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dissertation entitled

PHYLOGEOGRAPHY AND MANAGEMENT OF SNOW, ROSS'S, CANADA, AND CACKLING GEESE

presented by

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has been accepted towards fulfillment
of the requirements for the

Ph.D.	degree in	Fisheries and Wildlife Ecology, Evolutionary Biology and Behavior

Major Professor's Signature

6-27-05

Date

PHYLOGEOGRAPHY AND MANAGEMENT OF SNOW, ROSS'S, CANADA, AND CACKLING GEESE

By

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A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Fisheries and Wildlife

2005

ABSTRACT

PHYLOGEOGRAPHY AND MANAGEMENT OF SNOW, ROSS'S, CANADA, AND CACKLING GEESE

By

Rainy Inman Shorey

Identification of demographically and reproductively isolated populations is an important aspect of resource management and conservation. This is especially crucial for highly migratory species like waterfowl, as populations utilize several areas throughout the year, often co-occurring with individuals from other populations, and because rates of natality and survival may vary greatly among populations. Waterfowl species, subspecies, and management populations have traditionally been defined and managed based on morphology and plumage characteristics; and based on banding studies emphasizing commonalities in migratory patterns and fidelity to, and potential gene flow among, wintering and breeding areas. However, banding and morphometric techniques focus on contemporary attributes of species ecologies, and provide little information about historic population demographics. Thus, the management units defined for waterfowl based on morphology and banding may not be supported by species underlying population genetic structure.

With the development and greater accessibility of molecular techniques, genetic surveys can be conducted to determine the degree of genetic variation for currently defined populations, subspecies, and species of waterfowl. Molecular phylogenies based on maternally- (mitochondrial DNA) and bi-parentally- (neutral nuclear DNA) inherited markers can be examined in a spatial context, and be used to assess the relative influence

of historical processes and current behavioral and ecological factors on the spatial genetic structure revealed for specific waterfowl taxa.

This study focused on two co-distributed species groups of migratory waterfowl in North America that have similar historical geographic ranges. Populations, subspecies, and species of these two groups, including snow (*Chen caerulescens*) and Ross's geese (*Chen rossii*) and cackling (*Branta hutchinsii*) and Canada geese (*Branta canadensis*) were genetically characterized using mitochondrial and microsatellite molecular markers. These molecular surveys were designed to evaluate the degree of genetic variation at multiple spatial levels, and identify areas of genetic discordance within and among species. Hypotheses were then tested regarding the relative importance of causal historical and contemporary factors that have defined the genetic spatial structure observed. Finally, a determination was made as to whether the present species, subspecies, and management unit designations for each group of geese reflected the underlying spatial structure as seen at the level of genes.

Data collected as part of the phylogenetic investigation were then utilized to address specific issues of population management in snow geese and within cackling and Canada geese. For snow geese, information regarding the degree of genetic variation among Western populations was used to determine relative levels of historical and contemporary gene flow among populations of conservation concern, and to evaluate population structuring among breeding and wintering groups of these populations. To improve harvest management in the state of Michigan, established methods of genetic stock identification and nationally standardized sample collections were used to estimate proportional contributions of cackling and Canada geese to annual harvests.

ACKNOWLEDGEMENTS

I would like to express my gratitude to the many wonderful professors at Michigan State University that have offered me guidance and support throughout my degree. I thank all the wildlife managers and field biologists from many state, federal, and provincial agencies who donated their time, funding, sampling efforts, and wealth of knowledge to this project. I greatly appreciate the unending support provided by my family and friends during this period of my life. Finally, I am thankful I had the opportunity to discover my very special friend on the North Slope of Alaska during one of my many Ph.D. adventures.

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CHAPTER 1: INTRASPECIFIC PHYLOGEOGRAPHIES OF SNOW, ROSS'S, CANADA, AND CACKLING GEESE: DEFINING THE SPATIAL STRUCTURE OF BIOLOGICAL DIVERSITY

INTRODUCTION

Identification of demographically and reproductively isolated populations is an important aspect of resource management and conservation (Lande 1988). This is especially crucial for highly migratory species like waterfowl, as populations utilize several areas throughout the year, often co-occurring with individuals from other populations, and because rates of natality and survival may vary greatly among populations. Waterfowl species in North America vary in a number of characteristics that greatly influence the focus and implementation of management regulations for individual species. For instance, some species have populations that are very abundant and have wide geographic distributions, such as temperate nesting Canada geese (*Branta canadensis*; Ankney 1996, Rusch et al. 1996b) and Mid-Continent lesser snow geese (*Chen caerulescens*; North American Arctic Goose Conference 2001). Other species, such as spectacled eiders (*Somateria fisheri*; Scribner et al. 2001) and harlequin ducks (*Histionicus histionicus*; Lanctot et al. 1999) have populations that are threatened or declining and have limited distributions. Ecological traits of species also vary, such as migration patterns, levels of fidelity to breeding and wintering sites, and breeding behaviors including timing of pairing and strength of pairbond (Batt et al. 1992, Ely and Scribner 1994). Thus, successful management plans must consider the ecological traits and life history characteristics of each species.

Waterfowl management programs attempt to sustain a desirable level of harvest, while ensuring the long-term viability of contributing breeding populations and maintaining current levels of biological diversity within species. Challenges to waterfowl management include: 1) increases in numerical abundance for certain populations or species, while others have remained stable or have declined, and 2) recent geographic range expansions of nesting, molting, and wintering areas associated with growing numbers of waterfowl in certain populations. In addition, most waterfowl are harvested in locations distant from breeding grounds in flocks composed of several breeding populations (and possibly from different subspecies and species) from different geographic locations.

Species, subspecies, and management populations have traditionally been defined by morphology and plumage characteristics, and banding studies focused on migratory patterns and population distributions (Munro and Kimball 1982, Moser and Rolley 1990, Rusch et al. 1996a). However, banding and morphometric techniques focus on contemporary attributes of species ecologies, and provide little information about historic population demographics. Additionally, morphological traits can vary as a function of an individual's age (Thompson et al. 1999) and environmental factors such as climate and available food resources (Leafloor et al. 1998), while banding requires a large number of individuals are marked and resighted through observation or harvest to assess patterns of migration and population dispersal. Given the limitations of morphometrics and banding techniques, and the lack of historic population information provided by these data, an important question arises: Are the management units defined for waterfowl based on morphology and banding supported by the species underlying genetic structure?

The degree to which populations of waterfowl are spatially structured, and the utility of neutral genetic markers to describe gametic affinities among populations, varies among species. Populations can be influenced by historical vicariance and past dispersion events, and by current levels of gene flow, breeding systems, and ecological and behavioral characteristics (Avise et al. 1997, Avise 1998). Biogeographic theory postulates that species distributions and intraspecific relationships are the result of vicariance events and allopatric speciation, followed by dispersal from historically fragmented ranges (Wiley 1980, Endler 1982). Explanations for observations of levels of population structuring based upon measures of genetic divergence between waterfowl populations should incorporate information regarding separation times (e.g., times to mean common ancestors; Nielsen 1998) and locations of historical regions of geographic discordance (Thorpe et al. 1995). In addition, population structuring of waterfowl species may be influenced at regional scales by a variety of life history traits, including the timing and location of pair bonding, the degree (and sex-specificity) of breeding and wintering site philopatry, breeding behavior, and migration route fidelity (Anderson et al. 1992, Ely and Scribner 1994).

Utility of Genetic Markers

Biological diversity within waterfowl species, and the spatial distribution of populations, subspecies, and species has traditionally been defined by morphology and plumage characteristics (Bellrose 1980, Moser and Rolley 1990, Alisauskas 1998b, Giroux et al. 2001, Pearce et al. 2003), and based on banding studies emphasizing commonalities in migratory patterns and fidelity to, and potential gene flow among,

wintering and breeding areas (Raveling 1978, Hines et al. 1999, Kerbes et al. 1999, Drake and Alisauskas 2005). The development of new technologies, including stable isotope analysis of feathers (Caccamise et al. 2000), and molecular analysis techniques (e.g. polymerase chain reaction based sequencing of mitochondrial DNA, and neutral nuclear DNA markers), has offered additional insight as to how biological diversity may be spatially allocated among populations of waterfowl (Shields and Wilson 1987, Quinn et al. 1991, Quinn 1992, Baker 1998, Ruokonen et al. 2000, Scrinber et al. 2001, Paxinos et al. 2002, Scribner et al. 2003a).

Current molecular technologies have several advantages over other methods that have historically been used to delineate populations, subspecies, and species, and to quantitatively test hypotheses about the underlying causes of the spatial structure described. Unlike morphological delineations based on size and plumage characteristics which can vary with age and nutritional conditions, genetic markers are heritable and are maintained throughout an individuals lifetime. Morphological characteristics may also vary geographically, leading to different interpretations about the number of subspecies or races within a species (Larsson and Forslund 1991, Leafloor and Rusch 1997, Leafloor et al. 1998, Alisauskas 1998b). For instance, Canada geese have been defined as having between 8 subspecies (Palmer 1976) and 83 subspecies (Hanson 1997). An individual's DNA cannot be lost like a band, collar, or radio-transmitter (Samuel et al. 1990, Campbell and Becker 1991, Wiebe et al. 2000, Samuel et al. 2001). Virtually any cellular tissue can be used as a source for DNA. Sampling techniques can be non-destructive, and often very little tissue or blood is required to characterize the individual.

Most importantly, molecular markers allow statistical inferences to be made based upon measures of relatedness among groups, without direct observations of movements.

With the development and greater accessibility of molecular techniques (e.g. polymerase chain reaction based sequencing of mitochondrial DNA, and neutral nuclear DNA markers), molecular phylogenies can now be constructed (Avise et al. 1987, Avise 1992, Shields and Cotter 1998, Scribner et al. 2003a). Intra- and inter-specific phylogenies examined in a spatial context, can be used to evaluate the relative importance of historical events and current ecologic attributes in shaping phylogeographic observed patterns (Thorpe et al. 1995, Avise 1998, Bernatchez and Wilson 1998, Holder et al. 1999). Comparative analyses of phylogeographic structure across multiple species can be used to identify commonalities and differences between species relative to movements, life history and behavior, and locations and times of separations during Pleistocene or earlier vicariant events (Ploeger 1968, Avise and Walker 1998, Klicka and Zink 1997).

Microsatellites have several features that make them useful for evolutionary and ecological applications. These markers are loci which consist of a variable number of tandem repeat sequences of DNA. Typically, microsatellites consist of 10-50 copies of a repeat sequence 1-10 base pairs long. Microsatellite loci are codominant and are inherited in a Mendelian fashion, with one allele derived from each parent. Their abundance throughout the genome, high level of variance, and lack of physical linkage allow for statistically powerful calculations of allele frequencies (Scribner and Pearce 2000). Estimates of allele frequency allow assessments of levels of gene flow, and define relationships among individuals, populations, subspecies and species.

Mitochondrial (mt) DNA is maternally inherited and transmitted without recombination, and can be reliably used to reconstruct population genealogies and species phylogenies. Unique mtDNA sequences called haplotypes tend to evolve faster than nuclear DNA. Genetic differences accumulate between populations over short evolutionary time periods (Randi 2000). To identify individual haplotypes, DNA sequencing is utilized to determine actual base pair structure in targeted regions of the mtDNA genome. Mitochondrial DNA haplotypes can be used to construct haplotype trees that illustrate areas of genetic discordance within species. Hypotheses about the historical and contemporary factors underlying the patterns of genetic discordance may then be developed and tested based on haplotype trees branch lengths and topology (Templeton 1998).

PURPOSE OF PROJECT

The focus of this project is two co-distributed species groups of migratory waterfowl in North America, including two currently recognized species within each group. The first group is composed of snow geese (*Chen caerulescens*) and Ross's geese (*Chen rossii*). Current recognized taxonomy of snow and Ross's geese include the two species and two subspecies of snow goose, the lesser (*C. c. caerulescens*) and the greater (*C. c. atlantica*) (American Ornithologists' Union 1998, Ryder and Alisauskas 1995, Mowbray et al. 2000). In addition, the lesser snow goose subspecies is dimorphic, having recognized light (white) and dark (blue) color morphs. Lesser snow goose color morphs are controlled by a single gene locus where the dark allele is incompletely dominant to the light (Mundy et al. 2004). Snow and Ross's geese populations are currently managed

by species, subspecies, and in mixed groups based on common breeding and wintering areas (Ryder and Alisauskas 1995, Mowbray et al. 2000). There are four major management groups for these geese including the Western Arctic Population, the West Central Flyway Population, the Mid-Continent Population, and the Eastern Population (Figure 1).

The second group investigated includes cackling geese (*Branta hutchinsii*) and Canada geese (*Branta canadensis*). Four subspecies, *B. h. hutchinsii, B. h. leucopareia, B. h. taverneri, and B. h. minima*, are included as part of the cackling geese species. The Canada goose species is composed of subspecies *B. c. canadensis, B. c. interior, B. c. occidentalis, B. c. fulva, B. c. maxima, B. c. moffitti, B. c. parvipes* (Banks et al. 2003). Until 2003, the four subspecies of cackling geese were categorized as part of the Canada goose species group and referred to as "small-bodied subspecies" (Delcour 1956). Several genetic studies of mitochondrial DNA (VanWagner and Baker 1986, Shields and Wilson 1987, Quinn et al. 1991, Scribner et al. 2003a) verified previous subspecific taxonomic delineations based on difference in vocalizations, nesting habits, habitat, timing of migration, as well as color and size. The subspecies were historically treated as a single species, but actually constitute two species (Banks et al. 2003). Cackling geese and Canada geese are currently managed in North America on several levels including species, subspecies, by affiliation to one of the four migratory Flyways (Figure 2), and by management populations (n = 19 for cackling and Canada geese combined; Appendix 1; Dickson 2000, Moser and Caswell 2004).

The first objective of this project was to genetically characterize populations, subspecies, and species of snow and Ross's geese and cackling and Canada geese using

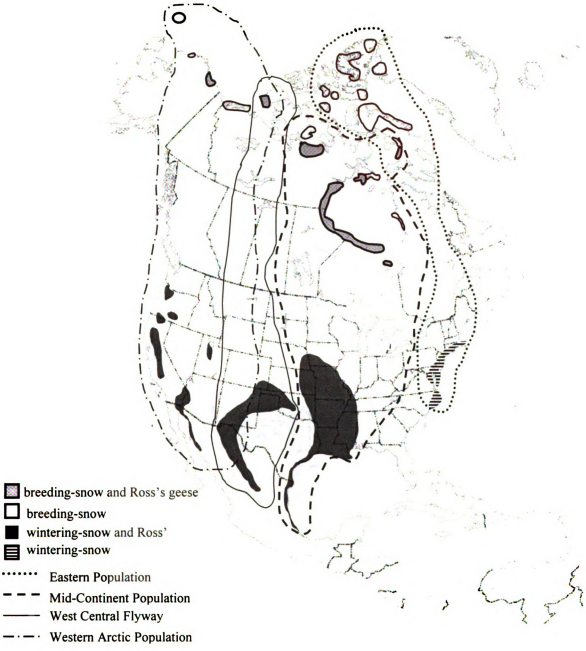

Figure 1. Breeding and wintering distributions and management population boundaries for snow geese (*Chen caerulescens*) and Ross's geese (*Chen rossii*).

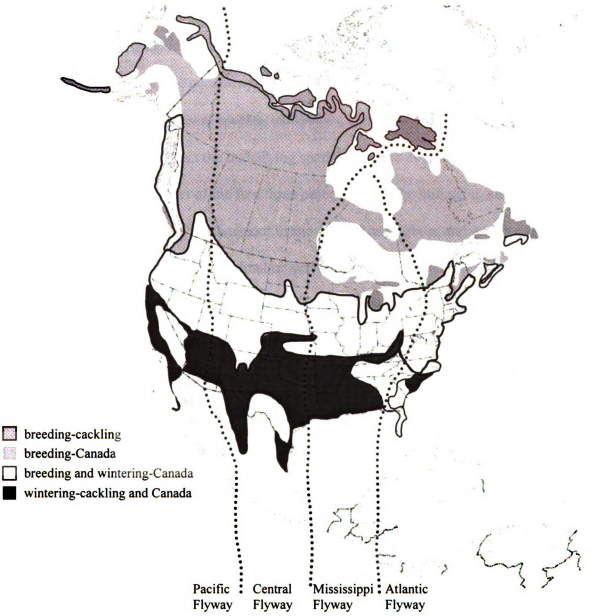

Figure 2. Breeding and wintering distributions and migratory Flyways for cackling geese (*Branta hutchinsii*) and Canada geese (*Branta canadensis*).

mitochondrial and microsatellite molecular markers. These molecular surveys were designed to evaluate the degree of genetic variation at multiple spatial levels, and identify areas of genetic discordance within and among species. The second objective is to test hypotheses regarding the relative importance of causal historical and contemporary factors that have defined the genetic spatial structure observed. The third objective was to determine whether the present species, subspecies, and management unit designations for each group of geese reflect the underlying spatial structure as seen at the level of genes. Data collected as part of the first three objectives will be utilized to address specific issues of population management in snow and Ross's geese and within cackling and Canada geese. Specifically, the final objective of this project was to use information of spatial genetic affinities among populations to estimate gene flow and to determine the composition of admixed groups during periods of harvest.

BACKGROUND

Defining Spatial Genetic Structure

Spatial patterns of genetic diversity within and among species are defined by historical and contemporary processes (Avise et al. 1987, Avise 1998). Past vicariant events, such as restrictions of populations within isolated refugia during Pleistocene or Pliocene glacial periods and subsequent range expansion during interglacial periods, influence phylogenetic structure within and among species (Avise and Walker 1998, Zink 1996, Klicka and Zink 1997, Voelker 1999). Smaller historic effective population sizes during and following glacial events likely increase levels of genetic drift within populations, and increase the variance in allele or haplotype frequency among

populations (Avise et al. 1988, Chesser et al. 1993, Chesser and Baker 1996). Drift and levels ofgenetic divergence will increase in a time-dependent fashion (Slatkin 1987, Arbogast et al. 2002).

Ecology and life history characteristics of a species including mating and breeding behaviors, fidelity to natal areas and breeding and wintering sites, and migratory behaviors can also have a profound effect on the degree of genetic drift and patterns of gene flow, and the resulting spatial patterns of genetic structuring (Chesser 1991a, Ely and Scribner 1994, Pearce et al. 2000). Genetic drift will decrease and gene flow will increase as more individuals interbreed across populations within a species (Chesser 1991b). High natal dispersal and low breeding site fidelity in one or both sexes will increase levels of gene flow among populations and decrease the degree of spatial genetic structure among populations within species (Greenwood 1980, 1987, Chesser 1991b). Additionally, pair bond formations that occur when individuals from different populations are sympatric will potentially increase gene flow among populations (Cooke et al. 1988, Robertson and Cooke 1999). Behaviors which discourage interbreeding among individual from different populations will increase genetic structuring between populations (Cooke et al. 1988, Chesser 1991a, Petrie and Kempenaers 1998, Miyatake and Shimizu 1999).

North American avian species including songbirds and Neotropical migrants (Zink 1996, Kimura et al. 2002), shorebirds (Wenink et al. 1994), wading birds (Rhymer et al. 2001), and migratory waterfowl (Avise et al. 1992, Quinn 1992, Scribner et al. 2001, Scribner et al. 2003a, Pearce et al. 2004, Peters et al. 2005, see review in Avise and Walker 1998) exhibit a variety of phylogeographic patterns (Zink 1997) ranging from

nearly panmictic species (Lanctot et al. 1999, Pearce et al. 2004) to species with strongly subdivided subspecies (Kimura et al. 2002) or populations (Wenink et al. 1994). Some phenotypically variable species, like the red-winged blackbird (*Agelaius phoeniceus*) and common grackle (*Quiscalus quiscula*), were found to lack spatial genetic structure (Ball et al. 1988, Zink 1996). Other species show evidence of population genetic structure, such as the fox sparrow (*Passerella iliaca*; Zink 1996), dunlin (*Calidris alpina*; Wenink et al. 1994).

Species that do not have congruent phylogeographic structure may have not been historically co-distributed, and may have inhabited different refuges during historic isolating events (Zink 1997). In addition, there is a correlation between elapsed time since sharing a common ancestor and current levels of spatial genetic structure within and among species. For instance, red-winged blackbirds may have only recently colonized their current range through dispersal from one panmictic historic population, while the fox sparrow likely experienced historical isolating events that genetically diverged populations prior to recent post-glacial dispersals (Zink 1996).

Arctic-Nesting Waterfowl

Patterns of spatial genetic structure vary greatly among co-distributed species of Arctic-nesting waterfowl. For instance, western and eastern populations of king eiders (*Somateria spectabilis*) are genetically homogeneous (Pearce et al. 2004), while spectacled eiders (*S. fischeri*) are characterized by significant genetic variation among their three primary nesting populations (Scribner et al. 2001). Species such as the northern pintail (*Anas acuta*; Cronin et al. 1996) and mallard (*Anas platyrhynchus*; Avise

et al. 1990) appear to be nearly panmictic over extensive geographic areas. In contrast, brant (*Branta bernicla*; Shields 1990) and common eiders (*S. mollissima*; Sonsthagen et al. 2005) have significant phylogenetically distinct haplotype groups that exhibit a geographic orientation reflecting past vicariance events. Differences in the degree of genetic divergence evident in co-distributed taxa points to the varying importance of historical factors and contemporary levels of gene flow in shaping genetic structure within different species (Avise and Walker 1998).

Within of waterfowl, cackling and Canada geese, and snow and Ross' geese exhibit several characteristics that make them useful groups for intraspecific phylogenetic analyses. First, they are independent, but co-distributed taxa that have similar historical geographic ranges (Ploeger 1968). This allows us to examine the degree of population structuring based on hypothetical glacial refugia and post-glacial dispersal. Secondly, cackling and Canada geese and snow and Ross's geese differ in a number of life history characteristics which may impact levels of genetic drift and gene flow among populations, and influence genetic variation at different spatial scales (Table 1; Ely and Scribner 1994).

There has been growing concern over the management of cackling and Canada geese, and snow and Ross's geese. Over the past few decades, both groups have seen tremendous increases in numerical abundance for certain populations (or subspecies), while other populations have remained stable or have declined (Ankney 1996, Pacific Flyway Council 1997, Alisauskas 1998a, Kelley et al. 1998, Kerbes et al. 1999, North American Arctic Goose Conference 2001). Geographic ranges of nesting, molting, and wintering areas have also recently increased in conjunction with growing numbers of

Table 1. Life history attributes of snow and Ross's geese and Canada and cackling geese that may influence spatial genetic structure (Ely and Scribner 1994).

Species	Natal Site Fidelity	Breeding Site Fidelity	Timing of Pairing	Family Stability	Nesting Behavior	Nesting Distribution	Molt Migration	Inter-Flyway Dispersal	POTENTIAL STRUCTURE
Snow / Ross's	F-biased*	F-biased	winter / spring	strong	colonial	interrupted	strong	high	LOW
Canada / Cackling	F-biased	F-biased	spring / summer	variable	dispersed	continuous	variable	low	HIGH

*F-biased = Fidelity is female biased.

geese (Bateman et al. 1988, Malecki and Trost 1998). Management directed to control expansions of overabundant populations of geese, while protecting others, emphasizes the necessity of using techniques that can differentiate populations, subspecies, and species that may be contributing to mixed migratory or wintering flocks. Canada geese have also become more prominent in urban areas, and are now considered over abundant in more than 100 urban areas in 37 states (Mowbray et al. 2002). Increasing mixing of resident Canada geese with migrant Canada and cackling geese during migration and on winter areas has resulted in uncertainty of racial composition of harvests that has created management problems, and potentially threatening the viability of numerically depressed populations of both species across their North American ranges (Mowbray et al. 2002).

Snow and Ross's Geese

Historical Processes

Climatic changes over time have likely had a large effect on the phylogeographic structure of snow geese and Ross's geese, as both species currently breed in high latitude regions of North America that were recolonized from refugia in Beringia and other ice-free areas north of major glaciers (Figure 3). Snow geese and Ross's geese likely utilized these high Arctic refuges during the last Pleistocene glacial event (26,000-18,000 ybp; Ploeger 1968), and may have been isolated in separate refugia in east Siberia and the Bering Sea area (snow geese), and in the Western Canadian Arctic Archipelago (Ross's geese) during the previous glacial maximum (150,000-130,000 ybp). Within the snow geese complex, greater snow geese may have occupied refuge breeding grounds in western Greenland during the last glacial, and were likely geographically isolated from

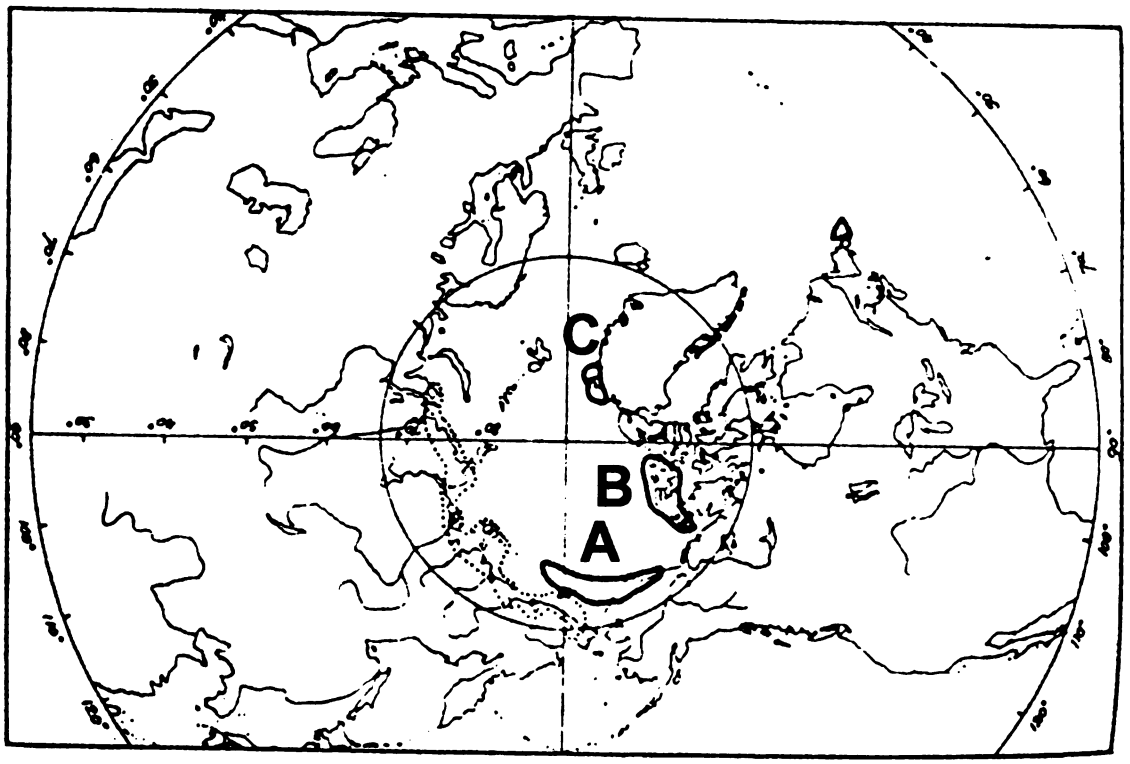

Figure 3. Breeding grounds for snow geese (*Chen caerulescens*) and Ross's geese (*C. rossii*) during the Last Glacial of the Pleistocene (Ploeger 1968). Refuge breeding areas for snow geese and Ross's geese included northeast Siberia and Bering Sea area (A): *C. c. caerulescens* (white color phase); the Canadian Arctic Archipelago (B): *C. c. caerulescens* (blue color phase) and *C. rossii*; and west Greenland (C): *C. c. atlanticus*.

lesser snow geese populations (Ploeger 1968). Blue-phase and white-phase lesser snow geese may have also been allopatric during this period, with blue-phase geese surviving in the Canadian Arctic Archipelago and white-phase geese inhabiting refuges farther west in Siberia and the Bering Sea region (Ploeger 1968, Cooke et al. 1988). Ploeger (1968) speculated that speciation occurred when snow and Ross's geese ancestors were isolated between the E. Siberia, Bering Sea area and the Canadian Arctic Archipelago, leading to

western and eastern populations from which lesser snow and Ross' geese subsequently arose.

Breeding Areas

About 95 percent of all Ross' geese breed in the central Canadian Arctic in the Queen Maud Gulf Migratory Bird Sanctuary (Kerbes 1994). Smaller numbers of Ross' also breed in other areas of the central Arctic including the west and south coasts of Hudson Bay, and on Southampton and Baffin Islands. Few Ross' geese are found breeding in the western Arctic on Banks Island and the north coast of Alaska (Ryder and Alisauskas 1995, Figure 1). Ross' geese nest in colonies interspersed with lesser snow geese, which breeds at very similar latitudes. Like Ross' geese, breeding populations of lesser snow geese are greatest in the central Canadian Arctic, and Ross's and snow geese breeding populations in this area are collectively termed the "mid-continent population". Lesser snow geese are more widely distributed across central and western Arctic breeding areas than Ross's geese, and are found at higher latitudes than Ross's geese. Greater snow geese breed in the high eastern Canadian Arctic, with the largest colony found on Bylot Island, and fewer numbers breeding on coastal areas of surrounding islands. Small numbers of lesser snow geese are found breeding in conjunction with greater snow geese colonies (Mowbray et al. 2000).

Wintering Areas

The Central Valley of California is the main wintering area for Ross's, though increasing numbers of these geese are wintering in Arkansas, Louisiana, New Mexico,

Texas, and the north-central highlands of Mexico (Turner et al. 1994, Figure 1). Lesser snow geese have a more extensive wintering range than Ross' geese, and are found within multiple wintering areas in Oregon, California, New Mexico, Oklahoma, Texas, numerous states along the Mississippi River in the Central and Mississippi Flyways, north and west Gulf Coast areas, and the highlands of Mexico (Figure 1). The largest numbers of lesser snow geese winter in coastal areas of Texas, Louisiana, and Mississippi (Mowbray et al. 2000, U.S. Fish and Wildlife Service 2001). Greater snow geese winter with small numbers of lesser snow geese in areas along the Atlantic coast from Massachusetts to South Carolina (Reed and Chagnon 1987, Cooke et al. 1995, Figure 1).

Population Size

In the early 1900s, the Ross' goose was considered a rare species, and hunting was prohibited in 1931 in an attempt to increase population sizes. Since that time, Ross' geese have increased from 2,000-3,000 birds to a current population of 700,000 (Ryder and Alisauskas 1995). Both Ross' geese and lesser snow geese have recently taken advantage of previously unavailable sources of food (agricultural plants and waste grain) on their wintering grounds and migration routes. Numbers of lesser snow geese have increased as much as 9 percent per year in some mid-continent populations, and current estimates are between 6 and 7 million birds (Mowbray et al. 2000). As lesser snow geese populations have increased, established colonies have expanded and new colonies have been established in western and central Arctic regions. Several breeding colonies have appeared south of Queen Maud Gulf (Alisauskas and Boyd 1994) and along Hudson Bay (Cooke et al. 1995) since 1950, and a colony was established on the North Slope of

Alaska during the early 1980s (Johnson 1995). Like Ross' geese, greater snow geese were estimated at 2,000-3,000 birds in the early 1900s (Hill and Frederick 1997). Greater snow geese have followed similar increasing trends as lesser snow geese, reaching 750,000 individuals in the late 1990's (Reed et al. 1998).

Ecology and Behavior

Female snow and Ross's geese exhibit a high degree of natal- and breeding site-fidelity compared to males, who are more likely to disperse (Rockwell and Cooke 1977, Geramita and Cooke 1982, Cooke 1987, Anderson et al. 1992, Drake and Alisauskas 2005). Males generally follow females to areas near their natal breeding colony after pairing on wintering grounds or during spring migration (Cooke et al. 1975, Greenwood 1980, Mowbray et al. 2000). Observers of lesser snow geese at LaPerouse Bay have documented up to twice as many adult females (75.8%) as males (33.7%) returning to a site in subsequent years (Cooke and Sulzbach 1978, Cooke et al. 1982), and fewer than 1% of males banded as goslings were resighted at their natal colony (Cooke et al. 1975). High levels of male mediated dispersal may considerably increase gene flow among breeding colonies of snow and Ross's geese (Rockwell and Barrowclough 1987).

Wintering site fidelity has been noted in several populations of snow and Ross's geese (Robertson and Cooke 1999). Winter affiliations of lesser snow geese nesting in the western Arctic have been examined using neck collar observations and degree of facial plumage staining acquired on winter feeding grounds (Baranyuk et al. 1999, Hines et al. 1999). In a banding study of Wrangel Island nesting lesser snow geese, Baranyuk et al. (1999) determined that 90% of marked birds with dark facial staining returned to

suspected wintering grounds in British Columbia and Washington; while 86% of marker birds with little or no facial staining returned to suspected wintering grounds in California. High rates of wintering ground fidelity (96-98%) were also estimated by Williams et al. (2005) based on banding observations for Wrangel Island and Banks Island geese.

For snow and Ross' geese, initial pairing occurs on the wintering grounds or during spring migration among 2 to 3-year-old-birds (Bellrose 1980, Cooke 1987, Cooke 2001, Ryder and Alisauskas 1995). Thus, pairs are formed when many regional populations are mixed, prior to their return to arctic breeding sites. Snow and Ross's geese exhibit long-term monogamy with strong pair bond stability (Anderson et al. 1992). Pair bonds last for life, but individuals will commonly pair and mate with a new individual if the partner dies (Prevett 1972, Bellrose 1980, Cooke et al. 1981).

In the fall and spring, lesser snow geese migrate primarily in the Mississippi and Pacific Flyways, and utilize the Central and Atlantic Flyways to a lesser extent. Ross' geese migrate along similar routes as lesser snow geese in the Mississippi and Pacific Flyways (Bellrose 1980). Greater snow geese are somewhat more isolated, as they travel down the Atlantic coast to the Carolinas in the fall, and return by the same route in the spring (Bellrose 1980, Reed et al. 1998). Some populations of snow and Ross' geese utilize more than one Flyway. For instance, approximately 80% of lesser snow geese from the Western Canadian Arctic and Wrangel Island migrate along the Pacific Flyway to California, while the remainder followed a path along the Central Flyway (Armstrong et al. 1999). Ross' geese from Queen Maud Island in the Central Canadian Arctic have

been documented migrating down the Missippi Flyway to the Gulf Coast, and along the Pacific Flyway to the California Coast (Alisauskas 1998a).

Genetic Studies

Mitochondrial markers employed to examine the genetic characteristics of snow and Ross' geese have been used in multiple studies to investigate the level of genetic structuring within and among these species (Avise et al. 1992, Quinn et al. 1992, Weckstein et al. 2002). Like cackling and Canada geese, two major clades of mtDNA haplotypes exist among white geese (Avise et al. 1992). However, mtDNA haplotypes within each white goose clade were found to be widespread among populations of snow and Ross' geese in all previous studies (Avise et al. 1992, Quinn 1992, Weckstein et al. 2002). Based on the wide distribution of haplotypes, Avise et al. (1992) concluded that snow and Ross' geese had no current phylogeographic structure, and hypothesized clade differences were a result of secondary introgression among the two species. Quinn (1992) argued that mtDNA sequences within one of the two haplotype clades were concordant with the geographic location of eastern and western populations of snow geese. Ten years later, Weckstein et al. (2002) added sampling locations and individuals to Quinn's dataset and concluded the level of mtDNA variation was consistent with the hypothesis that sharing of two mtDNA haplotype lineages between snow and Ross' geese resulted from secondary introgression, or hybridization (Avise et al. 1992). Weckstein et al. (2002) further stated that population structure found within one haplotype cluster supported the notion of past allopatry between blue and white phase lesser snow geese (Cooke et al. 1988). The slight discrepancies among these studies may be clarified by

increasing number of snow and Ross' populations, and number of individuals, sampled for phylogeographic analyses. In addition, biparentally inherited microsatellite markers could be used in conjunction with maternally inherited mtDNA to investigate the influence of contemporary verses historical influences on the genetic structure of these two species.

Cackling and Canada Geese

Historical Processes

Based on species ecology, nesting habits, and availability of unglaciated breeding habitat available during the Pleistocene, Ploeger (1968) identified four major breeding areas for cackling and Canada geese (Figure 4). He hypothesized that Canada geese inhabited refugia south of the major ice sheets, while cackling geese were found north of the glaciers in the Aleutian Islands and Canadian Arctic Archipelago. Canada geese were split between the "Western Southern Group" nested in the Pacific coastal region south of the Cordilleran ice sheet and included current subspecies *B. c. fulva* and *B. c. occidentalis*; and an "Eastern Southern Group" composed of current subspecies *B. c. canadensis*, *B. c. interior*, *B. c. maxima*, *B. c. moffitti*, and *B. c. parvipes* nested south of the Cordilleran and Laurentide ice sheets east of the Cascade and Sierra Nevada Mountains. Cackling geese were also said to inhabit two refugia including the "Aleutian Group" where *B. h. leucopareia* nested; and the "Northern Group" of the Canadian Archipelago which included the three remaining recognized subspecies, *B. h. minima*, *B. h. taverneri*, and *B. h. hutchinsii*. During the last glacial event, each of these four groups

was likely isolated, although intermixing between subspecies within a group was still possible (Ploeger 1968).

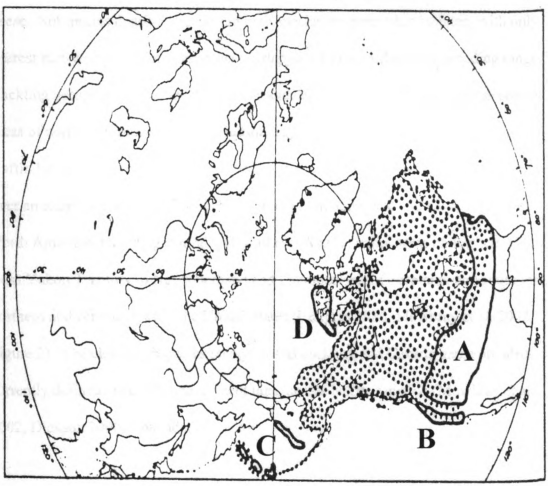

Figure 4. Breeding grounds for Canada geese (*Branta canadensis*) and cackling geese (*B. hutchinsii*) during the Last Glacial of the Pleistocene (Ploeger 1968). Refuge breeding areas for Canada geese included the Eastern Southern Group (A): *B. c. canadensis, B. c. interior, B. c. maxima, B. c. moffitti, B. c. parvipes*; and the Western Southern Group (B): *B. c. fulva, B. c. occidentalis*. Refuge breeding areas for cackling geese included the Aleutian Group (C): *B. h. leucopareia*; and the Northern Group (D): *B. h. minima, B. h. taverneri, B. h. hutchinsii*. Subspecies designations follow Banks et al. (2004). Stippled area represents the breeding range of Canada geese and cackling geese as defined by Ploeger (1968) in the late 1960's.

Breeding Areas

The breeding ranges for the four subspecies of Cackling geese are generally located at higher latitudes than the breeding ranges of the seven subspecies of Canada geese. Subspecies distributions within both species are somewhat isolated, with only nearest east-west neighbor subspecies overlapping a given subspecies breeding range. Cackling geese breed from the Aleutian Islands and coastal Alaska east across coastal areas of northern Canada and west Hudson Bay, and on Victoria, Southampton, and Baffin Islands (Mowbray et al. 2002, Banks et al. 2003, Figure 2). Canada geese breed over an extremely wide range of habitats throughout temperate and arctic regions of North American including central and southeast Alaska, many areas of northern Canada from Yukon Territory to Newfoundland and Labrador, west Greenland, and south into the northern and central areas of the United States (Bellrose 1980, Mowbray et al. 2002, Figure 2). The eleven subspecies recognized as cackling and Canada geese are also currently defined under 19 management units across North America (Mowbray et al. 2002, Dickson 2000, Appendix 1).

Wintering Areas

The wintering range of cackling geese includes southeast coastal Alaska, southern British Columbia, southern Washington state and northern Oregon, and the Central Valley of California for the western breeding populations; and southwest Texas, northern Mexico, and the western Gulf coast for cackling geese breeding in the central and eastern Arctic (Bellrose 1980, Banks et al. 2003, Figure 2). Wintering areas for Canada geese

include most of the United States, northern highlands of Mexico, and the Atlantic and Gulf coasts of Mexico (Bellrose 1980, Mowbray et al. 2002, Figure 2).

Population Size

Canada and cackling geese have generally increased in North America since the mid-century, resulting in current estimates of approximately 4.5 million for Canada geese and 600,000 for cackling geese (Mowbray et al. 2002). However, population indices are not available for some subspecies (i.e., *B. c. parvipes and B. c. fulva*), some subspecies are not well surveyed in portions of their range, and some local populations and subspecies (*B. h. minima*) have declined during this period (Drut and Trost 2001, Mowbray et al. 2002). Populations of local Canada geese breeding in the northern United States have rapidly increased in recent years, with some groups losing their migratory habits and becoming established as year-round residents.

Ecology and Behavior

Cackling and Canada geese exhibit strong female and male fidelity to breeding grounds, (Greenwood 1980, Lessells 1985, Sjoberg and Sjoberg 1998). Both Lessells (1985) and MacInnes and Lieff (1968) documented return rates to breeding grounds (50-60%) to be approximately equal for males and females. In contrast, rates of natal fidelity are female–biased, and much lower (3-10%) than rates of breeding ground fidelity (MacInnes and Lieff 1968, Surrendi 1970).

Wintering site fidelity has been documented for several subspecies of cackling and Canada geese. Raveling (1979) estimated winter site fidelity for Canada geese (*B.c.*

maxima) to be 80.0% for male and 76.7% for female yearlings, and 69.2% for male and 48.9% for female 2-year-olds. Similar proportions of marked cackling and Canada geese (juveniles-68%, adults-73%) returned to California wintering areas over a two year study (Johnson and Raveling 1988). In a study of eastern U.S. wintering areas for Canada geese populations, Hestbeck et al. (1991) found winter fidelity rates of *B. c. canadensis* to be 71.0% for mid-Atlantic states, 88.9% near the Chesapeake Bay, and 56.2% for the Carolinas.

Cackling and Canada geese may pair as yearlings, but are more likely to first pair and breed when they are in their second year (Craighead and Stockstad 1964, Raveling 1981). Initial pair bonds in cackling and Canada are formed in the spring during northward migrations or after the geese have returned to breeding sites (MacInnes 1966, Hanson 1997). Both cackling and Canada geese exhibit long-term monogamy (Anderson et al. 1992, Mowbray et al. 2002), and pairs will generally remain together through multiple breeding seasons, unless one of the pair dies (Bellrose 1980). Studies have illustrated, however, that pair bond stability is variable among subspecies of cackling and Canada geese (Johnson and Raveling 1988, Raveling 1988, Ely and Scribner).

Cackling and Canada geese show strong affiliation to particular migration routes, resulting in highly localized populations (Craven and Rusch 1983, Tacha et al. 1991, Didiuk and Caswell 1998, Gill et al. 1998). Their geographic migration patterns are so consistent that wildlife managers and biologists often refer to the recognized population groups that utilize each of the four Flyways in North America (Figure 2; Malecki and Trost 1998). Migration distances between breeding and wintering areas varies greatly, with individuals from Arctic and sub-Arctic areas of Canada and Alaska traveling the

greatest distances to midlatitude and southern areas of the United States. Populations nesting in southern Canada and northern states of the U. S. migrate shorter distances (Mowbray et al. 2002). Some populations of Canada geese winter within their breeding area, or have lost their migratory habit altogether (Mowbray et al. 2002). Northward molt-migrations have been documented for non-breeding Canada geese from populations in the northern U.S. and southern Canada (Abraham et al. 1999, Luukkonen et al. 2004).

Genetic Studies

Molecular studies of cackling and Canada geese have addressed subspecies distinctions and phylogeography of these two sister species as one taxonomic group previously recognized as one species, Canada geese (Delcour 1956, Bellrose 1980). Past projects focused on mitochondrial (mt) DNA illustrated large differences in haplotypes resolved for "small-bodied" Canada geese subspecies (now known as cackling geese) as compared to haplotypes found in "large-bodied" Canada geese subspecies (Shields and Wilson 1987, Van Wagner and Baker 1990, Quinn et al. 1991, Baker 1998, Shields and Cotter 1998). Although earlier studies suggested Canada geese subspecies could be unambiguously distinguished on the basis of haplotype, it is now recognized that common haplotypes are shared across multiple geographic locales and subspecies within the small-bodied clade (cackling geese) and within the large-bodied clade (Canada geese). No known mtDNA haplotypes are shared between cackling geese and Canada geese (Scribner et al. 2003a).

An investigation of the mtDNA and nuclear DNA of subspecies of cackling and Canada geese in western North America revealed considerable spatial genetic structure at

macro- and micro-geographic scales. In this region, differences between cackling and Canada geese were most influenced by historical population fragmentation, while isolation by distance and long-distance colonization events were the main factors driving genetic differences among subspecies within each species (Scribner et al. 2003a). Scribner et al. (2003b, 2003c) have completed several genetic-based investigations of management populations of cackling and Canada geese in the Mississippi and Atlantic Flyways, but no comprehensive, species-wide phylogeographic study has yet been conducted for cackling and Canada geese in North America.

OUTLINE OF CHAPTERS

Chapters 2 and 3 describe the comprehensive species-wide phylogenetic analyses of Canada geese and cackling geese, and snow geese and Ross's geese within North America. By utilizing molecular markers which differ in their mode of inheritance and evolutionary rates, I survey the degree of genetic variation at the levels of populations, subspecies, and species within Canada and cackling geese and within snow and Ross's geese. I assess the relative influence of historical processes and current behavioral and ecological factors on the spatial genetic structure revealed for both groups of taxa. Current population, subspecies, and species designations are then evaluated for snow and Ross's geese and for cackling and Canada geese based on the degree of phylogenetic structure resolved. These chapters build upon previous genetic studies for both taxonomic groups by expanding the number of individuals sampled, including sampling locations from all subspecies and major breeding populations within each species, and by

characterizing subspecies and populations sampled using both microsatellite and mtDNA markers.

Chapters 4, 5, and 6 utilize the genetics data collected as part of the phylogenetic analyses to address questions related to the harvest management of cackling and Canada geese. It has recently been demonstrated that the degree of genetic population structuring among localized groups of cackling and Canada geese can be used successfully for purposes of harvest derivation (Pearce et al. 2000, Scribner et al. 2003b). Potentially contributing populations and samples from harvest mixtures can be characterized using nuclear microsatellite loci, and compared using mixed stock analyses (Pella and Milner 1987, Smouse et al. 1990, Xu et al 1994) in order to estimate the proportional contributions of management populations, subspecies, and species in harvest mixtures. Two species (Richardson's cackling geese, and interior and giant subspecies of Canada geese) and four management populations [Tall Grass Prairie Population (TGPP), MVP, SJBP, and Michigan's Mississippi Flyway Giant Population (MI-MFGP)] of geese potentially contribute to mixed annual harvests in the state of Michigan. Harvest policies developed by the Michigan Department of Natural Resources seek to target the large and rapidly growing population of resident giant Canada geese (*Branta canadensis maxima*) and avoid harvest of migrant interior (*B. c. interior*) Canada geese and cackling geese (*B. hutchinsii hutchinsii*) (Soulliere et al. 1988, Luukkonen and Soulliere 2004).

Chapter 4 focuses on the joint use of standardized parts collections and genetic-based analyses for harvest derivations. I describe how statewide harvest samples collected through the United States Fish and Wildlife Service's Waterfowl Parts Survey can be used in conjunction with maximum likelihood methods to accurately estimate

proportional harvests of populations of cackling and Canada geese. Previous harvest studies in the state (Scribner et al. 2003b) collected harvested geese from a few private hunting areas and from state game area check stations (areas managed to attract migratory cackling and Canada geese). By utilizing the broad-based and systematic sampling provided by the Parts Survey, and by increasing the number of breeding populations in the baseline, I provide more representative statewide measures of the racial composition of goose harvest in Michigan as compared to previous harvest studies.

In Chapter 5, I utilize established methods of genetic stock identification and nationally standardized sample collections (as described in Chapter 4) to estimate proportional contributions of three subspecies (cackling geese, and interior and giant Canada geese) and four management populations (TGPP, MVP, SJBP, MI-MFGP) of geese to consecutive annual harvests over the period 1998-2002 in Michigan. The Michigan Department of Natural Resources has implemented special early and late goose seasons, and has shifted the opening date of the regular season from early October to mid-September in order to target a large and rapidly growing population of resident giant Canada geese and avoid harvest of migrant interior Canada geese and cackling geese (Soulliere et al. 1988, Luukkonen and Soulliere 2004). Thus, harvest derivations are conducted for multiple geographic and temporal breakdowns of statewide harvests, in order to evaluate harvest regulations in Michigan including special seasons and harvest zones.

Chapter 6 is a comparative analysis of harvest of cackling and Canada geese in Michigan estimated using three different derivation techniques. Results of the genetic-based harvest derivations from Chapter 5 will be compared and contrasted to harvest

estimates derived from morphological measures and band-return data for the same five year period in Michigan. An additional comparative analysis of a special early season harvest from 2000 – 2002 will be conducted using genetic and morphometric derivation techniques. A discussion of the efficacy of using each derivation technique at different spatial and temporal scales of harvest will follow.

Chapter 7 is focused on the management concerns surrounding the lesser snow goose breeding population located on Wrangel Island, Russia. In contrast to the Mid-Continent Population of lesser snow geese, and the Banks Island colony in the western Arctic, the Wrangel Island population has experienced considerable declines over the past 35 years (Kerbes et al. 1999). A better understanding of the population structure among breeding and wintering western arctic snow geese in terms of accurately defining appropriate management units, identifying demographic constraints on population dynamics, and determining the level of interaction and gene flow among populations, is important for the conservation and management of the Wrangel Island population.

Lesser snow geese on Wrangel Island form one of two large breeding colonies in the western arctic, and is the only remaining snow goose colony in Asia (Boyd 1995). In addition, the Wrangel Island population is composed of two subpopulations which nest in a single mixed colony, but winter in two separate locales in the Pacific Flyway (Bousfield and Syroechkovsky 1985). The more northern wintering group is found in Canada and northern Washington, and is exclusively Wrangel Island birds, while the southern wintering group in California includes lesser snow geese from Wrangel and Banks Islands, and Ross' geese and a small number of lesser snow geese from Queen Maud Gulf (central arctic) (Ryder and Alisauskas 1995, Mowbray et al. 2000). Further

complicating population assessment is the likely exchange of geese from the north and south wintering Wrangel Island population with the Banks Island population (Hines et al. 1999). The wealth of banding data available for these western Arctic populations (Armstrong et al 1999, Hines et al. 1999, Samuel et al. 2001), and the current availability of molecular markers, offers a unique opportunity to examine the degree of population structuring among the Wrangel Island and Banks Island colonies using multiple techniques. A genetic analysis of both the north and south wintering populations of Wrangel Island and the Banks Island population will be conducted using nuclear and mtDNA markers. Genetics data will be compared to recent mark-resight banding studies of Wrangel and Banks snow geese, to determine relative levels of historical and contemporary gene flow among populations, and to evaluate population structuring among breeding and wintering groups.

Appendix 1. Breeding and wintering ranges, migration routes and subspecific composition of 19 management units of cackling (*Branta hutchinsii*) and Canada (*Branta canadensis*) geese (adapted from Appendix 1, Mowbray et al. 2002).

North Atlantic (*B. c. canadensis*): Breeds from w. Greeland west and south to e. Labrador and Newfoundland; migrates down Labrador coast to Maritimes and south along New England coast; winters south along Atlantic Coast to Long Island Sound and in smaller numbers south to Pea Island, North Carolina.

Atlantic (*B. c. interior*): Breeds throughout Quebec, with highest breeding concentrations along coast of Ungava Bay and northeast coast of Hudson Bay; migrates south along east shore of Hudson and James Bays, across New York and e. Pennsylvania to Eastern Shore of Maryland; winters from New England south to South Carolina, with highest densities on Delmarva Penninsula.

Atlantic Flyway Resident (*B. c. canadensis*, *B. c. interior*, *B. c. maxima*): Breeds and winters from s. Quebec and Maritime Provinces south throughout states of Atlantic Flyway.

Southern James Bay (*B. c. interior*): Breeds on Akimiski Island and adjacent coastal lowlands of s. James Bay; migrates south from James Bay across central Great Lakes; winters from s. Michigan south to Mississippi, Alabama, Georgia, and South Carolina.

Mississippi Valley (*B. c. interior*): Breeds throughout n. Ontario, in coastal lowlands south of Hudson Bay; migrate from west shore of James Bay and south shore of Hudson Bay south down each side of Lake Michigan; winters from se. Wisconsin south, east of Mississippi River, to s. Illinois.

Eastern Prarie (*B. c. interior*): Breeds in Hudson Bay lowlands of ne. Manitoba; migrates from east coast of Hudson Bay southwest to interlakes region of Manitoba, then souther through w. Minnesota and e. Dakotas; winters from Minnesota south to Missouri.

Mississippi Flyway (*B. c. maxima*): Re-established throughout states of Mississippi Flyway; breeds and winters throughout region.

Western Prairie/Great Plains (*B. c. maxima*/*B. c. moffitti*): Breeds throughout Saskatchewan, North and South Dakota, Nebraska, Kansas, Oklahoma, and Texas; northernmost breeders migrate south to Missouri River, then along river; winters from Missouri River in South Dakota south to Texas.

Tallgrass Prairie (*B. h. hutchinsii*, possibly includes some *B. c. parvipes*): Breeds in n. Canada from Great Plain of the Koukdjuak on Baffin Island west to Queen Maud Gulf and south to McConnell and Maguse Rivers on west coast of Hudson Bay; migrates south from staging areas on west coast of Hudson Bay along a broad corridor down Mississippi River; winters from Louisiana west to ne. Mexico, with a major concentration in Oklahoma.

Shortgrass Prairie (*B. h. hutchinsii* and some *B. c. parvipes*): Breeds from Queen Maud Gulf westward to Mackenzie River delta, including s. Queen Victoria Island, and inland at lower densities in n. Alberta; migrates in separate eastern and western corridors from breeding areas to staging areas in se. Alberta and sw. Saskatchemwan and then in a single corridor south; winters in se. Colorado, ne. New Mexico, and panhandle ares of Oklahoma and Texas.

Hi-line (*B. c. moffitti*): Breeds in se. Alberta, sw. Saskatchewan, e. Montana, Wyoming, and n.-central Colorado; migrates just a short distance southward; winters from n.-central Colorado south to central New Mexico.

Appendix 1 (cont'd).

Rocky Mountain (*B. c. moffitti*): Breeds from sw. Alberta south through intermountain regions of w. Montana, Utah, Idaho, Nevada, Colorado, and Wyoming; migration a complex set of movements from higher elevations to lower elevations and in some cases a short distance south; winters from Montana south to s. California, s. Nevada, and Arizona.

Pacific (*B. c. moffitti*): Breeds and winters from s. British Columbia south, west of the Rockies and Idaho, w. Montana, Washington, and Oregon to nw. Nevada and n. California.

Dusky (*B. c. occidentalis*): Breeding restricted to Copper River delta and adjacent areas of se. Alaska; migrates south along Pacific coast; winters in Willamette River Valley of w. Oregon and along lower Columbia River in n.-central Oregon and s.-central Washington.

Cackling (*B. h. minima*): Breeds on Yukon-Kuskokwim Delta of w. Alaska; migrates from staging areas on shores of Bristol Bay, across Gulf of Alaska, south to Columbia River, Oregon; winters primarily in Willamette River valley of w. Oregon and lower Columbia River valley of n.-central Oregon and s.-central Washington, with small numbers (<10%) in central valleys of California.

Aleutian (*B. h. leucopareia*): Re-established and successfully breeds on several fox-free islands in Aleutians; migrates from staging areas in Aleutians south across Gulf of Alaska to n. California coast; winters primarily in San Joaquin Valley of central California, with small wintering concentrations along Oregon coast.

Pacific Flyway Lesser (*B. c. parvipes*): Breeds throughout much of central interior Alaska; migrates south from interior of Alaska along Pacific coast; winters in Washington, Oregon, and California.

Taverner's (*B. h. taverneri*): Breeds in w. Alaska and coastal tundra from Yukon-Kuskokwim Delta around to north slope of Alaska; migrates from coastal staging areas at tip of Alaska Peninsula south over water in fall, returns north through interior valleys of British Columbia and Yukon Basin in spring; winters primarily in Willamette River valley of w. Oregon and lower Columbia River valley of n.-central Oregon and s.-central Washington.

Vancouver (*B. c. fulva*): Breeds in extreme sw. Alaska and coastal areas of nw. British Columbia; winters over much of same area, from se. Alaska south along coast of British Columbia; occasionally to Willamette River valley of w. Oregon and lower Columbia River valley of n.-central Oregon and s.-central Washington.

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CHAPTER 2: CACKLING GEESE AND CANADA GEESE PHYLOGEOGRAPHY

INTRODUCTION

Spatial patterns of genetic diversity within and among species can be influenced by historical and contemporary processes (Avise et al. 1987, Avise 1998). Past vicariant events, such as restrictions of populations within isolated refugia during Pleistocene or Pliocene glacial periods and subsequent range expansion during interglacial periods, have likely contributed greatly to the phylogeographic structure of species and to cladogenic events (Avise and Walker 1998, Zink 1996, Klicka and Zink 1997, Voelker 1999). Other historical factors that may influence the genetic structure of species include size of populations during glacial and interglacial periods, length of time populations experienced geographic and reproductive isolation, and length of time since population separation (Avise et al. 1998, Emerson et al. 2001, Stewart and Lister 2001). Longer separation times and smaller effective population sizes in isolated populations increase the probability populations will accrue differences in gene frequencies and develop novel gene mutations (Avise et al. 1988). Historical population expansions occurring in a single, punctuated event, and with a low number of founding individuals, could appreciably change allele and haplotype frequencies in the founding population as compared to the population of origin. Alternatively, if expansion events included a large number of individuals over a prolonged time period, then gene frequencies may be similar among populations (Mila 2000, Hewitt 2001).

Ecology and life history characteristics that may affect species genetic structure include timing and location of pair bond formation, degree and sex-specificity of

philopatry, level of gene flow among contemporary breeding and/or wintering populations, and current sizes of populations (Greenwood 1980, Chesser 1991a, Chesser 1991b, Ely and Scribner 1994, Miyatake and Shimizu 1999). High natal and breeding site philopatry, and pair bond formation during periods when breeding populations are isolated, will tend to restrict gene flow and increase genetic structure among populations (Rockwell and Barrowclough 1987). Fidelity to wintering sites may increase among population genetic variation if populations are isolated in wintering areas, or homogenize gene frequencies if populations are admixed in wintering areas and pair bond formation occurs on these wintering sites (Robertson and Cooke 1999). Gene flow that is sex-biased may lead to differences in the degree of among population genetic variation revealed by maternally and bi-parentally inherited markers (Chesser 1991a, Scribner et al. 2001). Information on the degree of genetic discordance among mitochondrial (mt) DNA haplotypes, and the frequencies of shared and novel haplotypes and nuclear DNA alleles provides sources of inference to past events and species ecology. Large fundamental divisions in the topology of an intraspecific phylogeny reflect historical evolutionary splits within a taxa, while shallower molecular topologies are evidence of more recent population subdivisions (Avise 1992). The relative importance of ecological and historical factors in shaping spatial genetic structure is likely to be taxon specific.

Previous studies have shown that North American species exhibit a variety of phylogeographic patterns ranging from near panmictic [e.g., harlequin ducks (*Histrionicus histrionicus*) Lanctot et al. 1999; king eiders (*Somateria spectabilis*) Pearce et al. 2004] to species with strongly subdivided subspecies [Wilson's warblers (*Wilsonia pusilla*), Kimura et al. 2002) or population genetic structure within species [dunlins

(*Caldris alpine*), Wenink et al. 1994]. Phylogenetic investigations have been conducted for a wide variety of North American avian species (see review in Avise and Walker 1998), including songbirds and Neotropical migrants (Zink 1996, Kimura et al. 2002), shorebirds (Wenink et al. 1994), wading birds (Rhymer et al. 2001), and migratory waterfowl (Avise et al. 1992, Quinn 1992, Scribner et al. 2001, Scribner et al. 2003a, Pearce et al. 2004, Peters et al. 2005). Patterns of spatial genetic structure vary greatly among co-distributed avian species (Zink 1996, Avise and Walker 1998). Some species, like the song sparrow (*Melospiza melodia*), red-winged blackbird (*Agelaius phoeniceus*; Zink 1996), turnstone (*Arenaria interpres*; Wenink et al. 1994), and king eider (*Somateria spectabilis*; Pearce et al. 2004) exhibit little genetic differentiation across there geographic ranges, likely as a result of recent population expansions from a single glacial refugia and high levels of among population gene flow subsequent to the last Pleistocene glacial period. Significant intraspecies genetic variation consistent with population divergence in multiple glacial refugia has been found in fox sparrows (*Passerella iliaca*; Zink 1996), Wilson's warblers (*Wilsonia pusilla*; Kimura et al. 2002), rock ptarmigans (*Lagopus mutus*; Holder et al. 1999), dunlins (*Caldris alpine*; Wenink et al. 1994), and Canada geese (*Branta canadensis*; Scribner et al. 2003a). In some species genetic population structure is attributed strong natal and breeding philopatry (e.g., dunlin, Wenink et al. 1994) or to high fidelity to wintering sites [e.g., snow geese (*Chen caerulescens*) and Ross's geese (*Chen rossii*), see Chapter 6]. Thus, differences in the degree of genetic divergence evident in co-distributed North American avian species can result from both historical processes and species life history characteristics which influence contemporary levels of gene flow.

Two species of Arctic-nesting geese, Cackling geese (*Branta hutchinsii*) and Canada geese (*Branta canadensis*) (considered one species, *B. canadensis*, with 11 recognized subspecies until 2003; Banks et al. 2003), have highly variable phenotypes, ecology, and behavioral characteristics (Delacour 1954, Palmer 1976, Bellrose 1980, Owen 1980). Subspecies of cackling and Canada geese were originally defined on the basis of morphology and plumage characteristics (Delacour 1954, American Ornithologists' Union 1957). As these characters vary geographically, as few as 8 (Palmer 1976) and as many as 83 (Hanson 1997) subspecies have been recognized for cackling and Canada geese. Current subspecies include *B. h. hutchinsii*, *B. h. minima*, *B. h. taverneri*, and *B. h. leucoparia* for cackling geese; and *B. c. maxima*, *B. c. moffitti*, *B. c. interior*, *B. c. canadensis*, *B. c. parvipes*, *B. c. occidentalis*, and *B. c. fulva* for Canada geese (Banks et al. 2003). Breeding populations of cackling geese are primarily coastal, and are located on the Aleutian and Semidi Islands off the Alaskan coast, northern and western Alaska, coastal areas of northern Canada, and Southampton and Baffin Islands (Figure 1). Cackling geese winter from British Columbia south to California and east to north Mexico and western Louisiana (Mowbray et al. 2002). Canada geese breeding populations are found throughout Canada and the northern United States, and winter from the southern part of the breeding range through most of the United States and into Mexico (Figure 1; Mowbray et al. 2002).

Cackling geese and Canada geese are currently managed in North America by species, subspecies, by affiliation to one of the four migratory Flyways (Figure 1), and by management populations for cackling and Canada geese combined; Dickson 2000, Moser and Caswell 2004). Population affiliation to migratory Flyways and delineation of

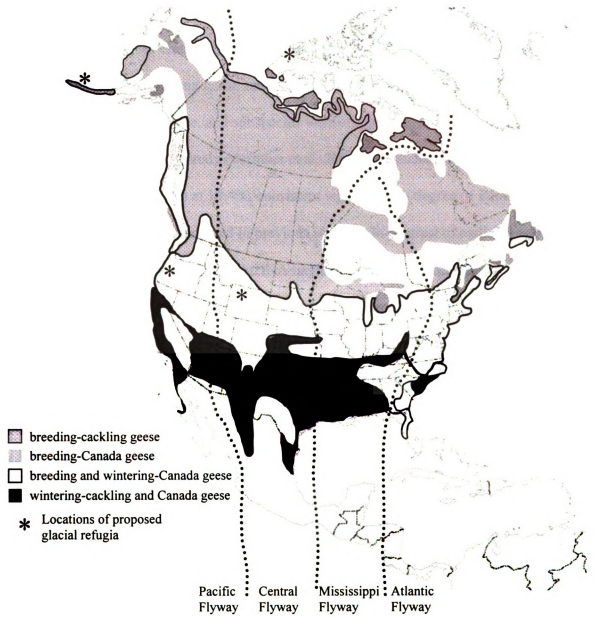

Figure 1. Breeding and wintering distributions and migratory Flyways for cackling geese (*Branta hutchinsii*) and Canada geese (*Branta canadensis*). Locations of Pleistocene glacial refugia proposed by Ploeger (1968) are indicated.

management populations has been determined by numerous migratory and breeding surveys, banding studies, and harvest data over the past 50 years (Moser and Caswell 2004). Early genetic studies based on mitochondrial DNA (mtDNA) supported current species and subspecies classifications (Shields and Wilson 1987, VanWagner and Baker 1990, Baker 1998). Cackling geese and Canada geese were found to differ by an average of 2.0% sequence divergence, and subspecies were characterized by distinct mtDNA haplotypes. A more recent study (Scribner et al. 2003a) estimated the sequence divergence between species at 14.4%, consistent with the high degree of interspecies genetic differentiation documented in previous studies. In contrast to earlier research, Scribner et al. (2003) found shared mtDNA haplotypes in high frequencies among subspecies of cackling geese and among subspecies of Canada geese. Differences in study results for subspecies may have been due to much larger sample sizes analyzed per subspecies in the work of Scribner et al. (2003a). Additionally, previous studies relied on characterization of mtDNA through restriction fragment analysis, which resolved sequence variation over a larger portion of the mtDNA molecule than in the Scribner et al. (2003) study, where a portion of the mtDNA genome was directly sequenced.

For Arctic-nesting waterfowl, current breeding areas and migratory pathways between breeding and wintering areas have evolved over relatively recent timescales (Ploeger 1968). High levels of genetic divergence documented previously between cackling geese and Canada geese is indicative of a fundamental geographic split that may have occurred during Pleistocene glacial events (Ploeger 1968). Based on species ecology, nesting habits, and availability of unglaciated breeding habitat available during the Pleistocene, Ploeger (1968) identified four major breeding areas for cackling and

Canada geese. He hypothesized that Canada geese inhabited refugia south of the major ice sheets, while cackling geese were found north of the glaciers in the Aleutian Islands and Canadian Arctic Archipelago. Canada geese were split between the "Western Southern Group" nested in the Pacific coastal region south of the Cordilleran ice sheet and included current subspecies *B. c. fulva* and *B. c. occidentalis*; and an "Eastern Southern Group" composed of current subspecies *B. c. canadensis*, *B. c. interior*, *B. c. maxima*, *B. c. moffitti*, and *B. c. parvipes* nested south of the Cordilleran and Laurentide ice sheets east of the Cascade and Sierra Nevada Mountains. Cackling geese were also said to inhabit two refugia including the "Aleutian Group" where *B. h. leucopareia* nested; and the "Northern Group" of the Canadian Archipelago which included the three remaining extant subspecies, *B. h. minima*, *B. h. taverneri*, and *B. h. hutchinsii*. Evidence of the biogeographic isolation of cackling and Canada geese in the four proposed glacial refugia would be reflected in a deep phylogenetic split between species and between subspecies groups associated with separate refugia.

In addition to historical separations based on glacial refugia, long-term family associations and strong male and female breeding site fidelity exhibited by cackling and Canada geese (Anderson et al. 1992, Ely and Scribner 1994, Mowbray et al. 2002) may reproductively isolate breeding populations and influence current partitioning of genetic variation. Initial pair bonds in cackling and Canada geese are formed in the spring during northward migrations or after the geese have returned to breeding sites (MacInnes 1966, Hanson 1997), and pairs exhibit long-term monogamy (Bellrose 1980). Significant spatial genetic structure among breeding populations may result from breeding site

fidelity and formation of pair bonds on breeding grounds, even though populations share migratory pathways and wintering areas (Ely and Scribner 1994, Scribner et al. 2003a).

Cackling and Canada geese show strong affiliation to particular migration routes, resulting in highly localized populations (Craven and Rusch 1983, Tacha et al. 1991, Didiuk and Caswell 1998, Gill et al. 1998). Their geographic migration patterns are so consistent that wildlife managers and biologists often refer to the recognized population groups that utilize each of the four migratory Flyways in North America (Figure 1; Malecki and Trost 1998). Populations that share migratory routes and common wintering areas within Flyways may experience a higher degree of among population gene flow than populations from different Flyways. Gene flow occurring among populations within the same Flyway via exchange of individuals during migration and wintering periods may increase the genetic similarity of breeding populations within a Flyway, and increase the spatial genetic structure among Flyway groups.

Both cackling and Canada geese are well-studied species (Mowbray et al. 2002) that are highly managed to maintain viable breeding populations for sustained harvests. The wealth of survey, banding, and harvest data have helped to develop the current administrative Flyway and management population definitions (Figure 1, Moser and Caswell 2004), and offer information on the life history characteristics of these species on which hypotheses of contemporary levels of gene flow may be based. We evaluate the phylogenetic structure within and among cackling geese and Canada geese due to historic geographic isolations in proposed glacial refugia and current levels of gene flow at population and Flyway scales by utilizing molecular markers which differ in their mode of inheritance and evolutionary rates. We build upon previous studies by sampling

breeding populations of cackling and Canada geese across their entire continental distribution. We genetically characterizing a large number of individuals from each location using bi-parentally inherited microsatellite loci and mtDNA sequence data from the maternally inherited mitochondrial control region. As all eleven subspecies and all four Flyway groups of cackling and Canada geese are represented in our analyses, we can estimate the degree of spatial genetic structure between species and among subspecies of cackling and Canada geese based on proposed glacial refugia, among Flyway groups of both species, and among breeding populations of throughout the continental range of cackling and Canada geese. Genetics data is used to characterize and interpret the phylogenetic structure of species, subspecies, and populations of geese utilizing each of the four migratory Flyways, and to predict the relative importance of historical and contemporary factors influencing phylogenetic structure.

METHODS

Sample Collection

Samples were collected from 6 breeding populations of cackling geese (*Branta hutchinsii*) and 16 breeding populations of Canada geese (*B. canadensis*) (Figure 2), representing each of the four subspecies of cackling geese and seven subspecies of Canada geese recognized in North America (Bellrose 1980, Banks et al. 2003). Geese were guided into catch nets using a helicopter or by walking during brood rearing, when geese were flightless (Cooch 1953, Timm and Bromley 1976). Blood or a blood quill (growing feather) was sampled from breeding adults or goslings at each location. Samples were placed into individual tubes containing high-salt buffer and stored at

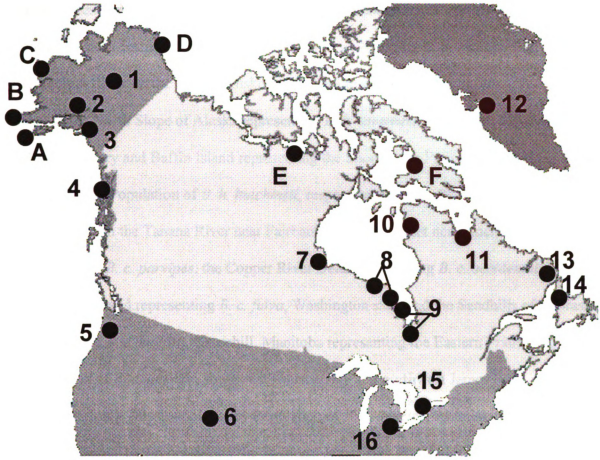

Figure 2. Sampling locations for subspecies of cackling geese (letters) and Canada geese (numbers) populations: A = Semidi Island (*Branta hutchinsii leucoparia*), B = Buldir Island (*B. h. leucoparia*), C = Yukon-Kuskokwim Delta (*B. h. minima*), D = North Slope (*B. h. taverneri*), E = Queen Maud Gulf Bird Sanctuary (*B. h. hutchinsii*, Short Grass Prairie Population), F = Baffin Island (*B. h. hutchinsii*, Tall Grass Prairie Population); 1 = Fairbanks (*B. canadensis parvipes*), 2 = Anchorage (*B. c. parvipes*), 3 = Copper River Delta (*B. c. occidentalis*), 4 = Admiralty Island (*B. c. fulva*), 5 = Washington (*B. c. moffitti*), 6 = Nebraska Sandhills (*B. c. moffitti*), 7 = Churchill (*B. c. interior*, Eastern Prairie Population), 8 = Hudson and James Bays (*B. c. interior*, Mississippi Valley Population), 9 = Akimiski Island and southern James Bay (*B. c. interior*, Southern James Bay Population), 10 = West Ungava Peninsula (*B. c. interior*), 11 = East Ungava Peninsula (*B. c. interior*), 12 = Greenland (*B. c. interior*), 13 = Newfoundland (*B. c. canadensis*, North Atlantic Population), 14 = Labrador (*B. c. canadensis*, North Atlantic Population), 15 = Ontario (*B. c. maxima*), 16 = southeast Michigan (*B. c. maxima*).

ambient temperatures in the field until frozen in the laboratory. Cackling geese were collected from Semidi Islands and Buldir Islands representing *B. h. leucopareia*, the Kashunuk River on the Yukon-Kuskokwim Delta representing *B. h. minima*, Prudhoe Bay of the North Slope of Alaska representing *B. h. taverneri*, and Queen Maud Gulf Bird Sanctuary and Baffin Island representing the Short Grass Prairie Population and Tall Grass Prairie Population of *B. h. hutchinsii*, respectively (Figure 2). Canada geese were collected from the Tanana River near Fairbanks and Cook Inlet near Anchorage, Alaska representing *B. c. parvipes*, the Copper River Delta representing *B. c. occidentalis*, Admiralty Island representing *B. c. fulva*, Washington state and the Sandhills of Nebraska representing *B. c. moffitti*, Churchill, Manitoba representing the Eastern Prairie Population of *B. c. interior*, southwest Hudson Bay and northwest James Bay representing the Mississippi Valley Population of *B. c. interior*, Akimiski Island and southern James Bay representing the Southern James Bay Population of *B. c. interior*, Greenland representing *B. c. interior*, western and eastern Ungava Peninsula representing the Atlantic Population of *B. c. interior*, Newfoundland and Labrador representing the North Atlantic Population of *B. c. canadensis*, and near Toronto, Ontario, and southeast Michigan representing *B. c. maxima* (Figure 2). Population names for *B. h. hutchinsii*, *B. c. canadensis*, and *B. c. interior* sampling locations are as defined in Dickson (2000). Sample sizes for each location are listed in Table 1.

Characterization of Microsatellite Loci

DNA was extracted from all samples using DNeasy extraction kits (Qiagen Inc., CA). Twenty nuclear microsatellite loci were initially screened for allelic variation.

Table 1. Measures of genetic diversity for Canada geese (*Branta canadensis*) and cackling geese (*Branta hutchinsii*) populations.

Breeding Location	Species	Population[a]	*n*	A	H_o	H_e	F_{IS}
Canada Geese							
Southeast Michigan	*B. c. maxima*	MISE	54	7.00	0.670	0.694	0.038
Ontario	*B. c. maxima*	ONGI	44	7.13	0.662	0.723	0.084*
Hudson and James Bays	*B. c. interior*	MVP	100	9.13	0.689	0.729	0.056*
Hudson and James Bays	*B. c. interior*	SJBP	116	9.00	0.709	0.751	0.056*
West Ungava Peninsula	*B. c. interior*	APUW	50	8.00	0.700	0.738	0.052
East Ungava Peninsula	*B. c. interior*	APUE	50	8.00	0.692	0.724	0.044
Churchill, Manitoba	*B. c. interior*	EPP	50	8.13	0.667	0.724	0.079*
Greenland	*B. c. interior*	GRLD	17	6.13	0.720	0.734	0.021
Labrador	*B. c. canadensis*	NAPL	51	7.25	0.687	0.705	0.025
Newfoundland	*B. c. canadensis*	NAPN	40	6.25	0.605	0.691	0.127*
Nebraska Sandhills	*B. c. moffitti*	NEMF	49	6.88	0.676	0.694	0.027
Washington	*B. c. moffitti*	WASH	18	6.13	0.747	0.755	0.010
Fairbanks, Alaska	*B. c. parvipes*	FAIR	20	6.38	0.778	0.737	-0.057
Anchorage, Alaska	*B. c. parvipes*	ANCH	45	7.25	0.703	0.741	0.052
Copper River Delta	*B. c. occidentalis*	CRD	51	7.63	0.685	0.736	0.070
Admiralty Island	*B. c. fulva*	ADMR	43	7.25	0.654	0.708	0.077
Cackling Geese							
Baffin Island	*B. h. hutchinsii*	TGPP	86	8.88	0.677	0.734	0.078*
Queen Maud Gulf	*B. h. hutchinsii*	SGPP	50	8.50	0.703	0.740	0.051
North Slope, Alaska	*B. h. taverneri*	NSLP	39	7.63	0.703	0.724	0.030
Yukon-Kuskokwim Delta	*B. h. minima*	YKD	38	6.50	0.608	0.692	0.128
Buldir Island	*B. h. leucoparia*	BULD	37	6.00	0.644	0.694	0.073
Semidi Island	*B. h. leucoparia*	SEMD	28	4.38	0.626	0.590	-0.061

n = sample size per population; A = mean number of alleles over 8 loci; H_o = observed heterozygosity; H_e = expected heterozygosity; F_{IS} = correlation of genes within individuals within populations with significant values ($P < 0.006$ after correction for multiple loci; represented by an asterisk) indicating possible inbreeding.

[a]Population abbreviations for samples from Scribner et al. (2003): FAIR = IN-AK, WASH = WA, ANCH = SC-AK, CRD = CRD, ADMR = SE-AK, NSLP = NS, YKD = YKD, BULD = BUL, SEMD = SEM.

Eight bi-parentally inherited loci proved to polymorphic in one or more breeding populations and were used for subsequent analyses. Loci used included Bcaμ1, Bcaμ7, Bcaμ9, Bcaμ11, Hhiμ1 (Buchholtz et al. 1998); TTUCG1, TTUCG5, (Cathey et al. 1998); and CR-G (A. Baker unpubl. data). Each locus was amplified using polymerase chain reaction (PCR) in 25 μl reaction volumes, including 100-150 ng DNA, 10-25 pmol of each primer, PCR buffer (10 mM Tris-HCl pH 8.3, 50 mM KCl, 100 μg/mL gelatin, 0.01%NP-40, 0.01% Triton-X 100), 0.5 U of AmpliTaq DNA Polymerase (Perkin-Elmer), and 100-200 μM dNTPs. Forward primers of each locus-specific primer pair were labeled with either Hex or Fluorescein by the manufacturer (IDT Technologies, Inc.). Thermocycler conditions included a denaturing step of 94 °C for 2 min, followed by 30-35 cycles of 94 °C for 1 min, annealing temperature for 1 min [49 °C (Bcaμ7), 51 °C (Hhiμ1), 54 °C (TTUCG-5), 56 °C (Bcaμ1, Bcaμ9, CR-G), 58 °C (Bcaμ11), 60 °C (TTUCG-1)], and 72 °C for 1 min. Products were visualized using a FMBIO II laser scanner (Hitachi Software Engineering Co.) after electrophoresis on denaturing 6% acrylamide gels. Genotypes were scored based on 20 base-pair standards and reference samples of known allelic size.

Characterization of MtDNA

A 143-bp fragment of the 5' end of the mitochondrial DNA control region was amplified using primers and conditions described in Pierson et al. (2000) and Pearce et al. (2000). These primers were designed to recognize sites flanking the hypervariable portion of the control region (3' end of domain; Baker and Marshall 1997), and additionally, to amplify and sequence only mitochondrial DNA sequences and not

nuclear DNA sequences originating from transposed mtDNA (Sorenson and Fleischer 1996). Approximately 50-100 ng DNA was used for the initial mtDNA amplification with primers L78 and H493 and the PCR protocol of Kocher et al. (1989). Thermocycler conditions included initial denaturation step of 94 °C for 2 min, followed by 40 cycles of 94 °C for 45 s, annealing at 60 °C for 1 min, 72 °C for 1 min, and extending at 72 °C for 7 min. Amplified PCR products were cleaned with QIA-quick spin column kits (Qiagen Inc., CA), and sequenced using SequiTherm Excel DNA sequencing kits (Epicentre, Inc., Madison, Wisconsin) by following product protocols for use of fluorescently labeled primers.

Gene Diversity and Population Differentiation

For each population, observed genotype frequencies for each of the eight microsatellite loci were tested for departure from Hardy-Weinberg expectations were implemented in the program FSTAT (Goudet 2001). Tests for genotypic linkage disequilibrium (a measure of independence across loci within a population) were performed as described in Goudet et al. (1996) using FSTAT. Estimates of measures of genetic diversity including number of alleles per locus (A), observed (H_O) and expected (H_E) heterozygosity were calculated using the program The Excel Microsatellite Toolkit (Park 2001).

The FSTAT program was used to estimate degree of spatial heterogeneity in gene frequency within and among cackling and Canada geese populations using hierarchical *F*-statistics (Weir and Cockerham 1984, Weir 1996) at three levels: (1) among individuals within populations (*f*), (2) among individuals within the total population (*F*),

and (3) among populations (θ). Significance of *F*-statistics was based on 95% confidence intervals determined by bootstrapping across loci. Confidence intervals that included zero were considered non-significant. Pair-wise estimates of population F_{ST} were used as summary measures of inter-population variance in allele frequency. Significance of pair-wise interpopulation differentiation was determined using the exact G-test (Goudet et al. 1996) in FSTAT, as the G-test is more powerful than exact F_{ST}-estimator tests for diploid populations (Goudet et al. 1996, Petit et al. 2001). For tests of Hardy-Weinberg, gametic disequilibrium, and *F*-statistics, nominal significance levels (alpha) were adjusted to account for multiple testing using sequential Bonferroni corrections (Rice 1989).

Genetic affinities among populations of cackling and Canada geese were assessed using several approaches. First, microsatellite allele frequencies across all eight loci were used to estimate Cavalli-Sforza and Edwards (1967) chord distances among all 24 populations of cackling and Canada geese. A multilocus population neighbor-joining tree based on interpopulation distances was then constructed using the program PHYLIP (version 3.6; Felsenstein 1993). Chord distances have been shown to produce robust tree topologies (Takezaki and Nei 1996). Statistical significance of branches was based on 1000 bootstrapped population trees constructed using PHYLIP.

A hierarchial analysis of molecular variance (AMOVA; Excoffier et al. 1992) was used to partition variance in mtDNA haplotype frequencies and nDNA allele frequencies among cackling geese and Canada geese populations. Estimates of variance among populations within groups (Φ_{SC}), among groups (Φ_{CT}) and among populations among groups (Φ_{ST}) were derived using AMOVA in the program ARLEQUIN (version 2.0,

Schneider et al. 2000). Groups were defined by species, subspecies, and migratory Flyway affiliation for hierarchical analyses.

MtDNA Sequence Data

Mitochondrial DNA sequences were obtained from 680 samples across all 11 subspecies and 22 breeding locales. Sequences were aligned manually, and haplotype designations were based on at least one base-pair substitution or insertion-deletion events. Additional haplotypes have been described previously (A-Z, Scribner et al. 2003a; S1-S23, Scribner et al. 2003b) for cackling geese and Canada geese in North America.

Phylogeographic Analyses

We used MODELTEST version 3.06 (Posada and Crandall 1998) to find the best available model of DNA evolution based on hierarchical likelihood-ratio tests. The model of Tamura and Nei (1993) that incorporates information on the shape parameter of the gamma distribution (G = 0.3362) provided the best fit to the data, and was used in tree reconstructions for analyses including all cackling geese and Canada geese populations. The best available model of DNA substitution when species were analyzed separately was the HKY (Hasegawa et al. 1985) incorporating information on the shape parameter of the gamma distribution (G = 0.0640) for Canada geese populations; and the HKY incorporating information on the proportion of invariable sites (I = 0.5168) for cackling geese populations. Phylogenetic analyses were conducted using PAUP*4.0b10 (Swofford 2000). We used maximum-likelihood and parsimony methods. Heuristic tree searches were conducted for each analysis, with 20 and 100 random additions of taxa for

maximum-likelihood and parsimony analyses, respectively, each followed by tree bisection-reconnection topological rearrangements. Robustness of nodes was assessed using tree reconstructions of bootstrap-resampled data (1000 replicates) under parsimony criteria, and (200 replicates) for maximum-likelihood criteria. We used sequence from lesser snow goose (*Chen caerulescens caerulescens*) from a homologous portion of the control region (GenBank accession number S70800; Quinn 1992) as an outgroup.

RESULTS

Genetic Variation

Allelic variation for the nine nuclear microsatellite loci ranged from 5 to 23 alleles . Both cackling geese and Canada geese populations were characterized by high levels of microsatellite diversity as evidenced by estimates of observed and expected heterozygosity and allelic diversity (Table 1). The mean number of alleles over the eight loci was slightly higher for Canada geese populations (6.13 – 9.13) as compared to populations of cackling geese (4.38 - 8.88). No loci deviated from Hardy-Weinberg expectations, and no evidence of linkage disequilibrium was observed. Inbreeding coefficients (F_{IS}) were low and non-significant for all populations of cackling geese except for the population from Baffin Island (F_{IS} = 0.078; Table 1). Significant inbreeding coefficients (heterozygote deficiency) were observed for five of the sixteen populations of Canada geese (Table 1). Three of these populations were *B. c. interior* geese breeding along Hudson and James Bays. Heterozygote deficiency in these populations may be a result of sampling within family groups, rather than an indication of population inbreeding.

Phylogenetic and Population Relationships

Estimates of spatial variation based on the eight biparental microsatellite loci were significant for individuals within populations (f), among populations (θ) and for individuals across the total population (F) of cackling geese and Canada geese combined (Table 2). Estimates of spatial variance were also significant for all three hierarchical levels of analysis when Canada geese populations and cackling geese populations were analyzed separately (Table 2).

Pairwise estimates of variance among populations (θ_P) were highly significant between populations of cackling geese and populations of Canada geese. Among population differences in allele frequency were greater among populations from different species (mean $\theta_P = 0.062$) than among populations within species (mean $\theta_P = 0.055$ for cackling geese population comparisons; mean $\theta_P = 0.032$ for Canada geese population comparisons) when all 22 populations were included. Allele frequencies were significantly different among all pairs of Canada geese populations except between two populations of *B. c. interior* breeding on the Ungava Peninsula (APUW and APUE), and between APUW and the *B. c. canadensis* population from Labrador (NAPL; Table 3). Within cackling geese, allele frequencies were not significantly different between the two *B. h. hutchinsii* populations (TGPP and SGPP), and between SGPP and *B. h. minima* from the Yukon-Kuskokwim Delta (YKD). Allele frequencies differed significantly among all other population comparisons for cackling geese (Table 3). Pairwise differences in allele frequencies were much greater between populations from different proposed glacial refugia (mean $\theta_P = 0.080$) than between populations from within the

Table 2. Estimates of hierarchical F-statistics (Weir and Cockerham 1984) for populations of cackling geese and Canada geese based on eight microsatellite loci. Variance partitioning: f = alleles within individuals; F = among individuals within the total population; θ = among populations. Statistically significant ($P < 0.01$) values over all loci are marked with an asterisk.

Locus	f	F	θ
All Populations ($n = 22$)			
Bcaμ1	0.035	0.069	0.035
Bcaμ7	0.077	0.104	0.029
Bcaμ9	0.057	0.104	0.049
Bcaμ11	-0.011	0.057	0.067
Hhiμ1	0.004	0.033	0.028
CR-G	0.004	0.041	0.037
TTUCG-1	0.114	0.164	0.057
TTUCG-5	0.127	0.147	0.023
All Loci	0.090*	0.039*	0.053*
Canada Populations ($n = 16$)			
Bcaμ1	0.039	0.065	0.026
Bcaμ7	0.075	0.093	0.02
Bcaμ9	0.052	0.075	0.025
Bcaμ11	-0.004	0.035	0.038
Hhiμ1	-0.018	0.01	0.028
CR-G	-0.011	0.024	0.035
TTUCG-1	0.144	0.169	0.029
TTUCG-5	0.141	0.155	0.017
All Loci	0.054*	0.079*	0.027*
Cackling Geese Populations ($n = 6$)			
Bcaμ1	0.024	0.025	0.028
Bcaμ7	0.087	0.126	0.043
Bcaμ9	0.072	0.146	0.079
Bcaμ11	-0.033	0.062	0.093
Hhiμ1	0.082	0.029	0.011
CR-G	0.053	0.091	0.041
TTUCG-1	0.011	0.043	0.032
TTUCG-5	0.087	0.117	0.033
All Loci	0.053*	0.095*	0.044*

Table 3. Pairwise estimates of inter-population variance in allele frequencies (mean θ_P across all loci). Bold values were insignificant after Bonferonni correction for multiple loci (Rice 1989). Population abbreviations are as listed in Table 1.

Canada Geese Populations (n = 16)

	B.c. maxima	*B. c. interior*						*B.c. canadensis*		*B.c. moffitti*		*B. c. parvipes*		*B. c. occidentalis*	*B. c. fulva*
	ONGI	MVP	SJBP	APUW	APUE	EPP	GRLD	NAPL	NAPN	NEMF	WASH	FAIR	ANCH	CRD	ADMR
MISE	0.016	0.014	0.022	0.018	0.012	0.021	0.066	0.022	0.024	0.040	0.049	0.021	0.066	0.033	0.032
ONGI		0.014	0.020	0.016	0.016	0.015	0.047	0.023	0.027	0.042	0.028	0.023	0.060	0.024	0.027
MVP			0.006	0.014	0.010	0.008	0.033	0.013	0.019	0.027	0.034	0.013	0.050	0.031	0.030
SJBP				0.011	0.014	0.008	0.024	0.009	0.018	0.028	0.039	0.012	0.046	0.023	0.022
APUW					**0.006**	0.016	0.022	**0.008**	0.012	0.037	0.046	0.025	0.052	0.028	0.023
APUE						0.012	0.042	0.007	0.016	0.047	0.052	0.016	0.066	0.036	0.029
EPP							0.036	0.014	0.021	0.021	0.041	0.003	0.054	0.027	0.019
GRLD								0.041	0.052	0.038	0.064	0.051	0.058	0.052	0.051
NAPL									0.008	0.045	0.058	0.024	0.079	0.039	0.028
NAPN										0.042	0.069	0.025	0.074	0.047	0.022
NEMF											0.058	0.026	0.060	0.043	0.048
WASH												0.049	0.082	0.037	0.067
FAIR													0.038	0.025	0.024
ANCH														0.043	0.049
CRD															0.019

Table 3 (cont'd).

Cackling Geese Populations (n = 6)

	B. h. hutchinsii	*B. h. taverneri*	*B. h. minima*	*B. h. leucoparia*	
	SGPP	NSLP	YKD	BULD	SEMD
TGPP	**0.000**	0.019	0.031	0.041	0.099
SGPP		0.011	**0.021**	0.035	0.095
NSLP			0.042	0.045	0.087
YKD				0.064	0.171
BULD					0.064

same refugia (mean $\theta_P = 0.027$) for cackling geese. In contrast, pairwise comparisons of allele frequencies for Canada geese were similar for populations within one refugia (mean $\theta_P = 0.031$) and between separate refugia (mean $\theta_P = 0.034$). Pairwise population comparisons of allele frequencies were also similar between populations within the same Flyway and between populations from different Flyways for Canada geese (within Flyway mean $\theta_P = 0.028$; between Flyway mean $\theta_P = 0.033$). Cackling geese exhibited more variation in allele frequencies between populations within a Flyway (mean $\theta_P = 0.068$) than between populations in different Flyways (mean $\theta_P = 0.033$).

Microsatellite allele frequencies and mitochondrial haplotype frequencies differed significantly between goose species (mtDNA $\Phi_{CT} = 0.947$, nDNA $\Phi_{CT} = 0.020$) and among populations within species (Table 4). Hierarchical analysis of cackling and Canada geese populations revealed variation in haplotype frequencies was much greater between species ($\Phi_{CT} = 0.947$) than among populations within a species ($\Phi_{SC} = 0.288$). The variability of haplotype frequencies was greater among populations within proposed glacial refugia than between refugia for cackling and Canada geese. In contrast, allele

Table 4. Hierarchical estimates of variance based on mtDNA clade frequencies. Variance partitioning: among populations within groups (Φ_{SC}), among populations among groups (Φ_{ST}), and among groups for multiple group analyses (Φ_{CT}). Statistically values ($P < 0.05$ for mtDNA; $P < 0.006$ for nDNA after corrections for mulitple loci) are marked with an asterisk.

	# of	# of	mtDNA			nDNA		
Contrasts	Pops	Groups	Φ_{SC}	Φ_{CT}	Φ_{ST}	Φ_{SC}	Φ_{CT}	Φ_{ST}
Non-Hierarchical Analyses								
Among Cackling Geese Populations	6	1	na	na	0.252*	na	na	0.007*
Among Canada Geese Populations	16	1	na	na	0.283*	na	na	0.025*
Hierarchical Analyses								
Species as a Component of Variance								
Between Cackling Geese and Canada Geese	22	2	0.288*	0.947*	0.962*	0.021*	0.020*	0.041*
Proposed Refugia as a Component of Variance								
Cackling Geese: Among Refugia and Populations	6	2	0.205*	0.148	0.322*	0.025*	0.055*	0.078*
Canada Geese: Among Refugia and Populations	16	2	0.267*	0.140	0.369*	0.024*	0.005	0.028*
Migratory Flyways as a Component of Variance								
Cackling Geese: Among Flyways and Populations	6	2	0.253*	0.002	0.251*	0.010*	-0.004	0.006*
Canada Geese: Among Flyways and Populations	16	4	0.299*	0.086*	0.233*	0.019*	0.006*	0.026*
Subspecies as a Component of Variance								
Cackling Geese: Among Subspecies and Populations	6	4	0.262*	0.062	0.213*	0.020*	-0.015	0.005*
Canada Geese: Among Subspecies and Populations	16	7	0.306*	0.147	0.186*	0.016*	0.013*	0.027*

[a]Pacific Flyway Populations: NLSP, YKD, BULD, SEMD; Central/Mississippi Flyway Populations: TGPP, SGPP

[b]Pacific Flyway Populations: ADMR, CRD, ANCH, FAIR, WASH; Central Flyway Populations:NEMF, EPP; Mississippi Flyway Populations: MISE, ONGI, MVP, SJBP; Atlantic Flyway Populations: APUW, APUE, GRLD, NAPL, NAPN

frequency differences were greater between cackling geese refugia than among populations within refugia, indicative of substantial variation between populations of *B. c. leucoparia* and the other three subspecies. When populations and subspecies of Canada geese were divided by migratory Flyway affinities, estimates of haplotype and allele frequency variance were greater among populations within Flyway groups, than between Flyways (Table 4). A hierarchical analysis of cackling geese among Flyways revealed similar results. Hierarchical estimates of variance based on haplotype and allele frequencies were greater among populations within subspecies than between subspecies for both cackling geese and Canada geese (Table 4).

Populations of cackling geese and Canada geese generally clustered by species within the consensus neighbor-joining tree based on chord distances derived from bi-parental loci (Figure 3). One population of Canada geese (*B. c. parvipes*, ANCH) fell within the cackling geese cluster, although statistical support for node placement was low. Significant genetic differentiation between the two populations of *B. h. leucoparia* and other cackling geese populations was evident based on the tree topology (95% bootstrap support). Within Canada geese, populations of *B. c. canadensis* clustered together with low support, but other subspecies with multiple populations were intermixed (Figure 3). No significant phylogeographic pattern was evident among Canada geese populations or cackling geese populations breeding in close geographic proximity (Figure 3).

Fifty-three haplotypes were characterized across 680 individuals from six populations of cackling geese and sixteen populations of Canada geese on the basis of 143 bp of mtDNA sequence data. Two major mtDNA haplotype clades representing

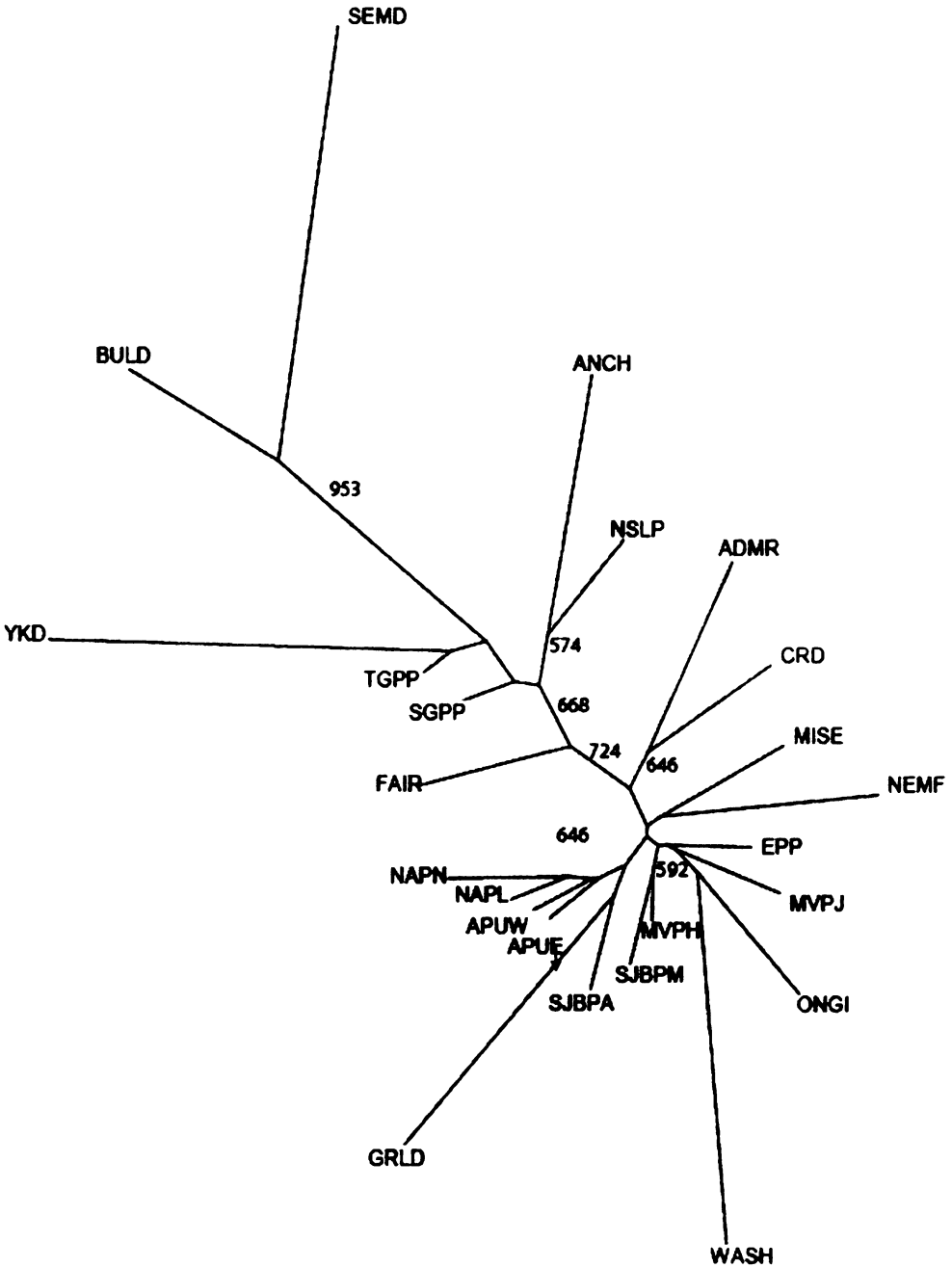

Figure 3. Neighbor joining tree describing overall genetic similarities among populations of cackling and Canada geese based on Cavalli-Sforza and Edwards (1967) chord distances across eight microsatellite loci. Bootstrap support (>50% out of 1000 replicates) for the consensus microsatellite tree is shown to the right of branches or identified by an arrow. Population abbreviations are as in Table 1.

cackling geese and Canada geese were strongly supported (98-100%) for both maximum likelihood and maximum parsimony analyses. The majority of haplotypes within each species clade were unresolved. Thirty-three of 53 haplotypes (62%) were found in a single sampling locale. Private alleles occurred in frequencies of 0.00 to 0.40 in Canada geese populations. Similar frequencies of private haplotypes were observed among Canada geese populations putatively from the "Western Southern" refugia (mean = 0.10) and Eastern Southern refugia (mean = 0.08). Private haplotypes were found in the highest frequencies within the Pacific Flyway (mean frequency = 0.16). Frequencies of private haplotypes in the remaining Flyways were 0.02 in the Central Flyway, 0.07 in the Mississippi Flyway, and 0.04 in the Atlantic Flyway. Haplotype A was the most common haplotype in Canada geese, and was found in six of seven subspecies and 15 of 16 populations (not found in B. c. occidentalis from CRD; Figure 4). Population frequencies of haplotype A ranged from a low of 0.00 in the CRD population to a high of 1.00 in the FAIR population. Haplotype A was much more common on average in populations from the proposed "Eastern Southern" refugia (mean = 0.63) than in populations from the "Western Southern" refugia (mean = 0.14). Mean frequency of the A haplotype was greatest for populations in the Atlantic Flyway (0.72), followed by 0.58 in the Central Flyway, 0.49 in the Pacific Flyway, and 0.41 in the Mississippi Flyway. Only one statistically supported haplotype clade was resolved within the Canada goose mtDNA haplotype tree, which included two private haplotypes (I and J) from the CRD (*B. c. occidentalis*) and ANCH (*B. c. parvipes*) populations.

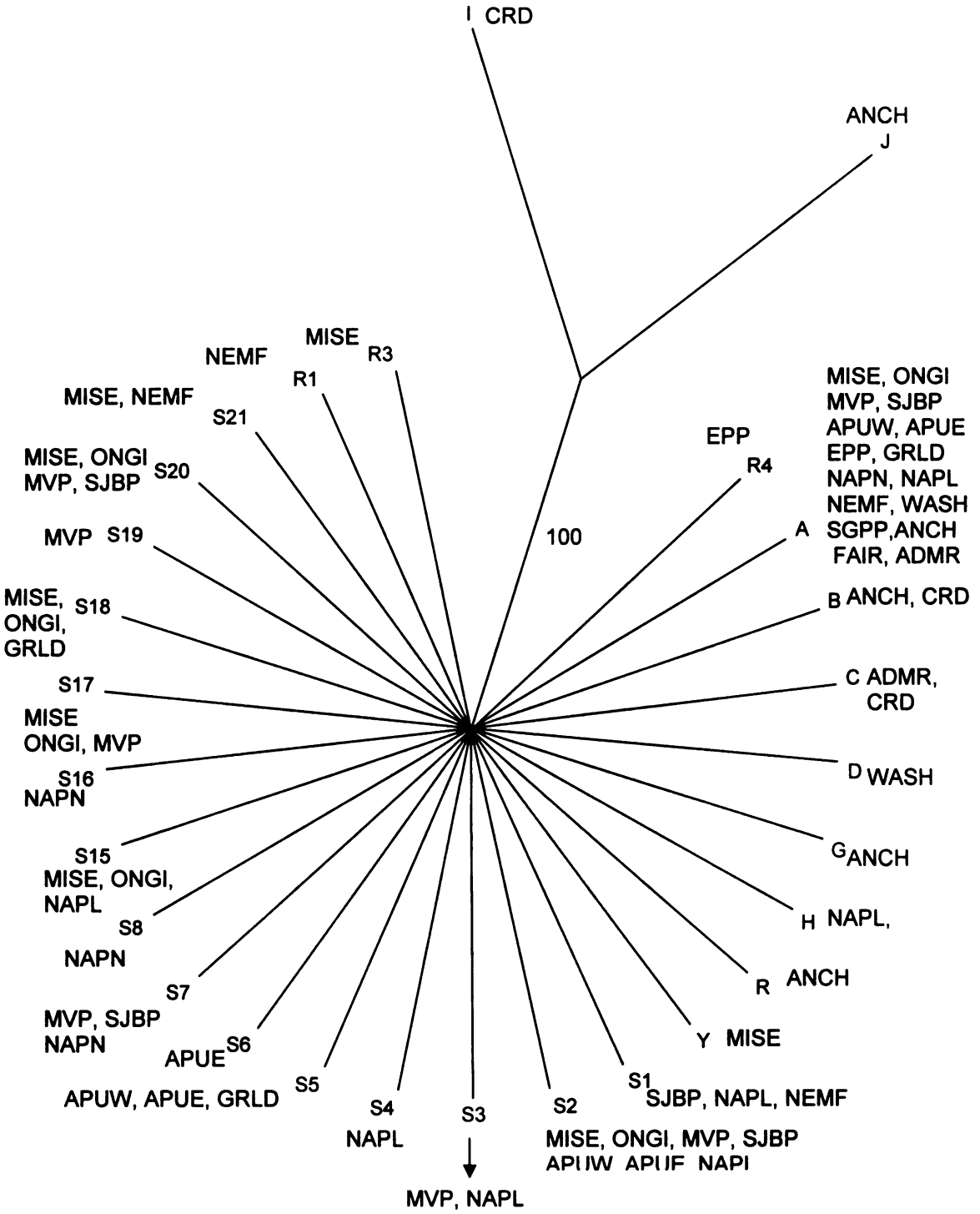

Figure 4. Mitochondrial DNA cladogram based on maximum likelihood analysis describing evolutionary relationships among 26 haplotypes of Canada geese resolved on the basis of mtDNA control region sequence data. Bootstrap values based on 200 replicates exceeding 50% and population locations for haplotypes are included.

For cackling geese, the most common haplotype (L) was found in all four subspecies and all six populations (Figure 5). Frequencies of the L haplotype in cackling geese populations were 20% for BULD and 79% for SEMD representing *B. h. leucoparia*, 55% for *B. h. minima* from YKD, 35% for *B. h. taverneri* from NSLP, and 34% for SGPP and 43% for TGPP representing *B. h. hutchinsii*. Seventeen of 25 cackling geese haplotypes (71%) were found in a single population, and nine haplotypes were observed only in geese from Baffin Island (TGPP; Figure 5). No private haplotypes were found in the NSLP population. Frequencies of private haplotypes in the remaining cackling geese populations were 40% for BULD, 7% for SEMD, 18% for YKD, 37% for SGPP, and 43% for TGPP. Frequencies of the L haplotype were similar between cackling geese populations from the proposed "Aleutian" refugia (mean = 0.50) and populations from the "Northern" refugia (mean = 0.39), as were frequencies of private haplotypes (mean = 0.24 in both refugia groups). Frequencies of the L haplotype were also similar between populations in the Pacific Flyway (mean = 0.45) and populations in the Central/Mississippi Flyway (mean = 0.39). The mean frequency of private haplotypes was twice as large in the Central/Mississippi Flyway populations (mean = 0.40) as in the Pacific Flyway populations (mean = 0.16).

DISCUSSION

Canada geese and cackling geese were considered large- and small-bodied forms of one species complex (*Branta canadensis*) until 2003 (Banks et al. 2003). Past genetic studies of geese based on mtDNA analyses (Shields and Wilson 1987, Van Wagner and Baker 1990, Baker 1998, Scribner et al. 2003a) supported the split of the Canada goose

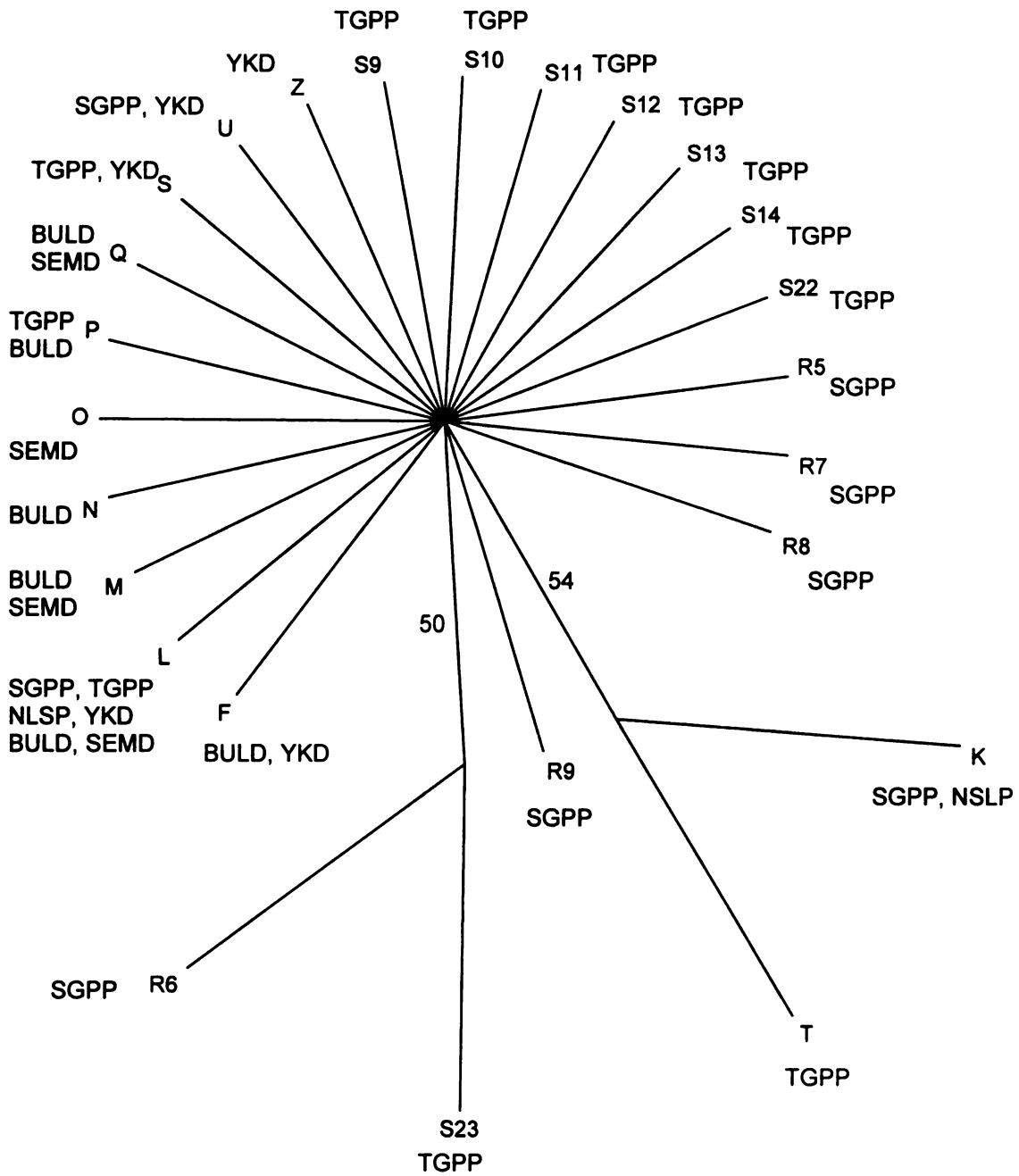

Figure 5. Mitochondrial DNA cladogram based on maximum likelihood analysis describing evolutionary relationships among 27 haplotypes of cackling geese resolved on the basis of mtDNA control region sequence data. Bootstrap values based on 200 replicates exceeding 50% and population locations for haplotypes are included.

species complex into two species, as evidenced by high levels of sequence divergence between large- and small-bodied forms (14%, Scribner et al. 2003a). It has even been suggested that the two newly recognized species of Canada geese and cackling geese have closer evolutionary ties to the Hawaiian goose and barnacle goose, respectively, rather than being each other's closest genetic relative (Paxinos et al. 2002).

The high degree of genetic divergence revealed in the above studies may be a result of species isolation that occurred during the Pleistocene. Based on species ecology, nesting habits, and availability of unglaciated breeding habitat available during the Pleistocene, Ploeger (1968) identified four major breeding areas for cackling and Canada geese. He hypothesized that Canada geese inhabited refugia south of the major ice sheets, while cackling geese were found north of the glaciers in the Aleutian Islands and Canadian Arctic Archipelago. Canada geese were split between the "Western Southern Group" nested in the Pacific coastal region south of the Cordilleran ice sheet and included current subspecies *B. c. fulva* and *B. c. occidentalis*; and an "Eastern Southern Group" composed of current subspecies *B. c. canadensis*, *B. c. interior*, *B. c. maxima*, *B. c. moffitti*, and *B. c. parvipes* nested south of the Cordilleran and Laurentide ice sheets east of the Cascade and Sierra Nevada Mountains. Cackling geese were also hypothesized to inhabit two refugia including the "Aleutian Group" where *B. h. leucopareia* nested; and the "Northern Group" of the Canadian Archipelago which included the three remaining extant subspecies, *B. h. minima*, *B. h. taverneri*, and *B. h. hutchinsii*.

Our findings of variation in mtDNA and nDNA based on analyses of molecular variance (Tables 2, 3 and 4), genetic distances among populations based on allele

frequencies (Figure 3) and haplotypes (Figures 3, 4, and 5) support a fundamental evolutionary split between Canada geese and cackling geese. Thus, our data is consistent with the findings of previous genetic studies that documented large genetic differences between species. Hierachical analyses of mtDNA haplotype variance (Table 4) and the deep phylogenetic split between species in our haplotype tree support Ploeger's (1968) hypotheses that ancestors of cackling and Canada geese were isolated in separate Pleistocene refugia.

Subspecies distinctions, however, were not well supported in either species group on the basis of our analyses. Topologies within the mtDNA haplotype tree for both species were weakly supported, and demonstrated a lack of phylogenetic structure based on subspecies classifications. Results of AMOVA for mtDNA indicated that higher levels of genetic variance were apportioned among populations within subspecies, than among subspecies within cackling and Canada geese (Table 4). Among population variation in haplotype frequencies was also greater than between group variance for hierarchical contrasts of proposed glacial refugia groups and Flyway groups (Table 4). Ancestral haplotypes within cackling geese (L) and Canada geese (A) were inferred based on interior orientation within haplotype clades (Figures 4 and 5), high frequency of occurrence, and broad geographic dispersion. For Canada geese, frequencies of the A haplotype varied considerably between groups of populations from the "Western Southern" and "Eastern Southern" glacial refugia proposed by Ploeger (1968), though the occurrence of private haplotypes was similar between both refugial groups. In contrast, populations of cackling geese putatively from the "Aleutian" refugia and "Northern" refugia had similar frequencies of the L haplotype, and similar frequencies of private

haplotypes. The large difference in frequency of the ancestral A haplotype between the two refugial groups of Canada geese, and the lack of the A haplotype in one of two populations from the "Western Southern Group" (CRD), suggest that Canada geese may have been separated in two isolated refugia during the Pleistocene, but that separation times were not long enough for complete lineage sorting to occur. The widespread occurrence of the L haplotype in similar frequencies within populations of cackling geese from the two proposed refugia argues that cackling geese may have resided together in one refugia, or that historical gene flow occurred between the two refugial groups.

In a genetic survey of cackling and Canada geese in western North America, Scribner et al. (2003a) also found a lack of evidence to support the existence of two refugia for cackling geese. Their conclusions were based on the widespread occurrence of the ancestral haplotype L in cackling geese subspecies putatively from the two different refugia. However, they stated genetic affinities between populations of Canada geese sampled from interior Alaska and Washington State were supportive of Ploeger's hypothesized "Eastern Southern Group", one of two proposed Pleistocene refugia for Canada geese. Based on our suite of microsatellite loci we found significant differences between populations in these regions (FAIR, WASH) and populations did not cluster together within the neighbor-joining tree based on affinities in microsatellite allele frequency (Figure 3). However, our data on the frequencies of the ancestral haplotype A within the refugial groups support the hypothesis that two isolated refugia may have existed for Canada geese.

In both cackling geese and Canada geese, we observed a large number of haplotypes that occurred in only one population, and that differed by only one or two site

changes from other haplotypes. Numerous "private" haplotypes (Slatkin and Maddison 1989) suggest that historical founder events and restricted gene flow have led to novel haplotypes in many populations. Our large samples sizes for each population lend confidence to frequency estimates of novel haplotypes and ancestral haplotypes for both cackling and Canada geese. Distribution of private haplotypes among contemporary populations of Canada geese and cackling geese is likely limited by the high level of natal area and breeding site philopatry that characterize these species (Anderson et al. 1992, Ely and Scribner 1994, Mowbray et al. 2002).

Previous studies documented that nominal subspecies within cackling and Canada geese could be unambiguously distinguished based on mtDNA haplotypes (Shields and Wilson 1987, Van Wagner and Baker 1990, Baker 1998). We did not find evidence of distinct mitochondrial DNA among subspecies of cackling and Canada geese (Figures 4 and 5). Our results are consistent with a mtDNA survey of cackling and Canada geese in western North America (Scribner et al. 2003a). Differing results may be attributed to differences in sample sizes among studies, and how samples were genetically characterized. Earlier studies utilized small numbers of samples per population, and additional shared haplotypes may have been undetected when few individuals were analyzed from each location even if geographic coverage of sampling was broad. Our study, and the work of Scribner et al. (2003a), had relatively larger sample sizes for all population collections, which provides greater confidence in inferred phylogeographic and population relationships (Funk and Omland 2003, Peters et al. 2005). Previous studies relied on characterization of mtDNA through restriction fragment analysis, which resolved sequence variation over a larger portion of the mtDNA molecule than in our

study, where a portion of the mtDNA genome was directly sequenced. Resolution among subspecies may be improved by sequencing a longer region of the mtDNA control region to increase the number of informative character states. Additionally, sequencing of mtDNA could be supplemented with sequences from informative nuclear genes, such as the Z-chromosome-linked chromo-helicase binding protein gene (Peters et al. 2005).

Long-term family associations and strong male and female breeding site fidelity exhibited by cackling and Canada geese (Anderson et al. 1992, Ely and Scribner 1994, Mowbray et al. 2002) could reproductively isolate breeding populations and lead to significant genetic differentiation among breeding populations over time due to genetic drift. Pair bond formation of cackling and Canada geese during spring when geese have returned to breeding grounds (Raveling 1969, Surrendi 1970, Ely and Scribner 1994) may serve to reinforce genetic isolation among populations. However, populations that share migratory routes and common wintering areas within Flyways may experience a higher degree of inter-population gene flow than populations from different Flyways. If a high level of genetic exchange occurs among populations within Flyways due to individuals dispersing to new populations during migration or wintering, the degree of spatial genetic structure within species may be greater among wintering Flyway groups than among breeding populations (Robertson and Cooke 1999). Hierarchical analyses revealed greater levels of mtDNA and nDNA genetic variation among breeding populations than among Flyway groups for both cackling and Canada geese (Table 4). Among population genetic differentiation was also significantly greater than genetic variability among subspecies. Our inter-population tree based on allele frequency differences had low support for phylogenetic structure based on subspecies or Flyways (Figures 3). In

addition, mean pairwise population differences in allele frequencies were similar between populations from different Flyways and between populations in the same Flyway for both cackling and Canada geese. Our data are consistent with studies that indicate strong fidelity to breeding sites and formation of pair bonds on breeding grounds likely increases reproductive isolation among breeding populations of cackling and Canada geese. The lack of genetic divergence between Flyways suggests that refugial populations were large in number and time since population separation has been relatively short on an evolutionary time scale, resulting in no greater genetic differences between subspecies and migratory Flyway populations as compared to populations within Flyways. Alternatively, cackling and Canada geese have only been utilizing contemporary migratory Flyways over relatively short evolutionary periods (i.e., subsequent to the last Pleistocene glaciation), and Flyway groups may not have experienced long enough separation times to develop measurable genetic differences in gene frequencies.

One subspecies, *B. c. leucoparia*, was well resolved based on nuclear genetic distances illustrated in the microsatellite neighbor-joining tree. The island populations of BULD and SEMD were distinguished from other populations and subspecies with 95% bootstrap support. A similar topology was not supported in the cackling geese mtDNA tree, as these populations have multiple shared haplotypes including the ancestral haplotype (L) found in all populations and subspecies of cackling geese (Figure 5). The *B. h. leucoparia* subspecies of cackling geese was extirpated from most of its historical range after the introduction of non-native predators for fur production from 1830 to 1930, and was listed as an endangered in 1967 (USFWS 1991). The genetic divergence

between *B. h. leucoparia* and other subspecies of cackling geese is likely a result of the severe population bottleneck that occurred in the mid 20th century. Our tests for excess heterozygosity indicating BULD had likely experienced a recent population bottleneck, and low levels of allelic diversity of the BULD and SEMD populations relative to other cackling geese (Table 1), is consistent with the findings of a previous genetic study on *B. h. leucoparia* (Pierson et al. 2000).

Some Arctic-nesting avian species have deeply diverged phylogenetic groups that are geographically widespread. In an investigation of the evolutionary relationship between mallard ducks (*Anas platyrhynchos*) and American black ducks (*Anas rubripes*), two fundamental, phylogenetically distinct mtDNA clades were described that were widely distributed in mallards from two geographically isolated breeding populations (Manitoba and California; Avise et al. 1990). The authors argued that the geographic uniformity suggested either recent colonization of Manitoba by birds from California after the last glacial retreat, or that recent gene flow had occurred between the two populations. A similar pattern of mtDNA variation was found in lesser snow geese and Ross's geese across their breeding ranges (Quinn 1992, Avise et al. 1992, Weckstein 2002, see Chapter 6). Two fundamental clades of mtDNA haplotypes suggestive of past vicariance and divergence were found in across the species breeding ranges, arguing for recent population expansion and high levels of contemporary gene flow.

Some Arctic species exhibit homogenized gene frequencies among nesting and wintering populations (harlequin duck, Lanctot et al. 1999; king eider, Pearce et al. 2004). For harlequin ducks, similar gene frequencies over a wide geography was hypothesized to be a result of the cumulative effects of low levels of gene flow over long

time periods, low levels of juvenile gene flow, or episodic dispersal attributed to habitat alteration. The genetic panmixia and lack of spatial structure in king eiders was attributed to historical gene flow and recent population growth following Pleistocene deglaciation (Pearce et al. 2004).

Cackling and Canada geese exhibit a fundamental genetic split between species related to their biogeographic isolation during the Pleistocene, and there is some evidence of a historical divergence between Canada geese restricted to two different glacial refugia. Additionally, our data revealed moderate levels of genetic variation among breeding populations and Flyway groups that have likely accrued due to strong male and female breeding site fidelity and pair bond formation that occurs when breeding populations are largely isolated from other populations. The spatial genetic structure of cackling and Canada geese is similar to phylogeographic structuring in dunlin (Wenink et al. 1994, 1996), which exhibit a strongly subdivided population genetic structure. Like cackling and Canada geese, the genetic variation in the dunlin is attributed to Pleistocene vicariant events combined with strong natal philopatry that has restricted contemporary gene flow among populations.

MANAGEMENT IMPLICATIONS

Management of cackling geese and Canada geese has traditionally been based on subspecies designations and management populations defined on the basis of migratory Flyway. Population and subspecies classifications were determined on the basis of morphological characteristics. There are not, however, definitive plumage characteristics and morphometric standards for all populations and subspecies of cackling and Canada

geese. In addition, morphologies can be subject to environmentally induced variation (Leafloor et al. 1998) and age-related variation (Thompson et al. 1999). Genetic markers can be used to document spatial patterns in allele or haplotype frequency within species, and determine if currently recognized management units adequately describe groups that are presumed to be demographically independent.

Genetic characterizations of cackling and Canada geese provide valuable information on past and present population structure that may be incorporated into management plans and conservation policies for these two species. Our data support previous findings of a fundamental genetic split between cackling geese and Canada geese species. Within species, our analyses revealed evidence of incomplete lineage sorting illustrated by the widespread distributions of ancestral haplotypes within cackling and within Canada geese. We also found indications that contemporary gene flow among breeding populations and Flyways may be restricted by breeding behaviors and strong fidelity to breeding grounds.

Current management efforts of cackling and Canada geese are focused largely on management populations defined by wildlife agencies based on breeding ground affliation and wintering ground distribution (Dickson 2000). These populations do not correspond precisely to subspecies or species. Some subspecies are split into multiple management populations (i.e., *B. c. interior* in AP, SJBP, MVP, EPP, and WPP populations), while other management populations may combine several subspecies or species into a single unit (i.e., SGPP population of *B. c. parvipes* and *B. h. hutchinsii*; see Appendix 1 in Chapter 1 for a summary of management populations). Large amounts of funds from federal, provincial, and state agencies are provided annually to support

research and regulations that attempt to maintain the diversity and viability of these management populations of cackling and Canada geese (Schmidt 2004). Results of our genetic survey suggest that there is much less genetic variability among breeding populations and subspecies than between species. Based on these results, we would recommend that future management efforts and monies be less focused on previously defined management populations (Dickson 2000) and more focused on identifying and maintaining the diversity within each species.

Both cackling and Canada geese are managed as game species, and the majority of harvest of these groups occurs on wintering grounds where populations and subspecies are admixed. Accurate discrimination among subspecies and populations based on morphology and band observations may be difficult when individuals are mixed in migratory or wintering groups (Pearce and Bollinger 2003, Scribner et al. 2003b). However, there is significant genetic structure for cackling and Canada geese at both macro- and micro-geographic scales that could be utilized in a management context. For example, genetic analysis techniques were recently combined with satellite telemetry to infer the geographic origin and racial composition of Canada geese in newly colonized habitats in Greenland (Scribner et al. 2003c). The authors used likelihood-based assignment tests based on multilocus genotypes, and observational data on seasonal movements, to determine that Canada geese in Greenland originated from the Atlantic Population of geese breeding near southern Ungava Bay in Quebec, Canada. It has also been demonstrated that genetic data provides a viable alternative to estimate proportional contributions of subspecies and populations to harvest (Pearce et al. 2000, Inman et al. 2003, Scribner et al. 2003b) at multiple temporal and spatial scales. In Chapter 5, we

provide an example of harvest derivations based on genetics data for seasonal cackling and Canada geese harvests in the State of Michigan from 1998-2002. This chapter is followed by a comparative analysis of cackling and Canada geese harvest estimates derived using three different techniques including genetic-based analyses, band recovery data, and morphological measurements (see Chapter 6).

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CHAPTER 3: PHYLOGEOGRAPHY OF SNOW GEESE AND ROSS'S GEESE

INTRODUCTION

Genetic variation within and among species can be influenced by both historical events and the ecology of the species (Avise et al. 1987, Avise 1998). Historical factors that may influence the spatial genetic structure of species include population isolation during glacial events, population expansions and dispersals during interglacial periods, size of populations during glacial and interglacial periods, length of time populations experienced geographic and reproductive isolation, and length of time since population separation (Avise et al. 1998, Emerson et al. 2001, Stewart and Lister 2001). Longer separation times and smaller effective population sizes in isolated populations increase the probability populations will accrue differences in gene frequencies and develop novel gene mutations (Avise et al. 1988). Historical population expansions occurring in a single, punctuated event, and with a low number of founding individuals, could appreciably change allele and haplotype frequencies in the founding population as compared to the population of origin. Alternatively, if expansion events included a large number of individuals over a prolonged time period, then gene frequencies may be similar among populations (Mila 2000, Hewitt 2001).

Ecology and life history characteristics that may affect species spatial genetic structure include timing and location of pair bond formation, degree and sex-specificity of philopatry, levels of gene flow among contemporary breeding and/or wintering populations, and current population size (Greenwood 1980, Chesser 1991a, Chesser 1991b, Ely and Scribner 1994, Miyatake and Shimizu 1999). High natal and breeding

site philopatry, and pair bond formation during periods when breeding populations are isolated, will tend to restrict gene flow and increase genetic structure among populations (Rockwell and Barrowclough 1987). Fidelity to wintering sites may increase among population genetic variation if populations are isolated in wintering areas, or homogenize gene frequencies across populations if populations are admixed in wintering areas and pair bond formation occurs on these wintering sites (Robertson and Cooke 1999). Gene flow that is sex-biased may lead to differences in the degree of among population genetic variation revealed by maternally and bi-parentally inherited markers (Chesser 1991a, Scribner et al. 2001). Information on the degree of genetic discordance among mitochondrial (mt) DNA haplotypes, and the frequencies of shared and novel haplotypes and nuclear DNA alleles provides sources of inference to past events and species ecology. Deeper subdivisions in an intraspecific phylogeny reflect historical evolutionary splits within a taxa, while shallower molecular separations are evidence of more recent population subdivisions (Avise 1992).

Phylogenetic investigations have been conducted for a wide variety of North American avian species (see review in Avise and Walker 1998), including songbirds and Neotropical migrants (Zink 1996, Kimura et al. 2002), shorebirds (Wenink et al. 1994), wading birds (Rhymer et al. 2001), and migratory waterfowl (Avise et al. 1992, Quinn 1992, Scribner et al. 2001, Scribner et al. 2003, Pearce et al. 2004, Peters et al. 2005). Patterns of spatial genetic structure vary greatly among co-distributed avian species (Zink 1996, Avise and Walker 1998). Some species, like the song sparrow (*Melospiza melodia*), red-winged blackbird (*Agelaius phoeniceus*; Zink 1996), turnstone (*Arenaria interpres*; Wenink et al. 1994), and king eider (*Somateria spectabilis*; Pearce et al. 2004)

exhibit little genetic differentiation across their geographic ranges, likely as a result of recent population expansions from a single glacial refugia, and high levels of gene flow among populations subsequent to the last Pleistocene glacial period. Significant levels of intraspecific genetic variation consistent with population divergence in multiple glacial refugia has been found in fox sparrows (*Passerella iliaca*; Zink 1996), Wilson's warblers (*Wilsonia pusilla*; Kimura et al. 2002), rock ptarmigans (*Lagopus mutus*; Holder et al. 1999), dunlins (*Caldris alpine*; Wenink et al. 1993), and Canada geese (*Branta canadensis*; Scribner et al. 2003). In several of these species (dunlin and Canada goose) genetic population structure was also attributed strong natal and breeding philopatry (Wenink et al. 1993; see Chapter 2 for Canada geese). Thus, differences in the degree of genetic divergence evident in co-distributed North American avian species can result from both historical processes and species life history characteristics which influence contemporary levels of gene flow.

Climatic changes over time have likely had a large effect on the phylogeographic structure of snow geese (*Chen caerulescens*) and Ross's geese (*Chen rossii*), as both species currently breed in high latitude regions of North America that were recolonized from refugia in Beringia and other ice-free areas north of major glaciers. Snow geese and Ross's geese likely utilized these high Arctic refuges during the last Pleistocene glacial event (26,000-18,000 ybp; Ploeger 1968), and may have been isolated in separate refugia in east Siberia and the Bering Sea area (snow geese), and in the Western Canadian Arctic Archipelago (Ross's geese) during the previous glacial maximum (150,000-130,000 ybp). Within the snow geese complex, greater snow geese (*C. c. atlantica*) may have occupied refuge breeding grounds in western Greenland during the last glacial, and were likely

geographically isolated from lesser snow geese (*C. c. caerulescens*) populations (Ploeger 1968). Blue-phase and white-phase lesser snow geese may have also been allopatric during this period (18,000-26,000 ybp), with blue-phase geese surviving in the Canadian Arctic Archipelago and white-phase geese inhabiting refuges farther west in Siberia and the Bering Sea region (Ploeger 1968, Cooke et al. 1988).

In addition to historical vicariant events, the phylogeographic structure of snow and Ross's geese has likely been influenced by current levels of gene flow among populations, degree of philopatry to nesting and wintering sites, breeding behavior, and recent range expansions and colonizations of new breeding and wintering grounds (Greenwood and Harvey 1982, Chesser 1991, Anderson et al. 1992, Ely and Scribner 1994, Robertson and Cooke 1999). Female snow and Ross's geese exhibit a high degree of natal- and breeding site- fidelity compared to males, who are more likely to disperse (Rockwell and Cooke 1977, Geramita and Cooke 1982, Cooke 1987, Anderson et al. 1992, Drake and Alisauskas 2005). Significant spatial genetic structure among breeding populations may result from strong female fidelity, even though populations share migratory pathways and wintering areas (Ely and Scribner 1994, Scribner et al. 2003a). Philopatry to wintering grounds may also be critical in defining population structure among snow and Ross's geese (Cooke et al. 1988, Robertson and Cooke 1999), as pair bond formation occurs principally on the wintering grounds where breeding populations are mixed (Prevett 1972, Cooke 1987, Ryder and Alisauskas 1995, Ganter et al. 2005). Fidelity to isolated wintering grounds by one or both sexes and associated young, followed by pair formation, may lead to spatial genetic structure among geese from different wintering regions rather than nesting areas. Currently, there are four major

management groups for snow and Ross's geese based on their affinities to regional wintering areas including the Western Arctic Population, the West Central Flyway Population, the Mid-Continent Population, and the Eastern Population (Figure 1).

Exponential growth of lesser snow geese populations nesting in the Mid-Continent region (Ankney 1996, Batt 1997, Abraham et al. 1999) and Western Arctic (Johnson 1995, Johnson 1996, Kerbes et al. 1999), and greater snow geese nesting in the Eastern Arctic (Ankney 1996) over the past 30 years have led to expansion of population boundaries in both breeding and wintering areas (Alisauskas 1998). Ross's geese have experienced similar range expansions (Fredrick and Johnson 1983) and colonizations of new breeding areas (Prevett and Johnson 1977, Alisauskas and Boyd 1994) during the same period. Before 1955, the total population of Ross's geese (6000 individuals) were though to be confined to a narrow and well defined area in the Queen Maud Gulf region (Dzubin 1965, Prevett and MacInnes 1972). An eastward shift of migration pathways and staging areas were recorded for Ross's geese by the late 1950's (Prevett and Johnson 1977, Campbell et al. 1990). Harvest records track the eastward progression of Ross's geese in North America. Ross's geese did not occur in the Central Flyway harvest survey until 1974, and were absent from harvest surveys in the Mississippi Flyway and Atlantic Flyway until 1982 and 1996, respectively (Sharp and Moser 1999). Similarly, populations of blue and white color phases of lesser snow geese may have been allopatric until the early 20th century (Cooke et al. 1988). Eastward expansions of white geese and westward expansions of blue geese have been recorded since 1940 (Lewis and Peters 1941, Cooch 1961, Dzubin 1979, Johnson and Troy 1987).

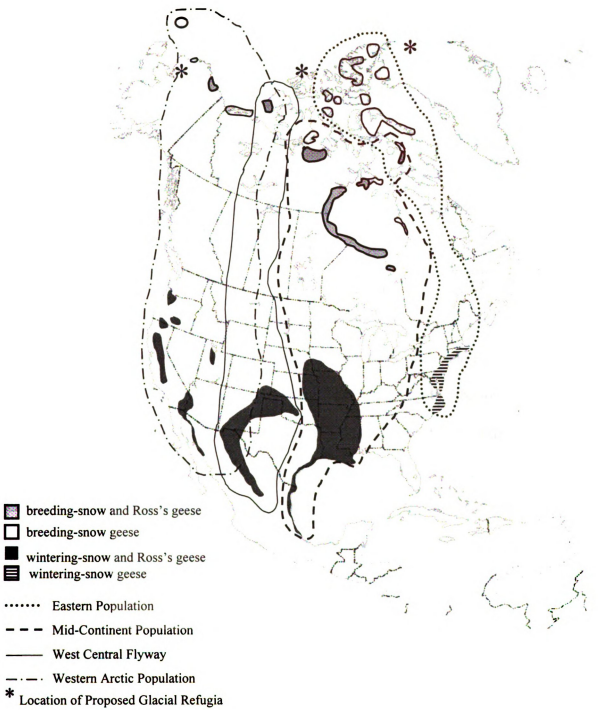

Figure 1. Breeding and wintering distributions and wintering / management population boundaries for snow geese (*Chen caerulescens*) and Ross's geese (*Chen rossii*). Locations of Pleistocene glacial refugia proposed by Ploeger (1968) are indicated.

One hypothesis regarding the spatial genetic structure of snow and Ross's geese is that present populations are genetically differentiated in a manner reflecting historical biogeographic isolating events proposed by Ploeger (1968). A second hypothesis is that contemporary population expansion events have been extensive and may mask any genetic signature of historical differentiation that may have occurred within and among species. In the absence of genetic variation attributed to historical processes, snow and Ross's geese may still exhibit genetic structure based on population affinities to breeding and wintering grounds. Several studies have focused on population structuring among breeding populations of snow geese and Ross's geese using maternally-inherited mtDNA data. Avise et al. (1992) found two phylogenetically distinct groups of haplotypes (designated clades I and II) which co-occurred in lesser snow geese and Ross's geese from different regions of their respective breeding and wintering distributions. Haplotypes of both clades were found in snow and Ross's geese from multiple geographic locales, both sexes, and among both color morphs of lesser snow geese. Clade frequencies were highly variable between snow geese (60% clade I, 40% clade II) and Ross's geese (10% clade I, 90% clade II) species , but were similar among populations within species. The deep phylogenetic split between clades without geographic localization was hypothesized to be a result of secondary hybridization and introgression among snow geese and Ross's geese from two allopatric populations that evolved during the Pleistocene, and from which geese subsequently dispersed and mixed widely (Avise et al. 1992). Quinn (1992) also observed the presence of two distinct mtDNA clades distributed across the lesser snow goose subspecies range (Ross's geese were not included) without detectable correlation with color-phase or sex of snow geese.

Quinn (1992) did, however, find a significant difference in clade frequencies between geese nesting in the western Arctic as compared to geese nesting in Hudson Bay. Based on an estimated 6.7% sequence divergence between clade I and clade II lineages, Quinn (1992) hypothesized that two formerly allopatric populations dispersed across the modern range of the lesser snow goose, likely during Pleistocene interglacial periods.

Weckstein et al. (2002) reanalyzed Quinn's (1992) data set including several new mtDNA sequences from lesser snow and Ross's geese, and identified two divergent lineages similar to Quinn's (1992) findings. Weckstein et al. (2002) also found significant genetic differences in clade frequencies between western and eastern nesting lesser snow geese, and concluded sharing of the two divergent haplotype lineages across species and geographies were consistent with two hybridization episodes between lesser snow and Ross's geese. Weckstein et al. (2002) further stated observed spatial variance in the frequency of clade II was consistent with Cooke et al.'s (1988) hypothesis that formerly allopatric populations of blue- and white-phase lesser snow geese had recently hybridized due to a change in winter feeding habits that caused both morphs to meet and pair on common wintering grounds. Weckstein et al. (2002) also hypothesized that clade II sequences were originally carried by lesser snow geese, while clade I sequences were originally carried by Ross's geese.

In each of these studies, conclusions were based on gene trees derived from a single locus (mtDNA) and relatively few individuals per locale. Our study builds upon previous work by employing multiple genetic markers (nuclear DNA microsatellites and mtDNA) that differ in their modes of inheritance and rates of evolution. We have increased the number of populations included in the analysis, and we sampled a large

number of individuals from each location. We examine the variation of bi-parentally inherited microsatellite loci and site substitutions of mtDNA sequence data from the maternally inherited mitochondrial cytochrome b gene to estimate the degree of population structuring between species of snow and Ross's geese, between subspecies of snow geese, between color morphs of lesser snow geese, and among breeding and wintering populations of snow geese and Ross's geese throughout the geographic range of both species. Genetics data is used to characterize and interpret the phylogenetic status of species, subspecies, and color phases of geese, and to predict the relative importance of historical and contemporary factors influencing population structure.

METHODS

Sample Collection

Samples were collected from breeding populations of lesser snow geese (*Chen caerulescens caerulescens*), greater snow geese (*C. c. atlantica*) and Ross's geese (*C. rossii*) during brood rearing, when geese were flightless. Geese were guided into catch nets using a helicopter or by walking (Cooch 1953, Timm and Bromley 1976). Blood or a blood quill (growing feather) was sampled from breeding adults or goslings at each location. Samples were placed into individual tubes containing high-salt buffer and stored at ambient temperatures in the field until frozen in the laboratory. White phase lesser snow geese were collected from Kolyma River Delta, Japan, Wrangel Island, Russia, Alaska's North Slope, Howe Island, Banks Island, Queen Maud Gulf Bird Sanctuary, Southampton Island, West Hudson Bay, LaPerouse Bay, Cape Henrietta Maria, Akimiski Island, and Baffin Island (Figure 2). Blue phase lesser snow geese were

Figure 2. Sampling locations for snow geese and Ross's geese breeding populations: 1 = Wrangel Island, Russia; 2 = North Slope, Alaska; 3 = Howe Island; 4 = Banks Island; 5 = Queen Maud Gulf Bird Sanctuary; 6 = Southhampton Island; 7 = West Hudson Bay; 8 = LaPerouse Bay; 9 = Cape Henrietta Maria; 10 = Akimiski Island; 11 = Baffin Island; 12 = Bylot Island. Sampling site not pictured: Kolyma River Delta, Japan. White phase lesser snow geese (*Chen caerulescens caerulescens*) were collected at locations 1-11 and the Kolyma River Delta. Blue phase lesser snow geese were collected at locations 5, 7, 9, 10, and 11. Greater snow geese (*C. c. atlantica*) were collected at location 12. Ross's geese (*C. rossii*) were collected at locations 5, 6, 7, 9, and 11.

collected concurrently at a portion of these locations including Queen Maud Gulf Bird Sanctuary, West Hudson Bay, Cape Henrietta Maria, Akimiski Island, and Baffin Island. Bylot Island was sampled for greater snow geese. Samples of Ross's geese were

collected from Queen Maud Gulf Bird Sanctuary, Southhampton Island, West Hudson Bay, Cape Henrietta Maria, and Baffin Island (Figure 2). Sample sizes for each location are listed in Table 1.

Characterization of Microsatellite Loci

DNA was extracted from all samples using DNeasy extraction kits (Qiagen Inc., CA). Twenty nuclear microsatellite loci were initially screened for allelic variation. Nine bi-parentally inherited loci proved to polymorphic in one or more breeding populations and were used for subsequent analyses. Loci used included Bcaμ1, Bcaμ5, Bcaμ9, Bcaμ11, Hhiμ1, Hhiμ3 (Buchholz et al. 1998); Aalμ1 (Fields and Scribner 1997); Sfiμ10 (S. Libants, unpubl. data); and CR-G (A. Baker, unpubl. data). Each locus was amplified using polymerase chain reaction (PCR) in 25 μl reaction volumes, including 100-150 ng DNA, 10-25 pmol of each primer, PCR buffer (10 mM Tris-HCl pH 8.3, 50 mM KCl, 100 μg/mL gelatin, 0.01%NP-40, 0.01% Triton-X 100), 0.5 U of AmpliTaq DNA Polymerase (Perkin-Elmer), and 100-200 μM dNTPs. Forward primers of each locus-specific primer pair were labeled with either Hex or Fluorescein by the manufacturer (IDT Technologies, Inc.). Most thermocycler conditions included a denaturing step of 94 °C for 2 min, followed by 30-35 cycles of 94 °C for 1 min, annealing temperature for 1 min [51 °C (Hhiμ1, Sfiμ10), 56 °C (Bcaμ1, Bcaμ9, Hhiμ3, CR-G), 58 °C (Bcaμ11), 60 °C (Bcaμ5)], and 72 °C for 1 min. Conditions for Aalμ1 included a denaturing step of 94 °C for 2 min, and 30 cycles of 94 °C for 1 min and 50 °C for 2 min. Products were visualized using a FMBIO II laser scanner (Hitachi Software

Table 1. Genetic diversity measures estimated for snow geese and Ross's geese populations. The species of each population sampled is designated as S = snow = Ross's geese or R geese. The color phase of each population sample is designated as W = white or B = blue.

Breeding Location	Species	Color Phase	Population	*n*	A	H_o	H_e	F_{IS}	P_B
Akimiski Island	S	B	AKBL	58	2.64	0.512	0.530	-0.04	0.23
Baffin Island	S	B	BFBL	53	2.74	0.504	0.487	0.04	0.53
Cape Henrietta Maria	S	B	CHBL	33	2.75	0.503	0.488	0.03	0.32
West Hudson Bay	S	B	WHBL	53	2.64	0.482	0.470	0.02	0.47
Queen Maud Gulf	S	B	QMBL	15	2.61	0.521	0.508	0.03	0.53
Akimiski Island	S	W	AKWH	24	2.68	0.480	0.477	0.01	0.85
Baffin Island	S	W	BFWH	41	2.69	0.521	0.483	0.07	0.53
Cape Henrietta Maria	S	W	CHWH	58	2.38	0.482	0.450	0.07	0.47
LaPerouse Bay	S	W	LPBA	48	2.59	0.503	0.511	-0.02	0.19
South Hampton Island	S	W	SHWH	54	2.54	0.501	0.479	0.04	0.10
West Hudson Bay	S	W	WHWH	40	2.79	0.510	0.476	0.07	0.68
Queen Maud Gulf	S	W	QMWH	54	2.44	0.493	0.498	-0.01	0.02*
Howe Island	S	W	HOWE	50	2.55	0.508	0.496	0.02	0.50
North Slope, Alaska	S	W	NSWH	34	2.67	0.499	0.422	0.16*	0.53
Banks Island	S	W	BKIS	81	2.58	0.493	0.485	0.02	0.85
Wrangel Island (N)	S	W	WRNO	76	2.65	0.503	0.509	-0.01	0.90
Wrangel Island (S)	S	W	WRSO	85	2.62	0.503	0.490	0.03	0.75
Kolyma, Japan	S	W	KOLY	31	2.49	0.491	0.470	0.04	0.41
Bylot Island	S[a]	W	BYIS	61	2.52	0.512	0.522	-0.02	0.10
Baffin Island	R	W	BFRO	22	2.98	0.535	0.519	0.03	0.88
Cape Henrietta Maria	R	W	CHRO	52	2.66	0.516	0.540	-0.05	0.50
South Hampton Island	R	W	SHRO	40	2.56	0.533	0.509	0.05	0.55
West Hudson Bay	R	W	WHRO	83	2.79	0.527	0.503	0.05	0.88
Queen Maud Gulf	R	W	QMRO	53	2.78	0.518	0.520	-0.01	0.75

n = sample size per population; A = mean allelic richness over 9 loci; H_o = observed heterozygosity; H_e = expected heterozygosity; F_{IS} = correlation of genes within individuals within populations as a test for deficit of heterozygotes ($P < 0.006$ after correction for multiple loci; represented by an asterisk) indicating possible inbreeding; P_B = P-value from one-tailed tests for heterzygote excess, with significant values ($P < 0.05$; represented by an asterisk) indicating a recent population bottleneck. [a]Greater snow geese (*Chen caerulescens atlantica*); all other populations of snow geese are lesser snow geese *(C. c. caerulescens)*.

Engineering Co.) after electrophoresis on denaturing 6% acrylamide gels. Genotypes were scored based on 20 base-pair standards and reference samples of known allelic size.

Characterization of MtDNA

Approximately 50-100 ng DNA was used for the initial mtDNA amplification (1173 bp) with Quinn's (1992) primers (16775L and 287H-M) and the PCR protocol of Kocher et al. (1989). Thermocycler conditions included initial denaturation step of 92 °C for 2 min, followed by 40 cycles of 92 °C for 40 s, annealing at 61 °C for 2 min, 72 °C for 2 min, and extending at 72 °C for 7 min. A restriction endonuclease, *Alu*I (Quinn 1992), was used to test for the presence or absence of a specific restriction site within the mtDNA control region amplified for all geese sampled. Quinn (1992) and Avise et al. (1992) demonstrated this restriction enzyme cleaves the DNA within one group of snow geese haplotypes (clade I) in this mtDNA region, while leaving the remaining haplotypes intact (clade II), with sequence divergence between these two mtDNA clades averaging 6.7% (Quinn 1992). Amplified mtDNA was digested with *Alu*1 according to manufacturer protocol (New England Biolabs, Inc.), and visualized using ultraviolet light after electrophoresis on 1% agarose gels stained with ethidium bromide.

Gene Diversity and Population Structuring

For each population, observed genotype frequencies for each of the nine microsatellite loci were tested for departure from Hardy-Weinberg expectations (ensures population genotype frequencies can be estimated based on estimates of allele frequencies) were implemented in the program FSTAT (Goudet 2001). Tests for

genotypic linkage disequilibrium (a measure of independence across loci within a population) were performed as described in Goudet et al. (1996) using FSTAT. The FSTAT program was also used to estimate degree of spatial heterogeneity in gene frequency within and among snow geese populations using hierarchical *F*-statistics (Weir and Cockerham 1984, Weir 1996) at three levels: (1) among individuals within populations (*f*), (2) among individuals within the total population (*F*), and (3) among populations (θ). Significance of *F*-statistics was based on 95% confidence intervals determined by bootstrapping across loci. Confidence intervals that included zero were considered non-significant. Pair-wise estimates of population F_{ST} were used as summary measures of inter-population variance in allele frequency. Significance of pair-wise interpopulation differentiation was determined using the exact G-test (Goudet et al. 1996) in FSTAT, as the G-test is more powerful than exact F_{ST}-estimator tests for diploid populations (Goudet et al. 1996, Petit et al. 2001). For tests of Hardy-Weinberg, gametic disequilibrium, and *F*-statistics, nominal significance levels (alpha) were adjusted to account for multiple testing using sequential Bonferroni corrections (Rice 1989).

Rapidly evolving markers like microsatellites are useful for detecting relatively recent population bottlenecks that may be indicative of founder events based on a low number of individuals (Cornuet and Luikart 1996). The program BOTTLENECK (Cornuet and Luikart 1996) was used to detect bottlenecks that may have resulted from natural colonization events associated with the recent range expansions of snow geese and Ross's geese populations. BOTTLENECK tests for significant excess in heterozygosity within each population. This excess is apparent when populations have experienced a recent genetic bottleneck causing the number of alleles to decrease faster

than levels of heterozygosity. A one-tailed Wilcoxon sign-rank test was used to test for heterozygosity excess under a two-phase mutation model (TPM), as this is the recommended model for microsatellite data (Cornuet and Luikart 1996). The TPM model was run four times with 80%, 85%, 90%, or 95% of the mutations occurring in one step, with the remaining proportion of the mutations occurring in multiple steps (variance = 30).

Microsatellite allele frequencies across all nine loci were used to estimate Cavalli-Sforza and Edwards (1967) chord distances among all 24 populations of snow and Ross's geese. A multilocus population neighbor-joining tree based on interpopulation distances was constructed using the program PHYLIP (version 3.6; Felsenstein 1993). Chord distances have been shown to produce robust tree topologies over a range of conditions (Takezaki and Nei 1996). Statistical significance of tree branches was based on 1000 bootstrapped population trees constructed using PHYLIP.

An analysis of molecular variance (AMOVA; Excoffier et al. 1992) was used to assess among population variation (Φ_{ST}) in mtDNA clade frequencies and nDNA allele frequencies. Hierarchial AMOVA contrasts were used to partition genetic variance among populations within groups (Φ_{SC}), among groups (Φ_{CT}) and among populations among groups (Φ_{ST}) in the program ARLEQUIN (version 2.0, Schneider et al. 2000). Hierarchical AMOVAs were conducted to exam several hypotheses related to the potential spatial genetic structure of snow and Ross's geese based on life history characteristics (Ely and Scribner 1994) and hypothesized Pleistocene refugia (Ploeger 1968) of both species. First, we hypothesized that genetic variation would be greater between species of snow and Ross's geese and between subspecies of lesser and greater

snow geese than among populations within species and among populations within subspecies. Secondly, we hypothesized that genetic variation would be greater between color-phases of lesser snow geese than among populations of the same color-phase. Finally, we hypothesized that genetic variation may be greater among populations of snow and Ross's geese wintering in different regions as compared to populations wintering in the same area. Hierarchical AMOVAs were conducted for (1) snow geese compared to Ross' geese ; (2) lesser snow geese compared to greater snow geese; (3) white-phase snow geese populations, blue-phase snow geese populations, and Ross's geese populations representing three different groups; (4) white-phase snow geese compared to blue-phase snow geese; and wintering populations of (5) snow and Ross's geese, (6) white-phase and blue-phase snow geese, and (7) white-phase snow geese. Breeding populations were assigned to regional wintering groups based on where the majority of each breeding population winters annually. Wintering populations included the Eastern Population represented by greater snow geese from BYIS; the Mid-Continent Population consisting of AKBL, BFBL, CHBL, WHBL, QMBL, AKWH, BFWH, CHWH, LPBA, WHWH, and SHWH lesser snow geese populations, and BFRO, CHRO, SHRO, and WHRO Ross's geese populations; and the West Central Flyway and Western Arctic Populations including lesser snow geese from NSWH, HOWE, BKIS, WRNO, WRSO, and KOLY, and Ross's geese from QMRO (Figures 1 and 2).

RESULTS

Genetic Variation

Allelic variation for the nine nuclear microsatellite loci ranged from 3 to 26 alleles. The number of alleles in each population was similar for seven of the nine microsatellite loci. For the remaining two loci, Bcaμ5 and CR-G, allelic variation was generally higher in Ross's geese populations as compared to snow geese populations (Table 1). Mean allelic richness (mean number of alleles independent of sample size to allow for comparison among population with different sample sizes; El Mousadik and Petit 1996, Petit et al. 1998) over the nine loci was similar across all populations (2.38 – 2.98), as were expected (0.422 – 0.540) and observed (0.480 – 0.535) heterozygosity values (Table 1). Only one locus (Sfiμ10) exhibited a departure from Hardy-Weinberg expectations, and no evidence of linkage disequilibrium was observed. Inbreeding coefficients (F_{IS}) were low and non-significant for all populations except for lesser snow geese sampled from the North Slope of Alaska (F_{IS} = 0.156; Table 1). Tests for significant excess in heterozygosity indicated the presence of a possible population bottleneck in only one population of white-phase lesser snow geese (QMWH, P_B = 0.019; Table 1).

Phylogenetic and Population Relationships

Estimates of genetic variation based on the nine biparental microsatellite loci were low for individuals within populations (f = 0.022), but showed a significant difference in allele frequencies among populations (θ = 0.035) and for individuals across the total population (F = 0.056) of snow geese and Ross's geese (Table 2). When snow geese and Ross's geese populations were analyzed separately, snow geese exhibited significant among population differences (θ = 0.008), but Ross's geese among

Table 2. Estimates of hierarchical F-statistics (Weir and Cockerham 1984) for populations of snow geese and Ross's geese based on nine microsatellite loci. Variance partitioning: f = alleles within individuals; F = among individuals within the total population; θ = among populations. Statistically significant ($P < 0.01$) values over all loci are marked with an asterisk.

Locus	f	F	θ
Snow and Ross's Geese Populations ($n = 24$)			
Aalμ1	0.002	0.035	0.033
Bcaμ1	0.016	0.058	0.044
Bcaμ9	0.002	0.046	0.044
Bcaμ5	-0.063	0.01	0.068
CR-G	-0.016	0.026	0.041
Hhiμ1	0.005	0.042	0.037
Hhiμ3	0.050	0.081	0.033
Sfi10μ	0.102	0.119	0.019
Bcaμ11	0.004	0.007	0.003
All Loci	0.022	0.056*	0.035*
Snow Geese Populations ($n = 19$)			
All Loci	0.023	0.031	0.008*
Ross's Geese Populations ($n = 5$)			
All Loci	0.015	0.019	0.004

populations variance was not significant. All pairwise estimates of variance among populations (θ_P) were highly significant between populations of lesser snow geese and Ross's geese (mean $\theta_P = 0.083$). Subspecies comparisons between the Bylot Island population of greater snow geese and all breeding populations of lesser snow geese were also significant (Table 3). Mean pairwise estimates of variance were greater between populations of greater and lesser snow geese (mean $\theta_P = 0.016$) than among populations of lesser snow geese (mean $\theta_P = 0.007$). Pairwise θ_P values between white-phase and blue-phase geese (mean $\theta_P = 0.007$) were on average greater than pairwise values

Table 3. Pairwise estimates of inter-population variance in allele frequencies (mean θ_P across all loci) for blue- and white-phase lesser snow geese (*C. c. caerulescens*), greater snow geese (*C. c. atlantica*), and Ross's geese (*C. rossii*). Bold values were statistically significant after Bonferonni correction for multiple loci (Rice 1989). Population abbreviations are as listed in Table 1.

	Blue Snow Geese Mid-Continent Population				White Snow Geese Mid-Continent Population							White Snow Geese West Central Flyway/Western Arctic Populations						Greater Snow[a]
	BFBL	CHBL	WHBL	QMBL	AKWH	BFWH	CHWH	LPBA	SHWH	WHWH	QMWH	HOWE	NSWH	BKIS	WRNO	WRSO	KOLY	BYIS
AKBL	-0.001	0.008	**0.005**	0.006	0.003	0.001	-0.002	0.002	**0.004**	-0.002	0.000	0.001	0.004	0.004	-0.001	-0.001	0.002	**0.013**
BFBL		**0.020**	0.011	0.019	0.006	0.007	0.004	**0.006**	**0.011**	0.003	0.001	0.013	0.015	0.010	0.003	0.001	0.012	**0.015**
CHBL			**0.012**	-0.004	0.007	0.007	0.001	0.011	**0.008**	0.006	**0.016**	0.005	0.007	**0.022**	**0.016**	**0.019**	0.001	**0.018**
WHBL				0.003	0.001	**0.010**	**0.007**	0.003	0.001	-0.004	**0.011**	0.003	0.002	**0.027**	**0.019**	**0.018**	0.000	**0.015**
QMBL					0.002	0.005	0.004	0.013	-0.001	0.001	**0.022**	0.001	0.006	**0.031**	0.025	0.025	0.003	**0.028**
AKWH						0.009	-0.002	0.002	0.004	0.000	0.005	0.000	-0.004	0.013	0.010	0.013	-0.005	**0.021**
BFWH							0.002	**0.004**	**0.008**	-0.003	0.007	0.003	0.008	**0.017**	0.011	**0.010**	0.004	**0.016**
CHWH								**0.008**	**0.005**	0.001	0.000	0.003	0.006	0.004	0.003	0.003	-0.001	**0.015**
LPBA									0.005	-0.003	**0.007**	0.004	0.000	**0.018**	**0.010**	**0.013**	0.002	**0.019**
SHWH										0.000	**0.006**	**0.002**	**0.006**	**0.025**	**0.017**	**0.015**	0.000	**0.013**
WHWH											**0.006**	-0.003	0.000	**0.017**	**0.010**	**0.010**	-0.004	**0.010**
QMWH												0.008	**0.009**	**0.010**	0.002	-0.001	0.004	**0.012**
HOWE													0.000	**0.017**	**0.010**	**0.011**	-0.003	**0.010**
NSWH														**0.023**	**0.015**	**0.016**	-0.004	**0.013**
BKIS															0.002	0.002	**0.020**	**0.028**
WRNO																0.000	**0.009**	**0.017**
WRSO																	0.013	**0.013**
KOLY																		**0.011**

Table 3 (cont'd).

	Ross's Geese[b]			
	CHRO	SHRO	WHRO	QMRO
BFRO	0.003	0.001	0.006	-0.002
CHRO		**0.006**	**0.011**	**0.009**
SHRO			0.002	-0.003
WHRO				0.000

[a]Greater snow geese represent the Eastern wintering Population.

[b]BFRO, CHRO, SHRO, and WHRO are part of the Mid-Continent wintering Population; QMRO is part of the West Central Flyway and Western Arctic Populations.

between white-phase populations of geese (mean $\theta_P = 0.006$), and less than pairwise values between blue-phase populations of geese (mean $\theta_P = 0.008$). Differences in allele frequencies between blue-phase and white-phase lesser snow geese populations breeding in the same geographic locale were only significant for the two populations from Queen Maud Gulf Bird Sanctuary ($\theta_P = 0.022$). Variation in allele frequency was greater between populations of snow geese known to winter in different regions (mean $\theta_P = 0.0094$) than between populations within the same wintering group (mean $\theta_P = 0.0056$; Table 3). Pairwise comparisons revealed Ross's geese from Cape Henrietta Maria (CHRO) had significantly different allele frequencies from Ross's geese in West Hudson Bay, Queen Maud Gulf Bird Sanctuary, and Southampton Island (Table 3). Allele frequencies were similar for all other Ross's geese population pairs.

Populations of snow geese and populations of Ross's geese formed two distinct clusters within the consensus neighbor-joining tree based on chord distances derived from bi-parental loci (Figure 3). Bootstrap support for the tree node separating the two species was 100%. Significant genetic differentiation between greater snow geese and

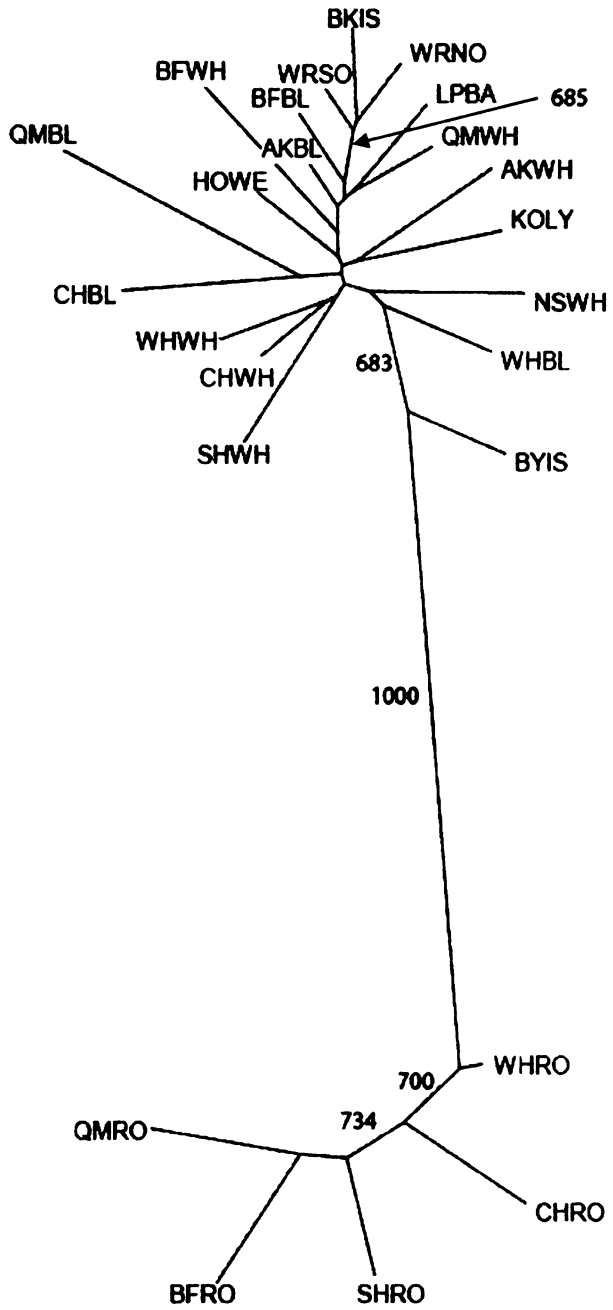

Figure 3. Neighbor joining tree describing overall genetic similarities among populations of snow and Ross's geese based on Cavalli-Sforza and Edwards (1967) chord distances across nine microsatellite loci. Bootstrap support (>50% out of 1000 replicates) for the consensus microsatellite tree is indicated. Population abbreviations are as in Table 1.

lesser snow geese populations was also evident based on the tree topology, although statistical support for differentiation between snow geese subspecies was less than between species. The only genetically distinct group within the lesser snow geese cluster included the BKIS, WRNO, and WRSO breeding populations from the Western Arctic wintering population (Figure 3). Lesser snow geese populations wintering in other regions did not cluster together on the neighbor-joining tree, and no significant phylogeographic pattern was evident among lesser snow geese populations breeding in close geographic proximity or among lesser snow geese populations of the same color phase (Figure 3).

Among population differences in mtDNA clade frequencies and nDNA allele frequencies were significant across all breeding populations of snow geese and Ross's geese (mtDNA $\Phi_{ST} = 0.093$, nDNA $\Phi_{ST} = 0.035$; Table 4). Among population differences in clade frequencies were significant for snow geese ($\Phi_{ST} = 0.058$), but not significant for Ross's geese ($\Phi_{ST} = -0.006$), when species were considered separately. Clade frequencies were equivalent among populations of blue-phase lesser snow geese ($\Phi_{ST} = 0.029$), but differed significantly among populations of white-phase lesser snow geese ($\Phi_{ST} = 0.059$). Hierarchical analyses of variance based on maternally and bi-parentally inherited DNA frequencies revealed significant levels of genetic variation among populations within groups (Φ_{SC}) when population groups were designated by species, subspecies, color phase of lesser snow geese, or wintering region (Table 4). Genetic variation between snow and Ross's gees species was significant, and proportionally larger, than variance among populations within species. In contrast, among population estimates of genetic variance (Φ_{SC}) were greater than among group

Table 4. Hierarchical estimates of variance based on mtDNA clade frequencies. Variance partitioning: among populations within groups (Φ_{SC}), among groups (Φ_{CT}), among populations for non-hierarchical analyses and among populations among groups for hierarchical analyses (Φ_{ST}). Statistically significant values ($P < 0.05$ for mtDNA; $P < 0.006$ for nDNA after corrections for mulitple loci) are marked with an asterisk.

Contrasts	# of Pops	# of Groups	mtDNA Φ_{SC}	mtDNA Φ_{CT}	mtDNA Φ_{ST}	nDNA Φ_{SC}	nDNA Φ_{CT}	nDNA Φ_{ST}
Non-Hierarchical								
Among All Snow and Ross's Geese Populations	24	1	na	na	0.093*	na	na	0.035*
Among All Snow Geese Populations	19	1	na	na	0.058*	na	na	0.008*
Among White-Phase Snow Geese Populations	14	1	na	na	0.059*	na	na	0.008*
Among Blue-Phase Snow Geese Populations	5	1	na	na	0.029	na	na	0.005*
Among Ross's Geese Populations	5	1	na	na	-0.006	na	na	0.004*
Hierarchical								
Species or Subspecies as a Component of Variance								
Between Snow Geese, Ross's Geese	24	2	0.051*	0.123*	0.167*	0.007*	0.076*	0.083*
Between Lesser Snow Geese, Greater Snow Geese	19	2	0.061*	-0.026	0.036*	0.007*	0.008	0.016*
Color Phase of Snow Geese as a Component of Variance								
Among White-Phase Snow Geese, Blue-Phase Snow Geese, Ross's Geese	24	3	0.045*	0.085*	0.127*	0.007*	0.047*	0.054*
Between White-Phase Snow Geese, Blue-Phase Snow Geese	19	2	0.053*	0.015	0.067*	0.008*	-0.000	0.007*
Wintering Population as a Component of Variance								
Among Snow and Ross's Geese Wintering Populations[a]	24	3	0.093*	-0.001	0.093*	0.036*	-0.003	0.033*
Among Snow Geese Wintering Populations	19	3	0.040*	0.031	0.071*	0.005*	0.004	0.010*
Among White-Phase Snow Geese Wintering Populations	14	3	0.046*	0.021	0.006*	0.006*	0.004	0.010*

[a]Wintering population comparisons for snow and Ross's geese were made with three groups including (1) the Western Arctic and West Central Flyway Populations, (2) the Mid-Continent Population, and (3) the Eastern Population. Breeding populations were assigned to regional wintering groups based on where the majority of individuals from each population winters annually.

variance estimates (Φ_{CT}), for subspecies, lesser snow geese color phase, and wintering population contrasts (Table 4).

DISCUSSION

Snow geese and Ross's geese may have been isolated in separate refugia in east Siberia and the Bering Sea area (snow geese), and in the Western Canadian Arctic Archipelago (Ross's geese) during the previous glacial maximum (150,000-130,000 ybp). Contemporary populations of both species often nest within the same colonies, and are admixed on wintering grounds during pair formation (Ryder and Alisauskas 1995, Mowbray et al. 2000) providing opportunity for species introgression. Molecular genetics data from bi-parentally and maternally inherited markers for snow geese and Ross's geese revealed considerable genetic differentiation between these species. The significant genetic divergence in mtDNA and nDNA frequencies is indicative of a historic divergence between snow geese and Ross's geese. Historical genetic differences between species may be maintained by differences in courtship and breeding behaviors (Palmer 1976, Prevett and MacInnes 1980, Owen 1980, Cooke et al. 1995) and morphology (Bellrose 1980, Owen 1980), rather than to geographic isolation on breeding and wintering grounds. Our data demonstrates that interbreeding between species is likely infrequent and interspecies genetic exchange is low, although mixed pairs and hybrids have been known to occur (Trauger et al. 1971, Hatch and Shortt 1976, Cooke et al. 1995).

Previous studies based on the mtDNA characteristics of snow and Ross's geese have offered two competing hypotheses about how the fundamental phylogenetic split

between clade I and clade II haplotypes had evolved. One hypothesis proposes that clade I haplotypes originated in lesser snow geese and clade II haplotypes originated in Ross's geese, and the widespread occurrence of both clades in snow and Ross's geese populations is a result of dispersal and secondary hybridization between the two species (Avise et al. 1992, Weckstein et al. 2002). The second hypothesis proposes that the divergence of clade I and clade II haplotypes occurred prior to speciation of snow and Ross's geese, and subsequent divergence in haplotype frequencies between the two species (Quinn 1992). Our analyses revealed populations of Ross's geese have 73 – 83% clade II haplotypes, whereas 18 of the 19 populations of snow geese have relatively equivalent proportions of clade I and clade II haplotypes or have greater proportions of clade I haplotypes. The northern wintering population of lesser snow geese breeding on Wrangel Island, Russia (WRNO) exhibited a much lower frequency of clade I haplotypes than all other snow geese populations. The small proportion of clade I birds present within the WRNO population is more consistent with the clade I frequencies documented for Ross's geese populations (0.10, Avise et al. 1992; 0.30, Weckstein et al. 2002; 0.18 – 0.27, Shorey unpublished data) than for snow geese populations. WRNO snow geese have been isolated historically and during contemporary periods from Ross's geese populations in North America based on putative Pleistocene refugia locations (Ploeger 1968) and known migratory pathways and wintering sites (Ryder and Alisauskas 1995, Mowbray et al. 2000). Given this geographic isolation, low frequencies of clade I haplotypes in the WRNO population similar to Ross's geese populations suggests that the evolutionary split between mtDNA clades occurred prior to speciation of snow and Ross's geese, supporting Quinn's (1992) evolutionary hypothesis.

Unlike Ross's geese, greater snow geese have minimal contact with lesser snow geese on breeding or wintering areas. Greater snow geese breed at higher latitudes in the northeast Arctic than most lesser snow populations (Reed and Chagnon 1987), and winter along the Atlantic Coast from Massachusetts to South Carolina in groups composed exclusively of greater snow geese (Veit and Petersen 1993, Reed et al. 1998). Both historical and contemporary geographic isolation between subspecies, and morphological differences in body size (greater snow geese are generally larger than lesser snow geese) between subspecies may limit potential pairing and gene flow between greater and lesser snow geese (Cooke et al. 1995, Reed et al. 1998). Genetic differentiation between greater and lesser subspecies of snow geese was low based on differences mtDNA clade frequencies, but was significant based on variation in microsatellite allele frequency. This suggests historic rates of gene flow among subspecies may have been greater than contemporary levels of genetic exchange. Hierarchical analyses of genetic variance indicated variation among populations within subspecies was greater than the level of variation between greater and lesser snow geese. However, our analyses only included one population of greater snow geese (BYIS), indicating that the higher degree of genetic variation within subspecies as compared to among subspecies could be attributed to differences among populations of lesser snow geese. Characterizing additional populations of greater snow geese, and sequencing mtDNA to determine individual haplotypes within greater and lesser snow geese may offer greater resolution of potential genetic variation between subspecies that we were not able to resolve based on clade frequencies.

Before 1955, total numbers of Ross's geese were estimated at 6000 individuals, and were though to be confined to a narrow and well defined area in the Queen Maud Gulf region (Dzubin 1965, Prevett and MacInnes 1972). An eastward shift of migration pathways and staging areas were recorded for Ross's geese by the late 1950's (Prevett and Johnson 1977, Campbell et al. 1990). Continued growth in the population numbers and eastward expansion of the species has led to new colonies on the west coast of Hudson Bay and on Southampton and Baffin Islands (Ryder and Cooke 1973, Prevett and Johnson 1977, Frederick and Johnson 1983), and migrations to new wintering areas (Ryder and Alisauskas 1995). Current populations include 1 million breeders in the Queen Maud Gulf region, 80,000 nesting on the west coast of Hudson Bay, and smaller (but unknown) numbers of individuals on the islands (R. Alisauskas, personal communication). Similarity in mtDNA clade frequencies among Ross's geese breeding populations support the hypothesis that Ross's geese were previously one panmictic group prior to recent population expansions, and is concordant with earlier mtDNA studies (Avise et al. 1992, Weckstein et al. 1992).

The majority (90%) of Ross's geese from Queen Maud Gulf (QMRO) winter in the Central California Valley as part of the Western Arctic Population. The remaining Ross's geese from Queen Maud Gulf and the other four populations of Ross's geese in our study migrate south with the Mid-Continent Population of snow and Ross's geese. If Ross's geese have strong fidelity to wintering areas, then genetic differences may accrue as a function of winter fidelity and time since colonization between the QMRO population and the four other populations wintering in a different region. We found significant genetic variation in allele frequencies between Ross's geese nesting in Cape

Henrietta Maria (CHRO) and all other Ross's populations based on pairwise θ_P comparisons and microsatellite chord distances. Differences in chord distances were also evident between Ross's geese breeding in west Hudson Bay (WHRO) and the remaining populations of Ross's geese. Gene frequencies were similar among QMRO, and Ross's geese on Southampton and Baffin Islands. Genetic differentiation between Ross's geese nesting in west Hudson Bay and Cape Henrietta Maria coastal populations compared to the putative ancestral population in Queen Maud Gulf and Southampton and Baffin Islands populations suggests the WHRO and CHRO populations may have been colonized by geese from Queen Maud earlier than the island populations. Alternatively, founding population sizes may have been smaller in WHRO and CHRO than on the islands, resulting in population bottlenecks that changed allele frequencies in WHRO and CHRO relative to the Queen Maud population. We found no evidence of population bottlenecks or lowered allelic diversity in the WHRO and CHRO populations relative to other Ross's geese. Thus, the WHRO and CHRO populations were likely colonized earlier than Southampton and Baffin Islands, and genetic drift has increased genetic variation between WHRO and CHRO and Ross's geese from Queen Maud. Future genetic divergence between the Queen Maud population and the other four recently established populations may increase over time as a function of wintering fidelity to different wintering areas.

Banding studies indicate lesser snow geese fidelity to breeding grounds is female-biased (70-80% annual return), with males more prone to dispersal (50-66% annual return) (Cooke and Sulzbach 1978, Cooke and Abraham 1980, Ganter and Cooke 1998). High male dispersal rates from natal breeding areas increases potential gene flow and

decreases spatial genetic structure among breeding populations. Phylogenetic structure at the level of breeding populations may also be diminished by the formation of breeding pairs on the wintering grounds or during spring migration when populations are mixed (Prevett 1972, Cooke 1987, Ganter et al. 2005). Thus, philopatry to wintering grounds may be more influencial in determining population structure in lesser snow geese than fidelity to breeding sites (Cooke et al. 1988, Robertson and Cooke 1999). Estimated annual fidelity to wintering areas varies among wintering regions, and is very high for male and female lesser snow geese in the Western Arctic wintering population (96-98% return in subsequent year; Armstrong et al. 1999, Baranyuk et al. 1999, Williams et al. 2005), and relatively lower for lesser snow geese in the Mid-Continent wintering population (43-72%; Alisauskas 1998).

If winter fidelity is an important factor influencing genetic structure of snow geese, we would expect a higher degree of genetic variation among wintering populations than among breeding populations sharing the same wintering grounds. Hierarchical analyses of mtDNA and nDNA variance indicated genetic differences were greater among breeding populations within a wintering group than among wintering groups. The hierarchical analysis calculated the proportional variance from with a "bottom-up" approach, beginning with the genetic variation among individuals. Both the mtDNA control region and microsatellite loci utilized for this analysis are highly polymorphic, and the high level of variation among individuals may make it difficult to resolve variation among the top hierarchical contrasts (i.e., among wintering groups). Pairwise comparisons of population θ_P values revealed that mean pairwise population differences were twice as large between lesser snow geese from different wintering areas as

compared lesser snow geese from the same wintering population. In addition, one wintering population was statistically supported among lesser snow geese in the population distance tree. The cluster was composed of three populations (WRNO, WRSO, BKIS) representing the majority of lesser snow geese contributing to the Western Arctic wintering population. There is also evidence that lesser snow geese from Japan (KOLY) which are reproductively isolated from all other snow geese populations during breeding periods, but share wintering grounds in the Central California Valley with other snow and Ross's geese populations (M. Samuel, personal communication), have similar gene frequencies as most North American populations. Additionally, populations of lesser snow geese nesting in one colony on Wrangel Island, Russia, but wintering in two geographically distinct areas (WRNO geese winter in southern British Columbia and northern Washington state and WRSO geese winter in the Central Valley of California), exhibit significant differences in allele and haplotype frequencies. Thus, fidelity to wintering areas is likely a more important influence on the genetic structure of snow geese than fidelity to geographically separated breeding sites. Contemporary wintering areas have likely only been utilized since the retreat of the last Pleistocene glacier, and wintering populations may not have been separated long enough to generate large genetic differences among all wintering groups. It is possible that genetic variation among wintering populations may continue to increase over time as a function of restricted gene flow among populations from different wintering areas.

The two color morphs of lesser snow geese were considered separate species until 1983 when studies revealed that the two forms were a single interbreeding, dimorphic species (Am. Ornithol. Union 1983) with the color dimorphism controlled by a single

gene, the melanocortin-1 receptor (Mundy et al. 2004). Historic data suggests blue-phase and white-phase lesser snow geese may have been isolated in two separate refugia during the last Pleistocene glacial period (18,000-26,000 ybp), with blue-phase geese surviving in the Canadian Arctic Archipelago and white-phase geese inhabiting refuges farther west in Siberia and the Bering Sea region (Ploeger 1968, Cooke et al. 1988). Color phases may have remained allopatric until the early 20th century (Cooke et al. 1988). Prior to the 1920's, 99% of the geese nesting in western colonies of Hudson Bay were white and 99% of geese within eastern colonies of Hudson and James Bays were blue (Barnston 1860, Sanders 1917). During this period, mixing of blue and white snow geese on major wintering grounds was extremely rare (Cooke et al. 1988). Eastward expansions of white geese and westward expansions of blue geese that have occurred since 1940 (Lewis and Peters 1941, Cooch 1961, Dzubin 1979, Johnson and Troy 1987), and increasing numbers of lesser snow geese across the continent (Ankney 1996, Batt 1997, Abraham et al. 1999) have increased opportunities for genetic exchange between blue and white snow geese. Lack of genetic differences among blue and white lesser snow geese populations in similar geographic locales indicate that the length of time blue and white snow geese may have been historically isolated was not long enough for significant genetic variation to develop between the two color morphs. In addition, mixed-mating between the color morphs during more recent evolutionary periods may have homogenized gene frequencies among blue and white geese wintering and breeding in similar regions.

Few avian species have deeply diverged phylogenetic groups which are geographically widespread as in snow and Ross's geese (Avise and Walker 1998). Several other species of Arctic-nesting birds exhibit significant genetic divergences

attributed to historical events that display a strong geographic orientation (dunlin, Wenink et al 1993; spectacled eider, Scribner et al. 2001; Canda geese; Scribner et al. 2003). Canada geese, for example, were shown to have a large genetic divergence between two mtDNA haplotype clades (14% sequence divergence), which was related to the division of large-bodied and small-bodied forms of geese within the species (Scribner et al. 2003; see also Chapter 2). This significant phylogenetic split was attributed to isolation of the two forms in separate glacial refugia during the Pleistocene. In contrast, some Arctic species exhibit homogenized gene frequencies among nesting and wintering populations [harlequin duck (*Histrionicus histrionicus*), Lanctot et al. 1999; king eider, Pearce et al. 2004]. For instance, king eiders are genetically panmictic across the species range, and lack of spatial structure was attributed to historical gene flow and recent population growth following Pleistocene deglaciation (Pearce et al. 2004). Our genetics data support the hypothesis of a fundamental genetic split between snow and Ross's geese species, but propose that speciation occurred subsequent to evolutionary divergence between the two, geographically widespread mtDNA haplotype clades.

We used multiple genetic markers which differed in mode of inheritance and rate of evolution to resolve historical signatures of genetic variation and detect contemporary changes in genetic divergence within and among snow and Ross's geese species. We investigated two hypotheses regarding the spatial genetic structure of snow and Ross's geese. Our first hypothesis proposed that the present populations of snow and Ross's geese are genetically differentiated in a manner reflecting historical biogeographic isolating events proposed by Ploeger (1968). We found significant phylogenetic divergences among species based on mtDNA clade frequencies and allele frequencies,

supporting Ploeger's hypothesis that snow and Ross's geese were isolated in separate glacial refugia during the Pleistocene. We also found evidence of genetic differentiation between greater and lesser snow geese, although the degree of genetic variation between subspecies was much less than between species. The lack of significant variation between subspecies based on mtDNA may indicate that greater snow geese were not completely isolated in the northeastern Arctic glacial refugia proposed by Ploeger (1968), or the period of subspecies separation was not long enough to accrue significant differences in gene frequencies. Alternatively, we may not have been able to resolve subspecies differences based on only one population of greater snow geese and without sequencing haplotypes within mtDNA clades.

Our second hypothesis stated that contemporary population expansion events within snow and Ross's geese have been extensive, and any genetic signature of historical differentiation that may have occurred within and among species may be masked by these expansions. Alternatively, snow and Ross's geese may still exhibit genetic structure based on population affinities to breeding and wintering grounds, despite expansions that may obscure genetic variation attributed to historical processes (Ely and Scribner 1994, Robertson and Cooke 1999). We were able to resolve historic divergence at the level of species, but not at the subspecies level or among color phases of lesser snow geese. Recent widespread expansions of snow geese populations may have diluted past genetic divergence between subspecies and between color phases. However, it is also possible that separation times between subspecies and between blue and white snow geese may have been too short to allow for significant genetic variation to accrue between groups. We provide evidence that the current population genetic

structure of snow and Ross's geese is strongly influenced by population affiliation to wintering regions, and hypothesize wintering populations may continue to diverge genetically over time.

Both historical vicariant events and recent demographic changes, including population expansions and colonization of new nesting and wintering sites, have greatly influenced contemporary levels of genetic differentiation among populations of snow and Ross's geese. By utilizing maternally and bi-parentally inherited genetic markers, our study provides inferences about the relative importance of historical and ecological factors that have shaped the spatial genetic structure of snow and Ross' geese across their species ranges. In previous studies (Quinn 1992, Avise et al. 1992, Weckstein et al. 2002), conclusions were based on gene trees derived from a single locus (mtDNA), relatively few individuals per locale, and a limited number of populations within each species. By increasing the number of populations included in the analysis, and sampling a large number of individuals from each location, we were able to examine hypothesis regarding the genetic differentiation of among species of snow and Ross's geese, between subspecies of snow geese, between color morphs of lesser snow geese, and among breeding and wintering populations of snow geese and Ross's geese throughout the geographic range of both species.

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CHAPTER 4: A NOVEL METHOD FOR CANADA GOOSE HARVEST DERIVATION USING GENETIC ANALYSIS OF TAIL FEATHERS

INTRODUCTION

Harvest management for Canada geese (*Branta canadensis*) attempts to meet species, population, and resource user goals by maintaining viable breeding populations that allow for sustained harvests. The success of Canada goose management may be increased by monitoring harvest composition in areas where birds from multiple breeding populations or subspecies mix during seasonal hunting periods. To accurately estimate proportional contributions of populations or subspecies within a mixed flock, the harvest must be unambiguously identified to population/subspecies of origin. In addition, harvest samples must be representative of the entire harvest at desired spatial and temporal scales.

Genetic markers have been recently used to estimate proportional contributions of Canada goose populations in harvest mixtures at multiple geographical scales (Pearce et al. 2000, Scribner et al. 2003). Scribner et al. (2003) were also able to estimate harvest composition for discrete time periods associated with early, regular, and late hunting seasons within each of several years and between managed and private lands in close proximity. However, sample sizes in some of the harvest mixtures analyzed were relatively small, and all hunter-harvested birds in both earlier studies were collected at a few private hunting areas and at state game area check stations that were managed for migrating Canada geese and other waterfowl. Restricted sampling of harvested geese may be a source of error if harvest derivations are assumed to represent the harvest

composition across larger geographic regions (e.g., entire states or Flyways). Thus, a more broad-based and systematic framework of sampling harvested birds is needed to increase the accuracy and precision of genetic-based estimates of harvest composition over large geographic areas. Annual collections of tail fans (feathers) of harvested geese from hunters participating in the U.S. Fish and Wildlife Service (USFWS) Waterfowl Parts Survey (Martin and Carney 1977) may provide sampling coverage necessary to determine population-specific Canada goose harvest estimates at spatial and temporal resolutions necessary to answer many research and management questions, and without the need to conduct additional directed collections.

The sex and age composition of harvest is needed to estimate differential susceptibility when evaluating harvest regulations (Pospahala et al. 1974, Reynolds and Sauer 1991). However, determining sex and age may be problematic when complete specimens or sex organs are not available for inspection, particularly in sexually monomorphic species like Canada geese (Bellrose 1980, Owen 1980). Tail fans may be used to discriminate large from small subspecies of Canada geese based on size morphology, but subspecies determinations may be inaccurate if both sexes are included in analyses (Tacha et al. 1987). Although Canada geese cannot be sexed from tail fans alone, the sex of each harvested Canada goose sample can be determined using genetic markers (e.g., Griffiths et al. 1998).

Our objectives were to (1) use nuclear microsatellite loci and likelihood methods based on mixed stock analyses to estimate proportional contributions of breeding populations of Richardson's, interior, and giant Canada geese using tail fans obtained from U.S. Fish and Wildlife Service Parts Survey for Michigan's 1998-99 harvest, and

(2) to use genetic markers to determine sex and estimate sex ratios of Canada geese harvested. We build upon the work of Scribner et al. (2003) by incorporating systematic Parts Survey collections to expand the geographical coverage of Canada goose harvest sampling in Michigan, and by providing methodology for molecular determination of sex that can be accomplished using Parts Survey samples. By increasing the number of breeding populations in our baseline, and by increasing sample size, we provide more representative state-wide measures of the racial composition of Canada goose harvests in Michigan.

METHODS

Sample Collection

Blood was sampled from feather quills taken from pre-fledging goslings collected according to methods outlined in Scribner et al. (2003). Specific sampling locations include the baseline breeding populations identified in Scribner et al. (2003), and four additional breeding populations including Baffin Island, and Michigan's eastern upper peninsula, northeast lower peninsula, and northwest lower peninsula. Collections of interior Canada geese included samples obtained within the Mississippi Valley Population (MVP) breeding range in both Hudson Bay (n = 100) and James Bay (n = 65) and within the breeding range of the Southern James Bay Population (SJBP) on the mainland (n = 100) and Akimiski Island (n = 83); Richardson's Canada geese were collected within the Tall Grass Prairie Population (TGPP) breeding areas on Baffin Island (n = 86). Giant Canada geese were sampled within breeding areas across Michigan including the southwest (n = 119), south-central (n = 129), southeast (n = 79), northwest

(n = 46), and northeast (n = 30) regions of the lower peninsula, areas surrounding Saginaw Bay (n = 78), and within western (n = 58) and eastern portions of the upper peninsula (n = 19).

Canada goose harvest samples were collected during the 1998-99 fall hunting season in Michigan through the USFWS Waterfowl Parts Survey (Martin and Carney 1977). The Waterfowl Parts Survey was initiated in 1961 in an effort to provide the USFWS with direct estimates of species, age, and sex composition of annual harvests that could not be accurately determined from the USFWS Hunter Questionnaire Survey, which has been used since 1952 for total harvest estimates. The Parts Survey also facilitates harvest analyses at finer geographical (e.g., state vs. flyway) and temporal (e.g., daily or weekly vs. entire season) scales than was possible through the Questionnaire Survey (Martin and Carney 1977, Geissler 1990). Cooperating hunters were asked to mail the USFWS primary wing tips and tail retrices for each goose harvested, and samples returned were cataloged by a unique identification number in the USFWS database associated with date and location of harvest. Biologists then categorize goose samples returned by species and age (juvenile or adult) (Carney 1964, 1992). The USFWS attempts to solicit hunter participation to collect samples from each state in proportion to that state's contribution to the total flyway harvest.

We obtained hunter-harvested samples of all Canada geese collected in Michigan during the 1998-99 USFWS Parts Survey (n = 481). Each sample envelope contained 1-12 tail feathers from geese harvested in 51 out of 83 possible counties in Michigan during the early (n = 259), regular (n = 201) and late (n = 11) hunting seasons (date range:

9/1/98-2/3/99). Samples were presumed to represent a mixture from all sampled baseline locations.

Genetic Analyses

We extracted DNA from 3 tail fan feathers (when available) for each harvested Canada goose to maximize quantities of DNA. Use of multiple feathers may lead to contamination (Pearce et al. 1997) if hunters inadvertently placed feathers from multiple individuals in each envelop. However, given the high allelic diversity of loci surveyed (Scribner et al. 2003), we would expect to observe evidence of amplification of >2 alleles from DNA of contaminated samples, inconsistent with known Mendelian inheritance (Cathey et al. 1998, Buchholz et al. 1998). Feathers were dissected on a clean glass plate. The feather rachis was diced into 0.30 cm pieces using a sterile blade that was flamed between samples to prevent contamination. These pieces were subsequently placed into a 1.5 mL Eppendorf tube, and Qiagen Dneasy kits and protocols (QIAGEN Incorporated, Valencia, CA, USA) were used to extract DNA. We quantified DNA concentration using a fluorometer or spectrophotometer, and diluted samples to working concentrations of 50 ng/μL for subsequent analyses.

We used five bi-parentally inherited microsatellite DNA loci (Bcaμ7, Bcaμ9, Bcaμ11, and Hhiμ1 [Buchholz et al. 1998], and TTUCG-1 [Cathey et al. 1998]) to estimate allele and genotype frequencies for all baseline breeding populations and hunter-harvested samples. Loci were amplified using polymerase chain reaction (PCR), and products were electrophoresed on denaturing 6% polyacrylamide gels and visualized using a FMBIO II laser scanner (Hitachi Software Engineering, Alameda, California,

USA). Resulting genotypes were scored based on 20 base-pair standards and reference samples of known genotype.

Sex of all hunter-harvested samples was determined using the chromo-helicase-DNA-binding (CHD) locus (Griffiths et al. 1998). Primers amplify portions of the CHD locus on the W and Z sex chromosomes (females are ZW and males are ZZ) within non-coding intron regions whose lengths differ between the chromosomes. Thus, males can be identified by the presence of one band (two introns of the same size), while females are characterized by two bands (two introns of different sizes).

Statistical Analyses

We conducted mixed stock analyses of the harvest using maximum likelihood methods (Pella and Milner 1987, Scribner et al. 2003). We sampled all three subspecies and four managed populations of Canada geese [MVP, SJBP, TGPP, Michigan Mississippi Flyway Giant Population (MI-MFGP)] likely to contribute to Michigan's harvest (Luukkonen and Soulliere 2002). In order to ensure genetic markers used were independent, tests for genotypic linkage disequilibrium were conducted as described by Weir (1996) using the program GENEPOP (Raymond and Rousset 1995). For each breeding population, we used a Fisher's Exact Test implemented in program GENEPOP to test observed genotype frequencies in each of the five microsatellite loci utilized for deviations from Hardy-Weinberg expectations. In addition, we used simulated harvest mixtures to estimate accuracy and precision of the harvest mixture composition based on resampling of baseline populations.

We used hierarchical F-statistics (Weir 1996) in the program F-STAT (Goudet 2000) to estimate degree of genetic differentiation among subspecies and among management populations. Measures of variance in allele frequency among subspecies and among management populations were summarized as pair-wise estimates of population F_{st}, and significance of mean F_{st} values (across the five microsatellite loci) was determined by jackknifing procedures (Weir 1996). To account for multiple testing, sequential Bonferroni procedures (Rice 1989) were used to adjust nominal significance levels in tests of Hardy-Weinberg, gametic disequilibrium, and F-statistics.

Harvest derivations were calculated using the Statistics Program for Analyzing Mixtures (Debuvec et al. 2000), which compares the distributions of genotypic frequencies of each baseline population with the genotypic frequencies observed in harvest mixtures (see Scribner et al. 2003 for details). Proportional contributions of each subspecies were calculated as the mean over 500 replicate resamplings (with replacement) of baseline populations and the harvest mixture, and confidence limits (SE) for harvest estimates were calculated using Monte Carlo bootstrapping.

RESULTS

Each of the five microsatellite loci were polymorphic (4-13 alleles per locus; mean heterozygosity per locus 0.406-0.806; specific data not shown). Tests for each locus in each of the baseline breeding populations revealed approximately 95% of individual tests, and cumulative tests across all loci for each baseline population, were within Hardy-Weinberg expectations ($P > 0.05$). No linkage was evident for any locus pair in any population, indicating microsatellite loci used in harvest mixture analyses

were independent. We observed no evidence of cross-sample contamination (data not shown).

Pair-wise comparisons among the thirteen Canada geese breeding areas revealed significant differences in allele frequencies (mean F_{st} across all populations = 0.025, $P < 0.001$). Differences were greater among subspecies (interior, Richardson's, and giant Canada geese; mean pair-wise $F_{st} = 0.039$, $P < 0.005$) than among management populations (MVP, SJBP, TGPP, MI-MFGP; mean pair-wise $F_{st} = 0.033$, $P < 0.005$). Simulations based on allele frequencies of breeding populations indicated that allocating a mixed harvest to populations of origin can be accomplished with high accuracy (85-96%). The majority of misclassifications within the simulations were to other breeding populations within the same subspecies (interior to interior, giant to giant; specific data not shown). Therefore, we were able to more accurately and precisely assign the mixed harvests to subspecies (interior, Richardson's, and giant).

DNA concentrations were sufficient for PCR and analysis for 471 of the 481 (98%) Canada geese sampled through the Parts Survey. Maximum likelihood estimates (±SE) for the 1998-99 fall harvest of Canada geese in Michigan were 69.2 ± 6.2% giant Canada geese, 26.3 ± 5.8% interior Canada geese, and 3.8 ± 1.2% Richardson's geese (Figure 1). Of the 471 tail fan samples used in the sexing analysis, 224 were female and 239 were male, resulting in a harvest ratio of 0.937 females for every 1 male.

DISCUSSION

Management agencies use harvest derivations to determine if current hunting regulations meet species and population goals for sustainable harvests while maintaining

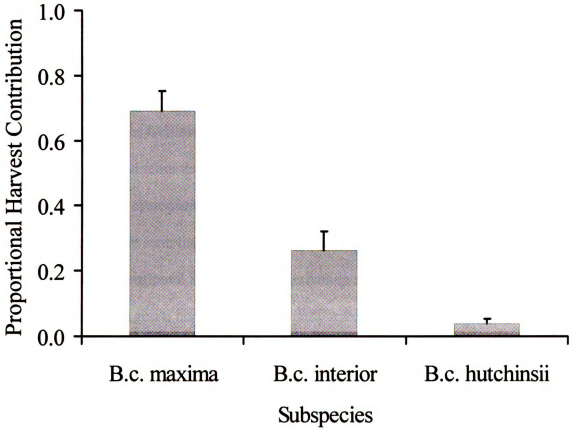

Figure 1. Mean proportional contributions (±SD) of subspecies (*Branta canadensis maxima, B. c. interior, and B. hutchinsii hutchinsii*) of Canada geese to the 1998-99 season harvest in Michigan.

diversity and viability of breeding populations. For harvest derivation techniques to be reliable and widely applicable, harvest sampling regimes must enable managers to accurately estimate harvest by subspecies and population. Use of genetic markers and mixed stock analyses allows for accurate discrimination among subspecies and populations of Canada geese contributing to harvests. As problems of differentiating Canada goose populations and subspecies are not unique to Michigan or the Mississippi

Flyway (Rusch et al. 1995), the derivation techniques employed in Michigan's Canada goose harvest could be applied to many areas of North America where multiple subspecies or populations co-occur during harvest.

Long-term, adaptive management of Canada geese necessitates that harvest derivation techniques facilitate collections of sufficient data to provide evaluations of the harvest at spatial and temporal scales relevant to management objectives. Incorporating a comprehensive and systematic sampling methodology such as the USFWS Waterfowl Parts Survey reduces sampling bias, and Canada geese harvest estimates can be derived at desired spatial and temporal scales. As the derivation techniques employed in Michigan's Canada goose harvest allow for multi-scale analyses, these techniques could be used to evaluate annual harvest regulations, including harvest quotas, harvest zones, and seasonal harvest periods.

The sex ratio of Canada geese harvested in Michigan during the 1998-99 was nearly 1:1. Multiple studies have documented nearly even proportions of sexes among several age groups of Canada geese (Hanson and Smith 1950, Sherwood 1965, Vaught and Kirsch 1966, see Bellrose 1980 for review). An even sex ratio would be expected given both sexes actively participate in parental care of offspring, family groups often migrate together (Raveling 1988, Raveling et al. 2000), and hunting mortality is similar among males and females (Bellrose 1980, but see Imber 1968). This is in contrast to sexually dimorphic ducks, where females incur higher mortality during nesting, brood rearing, and hunting, leading to a 2:1 sex ratio (males:females) in harvests of many species (Bellrose et al. 1961, Bellrose 1980). Hunter selectivity for one sex in dimorphic species may also account for skewed sex ratios in ducks.

MANAGEMENT IMPLICATIONS

Increasing the accuracy of harvest derivations across multiple spatial scales and time periods of relevance to managers will improve evaluations of the impacts that alternative harvest regimes have on co-occurring populations of Canada geese. Such knowledge is essential when management objectives differ among populations. By combining samples from the USFWS Parts Survey with genetic analyses, we increased spatial coverage of state-wide harvest samples, reducing sampling bias encountered when harvest derivations estimated from samples obtained from a few selected harvest locations were extrapolated to other non-sampled areas or time periods. If sufficient genetic differences exist among breeding populations, and if sufficient samples are available, genetic-based harvest derivation techniques could be applied in other states, and for other migratory species at many temporal and geographic scales. Molecular methods of sex determination would eliminate gender-based biases inherent in morphologically-based methods of subspecific or population classification.

ACKNOWLEDGEMENTS

Funding for this study was provided by the Michigan Department of Natural Resources (MDNR) and through the Partnership for Ecosystem Research and Management (PERM) Program between the MDNR and the Department of Fisheries and Wildlife at Michigan State University. Baseline samples were collected by many individuals associated with the MDNR, including B. Odum, S. Schmidt, T. Cooley, J. Gormley, J. Lerg, A. Karr, B. Voyle, T. Gearman, and J. Dastack. Additional baseline

samples were obtained by K. Abraham, D. Caswell, and J. Leafloor. We also thank the Michigan State University students who assisted with baseline sample collection including J. Niewoonder, M. Monfils, L. Briggs, M. Wasilco, R. White, A. Bump, L. Gay, E. Butler, J. Lemson, D Gaebel, and J. Murphy. Hunter-harvested samples were collected by the U.S. Fish and Wildlife Service. We acknowledge J. Martz and C. Bennett, Jr., MDNR, for their assistance throughout the project.

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CHAPTER 5: COMPOSITION OF CANADA AND CACKLING GOOSE HARVESTS IN MICHIGAN 1998-2002: A GENETIC ANALYSIS OF USFWS WATERFOWL PARTS SURVEY SAMPLES

INTRODUCTION

The number of states where harvest regulations for cackling geese (*Branta hutchinsii*, Banks et al. 2003) and Canada geese (*Branta canadensis*) include special seasons and hunting zones is growing in response to requests for increased hunting opportunities and decreased human-geese conflicts, and the need to target overabundant non-migratory resident populations while protecting smaller migratory populations (Lindberg and Malecki 1994, Williams and Johnson 1995, Ankney 1996, Heusmann 1999, Luukkonen and Souillere 2004a). Agencies across North America including the Michigan Department of Natural Resources have implemented special early and late goose seasons, and has shifted the opening date of the regular season from early October to mid-September to target a large and rapidly growing population of resident giant Canada geese (*Branta canadensis maxima*) and to minimize harvests of migrant interior (*B. c. interior*) Canada geese and cackling geese (*B. hutchinsii hutchinsii*) (Soulliere et al. 1988, Luukkonen and Soulliere 2004a). Current understanding of migration patterns and timing of interior Canada geese and cackling geese based on banding studies suggest these birds remain on their northern breeding grounds until late September (Tacha et al. 1991, Mowbray et al. 2002, Leafloor et al. 2004), and generally do not arrive in major harvest areas of southern Michigan until early October (Luukkonen and Soulliere 2004a). Daily limits are more liberal during early and late seasons as compared to the regular

season to in an attempt to increase harvest of resident Canada geese during periods of low migrant abundance (Luukkonen and Soulliere 2004b). As harvest regulations may vary among seasons, it would be important to determine if arrival times of migrants are similar among years, or if arrival times vary annually. Derivation techniques that provide accurate estimates of harvest at fine temporal scales are necessary to evaluate harvests of resident Canada geese and migrant Canada and cackling geese within and among hunt seasons. Additionally, it is important to determine if harvest sampling is spatially uniform among years, or if there is large variation in annual sample collections. If sampling among years is equivalent, then differences in annual harvests may be attributed to biological factors (i.e., chronology of migration of interior Canada geese and cackling geese) that lead to changes in the proportion of migrant and resident geese harvested each year. If sampling among years is highly variable, then annual harvest differences may be a result of sampling variation.

In addition to the seasonal changes implemented to increase resident goose harvests and protect migratory geese, special harvest zones and game management units (GMUs) have been created. Michigan has been divided into two harvest management zones; the Mississippi Valley Population (MVP) zone in the Upper Peninsula and northwest Lower Peninsula and the Southern James Bay Population (SJBP) zone in the southeast Lower Peninsula (Figure 1). The MVP and SJBP zones were defined based on long-term banding and radio-telemetry data (Tacha et al. 1991) and range descriptions (Bellrose 1980) that defined migratory corridors utilized by MVP and SJBP geese (*B. c. interior*). The MVP and SJBP zones have been used to regulate harvests of birds that breed within geographically defined breeding populations by adjusting season length and

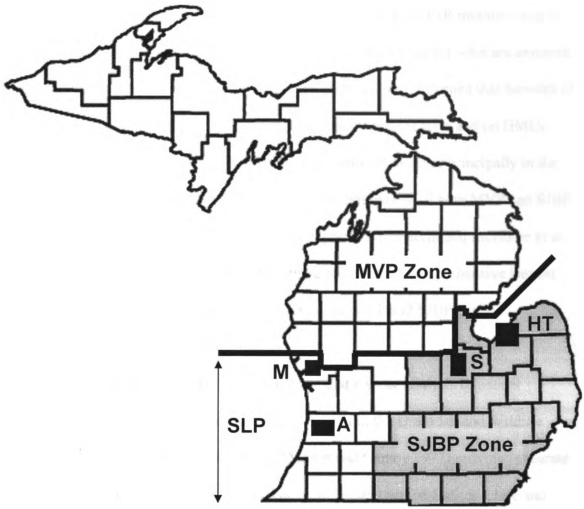


Figure 1. Four local goose management units (GMUs) designed to attract migrating waterfowl are located in the southern Lower Peninsula (SLP) of Michigan, including Muskegon County Wastewater (M) and Allegan (A) in the Mississippi Valley Population (MVP) harvest management zone, and Saginaw (S) and Tuscola/Huron (HT) within the Southern James Bay Population (SJBP) harvest management zone. Counties within the MVP zone are white, while counties within the SJBP zone are shaded. GMUs within these zones are designated by black rectangles.

timing and daily limits within these zones, and implementing closures in areas where Federally imposed state quotas have been reached for the annual harvest. GMUs are smaller public hunting areas within harvest management zones traditionally managed to attract migrant geese through the supplementation of browse foods and by providing open

water refuges (Luukkonen and Soulliere 2004b). The Michigan DNR monitors annual harvests within GMUs, and the season is closed when state quotas for what are assumed to migrant geese are achieved. Management prescriptions have assumed that harvests of MVP geese occurs mostly within the MVP harvest management zone and on GMUs within that zone, while harvests of SJBP geese are assumed to occur principally in the SJBP zone. However, recent studies have indicated that harvest of both MVP and SJBP geese may be more widespread in Michigan than previously determined (Scribner et al. 2003, Fritzell and Luukkonen 2004). Thus, there is a need for comprehensive harvest evaluations across public and private areas within the MVP and SJBP harvest management zones and within local GMUs.

Inman et al. (2003) recently demonstrated that genetic analysis of annual collections of tail fans (feathers) of harvested geese from the U.S. Fish and Wildlife Service (USFWS) Waterfowl Parts Survey (Martin and Carney 1977) provided accurate discrimination among subspecies and management populations of Canada geese and cackling geese contributing to Michigan harvests. Through this comprehensive sampling methodology, hunters from across the state mail the USFWS tail retrices from harvested geese from public and private hunting areas within both harvest management zones, and throughout all seasonal harvest periods. The broad temporal and spatial coverage of these harvest samples combined with genetic-based mixed stock analysis (Pearce et al. 2000, Scribner et al. 2003) can be used to estimate proportional contributions of resident and migrant geese to special harvest seasons and within local GMUs and harvest management zones.

Our first objective was to utilize nuclear microsatellite loci and mixed stock analyses to estimate proportional contributions of three subspecies (cackling geese, and interior and giant Canada geese) and four management populations [Tall Grass Prairie Population (TGPP), MVP, SJBP, and Michigan's Mississippi Flyway Giant Population (MI-MFGP)] of geese that are potentially harvested during special seasons and within defined harvest zones. We estimate seasonal and annual variation in population and subspecies contribution to annual harvests using genetic markers and established mixture analysis (Pella and Milner 1987, Pella and Masuda 2001) for early, regular and late seasons, and for six discrete time periods from the beginning of the early season to the end of the regular season. Additionally, we derive harvest estimates for local GMUs and surrounding private areas, and for the MVP and SJBP harvest management zone for annual, early season, and regular season harvest periods. Our second objective was to test the equality of harvest estimates derived for harvest mixtures collected at different times or from different harvest zones. We present results based on Monte Carlo likelihood ratio tests to assess significant changes in harvest composition among the five years sampled. Our final objective was to determine if bias exists among harvest sample collections. Variograms, which illustrate the average degree of similarity among number of individuals sampled as a function of distance separating sampling locales (Rossi et al. 1992), were used to determine if the spatial pattern of harvest samples collected across the state was consistent among years.

METHODS

Sample Collection

Baseline samples were collected from pre-fleging goslings in breeding populations of cackling geese, and interior and giant Canada geese according to methods outlined in Scribner et al. (2003), including all sampling locations outlined in Inman et al. (2003). A total of 964 individuals were collected from baseline breeding populations of cackling geese (n = 1 population), and interior (n = 4) and giant (n = 8) Canada geese. Samples from the goose harvest were collected during the 1998-2002 annual hunting seasons in Michigan using the United States Fish and Wildlife Service (USFWS) Waterfowl Parts Survey (Martin and Carney 1977) (see Inman et al. 2003 for Survey details). We obtained hunter-harvested samples of all geese collected in Michigan during the 1998-99 (n = 471), 1999-2000 (n = 406), 2000-01 (n = 324), 2001-02 (n = 486), and 2002-03 (n = 585) USFWS Parts Surveys (Figure 2). Each sample envelope contained 1-12 tail feathers, and were identified by date and county of harvest within Michigan. Samples were presumed to represent a mixture from all sampled baseline locations.

Genetic Analyses

We extracted and quantified DNA from geese tail fan feathers using techniques detailed in Inman et al. (2003). Five bi-parentally inherited microsatellite DNA loci (Bcaμ7, Bcaμ9, Bcaμ11, and Hhiμ1 [Buchholz et al. 1998], and TTUCG-1 [Cathey et al. 1998]) were used to estimate allele and genotype frequencies for all baseline breeding populations and hunter-harvested samples. Loci were amplified using polymerase chain reaction (PCR), and products were electrophoresed on denaturing 6% polyacrylamide gels and visualized using a FMBIO II laser scanner (Hitachi Software Engineering,

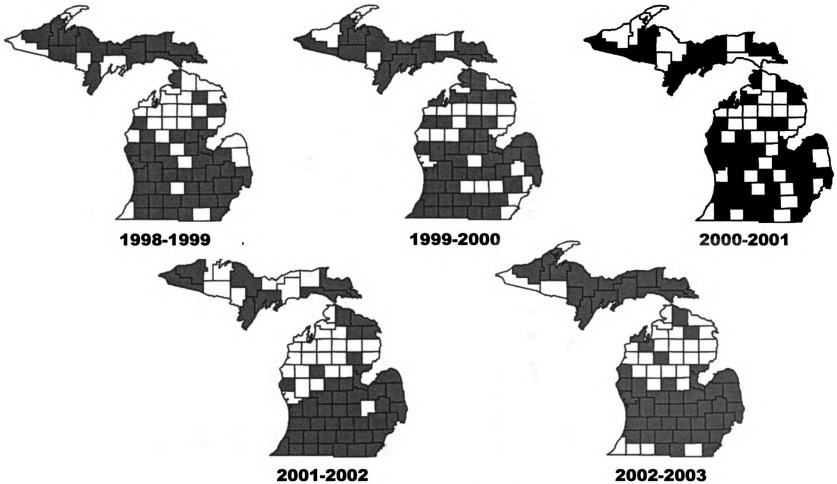


Figure 2. Distribution of cackling geese and Canada geese harvest samples collected in Michigan through the U. S. Fish and Wildlife Service Waterfowl Parts Survey. Shaded counties indicate at least one sample was collected within that county during the annual harvest season referenced below each map.

Alameda, California, USA). Resulting genotypes were scored based on 20 base-pair standards and reference samples of known genotype.

Sex of all hunter-harvested samples was determined using the chromo-helicase-DNA-binding (CHD) locus (Griffiths et al. 1998). Males were identified by the presence of one amplified band (two introns of the same size), while females were characterized by two bands (two introns of different sizes).

Harvest Derivations

We first used variograms to determine if harvest sampling is spatially uniform among years, or if there is large spatial variation in annual sample collections for the total harvest, early season harvest, regular season harvest, and harvest within the MVP and SJBP harvest management zones. Similar to spatial covariance and correlation functions, variograms model the average degree of similarity (e.g., level of variability) among number of individuals sampled as a function of distance separating sampling locales (Rossi et al. 1992). Each variogram was constructed as a plot of half the average squared difference among harvest sample sizes for counties separated by about the same distance (distance between county pairs). Geographic distances between each pair of Michigan counties were calculated using x,y coordinates (in meters) from the MIGeoref projection (MDNR Spatial Data Library 2005). Variograms were constructed using the program SAS (SAS Institute 2005). Ten distance classes were included in all variograms except for the SJBP harvest zone total harvest variogram (7 distance classes), and were determined by the lag distance (30 km for SJBP, 40 km for all others) multiplied by the number of lags, or distance classes. Distance classes included harvest samples from

pairwise county comparisons whose geographic distance between counties were within each distance interval ± half the lag distance.

We conducted mixed stock analyses of annual harvests using conditional maximum likelihood methods (Pella and Milner 1987) within the Statistics Program for Analyzing Mixtures (SPAM 3.7, Debuvec et al. 2000), which compares the distributions of genotypic frequencies of each baseline population with the genotypic frequencies observed in harvest mixtures (see Scribner et al. 2003 for details). We utilized Bayesian modeling of baseline allele frequency distributions (Pella and Masuda 2001) prior to maximum likelihood estimation of the harvest to accommodate the possibility of alleles that are found in mixtures but not present in the baseline. This method is an improvement over conditional maximum likelihood methods, as absence of an allele from a particular baseline population sample implies it is only rare and was missed in sampling rather than assuming it is nonexistent. Proportional contributions of cackling and Canada geese were calculated as the mean (±SD) over 1000 replicate resamplings (with replacement) of baseline populations and the harvest mixture, and confidence limits for harvest estimates were calculated using Monte Carlo bootstrapping.

Harvest derivations were conducted for multiple geographic and temporal subdivisions of statewide harvests. For each of the five harvest years (1998-2002), proportional contributions of cackling and Canada geese were estimated for each annual period, and for early (September 1-15), regular (September 16 – December 31), regular + late (September 16 – January 31; except 1998 which included samples until February 3), and late (January 1 – 31; 2001 only) seasons within each annual harvest. Annual collections of statewide harvest samples were also analyzed within six discrete time

periods: September 1 – 7, September 8– 15, September 16– 22, September 23 – 29, September 30 – October 6, and October 7 – December 31.

Similar statewide harvest derivations were conducted on an annual basis for samples harvested within Michigan's MVP and SJBP harvest management zones (Figure 1). Seasonal harvests were analyzed for early and regular seasons only due to the low number of geese harvested in the late season within both of these areas. Proportional contributions of each of the four management populations were estimated within the MVP and SJBP harvest zones for statewide and seasonal derivations.

Four local Goose Management Units (GMU) within the southern Lower Peninsula (SLP) of Michigan, including Huron/Tuscola, Saginaw, Muskegon Wastewater, and Allegan, were compared to non-GMU county harvests at the statewide level and within SLP counties (Figure 1). Analyses were conducted for regular seasons 1998-2002, as local GMUs were only open to hunting during the regular season in these years. Geese harvested within Huron, Tuscola, Saginaw, Muskegon, and Allegan counties during the regular season were defined as GMU samples for this analysis. Proportional contributions of subspecies were estimated in the regular season for all four local GMUs combined (HTSMA), non-GMU counties statewide, and non-GMU counties within the SLP.

Monte Carlo likelihood ratio tests were conducted in SPAM 3.7b (Debuvec et al. 2000) to test the equality of harvest mixtures (i.e., did harvest mixtures collected at different times or from different spatial locales originate from the same underlying mixture). This test is more powerful for detecting differences among mixtures than overlap in the confidence interval estimates for each population contribution from each

mixture. The latter technique suffers from inflated Type I error rates arising from the simultaneous inferences, and inflated Type II error rates due to the use of marginal (region-specific) measures of mixture difference (Reynolds and Templin 2004). The likelihood ratio compares the likelihood of the observed mixture samples under two different models: (1) the null model, where each of the M mixture samples comes from a common mixture, and (2) the alternative model, where each of the M mixture samples comes from a (possibly) different mixture. The observed likelihood ratio is obtained by fitting both models and forming the ratio of their likelihoods. This observed likelihood ratio is then compared to the reference distribution of likelihood ratio expected under the null model to calculate a P-value. This method assumes all mixture samples were gathered independently and randomly, all populations contributing to the mixtures are represented in the baseline, and that the genetic markers used to characterize samples are in Hardy-Weinberg equilibrium within each contributing population (Reynolds and Templin 2004).

Likelihood ratio tests of equality among potentially different mixture samples were conducted for several different spatial and temporal harvest derivations of cackling and Canada geese. Yearly mixtures (n = 5, 1998-2002 harvests) were tested for equality within three geographic areas: (1) statewide, (2) within the MVP harvest management zone, and (3) within the SJBP harvest management zones. Similarly, yearly mixtures (n = 5, 1998-2002 harvests) were tested for equality over four time periods of the statewide harvest: (1) annual harvest, (2) early season, (3) regular season, and (4) regular + late seasons. For each likelihood ratio test, parametric bootstrapping was used to test the null hypothesis that the harvest samples collected each year (n = 5) came from a common

mixture (n = 5000 simulations). Mixture simulations and model fitting were done in SPAM 3.7b, and final analysis of simulation results was conducted in Microsoft Excel (Microsoft Office, Microsoft, Inc., Redmond, WA.).

RESULTS

Baseline Population Differentiation

Inman et al. (2003) previously determined the 5 microsatellite loci used to characterize baseline populations were independent, polymorphic, and did not deviate from Hardy-Weinberg expectations. These determinations were made using several tests within the program GENEPOP (Raymond and Rousset 1995). Hierarchical F-statistics (Weir 1996) calculated in the program F-STAT (Goudet 2000) revealed significant differences in allele frequencies among subspecies and among management populations (Inman et al. 2003). Inman et al. (2003) demonstrated that allocating mixed harvest groups to population of origin could be accomplished with high accuracy (85-96%) based on allele frequency distributions of baseline breeding populations.

Harvest Derivations

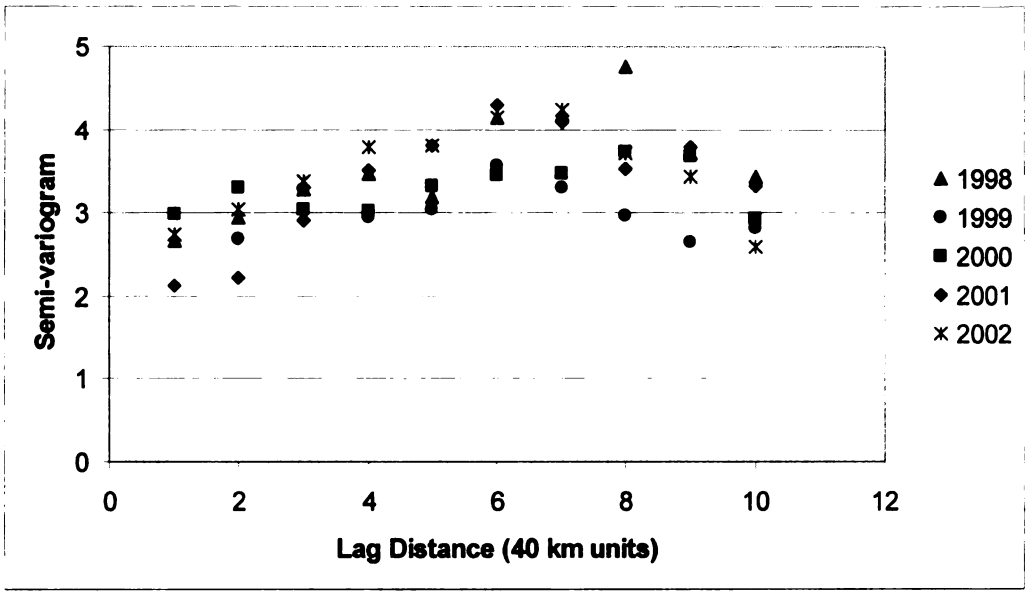
Statewide distributions of goose harvest samples included 54 counties in 1998-99, 56 counties in 1999-2000, 46 counties in 2000-01, 51 counties in 2001-02, and 54 counties in 2002-03 (Figure 2). Annually, the number of counties sampled within MVP and SJBP harvest zones (Figure 1) were: 1998-99 (35 MVP, 19 SJBP), 1999-2000 (29 MVP, 18 SJBP), 2000-01 (30 MVP, 16 SJBP), 2001-02 (28 MVP, 23 SJBP), and 2002-03 (31 MVP, 23 SJBP). Numbers of geese sampled annually within MVP harvest zone

counties were as follows: 1998-99 (n=284), 1999-2000 (n=276), 2000-01 (n=194), 2001-02 (n=202), and 2002-03 (n=327), Annual sample sizes within SJBP harvest zone counties were: 1998-99 (n=174), 1999-2000 (n=127), 2000-01 (n=134), 2001-02 (n=291), and 2002-03 (n=255).

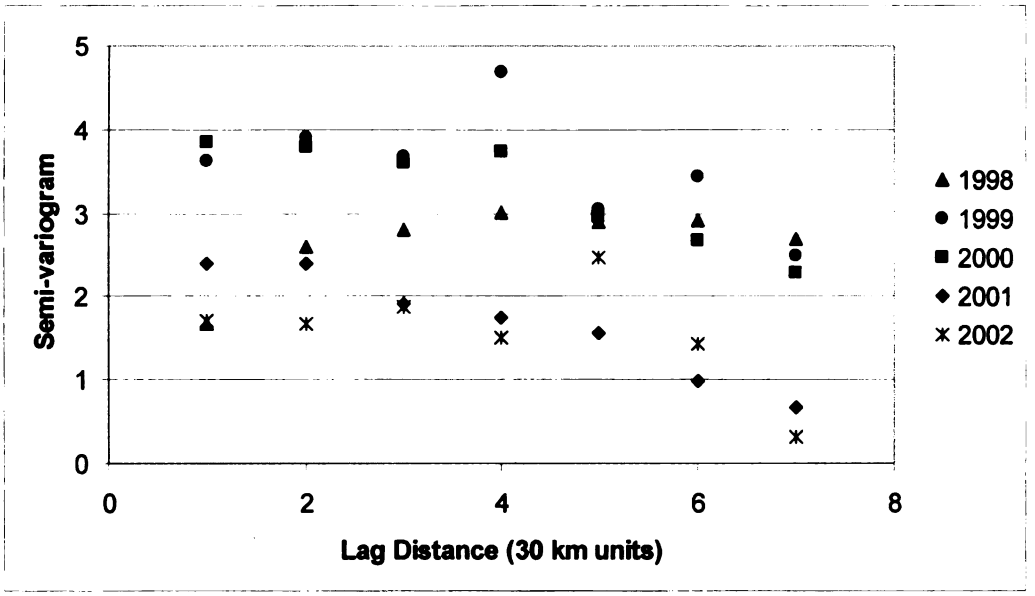
The variogram analysis illustrated that there is less variance in the sample size of harvested geese among counties in close geographic proximity to one another than among counties separated by larger distances (Figure 3). The variance in harvest sample size increases in a curvilinear fashion as a function of intervening distance among counties sampled. This pattern is consistent across all five years of harvest sampling. Early and regular season samples showed no marked differences in spatial patterns across years, and sampling variability within early and regular seasons was similar to statewide sampling variances (data not shown). Spatial patterns of harvest samples collected within the MVP harvest zone were similar across years, and sampling variance was consistent across years within the MVP harvest zone. Number of samples collected within the SJBP harvest zone were somewhat more variable (among counties) in 1999 and 2000 than the remaining three years (Figure 3). Similar patterns in sampling variation across multiple years and spatial scales indicates the USFWS Waterfowl Parts Survey is consistent across years. Thus, variation in annual harvest estimates can be attributed to biological phenomenon rather than inter-annual sampling bias.

Statewide

Total annual harvests (±SD) were composed mainly of giant Canada geese (67.4 ± 6.5% - 82.4 ± 4.2%), with lesser proportions of interior Canada geese (16.2 ± 4.1% -



Statewide



SJBP Harvest Zone

Figure 3. Variograms for the spatial distribution of annual harvest samples of cackling geese and Canada geese collected in Michigan from 1998-2002 Statewide, and within the Southern James Bay (SJBP) Harvest Zone.

30.5 ± 6.5%) and cackling geese (0.3 ± 0.4% - 3.8 ± 1.5%) (Figure 4). Giant Canada geese dominated statewide early season harvests, with contributions ranging from 76.2 ± 5.8% to 91.0 ± 4.6% (Figure 5). Proportional harvests of interior Canada geese increased greatly from the early to the regular season in all five years. The largest increase (33.7%) between seasons occurred in 2002, which was also the year of the largest proportional contribution of interior birds to the regular season harvest. Proportions of cackling geese increased slightly from the early to the regular season in three of the five years analyzed, although all estimates were less than 10% (Figure 5). Likelihood ratio tests rejected the null model that the five yearly harvest mixtures were sampled from a common mixture of cackling geese and Canada geese for the statewide harvest during annual ($P = 0.0096$) and early season ($P = 0.0048$) harvest periods. In contrast, regular season harvest mixtures were not significantly different among the five years sampled ($P = 0.1745$).

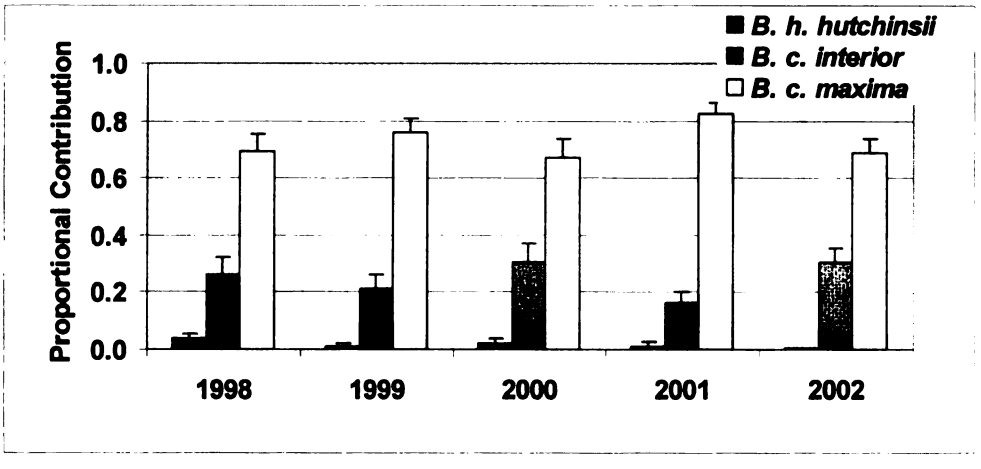


Figure 4. Mean proprotional contributions (±SD) of *Branta hutchinsii hutchinsii*, *B. canadensis interior*, and *B. c. maxima* to annual statewide Michigan harvests from 1998-2002. Annual harvests include samples collected September 1 – December 31 during the year indicated, as well as samples collected in January of the following year (e.g., 1998 includes September 1 – December 31, 1998 and January 1 – 31, 1999). Sample sizes for each year: 1998 ($n = 471$), 1999 (406), 2000 (324), 2001 (486), 2002 (585).

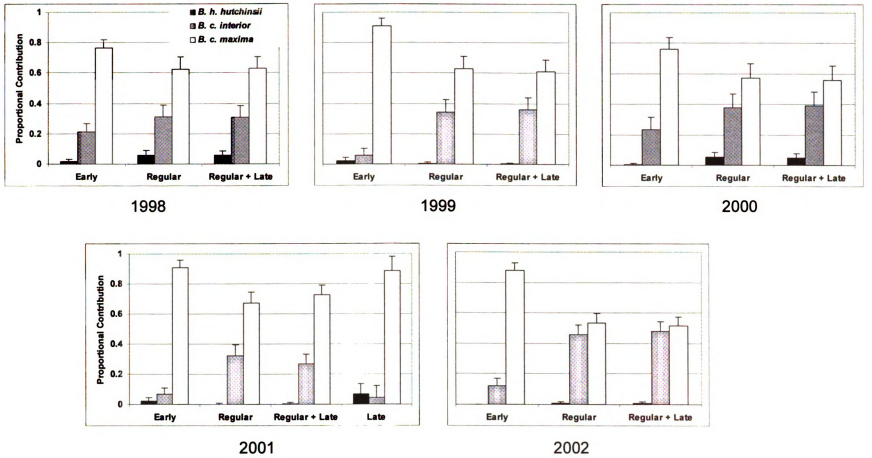


Figure 5. Mean proportional contributions (±SD) of *Branta hutchinsii hutchinsii*, *B. canadensis interior*, and *B. c. maxima* to early (September 1 - 15), regular (September 16 – December 31), regular + late (September 16 – January 31), and late (January 1 – 31; 2001 only) seasonal harvests from 1998-2002 in Michigan. Sample sizes for seasonal harvests in each year: early season 1998 (n = 255), 1999 (195), 2000 (170), 2001 (255), 2002 (261); regular season 1998 (194), 1999 (196), 2000 (143), 2001 (193), 2002 (310); regular + late seasons 1998 (206), 1999 (207), 2000 (154), 2001 (231), 2002 (323); late season 2001 (38).

Sample sizes during the late season were too low to perform individual season analyses in four of five annual harvests. For all five years we combined regular and late seasons for derivations, and found that proportional estimates of all three subspecies were similar within years between the regular and regular + late seasonal derivations. Unlike annual regular season harvest estimates, proportional estimates were significantly different among years for the regular + late season ($P = 0.0385$) harvest. The harvest pattern in 2001, the only year the late season was analyzed separately from the regular season, indicated proportional contribution of interior geese decreased in the late harvest, while giant Canada geese and cackling geese proportions increased (Figure 5).

Estimated proportions of giant Canada geese harvested statewide decreased after the early season (i.e., two weeks) in 1998, 2001, and 2002, and decreased after the first month of harvest in 1999 and 2000 (Figure 6). Proportional contributions of giants continued to decrease, and interior contributions increased, into early October in 1999 and through the regular hunting season in 2000 and 2001, while estimates for giants and interiors remained relatively constant after September for 2002. In 1998, estimates of giant Canada geese harvested increased, and estimates of interiors decreased, from October through then end of the regular hunting season in December. Proportional harvest estimates of interior Canada geese were much greater during the first week of the early season in 1998 and 2000 as compared to the remaining three years. This suggests a larger number of interiors were present in Michigan during the early season in 1998 and 2000 than in 1999, 2001, and 2002.

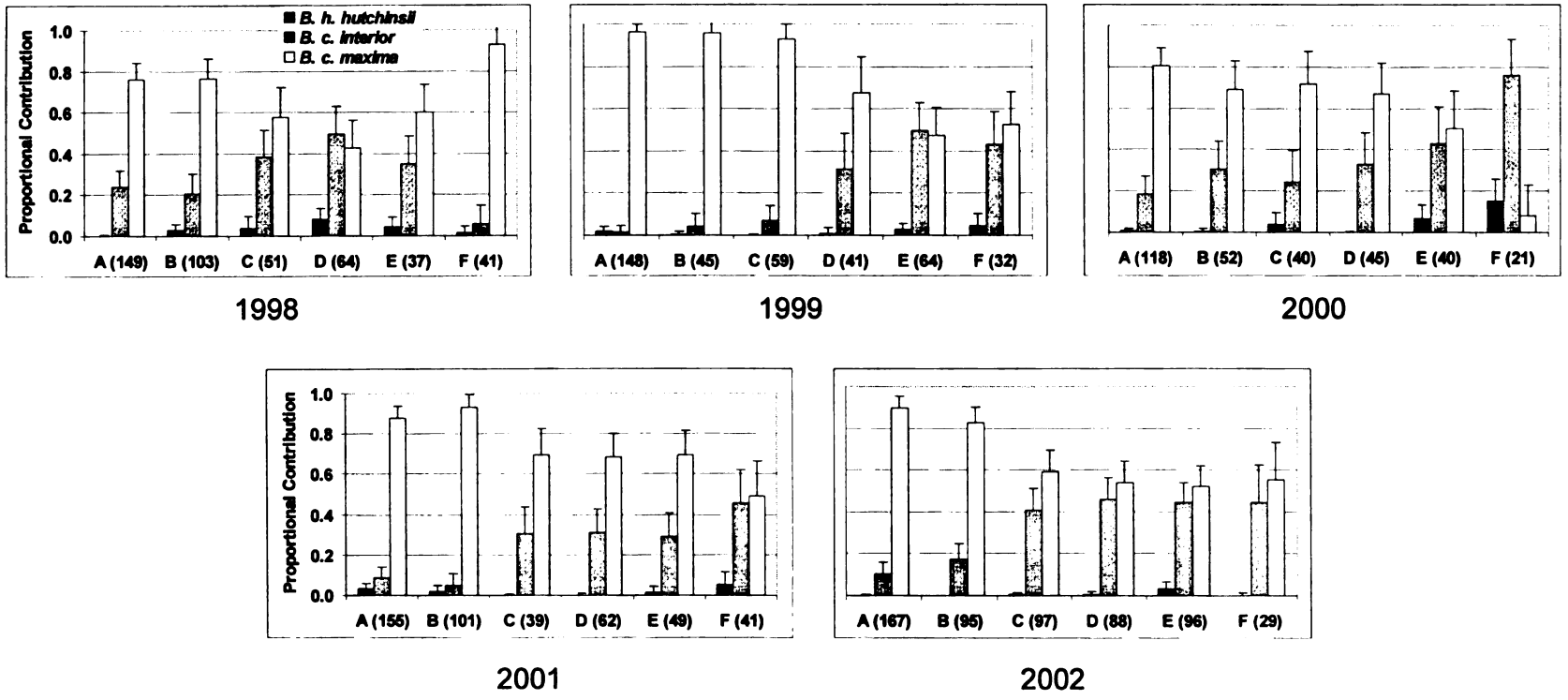


Figure 6. Mean proportional contributions (±SD) of *Branta hutchinsii hutchinsii*, *B. canadensis interior*, and *B. c. maxima* to each annual hunting season in Michigan from 1998-2002 during six discrete time periods: A (September 1–7), B (September 8–15), C (September 16-22), D (September 23-29), E (September 30-October 6), and F (October 7-December 31). Sample sizes for each hunting period are listed by date parenthetically for each year.

MVP and SJBP Harvest Zones

Proportional harvest estimates for geese originating from the MVP and SJBP management populations varied greatly within and among years for designated MVP and SJBP harvest zones (Figure 7). Birds of MVP origin were harvested in greater proportions than birds of SJBP origin within the SJBP harvest zone in four of five years in the early season and in three years during the regular season (Table 1). Estimated proportional harvests of geese originating from the MVP population were greater in the SJBP harvest zone in both seasons in 1999 and 2002. Alternatively, we estimated that geese originating from the SJBP population had higher estimated harvests in the MVP harvest zone in early and regular seasons in 1998 and 2001. Overall, proportional contributions of MVP Canada geese were greater than contributions of SJBP geese to statewide harvests and in the MVP and SJBP harvest zones in 1999 and 2002 (over all seasons and total annual harvest), while SJBP geese were harvested more often than MVP geese statewide and in both harvest zones in 2001 (Figure 7, Table 1). Proportional harvests of giant Canada geese were similar in the MVP and SJBP harvest zones within years, and followed proportional statewide harvest trends among years . Cackling geese had low proportional harvest estimates in both MVP and SJBP harvest zones (Figure 7). Likelihood ratio tests rejected the null model of equality among annual harvests estimates within the MVP harvest management zone ($P = 0.0022$). In contrast, annual harvests estimates within the SJBP harvest management zone were not significantly different ($P = 0.1384$). Annual variations in harvest estimates of migrants within the MVP zone can be linked to variations in proportional contributions of migrants during the early and regular seasons. In the SJBP zone, fluctuations in the annual harvest of migrants were more

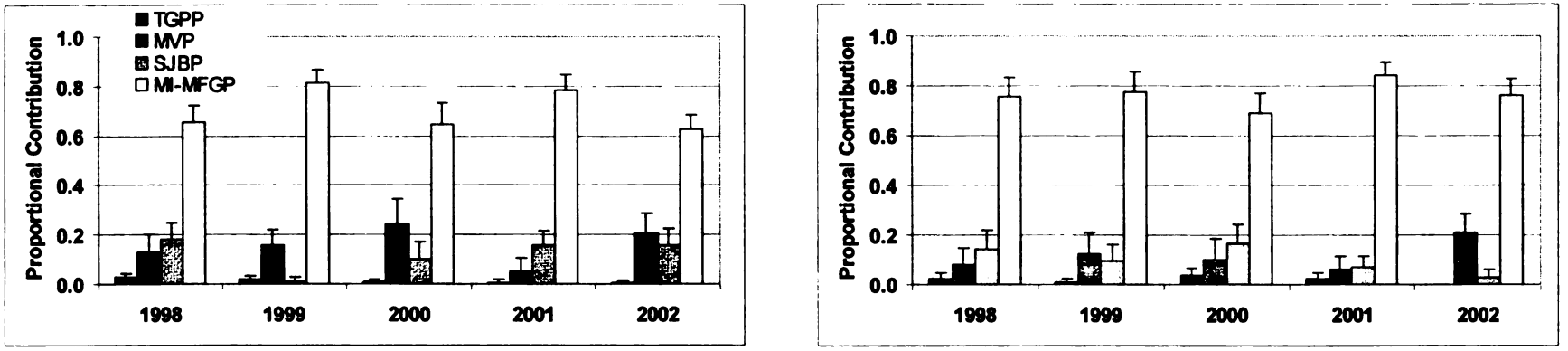


Figure 7. Mean proportional contributions (±SD) of Canada geese from the Tall Grass Prairie Population (TGPP), Mississippi Valley Population (MVP), Southern James Bay Population (SJBP), and Michigan-Mississippi Flyway Giant Population (MI-MFGP) to annual harvests (1998-2002) in Michigan within the MVP Goose Management Unit (GMU) and the SJBP GMU. Sample sizes for each year: Mississippi Valley Population Zone - 1998 (n = 284), 1999 (276), 2000 (194), 2001 (202), 2002 (327); Southern James Bay Population Zone – 1998 (174), 1999 (127), 2000 (134), 2001 (291), 2002 (255).

Table 1. Mean proportional contributions (±SD) of geese from the Mississippi Valley Population (MVP), Southern James Bay Population (SJBP), Michigan Mississippi Flyway Giant Population (MI-MFGP), and Tall Grass Prairie Population (TGPP) to early (Sept 1-15) and regular season (Sept 16-Dec 31) harvests in MVP and SJBP Goose Harvest Zones in Michigan from 1998-2002. Harvest estimates and standard deviations (SD) were calculated over 1000 bootstrap replications.

GMU Harvest	Population	1998 Estimate (SD)	1999 Estimate (SD)	2000 Estimate (SD)	2001 Estimate (SD)	2002 Estimate (SD)
MVP Early	MVP	0.085 (0.076)	0.023 (0.034)	0.170 (0.091)	0.019 (0.037)	0.075 (0.069)
	SJBP	0.116 (0.074)	0.008 (0.019)	0.031 (0.047)	0.049 (0.049)	0.072 (0.063)
	MI-MFGP	0.791 (0.081)	0.945 (0.044)	0.796 (0.084)	0.914 (0.057)	0.854 (0.066)
	TGPP	0.008 (0.010)	0.024 (0.021)	0.002 (0.008)	0.018 (0.023)	0.000 (0.001)
		(*n*=164)	(*n*=150)	(*n*=119)	(*n*=110)	(*n*=138)
MVP Regular	MVP	0.193 (0.101)	0.341 (0.093)	0.377 (0.188)	0.102 (0.094)	0.300 (0.110)
	SJBP	0.274 (0.102)	0.017 (0.036)	0.324 (0.176)	0.317 (0.110)	0.203 (0.088)
	MI-MFGP	0.452 (0.094)	0.628 (0.088)	0.271 (0.142)	0.580 (0.104)	0.483 (0.074)
	TGPP	0.081 (0.044)	0.014 (0.019)	0.029 (0.035)	0.001 (0.007)	0.015 (0.016)
		(*n*=118)	(*n*=121)	(*n*=75)	(*n*=80)	(*n*=180)
SJBP Early	MVP	0.027 (0.055)	0.032 (0.053)	0.218 (0.142)	0.047 (0.049)	0.102 (0.069)
	SJBP	0.241 (0.098)	0.016 (0.044)	0.111 (0.104)	0.027 (0.042)	0.018 (0.032)
	MI-MFGP	0.675 (0.104)	0.951 (0.068)	0.657 (0.127)	0.888 (0.064)	0.879 (0.065)
	TGPP	0.056 (0.058)	0.001 (0.008)	0.013 (0.020)	0.037 (0.034)	0.000 (0.002)
		(*n*=87)	(*n*=48)	(*n*=58)	(*n*=150)	(*n*=124)
SJBP Regular	MVP	0.118 (0.091)	0.215 (0.129)	0.029 (0.049)	0.116 (0.095)	0.283 (0.116)
	SJBP	0.039 (0.057)	0.137 (0.099)	0.196 (0.093)	0.151 (0.085)	0.096 (0.092)
	MI-MFGP	0.842 (0.094)	0.637 (0.118)	0.706 (0.100)	0.726 (0.091)	0.617 (0.095)
	TGPP	0.001 (0.007)	0.011 (0.018)	0.069 (0.045)	0.008 (0.015)	0.004 (0.012)
		(*n*=77)	(*n*=79)	(*n*=71)	(*n*=116)	(*n*=126)

likely a result of fluctuations in the early season harvest, as regular season estimates of migrant harvest were fairly constant among years (Table 1).

Local GMUs

Migrant interior geese were harvested in greater proportions during the regular season within local GMUs (HTSMA) than within non-GMU counties in the SLP (Figure 8). Proportional contributions of migrant geese were also greater in non-GMU counties statewide as compared to non-GMU counties within the SLP. Giant Canada geese had the highest estimated harvest proportions in all areas and years except for the 2000 regular season local GMU harvest (70.4% ± 15.1% *B. c. interior*, 19.3% ± 14.6% *B. c. maxima*, 10.3% ± 7.0% *B. h. hutchinsii*).

Sex Determination

Statewide geese sex ratios were slightly male biased in 2001 and 2002. Approximately equal harvests of the sexes occurred during 1998, 1999, and 2000. Specific annual ratios of females to males were as follows: 1998-99 (0.937), 1999-2000 (1.020), 2000-01 (0.929), 2001-02 (0.800), 2002-03 (0.807).

DISCUSSION

In response to Michigan's rapidly growing giant Canada goose population, special late and early goose seasons were implemented in the late 1970's and mid 1980's respectively (Soulliere et al. 1988). Michigan's resident goose population continued to grow at a rate of approximately 14% per year, and regular harvest seasons were extended

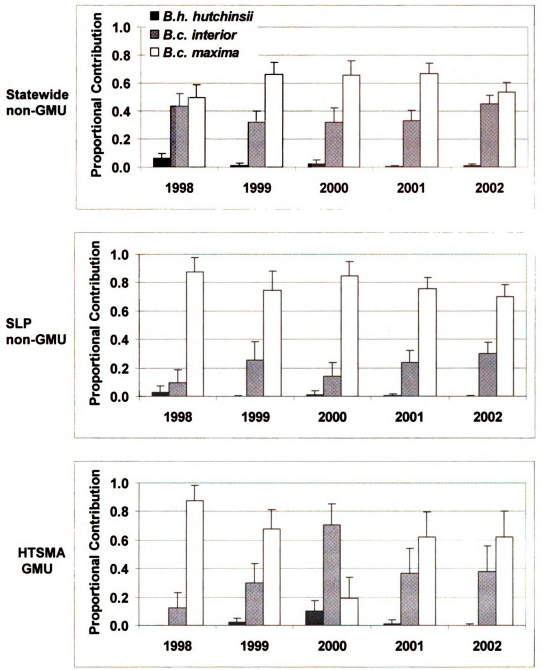


Figure 8. Mean proprotional contributions (±SD) of *Branta hutchinsii hutchinsii*, *B. canadensis interior*, and *B. c. maxima* to regular season harvests (September 16 – December 31) in Michigan's four local Goose Management Units (GMU) including Huron/Tuscola, Saginaw, Muskegon, and Allegan (HTSMA); and Michigan's non-GMU counties statewide and in the Southern Lower Peninsula (SLP) from 1998-2002. Sample sizes for each year: Statewide non-GMU – 1998 (n = 148), 1999 (145), 2000 (115), 2001 (152), 2002 (277); SLP non-GMU – 1998 (57), 1999 (50), 2000 (65), 2001 (116), 2002 (163); HTSMA GMU – 1998 (51), 1999 (55), 2000 (31), 2001 (44), 2002 (30).

in 1998 to include the latter two weeks of September (Luukkonen and Souillere 2004a). As these seasonal changes were established in order to target giants and avoid harvest of migrant cackling and Canada geese, harvest derivations must accurately estimate contributions of species, subspecies and populations during multiple time periods of annual hunts. Adding to the temporal complexity of Michigan's harvests are local GMUs traditionally managed to attract migrant geese, and regional harvest zones established to better manage harvest of interior geese originating from the MVP and the SJBP. We utilized genetic markers and mixed stock analyses, which allow for accurate discrimination among species, subspecies and populations of geese contributing to harvests, to assess special season and hunt zone regulations in Michigan.

Variograms of harvest sampling suggests variance in the spatial pattern of samples is consistent among years for multiple temporal and geographic scales. Spatial correlations between sample size variance and pairwise distance between counties indicate sampling variance decreases as a function of decreasing distance between counties sampled. Thus, differences among proportional estimates of harvest among years are not likely a result of spatial or temporal sampling bias among years. Differences in estimates of proportional contributions to annual harvests were due to biological phenomenon including arrival timing of migratory interior Canada geese and cackling geese into Michigan and the duration of their stay in the state. Early spring weather, such as levels of precipitation, daily mean temperature, and relative humidity strongly influence the arrival of migratory geese on their northern breeding grounds and timing of nest initiation (Blokpoel and Gauthier 1980, Wege and Raveling 1983). Nest initiation date is closely correlated with timing of fall migrations (K. Abraham, personal

communication), with earlier nest initiation leading to earlier fall migrations to staging areas and southern wintering grounds. Annual inconsistencies in climatic conditions would cause nest initiation dates to vary among years, and migrations of interior Canada geese and cackling geese into Michigan would be earlier in some years than others. Subsequent harvest of migratory geese would increase during the early season in years of early arrival. Our discrete time analyses indicated there were annual fluctuations in the initial arrival time of migratory geese. Interior Canada geese began arriving in Michigan prior to the early season in 1998 and 2000, as evidenced by the greater estimated harvest of interiors during the first week of the early season during these two years as compared to 1999, 2001, and 2002.

Among year differences in early and regular season estimates of interior and giant Canada geese were reflected in the pattern of among year differences in total annual estimates. Annual variation in timing of migration of interior Canada geese and cackling geese and subsequent early season harvest could have a large effect on total annual harvest estimates, as early season bag limits are much more liberal than regular season limits. However, annual harvests of interior Canada geese are greatest during the regular season, so changes in harvest regulations during this season may have the most impact on total take of interior Canada geese. Future harvest regulations may benefit from directed research focused on how variations in the opening date, duration, and bag limits during early and regular seasons would effect overall annual harvests of resident and migratory geese.

Initial arrival date of migratory interior Canada geese may be an important factor determining residence time in Michigan and susceptibility to harvest throughout the

hunting season. However, in years of higher estimated proportional interior harvest during early seasons, and likely earlier initial arrival of migrant interiors to Michigan, regular and regular + late season interior harvests were not proportionally greater as compared to regular and regular + late seasons in other years. Thus, initial arrival date of migratory interiors may influence susceptibility to harvest in the early season, but may not strongly affect regular and late season harvest of migrants.

Influence of late season hunts on total annual harvests is likely small given low harvest levels during January/February. However, during 2001 when adequate sample size allowed an analysis of late season harvest alone, higher proportions of the harvest were comprised of giants compared to the regular season. Thus, migratory interior Canada geese may exhibit greater proclivity for southerly migration during the winter months. Special seasons during the winter period could be successful in targeting resident giants.

The change in subspecies harvest proportions from the regular to the late season in 2001 may indicate late season sample sizes were too low in the other three years to resolve late season trends when combined with regular season harvest samples. This lack of late season resolution is also apparent from likelihood ratio tests results that indicate that regular + late season harvest mixtures vary annually, while regular season harvest mixtures have relatively equal contributions of migratory and resident geese among years. Differences in mid-winter weather conditions among years could lead to different migration patterns if propensities for migration further south differ between subspecies.

Selectively managing harvests of MVP and SJBP may be difficult using Michigan's current harvest management zones because of the broad overlap and annual

variation in population-specific harvests within these zones. Harvest mixtures differed from year to year within the MVP harvest zone, while staying relatively uniform over time within the SJBP harvest management zone. In 1999 and 2002, MVP birds comprised the majority of the interior Canada geese harvest in the MVP and SJBP harvest zones, while SJBP birds were harvested in greater proportions in both harvest zones in 2001. The repeated occurrence of greater proportional harvests of MVP birds than SJBP birds in the SJBP harvest zone, and greater proportional harvests of SJBP birds than MVP birds in the MVP harvest zone, in multiple seasons and years, suggests the fall distribution of these populations extends well beyond previously defined migratory corridors in Michigan based on previous banding and radio-transmitter studies (Tacha et al. 1991) and range descriptions (Bellrose 1980). Concurrent with our findings, Fritzell and Luukkonen (2004) recently documented that MVP geese were harvested across a larger proportion of the state of Michigan than previously estimated based on 1980-1989 band recovery data. MVP band recoveries increased in number and geographic distribution in the Lower Peninsula of Michigan, following an increase in the amount and distribution of banding on eastern MVP breeding grounds on James Bay in 1990. Scribner et al. (2000, 2003), also documented substantial harvests of MVP and SJBP geese beyond traditional MVP and SJBP harvest zones in Michigan using genetic-based derivation techniques. They estimated contributions of MVP geese to harvests in southeastern Michigan game management areas, and SJBP harvests at southwestern Michigan game management areas, were greater than 30% in some years.

If there is greater mixing of migrants originating from the MVP and SJBP populations in the southwest Lower Peninsula relative to the northwest Lower Peninsula,

then the occurrence of higher proportions of birds originating from the SJBP population (relative to birds originating from the MVP population) in the MVP harvest zone in 1998 and 2001 could be explained by relatively lower numbers of counties and individual harvested geese sampled in the northwest Lower Peninsula in those years as compared to the number and distribution of samples collected from the southwest Lower Peninsula. However, estimates of harvested birds originating from the MVP population were not always greater in the northwest Lower Peninsula as compared to the southwest Lower Peninsula within each year, and estimated proportions of birds originating from the SJBP population were greater in the northwest Lower Peninsula than the southwest Lower Peninsula in four of five years sampled (data not shown). This indicates that potential sampling bias in 1999 and 2001 is not the dominate factor influencing estimates of SJBP migrants harvested within the MVP harvest zone, and mixing of birds from SJBP and MVP populations may not be measurably greater in southwest Michigan relative to mixing of both populations in the northwest Lower Peninsula.

Local GMUs were traditionally managed to attract interior Canada geese through provisions of browse foods and open-water refuges (Luukkonen and Souillere 2004a). Results of GMU harvest derivations indicate these areas continue to draw greater proportions of interior geese than surrounding non-GMU areas. A comparison of derivation results from non-GMU statewide harvests to non-GMU estimates in the SLP revealed that greater numbers of interior Canada geese and cackling geese are harvested in Michigan's Upper Peninsula (UP) and northern portion of the Lower Peninsula (NLP) as compared to the southern portion of the Lower Peninsula in all annual harvests. This

suggests an increased vulnerability to harvest and/or increased presence of migrant geese in the UP and NLP, and lower numbers of resident giant Canada geese in these areas.

MANAGEMENT IMPLICATIONS

Harvest is the most direct way to impact population dynamics of Canada geese (Williams and Nichols 1990). Michigan has approximately 50,000 goose hunters (Soulliere and Frawley 2001) that can be utilized as a practical means of controlling large populations of giant Canada geese. By combining samples from the USFWS Parts Survey with genetic analyses, we describe results from an extensive study designed to monitor annual harvest levels including special seasons and within defined management zones. We expand previous studies that have used genetic methodology to monitor Michigan cackling geese and Canada geese harvests by incorporating new methods to assess sampling bias and through the use of likelihood ratio tests that assess the magnitude of variance in harvest composition among spatial and temporal samples.

Harvest estimates suggest that the number of resident and migratory Canada geese, as a proportion of the total goose population, varies in different hunt zones of Michigan and different time periods of the season. Annual and seasonal variation in proportional harvest estimates of cackling and Canada geese is likely influenced by several factors. Relative population sizes are likely to fluctuate over time, as is population productivity. Increased productivity in a given year leads to higher proportions of juveniles which tend to be more susceptible to harvest than adults. Variation in annual climatic conditions during spring migration and nesting of migratory geese will lead to differences in nest initiation dates. Weather in the late summer will

also cause fall migrations to shift temporally. Initial arrival dates of migratory cackling and Canada geese may be an important factor determining early season susceptibility of migratory geese, and should be considered in future management of early season hunts.

Policies aimed at reducing numbers of giant Canada geese may benefit from increased hunting pressure in non-GMU areas in southern lower Michigan, especially during early and late season harvests. Harvest derivations within the MVP and SJBP harvest zones indicate MVP and SJBP Canada geese likely migrate through both Michigan harvest zones frequently, making both populations susceptible to harvest in both zones. Management of interior Canada geese may be improved by redefining breeding population management units based on genetics information.

We introduce a novel approach for detection of sampling variance as a source of bias in data. In the absence of spatial heterogeneity of harvest samples among years, annual variance in harvest proportions can be attributed to biological phenomenon. This is also useful information for USFWS managers, in that sampling methodology is targeting a consistent cross-section of Michigan hunters annually.

Annual variation in proportions of giant and interior Canada geese in early and regular + late season harvests indicate that a single opening date may not be appropriate to achieve desired targeted harvests. Additional studies of impacts of nest initiation date, and investigations of late summer weather as it correlates to the initiation of fall migration of interior Canada geese and cackling geese, are warranted.

Differences in migratory tendencies between resident and migratory geese during mid-winter could lead to different harvest proportions if late seasons are used as a management tool. Further research of the effects of weather on migratory behavior of

geese is necessary. Managers can use this information to ascertain the impacts of annual harvest regulations and determine if current regulations are successful in directing hunters to target giant Canada geese while protecting migratory geese. Adaptive harvest management of resident Canada geese and migratory Canada and cackling geese will benefit from the information gained through this analysis and similar future studies.

ACKNOWLEDGEMENTS

The Michigan Department of Natural Resources (DNR) and the Partnership for Ecosystem Research and Management (PERM) Program between the Michigan DNR and the Department of Fisheries and Wildlife at Michigan State University provided funding for this study. Baseline samples were collected by many individuals associated with the MDNR, Michigan State University, K. Abraham and J. Leafloor from the Ontario Ministry of Natural Resources, and individuals from the Canadian Wildlife Service and Environment Canada including D. Caswell and K. Dickson. We thank all participants of the Mississippi Flyway Wing Bee who assisted in cataloging hunter-harvested samples collected by the U.S. Fish and Wildlife Service, especially Barb Lercel Avers and Bill Scullon of the Michigan DNR, and Dave Rave of the Minnesota DNR.

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CHAPTER 6: A COMPARATIVE ANALYSIS OF WATERFOWL HARVEST DERIVATION TECHNIQUES: ASSESSING MICHIGAN'S CANADA GOOSE AND CACKLING GOOSE HARVEST USING BAND RETURNS, MORPHOMETRICS, AND GENETICS

INTRODUCTION

Harvest management is a key component in the conservation of Canada geese (*Branta canadensis*) and cackling geese (*Branta hutchinsii*), which are continentally distributed and composed of multiple subspecies and management populations (Bellrose 1980, Banks et al. 2003). In many states and provinces there is a growing need to target overabundant resident populations of geese while protecting smaller migratory populations to ensure populations remain viable and harvests are sustainable over time (Williams and Johnson 1995, Ankney 1996). The number of states/provinces where harvest regulations include special seasons and hunting zones has increased in response to requests for increased hunting opportunities and decreased human-resident geese conflicts (Luukkonen and Soulliere 2004).

In response to Michigan's rapidly growing giant Canada goose (*B. c. maxima*) population, Michigan's Department of Natural Resources (DNR) established a special early season harvest in the Lower Peninsula of Michigan in 1986. The 15-day season beginning September 1 was designed to focus harvest on resident and molt-migrant giant Canada geese, and avoid migratory interior Canada geese (*B. c. interior*) and cackling geese (*B. h. hutchinsii*) that were assumed to arrive in Michigan later in the hunting season (Soulliere and Martz 1997). Michigan's DNR also requested and was granted

regular goose season opening dates in mid-September beginning in 1998 as a further attempt to target resident geese during periods of low interior and cackling migration (Luukkonen and Soulliere 2004). In order to assess if current hunt regulations were meeting prescribed state and federal management goals, accurate harvest derivation techniques were needed to assess the proportion of resident giant Canada geese and migratory interior Canada and cackling geese harvested during experimental early seasons and during extended regular seasons.

A variety of techniques have been employed by biologists seeking to differentiate populations or subspecies of Canada and cackling geese contributing to harvests. These techniques have included marking geese with leg bands and neck collars (Lindberg and Malecki 1994, Fritzell and Luukkonen 2004) or satellite transmitters (Luukkonen et al. 2004), measuring morphometric characters (Johnson et al. 1979, Moser and Rolley 1990, Merendino et al. 1994), stable isotope analysis of feather tissue (Caccamise et al. 2000), and genetic discrimination (Pearce et al. 2000, Scribner et al. 2003, Inman et al. 2003). No comparative studies have been conducted to investigate the concordance of results across independent harvest derivation techniques. Michigan is uniquely suited to address this issue, as band recovery data, morphometric measures, and genetics information has been simultaneously collected for the regular season statewide goose harvest during a five year period after implementation of the mid-September season opening in 1998. In addition, a local study of the morphometric and genetic characteristics of geese harvested during the experimental early seasons in the Saginaw Bay region was carried out from 2000-2002. Our main objectives were to compare proportional harvest estimates of interior and giant Canada geese and cackling geese derived from multiple data sources

for the regular hunt season statewide and for the early season in the Saginaw Bay area. We discuss the degree of similarity among estimated harvests derived from different methods, and the efficacy of using each harvest derivation technique at statewide and local geographic scales. Our secondary objectives were to assess potential biases in estimates that may result from assumptions of harvest sampling dispersion, sample sizes, and harvest derivation calculations. We discuss potential sources of bias for each derivation technique. Additionally, we use variograms, which illustrate the average degree of similarity among number of individuals sampled as a function of distance separating sampling locales (Rossi et al. 1992), to determine if the spatial pattern of harvest samples collected across the state was consistent among years.

METHODS

Band Return Analyses

Sample Collection

We analyzed the harvest composition of banded Canada geese shot during the regular hunting season in Michigan. Only direct recoveries of geese (i.e., banded bird recovered the first hunting season after banding; Munro and Kimball 1982) shot or found dead were included in the harvest derivation estimates. Counts of band recoveries from each state or province were corrected for estimates of reporting rates for solicited and unsolicited bands. Solicited band recoveries are those reported by someone other than the hunter, such as natural resource agency employees, while unsolicited band recoveries are reported directly by the hunter. As only limited information regarding differential reporting rates of solicited verses unsolicited bands on geese is available, reporting rates

recorded for banded mallard ducks harvested during the same hunting period were used as a general estimate of reporting rates for geese recoveries (reporting rate approximately 76%, Royal and Garrettson 2005). To estimate the actual number of banded geese harvested from each state/province, reporting rates of solicited leg bands were assumed to be 100%, while reporting rates of unsolicited leg bands or neck collars were assumed to be 80%. No differential reporting rates for goose body size or population of origin were included in the band recovery analysis, but could be incorporated in future derivations as additional data become available. Sexes of geese were determined at the time of banding by cloacal examination.

Harvest Derivation

Contributions of giant and interior Canada geese and cackling geese to Michigan's regular season harvests from 1998-2002 were derived using weighted band recoveries (see Rusch et al. 1996), similar to methods outlined in Munro and Kimball (1982) developed to estimate derivation of mallard harvests. Derivation of the harvest was calculated by using estimates of spring population size and annual production to estimate the fall flight of each population of geese. These population estimates were then used to "weight" the number of bands applied to geese in each population, or estimate the number of geese in a particular population represented by each banded bird that is shot and reported. The number of band recoveries, multiplied by the respective weight for each population, provided a weighted harvest estimate. Weighted estimates were then converted into percentages to reflect the subspecies composition of the harvest within Michigan (Rusch et al. 1996). Geese without young that were banded on migrant goose

(interior and cackling) breeding areas were considered possible molt migrants (Abraham et al. 1999), and were excluded from derivations. We attempted to exclude molt-migrant giant Canada geese from our samples of interior Canada geese by excluding geese judged to be giant Canada geese based on morphological characters at the time of banding, (pers. comm. Lyle Walton, Ontario Ministry of Natural resources) and by including only adults banded within the same 10 minute degree block in which goslings were banded on the same date as adults (obtained from banding records). Annual derivations were calculated for adult or after hatch-year (AHY) geese: 1998 (n = 61), 1999 (n = 52), 2000 (n = 34), 2001 (n = 59), and 2002 (n = 48). AHY geese were distinguished from juveniles or hatch-year (HY) geese based on banding records.

Morphometric Analyses

Sample Collection

Samples for this analysis were obtained through requests in the Michigan Waterfowl Hunting Guide and through news releases and other advertisements (e.g., postings in DNR field offices, personal communication to hunters). Participating hunters provided goose heads and tails with cloaca attached to DNR field offices, and samples were transferred to staff at the Rose Lake Pathology Laboratory for processing. Goose gender and age class (HY or AHY) were determined by cloacal exam and culmen and skull measurement techniques outlined in Dzubin and Cooch (1992). Mean culmen lengths of harvested geese were first estimated in each of Michigan's three hunting zones for the period 1997-2002. Annual statewide mean culmen length was then estimated by weighting zone means by the proportion of the Canada goose harvest that occurred in

each of Michigan's three geographic hunting zones. This improved the accuracy of statewide culmen length estimates by helping to prevent bias due to over- or under-sampling harvest in a particular zone. A database containing estimates of Michigan's Canada goose harvest in each zone was provided by the USFWS for 1998-2002.

Harvest Derivation

Although other populations of interior geese contribute to Michigan's harvest, giants and MVP geese account for >90% of the statewide regular season harvest (Fritzell and Luukkonen 2004). Thus, the contribution of interior and giant Canada geese to annual regular season harvests was estimated from culmen measurement standards for Michigan giant and Mississippi Valley Population (MVP) interior geese (Moser and Rolley 1990) using the techniques described by Trost et al. (1992). Because of the potential for incomplete development of HY geese during the regular season, we only used measurements from AHY-aged birds in the analysis: 1998 (n = 142), 1999 (n = 179), 2000 (n = 232), 2001 (n = 164), and 2002 (n = 113). Female geese with culmen measurements $\leq$41.3 mm and male geese with measurements $\leq$43.0 mm were assumed to represent cackling geese (K. Bataille, Missouri Dept. of Conservation, personal communication).

Similar to the statewide morphometric harvest derivation, only AHY geese were used in the local analysis: 2000 (n = 117), 2001 (n = 126), and 2002 (n = 48). A limitation of using Moser and Rolley's (1990) morphometric technique to estimate harvest composition for early season samples from the Saginaw Bay area is that the proportional contribution of only two populations can be estimated. This makes choosing

reference populations somewhat problematic in an area like Saginaw Bay that has more than two potential populations contributing to harvest (e.g., Michigan giants, molt-migrant giants from other states and provinces, Northwest James Bay MVP, Akimiski Island SJBP, mainland SJBP, and Richardson's cackling geese). Canada goose size varies among populations (Moser and Rolley 1990), subpopulations (Leafloor and Rusch 1997), and sometimes within populations in response to environmental variation (Leafloor et al. 1998). Significant differences in the size of Michigan giants has also been described across different regions of the state (Soulliere et al. 1995). Consistent with findings of Leafloor and Rusch (1997) with interior and other giant populations, the largest Michigan giants occur in the southern part of the state. Thus, we needed to accommodate multiple giant and interior reference populations. This problem was further exacerbated by the relatively large body size of mainland SJBP, which results in more overlap in size distributions with giant Canada goose populations (Leafloor and Rusch 1997).

Culmen measurements were not available for all reference baseline populations of Canada geese that may contribute to harvests in Saginaw Bay because Leafloor and Rusch (1997) reported only skull measurements for Northwest James Bay MVP and mainland SJBP. Thus, mean culmen length was predicted from mean skull length using values in the literature (Leafloor and Rusch 1997) and linear regression. Six sets of means for culmen and skull length were taken from two studies (Moser and Rolley 1990 and Merendino et al. 1994) to develop equations to predict mean culmen length from mean skull length. Mean culmen length was predicted from skull length for geese from Northwest James Bay and the Southern James Bay mainland (Leafloor and Rusch 1997).

These estimates, and documented mean culmen length for Akimiski Island geese (Merendino et al. 1994), were used as references to estimate and compare proportional contribution of interior and giant populations in the early season harvest on the study area.

Genetic Analyses

Sample Collection

Baseline samples were collected from pre-fleging goslings in breeding populations of cackling geese, and interior and giant Canada geese according to methods outlined in Scribner et al. (2003), and included all sampling locations outlined in Inman et al. (2003). A total of 964 individuals were collected from baseline breeding populations of cackling geese (n = 1 population), and interior (n = 4), and giant (n = 8) Canada geese. Statewide goose harvest samples were collected during regular hunting seasons (September 16 – December 31) in Michigan through the United States Fish and Wildlife Service (USFWS) Waterfowl Parts Survey (Martin and Carney 1977) (see Inman et al. 2003 for Survey details). We obtained hunter-harvested samples of geese collected in Michigan during regular seasons from 1998-2002. Each sample consisted of 1-12 tail feathers pulled from each goose harvested, and were identified by date and county of harvest within Michigan. Similar to banding and morphometric investigations, only samples from AHY geese were used for genetic analysis. Trained waterfowl biologists identified the age class (AHY or HY) of each harvested sample by independently aging tail feathers and primary feathers provided by participating hunters (P. Padding, unpublished USFWS report). As primary wing tips provide a more accurate

assessment of age for Canada geese than tail feathers (Tacha et al. 1989), age classification determined by primary feathers was first used to separate AHY and HY samples. Remaining samples for which primary feathers were not included by the hunter were separated into age classes according to tail feather aging.

Early season harvest samples from the Saginaw Bay area were submitted by area hunters as part of the morphometric analysis of geese described above. We utilized tongue tissue sampled from these AHY harvested geese for genetic analyses. Tongues were clipped from geese during head and tail collections at regional DNR field offices. Tongue samples were placed in individual vials containing a high-salt buffer (100 mM Tris, pH 8.0, 100 mM EDTA, 0.5% sodium dodecyl sulfate, 50 mM NaCl) and were frozen at -20°C until analyzed.

Lab Analysis

We extracted and quantified DNA from geese tail fan feathers using techniques detailed in Inman et al. (2003). DNA was extracted from early season tongue samples using Qiagen Dneasy kits and protocols (QIAGEN Incorporated, Valencia, CA). Five bi-parentally inherited microsatellite DNA loci (Bcaμ7, Bcaμ9, Bcaμ11, and Hhiμ1 [Buchholz et al. 1998], and TTUCG-1 [Cathey et al. 1998]) were used to estimate allele and genotype frequencies for all baseline breeding populations and hunter-harvested samples. Loci were amplified using polymerase chain reaction (PCR), and products were electrophoresed on denaturing 6% polyacrylamide gels and visualized using a FMBIO II laser scanner (Hitachi Software Engineering, Alameda, California, USA). Resulting

genotypes were scored based on 20 base-pair standards and reference samples of known genotype.

Sex of all hunter-harvested samples was determined using the chromo-helicase-DNA-binding (CHD) locus (Griffiths et al. 1998). Males were identified by the presence of one amplified band (two introns of the same size), while females were characterized by two bands (two introns of different sizes). For early season samples, sex was determined by cloacal exam at the time morphometric measurement were taken.

Harvest Derivation

We conducted mixed stock analyses of annual harvests using conditional maximum likelihood methods (Pella and Milner 1987) within the Statistics Program for Analyzing Mixtures (SPAM 3.7b, Debuvec et al. 2000), which compares the distributions of genotypic frequencies of each baseline population with the genotypic frequencies observed in harvest mixtures (see Scribner et al. 2003 for details). We utilized a pseudo-Bayes method (Pella and Masuda 2001) to estimate baseline allele frequency distributions, which are calculated as the average of observed allele frequencies in each population and the unweighted arithmetic mean of the allele frequencies among baseline populations at each locus. All mean allele frequency estimates are positive as a result of this calculation, so absence of an allele from a particular baseline population sample implies it is only rare and was missed in sampling rather than assuming it is nonexistent. Proportional contributions of interior and Canada geese and cackling geese were calculated as the mean (±SD) over 1000 replicate resamplings (with replacement) of baseline populations and the harvest mixture. Annual harvest derivations were calculated

for all AHY geese which included 754 individuals: 1998 (n = 142), 1999 (n = 158), 2000 (n = 111), 2001 (n = 126), and 2002 (n = 217). Harvest derivations for the three early seasons in the Saginaw Bay area included 274 adult geese: 2000 (n = 102), 2001 (n = 124), and 2002 (n = 48).

Monte Carlo likelihood ratio tests were conducted in SPAM 3.7b (Debuvec et al. 2000) to test the equality of harvest mixtures (Reynolds and Templin 2004; see Chapter 5 Methods for summary of likelihood ratio tests assumptions and design). Likelihood ratio tests were completed for statewide regular season harvests and early season harvests from Saginaw Bay. For each likelihood ratio test, parametric bootstrapping was used to test the null hypothesis that the harvest samples collected each year came from a common mixture (n = 5000 simulations). Mixture simulations and model fitting were done in SPAM 3.7b, and final analysis of simulation results was conducted in Microsoft Excel (Microsoft Office, Microsoft, Inc., Redmond, WA.).

Variograms

We used variograms (Rossi et al. 1992) to test for consistency among annual spatial distribution patterns of regular season harvest samples for morphometric datasets and for genetic-based datasets. Each variogram was constructed as a plot of half the average squared difference among harvest sample sizes for counties separated by about the same distance (distance between county pairs). Geographic distances between each pair of Michigan counties were calculated using x,y coordinates (in meters) from the MIGeoref projection (MDNR Spatial Data Library 2005). Variograms were constructed using the program SAS (SAS Institute 2005). Ten distance classes were included in each

variogram, and were determined by the lag distance (40 km) multiplied by the number of lags, or distance classes. Distance classes included harvest samples from pairwise county comparisons whose geographic distance between counties were within each distance interval ± half the lag distance.

Variance in Harvest Estimates

Several factors may influence the variance and bias in harvest estimates regardless of the technique used to derive these estimates. First, all derivation techniques assume that all populations putatively contributing to the harvest have been adequately sampled in terms of numbers of individuals collected and spatial distribution of the samples. Non-representative sampling of baseline populations (numerical or geographic) contributing to harvest may increase variance of harvest estimates (Crissey 1955, Dufour et al. 1993, Fritzell and Luukkonen 2004). A second assumption is that samples collected from harvest mixtures adequately characterize the true harvest mixture. The accuracy and precision of harvest derivation estimates could be compromised if harvest samples do not adequately cover locations where harvest is occurring, or if sample sizes are too low to include all populations represented in the mixture. Thus, it is important that derivations incorporate a comprehensive and systematic sampling scheme for collecting harvested individuals to reduce possible sampling bias (Inman et al. 2003). A third issue is that all three derivation techniques rely on voluntary contributions of samples from hunters. There is a potential to increase bias in harvest estimates if there are temporal or spatial inconsistencies in volunteer contributions. For instance, there may be a tendency for hunter effort in submitting samples to decrease over the season, submitting more

samples early in the harvest and less toward the end of the season as their interest declines. One example of this bias could arise for genetic samples collected through the USFWS Waterfowl Parts Survey, as hunters who run out of return envelopes may not request more even if they harvest more geese. It is also possible that hunters selectively submit samples based on their impression of how "good" an individual bird may be in terms of coloration or size. Selectively submitting samples in this manner may occur more often with morphometic techniques, as whole birds are generally handed to biologists for sampling. Finally, the accuracy and precision of harvest estimates is highly dependent on the number of potentially contributing populations, whether all the potentially contributing populations are known, and the actual composition of the mixture (Pella and Milner 1987). Based on numerous previous studies of cackling and Canada geese, we are confident that only three subspecies (*B. h. hutchinsii*, *B. c. interior*, *B. c. maxima*) are potentially harvested in Michigan during annual hunts, thus minimizing error in harvest estimates.

Harvest derivation calculations based on band returns for AHY geese include estimations of the size of spring adult cackling and Canada geese populations. Interior Canada geese population estimates were based on aerial surveys of stratified, fixed-wing transects conducted in early spring on breeding grounds, while giant Canada geese population estimates were based on transect counts from fixed-wing aircraft, helicopters, or ground checking during nesting periods on breeding grounds. Estimates of the spring population size of adult cackling geese were based on helicopter transect counts conducted on Baffin Island breeding grounds in the fall prior to the southward migration of geese. While interior and giant Canada geese population transect counts would

include only AHY birds, fall counts of cackling geese would include both AHY and HY individuals. Estimates of the spring goose population for each subspecies are likely the predominant source of variation in adult harvest estimates based on band recoveries. The precision and accuracy of harvest estimates based on band recoveries may also be influenced by temporal and geographic differences in banding efforts (Fritzell and Luukkonen 2004) and band recovery and reporting rates (Conroy and Blandin 1984, Caswell et al. 1987, Royal and Dubovsky 2001). We attempted to limit variance attributed to band reporting rates by including rate correction factors for solicited and unsolicited bands based on previous band reporting studies (Royal and Garrettson 2005).

Sources of variation in harvest estimates based on culmen measurements include variation in culmen lengths among populations of interior Canada geese (Merendino et al. 1994, Leafloor et al. 1996, Leafloor and Rusch 1997) and among populations of giant Canada geese contributing to harvests (Moser and Rolley 1990); variation among individual culmen lengths within populations due to environmental influences (Leafloor et al. 1998) and age of individuals (Thompson et al. 1999); and measurement error of harvest samples. Measurement error includes variation in measurements conducted by different observers (Rasmussen et al. 2001), though this possible error was addressed by limiting the number of people conducting measurements (2 individuals). Errors in assigning individual birds to sex and age categories could also introduce variation and bias into harvest estimates as subspecies classification was based on culmen measurement standards for AHY geese, and female and male standards differ within a subspecies. We attempted to limit this type of error by restricting our observers to only those individuals that were very experienced in sexing and aging techniques.

The level of variance and bias associated with genetic-based harvest estimates is greatly dependent on the amount of genetic divergence among potentially contributing populations of geese (Pella and Milner 1987, Wood et al. 1987). Bias in estimates will be largest when baseline populations that are similar in their genetic characteristics differ greatly in abundance (Millar 1987). We attempted to limit this bias by employing a suite of microsatellite markers which have demonstrated differences in allele frequencies among cackling geese, and interior and Canada geese (Inman et al. 2003). If the true composition of a harvest mixture is highly skewed toward one population (near 100%), genetic-based derivations may underestimate harvest contributions of the prevalent population and overestimate harvest contributions of other putative populations, even when baseline populations are sufficiently differentiated by a suite of genetic markers (Marlowe and Busack 1995, Scribner et al. 2003). The program SPAM used to calculate harvest composition accounts for the effects of baseline and mixture sampling variation by repeatedly drawing samples with replacement from the baseline and mixture groups so final harvest composition estimates are a mean of multiple likelihood estimates, with related confidence intervals. Additionally, we addressed the issue of sampling variance leading to potential bias of genetic-based harvest estimates by having a large number of samples representing baseline populations and harvest mixtures.

RESULTS

Based on USFWS harvest estimates, Michigan hunters took an estimated 57,200, 50,100, 57,800, 55,600, and 52,400 Canada geese during the 1998, 1999, 2000, 2001, and 2002 regular seasons, respectively. Variograms for regular season, statewide harvests

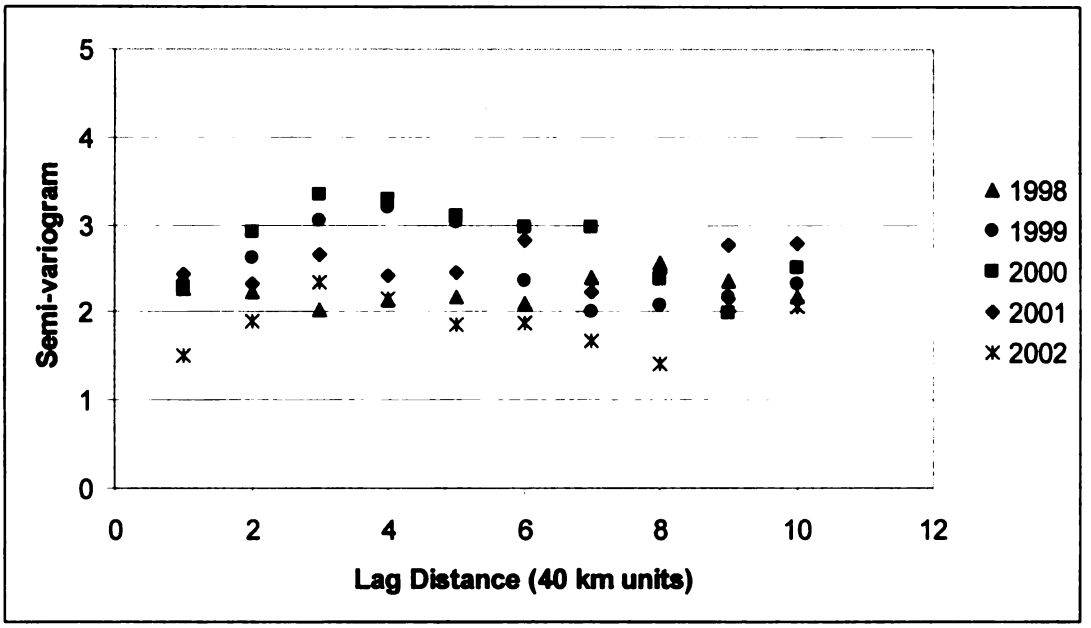
illustrated less variance in the sample size of harvested geese among counties in close geographic proximity to one another than among counties separated by larger distances for morphology- and genetic-based analyses (Figure 1). The variance in harvest sample size increased in a curvilinear fashion as a function of increasing distance between counties sampled. This pattern was consistent across all five years of harvest sampling, although the range of sampling variance among years was slightly greater for the morphology sample dataset than the genetic sample dataset.

Band Recovery Analyses

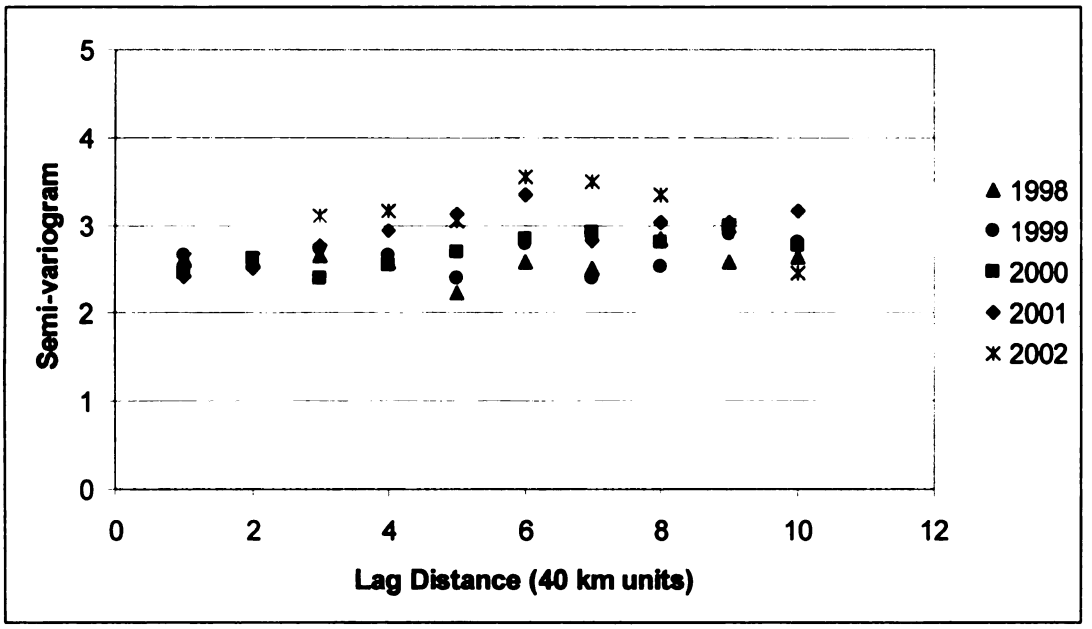
A total of 254 bands were recovered for adult geese from the 1998-2002 regular hunt seasons. No banded cackling geese were recovered in any of the five harvest seasons in Michigan. Estimated proportional harvests of interior Canada geese were greater than estimated proportions of giant Canada geese harvested in 1999 (interiors: 59.3%), 2000 (62.3%), and 2002 (51.7%) (Table 1). In 1998 and 2001, estimated proportions of giant Canada geese harvested were 53.7% and 61.3%, respectively (Table 1). Sex ratios of the banded harvest were male dominated in 1998 (female to male ratio: 0.65), 1999 (0.77), and 2001 (0.83), and female dominated in 2000 (1.19) and 2002 (1.5).

Morphometric Analyses

Based on culmen measurements from both sexes, the proportion of giants in the Michigan regular season harvest has increased since the shift of the regular season opening to mid-September which occurred after 1997 (46% giants). Proportional harvests of giants were estimated to be 61% in 1998, 76% in 1999, 83% in 2000 and 90%



Morphology Samples



Genetic Samples

Figure 1. Omnidirectional variograms for the spatial distribution of two collections of regular season harvest samples of cackling geese and Canada geese in Michigan from 1998-2002. Harvest samples used for morphology-based analyses were collected through the Michigan Department of Natural Resources, and harvest samples used for genetic-based analyses were collected through the United States Fish and Wildlife Service Waterfowl Parts Survey.

in 2001 (Table 1). During 2002, the proportion of giants in the harvest declined to 61%, but remained above the estimate in 1997 and was similar to the 1998 estimate. The proportion of samples classified as cackling geese was highest in 1997 and lowest in 1999 (Table 1). However, this result is based on small numbers of geese meeting the culmen length criteria for this subspecies (n = 22 from 1997-2002). Estimated interior Canada goose harvest decreased each year from 1998 through 2001 while estimated giant harvest increased (Table 1). Based on morphology samples, estimates of adult sex ratios for regular season harvests were strongly male biased in 1998 (female to male ratio: 0.53) and 1999 (0.64). Approximately equal harvests of the sexes occurred during 2000 (1.11), 2001 (1.08), and 2002 (0.95).

Culmen measurements were collected from 291 AHY birds in the Saginaw Bay area during the three years of early seasons (Table 2). No geese met the culmen measurement criteria for cackling geese. Estimates of mean adult culmen lengths from the harvest sample differed from means reported for Michigan giants (Moser and Rolley 1990) by less than 0.5 mm for both sexes and were larger than reference means from northern Michigan giants (Soulliere et al. 1995).

Estimates of the contribution of giant Canada geese in the early season harvest ranged from 90 to 100% for females and from 87 to 100% for males depending on reference populations in the morphometric analysis and sample year (Table 2). The lowest estimate of the contribution of giants was for male harvest samples in 2000 under the assumption that all geese harvested were either giants from Michigan only or interiors from the Southern James Bay mainland. Michigan giants have relatively large culmens (Moser and Rolley 1990) and geese from the Southern James Bay mainland were the

Table 1. Comparison of harvest estimates (%) of adult cackling (*B. h. hutchinsii*) and Canada (*B. c. interior* and *B. c. maxima*) geese based on band recovery, morphometric, and genetic derivation techniques for the regular hunt season in Michigan from 1998-2002. Genetic estimates include standard deviation in parentheses based on 1000 bootstrap replicates. Sample sizes are listed below estimates.

	Band Recovery	Morphometric	Genetic Analysis
1998			
B.c. interior	46.3	36.3	27.7 (8.1)
B.c. maxima	53.7	61.3	68.7 (8.2)
B.h. hutchinsii	0.0	2.4	3.6 (2.5)
	(n = 61)	(n = 142)	(n = 142)
1999			
B.c. interior	59.3	24.2	24.8 (7.5)
B.c. maxima	40.7	75.8	73.5 (7.7)
B.h. hutchinsii	0.0	0.0	1.8 (1.8)
	(n = 52)	(n = 179)	(n = 158)
2000			
B.c. interior	62.3	16.0	45 (10.2)
B.c. maxima	37.7	83.6	54.2 (10.3)
B.h. hutchinsii	0.0	0.4	0.8 (1.6)
	(n = 34)	(n = 232)	(n = 111)
2001			
B.c. interior	38.7	8.6	29.1 (8.8)
B.c. maxima	61.3	90.3	69.7 (8.8)
B.h. hutchinsii	0.0	1.1	1.3 (1.9)
	(n = 59)	(n = 164)	(n = 126)
2002			
B.c. interior	51.7	37.8	49.5 (7.1)
B.c. maxima	48.3	61.1	50.4 (7.1)
B.h. hutchinsii	0.0	1.1	0.1 (0.5)
	(n = 48)	(n = 113)	(n = 217)

Table 2. Comparison of harvest estimates (%) of adult cackling (*B. h. hutchinsii*) and Canada (*B. c. interior* and *B. c. maxima*) geese based on genetic and morphometric derivation techniques for the early hunt season in Saginaw Bay from 2000-2002. Morphometric harvest estimates were calculated using three different interior and two giant culmen reference lengths-estimates listed in this table represent the range of results from these six morphometric derivations. Genetic estimates include standard deviation in parentheses based on 1000 bootstrap replicates. Samples sizes are listed below estimates.

	Genetic Analysis	Morphometric
2000		
B.c. interior	20.6 (8.3)	2-13
B.c. maxima	79.1 (8.6)	87-98
B.h. hutchinsii	0.3 (1.2)	0
	(n = 102)	(n = 117)
2001		
B.c. interior	30.6 (7.9)	0-3
B.c. maxima	69.1 (8.0)	97-100
B.h. hutchinsii	0.3 (0.9)	0
	(n = 124)	(n = 126)
2002		
B.c. interior	12.9 (9.4)	0-7
B.c. maxima	86.5 (9.4)	93-100
B.h. hutchinsii	0.6 (1.5)	0
	(n = 48)	(n = 48)

largest interiors recorded. Using the largest reference means for interior Canada geese results in the most conservative estimate of giants in the calculated harvest composition. Assuming that interior geese migrating through the study area are affiliated with SJBP Akimiski Island and Southern James Bay mainland in proportion to abundance on the breeding ground (about 30% of SJBP occur on Akimiski), then a reference size based on

the weighted average of the two SJBP segments may be the most realistic interior reference. Using this SJBP weighted average reference, the southern Michigan giant reference, and the average culmen sizes of samples from adult birds, an estimated 98% of female and 96% of male geese were giants for the entire 3-year experiment. Sex ratios of harvested samples collected for morphometric analyses were male biased in 2000 (females to males: 0.67) and 2002 (0.41), and female biased in 2001 (1.17).

Genetic Analyses

Statewide distributions of Canada geese regular season harvest samples varied among years, and included 40 counties in 1998, 42 counties in 1999, 27 counties in 2000, 33 counties in 2001, and 44 counties in 2002. Regular season harvests of adults were composed mainly of giant Canada geese (50.4% - 73.5%), with lesser proportions of interior (24.8% - 49.5%) Canada geese and cackling geese (0.1% - 3.6%) (Table 1). Estimates of giant harvest were greatest in 2001, but did not indicate harvests of resident geese steadily increased from 1998-2001 as illustrated by morphometric derivation results. Contributions of cackling geese to regular season harvests varied among years, but were always less than 10% of the total harvest (Table 1). Likelihood ratio tests of regular season harvests indicated that proportional estimates of adult giant and interior Canada geese and cackling geese harvested annually differed significantly among years ($P = 0.039$). Estimates of adult sex ratios for regular season harvests were slightly male biased in 2001 and 2002. Approximately equal proportions of males and females were harvested during 1998, 1999, and 2000. Specific annual ratios of females to males were as follows: 1998 (0.937), 1999 (1.020), 2000 (0.929), 2001 (0.800), 2002 (0.807).

Tongues were clipped for genetic-based analyses from 274 of the adult geese collected for morphometric analyses. Similar to morphometric analyses, proportional harvest estimates were greater for giant Canada geese than interior Canada geese during all three years (Table 2). However, proportional harvest estimates of giant Canada geese based on genetic analyses (69.1 -86.5%) were consistently lower than morphometric-based estimates. Estimated proportions of interior Canada geese harvested during the three early seasons were higher than estimates from morphometric derivations, and ranged between 12.9 – 30.6%. Cackling geese were estimated to compose than 1% of the early season harvest each year (Table 1). Likelihood ratio tests revealed no significant differences in proportional harvest estimates of cackling geese and interior and giant Canada geese among years for genetic derivations ($P = 508$). Female to male sex ratios in early season harvests as determined by genetic sexing for 2000 (females to males: 0.54) and 2002 (0.34) samples were similar to sex ratios determined by cloacal examination in the field. The sex ratio for 2001 was 0.91, which contrasted with the morphology-based sex ratio of 1.17 for the same year.

DISCUSSION

All three derivation techniques provide estimates of the harvest composition and it would be inappropriate to view estimates derived from one type of data as a "check" on estimates derived from other datasets. However, we have greater confidence in our harvest derivations when these independently obtained estimates agree with each other. Regular season harvest estimates of each subspecies were most similar among all three derivations in 1998 and 2002, and least similar in 2000. In 1999, morphometric and

genetic derivations produced equivalent results, while estimates of harvests were more comparable between band recovery and genetic derivations in 2001.

Harvest estimates may be consistent across techniques in some years and disparate in others due to inadequate baseline collections. Baseline populations included samples from relatively small portions of the geographic ranges for interior Canada geese and cackling geese, as sampling focused on coastal areas and excluded most inland populations. Giant Canada geese in the baseline were represented by Michigan populations only. Influxes of birds from populations that were not represented in the baseline (e.g., interior Canada geese and cackling geese from inland breeding areas, giant Canada geese from Ontario) may result in harvest estimates that are not concordant among multiple derivations, especially if the ability to correctly categorize birds from non-represented populations varies among derivation techniques.

Potential temporal and geographic biases of harvest mixture samples discussed in the methods may also lead to differences among harvest estimates derived from various techniques. We may assume that in years of concordant estimates harvest samples collected independently for each derivation are more likely to represent similar geographic areas and temporal coverage of the regular season harvest than in years where estimates disagree among derivation results. It is possible that in years of discordant estimates, harvest samples for each derivation do not equally represent the harvest mixture in time and/or space. Temporal and spatial sampling biases may be created by hunters in terms of selectively submitting samples, or failing to submit samples later in the season due to hunter "burn out". Geographic and temporal biases may also be present in the sampling methodology for each derivation method. However, sampling biases

inherent in each technique would not likely change from year to year, and differences among annual harvest estimates derived from each technique would then be consistent over the five years analyzed. In addition, spatial patterns of variance for harvest samples were similar between morphology and genetic collections among years of concordant and discordant estimates, as indicated by comparative variograms (Figure 1).

Band recovery derivations consistently estimated higher proportional regular season harvests of interior Canada geese as compared to harvest estimates of interiors based on morphometric and genetic derivations. Estimates of interiors harvested were lowest, and harvest estimates of giant Canada geese were highest, in 4 of the 5 years analyzed based on morphometric derviations as compared to annual results of the other two techniques. Morphology-based harvest derivations may underestimate contributions of interior Canada geese, as the morphometric technique employed (Moser and Rolley 1990) is designed to separate only two populations of geese. This technique is difficult to apply to the multiple populations of interior Canada geese that have measurable differences in size (Leafloor and Rusch 1997, Leafloor et al. 1998), and likely contribute to annual harvests in Michigan. Observed and potentially unobserved geographic variation in the size of interiors may skew harvest estimates of interior Canada geese based on morphometric derivations.

Regular season harvests of cackling geese were estimated to be less than 5% of the harvest in all years for all derivations. However, no cackling geese were recorded during the five regular seasons of band recoveries, indicating no presence of this subspecies in the harvests. The annual number of individuals sampled through band recoveries was much less than the annual sample sizes for morphometric and genetic

derivations. If cackling geese are rare but present in harvests as indicated by morphometric and genetic analyses, larger numbers of band returns may be necessary to detect low levels of these geese.

Early season harvest comparisons utilized the same set of harvest samples for morphometric and genetic derivations, reducing potential sampling biases between the two derivations. Both early season derivations resulted in relatively high estimates of proportions of giant Canada geese as compared to interior Canada geese harvest estimates, but morphology-based analyses resulted in consistently higher estimates of giants and lower estimates of interiors than harvest results derived from genetic characteristics. This suggests that there may be underlying differences in these two techniques causing bias in one, or both, sets of estimates. Bias may result from inadequate sampling of interior and/or giant populations used to develop baseline references for morphometric and genetic derivations, as discussed above for the regular season harvest. The problem of applying morphometric analysis to mixtures potentially involving more than two populations is also relevant for early season harvests, although multiple culmen measurements for interior and Canada geese were used in this analysis to minimize potential error.

The efficacy of using each of the derivation techniques may vary depending on the goals of the harvest evaluation. For instance, only adult harvests can be assessed using morphology-based methods, whereas band recovery and genetic harvest derivations can also incorporate estimates of juvenile harvests or combined harvests of adults and juveniles. Although only adults were included in our analyses for comparative purposes, annual sample collections of geese from regular season harvests in Michigan were

composed of 19-35% juveniles in genetic datasets, 13-56% juveniles in morphology datasets, and 67-73% juveniles in band recovery datasets. Early season harvest collections included 34-44% juveniles. By excluding juveniles, we lose a large number of harvest samples that may be informative in harvest assessments and potentially skew estimates of harvest composition for each subspecies.

MANAGEMENT IMPLICATIONS

It is challenging to manage a highly mobile biological resource like cackling geese and Canada geese that are distributed across heterogeneous, changing environments, and characterized by complex, only partially recognized biotic/environmental interactions (Williams and Nichols 1990). Successful management of these species requires accurate and precise estimates of harvest composition that may be used to direct future harvest policies. Partially blind management, based on imprecise and/or biased monitoring programs, will fail to consistently recognize the need for harvest restrictions, or to respond to harvest opportunities when they arise (Williams et al. 1996). It is therefore important to contrast harvest estimates derived by multiple techniques currently being used to evaluate the harvest of cackling and Canada geese in order to investigate potential biases associated with each derivation method.

Band recovery, morphometric, and genetic analyses all provide estimates of the "true" harvest composition. It is difficult, however, to assess the accuracy and precision of estimates calculated from each derivation technique if only one type of derivation is used to analyze a harvest mixture. By comparing the results of multiple harvest derivation techniques applied to goose harvests in Michigan over similar temporal and

geographic scales, we were able to assess how potential biases associated with each derivation technique may influence resulting harvest estimates. Additional study is needed to determine why estimates among techniques are concordant in some years, and dissimilar in others, and to fully explain differences in derivation patterns that are consistent among years (i.e., higher proportional estimates of giant Canada geese resulting from morphometric derivations) in order to improve harvest monitoring.

ACKNOWLEDGEMENTS

Funding for this study was provided by the Michigan Department of Natural Resources (MDNR) and through the Partnership for Ecosystem Research and Management (PERM) Program between the MDNR and the Department of Fisheries and Wildlife at Michigan State University. Baseline samples were collected by many individuals associated with the MDNR, Michigan State University, and individuals from the Canadian Wildlife Service and Environment Canada including K. Abraham, D. Caswell, K. Dickson, and J. Leafloor. We thank all participants of the Mississippi Flyway Wing Bee who assisted in cataloging hunter-harvested samples collected by the U.S. Fish and Wildlife Service, especially Barb Lercel Avers and Bill Scullon of the MDNR, and Dave Rave of the Minnesota DNR.

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CHAPTER 7: DISPERSAL AND GENE FLOW AMONG WRANGEL ISLAND AND BANKS ISLAND LESSER SNOW GEESE

INTRODUCTION

Exponential growth of Mid-Continent lesser snow geese (*Chen caerulescens caerulescens*) populations (Ankney 1996, Batt 1997), and some Western populations (Kerbes et al. 1999) over the past 30 years have led to expansion of population boundaries in both breeding and wintering areas (Alisauskas 1998). Expansions of lesser snow geese populations could increase dispersal and potential gene flow among breeding colonies and/or wintering groups. Current management policies directed to control overabundant populations through harvest on wintering grounds and migratory pathways when populations are mixed could significantly impact the diversity and long-term viability of lesser snow geese if population dynamics among breeding and wintering groups are not well understood.

The two largest breeding colonies of lesser snow geese in the Western Arctic are currently experiencing very different population trends. The population nesting on Wrangel Island (WI) off the northeast coast of Russia has greatly declined in abundance over the past 35 years. Population numbers have decreased from 150,000 geese in the late 1960's to 65,000 in the mid-1990's. In contrast, the colony on Banks Island, Canada has grown from 170,000 individuals to 486,000 individuals during the same time period (Kerbes et al. 1999, Hines et al. 1999b). The WI breeding colony consists of two wintering groups. The northern group which comprises an estimated 50% of the total Wrangel population migrates to the Fraser River Delta, British Columbia and the Skagit

River Delta, Washington. The southern group migrates 600 km farther south to winter in California's Central Valley (Figure 1, Kuznetsov et al. 1998, Armstrong et al. 1999). The southern WI group (SWI) shares its wintering grounds with approximately 75% of the lesser snow geese population from BI and other smaller Western Canadian Arctic breeding populations, while the northern WI wintering group (NWI) is isolated from other breeding populations (Syroechkovsky et al. 1994, Hines et al. 1999a). In the spring, the NWI population reverses its fall migration pathway, following the Pacific coast north, while the SWI population follows a more inland route typical of the BI population wintering in the Pacific and Central Flyways (Bousfield and Syhroechkovsky 1985, Armstrong et al. 1999). During spring migration the NWI and SWI populations remain isolated until at least the Yukon-Kuskokwim Delta in Alaska, and may arrive separately on WI in some years (Ganter et al. 2005).

Identifying the degree of dispersal and population structure among breeding and wintering groups of NWI, SWI, and BI geese is essential to the successful management of these populations. Both breeding and wintering patterns of these populations likely influence the interactions among NWI, SWI, and BI birds and potential gene flow among populations. Currently the WI population is of conservation concern due to its declining abundance and because it is the only significant snow goose colony nesting on the Asian continent (Kuznetsov et al. 1998). In addition, the NWI population is the only group of lesser snow geese wintering in Canada (Mowbray et al. 2000). Without an understanding of the potential genetic exchange and population structure among NWI, SWI, and BI lesser snow geese, the abundance and diversity of the WI population may be negatively impacted if harvest limits in California are increased in an effort to control the growth of

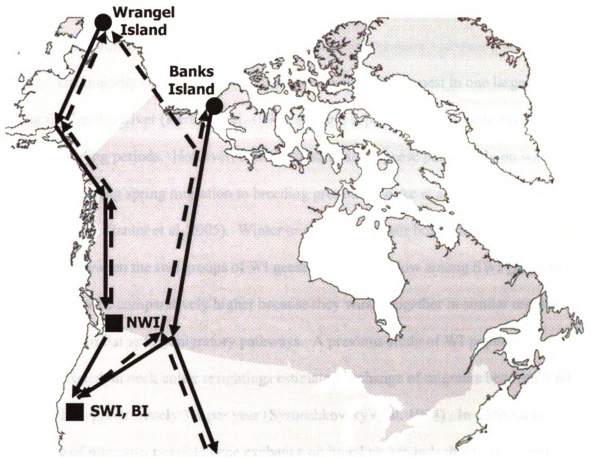

Figure 1. Breeding (circles) and wintering (squares) populations of lesser snow geese from Wrangel Island and Banks Island. Fall migratory pathways south to wintering grounds are marked by solid arrows, and spring migratory routes north to breeding areas are marked by dashed arrows. Approximately equal proportions of geese breeding on Wrangel Island winter in the British Columbia / Washington region (NWI) and in California's Central Valley (SWI). Lesser snow geese from Banks Island (BI) winter in the Central Valley (75% of the population) with the SWI population.

the BI population. Thus, it is important to quantify gene flow between SWI and BI populations potentially occurring during admixture on wintering grounds and spring migration. Genetic exchange between NWI and SWI populations could occur as a result of mixing on breeding grounds, during fall migration, and due to movement of birds

between north and south wintering areas. A measure of this gene flow is vital in defining management units of lesser snow geese.

The majority of NWI and SWI (90%) lesser snow geese nest in one large colony along the Tundra River (Kerbes et al. 1999), so there is potential for genetic exchange during breeding periods. However, colonial nesting snow geese pair mainly on wintering grounds or during spring migration to breeding grounds (Cooke et al. 1975, Ely and Scribner 1994, Ganter et al. 2005). Winter or early spring pair bond formation may limit gene flow between the two groups of WI geese, while gene flow among SWI geese and BI geese may be comparatively higher because they winter together in similar regions and follow similar spring migratory pathways. A previous study of WI population structure based on neck collar resightings estimated exchange of migrants between SWI and NWI at approximately 3% per year (Syroechkovsky et al. 1994). In addition to exchange of migrants, possible gene exchange on breeding grounds due to extra-pair copulation, intraspecific nest parasitism, and fostering, increases the amount of potential gene flow between the two WI populations to 9% per generation (Syroechkovsky et al. 1994). This level of exchange is likely too high to allow for appreciable genetic differences to accrue between the populations. Allozyme analyses of biparentally inherited blood proteins and esterases from samples of NWI and SWI geese found no statistical differences in allele frequency between populations (Kuznetsov et al. 1998), supporting conclusions based on banding observations.

Our study of Western Arctic lesser snow geese builds upon previous investigations by employing multiple genetic markers (nDNA microsatellites and maternally inherited mtDNA) and sampling a large number of individuals from NWI,

SWI and BI populations, to quantify levels of gene flow among these three populations and assess historical and contemporary levels of dispersal among breeding and wintering groups. We are able to compare our indirect measures of dispersal to direct measures of movement of NWI, SWI, and BI lesser snow geese quantified by Williams et al. (2005) in a mark-recapture study of geese banded on WI and BI breeding grounds. Geese for the Williams et al. (2005) study were banding during the same period samples were collected for our genetic analyses. Estimates of dispersal among the NWI, SWI, and BI populations could potentially differ between the two techniques as banding methods measure degree of movement among populations, whereas genetic methods measure gene flow mediated by immigrants who disperse from source populations and subsequently breed with individuals from receiving populations. Estimates may also differ because genetic analyses based on bi-parentally and maternally inherited markers provide indirect estimates of contemporary and historical rates of dispersal, while banding observations provide direct estimates of contemporary dispersal only. However, valuable information about the population dynamics of NWI, SWI, and BI lesser snow geese may be gained from both direct and indirect measures of dispersal even if resulting estimates vary between the two techniques. Previous studies have utilized either direct or indirect measures of dispersal among Western Arctic nesting lesser snow geese (Syroechkovsky et al. 1994, Kuznetsov et al. 1998, Armstrong et al. 1999, Baranyuk et al. 1999), but have not combined the two techniques to provide a more thorough analyses of past and current interactions among populations.

METHODS

Sample Collection

Samples for genetic analysis were collected in 1994 from flightless lesser snow geese breeding populations during mid-summer brood drives. Collections were made from July 19 to July 23 on BI and from July 25 to August 1 on WI. Geese were aggregated in mobile corral nets in catch areas using an all-terrain vehicle or on foot on WI and using helicopter-drive techniques on BI (Cooch 1953, Timm and Bromley 1976). Numbers of birds sampled at each location were: NWI (n=71), SWI (n=79), and BI (n=79) (Figure 1). Blood or a blood quill (growing feather) was sampled from breeding adults. Samples were placed into individual tubes containing high-salt buffer and stored at ambient temperatures in the field until frozen in the laboratory.

All geese captured from 1993-1996 on WI and from 1994-1996 on BI were marked with metal United States Fish and Wildlife Service legbands, and most adults were fitted with colored plastic neckbands as part of a larger study of populations of Western Canadian Arctic and Wrangel Island nesting snow geese (Kerbes and Meeres 1999). Neckband color was red with white characters for WI birds, and black with white characters for BI (Samuel et al. 2001).

On the WI breeding colony, north wintering geese can be reliably distinguished from south wintering geese by the degree of reddish-staining on their head and face (Baranyuk and Syroechkovsky 1994, Baranyuk et al. 1999). Geese from northern wintering grounds forage in tidal marshes, and acquire a red stain due to the mineral salts in the soils and water of these coastal areas (Hohn 1955, Baranyuk and Syroechkovsky 1994, Baranyuk et al. 1999). Southern wintering geese feed mainly in agricultural fields

on waste grain, retaining their white plumage (Pacific Flyway Technical Committee 1992, Baranyuk et al. 1999). Facial staining is associated with a color score from 1-6, with 1 being completely white and 6 being strongly red. Past neckband observations have recorded high fidelity (86-90%) of WI geese with face plumage scores 1-3 to southern wintering areas, and WI geese with scores of 4-6 to northern wintering areas (Baranyuk et al. 1999). For our analyses, we included geese scored as 1 or 2 (southern) and 5 or 6 (northern), and eliminated intermediate-stained (plumage scores of 3 or 4) geese that had higher likelihoods of being incorrectly classified to wintering regions (Kuznetsov et al. 1998, Baranyuk et al. 1999, Williams et al. 2005). Face stain score was recorded by one trained biologist (V. V. Baranyuk) for all individuals sampled for genetic analysis and all individuals banded (Williams et al. 2005).

Analysis of Microsatellite Loci

DNA was extracted from all samples using DNeasy extraction kits (Qiagen Inc., CA). Twenty nuclear microsatellite loci were initially screened for allelic variation. Nine bi-parentally inherited loci proved to be polymorphic in one or more breeding populations and were used for subsequent analyses. Loci used included Bcaμ1, Bcaμ5, Bcaμ9, Bcaμ11, Hhiμ1, Hhiμ3 (Buchholz et al. 1998), Aalμ1 (Fields and Scribner 1997), Sfiμ10 (S. Libants, unpubl. data), and CR-G (A. Baker, unpubl. data). Each locus was amplified using polymerase chain reaction (PCR) in 25 μl reaction volumes, including 100-150 ng DNA, 10-25 pmol of each primer, PCR buffer (10 mM Tris-HCl pH 8.3, 50 mM KCl, 100 μg/mL gelatin, 0.01%NP-40, 0.01% Triton-X 100), 0.5 U of AmpliTaq DNA Polymerase (Perkin-Elmer), and 100-200 μM dNTPs. Forward primers of each

locus-specific primer pair were labeled with either Hex or Fluorescein by the manufacturer (IDT Technologies, Inc.). Most thermocycler conditions included a denaturing step of 94 °C for 2 min, followed by 30-35 cycles of 94 °C for 1 min, annealing temperature for 1 min [51 °C (Hhiμ1, Sfiμ10), 56 °C (Bcaμ1, Bcaμ9, Hhiμ3, CR-G), 58 °C (Bcaμ11), 60 °C (Bcaμ5)], and 72 °C for 1 min. Conditions for Aalμ1 included a denaturing step of 94 °C for 2 min, and 30 cycles of 94 °C for 1 min and 50 °C for 2 min. Products were visualized using a FMBIO II laser scanner (Hitachi Software Engineering Co.) after electrophoresis on denaturing 6% acrylamide gels. Genotypes were scored based on 20 base-pair standards and reference samples of known allelic size.

Analysis of MtDNA

Approximately 50-100 ng DNA was used for the initial mtDNA amplification (1173 bp) with primers 16775L and 287H-M (Quinn 1992) and PCR protocols of Kocher et al. (1989). Thermocycler conditions included an initial denaturation step of 92 °C for 2 min, followed by 40 cycles of 92 °C for 40 s, annealing at 61 °C for 2 min, 72 °C for 2 min, and extension at 72 °C for 7 min. Previous studies of snow geese phylogeographic structure based on control region mtDNA sequences revealed two major mtDNA clades (clade I and clade II) that differed by an average of 6.7% sequence divergence (Avise et al. 1992, Quinn 1992, Weckstein et al. 2002). Of the 22 variable sites between clade I and clade II mtDNA haplotypes, seven differences were fixed between the two clades. Two of the fixed differences fall within the recognition sequence for the restriction enzyme *Alu*I (Quinn 1992). This restriction enzyme cleaves the mtDNA of haplotypes within clade I, but does not cleave the mtDNA of haplotypes within clade II. Restriction

digests were performed using *Alu*I to test if the amplified region of mtDNA for was cut by the enzyme in order to classify individual snow geese as belonging to clade I or clade II. Amplified mtDNA was digested with *Alu*1 according to manufacturer protocol (New England Biolabs, Inc.) and visualized using ultraviolet light after electrophoresis on 1% agarose gels and staining with ethidium bromide.

Estimates of Gene Diversity and Degree of Population Structuring

Departure from Hardy-Weinberg expectations was tested using the program FSTAT (Goudet 2001) For each of the nine microsatellite loci in all three snow geese populations. Tests for genotypic linkage disequilibrium, a measure of independence across loci within a population, were performed as described in Goudet et al. (1996) using FSTAT. The FSTAT program was also used to estimate degree of spatial heterogeneity in gene frequency within and among snow geese populations using hierarchical *F*-statistics (Weir and Cockerham 1984, Weir 1996) at three levels: (1) among individuals within populations, (2) among individuals within the total population, and (3) among populations. Significance of *F*-statistics were based on 95% confidence intervals determined by bootstrapping across loci. Confidence intervals that included zero were considered non-significant. Pair-wise estimates of population F_{ST} were used as summary measures of inter-population variance in allele frequency. Significance of pair-wise interpopulation differentiation was determined using the exact G-test (Goudet et al. 1996) in FSTAT, as the G-test is more powerful than exact F_{ST}-estimator tests for diploid populations (Goudet et al. 1996, Petit et al. 2001). For tests of Hardy-Weinberg, gametic disequilibrium, and *F*-statistics, nominal significance levels (alpha) were adjusted to

account for multiple testing using sequential Bonferroni corrections (Rice 1989). A hierarchial analysis of molecular variance (AMOVA; Excoffier et al. 1992) was used to partition variance in mtDNA clade frequencies (clade I versus clade II) among snow geese populations (Phi_{ST}).

Estimates of Rates of Migration Among Populations

Coalescent-based methods (Beerli and Felsenstein 2001) were used to estimate relative measures of θ ($4N_e\mu$, a composite measure of effective population size and mutation rate) and interpopulation migration rates (4Nm, number of immigrants per generation) based on microsatellite data. Estimates were made using maximum likelihood methods based on a stepwise mutation model in program MIGRATE (v1.5, Beerli 2002). Twenty individuals were randomly selected from each population, including NWI, SWI, and BI. The goodness of fit of data was evaluated under several different models of θ and migration rates. The models tested included: A) Full model with unrestricted migration among all populations and unrestricted estimates of effective population size. B) N-dimensional island model assuming equal migration among all populations and equal effective population sizes. C) Restricted migration model assuming equal migration among all populations, but unrestricted estimates of effective population size. D) Model with unrestricted migration among all populations, but equal effective population sizes. The full model was run three times with progressively more extensive search strategies to ensure estimates were not based on convergence within local maximums. We then ran the full model three times with the following search parameters: 10 short chains, each with a total of 100,000 geneologies and a sampling

increment of 100 geneologies; and 3 long chains which were combined, each with a total of 1,000,000 geneologies and a sampling increment of 1000 geneologies. The first 10,000 geneologies in each chain were discarded. Initial parameters for each of these three runs were the resulting migration and θ estimates from the previous run. Alternative models were each run once, with initial parameters of migration and θ set as the mean of resulting estimates from the three full model runs. Likelihood estimates of each alternative model were compared to the full model using a likelihood-ratio test to evaluate goodness-of-fit of each model, and determine which model of gene flow and population size was statistically supported by the data. Each likelihood-ratio test was compared to a Chi-square distribution with degrees of freedom equal to the difference in the number of parameters between the two models being tested (Beerli and Felsenstein 2001).

RESULTS

Eight of the nine microsatellite loci used were polymorphic in all three populations, with two to seventeen alleles present within each population (Table 1). Each of the bi-parental loci used did not deviate significantly from Hardy-Weinberg equilibrium, and were determined to be genetically independent, as no evidence of gametic disequilibrium was detected for any locus combination in any population. Hierarchical *F*-statistics showed no evidence of significant variation among individuals within populations (*f*), among individuals within the total population (*F*), or among populations (F_{ST}) based on microsatellite loci (Table 1).

Table 1. Lesser snow geese allele frequencies and F-statistics for nine biparental and one maternally inherited marker from three populations of lesser snow geese breeding within the West Arctic region. Populations include north and south wintering Wrangel Island and Banks Island.

					Variance partitioning[a]		
Locus	Allele/ mtDNA Clade	Banks Island	Wrangel North	Wrangel South	Alleles within individuals within populations	Among individuals within total population	Among populations
Aalμ1	82	0.196	0.180	0.190	-0.124	-0.126	-0.002
	84	0.044	0.073	0.065			
	86	0.101	0.180	0.119			
	88	0.456	0.407	0.423			
	90	0.184	0.127	0.173			
	92	0.019	0.033	0.030			
	n	79	75	84			
Bcaμ1	112	0.006	0.013	0.000	0.005	0.013	0.008
	114	0.045	0.013	0.030			
	116	0.064	0.113	0.095			
	118	0.391	0.253	0.280			
	120	0.058	0.060	0.042			
	122	0.122	0.067	0.131			
	124	0.051	0.160	0.131			
	126	0.083	0.120	0.131			
	128	0.071	0.047	0.071			
	130	0.064	0.087	0.065			
	132	0.019	0.053	0.012			
	134	0.026	0.013	0.012			
	n	78	75	84			
Bcaμ9	98	0.000	0.000	0.006	0.016	0.015	-0.001
	102	0.411	0.487	0.423			
	104	0.013	0.013	0.006			
	106	0.196	0.173	0.131			
	108	0.070	0.033	0.054			
	110	0.127	0.127	0.149			
	112	0.171	0.160	0.232			
	114	0.013	0.007	0.000			
	n	79	75	84			
Bcaμ5	200	1.000	0.987	0.994	-0.005	-0.004	0.001
	202	0.000	0.013	0.006			
	n	81	76	84			

Table 1 (cont'd).

Locus	Allele/ mtDNA Clade	Banks Island	Wrangel North	Wrangel South	Variance partitioning[a]: Alleles within individuals within populations	Variance partitioning[a]: Among individuals within total population	Variance partitioning[a]: Among populations
CR-G	164	0.975	0.993	0.994	-0.008	-0.008	0.000
	166	0.012	0.000	0.000			
	168	0.012	0.007	0.006			
	n	81	76	84			
Hhiμ1	174	0.006	0.000	0.012	-0.006	-0.001	0.005
	178	0.006	0.007	0.000			
	180	0.006	0.000	0.000			
	182	0.012	0.020	0.018			
	184	0.000	0.007	0.006			
	186	0.019	0.020	0.006			
	188	0.062	0.092	0.071			
	190	0.031	0.020	0.054			
	192	0.062	0.066	0.143			
	194	0.451	0.421	0.333			
	196	0.105	0.125	0.107			
	198	0.080	0.072	0.071			
	200	0.031	0.033	0.030			
	202	0.080	0.066	0.060			
	204	0.012	0.020	0.030			
	206	0.025	0.026	0.042			
	208	0.006	0.000	0.006			
	210	0.000	0.007	0.006			
	212	0.000	0.000	0.006			
	214	0.006	0.000	0.000			
	n	81	76	84			
Hhiμ3	115	0.235	0.237	0.292	0.111	0.109	-0.002
	117	0.012	0.020	0.006			
	121	0.006	0.007	0.000			
	123	0.235	0.171	0.196			
	125	0.500	0.553	0.488			
	127	0.012	0.013	0.018			
	n	81	76	84			

Table 1 (cont'd).

Locus	Allele/ mtDNA Clade	Banks Island	Wrangel North	Wrangel South	Variance partitioning[a]: Alleles within individuals within populations	Among individuals within total population	Among populations
Sfiμ10	126	0.481	0.507	0.560	0.135	0.136	0.001
	128	0.000	0.026	0.000			
	130	0.519	0.467	0.440			
	n	81	76	84			
Bcaμ11	134	0.000	0.000	0.006	-0.057	-0.062	-0.005
	138	0.006	0.020	0.018			
	140	0.883	0.862	0.887			
	142	0.111	0.118	0.089			
	n	81	76	84			
All Biparental Loci					0.011 (NS)	0.012 (NS)	0.001 (NS)
mtDNA	clade I	0.568	0.182	0.439	na	na	0.098
	clade II	0.432	0.818	0.561			($P < 0.001$)
	n	74	66	82			

[a] *F*-statistics for biparental loci and maternally inherited mtDNA. Nomenclature is as follows: Alleles within individuals within populations represented by *f*, among individuals within total population represented by *F*, and among populations represented by F_{ST} and Phi_{ST} (Weir and Cockerham 1984, Excoffier et al. 1992). NS = nonsignificant (i.e. $P > 0.05$); na indicates that no *F*-statistic was applicable for mtDNA clade frequency data.

Pair-wise population differences in allele frequency were summarized across the nine microsatellite loci as the proportion of total genetic diversity partitioned between each pair of populations. No pair-wise comparisons (Table 2) were significant, indicating allele frequencies were similar across populations (mean F_{st} across all populations = 0.0018, $P > 0.05$). In contrast to results based on microsatellites, mtDNA clade frequencies were significantly different among populations ($Phi_{ST} = 0.098$, $P < 0.001$; Table 1). Notably, there were large differences between northern and southern wintering

Table 2. Above diagonal: Pairwise F_{ST} comparisons[a] among lesser snow geese populations based on 9 bi-parentally inherited microsatellite loci. Below diagonal: Pairwise Phi_{ST} comparisons[b] among lesser snow geese populations based on maternally inherited mtDNA. *P*-values for each pairwise comparison are indicated below estimates in parentheses. Significant *P*-values are marked with an asterisk.

	Wrangel North	Wrangel South	Banks Island
Wrangel North	---	-0.0008 (0.5833)	0.0016 (0.3000)
Wrangel South	0.1047 (0.0000)*	---	0.0029 (0.3667)
Banks Island	0.1932 (0.0000)*	0.0047 (0.0999)	---

[a]Weir and Cockerham 1984

[b]Excoffier et al. 1992

populations of lesser snow geese breeding on WI (pair-wise $Phi_{ST} = 0.1047$, $P < 0.0001$), and between NWI and BI (pair-wise $Phi_{ST} = 0.1932$, $P < 0.0001$; Table 2).

In the comparison of competing models of migration and effective population size, only Model B, the N-dimensional island model [Ln(L) = -565], was found to have significantly higher likelihood than Model A, the full model [Ln(L) = -678; $P < 0.0001$]. Models C [Ln(L) = -817] and D [Ln(L) = -767] had lower likelihoods than Model A, and both likelihood ratio tests were non-significant. Genetic-based estimates of effective population size and migration rate are based on microsatellite data, which reflect contemporary evolutionary patterns for each population. This suggests that effective population sizes and exchange of migrants and potential gene flow is equivalent among

NWI, SWI, and BI populations over recent evolutionary periods. These results are consistent with the lack of differentiation in microsatellite loci frequencies among the three populations, and the equivalent rates of migration among the three populations documented by Williams et al. (2005). For the N-dimensional island model, mean effective population size (θ or $4N_e\mu$) was estimated at 0.50 (95% CI: 0.46, 0.56) and mean migration (4Nm) among the three populations was estimated to be 9.23 (95% CI: 8.72, 9.79) individuals per generation.

DISCUSSION

The NWI population wintering in British Columbia and Washington State was highly differentiated genetically from the SWI and BI populations wintering together in the Central Valley of California as evidenced by significant differences in mtDNA clade frequencies. Previous studies comparing the mtDNA characterisitics of lesser snow geese populations, including geese from WI, observed that two distinct mtDNA clades (6.7% sequence divergence) were distributed across the lesser snow goose subspecies range without geographic localization (Avise et al. 1992, Quinn 1992, Weckstein et al. 2002). Two different hypotheses were raised to explain the lack of geographic pattern among the highly divergent mtDNA clades. Quinn (1992) stated that two ancestral lesser snow goose populations likely occupied different historic refugia during glacial events (Ploeger 1968) and subsequently dispersed across the modern range of lesser snow geese during interglacial periods. An implication of this hypothesis is that speciation of snow geese and Ross's geese would have been recent, postdating the split in the mtDNA gene tree, with both species retaining the ancestral polymorphism (Avise et al. 1992). Both

Avise et al. (1992) and Weckstein et al. (2002) supported an alternative hypothesis of secondary introgression and hybridization between formerly allopatric populations of snow and Ross's geese that were isolated during the Pleistocene.

In the previous studies, snow geese with clade I and clade II haplotypes were identified at every population surveyed, but the proportions of individuals within each mtDNA clade differed among populations. Frequencies of clade I haplotypes were 0.37 for WI snow geese and 0.50 for geese from LaPerouse Bay in a study conducted by Quinn (1992). Weckstein et al. (2002) added to Quinn's (1992) data by sampling snow geese from Queen Maud Gulf, where the frequency of clade I haplotypes was 0.22. Avise et al. (2002) surveyed snow geese from WI, Queen Maud Gulf, and Anderson River, where clade I frequencies were 0.40, 0.64, and 0.71, respectively. Similar to these previous studies, we documented a higher number of WI snow geese with clade II haplotypes than clade I haplotypes. We estimated the frequency of clade I haplotypes to be 0.32 for the WI breeding population, 0.18 for the NWI wintering population, and 0.44 for SWI wintering population. In contrast to WI birds, most geese from BI were identified as having clade I haplotypes (frequency = 0.57), similar to geese from LaPerouse Bay (Quinn 1992, Weckstein et al. 2002) and Queen Maud Gulf (Avise et al. 1992). Quinn (1992) and Weckstein et al. (2002) found mtDNA clade frequencies were significantly different between WI and LaPerouse Bay and between WI and Queen Maud Gulf snow geese populations. In our study, significant differences in clade frequencies were documented between NWI and SWI populations and between NWI and BI populations, but frequencies were similar between SWI and BI populations sharing the same wintering areas. Avise et al. (1992) reported clade frequencies were statistically

similar among the WI, Anderson River, and Queen Maud Gulf breeding populations, but sample sizes were low for the WI population (n = 10).

The frequency of clade I haplotypes is much lower in the NWI population than other regional snow geese populations. The small proportion of clade I birds present within the NWI population is more consistent with the clade I frequencies documented for Ross's geese populations (0.10, Avise et al. 1992; 0.30, Weckstein et al. 2002; 0.18 – 0.27, Shorey unpublished data) than for snow geese populations. NWI snow geese have been isolated historically and during contemporary periods from Ross's geese populations in North America based on putative Pleistocene refugia locations (Ploeger 1968) and known migratory pathways and wintering sites (Ryder and Alisauskas 1995, Mowbray et al. 2000). Given this geographic isolation, low frequencies of clade I haplotypes in the NWI population similar to Ross's geese populations suggests that the evolutionary split between mtDNA clades occurred prior to speciation of snow and Ross's geese, supporting Quinn's (1992) evolutionary hypothesis.

NWI and SWI lesser snow geese may have originated in two different glacial refugia, and retain some genetic signature of their formerly allopatric state as evidenced by significant differences in mtDNA clade frequencies. Kuznetsov et al. (1998) hypothesized that the NWI and SWI populations were once allopatric, and the SWI population may have originated from geese nesting on the Russian coast near Wrangel Island known to winter in California. These mainland geese may have joined the WI colony after being displaced from their coastal breeding area prior to the 1930s (Bousfield and Syroechkovsky 1985). In addition to possible historical differences in origin between NWI and SWI geese, these populations may have been largely isolated in

different colonies that existed on Wrangel Island until the late 1950s when one of the two remaining colonies on the island was disrupted by a geologic expedition (Syroechkovsky and Krechmar 1981, Kuznetsov et al. 1998). Since 1969 the majority of nesting geese on Wrangel Island have inhabited a single large colony (Bousfield and Syroechkovsky 1985), increasing the potential for mixing of geese from NWI and SWI populations on the breeding grounds. Lack of nDNA allele frequency differences between the two populations indicate that genetic differences that accrued during historic isolation have decayed at a faster rate for microsatellite markers than maternally-inherited markers due to male-biased gene flow (Cooke and Sulzbach 1978, Cooke and Abraham 1980, Rockwell and Barrowclough 1987) and a much greater mutation rate for microsatellites as compared to mtDNA. Contemporary increases in gene flow between NWI and SWI populations may be due to loss of breeding areas and recent changes in the spatial structure of the breeding colony on WI.

High rates of fidelity (96-98%) of NWI lesser snow geese to northern wintering grounds and SWI and BI populations to southern wintering grounds were estimated by Williams et al. (2005) based on banding observations and documented previously for these groups in similar banding studies (Baranyuk et al. 1999, Armstrong et al. 1999). Rates of winter fidelity were equivalent for males and females from NWI, SWI, and BI populations, and greater than rates of fidelity to breeding areas for female (70-80%) and male (50-66%) lesser snow geese (Cooke and Sulzbach 1978, Cooke and Sulzbach 1978, Cooke and Abraham 1980, Ganter and Cooke 1998). Based on rates of fidelity to wintering grounds as compared to rates of fidelity to breeding grounds, we would expect greater spatial genetic structure among wintering populations than among breeding

populations of Western Arctic lesser snow geese. Genetic analyses indicate wintering populations NWI and SWI are more highly structured than WI and BI breeding populations of lesser snow geese in the Western Arctic, supporting the thesis of Robertson and Cooke (1999) that patterns of population structure and gene flow may be defined by wintering regions rather than fidelity to breeding site.

Both banding data and genetic analyses based on nDNA provide estimates of contemporary dispersal among populations, but do not provide information about historic dispersal or gene flow among the populations which may or may not be similar to current patterns. Alternative markers, such as mtDNA, must be utilized in order to assess how historic factors may have influenced the exchange of individuals among populations and shaped current genetic structure. As a maternally-inherited marker, mtDNA also provides a measure of female-mediated dispersal and gene flow. Williams et al. (2005) found low (2%) and equal rates of exchange of migrants among NWI, SWI, and BI populations for both male and female snow geese. Our coalescence-based analysis of microsatellite data also indicated an equal rate of gene exchange among these three populations in concordance with Williams et al. (2005) direct observations of dispersal. In contrast, significant variation in mtDNA clade frequencies among NWI, SWI, and BI populations suggests that rates of dispersal and subsequent gene flow may not be equivalent among populations and is male-biased. These results are more reflective of earlier banding research conducted from 1974-1979 documenting male-biased dispersal from the SWI population (Syroechkovsky et al. 1994). Two hypotheses may explain the differential results from our mtDNA analyses as compared to our nDNA analyses and the banding observations of Williams et al. (2005). If dispersal and gene flow among the

three populations are male-biased, but dispersal rates are low for both sexes, Williams et al. (2005) banding study may not have provided the resolution necessary to detect a difference in dispersal between males and females. Alternatively, both banding and genetic studies results may be accurate, and indicate historic dispersal and gene flow among NWI, SWI, and BI lesser snow geese populations were more restricted than during evolutionary recent periods.

Degree of face staining has been a reliable indicator of population affiliation for NWI and SWI lesser snow geese (Kuznetsov et al. 1998, Baranyuk et al. 1999). Banding studies have documented high fidelity (82 – 90 % return rate in subsequent winters) of WI geese with little or no face staining to southern wintering areas in Oregon and California, and WI geese with dark red staining to northern wintering areas in the Fraser-Skagit region (Baranyuk et al. 1999, Williams et al. 2005). Past studies conducted to investigate the relationship between the degree of face staining and genetic population structuring have found no evidence of genetic differentiation between NWI and SWI snow geese based on pairing observations (Syroechkovsky et al. 1994) and electrophoretic analysis of blood proteins and esterases (Kuznetsov et al. 1998). We also found a lack of genetic variation between NWI and SWI populations based on microsatellite allele frequencies. However, mtDNA clade frequencies differed significantly between the two populations, suggesting face staining is indicative of genetic isolation and population structuring between geese from the NWI and SWI wintering regions.

Data from our study illustrates the importance of both past vicariance and ongoing demographic changes and range expansions within and among populations in shaping the

current population genetic structure of Western Arctic lesser snow geese. This study highlights how the combination of direct and indirect measures of dispersal and genetic exchange, and the use of multiple genetic markers with different patterns of inheritance, can provide a more comprehensive picture of demographic patterns through time and aid in population assessment. Our results suggest there is a low level of male-mediated gene flow occurring between the NWI and SWI lesser snow geese population, and that current levels of population and genetic exchange may be greater than during historic periods. However, significant genetic differences between the NWI and SWI populations indicate that these populations should be currently managed as separate populations, or subpopulations, even though most individuals nest within one large breeding colony on WI. Genetic differences between NWI and BI snow geese, and the lack of genetic variation between SWI and BI geese wintering in the same region, could be used to argue that management units of lesser snow geese should be defined by wintering sites rather than breeding areas. If BI and SWI birds were managed as one unit, we would caution that policies directed to control the overabundant BI population through harvest on wintering grounds when geese from the SWI population are present could significantly impact the long-term viability of the WI breeding population. Factors influencing the decline of the WI population are not well understood, and management plans should minimize potential harvests of both NWI and SWI geese until further investigations can be conducted.

ACKNOWLEDGMENTS

We thank the following individuals for assistance in conducting field sampling: V. V. Baranyuk, D. R. Goldberg, B. Ganter, J. Takekawa, E. G. Cooch. A special thanks

to L. Main for extensive laboratory assistance. Financial support was provided by the United States Geological Survey, Environment Canada, Michigan State University, and the Arctic Goose Joint Venture.

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