution of immigration to population growth rates of Karrak Lake and McNaughton (Colony 10) breeding colonies, Queen Maud Gulf Migratory Bird Sanctuary, Nunavut, Canada. Population growth rates (λ) were derived from annual population estimates based on nest plot sampling (Alisauskas unpublished data), or from periodic photo inventory surveys (Kerbes et al. 2006). Population growth rates pertain to Ross's and Lesser Snow Geese, collectively light geese (LG), or to Ross's Geese only (RG), for the range of years presented next to the estimate. Contribution of immigration (I) to λ was obtained by solving a balance equation where *per capita* female recruitment (F), adult female survival during conservation order years (S), and colony-specific emigration rate (E) were known, and immigration was the one unknown parameter. λ, F, and S were held constant while the point estimate of emigration rate, and its lower and upper 95% confidence levels were used to calculate the upper and lower bounds for the contribution of immigration to λ.

Colony	Data	Spp.	Years	$\hat{\lambda}$	$\hat{F}$	$\hat{S}$	$\hat{E}$	$\hat{I}$
				Population Parameters Estimates				
Karrak	Plots	LG	1993-2005	1.087	0.214	0.811	0.110	0.172
	Plots	LG	1999-2005	1.072	0.214	0.811	0.110	0.157
	Photo	LG	1988-1998	1.075	0.214	0.811	0.110	0.159
	Photo	RG	1988-1998	1.098	0.214	0.811	0.110	0.183
	Plots	LG	1993-2005	1.087	0.214	0.811	0.050	0.112
	Plots	LG	1999-2005	1.072	0.214	0.811	0.050	0.097
	Photo	LG	1988-1998	1.075	0.214	0.811	0.050	0.099
	Photo	RG	1988-1998	1.098	0.214	0.811	0.050	0.123
	Plots	LG	1993-2005	1.087	0.214	0.811	0.170	0.232
	Plots	LG	1999-2005	1.072	0.214	0.811	0.170	0.217
	Photo	LG	1988-1998	1.075	0.214	0.811	0.170	0.219
	Photo	RG	1988-1998	1.098	0.214	0.811	0.170	0.243
Col. 10	Photo	LG	1988-1998	1.157	0.214	0.811	0.250	0.382
	Photo	RG	1988-1998	1.131	0.214	0.811	0.250	0.356
	Photo	LG	1988-1998	1.157	0.214	0.811	0.110	0.242
	Photo	RG	1988-1998	1.131	0.214	0.811	0.110	0.216
	Photo	LG	1988-1998	1.157	0.214	0.811	0.390	0.522
	Photo	RG	1988-1998	1.131	0.214	0.811	0.390	0.496

could compensate for immigration to sustain the observed population growth rate at Colony 10.

6.5 CONCLUDING REMARKS

6.5.1 Are Current Rates of Movement Greater Than Historical Levels?

Breeding dispersal by adult Ross's Geese clearly influences the species' distribution, and behavioral evidence for breeding dispersal (Chapter 2) is consistent with genetic evidence of extensive subpopulation connectedness (Avise et al. 1992). It is unknown whether these results reflect a long-term evolutionary history of extensive movement, or more recent selection favoring behavioral flexibility in patterns of philopatry. Historic rates of dispersal during any portion of the annual cycle are unknown, but populations of light geese were once smaller and more restricted in distribution (Dzubin 1965, Alisauskas and Ryder 1995) when migration and winter food were more limited, so it is possible that historic rates of philopatry differed from current levels. For light geese, the cost-benefit relationship of philopatry during the nonbreeding period has likely changed as food has increased in abundance and quality along migration routes and on wintering areas (Abraham and Jefferies 1997, Alisauskas et al. 1988); thus, dispersal decisions during the nonbreeding period probably carry less risk than they did historically. Increased dispersal has undoubtedly been a favorable trait during the nonbreeding period judging from the marked expansion of winter range, whether positive outcomes of dispersal during one portion of the annual cycle has any impact on breeding philopatry remains unknown.

Based on mitochondrial DNA markers, Avise et al. (1992) presented evidence suggesting allopatric evolution of Ross's and Lesser Snow Geese. At present, light goose breeding colonies in the QMG region are composed of Ross's and Lesser Snow Geese. These species have very similar life histories, now co-occur throughout the annual cycle, and interbreed; thus, social facilitation may presently influence the evolution of life history traits. Historically, Ross's Geese nested on islands in shallow lakes perhaps to avoid nest predation by Arctic Fox (Ryder 1969b). With the concurrent increase of Ross's Goose and Snow Goose populations, terrestrial area occupied by nesting geese expanded into previously unused island and mainland habitats (Kerbes et

al. 1983, McLandress 1983, Kerbes 1994). Early expansion of nesting area from islands to the mainland involved mostly Snow Geese, probably because they are larger and more capable at deterring foxes than smaller Ross's Geese (McLandress 1983). Similarly, social facilitation may have had a role in the winter expansion of Ross's Geese into mid-continent flyways (Alisauskas 1998, Alisauskas et al. 2006a).

In species of arctic-nesting geese for which proper estimates of breeding philopatry exist, female philopatry appears to be highly variable (≥0.93 for Black Brant, Lindberg et al. 1998; and ≥0.63 for Ross's Geese, Chapter 2), but in no case is it absolute. Estimates of colony-level philopatry by Lesser Snow Geese are absent, but they are considered to "show a high degree of breeding-site fidelity" at LPB (Ganter and Cooke 1998), based on the fact that 73% of detected females had nested ≤500 m of their previous nest site (Abraham 1980, Cooke and Abraham 1980). Female emigration from this subarctic colony was thought to occur at very low rates (Cooke et al. 1975, Rockwell et al. 1977), but coinciding with extensive habitat degradation, emigration from LPB has increased over time (Francis and Cooke 1993, Cooch et al. 2001). Thus, even in a population where female geese show a "high degree" of philopatry, dispersal is likely to persist.

Dispersal patterns result from cumulative decisions during the process of habitat selection; this decision process is bound to overlap at different spatial scales. For geese philopatric to their breeding colony, there appears to be substantial flexibility with regard to affinity to previous nest location (Abraham 1980, Lindberg and Sedinger 1997, Chapter 3). In general, locations of breeding colonies remain stable, but colony-specific breeding distributions of arctic-nesting geese are spatially and temporally dynamic (Abraham 1980, Alisauskas and Boyd 1994, Lindberg and Sedinger 1997, Ganter and Cooke 1998). These local distributional changes result from changes in suitability and availability of habitat (Lindberg and Sedinger 1997, Ganter and Cooke 1998), settling patterns of new recruits into the breeding population (Lindberg and Sedinger 1997, Ganter and Cooke 1998), and from intra-colony breeding dispersal by adults (Ganter and Cooke 1998, Chapter 3).

The motivation for inter-colony breeding dispersal by female arctic-nesting geese is not known, but the outcomes of such movement can have a large influence on

local population dynamics of breeding Ross's Geese; a portion of most breeding populations is composed of migrant females, but it should not be assumed that emigration and immigration are equal. A more complete understanding of the role of dispersal in population dynamics, and in the evolution of life history strategies, requires additional study because several questions remain unanswered. Further work is needed to assess the potential for spatial variability in recruitment, as this may be linked to movement decisions. To this end, information on natal philopatry is needed because *in situ* recruitment requires the return of individuals to their natal colony. Delayed sexual maturity may be adaptive not only to permit young geese to exceed physiological thresholds for breeding (Reynolds 1972, Alisauskas and Ankney 1992), but also may afford young geese the opportunity to prospect new areas before sexual maturity, after which time constraints of breeding may interfere with exploration.

Of interest is the question about whether variability in dispersal probability (Abraham 1980, Lindberg and Sedinger 1997, Chapter 3) has a genetic basis, or largely is the result of phenotypic plasticity. Further work should focus on identifying factors that cue dispersal decisions, which would assist our understanding of what serves as the impetus for dispersal. In addition, information on the reproductive outcome following inter-colony movements by breeding geese is required to assess of the adaptive significance of dispersal. For example, I found that reproductive success influences dispersal distance (Chapter 3), but do dispersing individuals have better lifetime reproductive success than philopatric individuals? Adaptiveness and genetic variance of dispersal may change over time in a density-dependent fashion, similar to arguments made by Gloutney et al. (1999) about variable anorexia in this same species.

Avian philopatry should be correlated with stability of the habitat (McNicholl 1975), so among-colony differences in philopatry may arise in part from spatial variation in chronology of habitat availability. Given a lack of attachment to previous nest sites (Chapter 3), homogeneous nature of lowland tundra habitat, and the importance of early onset of breeding, I imagine that some between-colony breeding dispersal by Ross's Geese results from a lack of available habitat prompting a dispersal event that is related to maintaining a pair's reproductive status. This may result from individuals arriving at their previous breeding colony to find poor habitat conditions,

and then deciding to attempt to breed at another colony. This speculation arises from the apparent directional movement towards Karrak Lake and a west-east cline in timing of snowmelt. Although this serves as a working hypothesis to explain the directional westward movement of Ross's Geese in the QMG region, it does not explain the movement of geese from Karrak Lake to other more easterly-located colonies.

Clearly movement has a substantial role in population dynamics of breeding geese. My studies of Ross's Goose dispersal on their breeding grounds highlight the importance of movement in determining their distributional patterns, and influencing gene flow, on a continental scale. I hope this work serves as a springboard to further investigation pertaining to spatial aspects of population dynamics.

6.5.2 Management Implications of Inducing Nest Failure

Several alternative strategies for reducing light goose populations have been proposed (Johnson 1997, Johnson and Ankney 2003). One of the strategies considered was the taking of eggs on the breeding grounds (Johnson 1997), but if breeding failure causes dispersal, induced nest failure might produce the undesirable result of geese moving, and exporting the 'problem' to other breeding areas. My results suggest that egg removal would not result in widespread dispersal if it were implemented as a method to reduce light goose populations.

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APPENDIX A. NECKBANDS AS A MARKING TECHNIQUE: ARE THEY WORTH THE EFFORT?

Neckbands are useful markers that permit the identification of individual geese without having to physically capture them. In most cases, neckbands negatively affect the survival of adult geese (Alisauskas and Lindberg 2002 and references therein, Alisauskas et al. 2006a, but see Menu et al. 2000), and neckbands have also been shown to negatively influence breeding probability and clutch size in Greater Snow Geese (Reed et al. 2004). The potential for negative effects of neckbands to bias the estimation of population parameters has been discussed previously (Alisauskas and Lindberg 2002, Reed et al. 2004). Negative effects of neckbands on survival should not necessarily bias estimates of movement because the processes of survival and movement are separate in multistate models (Clobert and Lebreton 1991, Nichols and Kendall 1995).

As an alternative to neckbands, tarsal bands have been used effectively as a marker in population studies of other geese, but because they are smaller and placed on the leg, tarsal bands are more difficult to detect and read. In order for an observer to detect a tarsal band on a nesting female goose, the bird must be standing. Based on my experience with sightings of tarsal-banded Ross's Geese, I suggest that tarsal bands do not result in sufficiently high detection of individual codes, at least in situations of density and numbers of geese encountered during my study. In the case of Ross's Geese, and the midcontinent population of Lesser Snow Geese, most birds nest at large colonies (Alisauskas and Boyd 1994, Kerbes 1994), some having upwards of a million birds. In order to conduct studies based on marked individuals, at these colonies markers need to be: (1) conspicuous, (2) readable from long distances (500 m), and (3) detectable without having to flush every bird from its nest. Tarsal bands may prove to be a useful marker for estimating vital rates at smaller colonies with lower densities of

light geese, but the trade-off is restricted inference from sampling a smaller proportion of the population of interest.

I tested whether reproduction by Ross's Geese after they were marked was independent of marker type (legband vs. neckband) by comparing the presence/absence of a brood patch in females with differing marker types ($n = 197$). Of the 197 recaptures, 85.2% (98/115) of legbanded females had visible evidence of a brood patch, whereas 92.7% (76/82) of neckbanded females had a brood patch. These results are opposite of the predicted relationship, suggesting that neckbands do not have a negative effect on breeding probability (likelihood ratio $\chi^2 = 2.72$, df = 1, $P = 0.099$).

I also compared estimates of mean nest initiation date, clutch size, and nest success of neckbanded females, 2000-2004, to those estimated from systematically-spaced plots for the same range of years (Alisauskas unpublished data). Nest initiation dates were consistently earlier for neckbanded geese in all years (range 0.90–1.98 days), and clutch size differed only in 2002 when clutch size within nest plots was 0.1 egg greater than clutch size of neckbanded birds. Nest success of neckbanded females was 0.06 greater than that of nests within plots in 2000, but during 2001-2003, nest success within plots ranged 0.05-0.17 higher than that of neckbanded females. There was no difference between nest success of neckbanded females and nests within plots during 2004.

Neckbands negatively influence the survival of Ross's Geese (Alisauskas et al. 2006a), but they do not appear to negatively influence breeding probability, nest initiation date, or clutch size. In three of five years, estimates of nest success for neckbanded geese were lower than those of unmarked birds (nest plot data), but inconsistent results preclude making generalities about an effect of neckbands on nest success; this effect appears to be year-specific.