A hybrid zone between Canada Geese (*Branta canadensis*) and Cackling Geese (*B. hutchinsii*)

(Zone d'hybridation entre *Branta canadensis* et *B. hutchinsii*)

Author(s): James O. Leafloor, Jennifer A. Moore and Kim T. Scribner

Source: *The Auk*, Vol. 130, No. 3 (July 2013), pp. 487-500
Published by: University of California Press on behalf of the American Ornithologists' Union
Stable URL: http://www.jstor.org/stable/10.1525/auk.2013.12196
Accessed: 18/08/2013 22:23

The Auk 130(3):487–500, 2013

A HYBRID ZONE BETWEEN CANADA GEESE (*BRANTA CANADENSIS*) AND CACKLING GEESE (*B. HUTCHINSII*)

James O. Leafloor,[1,3] Jennifer A. Moore,[2,4] and Kim T. Scribner[2]

[1]*Canadian Wildlife Service, 150-123 Main Street, Winnipeg, Manitoba R3C 4W2, Canada; and*
[2]*Department of Fisheries and Wildlife, Michigan State University, East Lansing, Michigan 48824, USA*

Abstract.—We studied patterns of geographic variation in structural size and genetic characteristics of white-cheeked geese inhabiting coastal areas of Hudson Bay, Canada, from northern Manitoba to southern Nunavut to determine the degree of morphological and spatial overlap, if any, between Cackling Geese (*Branta hutchinsii*) and Canada Geese (*B. canadensis*) in this region. Most Canada Geese occurred in sub-Arctic habitats south of 59°N latitude, and most Cackling Geese occurred in Arctic habitats north of 60°N, but the two species overlapped in a narrow zone between 59°N and 60°N latitude that coincided with the ecotone between sub-Arctic and Arctic ecozones. Mismatches between morphological and genetic characteristics of some individual females suggested that introgression had occurred in this area, and contrasting patterns in the nuclear and mitochondrial DNA (mtDNA) were consistent with female natal philopatry and male-biased dispersal. Evidence of introgression in the nuclear genome was geographically more widespread than evidence of introgression in the mtDNA genome. We suggest that the persistence of Canada Goose mtDNA in phenotypic Cackling Geese is a result of historical hybridization events that occurred when the Arctic–sub-Arctic ecotone was located farther north during a warmer climatic period. Despite evidence of introgression, most birds that we sampled appeared to belong to one or the other parental species, on the basis of their consistent identification using morphological, mtDNA, and nuclear DNA characteristics. We suggest that the area of overlap represents a tension zone between Canada Geese and Cackling Geese that is maintained by behavioral and ecological factors that limit effective dispersal. *Received 17 October 2012, accepted 29 March 2013.*

Key words: *Branta canadensis*, *B. hutchinsii*, Cackling Goose, Canada Goose, genetics, hybrid zone, phenotype, phylogeography, secondary contact.

Zone d'hybridation entre *Branta canadensis* et *B. hutchinsii*

Résumé.—Nous avons étudié les patrons de variation géographique des caractéristiques génétiques et de la taille structurelle de bernaches habitant les zones côtières de la baie d'Hudson, du nord du Manitoba au sud du Nunavut, au Canada, afin de déterminer le degré de chevauchement morphologique et spatial, s'il y a lieu, entre *Branta hutchinsii* et *B. canadensis* dans cette région. La plupart des *B. canadensis* étaient présentes dans les habitats subarctiques, au sud du 59°N de latitude, et la majorité des *B. hutchinsii* se trouvaient dans des habitats arctiques au nord du 60°N. Les deux espèces se chevauchaient dans une zone étroite entre le 59°N et le 60°N, qui coïncidait avec l'écotone entre les écozones subarctiques et arctiques. Un décalage entre les caractéristiques morphologiques et génétiques chez certaines femelles suggère que de l'introgression s'était produite dans cette région. Les évolutions contrastées de l'ADN nucléaire et de l'ADN mitochondrial (ADNmt) concordaient avec la philopatrie natale chez la femelle et la dispersion biaisée en faveur des mâles. Les preuves d'introgression du génome nucléaire étaient plus répandues sur le plan géographique que celles du génome de l'ADNmt. Nous suggérons que la persistance de l'ADNmt de *B. canadensis* dans le phénotype de *B. hutchinsii* est un résultat d'événements d'hybridation historiques qui ont eu lieu lorsque l'écotone Arctique–Subarctique était situé plus au nord lors d'une période climatique plus chaude. Malgré les preuves d'introgression, la plupart des oiseaux que nous avons échantillonnés semblaient appartenir à l'une ou l'autre des espèces parentales, sur la base de leur identification cohérente avec des caractéristiques morphologiques, de l'ADNmt et de l'ADN nucléaire. Nous suggérons que la zone de chevauchement représente une zone de tension entre *B. canadensis* et *B. hutchinsii* maintenue par des facteurs comportementaux et écologiques qui limitent la dispersion effective.

[3]E-mail: jim.leafloor@ec.gc.ca
[4]Present address: Biology Department, Grand Valley State University, 317 Henry Hall, Allendale, Michigan 49401, USA.

The Auk, Vol. 130, Number 3, pages 487–500. ISSN 0004-8038, electronic ISSN 1938-4254. DOI: 10.1525/auk.2013.12196

Hybridization is common in birds, occurring in ~10% of all bird species, and is particularly common among waterfowl species, about half of which are known to hybridize (Grant and Grant 1992). In some cases, hybrid zones may form in areas where closely related but usually allopatric species come into secondary contact, and the zone of overlap represents an area of phenotypic and genotypic change that separates otherwise distinctive taxa (Jiggins and Mallet 2000). Such zones can be stable over long periods and can be maintained by a balance between selection and dispersal (Barton and Hewitt 1989). The outcome of interactions between closely related species in a zone of secondary contact may be influenced by behavioral, demographic, and environmental factors, and range from complete or near complete reproductive isolation (e.g., Irwin et al. 2001, Toews and Irwin 2008) to extensive hybridization and introgression (e.g., Irwin et al. 2009, Vallender et al. 2009, den Hartog et al. 2010).

Recently, the American Ornithologists' Union (AOU) split white-cheeked geese into two species: the Cackling Goose (*Branta hutchinsii*), a small-bodied form that nests in the Arctic, and the Canada Goose (*B. canadensis*), a large-bodied form that nests mainly in sub-Arctic and temperate regions of North America; we follow the nomenclature of Banks et al. (2004) here. The degree to which Canada Geese and Cackling Geese might overlap in their nesting distributions is not known. Some early authors reported that large-bodied and small-bodied forms of Canada Geese (i.e., those now recognized as Canada Geese and Cackling Geese, respectively) sometimes nested in proximity but that they remained isolated from one another because of behavioral and ecological differences (e.g., Sutton 1932, Mayr 1942:242, Brandt 1943). Smaller forms were usually described as tundra-nesting birds that nested in coastal habitats and on islands in coastal lakes, whereas large-bodied birds were thought to nest farther inland. Palmer (1976:187) reported that *B. c. parvipes*, currently identified through mitochondrial DNA (mtDNA) as a Canada Goose (Scribner et al. 2003b, Banks et al. 2004), overlapped with *B. c. hutchinsii* (now recognized as *B. hutchinsii hutchinsii*, a Cackling Goose) during different seasons, "resulting in a spectrum of individuals that grade imperceptibly from one 'pure' stock to the other." Although *parvipes* and *hutchinsii* were both considered subspecies of the Canada Goose at the time, Palmer's (1976) comments suggested that perhaps historically there was introgression between small-bodied and large-bodied forms of white-cheeked geese. *Branta c. parvipes* was thought to nest from interior Alaska eastward to the west coast of Hudson Bay, largely inland of *B. h. hutchinsii*, which was thought to nest mainly in tundra habitats along Canada's northern coast (Delacour 1954). Similarly, *B. c. interior* was thought to overlap with *B. h. hutchinsii* on nesting areas near the west coast of Hudson Bay at about 60°N latitude, but there they were thought to maintain separate identities (Palmer 1976).

Canada Geese and Cackling Geese are clearly separable on the basis of differences in their mitochondrial DNA (e.g., Shields and Wilson 1987, Van Wagner and Baker 1990, Quinn et al. 1991, Shields and Cotter 1998, Paxinos et al. 2002, Scribner et al. 2003b), but the degree to which the two species overlap geographically and morphologically is still incompletely known. One area where the two species are likely to overlap is on the west coast of Hudson Bay, Canada, which has been included in the breeding-range descriptions of at least three subspecies of white-cheeked geese and both species (*B. c. interior*, *B. c. parvipes*, and *B. h. hutchinsii*; AOU 1957, Banks et al. 2004). MacInnes (1963) believed that the small geese on the west coast of Hudson Bay near McConnell River were all *hutchinsii* but attempted to highlight uncertainty that existed in the literature by using the term "*hutchinsii–parvipes* complex" in his published reports (e.g., MacInnes 1962, 1966; MacInnes et al. 1974; C. D. MacInnes pers. comm.). MacInnes (1963) indicated that both on the western coast of Hudson Bay and on Southampton Island, the range of variation among adult specimens collected from nests, and larger samples from groups with goslings captured for banding, covered the size ranges of both *B. h. hutchinsii* and *B. c. parvipes*, yet the combined distributions of measurements fit a single normal distribution. Thus, he questioned the existence of *B. c. parvipes* in the area.

There remains some confusion about what species of white-cheeked goose might nest on the west coast of Hudson Bay. Even though this area is included in the breeding range of *B. c. parvipes*, this subspecies (i.e., the smallest subspecies of Canada Goose) has only been conclusively demonstrated to exist in parts of Alaska (Shields and Cotter 1998, Pearce and Bollinger 2003, Scribner et al. 2003b). No such small specimens, identified as Canada Geese using mtDNA, have been sampled during the nesting period or in the company of goslings in Canada, with one exception: a family of small white-cheeked geese that was captured in 2006 near Cape Henrietta Maria, Ontario, contained an adult female and two flightless goslings (identified as *B. canadensis* from mtDNA) and an adult male (identified as *B. hutchinsii* from mtDNA; K. F. Abraham pers. comm.). Likewise, evidence of hybridization between Cackling Geese and Canada Geese has not otherwise been reported, though hybridization between small Canada Geese (or Cackling Geese) and Snow Geese (*Chen caerulescens*) has been documented on the west coast of Hudson Bay (Prevett and MacInnes 1973).

We studied patterns of geographic variation in structural size of white-cheeked geese inhabiting coastal areas of southwestern Hudson Bay from northern Manitoba to southern Nunavut to determine the degree of morphological and spatial overlap, if any, between Cackling Geese and Canada Geese in this region. We also compared band-recovery distributions between small-bodied and large-bodied forms to investigate the degree to which they overlapped during the non-breeding period. Although it has often been assumed that hybrids exhibit phenotypic characteristics that are intermediate to those of parental forms, this is not always the case in hybrid zones, where hybrids may have characteristics of either of the parental species (e.g., Jiggins and Mallet 2000, Rohwer et al. 2001, Vallender et al. 2009). In such cases, joint examination of biparentally inherited nuclear DNA (nuDNA) and maternally inherited mtDNA has been important for identifying cases of introgression, and contrasting patterns of inheritance in molecular markers have allowed inference about the direction and incidence of hybridization and differential dispersal by males and females. We examined morphological measurements, microsatellite genotypes, and mtDNA haplotypes of adult birds to aid in species identification and to determine the relative distribution of Canada Geese and Cackling Geese in our study area. In addition, we searched for mismatches between morphological and genetic methods of species identification, using both nuclear DNA and mtDNA, to determine whether there was evidence of current (e.g., presence of F_1 hybrids) or historical (e.g., presence of cytonuclear

genotypes consistent with F_2, backcross or higher filial generations) hybridization between Cackling Geese and Canada Geese within and outside areas of sympatry.

If only Canada Geese occupied coastal areas of Hudson Bay in northern Manitoba and southern Nunavut, we expected to see a gradual decline in structural size of birds with increasing latitude, as has been found for Canada Geese that nest farther south along the coasts of James Bay and Hudson Bay (Leafloor and Rusch 1997). In this case, we would expect mtDNA haplotypes and microsatellite genotypes to match those of large-bodied Canada Geese found in all other studies of Canada Goose genetics to date. If both Cackling Geese and Canada Geese were present, we expected to find evidence of a disjunction in the size distribution of birds, or bimodality, and a corresponding change in their mtDNA haplotypes and microsatellite genotypes, as one species was replaced by another as we sampled northwestward along the coast.

METHODS

Field collections.—We captured Canada Geese and Cackling Geese from 3 to 10 August 2007 in near-coastal areas along Hudson Bay, Canada, between Cape Churchill, Manitoba, and the mouth of the McConnell River in Nunavut (approximately 58°33′N, 93°11′W to 60°43′N, 94°50′W; Fig. 1). The location of each banding drive was recorded using a global positioning system. We captured all groups encountered that consisted of at least four pairs of adult birds and their goslings, and the timing of our activities was intended to be late enough to avoid flightless molt-migrant Canada Geese from elsewhere (e.g., Sterling and Dzubin 1967, Davis et al. 1985), most of which have regained flight capabilities by early August. Molt migrations of non-breeding or failed nesting Canada Geese from southern Canada and the United States occur annually and may involve hundreds of thousands of

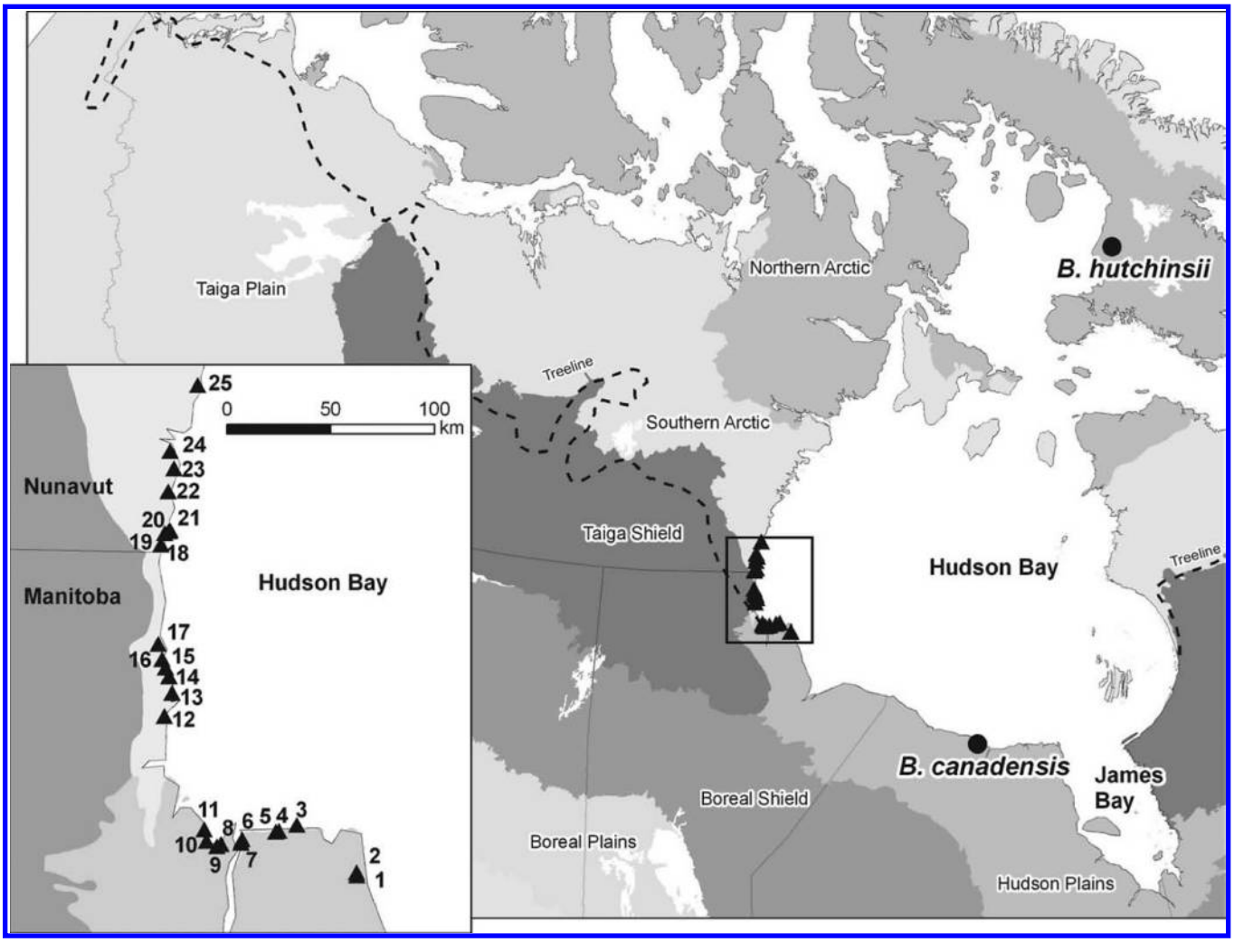

FIG. 1. Capture locations in 2007 of Canada Geese and Cackling Geese along the Hudson Bay coast in northern Manitoba and southern Nunavut. Geese were captured in coastal locations on both sides of the transition area between Southern Arctic and Taiga Shield ecozones, which coincided with a zone of overlap between Canada Geese and Cackling Geese, between 59° and 60° latitude. Source of parental populations for BAPS and STRUCTURE analyses are shown in northern Ontario for Canada Geese, and on Baffin Island for Cackling Geese.

geese (e.g., Abraham et al. 1999, Luukkonen et al. 2008), but we avoided capturing molt migrants to ensure that our results applied only to locally nesting birds. The sex of each bird was determined by cloacal characteristics (later confirmed by genetic analysis; see beyond), and all birds received standard aluminum leg bands. Band size for adult birds was determined on the basis of our general impression of body size, with birds deemed to be small receiving size-7B bands, and large birds receiving size-8 bands. In cases where it was difficult to decide, we made a judgment based on the size of the majority of the birds in the flock. In most cases, birds tended to be either all large or all small within a given flock, with only a few exceptions (J. Leafloor unpubl. data). Of 518 adults for which we had complete morphological data, our chosen band size agreed with our phenotypic classification of the two species based on skull length (see below) in all but five cases, indicating that we could identify most geese to species by physical appearance alone. A blood quill was collected from the secondary coverts of all adult birds and stored in a buffer solution (Longmire et al. 1993) at ambient temperature for later genetic analysis. One person (T. J. Moser) measured culmen length, head length, and length of the tarsus bone of all adult birds to the nearest 0.1 mm according to Dzubin and Cooch (1992), and all birds were released together after banding. These univariate measures are all positively correlated with skeletal volume and other multivariate measures of body size (Moser and Rusch 1988, Moser and Rolley 1990), and skull length has previously been used to differentiate between taxonomic or other geographic groups of Canada Geese (Moser and Rolley 1990, Merendino et al. 1994, Leafloor and Rusch 1997).

DNA extraction.—DNA was extracted from all samples using DNeasy extraction kits (Qiagen, Valencia, California). DNA concentrations were determined using fluorimetry, and all DNA samples were diluted to a working concentration of 20 ng μL^{-1} for genotyping. All DNA samples were stored at –20°C until genotyping was performed. Sex of all adult birds was verified using the chromo-helicase-DNA-binding (CHD) locus (Griffiths et al. 1998) with males being identified by the presence of one amplified band (two introns of the same size) and females by two bands (two introns of different sizes).

Microsatellite genotyping.—Eight polymorphic microsatellite loci were used for subsequent analyses. Loci included Bcaμ1, Bcaμ7, Bcaμ9, Bcaμ11, Hhiμ1 (Buchholz et al. 1998); TTUCG1, TTUCG5, (Cathey et al. 1998); and CR-G (A. Baker pers. comm.). 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^{-1} gelatin, 0.01%NP-40, 0.01% Triton-X 100), 0.5 U of AmpliTaq DNA Polymerase (Perkin-Elmer, Waltham, Massachusetts), 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, Coralville, Iowa). 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, South San Francisco, California) after electrophoresis on denaturing 6% acrylamide gels. Genotypes were based on 20-base-pair (bp) standards and reference samples of known allelic size.

Mitochondrial DNA sequencing.—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 an 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), and sequenced using SequiTherm Excel DNA sequencing kits (Epicentre, Madison, Wisconsin) by following manufacturer's protocols for use of fluorescently labeled primers.

Admixture analysis using microsatellites.—We used Bayesian admixture analyses to estimate the proportion of each individual's genotype, with unknown taxonomic status, that was attributable to each of the parental species (i.e., Canada Geese or Cackling Geese), and to examine the degree of overall mixed ancestry. We used a sample of Canada Geese (n = 54) from the Hudson Bay coast of northern Ontario (approximate coordinates 55.1°N, 83.4°W) and a sample of Cackling Geese (n = 86) from western Baffin Island (approximate coordinates 66.8°N, 72.5°W) as baseline populations to assign unknown female individuals from our study area to their respective species (Fig. 1). We first examined deviations from Hardy-Weinberg equilibrium (HWE) and calculated allelic diversity, observed heterozygosity, and genetic differentiation (F_{ST}) of the baseline populations using GENALEX, version 6.3 (Peakall and Smouse 2006). Probabilities of assignment (q) of unknown individuals to baseline populations were calculated in STRUCTURE (Pritchard et al. 2000) using the admixture analysis option with the correlated allele frequency model, k = 2, and a Markov chain Monte Carlo burn-in of 100,000 steps and 1 million steps after the burn-in. We used the USEPOPINFO model to specify the population of origin of the baseline samples, while keeping the birds from our study area as unknown origin. Under this model, STRUCTURE is forced to treat the baseline populations as pure (not admixed) individuals, while assigning a proportion of each unknown individual to the baseline populations. For comparative purposes, we performed a similar admixture analysis in BAPS, version 5.2 (Corander et al. 2008), with k = 2 and with the above reference populations as baselines. Both of these programs use model-based Bayesian approaches to assign individuals to baseline populations, yet with slightly different algorithms (Corander and Marttinen 2006). BAPS performs a further simulation analysis to test the significance of each individual's admixture. We used 200 iterations to estimate the admixture coefficients and simulated 200 reference individuals with 200 iterations each for significance testing in BAPS.

Geographic patterns of morphological variation, and identification of hybrids.—We examined the geographic distribution of morphological variation, mtDNA haplotypes, and microsatellite genotypes for evidence of hybrid individuals and to clarify the distribution and degree of overlap between Cackling Geese

and Canada Geese within our study area. On the basis of the bimodal distribution of skull lengths that we found, adult females were categorized as having a *hutchinsii* phenotype if their skull length was ≤100 mm, and as *canadensis* if skull length was >100 mm (Fig. 2). For adult males, we classified those with skull lengths ≤104 mm as Cackling Geese, and those with skull lengths >104 mm as Canada Geese.

Mitochondrial DNA provides diagnostic markers for the identification of allopatric Canada Geese and Cackling Geese, and mtDNA differences are correlated with differences in body size between species (Shields and Wilson 1987, Van Wagner and Baker 1990, Shields and Cotter 1998, Paxinos et al. 2002, Scribner et al. 2003b), so we expected that in the absence of hybridization, small birds would have mtDNA haplotypes associated with Cackling Geese, and that large birds would have mtDNA haplotypes associated with Canada Geese. We compared species assignments based on mtDNA to morphological and microsatellite species assignments to examine potential introgression. Potential hybrids were determined to be those individuals that were either identified as hybrids by the BAPS analysis (i.e., when species assignment was equivocal based on microsatellite allele frequencies) or whose species assignment differed between the mtDNA or nuDNA and morphometric data (i.e., genotype–phenotype mismatches). In most phenotypic comparisons, we excluded males in order to

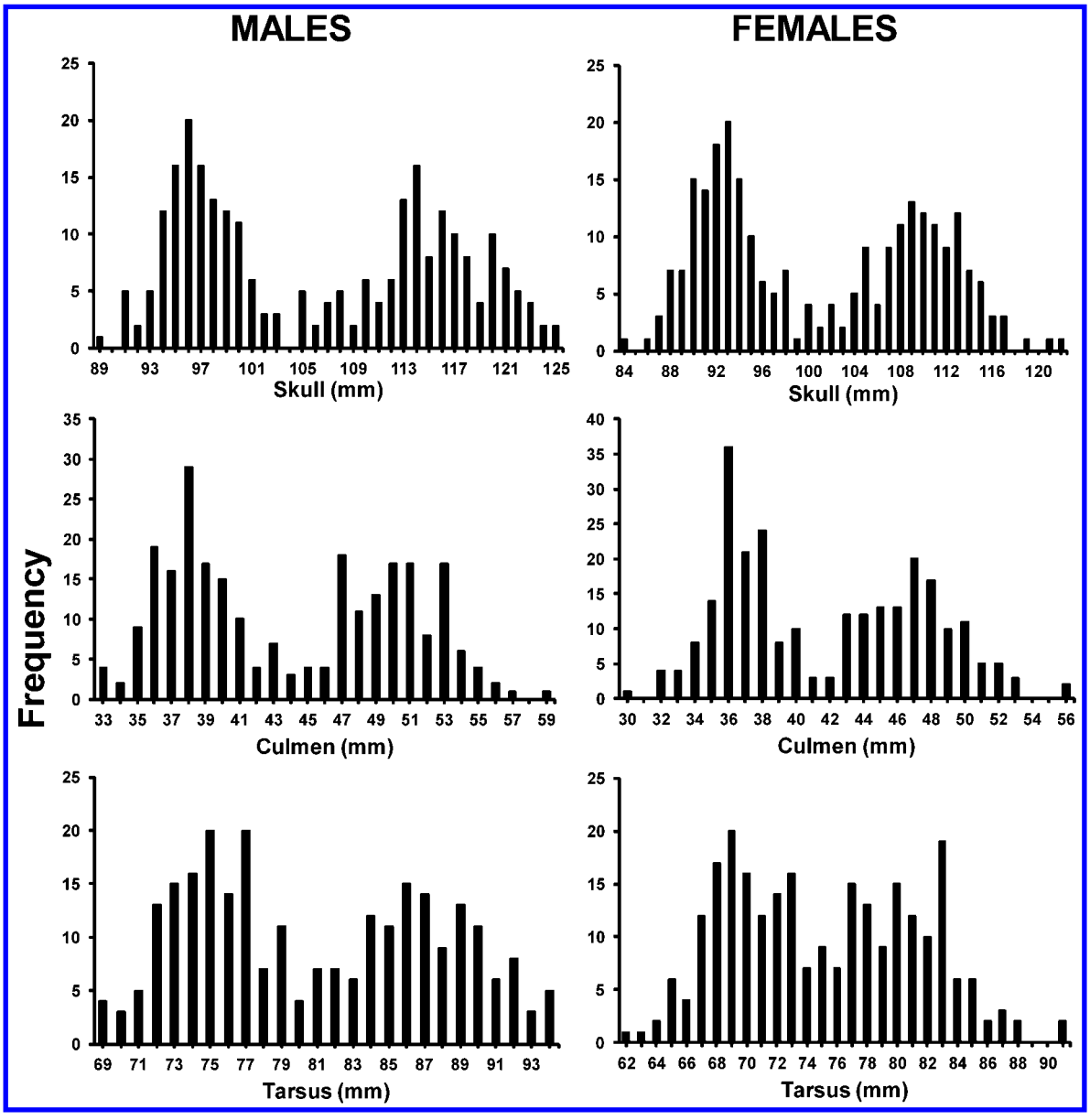

FIG. 2. Frequency distributions of morphometric measurements of adult male (n = 259) and female (n = 259) Canada Geese and Cackling Geese from geese measured in near-coastal areas along Hudson Bay, Canada, between Cape Churchill, Manitoba, and the mouth of the McConnell River in Nunavut. All measurements were rounded to the nearest millimeter.

reduce overlap among size classes of birds, and thereby controlled for any confounding issues related to sexual dimorphism.

Degree of spatial autocorrelation.—To test for patterns of spatial genetic structure at the individual level, we performed multilocus spatial autocorrelation analyses, following the methods of Smouse and Peakall (1999) in GENALEX, version 6.3 (Peakall and Smouse 2006). This technique calculates an autocorrelation coefficient (*r*) for individuals collected within the bounds of predefined distance classes. Under a model of restricted dispersal, the expectation is that genetic and geographic distance will be positively autocorrelated at short distances. We tested for significance using 9,999 random permutations of the data, and 95% confidence intervals for estimates of *r* were determined by 9,999 bootstraps. Ten distance classes at 20-km intervals were used. We performed analyses for all individuals and for each sex separately, to test for any patterns of sex-biased dispersal. In addition, we plotted the geographic distribution of band recoveries from hunter-shot birds and birds found dead to determine the extent of overlap that existed among large-bodied and small-bodied birds during fall and winter.

RESULTS

We captured and measured 518 adult geese and banded another 815 goslings in 25 banding drives along the Hudson Bay coast of northern Manitoba and southern Nunavut (Fig. 1). Gaps in the distribution of captured birds were areas where no brood flocks were found, despite repeated visits to all portions of our study area. On the basis of frequency distributions of morphometric measurements of adult birds, there appeared to be two size phenotypes present on our study area. Bimodality was evident in all three structural measures, and the two groups were most clearly differentiated by their skull lengths (Fig. 2). Of the 259 adult females examined, 128 were classified as Canada Geese on the basis of our skull-length criterion, and 131 were considered Cackling Geese (Table 1). On the basis of mtDNA haplotype ($n = 6$ *canadensis* and 9 *hutchinsii* haplotypes), we classified 118 adult females as Canada Geese and 141 adult females as Cackling Geese.

No microsatellite loci showed consistent deviations from HWE across both baseline populations. The average number of alleles per locus was 8.3 for the *canadensis* baseline population (i.e., those from northern Ontario) and 8.9 alleles locus^{-1} for the *hutchinsii* baseline population (i.e., those from Baffin Island). Observed heterozygosity was moderate ($H_o = 0.67$ for *canadensis*, and 0.68 for *hutchinsii*). Baseline populations showed considerable differentiation, with a significant F_{ST} of 0.05 ($P < 0.017$), from an analysis of molecular variance. We observed 5 mtDNA haplotypes in the *canadensis* baseline from northern Ontario, predominated by a haplotype (A) that was commonly observed in large-bodied subspecies in western North America (Scribner et al. 2003b). We observed 12 mtDNA haplotypes in the *hutchinsii* baseline from Baffin Island. Four haplotypes (L, S, U, and P) that were found in the majority of the birds sequenced (57%) have previously been described in small-bodied subspecies in western North America (Scribner et al. 2003b). Estimates of sequence divergence between all *canadensis* and *hutchinsii* haplotypes was ≥7%, and no haplotypes were shared between baselines (see Appendix 1 for microsatellite allele and mtDNA haplotype frequencies, and Appendix 2 for mtDNA haplotype sequences; see Acknowledgments).

In the STRUCTURE analysis, 59 of 259 females (22.7%) had probabilities of assignment to either species that ranged from 0.4 to 0.6, which suggests considerable admixture (Fig. 3A). BAPS assigned species status to 250 adult females with 100% probability (105 as *B. canadensis* and 145 as *B. hutchinsii*; Fig. 3B). Only nine individuals were assigned by BAPS as having considerable admixed ancestry, two of which were significantly admixed at $P < 0.05$, and another four showed significant admixture at $P < 0.1$.

Species identification based on skull length, mtDNA haplotype, and microsatellite allele frequencies (BAPS results) were all in agreement for 156 of 259 (60%) adult females examined. Phenotype and mtDNA species assignments were consistent for 204 of 259 females (79%); nuDNA and mtDNA were consistent in 174 of 259 females (67%); nuDNA and phenotype were in agreement for only 99 of 259 females (38%). Sixteen females identified as Cackling Geese by their mtDNA haplotypes were classified as Canada Geese according to their skull length, and 39 females identified as Canada Geese by their mtDNA haplotypes had skull lengths ≤100 mm that are characteristic of adult female Cackling Geese (Fig. 4). Mismatched individuals identified by mtDNA as Canada Geese were found among all size classes of phenotypic Cackling Geese, but mismatched individuals identified by mtDNA as Cackling Geese were limited to the smaller size classes of phenotypic

TABLE 1. Frequency of adult female Canada Geese (*canadensis*) and Cackling Geese (*hutchinsii*) from samples taken in 2007 from near-coastal areas along Hudson Bay, Canada, between Cape Churchill, Manitoba, and the mouth of the McConnell River in Nunavut. Individuals are identified according to phenotype, mtDNA haplotype, and nuDNA (based on microsatellite allele frequencies; birds with evidence of considerable admixture from BAPS analysis in parentheses) in three portions of the study area in northern Manitoba and southern Nunavut.

	Phenotype		mtDNA haplotype		nuDNA	
Latitude	*canadensis*	*hutchinsii*	*canadensis*	*hutchinsii*	*canadensis*	*hutchinsii*
60°N to 61°N ($n = 89$)	1	121	4	118	19	101 (2)
59°N to 60°N ($n = 48$)	39	9	28	20	22 (2)	24
58°N to 59°N ($n = 122$)	88	1	86	3	64	21 (4)
Total	128	131	118	141	107	152

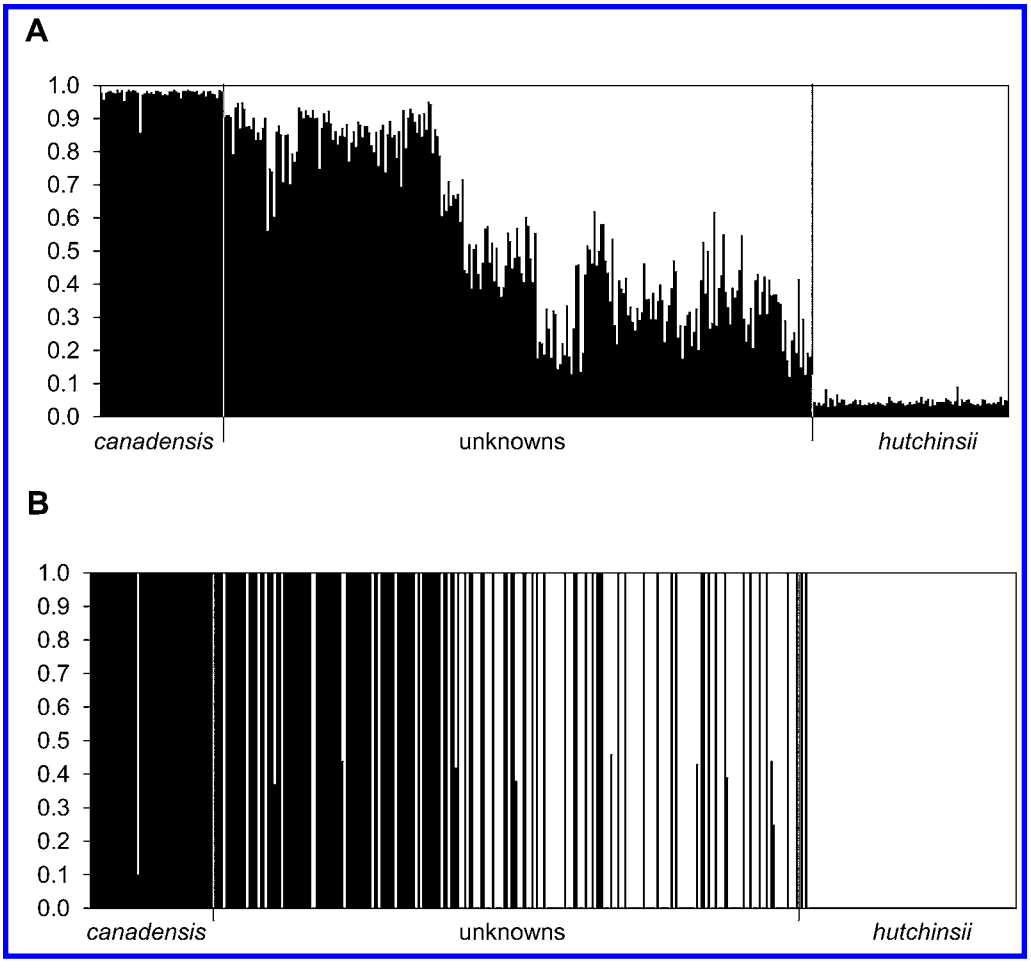

FIG. 3. Bar plots of the posterior probabilities of assignment of individuals to *Branta canadensis* (black) or *B. hutchinsii* (white), based on admixture analyses from (A) STRUCTURE and (B) BAPS. Each vertical bar represents an individual; baseline populations are on the left and right sides of the figures; and unknowns are arranged by sampling site, in an approximate southeast to northwest direction along the *x*-axis.

Canada Geese (Fig. 4A). Mismatches between phenotypic and nuDNA species assignments were more evenly distributed across all size classes of birds, and birds identified statistically as having considerable admixture in the BAPS analysis were found in both phenotypic groups (Fig. 4B).

Geographic distribution of the two phenotypes was clearly nonrandom on our study area, with Cackling Goose phenotypes predominating in coastal areas north of the Nunavut–Manitoba border at 60°N latitude. Only one adult female with a Canada Goose phenotype was captured north of 60°N (Fig. 5A), and of the four adult males with a Canada Goose phenotype that were captured north of 60°N, the northernmost was at 60°06′N. Canada Goose phenotypes predominated in areas south of 59°N latitude; only one adult female with a Cackling Goose phenotype was found south of 59°N, and a mixture of phenotypes was present in four of six flocks captured between 59°N and 60°N latitude (Table 1 and Fig. 5A). Among males with a Cackling Goose phenotype, only five were captured south of 60°N, and the southernmost was at 59°30′N.

Geographic distribution of species identified by their mtDNA haplotypes differed somewhat from phenotypic distributions. There was evidence of introgression of Canada Goose mtDNA in seven of eight flocks captured north of 60°N latitude, and evidence of introgression of Cackling Goose mtDNA in seven of 14 flocks captured south of 60°N latitude, not all of which was evident on the basis of phenotype alone (Fig. 5B). Species assignments based on BAPS and STRUCTURE analyses also suggested introgression in the nuclear DNA genome, over a wider geographic area than was evident based on distributions of size phenotypes or mtDNA haplotypes (Fig. 5C).

Spatial autocorrelation analysis was consistent with an overall pattern of male-biased dispersal and female natal philopatry. The analysis based on all individuals showed significant local spatial autocorrelation at distance classes of <60 km. However, when separate analyses were done for each sex, there was no significant autocorrelation for males, but significant spatial autocorrelation at distance classes <40 km for females (Fig. 6).

Band-recovery distributions of Cackling Geese and Canada Geese banded during our study suggested little, if any, overlap between species on migration and wintering areas; Cackling Geese were usually recovered farther west during fall and winter than were Canada Geese from our study area (Fig. 7).

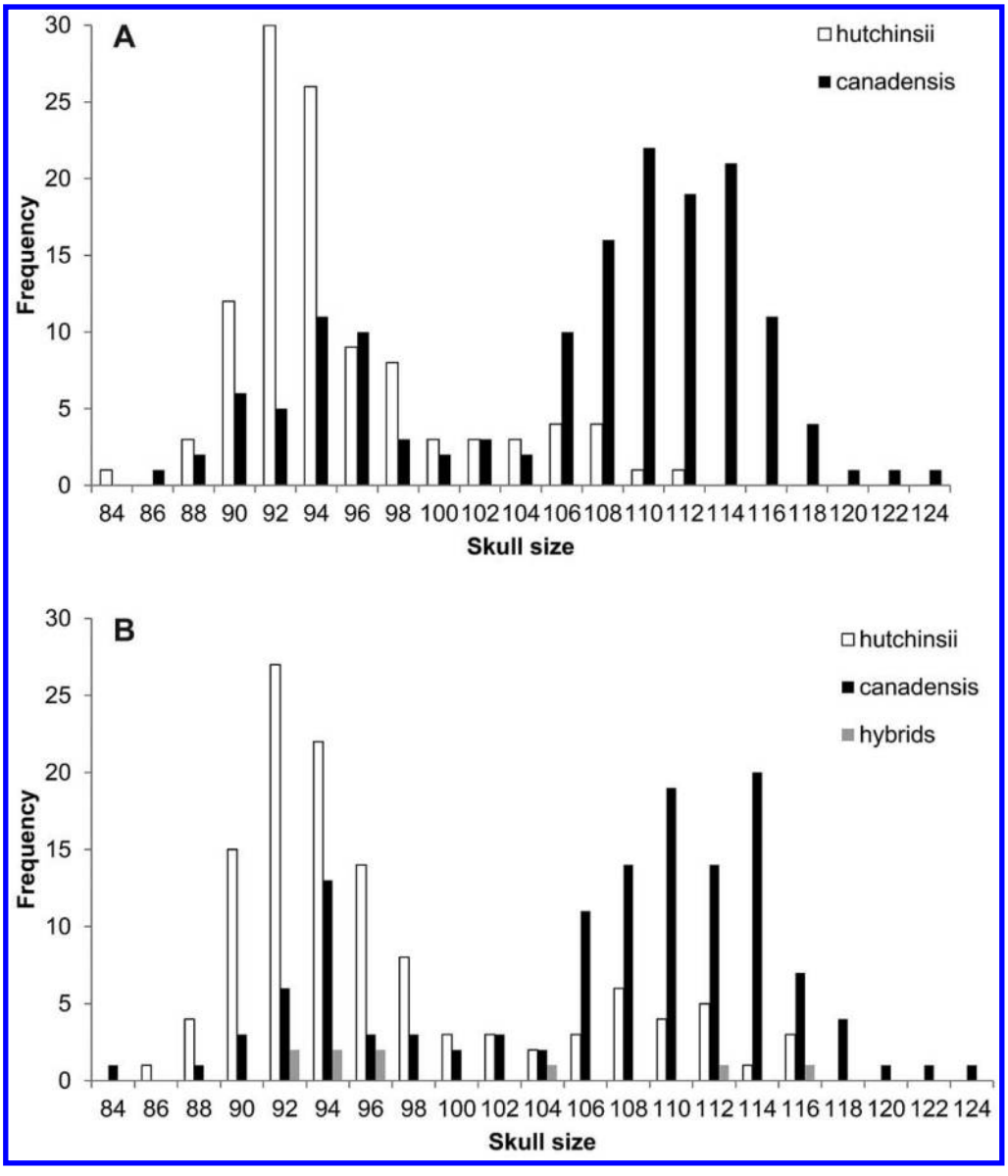

Fig. 4. Frequency distributions of skull lengths for adult female Canada Geese and Cackling Geese showing (A) species assignment based on mtDNA haplotypes and (B) species assignment based on BAPS analysis of microsatellite allele frequencies.

Discussion

Distribution of species and area of overlap.—Most Canada Geese in North America nest between 30°N and 60°N latitude (Mowbray et al. 2002), but some are known to nest north of 60°N along the Tanana River in central Alaska (Scribner et al. 2003b), along some rivers in northern Quebec (Québec Breeding Bird Atlas; see Acknowledgments), and on west Greenland, at least as far north as 67°N (Fox et al. 1996, Malecki et al. 2000, Scribner et al. 2003a). By contrast, Cackling Geese in our study area are among the southernmost nesting birds known for this species, and the vast majority nest well north of 60°N latitude. A few broods of Cackling Geese have been captured during Canada Goose banding drives near the mouth of the Kogaluk River in northern Quebec (approximately 59°38′N) over many years, but there they were rare compared with Canada Geese (J. Hughes, Canadian Wildlife Service, Ottawa, pers. comm.). Likewise, Cackling Geese have only rarely been captured with Canada Geese in coastal areas of northern Manitoba and Ontario, despite annual banding operations and despite tens of thousands of Canada Geese having been banded there since the mid-1970s (K. F. Abraham, F. B. Baldwin, and M. M. Gillespie pers. comm.; J. O. Leafloor pers. obs.; see below). Thus, our study area coincided with the northern periphery of nesting by Canada Geese, and the southern extent of nesting by Cackling Geese in this area.

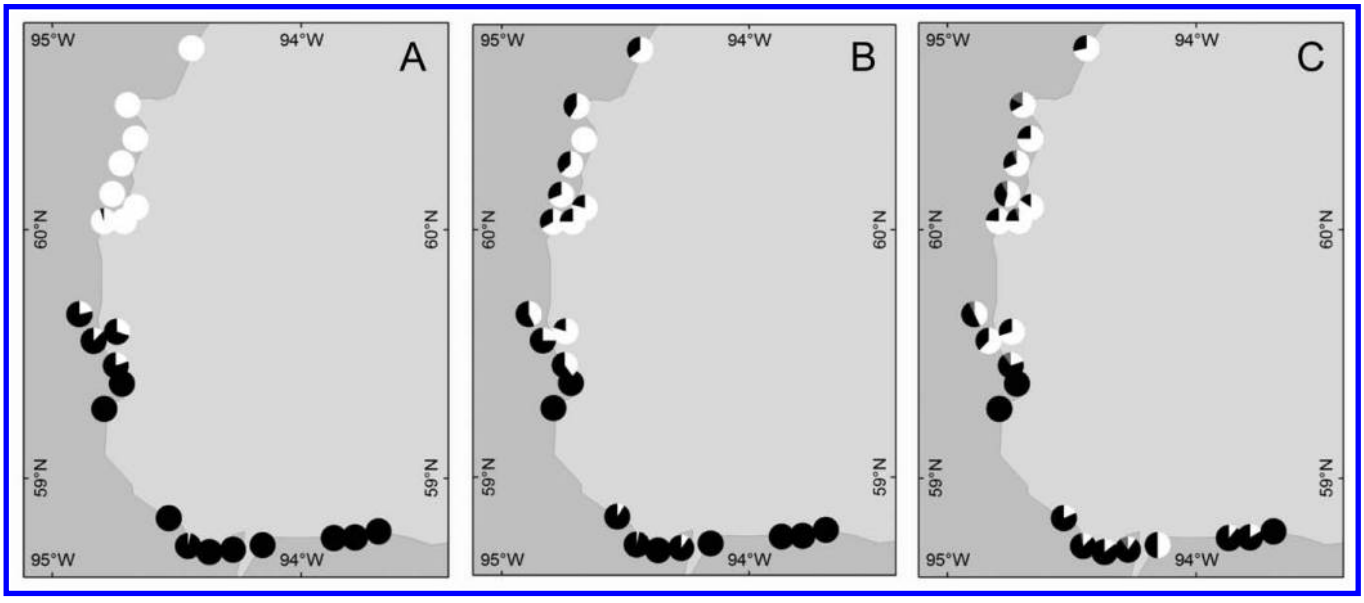

FIG. 5. Geographic distribution and frequency of adult female Canada Geese and Cackling Geese by capture location. Species assignments were based on (A) phenotype (i.e., skull length ≤100 mm = Cackling Goose; skull length >100 mm = Canada Goose), (B) mtDNA haplotypes, and (C) BAPS analysis of microsatellite allele frequencies. Black = Canada Goose, white = Cackling Goose, and gray = probable hybrids identified by BAPS analysis.

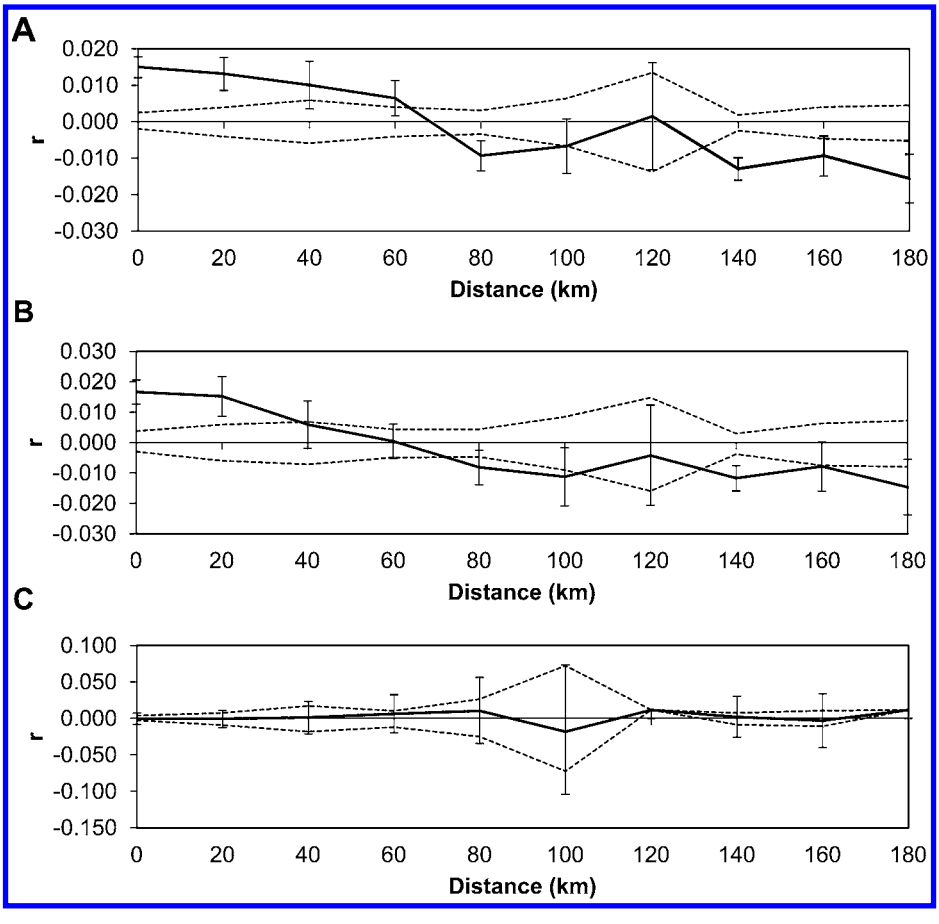

FIG. 6. Correlograms of correlation coefficients (*r*) of geographic and genetic distance at variable distance classes for (A) all geese, (B) females only, and (C) males only. Upper and lower error bars are bound by 95% confidence intervals around each *r*, and dashed lines indicate 95% confidence limits around the null hypothesis of a random spatial distribution of genotypes.

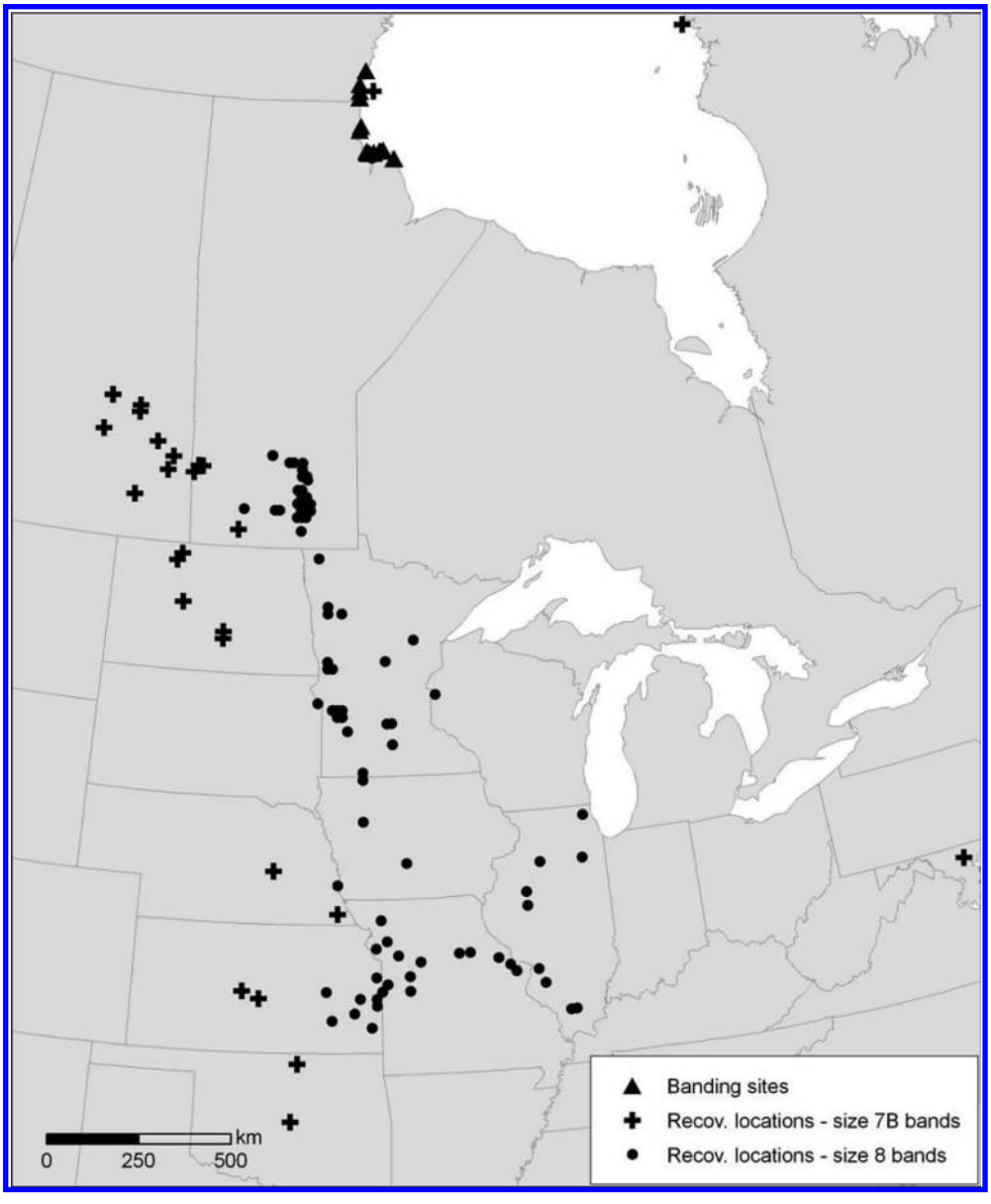

Fig. 7. Band-recovery distributions of Canada Geese and Cackling Geese banded along the Hudson Bay coast of northern Manitoba and southern Nunavut in August 2007. All recoveries (n = 161) were hunter-shot birds or birds found dead between August 2007 and November 2010.

In the distribution of large- and small-bodied phenotypes that we found, Canada Geese tended to occur most commonly in coastal areas of northern Manitoba but overlapped with Cackling Geese in a relatively narrow region on the southwest coast of Hudson Bay between 59°N and 60°N latitude. North of the Nunavut–Manitoba border at 60°N, Cackling Geese predominated. The presence of Cackling Goose mtDNA haplotypes in large-bodied birds was limited mainly to the area of overlap, but Canada Goose haplotypes were found in small-bodied birds over a wider geographic area that extended northward to our northernmost banding site, at approximately 60°44′N latitude. Thus, introgression in the mtDNA genome appeared to be somewhat directional and was more likely to involve dispersal of Canada Goose mtDNA haplotypes into nesting areas north of 60°N rather than dispersal of Cackling Goose mtDNA haplotypes to nesting areas south of 59°N latitude. None of these mismatched individuals was identified statistically as a first-generation hybrid by the BAPS analysis. Despite this pattern, we captured only one Canada Goose female north of 60°N and one Cackling Goose female south of 59°N that were identifiable on the basis of phenotype. Presence of Canada Goose mtDNA haplotypes north of 60°N, and of Cackling Goose mtDNA haplotypes south of 59°N, may be largely a result of backcrosses between hybrid offspring and parental species in their respective nesting ranges. We elaborate on this hypothesis below.

It is possible that in years when spring phenology is early, the area of overlap between Cackling Geese and Canada Geese widens as more Canada Geese disperse northward to nest. Our study area encompassed an ecotone between Southern Arctic and Taiga Shield ecozones (Fig. 1), and spring phenology is obviously influenced by patterns of snow disappearance in this area (Appendix 3; see Acknowledgments), so Canada Geese may not disperse north of 60°N in most years, unless spring conditions arrive early enough to allow nesting. Cackling Geese, on the other hand, arrive on nesting areas later in spring than do most Canada Geese, and presumably are adapted to shorter growing seasons associated with many Arctic environments. Most Cackling Geese nest later than most Canada Geese to the south, and yet Cackling Geese usually do not appear to nest outside of the Arctic ecozones, even though suitable nesting habitat is available, particularly in coastal areas to the south.

Patterns of spatial genetic structure were consistent with female natal philopatry and male-biased dispersal, though we found little contemporary evidence of dispersal by males or females between areas occupied by Canada Geese and Cackling Geese, respectively, based on either the geographic distribution of small- and large-bodied phenotypes or based on location of statistically identified first generation hybrids. Leafloor (1998) examined 20 years of banding records for Canada Geese captured in coastal areas of northern Ontario and found that both males and females banded as goslings tended to be recaptured in later years within ~20 km of their initial capture location. Despite similar recapture patterns, males were recaptured at lower rates than were females, and Leafloor (1998) suggested that although males tended to be philopatric to the natal area in general, they dispersed farther, on average, than females. This pattern was consistent with the spatial autocorrelation analyses conducted for males and females separately (Fig. 6), and this could partly explain why evidence of hybridization appeared to be more widespread on the basis of nuDNA frequencies rather than the distribution of mtDNA haplotypes (i.e., parental males or male hybrids tended to disperse farther than parental females or female hybrids).

We think that it is more likely that the hybrid zone has moved over time and that the distribution of Canada Goose haplotypes north of 60°N is an indication that Canada Geese have nested farther north in the past than most do now. Reports of large-bodied Canada Geese nesting on Southampton Island in the early 1900s were anecdotal, and no large-bodied Canada Geese were collected while they were nesting (e.g., Sutton 1932), but it is possible that nesting by large-bodied Canada Geese could have occurred farther north during warmer periods, and that hybridization with Cackling Geese may also have occurred farther north than present-day distributions of the two species might suggest. The persistence of Canada Goose mtDNA haplotypes among small-bodied geese in the Arctic may be the "ghost" of historical hybridization events, similar to the situation described by Rohwer et al. (2001) of a moving hybrid zone between two species of warblers in western North America. This hypothesis is consistent with what is known about climatic changes that have occurred in this area (see below).

Bryson et al. (1969) used radiocarbon isochrones to map approximate dates of deglaciation following the retreat of the Laurentide ice sheet in eastern North America over the past 13,000 years, and their map indicates that our coastal study area was probably covered by ice until 7,000–7,500 years BP. By 6,000 years BP, ice had retreated ~200 km inland from the Hudson Bay coast, and all of the Hudson Bay coast and the northern mainland coast of Canada was ice free by then (Bryson et al. 1969). During the last glacial maximum, Cackling Geese were thought to nest in Arctic refugia located in Beringia, north and west of mainland North America, whereas most Canada Geese were thought to be isolated in areas south of the Laurentide ice sheet and in coastal areas of western North America (Ploeger 1968). If this was indeed the case, then Canada Geese and Cackling Geese can be only recent inhabitants of much of the area around Hudson Bay (MacInnes 1966), and secondary contact between the two species has probably occurred here only within the past 6,000 years at most. During this time, there is evidence from radiocarbon dating of podzol soils associated with forest cover to suggest that the forest extended as much as 280 km north of the present tree line, to at least 63°N, and persisted there until about 1,500 years BP (Bryson et al. 1965, Sorenson et al. 1971). The presence of charcoal on podzol soils suggested that following fires at about 1,500 years BP, the forest apparently failed to regenerate, and the tree line retreated south of Ennadai Lake, Nunavut (60°45′N, 101°W), after which it again advanced northward to about 61°30′N or 62°N by 1,000 years BP. Movement of the tree line northward was thought to be associated with periods of milder climate (Bryson et al. 1965), and under such conditions, it is plausible that the nesting range of Canada Geese extended farther north along the Hudson Bay coast than it does now. Cackling Geese would have nested north of the tree line at that time, and thus it is likely that secondary contact first occurred in the Arctic–sub-Arctic ecotone north of the present area of overlap.

Hybridization and maintenance of the hybrid zone.—The timing of pair formation can have important implications for gene flow and the genetic structuring of goose populations (Anderson et al. 1992, Ely and Scribner 1994). For hybrid pairs to form, Canada Geese and Cackling Geese must choose mates at a time of year when the two species overlap in time and space, and our data suggest that pair formation is unlikely to occur during fall or winter, because large- and small-bodied birds from our study area overlapped little, or not at all, during that time (Fig. 7). MacInnes (1966) suggested that pair formation in Canada Geese (Cackling Geese) occurred in spring, during northward migration when birds from many nesting areas were mixed together, but other authors have suggested that pair formation likely occurred on the breeding grounds among birds from the same or nearby natal areas (e.g., Hanson 1965), and that natal philopatry by both sexes and pairing on natal areas promoted the geographic structuring of morphological variation in Canada Geese (Leafloor 1998). Even if pairing occurred at other times of year, associations formed on nesting areas may be maintained throughout the year by the strong migratory traditions and social structure of Canada Geese (e.g., Raveling 1978, 1979), and as a result most pairs are likely to consist of birds from the same nesting areas, as occurs in Barnacle Geese (*Branta leucopsis*; Owen et al. 1988, Choudhury and Black 1994). By contrast, Lesser Snow Geese (hereafter "Snow Geese") are thought to pair mainly in winter, when birds from many nesting colonies are mixed, and males usually follow females to their natal colony (Cooke et al. 1975). Even though female-biased natal philopatry is the norm in Snow Geese, occasionally females also disperse and nest at non-natal colonies (Geramita and Cooke 1982). As a result, there is considerable gene flow among

nesting colonies of Snow Geese, and little evidence of morphological differences among birds from different colonies (Cooke et al. 1975). Winter pair formation also explains the geographically widespread occurrence of hybrids between Snow Geese and the closely related Ross's Goose (*Chen rossii*; Trauger et al. 1971).

Lack of geographic variation in morphology of Snow Geese differs greatly from patterns of geographic variation present in Canada Geese and Cackling Geese, which both vary clinally in size (MacInnes 1966, Leafloor and Rusch 1997, J. Leafloor unpubl. data), and suggests that gene flow in white-cheeked geese may be much more restricted than it is in Snow Geese because pairing usually occurs on or near natal areas. Restricted gene flow would be further reinforced by high rates of natal philopatry in both sexes of white-cheeked geese (Leafloor 1998) and would limit the occurrence of heterospecific pairing to areas where Canada Geese and Cackling Geese nest in sympatry. Our data suggest that barriers to interspecific pair formation between Canada Geese and Cackling Geese are incomplete and that some hybrid pairs have produced viable offspring. At the same time, most birds that we sampled appeared to be pure parental species, given their consistent identification by phenotype, mtDNA haplotype, and microsatellite genotypes, which suggests that hybridization was not as extensive as might be expected if mating were random with respect to species. Furthermore, parental phenotypes and genotypes were nonrandomly distributed across an ecotone between Arctic and sub-Arctic habitats; Canada Geese were mainly associated with sub-Arctic habitats south of 60°N, and Cackling Geese were mainly associated with Arctic habitats north of 60°N. Thus, environmental factors may also play a role in determining range limits and the extent of overlap between these species (Cicero 2004).

MacInnes (1966) suggested that mating was assortative in Canada Geese, given that males were always larger than females in mated pairs, even though larger females were available in the population. If this were strictly the case, we might expect pairing between female Canada Geese and male Cackling Geese to be quite rare, because most female Canada Geese were larger than most male Cackling Geese in our study area. However, the presence of Canada Goose mtDNA haplotypes, which are maternally inherited without recombination, in birds with Cackling Goose phenotypes suggests that some heterospecific mating must have involved Canada Goose females and Cackling Goose males. The reverse scenario, involving male Canada Geese and female Cackling Geese, may be more likely, but we found that introgression of Cackling Goose mtDNA into birds with Canada Goose phenotypes also appeared to be geographically limited.

The presence of Canada Goose mtDNA haplotypes in most flocks in which only phenotypic Cackling Geese were found suggests that introgression has occurred over many generations, but that persistence of these haplotypes is mainly the result of backcrosses between hybrids and Cackling Geese. Conversely, the relative scarcity of Cackling Goose mtDNA haplotypes among phenotypic Canada Geese may be an indication that small-bodied females are at a selective disadvantage in sub-Arctic nesting areas occupied mainly by large-bodied geese. These observations agree with those of MacInnes (1966:551), who said that

> I have already advanced the hypothesis that smaller Canada geese may be favored over larger forms when the summer season is shortened. If this is true, populations living under shorter seasons should consist of smaller geese than those living under less rigorous conditions. Large immigrants coming into the short-season environment will be selected against by climate, while small immigrants moving into longer-season environments will probably be affected only by intraspecific competition.

Thus, the scarcity of Cackling Geese in sub-Arctic nesting areas, despite the availability of apparently suitable habitat, may be a result of competition with Canada Geese. We believe that the area of overlap represents a tension zone between Canada Geese and Cackling Geese (Barton and Hewitt 1989) and is maintained mainly by behavioral and environmental factors that limit effective dispersal.

The hybrid zone that we have identified represents only a tiny fraction of the respective breeding ranges of Canada Geese and Cackling Geese in North America, and we believe that the incidence of hybridization between these species is likely to be limited mostly to areas where Canada Geese and Cackling Geese nest in sympatry. The northern boundary of nesting by Canada Geese and the southern boundary of nesting by Cackling Geese are incompletely known, but it is possible that the two species could come into contact in transitional habitats along the Arctic–sub-Arctic ecotone that stretches across much of northern Canada at the tree line. Information about nesting by either species is very limited in all inland areas north of 60°N between the west coast of Hudson Bay and the Rocky Mountains to the west, and we know of no nesting specimens from which morphological measurements or genetic samples have been taken in this area that might assist in their identification to species. Until such data are collected, knowledge of breeding distributions and the extent of hybridization between Canada Geese and Cackling Geese in Canada will remain incomplete. However, the two species differ greatly in size, have diagnostic differences in their mtDNA, differ in their nuDNA characteristics, and have mostly allopatric breeding ranges that are clearly delineated by climatic zones over much of North America. The existence of a narrow hybrid zone (i.e., type 3 hybridization of Allendorf et al. 2001) between two otherwise evolutionarily distinct lineages should not preclude their recognition as distinct species.

Acknowledgments

Appendices 1-3 are available online at dx.doi.org/10.1525/auk.2013.12196. This research was funded by the Canadian Wildlife Service and U.S. Fish and Wildlife Service through the Arctic Goose Joint Venture. Manitoba Conservation generously provided field accommodations at Cape Churchill. We thank A. Didiuk, M. Gillespie, and G. Ball for identifying our study area as a potential area of overlap between nesting Canada Geese and Cackling Geese, and B. Batt, A. Davidson, M. Gillespie, and T. Moser for field assistance. We thank K. Meeres and M. Schuster for their help with data presentation and figures. K. Abraham, D. Ankney, F. Baldwin, R. Buss, K. Dickson, A. Didiuk, J. Hughes, D. Kellett, C. MacInnes, T. Moser, J. Pearce, and R. Zink provided reviews of earlier drafts and/or helpful discussion. This research was approved under permits issued by the Nunavut Wildlife Management Board, the Canadian Wildlife Service, and the U.S. Fish and Wildlife Service. The Québec Breeding Bird Atlas is at www.atlas-oiseaux.qc.ca/donneesqc/cartes.jsp?lang=en.

Literature Cited

Abraham, K. F., J. O. Leafloor, and D. H. Rusch. 1999. Molt migrant Canada Geese in northern Ontario and western James Bay. Journal of Wildlife Management 63:649–655.

Allendorf, F. W., R. F. Leary, P. Spruell, and J. K. Wenburg. 2001. The problem with hybrids: Setting conservation guidelines. Trends in Ecology & Evolution 16:613–622.

American Ornithologists' Union. 1957. Check-list of North American Birds, 5th ed. American Ornithologists' Union, Washington, D.C.

Anderson, M. G., J. M. Rhymer, and F. C. Rohwer. 1992. Philopatry, dispersal, and the genetic structure of waterfowl populations. Pages 365–395 *in* Ecology and Management of Breeding Waterfowl (B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, Eds.). University of Minnesota Press, Minneapolis.

Baker, A. J., and H. D. Marshall. 1997. Mitochondrial control region sequences as tools for understanding evolution. Pages 51–82 *in* Avian Molecular Evolution and Systematics (D. P. Mindell, Ed.). Academic Press, New York.

Banks, R. C., C. Cicero, J. L. Dunn, A. W. Kratter, P. C. Rasmussen, J. V. Remsen, Jr., J. D. Rising, and D. F. Stotz. 2004. Forty-fifth supplement to the American Ornithologists' Union *Check-list of North American Birds*. Auk 121:985–995.

Barton, N. H., and G. M. Hewitt. 1989. Adaptation, speciation and hybrid zones. Nature 341:497–503.

Brandt, H. 1943. Alaska Bird Trails. Bird Research Foundation, Cleveland, Ohio.

Bryson, R. A., W. N. Irving, and J. A. Larsen. 1965. Radiocarbon and soil evidence of former forest in the southern Canadian tundra. Science 147:46–48.

Bryson, R. A., W. M. Wendland, J. D. Ives, and J. T. Andrews. 1969. Radiocarbon isochrones on the disintegration of the Laurentide ice sheet. Arctic and Alpine Research 1:1–14.

Buchholz, W., J. M. Pearce, B. J. Pierson, and K. T. Scribner. 1998. Dinucleotide repeat polymorphisms in waterfowl (family Anatidae): Characterization of a sex-linked (z-specific) and 14 biparentally inherited loci. Animal Genetics 29:323–325.

Cathey, J. C., J. A. DeWoody, and L. M. Smith. 1998. Microsatellite markers in Canada Geese (*Branta canadensis*). Journal of Heredity 89:173–175.

Choudhury, S., and J. M. Black. 1994. Barnacle Geese preferentially pair with familiar associates from early life. Animal Behaviour 48:81–88.

Cicero, C. 2004. Barriers to sympatry between avian sibling species (Paridae: *Baeolophus*) in local secondary contact. Evolution 58:1573–1587.

Cooke, F., C. D. MacInnes, and J. P. Prevett. 1975. Gene flow between breeding populations of Lesser Snow Geese. Auk 93:493–510.

Corander, J., and P. Marttinen. 2006. Bayesian identification of admixture events using multilocus molecular markers. Molecular Ecology 15:2833–2843.

Corander, J., P. Marttinen, J. Sirén, and J. Tang. 2008. Enhanced Bayesian modelling in BAPS software for learning genetic structures of populations. BMC Bioinformatics 9:539.

Davis, R. A., R. N. Jones, C. D. MacInnes, and A. J. Pakulak. 1985. Molt migration of large Canada Geese on the west coast of Hudson Bay. Wilson Bulletin 97:296–305.

Delacour, J. 1954. The Waterfowl of the World. Country Life, London.

den Hartog, P. M., A. M. den Boer-Visser, and C. ten Cate. 2010. Unidirectional hybridization and introgression in an avian contact zone: Evidence from genetic markers, morphology, and comparisons with laboratory-raised F_1 hybrids. Auk127:605–616.

Dzubin, A., and E. G. Cooch. 1992. Measurements of Geese: General Field Methods. California Waterfowl Association, Sacramento.

Ely, C. R., and K. T. Scribner. 1994. Genetic diversity in Arctic-nesting geese: Implications for management and conservation. Transactions of the North American Wildlife and Natural Resources Conference 59:91–110.

Fox, A. D., C. Glahder, C. R. Mitchell, D. A. Stroud, H. Boyd, and J. Frikke. 1996. North American Canada Geese (*Branta canadensis*) in west Greenland. Auk 113:231–233.

Geramita, J. M., and F. Cooke. 1982. Evidence that fidelity to natal breeding colony is not absolute in female Snow Geese. Canadian Journal of Zoology 60:2051–2056.

Grant, P. R., and B. R. Grant. 1992. Hybridization of bird species. Science 256:193–197.

Griffiths, R., M. C. Double, K. Orr, and R. J. G. Dawson. 1998. A DNA test to sex most birds. Molecular Ecology 7:1071–1076.

Hanson, H. C. 1965. The Giant Canada Goose. Southern Illinois University Press, Carbondale.

Irwin, D. E., S. Bensch, and T. D. Price. 2001. Speciation in a ring. Nature 409:333–337.

Irwin, D. E., A. Brelsford, D. P. L. Toews, C. MacDonald, and M. Phinney. 2009. Extensive hybridization in a contact zone between MacGillivray's Warblers *Oporornis tolmiei* and Mourning Warblers *O. philadelphia* detected using molecular and morphological analyses. Journal of Avian Biology 40:539–552.

Jiggins, C. D., and J. Mallet. 2000. Bimodal hybrid zones and speciation. Trends in Ecology & Evolution 15:250–255.

Kocher, T. D., W. K. Thomas, A. Meyer, S. V. Edwards, S. Pääbo, F. X. Villablanca, and A. C. Wilson. 1989. Dynamics of mitochondrial DNA evolution in animals: Amplification and sequencing with conserved primers. Proceedings of the National Academy of Sciences USA 86:6196–6200.

Leafloor, J. O. 1998. Philopatry, geographic variation in body size, and genetic structure of Canada Geese. Ph.D. dissertation, University of Wisconsin, Madison.

Leafloor, J. O., and D. H. Rusch. 1997. Clinal size variation in Canada Geese affects morphometric discrimination techniques. Journal of Wildlife Management 61:183–190.

Longmire, J. L., N. C. Brown, L. J. Meincke, M. L. Campbell, K. L. Albright, J. J. Fawcett, E. W. Campbell, R. K. Moyzis, C. E. Hildebrand, G. A. Evans, and L. L. Deaven. 1993. Construction and characterization of partial digest DNA libraries made from flow-sorted human chromosome 16. Genetic Analysis: Biomolecular Engineering 10:69–76.

Luukkonen, D. R., H. H. Prince, and R. C. Mykut. 2008. Movements and survival of molt migrant Canada Geese from southern Michigan. Journal of Wildlife Management 72:449–462.

MacInnes, C. D. 1962. Nesting of small Canada Geese near Eskimo Point, Northwest Territories. Journal of Wildlife Management 26:247–256.

MacInnes, C. D. 1963. Interaction of local units within the eastern Arctic population of small Canada Geese. Ph.D. dissertation, Cornell University, Ithaca, New York.

MacInnes, C. D. 1966. Population behavior of eastern Arctic Canada Geese. Journal of Wildlife Management 30:536–553.

MacInnes, C. D., R. A. Davis, R. N. Jones, B. C. Lieff, and A. J. Pakulak. 1974. Reproductive efficiency of McConnell River small Canada Geese. Journal of Wildlife Management 38:686–707.

Malecki, R. A., A. D. Fox, and B. D. J. Batt. 2000. An aerial survey of nesting Greater White-fronted Geese and Canada Geese in west Greenland. Wildfowl 51:49–58.

Mayr, E. 1942. Systematics and the Origin of Species. Columbia University Press, New York.

Merendino, M. T., C. D. Ankney, D. G. Dennis, and J. O. Leafloor. 1994. Morphometric discrimination of giant and Akimiski Island Canada Geese. Wildlife Society Bulletin 22:14–19.

Moser, T. J., and R. E. Rolley. 1990. Discrimination of Giant and Interior Canada Geese of the Mississippi Flyway. Wildlife Society Bulletin 18:381–388.

Moser, T. J., and D. H. Rusch. 1988. Indices of structural size and condition of Canada Geese. Journal of Wildlife Management 52:202–208.

Mowbray, T. B., C. R. Ely, J. S. Sedinger, and R. E. Trost. 2002. Canada Goose (*Branta canadensis*). *In* The Birds of North America, no. 681 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

Owen, M., J. M. Black, and H. Liber. 1988. Pair bond duration and timing of its formation in Barnacle Geese (*Branta leucopsis*). Pages 23–38 *in* Waterfowl in Winter (M. W. Weller, Ed.). University of Minnesota Press, Minneapolis.

Palmer, R. S. 1976. Handbook of North American Birds, vol. 2. Yale University Press, New Haven, Connecticut.

Paxinos, E. E., H. F. James, S. L. Olson, M. D. Sorenson, J. Jackson, and R. C. Fleischer. 2002. MtDNA from fossils reveals a radiation of Hawaiian Geese recently derived from the Canada Goose (*Branta canadensis*). Proceedings of the National Academy of Sciences USA 99:1399–1404.

Peakall, R., and P. E. Smouse. 2006. GENALEX 6: Genetic analysis in Excel. Population genetic software for teaching and research. Molecular Ecology Notes 6:288–295.

Pearce, J. M., and K. S. Bollinger. 2003. Morphological traits of Pacific Flyway Canada Geese as an aid to subspecies identification and management. Journal of Field Ornithology 74:357–369.

Pearce, J. M., B. J. Pierson, S. L. Talbot, D. V. Derksen, D. Kraege, and K. T. Scribner. 2000. A genetic evaluation of morphology used to identify harvested Canada Geese. Journal of Wildlife Management 64:863–874.

Pierson, B. J., J. M. Pearce, S. L. Talbot, G. F. Shields, and K. T. Scribner. 2000. Molecular genetic status of Aleutian Canada Geese from Buldir and the Semidi islands, Alaska. Condor 102:172–180.

Ploeger, P. L. 1968. Geographical differentiation in Arctic Anatidae as a result of isolation during the last glacial. Ardea 56:1–159.

Prevett, J. P., and C. D. MacInnes. 1973. Observations of wild hybrids between Canada and blue geese. Condor 75:124–125.

Pritchard, J. K., M. Stephens, and P. Donnelly. 2000. Inference of population structure using multilocus genotype data. Genetics 155:945–959.

Quinn, T. W., G. F. Shields, and A. C. Wilson. 1991. Affinities of the Hawaiian Goose based on two types of mitochondrial DNA data. Auk 108:585–593.

Raveling, D. G. 1978. Dynamics of distribution of Canada Geese in winter. Transactions of the North American Wildlife and Natural Resources Conference 43:206–225.

Raveling, D. G. 1979. Traditional use of migration and winter roost sites by Canada Geese. Journal of Wildlife Management 43:229–235.

Rohwer, S., E. Bermingham, and C. Wood. 2001. Plumage and mitochondrial DNA haplotype variation across a moving hybrid zone. Evolution 55:405–422.

Scribner, K. T., R. A. Malecki, B. D. J. Batt, R. L. Inman, S. Libants, and H. H. Prince. 2003a. Identification of source population for Greenland Canada Geese: Genetic assessment of a recent colonization. Condor 105:771–782.

Scribner, K. T., S. L. Talbot, J. M. Pearce, B. J. Pierson, K. S. Bollinger, and D. V. Dirksen. 2003b. Phylogeography of Canada Geese (*Branta canadensis*) in western North America. Auk 120:889–907.

Shields, G. F., and J. P. Cotter. 1998. Phylogenies of North American geese: The mitochondrial DNA record. Pages 405–411 *in* Biology and Management of Canada Geese (D. H. Rusch, M. D. Samuel, D. D. Humburg, and B. D. Sullivan, Eds.). Proceedings of the International Canada Goose Symposium, Milwaukee, Wisconsin.

Shields, G. F., and A. C. Wilson. 1987. Subspecies of the Canada Goose (*Branta canadensis*) have distinct mitochondrial DNA's. Evolution 41:662–666.

Smouse, P. E., and R. Peakall. 1999. Spatial autocorrelation analysis of individual multiallele and multilocus genetic structure. Heredity 82:561–573.

Sorenson, C. J., J. C. Knox, J. A. Larsen, and R. A. Bryson. 1971. Paleosols and the forest border in southern Keewatin, N.W.T. Quaternary Research 1:468–473.

Sorenson, M. D., and R. C. Fleischer. 1996. Multiple independent transpositions of mitochondrial DNA control region sequences to the nucleus. Proceedings of the National Academy of Sciences USA 93:15239–15243.

Sterling, T., and A. Dzubin. 1967. Canada Goose molt migrations to the Northwest Territories. Transactions of the North American Wildlife and Natural Resources Conference 32:355–373.

Sutton, G. M. 1932. The exploration of Southampton Island, Hudson Bay. Memoirs of the Carnegie Museum, vol. XII, part II, section 2.

Toews, D. P. L., and D. E. Irwin. 2008. Cryptic speciation in a Holarctic passerine revealed by genetic and bioacoustic analyses. Molecular Ecology 17:2691–2705.

Trauger, D. L., A. Dzubin, and J. P. Ryder. 1971. White geese intermediate between Ross' Geese and Lesser Snow Geese. Auk 88:856–875.

Vallender, R., S. L. Van Wilgenburg, L. P. Bulluck, A. Roth, R. Canterbury, J. Larkin, R. M. Fowlds, and I. J. Lovette. 2009. Extensive rangewide mitochondrial introgression indicates substantial cryptic hybridization in the Golden-winged Warbler (*Vermivora chrysoptera*). Avian Conservation and Ecology 4(2):4.

Van Wagner, C. E., and A. J. Baker. 1990. Association between mitochondrial DNA and morphological evolution in Canada Geese. Journal of Molecular Evolution 31:373–382.

Associate Editor: J. T. Klicka