

A Tale of Two Refugia

How Quaternary fluctuations have shaped conservation and management of Arctic nesting geese in North America

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A very large number of field and laboratory collaborators

ARDEA

TIJDSCHRIFT DER NEDERLANDSE
ORNITHOLOGISCHE UNIE

JAARGANG 56

FEBRUARI 1968

AFLEVERING 1-2

GEOGRAPHICAL DIFFERENTIATION IN ARCTIC
ANATIDAE AS A RESULT OF ISOLATION DURING THE
LAST GLACIAL

by

P. L. PLOEGER

Zoological Museum, University of Amsterdam

“I have confined myself to the last glaciation as this is the only Pleistocene glacial period of which the effects are still to be seen in the present distribution of present geographical forms.” (p. 4).

Geese in Eastern Beringia

- *Anser*

- Lesser Snow Goose (*A. caerulescens caerulescens*): 2 refugia (for the subspecies)
- Greater White-fronted Goose (*A. albifrons*): 5 refugia for the species

- *Branta*

- Cackling Goose (*B. hutchinsii*): 2 refugia
- Canada Goose (*B. canadensis*): 2 refugia
- Black Brant (*B. bernicla nigricans*) 2 refugia for the subspecies

- *Chen*

- Emperor Goose (*Chen canagica*): 1 refugium



Geese in Eastern Beringia

- *Anser*

- Lesser Snow Goose (*A. caerulescens caerulescens*): 2 refugia
- Greater White-fronted Goose (*A. albifrons*): 5 refugia

- *Branta*

- Cackling Goose (*B. hutchinsii*): 2 refugia
- Canada Goose (*B. canadensis*): 2 refugia
- Black Brant (*B. bernicla nigricans*) 2 refugia

- *Chen*

- Emperor Goose (*Chen canagica*): 1 refugium



Geese in North America

Management on Wintering Grounds



Arctic nesting geese aggregating on wintering grounds in Klamath, Oregon

Geese in North America

Management By Flyways



Administrative Flyways



Biological Flyways

Geese in Eastern Beringia



Four species of Arctic-nesting geese captured together in molting flocks on the Yukon-Kuskokwim Delta, Alaska. Photograph by Craig Ely, USGS.

Geese in Eastern Beringia (*Branta*)



White-cheeked geese

- Canada Goose (*Branta canadensis*)
- Cackling Goose (*B. hutchinsii*)



Black Brant
(*Branta bernicla nigricans*)

The Genetics of Species and Subspecies in White-Cheeked Geese: New Data to Inform Management of Pacific Flyway Populations

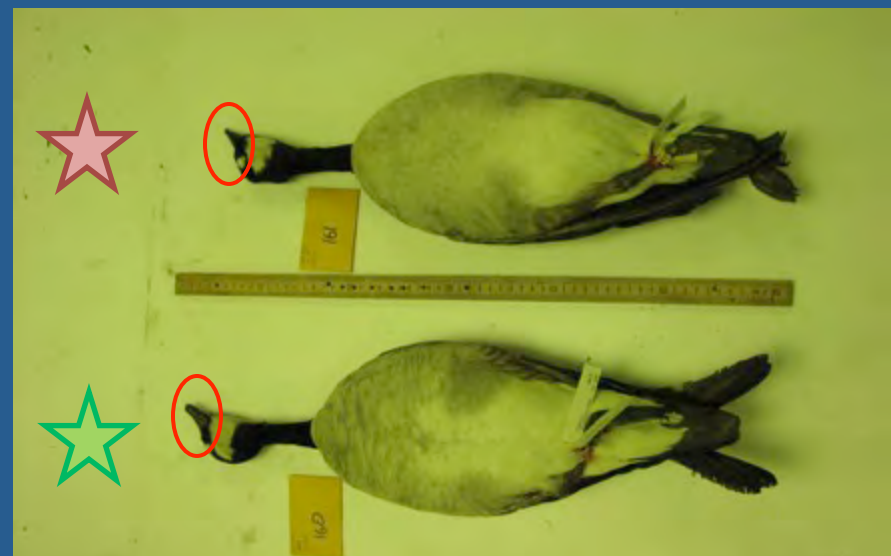
**John M. Pearce, Craig Ely,
Sandra Talbot, Kevin Sage**
*USGS, Alaska Science Center
Anchorage, Alaska*

Jeffrey Peters
*Wright State University
Dayton, Ohio*

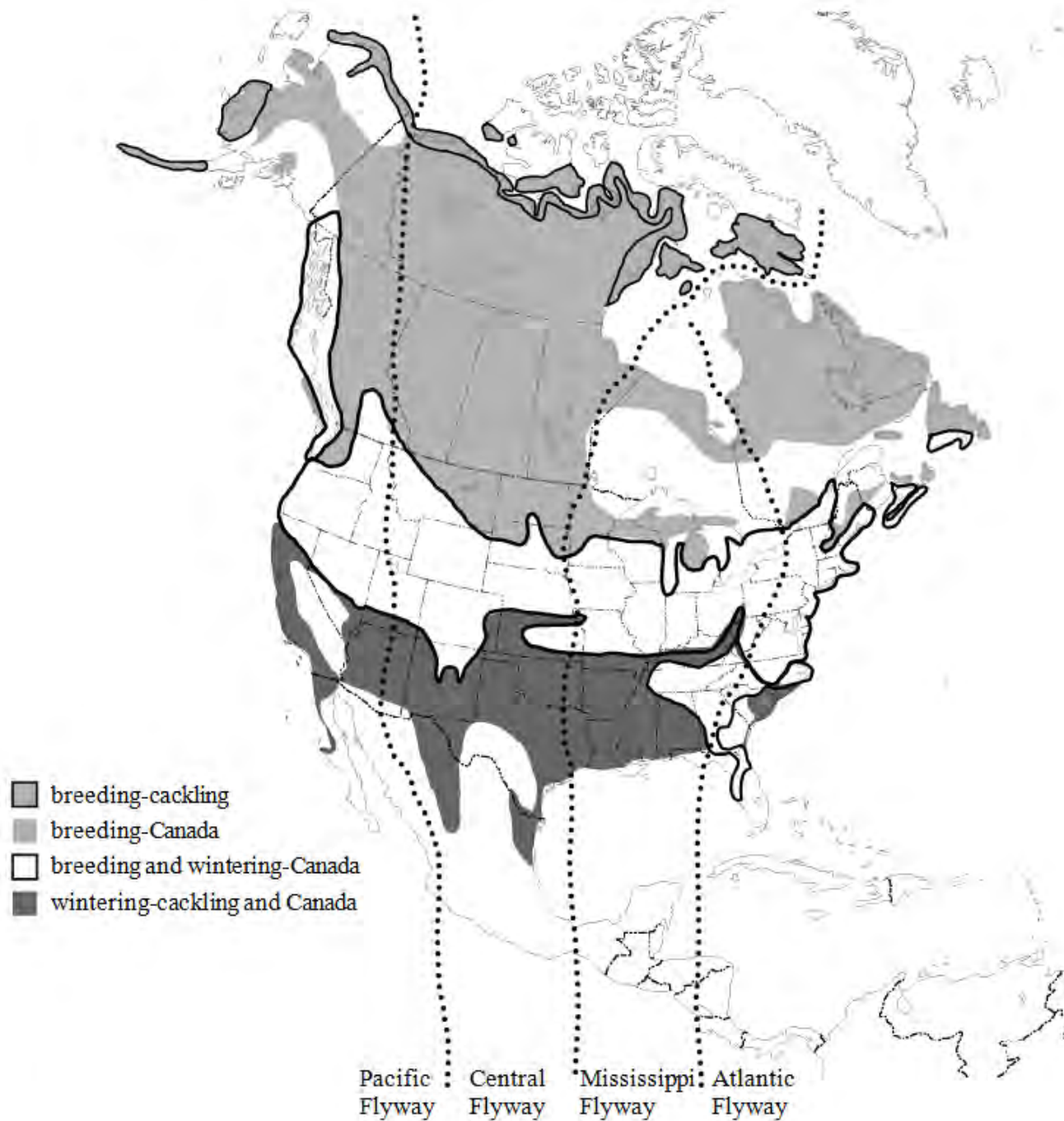


Morphological Variation in Original Species (Canada Geese)

Across 11 subspecies

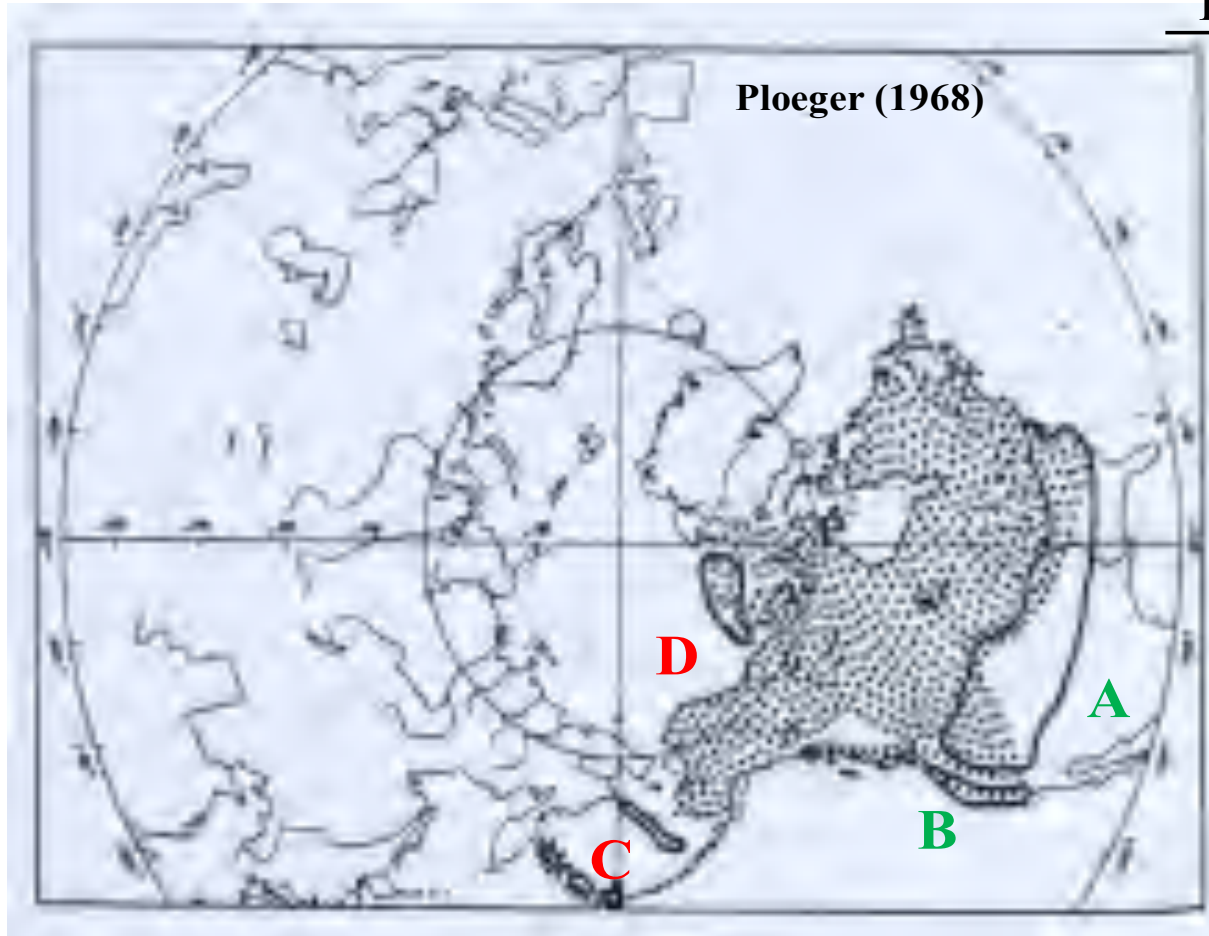


Access to H. Hanson collection provided by the Illinois Natural History Survey



Evolutionary origins of Canada goose phylogeographic diversity¹

Last glacial breeding grounds



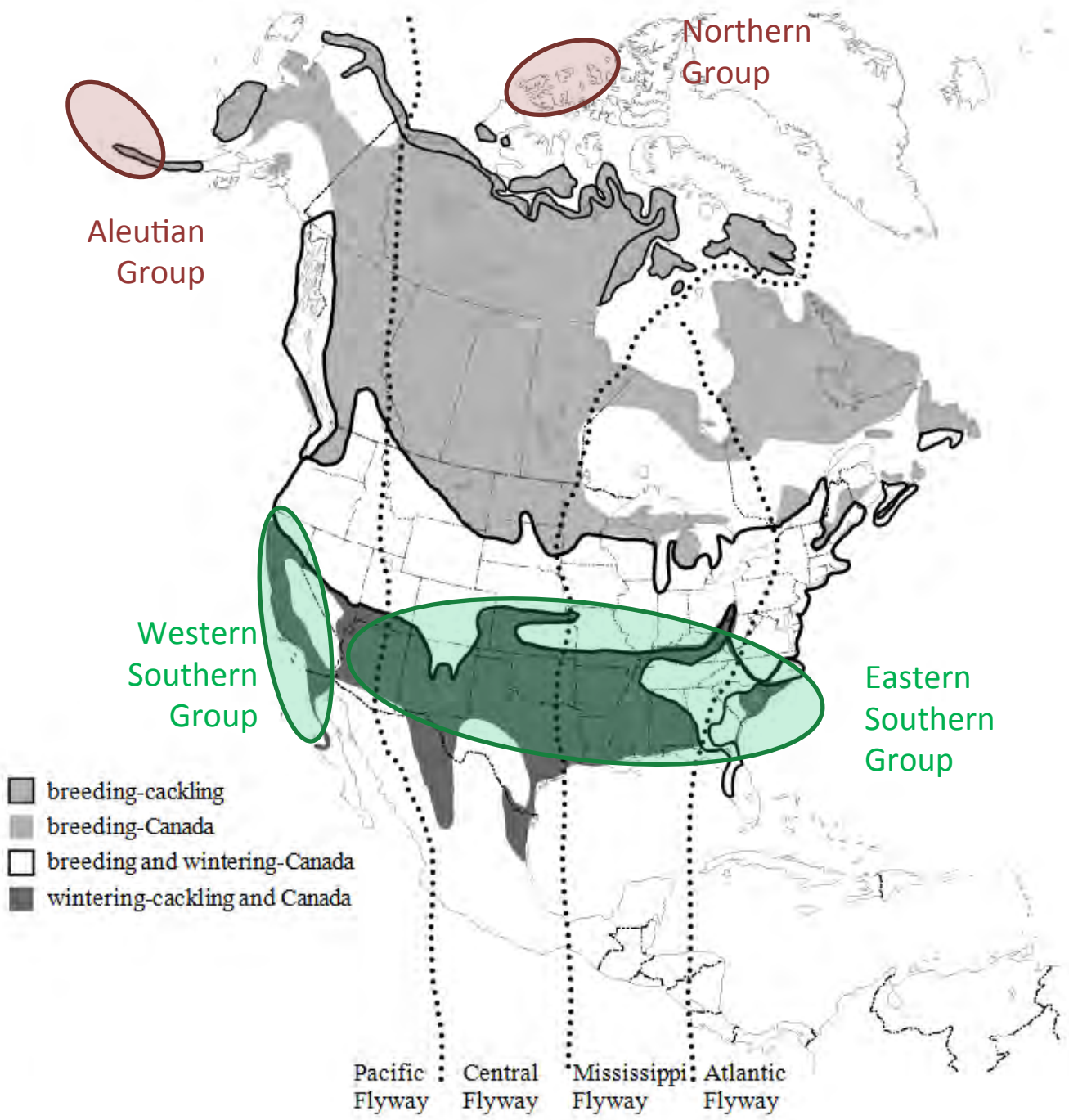
- A. Eastern Southern Group
- *canadensis*
 - *interior*
 - *maxima*
 - *moffitti*
 - *parvipes*

- B. Western Southern Group
- *fulva*
 - *occidentalis*

- C. Aleutian Group
- *leucopareia*
 - *asiatica*

- D. Northern Group
- *minima*
 - *hutchinsi*

¹Subspecies designations after Delacour (1954)



The species split by AOU



The Auk 121(3):985–995, 2004
© The American Ornithologists' Union, 2004.
Printed in USA.

FORTY-FIFTH SUPPLEMENT TO THE AMERICAN ORNITHOLOGISTS' UNION CHECK-LIST OF NORTH AMERICAN BIRDS

RICHARD C. BANKS,^{1,9,10} CARLA CICERO,² JON L. DUNN,³ ANDREW W. KRATTER,⁴
PAMELA C. RASMUSSEN,⁵ J. V. REMSEN, JR.,⁶ JAMES D. RISING,⁷
AND DOUGLAS F. STOTZ⁸

pp. 59–60. Several genetic studies of geese, including recent work with mitochondrial DNA (van Wagner and Baker 1986, Shields and Wilson 1987, Quinn et al. 1991, Paxinos et al. 2002, Scribner et al. 2003) have verified previous suggestions based on differences in voice, nesting habits, habitat, and timing of migration, as well as in color and size (e.g. Brooks 1914, Aldrich 1946, Hellmayr and Conover 1948), that the forms treated as the single species *Branta canadensis* by all previous AOU Check-lists and most other works actually constitute at least two species, and further that each of the two species may be more closely related to another member of the genus than to each other. Thus, we divide *B. canadensis* by recognizing a set of smaller-bodied forms as the species *B. hutchinsii*, and rearrange our representatives of the genus in the sequence *bernicla*, *leucopsis*, *hutchinsii*, *canadensis*, *sandvicensis*. Additional analysis may result in further splitting.

Canada Goose



Canada Goose

B. canadensis

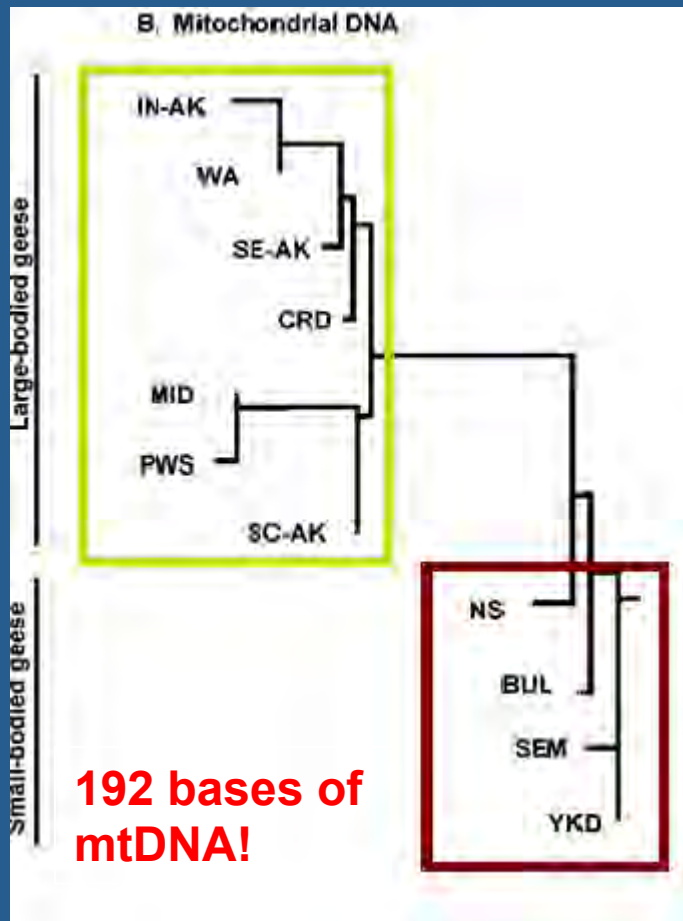
Cackling Goose

B. hutchinsii

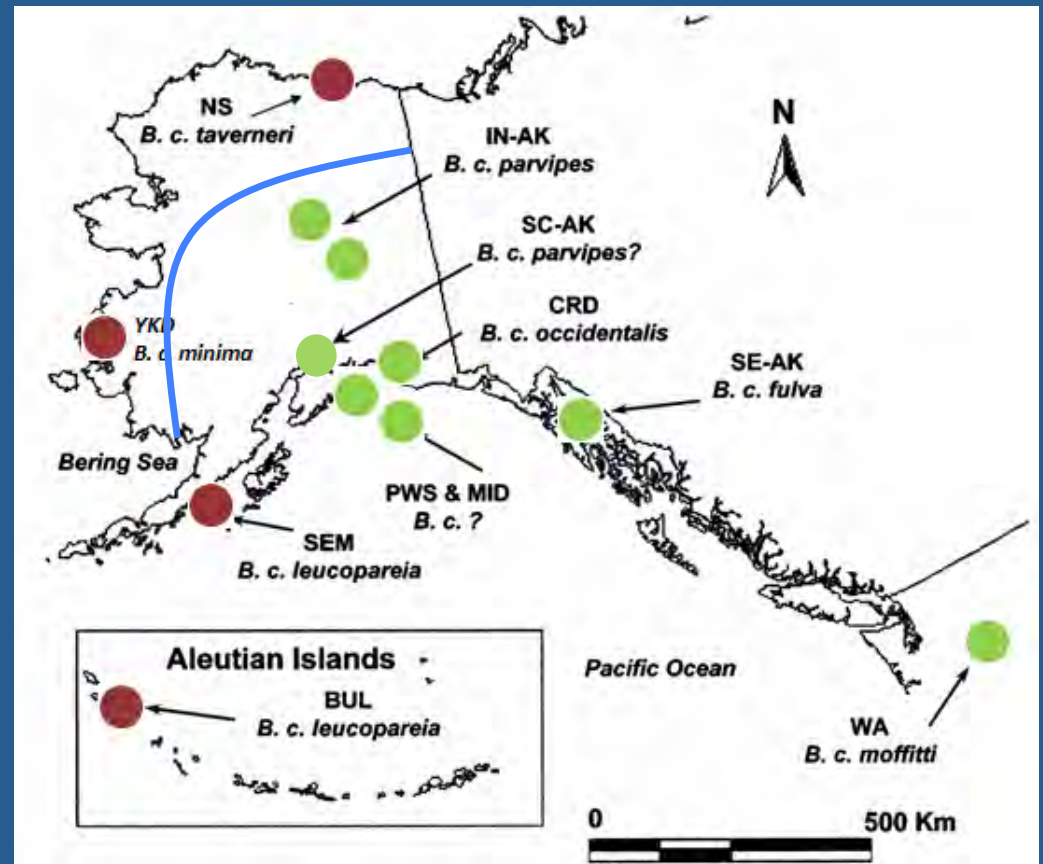
“...genetic studies...[1986 through 2003]”

The species split: "Recent" genetic analyses

Scribner et al. 2003; Auk



Johnson et al. 1979



The species split: AOU's decision



The Auk 121(3):985-995, 2004
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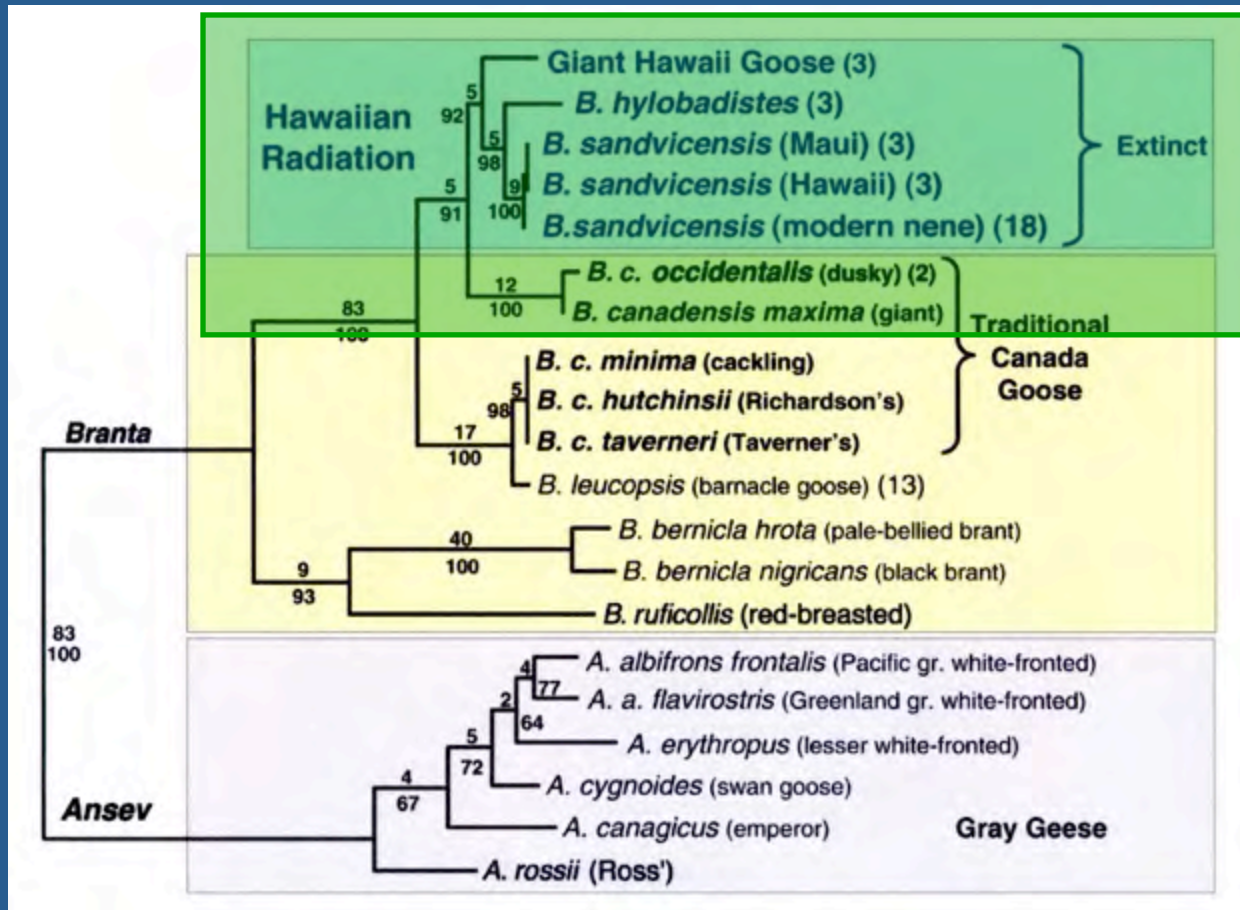
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“...and further that each of the two species may be more closely related to another member of the genus [*Branta*] than to each other.”

The species split: Recent genetic analysis

Paxinos et al. 2002; PNAS

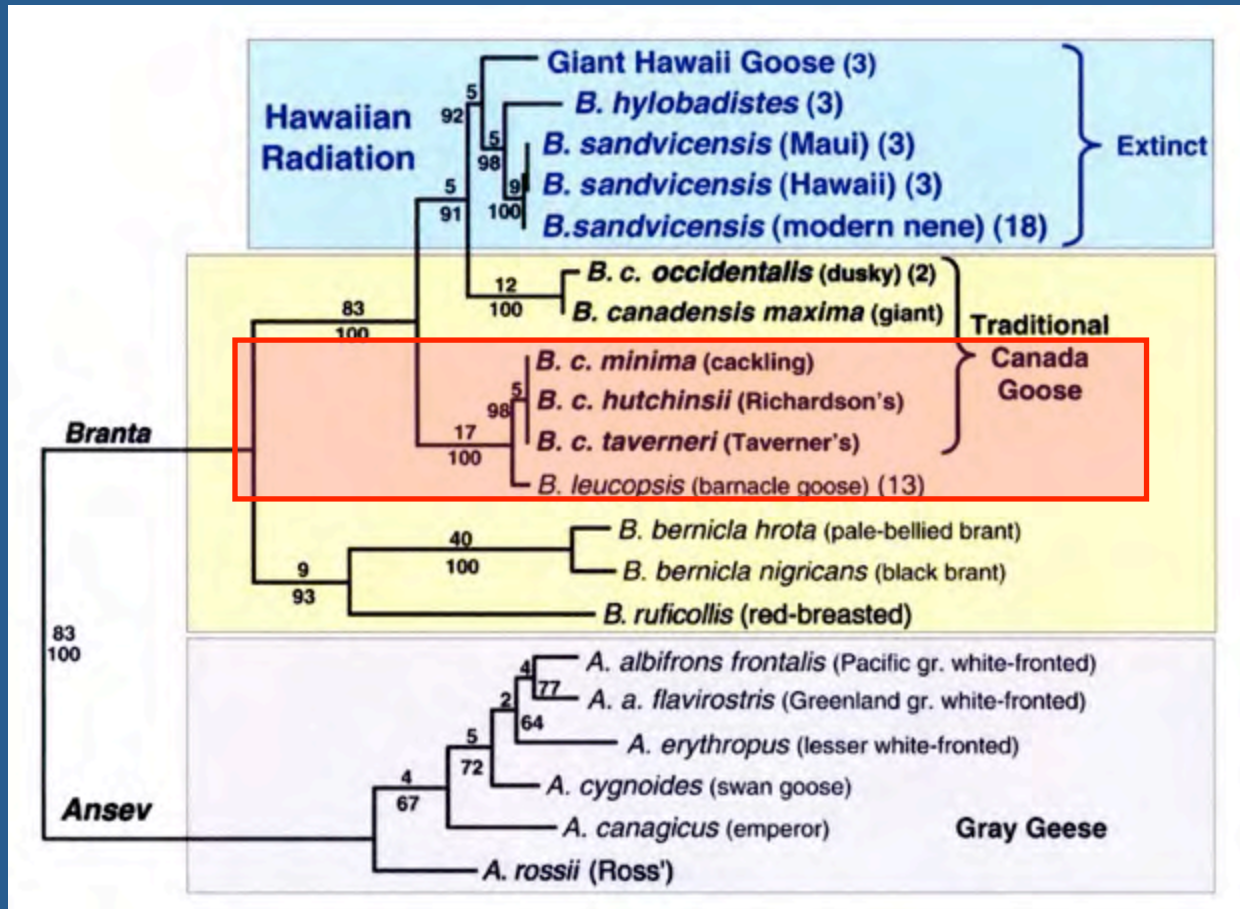
1,348 bases of mtDNA



The species split: Recent genetic analysis

Paxinos et al. 2002; PNAS

1,348 bases of mtDNA



The species split: USFWS response?



Federal Register

Monday,
March 1, 2010

Part II

Department of the Interior

Fish and Wildlife Service

50 CFR Parts 10 and 21
General Provisions; Migratory Birds
Revised List and Permits; Final Rules

“It was the best of times, it was the worst of times, it was the age of wisdom, it was the age of foolishness, it was the epoch of belief, it was the epoch of incredulity...”

The species split: USFWS response



Federal Register

Monday,
March 1, 2010

Part II

Department of the Interior

Fish and Wildlife Service

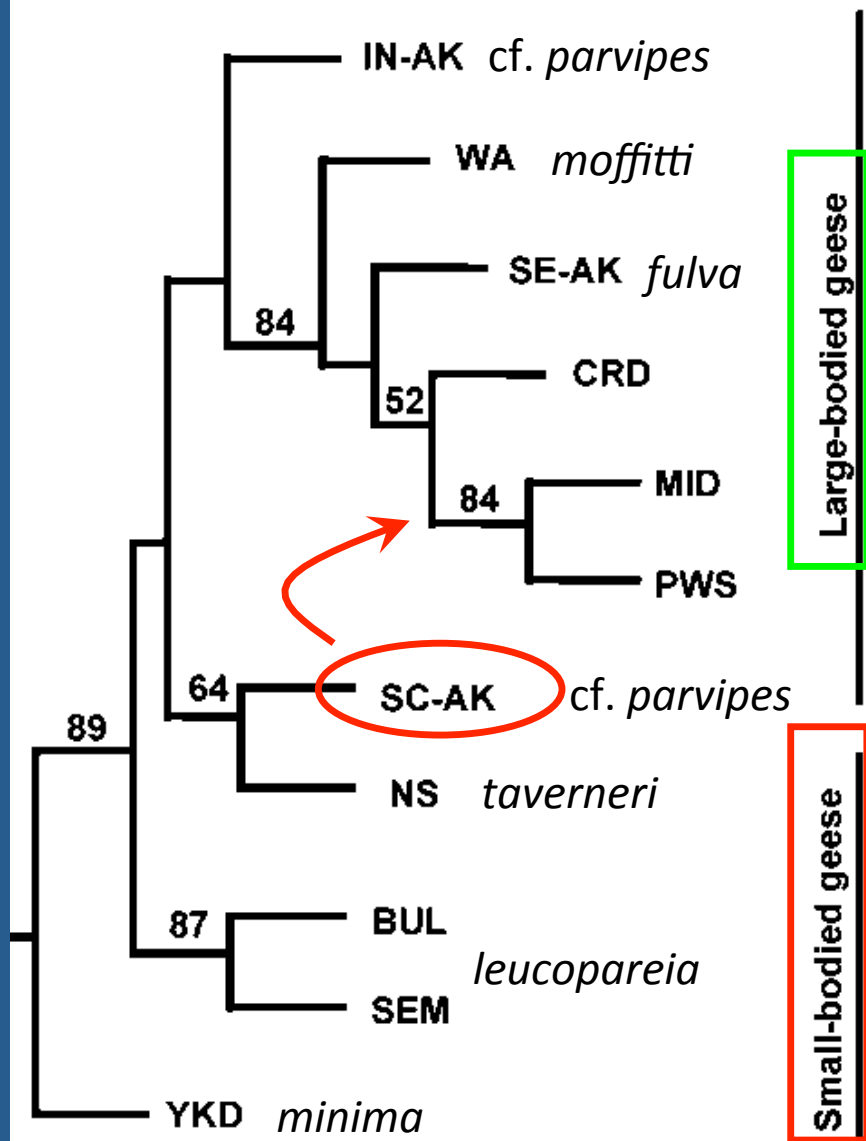
50 CFR Parts 10 and 21
General Provisions; Migratory Birds
Revised List and Permits; Final Rules

“We continue to consider all previously recognized subspecies of the Canada Goose as one species.”

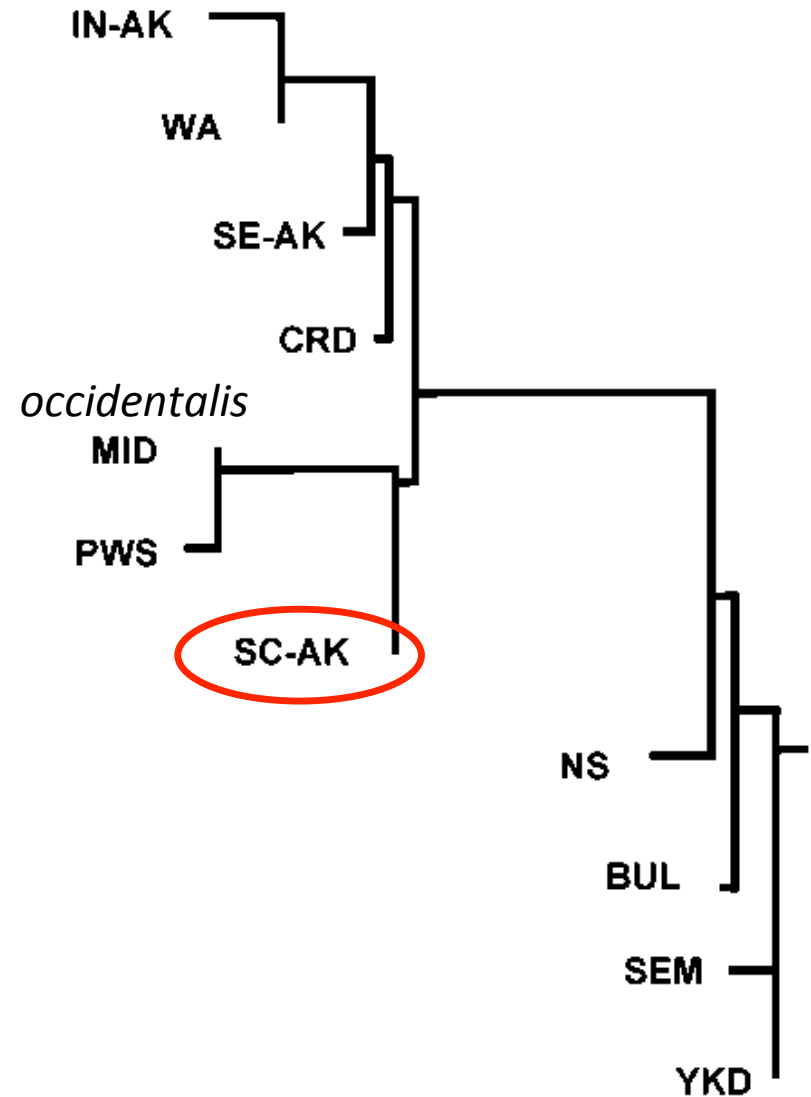
“We believe the mtDNA ...indicate substantial evolutionary distance between Cackling and Canada Geese.”

“However, the nuclear DNA in Scribner et al. suggests either that the nuDNA has not yet sorted...or that this division is not being maintained because hybridization is occurring.”

A. Nuclear microsatellite DNA



B. Mitochondrial DNA



Mismatch between mtDNA and nuclear loci suggestive of hybridization or lineage sorting

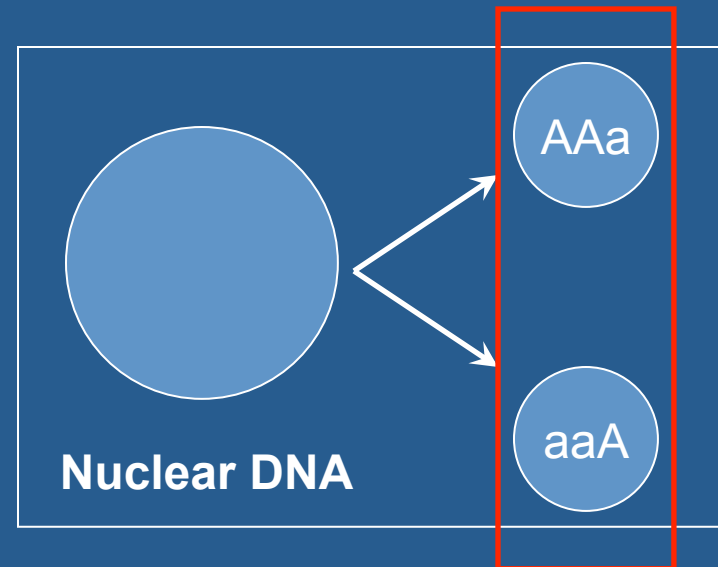
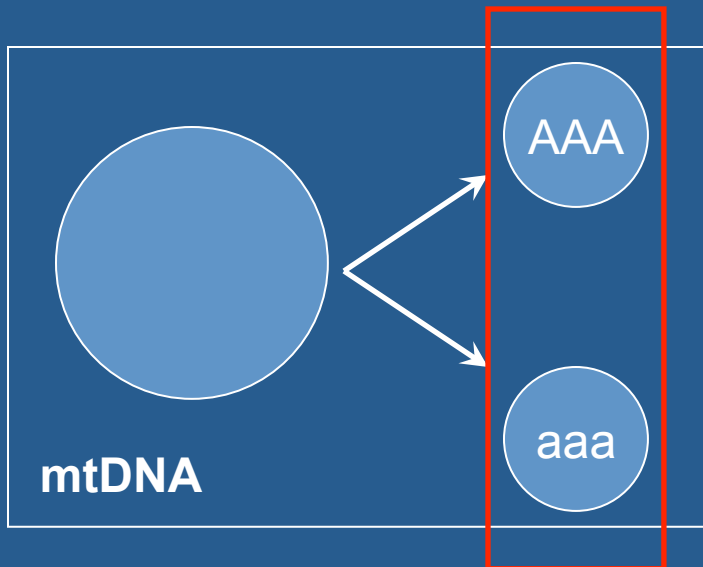
The species split: the mitogenome vs. the nuclear genome

Such differences are common in the literature

The two molecules are different in terms of:

- effective population size
- mode of transmission
- levels of recombination
- mutation rates

**gene flow
or
incomplete sorting?**



The species split: USFWS response



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“We suggest additional analysis of samples collected at several potential *zones of integration*...

...including [samples from] (*B. h. taverneri* and *B. c. parvipes*)...”

Hybrids and Policy

- Definitions

- *Hybridization*: Interbreeding of individuals from genetically distinct populations, regardless of taxonomic status (Haig and Allendorf 2006)
- *Introgressive Hybridization*: A taxon's genetic material enters the gene pool of another, introducing genetic novelty ('species' rather than taxon, Rheindt and Edwards 2011)
- *Hybrid Zone*: An area of contact between two genetically distinct population where hybridization occurs (Haig and Allendorf 2006)
 - USFWS: “zones of intergradation”
- *Suture Zone*: An area of congruence among several hybrid zones (Rheindt and Edwards 2011)

Haig, S., and F. Allendorf. 2006. Hybrids and Policy. *The Endangered Species Act at Thirty, Vol 2: Conserving Biodiversity in Human-Dominated Landscapes* (Scott, Goble & Davis, Eds). Washington: Island Press.

Rheindt, F. E. and S. V. Edwards. Genetic Introgression: An integral but neglected component of speciation in birds. *Auk* 128:620-632.

Hybrids and Policy

- Hybridization is often seen as negative
 - Increased rates of hybridization because of human activities have led to the extinction of populations and species (Rhymer and Simberloff 1996; Allendorf et al. 2001)
- Hybridization is an important and pervasive mechanism in speciation (Rheindt and Edwards 2011)
 - Maintenance of genetic diversity
 - Introduction of advantageous novelty

Hybrids and Conservation/ Management Policy

- Conservation Policies: Conundrum
 - Treat problems caused by increased anthropogenic hybridization
 - Recognize the important evolutionary role of hybridization, particularly within the context of species response to changing climates

The species split: USFWS response



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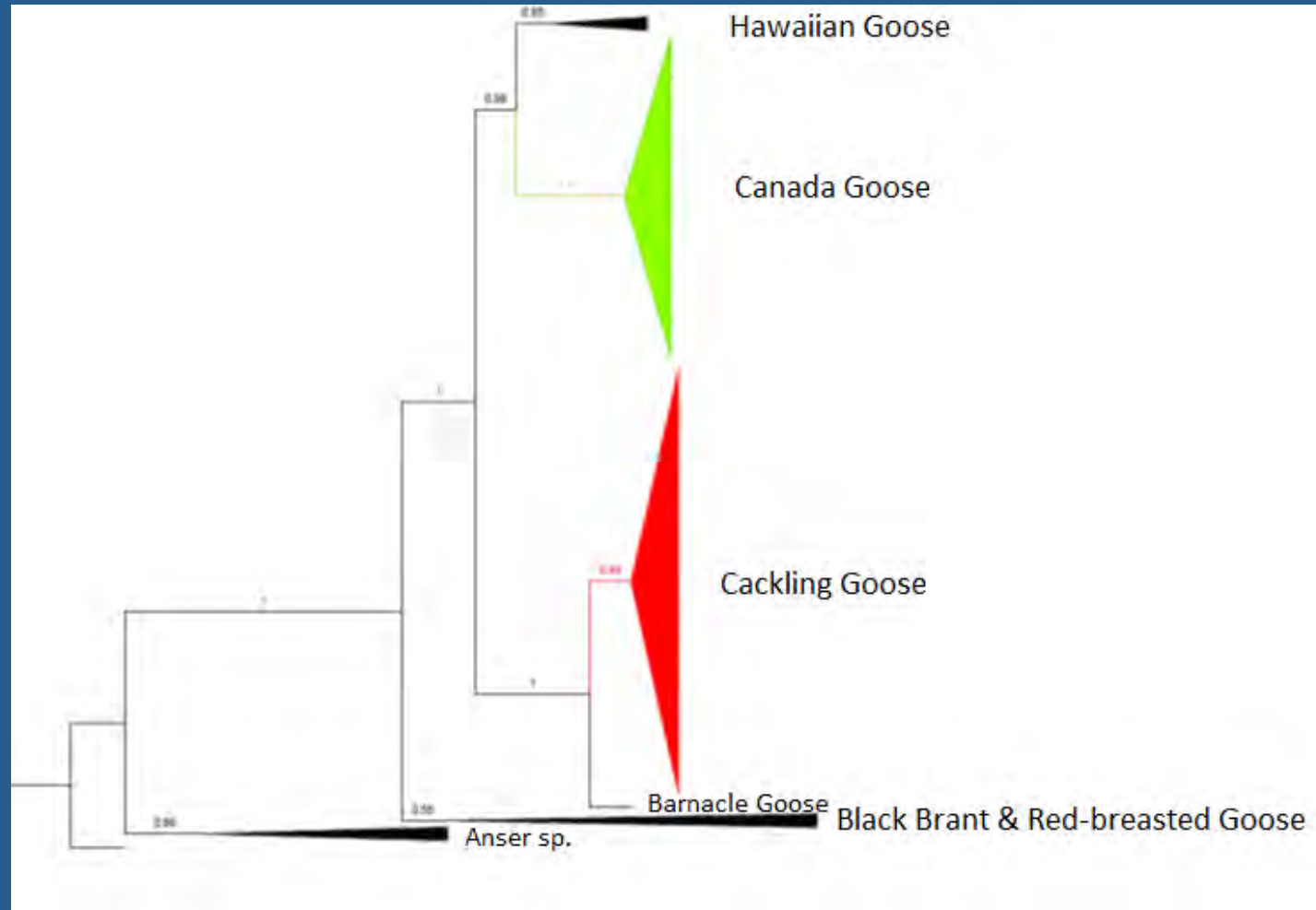
“We suggest additional analysis of samples collected at several potential **zones of integration...**

...including [samples from] (*B. h. taverneri* and *B. c. parvipes*)...”

The species split: additional mtDNA confirms deep divergence

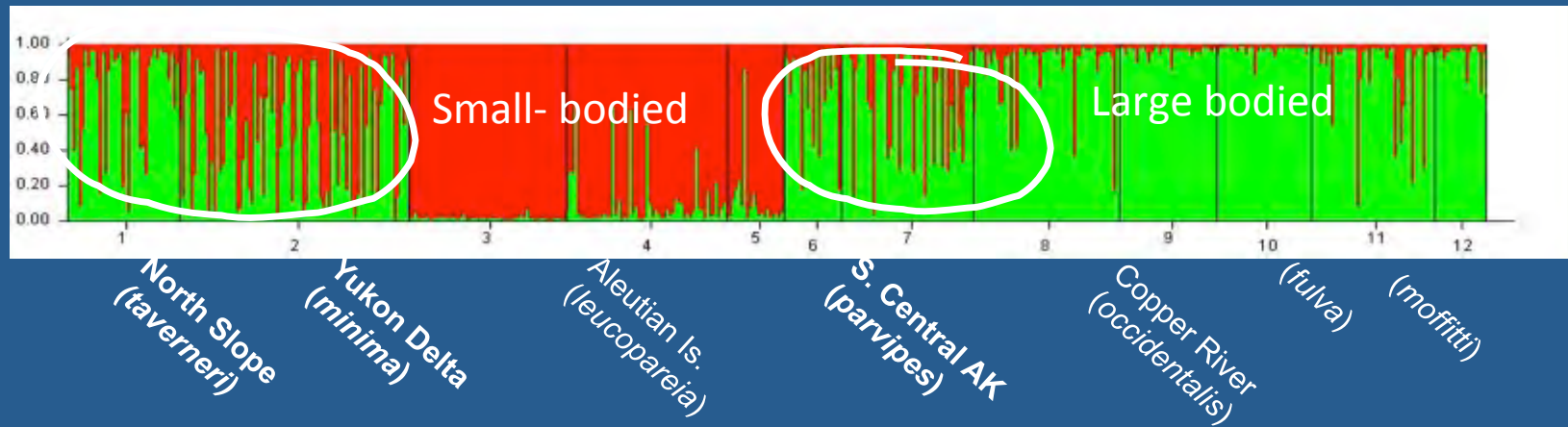
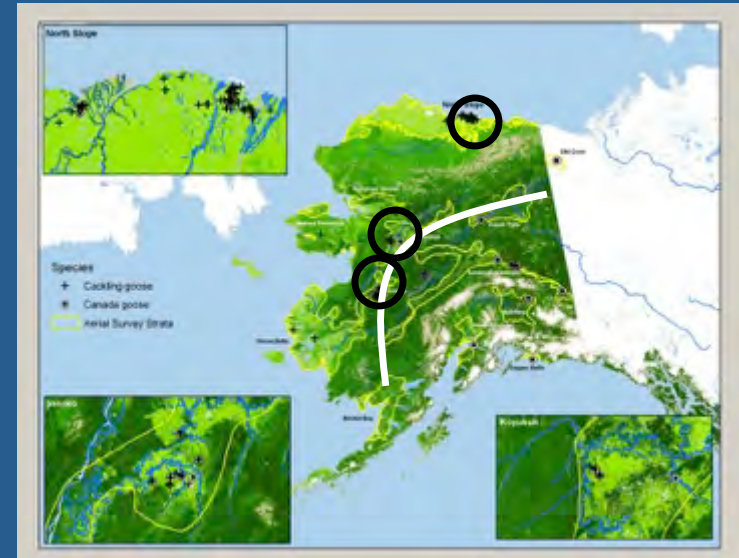
2011: Additional mtDNA (810 bases) = same result as Paxinos et al. (2002)

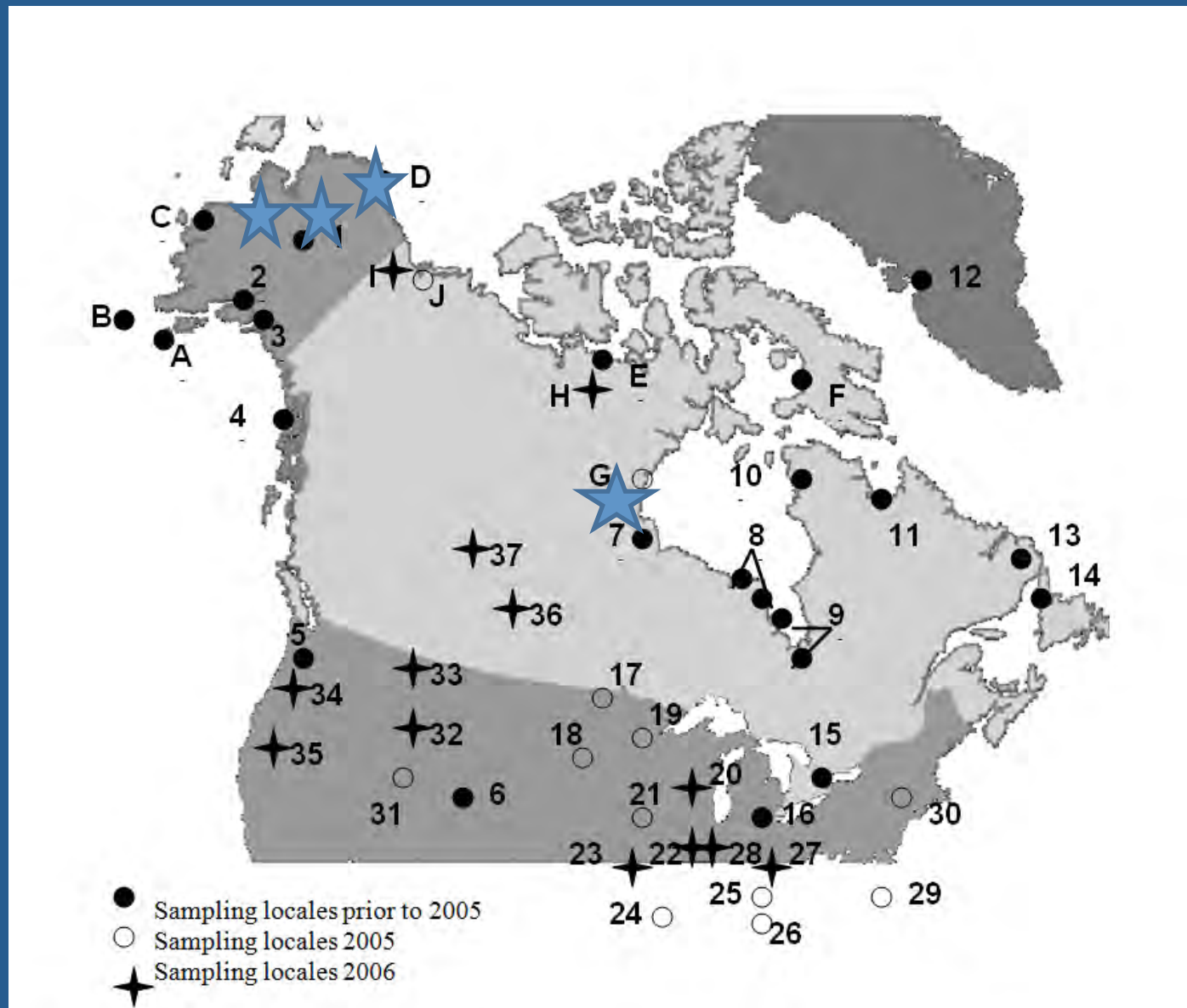
2014: Entire mitogenome (>16,700 bases) = preliminary results suggest same result as Paxinos et al. (2002)



Results and Conclusions: mtDNA and nuclear data

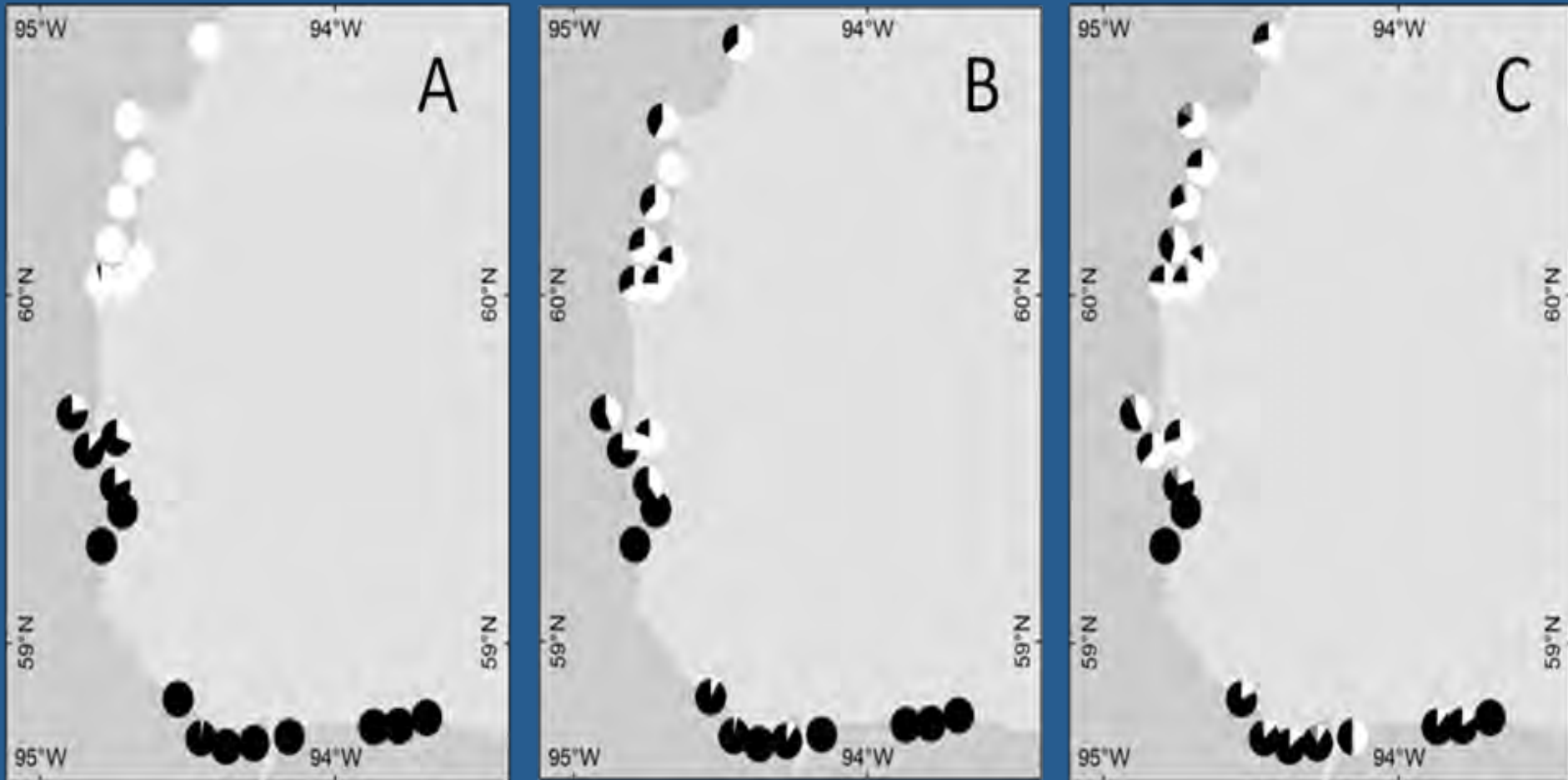
- We found evidence of sympatry in different areas of Alaska.
- Bayesian cluster analysis of microsatellite DNA and sequence data from 5 nuclear introns also suggest 2 groups, as well as admixture in areas of overlap.
- Gene flow or lineage sorting?
 - Microsatellites identify what appear to be contemporary hybrids, but only a few.
 - “Isolation with Migration” (IM) analysis of 5 introns suggest gene flow between the species is not significantly different from zero, supporting the lineage sorting hypothesis.





Leafloor et al. (2013). A hybrid zone between Canada Geese (*Branta canadensis*) and Cackling Geese (*B. hutchinsii*). *Auk* 130: 487-500.

Geographic distribution and frequency of adult female Canada Geese and Cackling Geese by capture location



phenotype

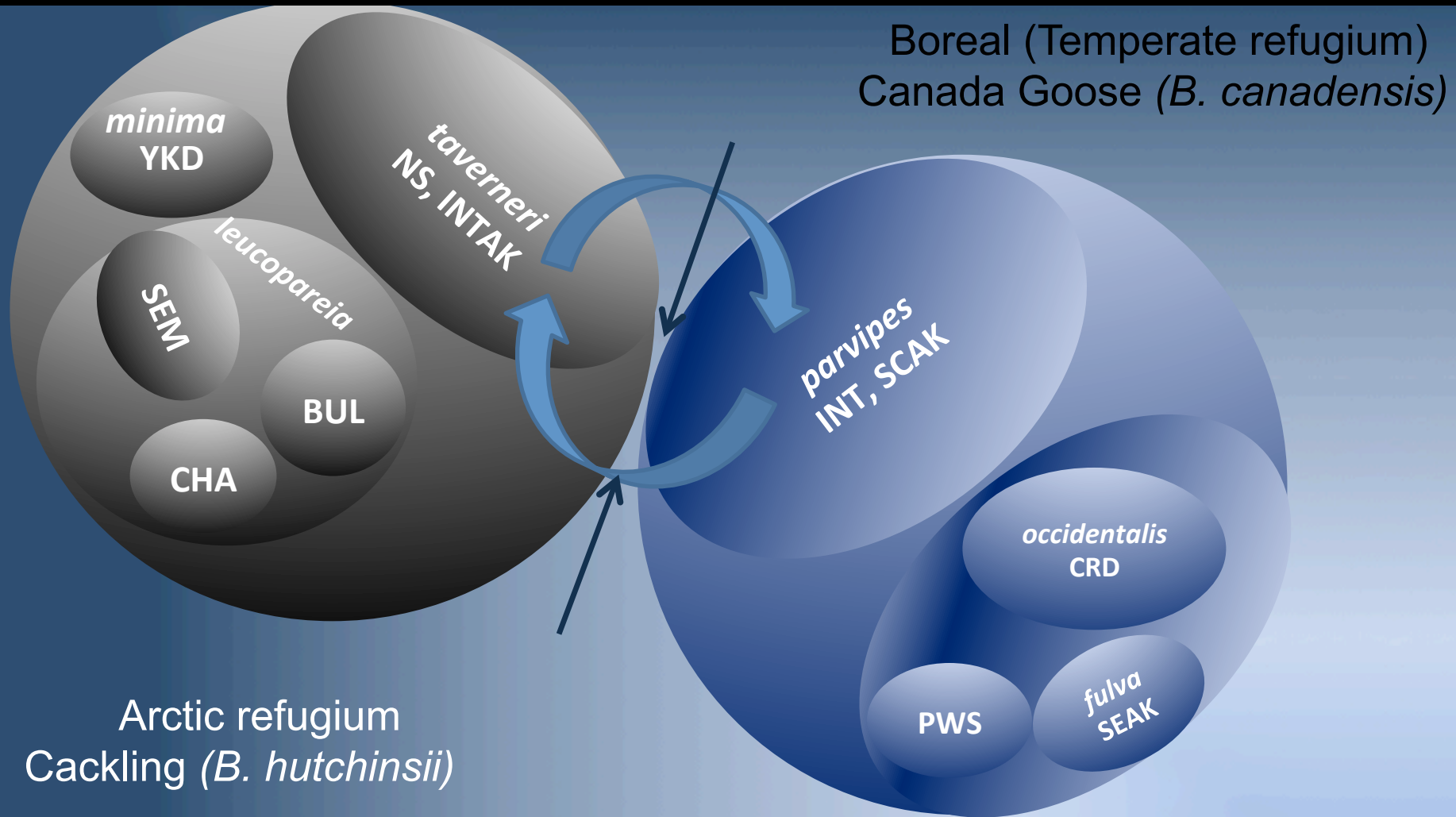
mtDNA haplotypes

BAPS -- μ sats

Summary-Leafloor et al. 2013

- Most Canada Geese occurred in sub-Arctic habitats, south of 50° N latitude
- Most Cackling Geese occurred in Arctic habitats, north of 60° N latitude
- The two species overlapped in a narrow zone between 59 ° N and 60 ° N latitude that coincides with an subarctic/Arctic ecotone
- Mismatches between morphology and genetic characteristics (some females) suggested introgression has occurred in the region
- Contrasting patterns of nuclear and mtDNA consistent with female philopatry and male biased dispersal
- Evidence of introgression in the nuclear genome more geographically widespread than evidence of introgression based on mtDNA genome.
- The persistence of Canada Goose mtDNA in phenotypic Cackling geese results from historical hybridization events that occurred when the Arctic/subarctic ecotone was located farther north (warmer climatic period)
- Despite evidence of introgression, its frequency appears low; the area of overlap represents a tension zone between the two species maintained by behavioral and ecological factors that limit effective dispersal.

Hypothesized Beringian Relationships Among White-cheeked Geese



Working Model: Separation and divergence of lineages in different glacial refugia followed by expansion, secondary contact and introgressive hybridization during warm periods

Phylogeography and Population Structure of North American Brant (*Branta bernicla*)



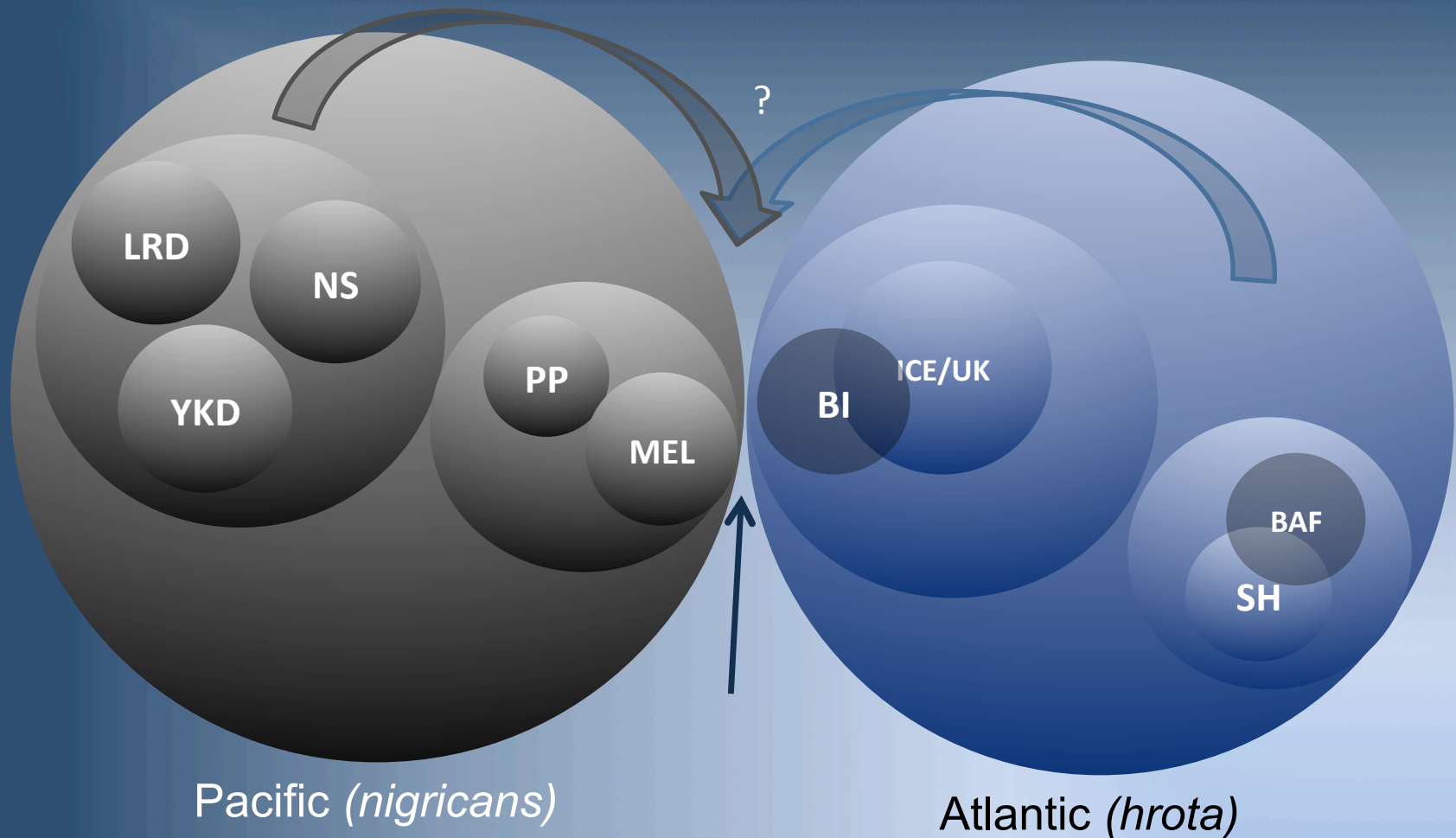
S. L. Talbot, G. K. Sage, J. R. Gust, J. R. Rearick, D. Ward, D. V. Derksen- Alaska Science Center, U. S. Geological Survey, Anchorage, Alaska, USA

W.S. Boyd, K. Dickson- Canadian Wildlife Service, Canada

Kendrew Colhoun- Wildfowl and Wetlands Trust, Slimbridge, UK

Black Brant

AMOVA Summary: Hypothesis Testing



mtDNA: $\phi_{CT} = 0.667, P < 0.001$

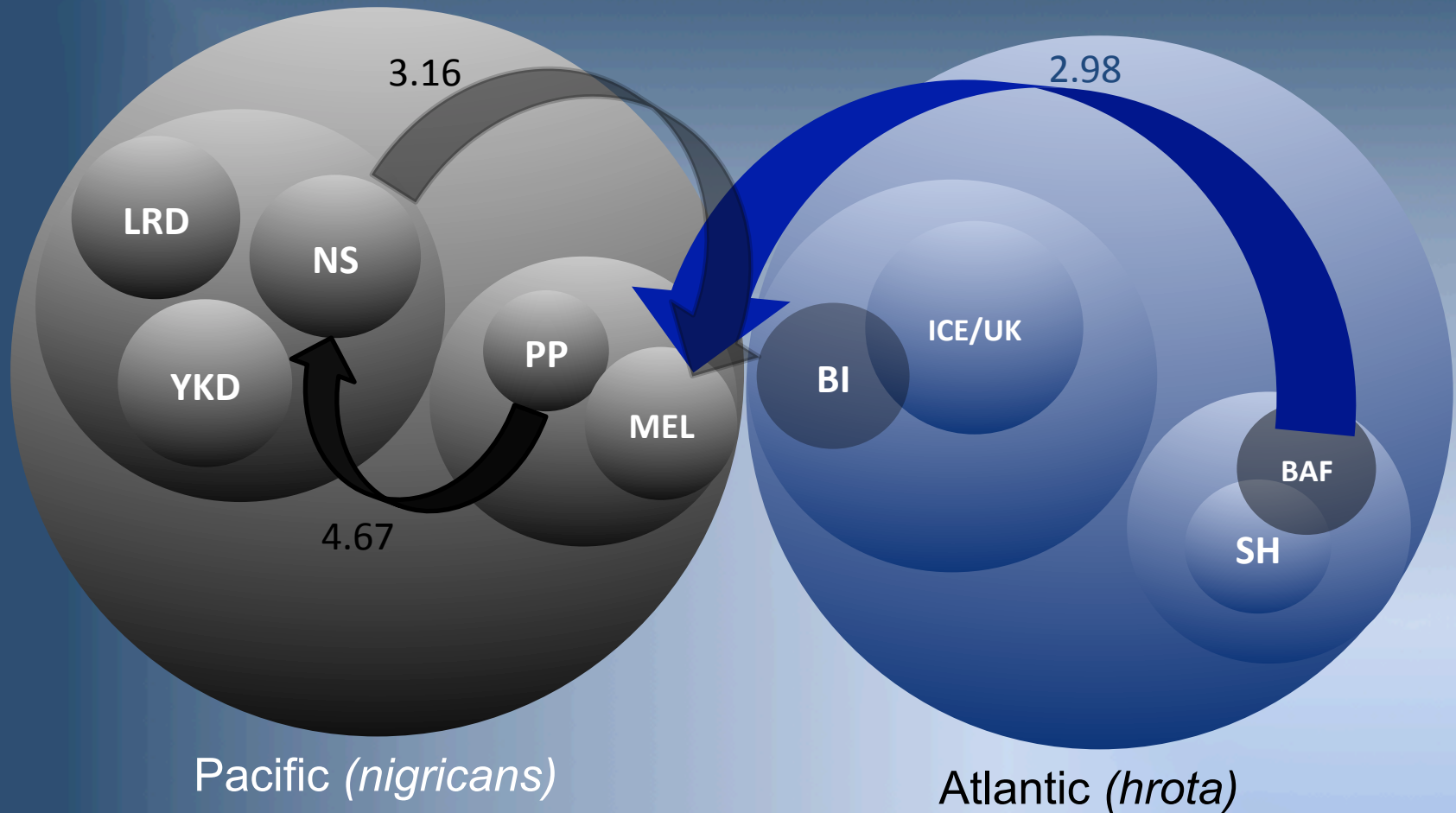
μsat loci: $\theta_{CT} = 0.046, P < 0.001$

[(PP, MEL) (YKD, NS, LRD)] [(ICE, BI, UK) (SH, BAF)]

[PP, MEL, YKD, NS, LRD] [(ICE, BI, UK) (SH, BAF)]

Black Brant

MIGRATE Summary: Gene Flow Polarity (4 population model)



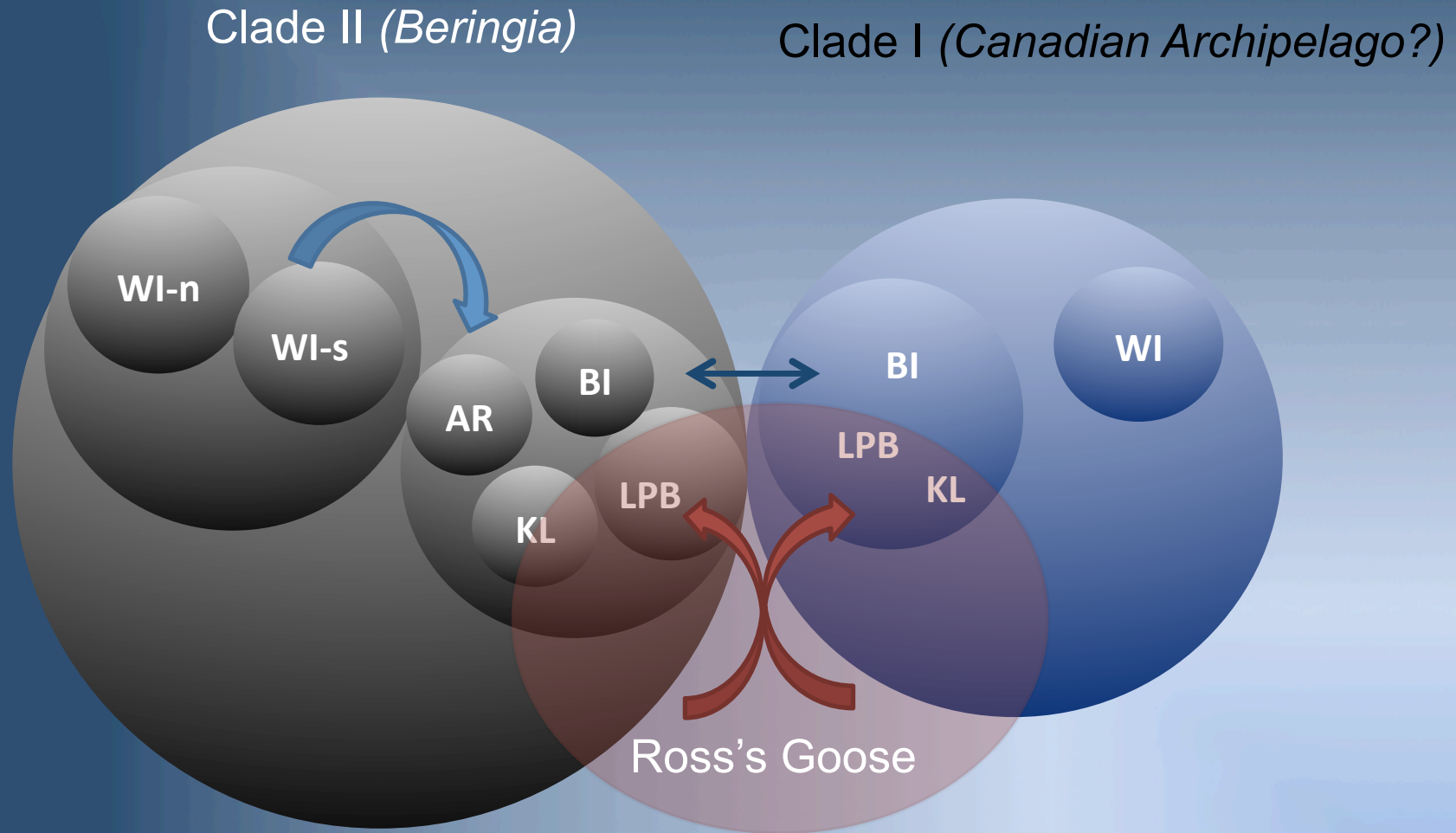
Working Model: Separation and divergence of lineages in different glacial refugia followed by expansion, secondary contact and introgressive hybridization during warm periods

Lesser Snow Goose

(*Anser [Chen] caerulescens caerulescens*)

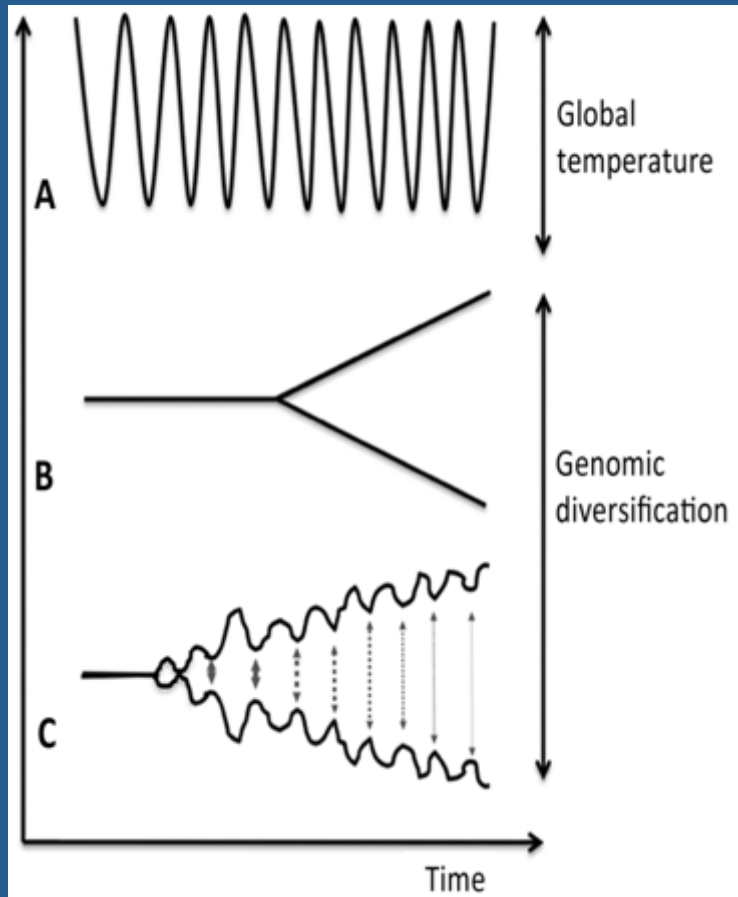


Lesser Snow Goose: Hypothesized Model of Lineage Dynamics



Working Model: Separation and divergence of lineages in different glacial refugia followed by expansion, secondary contact and introgressive hybridization during warm periods

Speciation Scenarios Arctic Nesting Geese



- Separation and divergence of lineages during cooling (glacial) periods
- Secondary contact and introgressive hybridization during warming periods (interglacial)

Future Directions

Arctic Nesting Geese

- Incorporate climate models into speciation and phylogeographic reconstructions (Hope et al., this session)
- Incorporate introgression into reconstructions
 - Introgression often driven by climate change and shifting habitats
 - Recognition that introgression is an integral part of the evolutionary process

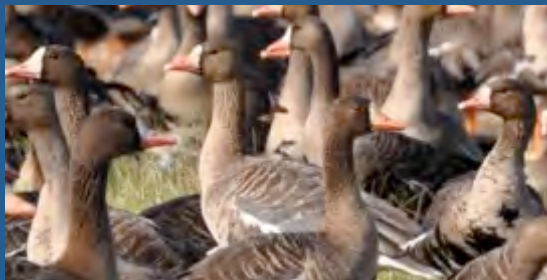
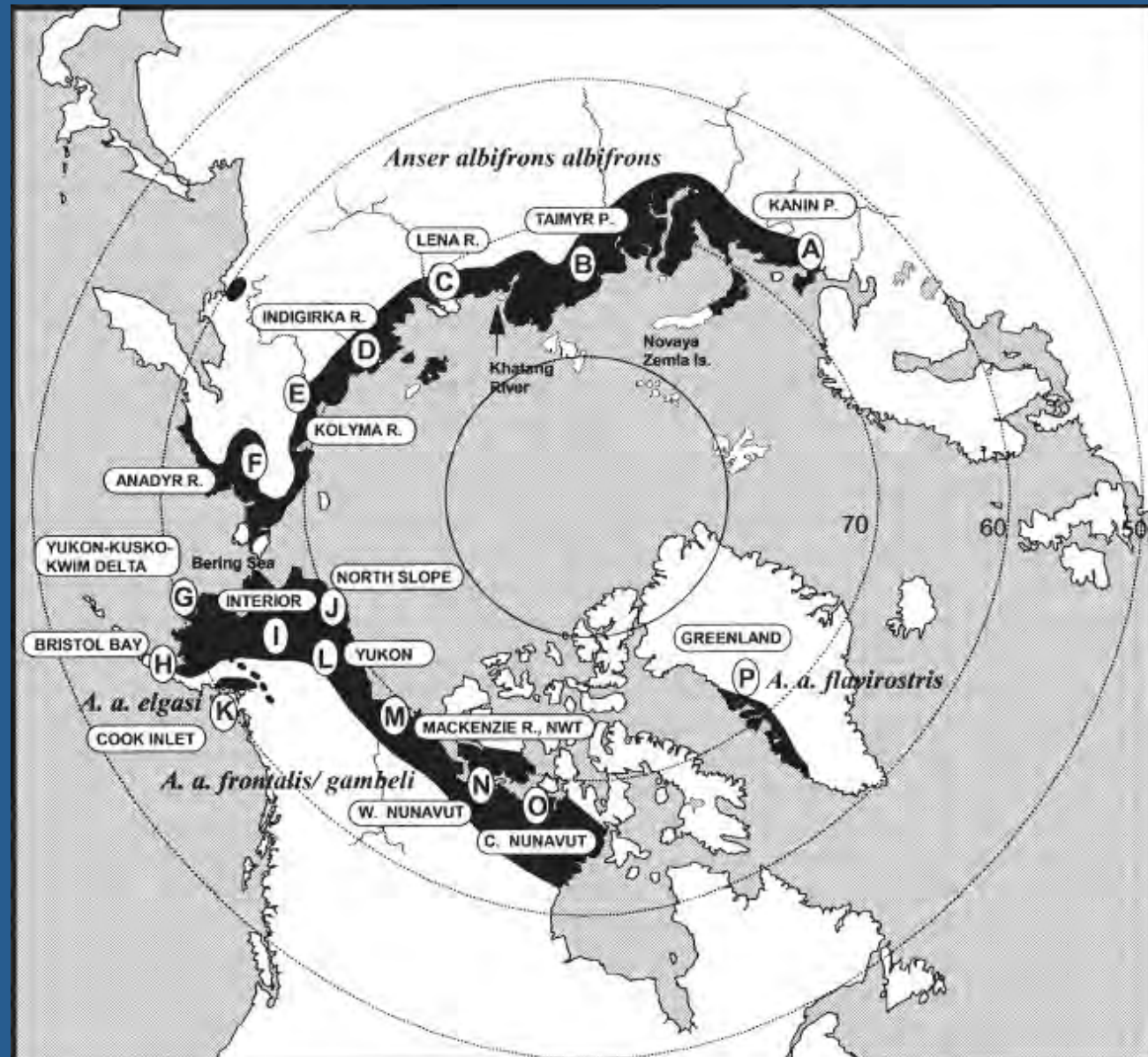
Thank you.

Extra slides

Geese in Eastern Beringia (*Anser*)

Greater White-fronted Goose (*Anser albifrons*)

- *A. a. albifrons*
- *A. a. frontalis/gambelli*
- *A. a. flavirostris*
- *A. a. elgasi*



Geese in Eastern Beringia (*Anser*)



Greater White-fronted Goose
(*Anser albifrons*)

<http://bna.birds.cornell.edu/bna/species/131/articles/introduction>



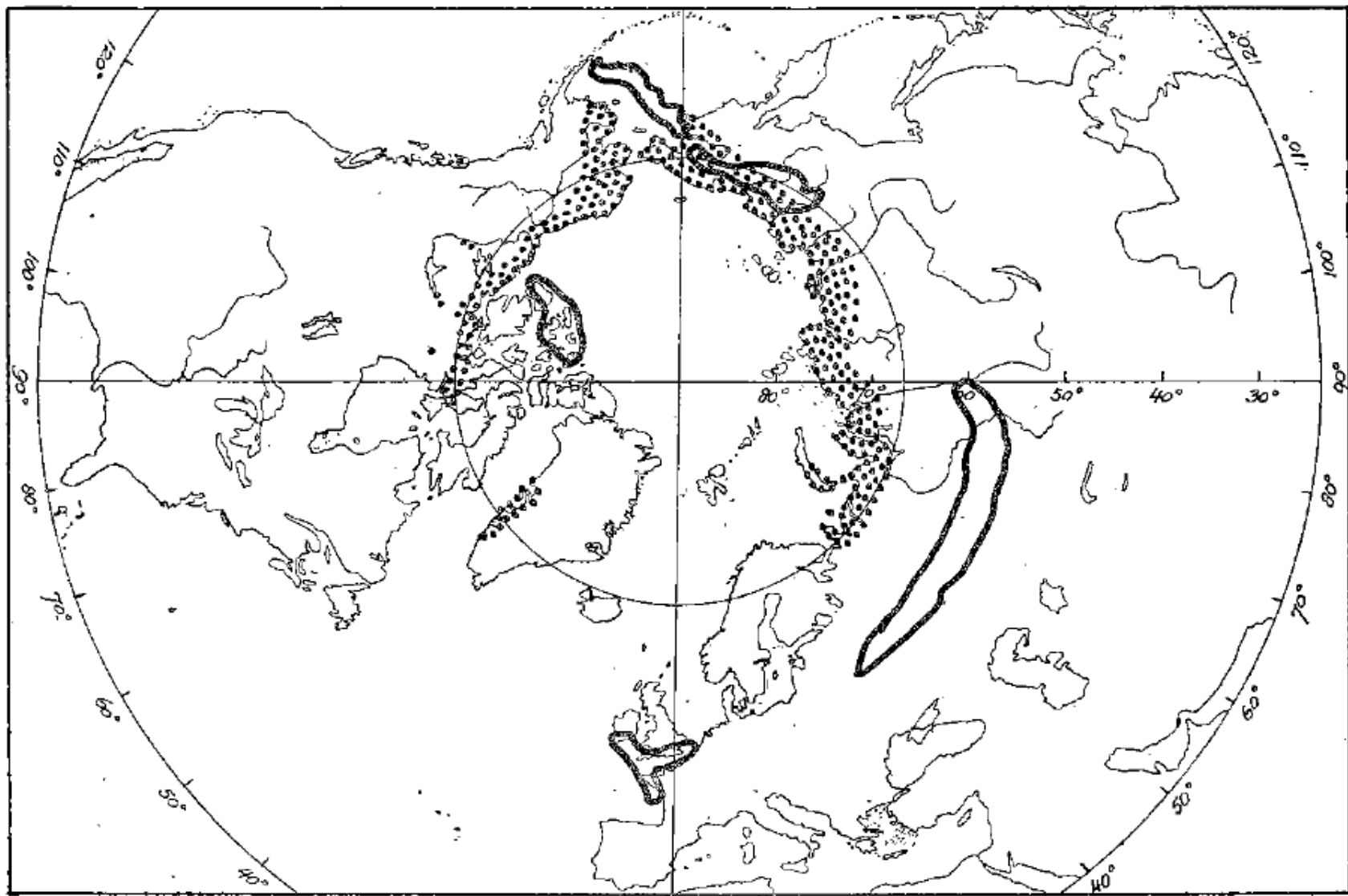
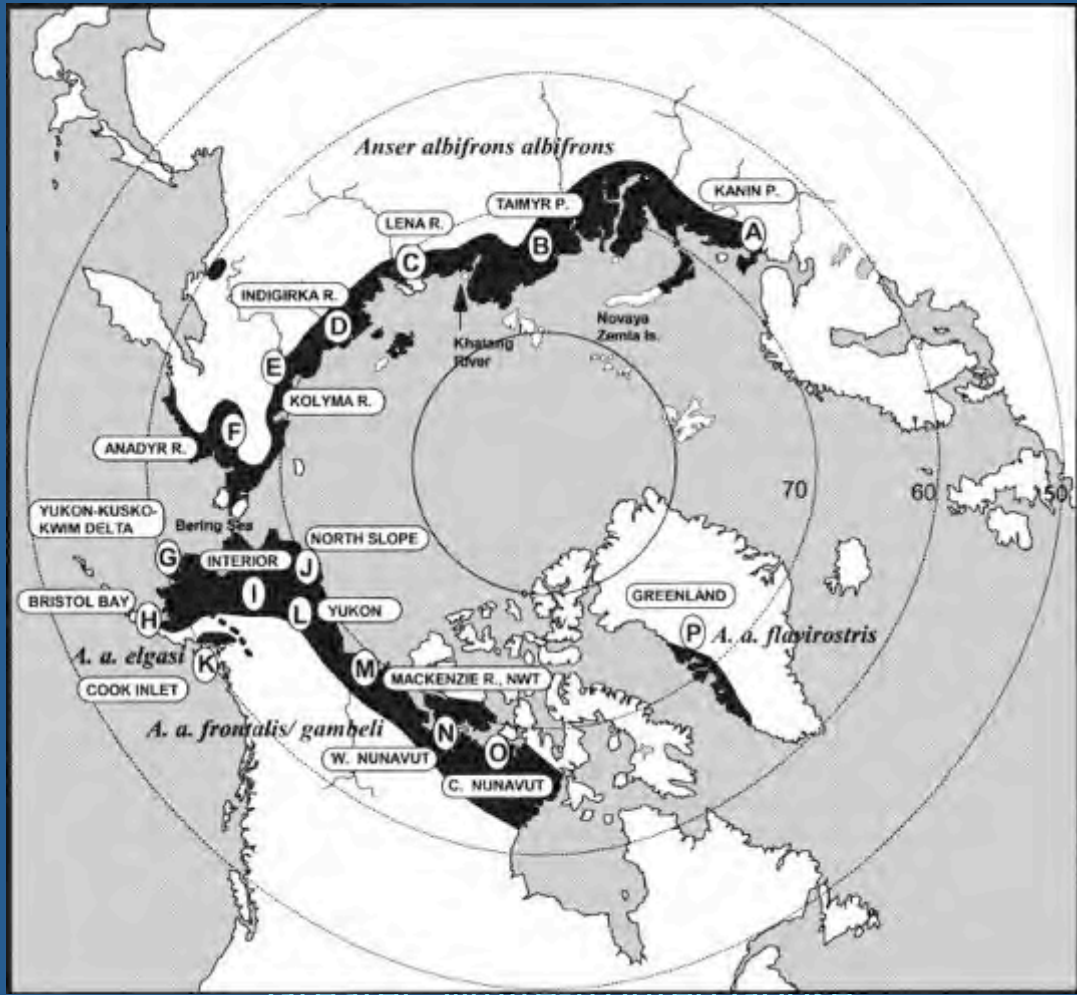
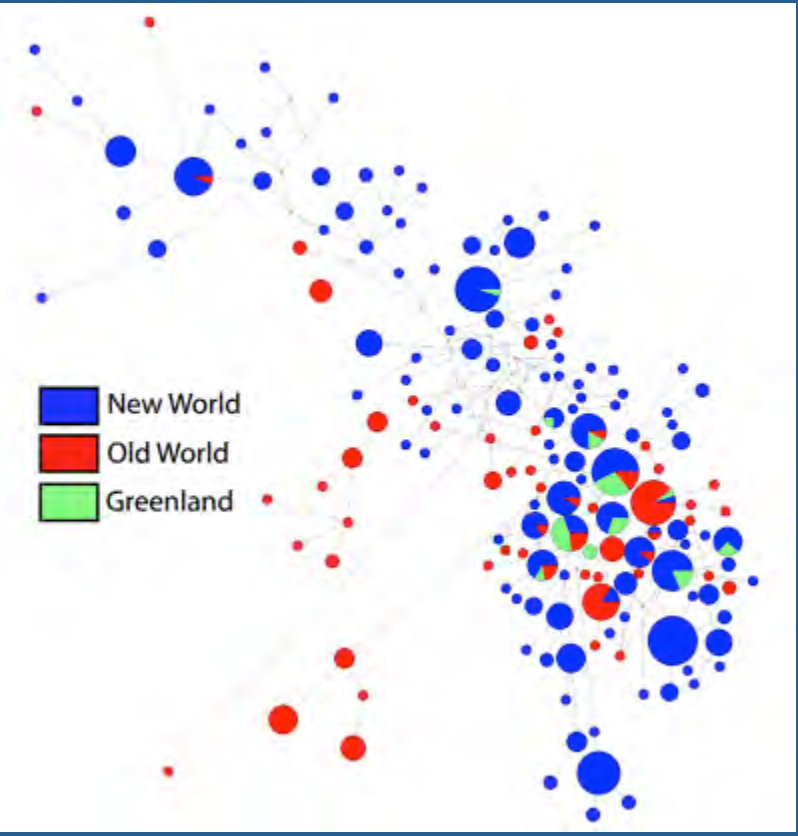
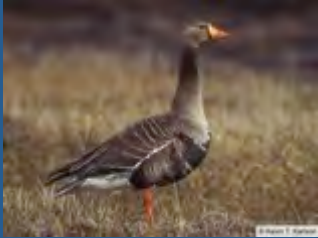


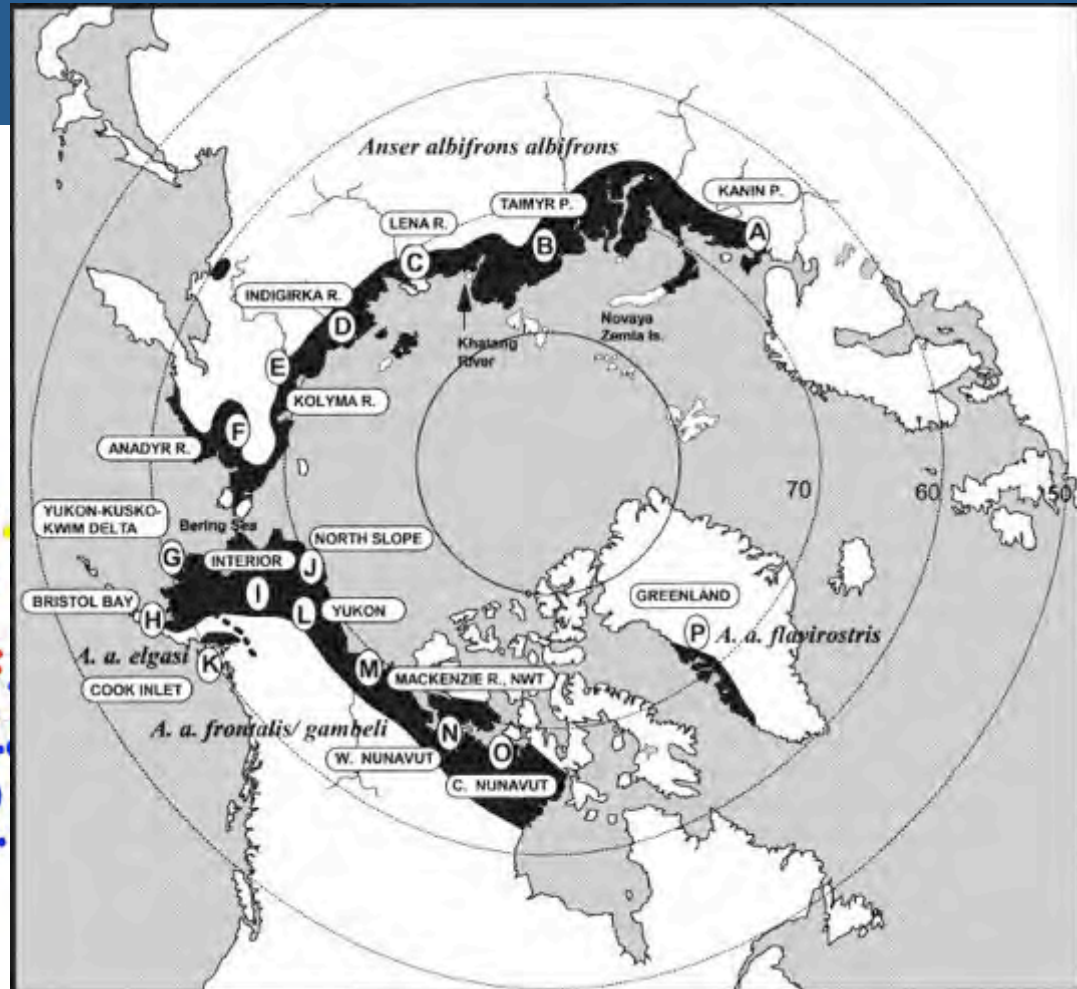
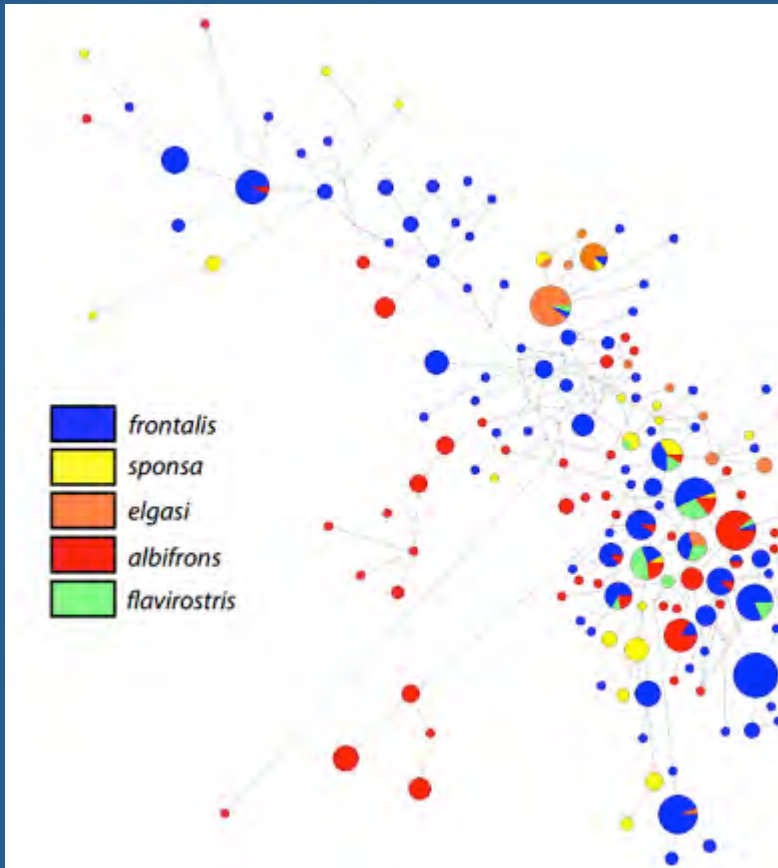
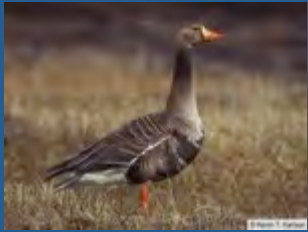
FIGURE 20. *Anser albifrons* (Scopoli). Stippled area = present breeding range. Solid lines = borders of potential Last-Glacial breeding grounds.

Geese in Eastern Beringia (*Anser*)



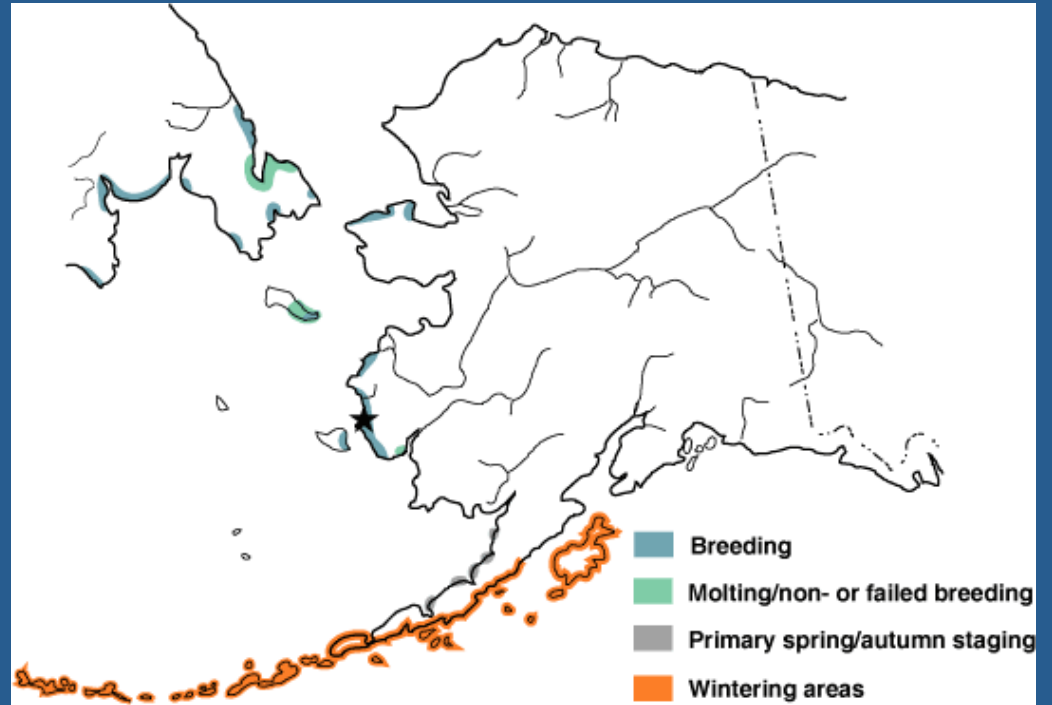
Greater White-fronted Goose
(*Anser albifrons*)

Geese in Eastern Beringia (*Anser*)



Greater White-fronted Goose (*Anser albifrons*)

Distribution and Demography (*Chen*)



Chen canagica (Emperor Goose)
Low Arctic

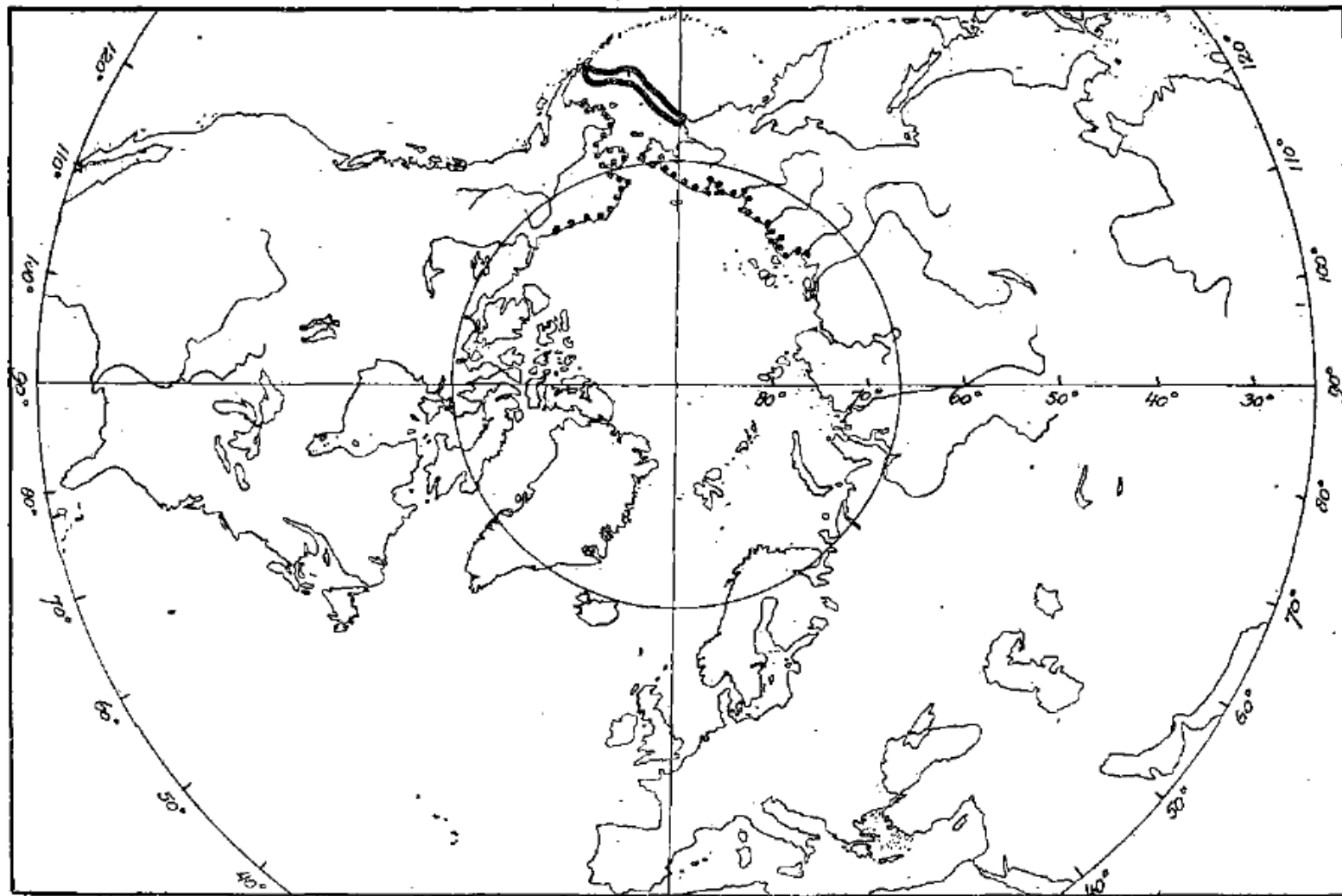
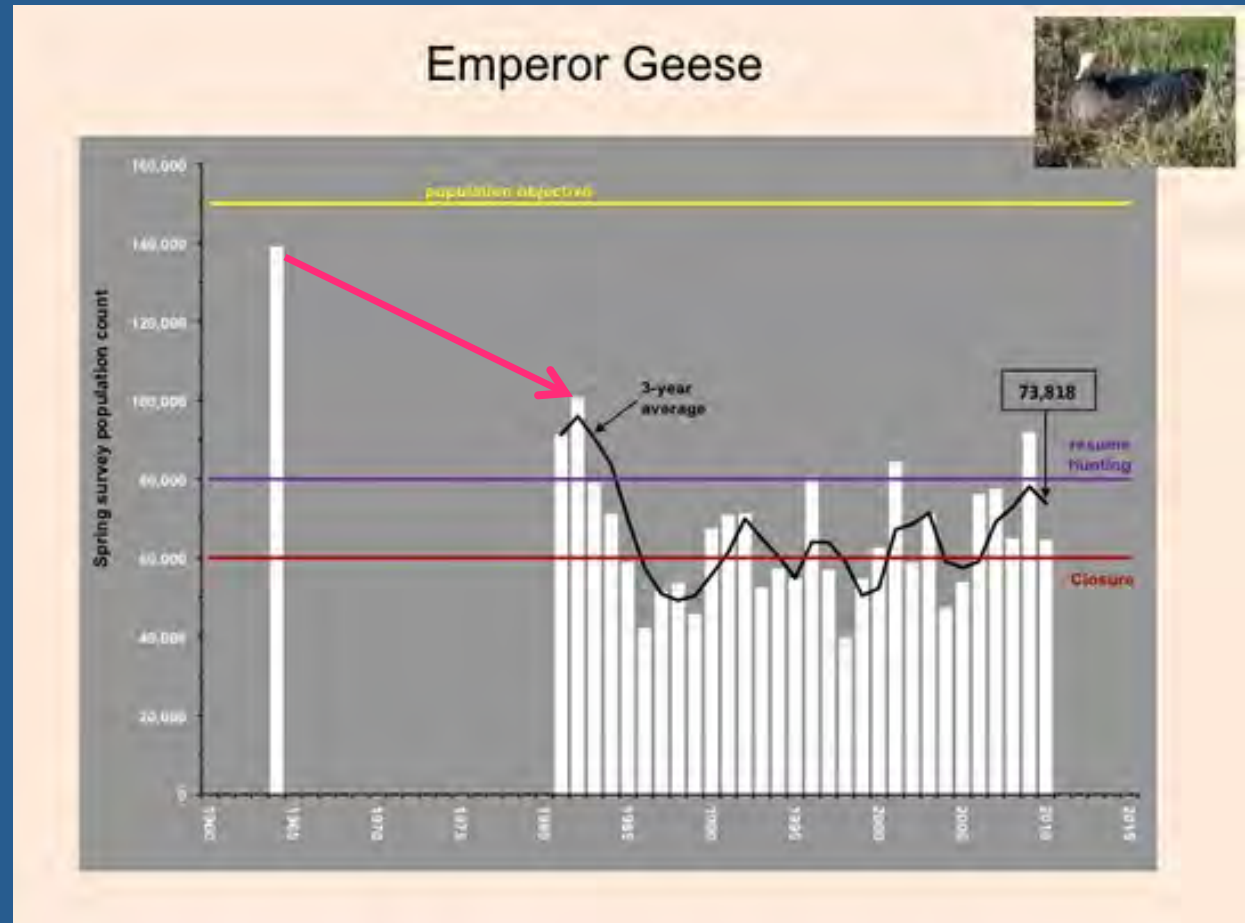


FIGURE 26. *Anser canagicus* (Sewastianow). Dots = present breeding range. Solid line = border of potential Last-Glacial breeding grounds.



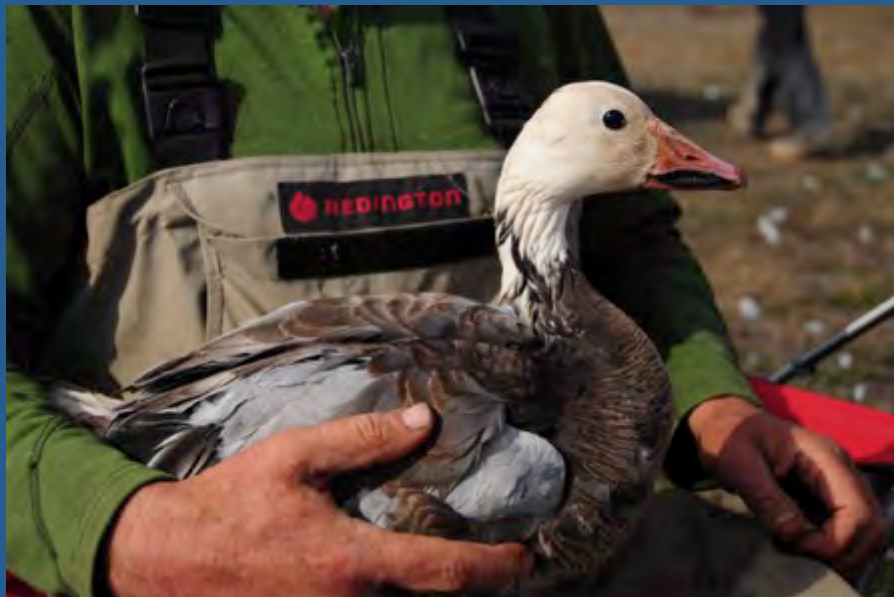
Emperor Goose



*Emperor Goose Population Size
Schmutz BNA revision (2011)*

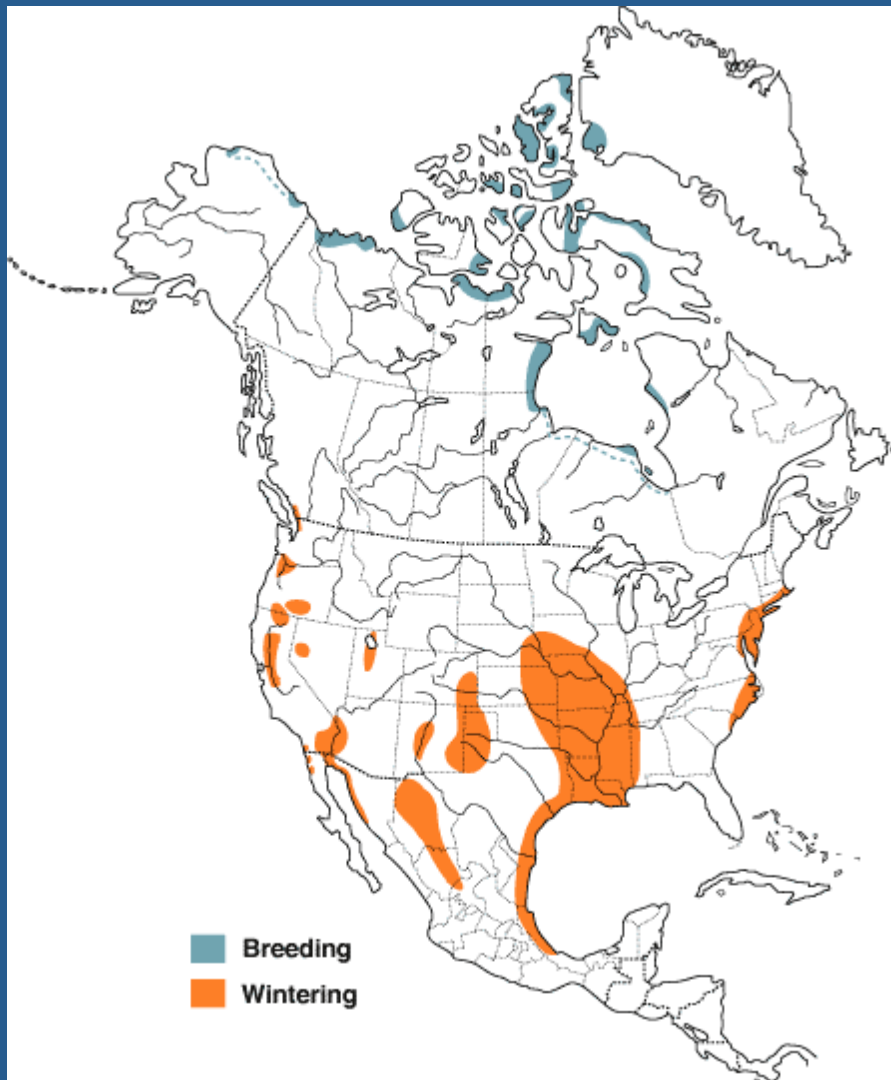
<http://bna.birds.cornell.edu/bna/species/097/articles/demography>

Geese in Eastern Beringia (Lesser Snow Goose)



- Morphology Studies
 - Two color morphs treated as two species
 - *Chen hyperborea*
 - *C. caerulescens*
- Genetic studies
 - revealed the 2 morphs represented a single interbreeding, dimorphic species
 - due to a single gene (MC1R, primary plumage color)

Geese in Eastern Beringia (*Anser*)



- Two subspecies currently recognized for management purposes
 - *C. c. caerulescens* (Linnaeus, 1758)*
 - Lesser Snow Goose, easternmost Siberia to Baffin Island
 - *C. c. atlantica* (Kennard 1927)*
 - Greater Snow Goose, eastern Canadian Arctic Archipelago to Thule district, NW Greenland.

North American Distribution of Lesser Snow Goose
(*Anser caerulescens caerulescens*)

Geese in Eastern Beringia (*Anser [Chen] caerulescens*)

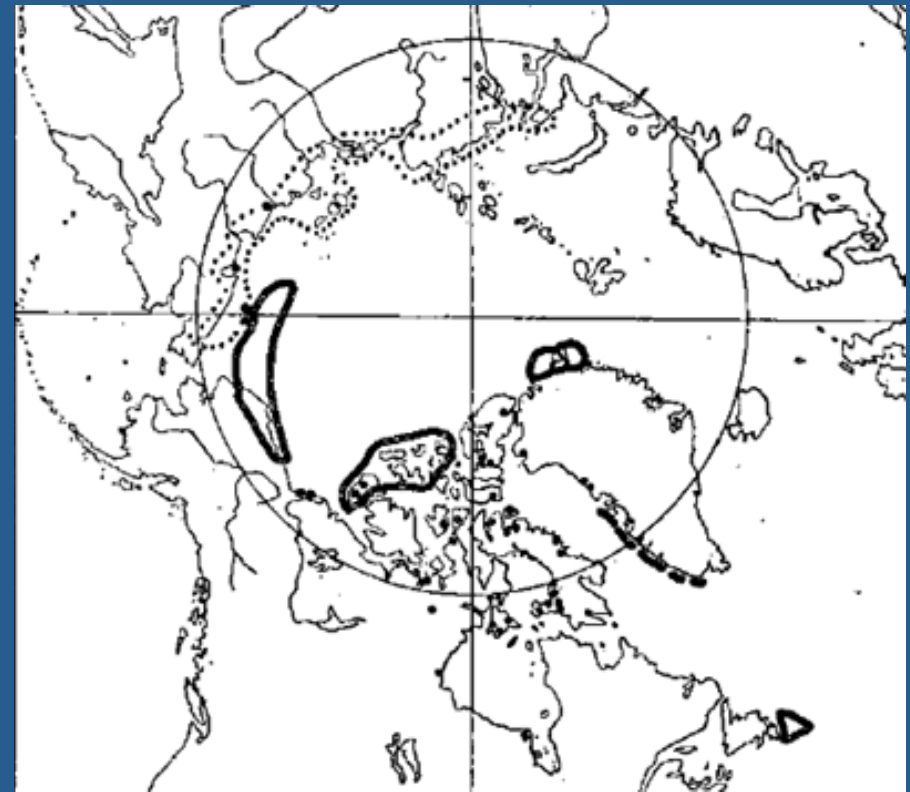
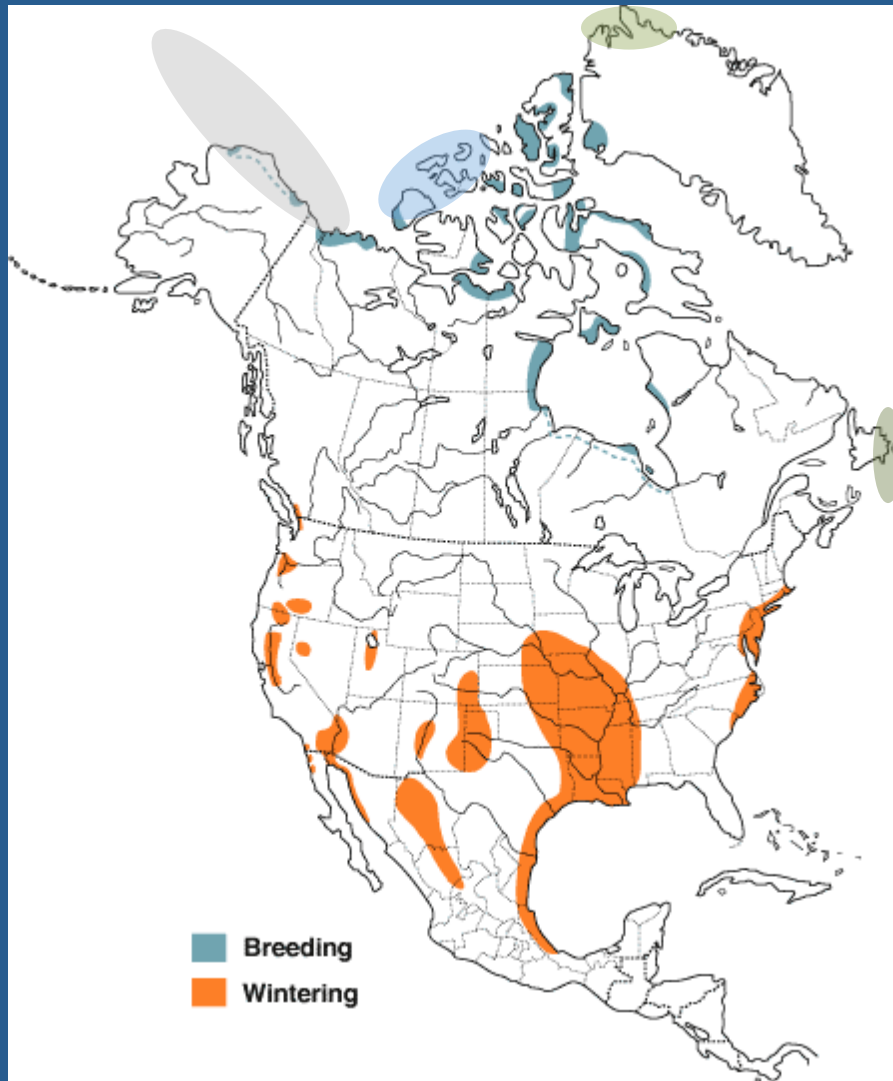


FIGURE 24. *Anser caerulescens* Linnaeus. Dots = present breeding distribution. Dotted line = borders of supposed former breeding range in Eurasia (USPENSKI 1965). Solid lines = borders of potential Last-Glacial breeding grounds.

Proposed Refugia for Snow Goose
(*Anser caerulescens*)

Lesser Snow Goose

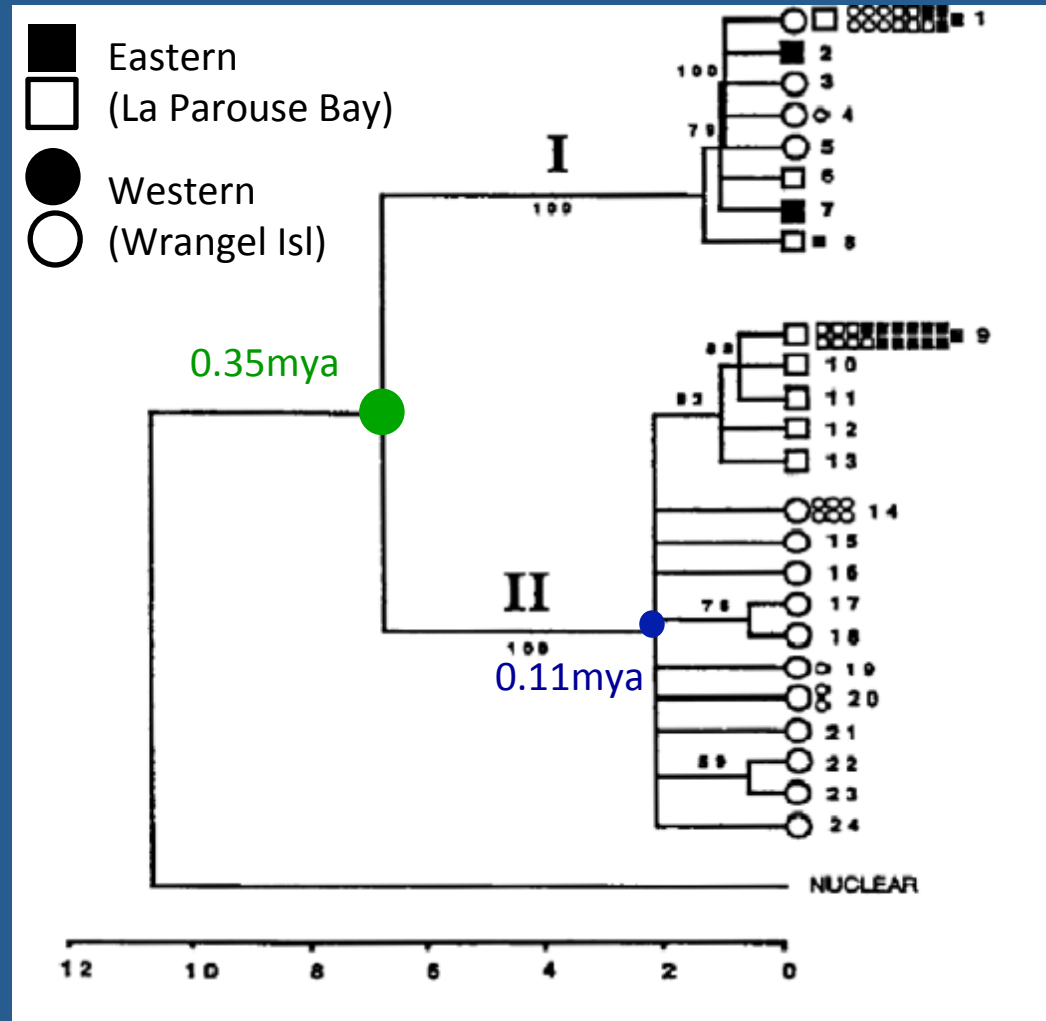
- Geographic variation

- Lesser Snow Goose (mid continent and western, including Beringia)
- Greater Snow Goose (Eastern)

- Clade Structure (mtDNA)

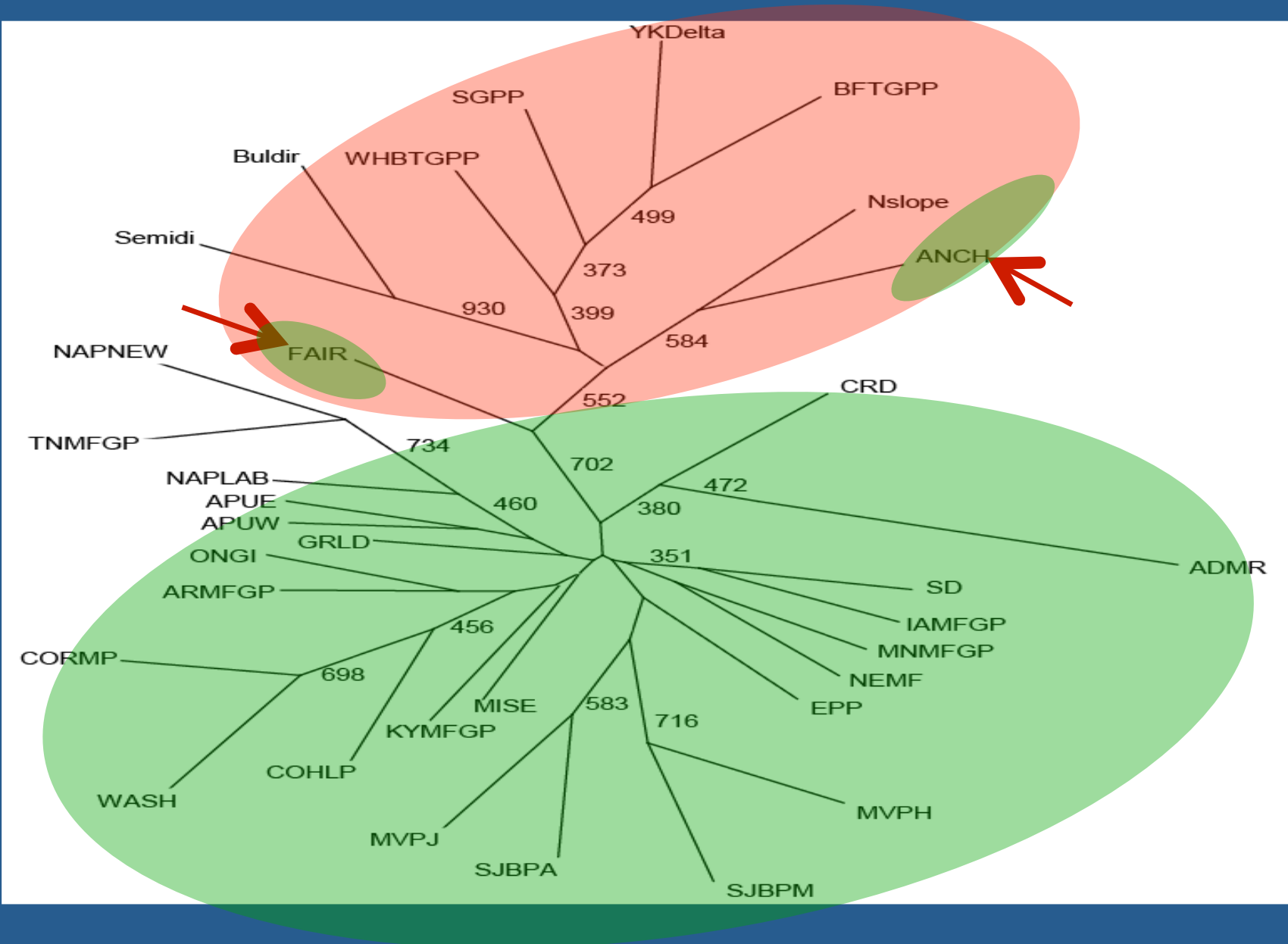
- 2 clades (6.8% distance)
 - Clade I: no consistent geographic structuring
 - Clade II: sequences among mtDNA types concordant with geographic distribution

Quinn (1992). *Molecular Ecology* 1: 105-117



Genetic Studies of Snow Geese

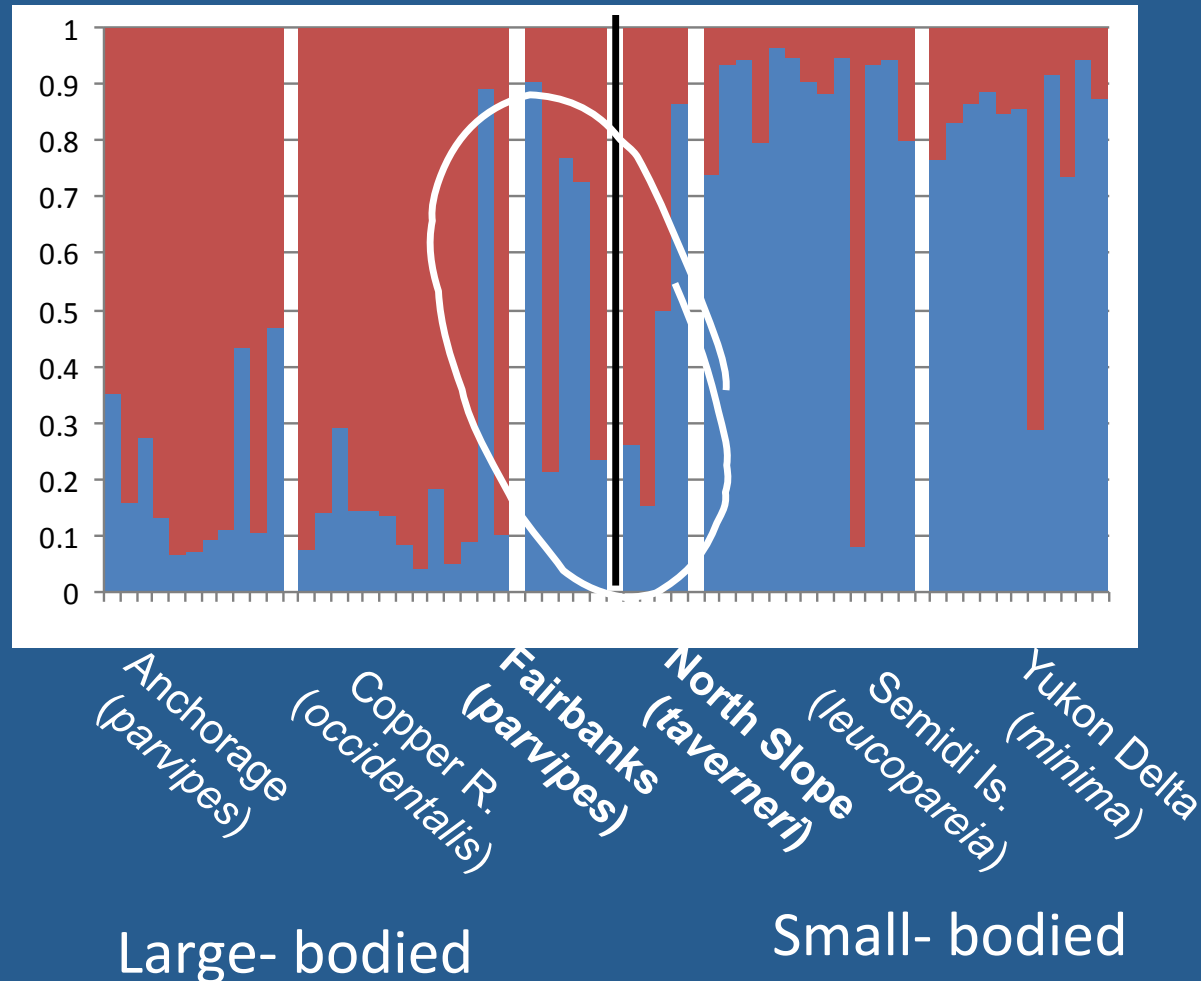
- Quinn (1992): 2 ancestral Snow Goose populations
- Cooke et al. (1988): white- and blue morphs allopatric until very recently (about 70 years ago), after which the group is characterized by sympatry and gene flow
 - Changing agricultural practices
 - Similar changes not observed in Beringian populations
- Weckstein et al. (2002): Reanalysis of Quinn's (1992) and Cooke et al. (1988) data
 - Same divergent lineages as Quinn
 - Past allopatry between Lesser and Greater Snow Goose (Cooke et al.)
 - Hybridization episodes
 - Ross's Goose (*Anser/Chen rossii*) x Lesser Snow Goose
- Rainey et al. (2011): Added population-level analyses of western lineage
 - Same divergent lineages as Quinn
 - Fine-scaled population structuring between Wrangel Island populations
 - Asymmetry in gene flow



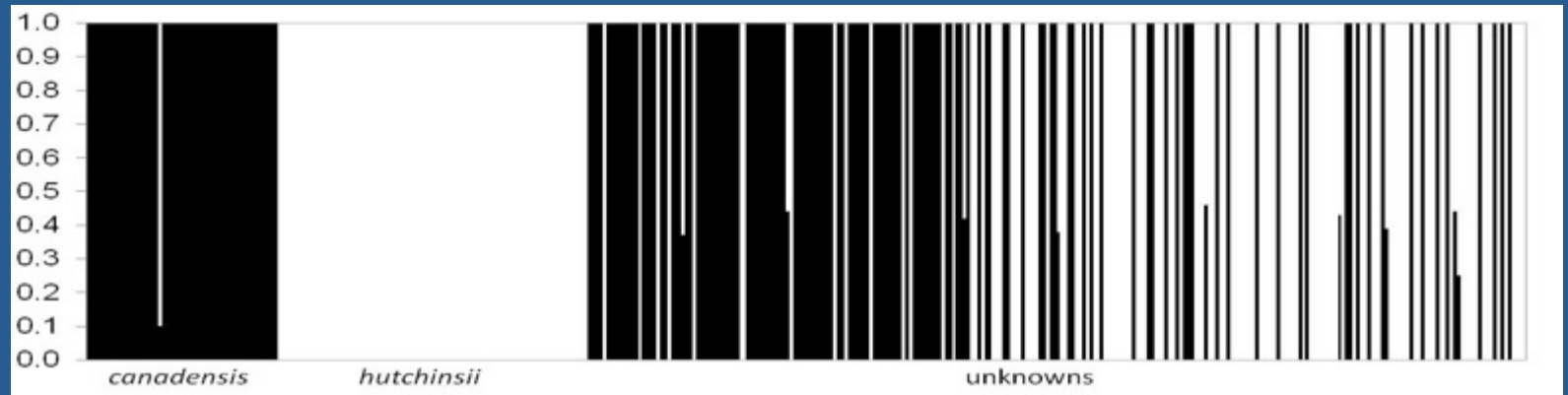
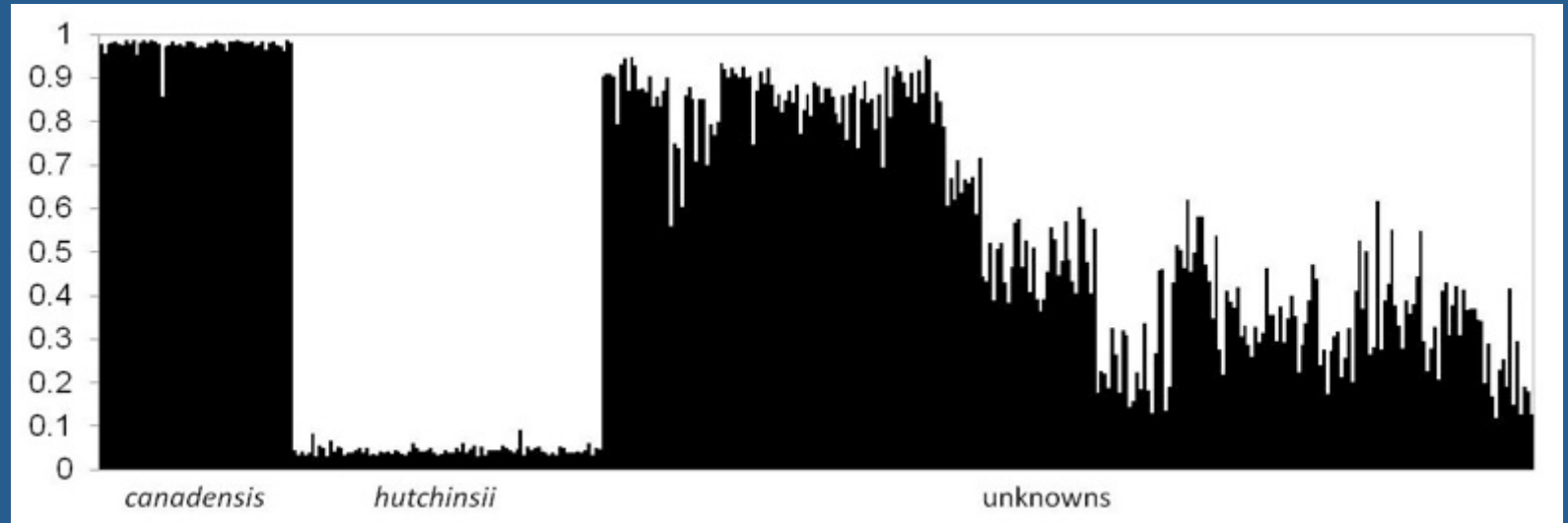
Neighbor-joining Tree
based on 8 microsatellite loci

Results and Conclusions: data from 5 nuclear introns

- Intron data: also suggest 2 clusters and admixture
- Isolation with Migration (IM)
 - $M = \sim 2/\text{generation}$
 - but 95% CIs overlap zero
 - » Reject gene flow
 - » Support incomplete sorting of nuclear DNA



BAYESIAN CLUSTER ANALYSIS STRUCTURE AND BAPS



Southeast



Northwest

Baseline populations

Unknowns

Hybrids and Policy

- Species legislation history (example: ESA) (Haig and Allendorf 2006)
 - 1973: No mention of hybrids in passage of ESA
 - 1977: US-DOI defines ‘wildlife’ to include hybrids
 - 1977, 1983: US Solicitor states hybrids not protected under ESA
 - Pre-1990: USFWS discourages conservation efforts for hybrids
 - “Might not help and could hinder recovery...”
 - 1990: USFWS: “rigid standard should be revisited because issue of hybrids more properly a biological issue than a legal one”
 - 1996: USFWS and NMFS propose intercross policy for protection of hybrids
 - 2000: USFWS and NMFS render policy on controlled propagation of captive populations
 - Present: Proposed intercross policy not approved or disapproved.

Phylogeography and Population Structure of North American Brant (*Branta bernicla*)



S. L. Talbot, G. K. Sage, J. R. Gust, J. R. Rearick, D. Ward, D. V. Derksen- Alaska Science Center, U. S. Geological Survey, Anchorage, Alaska, USA

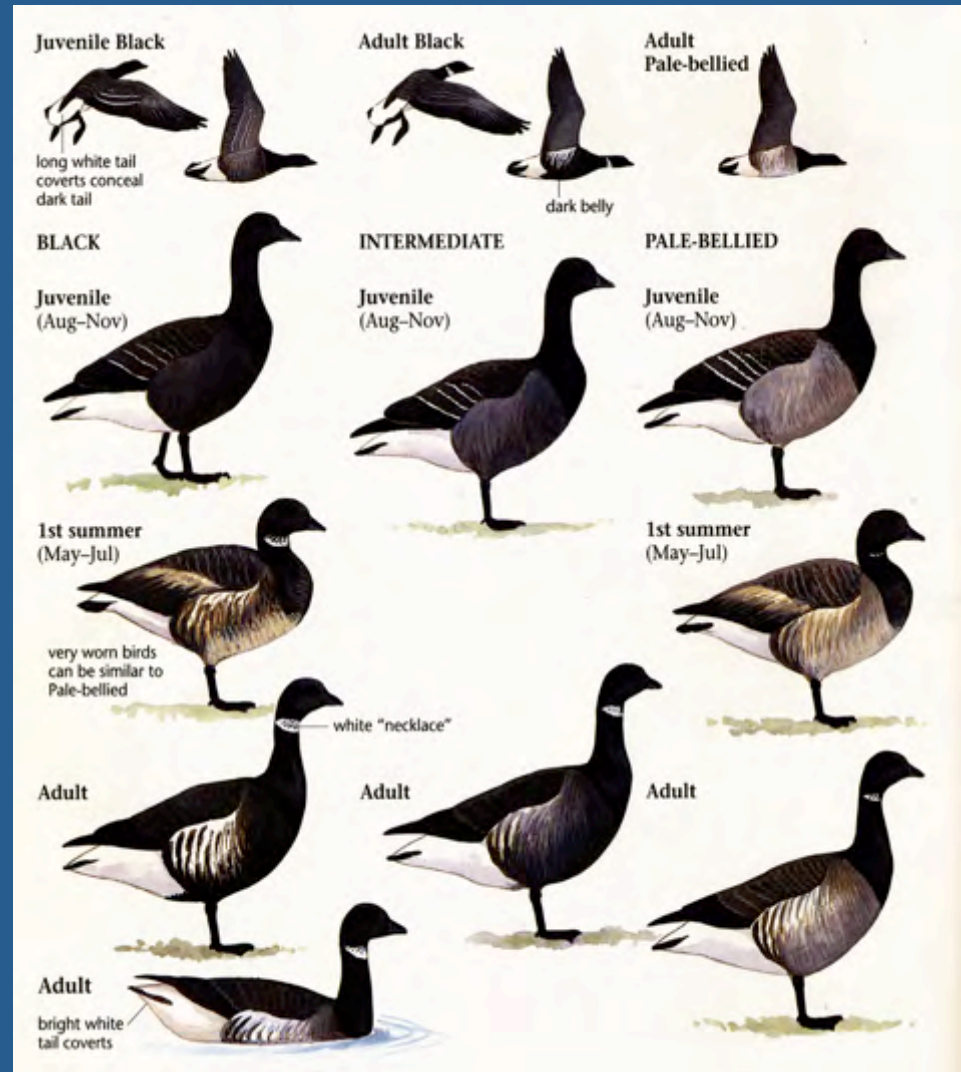
W.S. Boyd, K. Dickson- Canadian Wildlife Service, Canada

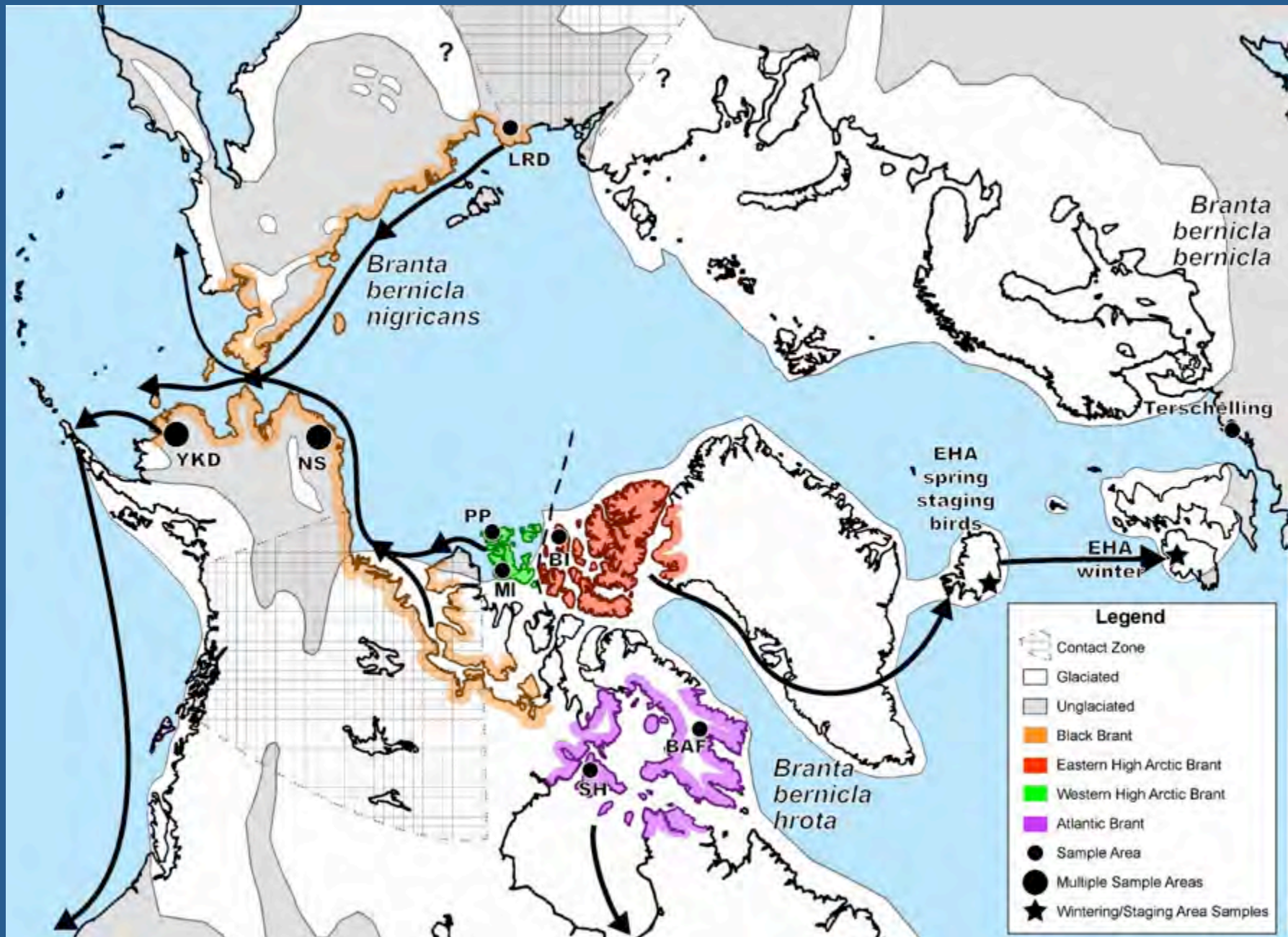
Kendrew Colhoun- Wildfowl and Wetlands Trust, Slimbridge, UK

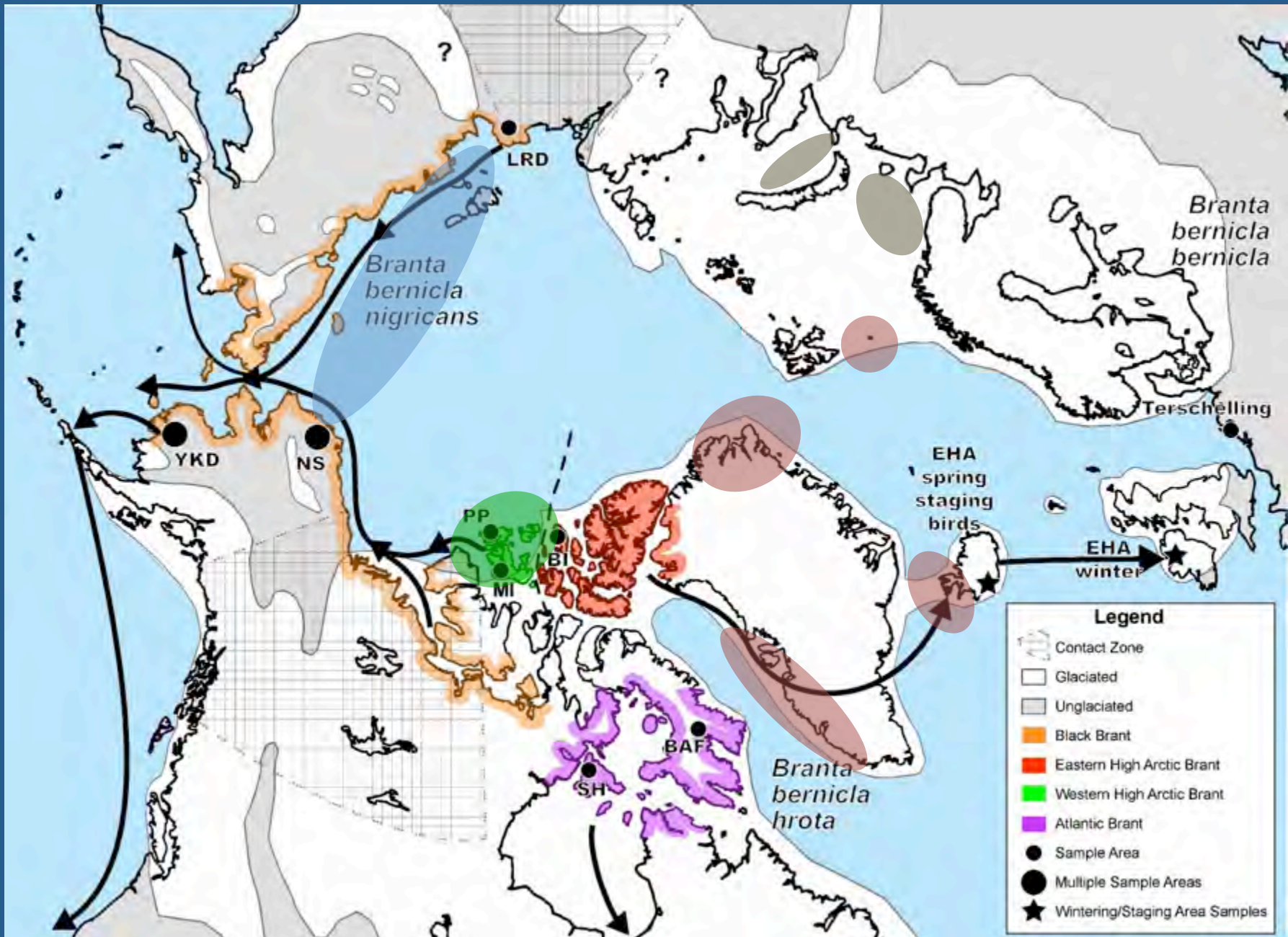
Taxa/stocks for management/conservation

Three subspecies/four stock (hypothesis)

- Dark Bellied Brant Goose (*Branta bernicla bernicla* Linnaeus)
 - Western Siberia and Europe
- Black Brant (*B. b. nigricans* Lawrence)
 - Northwestern Canada
 - Northern and western Alaska
 - Northeastern Siberia
- Light-Bellied Brant Goose (*B. b. hrota* Müller)
 - Eastern and western Atlantic
 - Four Stocks
 - Eastern Atlantic High Arctic
 - Eastern Canadian Low Arctic
 - Eastern Canadian High Arctic
 - Western Canadian High Arctic







Legend

- Contact Zone
- Glaciated
- Unglaciated
- Black Brant
- Eastern High Arctic Brant
- Western High Arctic Brant
- Atlantic Brant
- Sample Area
- Multiple Sample Areas
- Wintering/Staging Area Samples

Black Brant (*B.b. nigricans*)



Melville Is. Canada

WHA (Grey-belly) Brant



Melville Is. Canada

Light-bellied Brant (*B.b. hrota*)

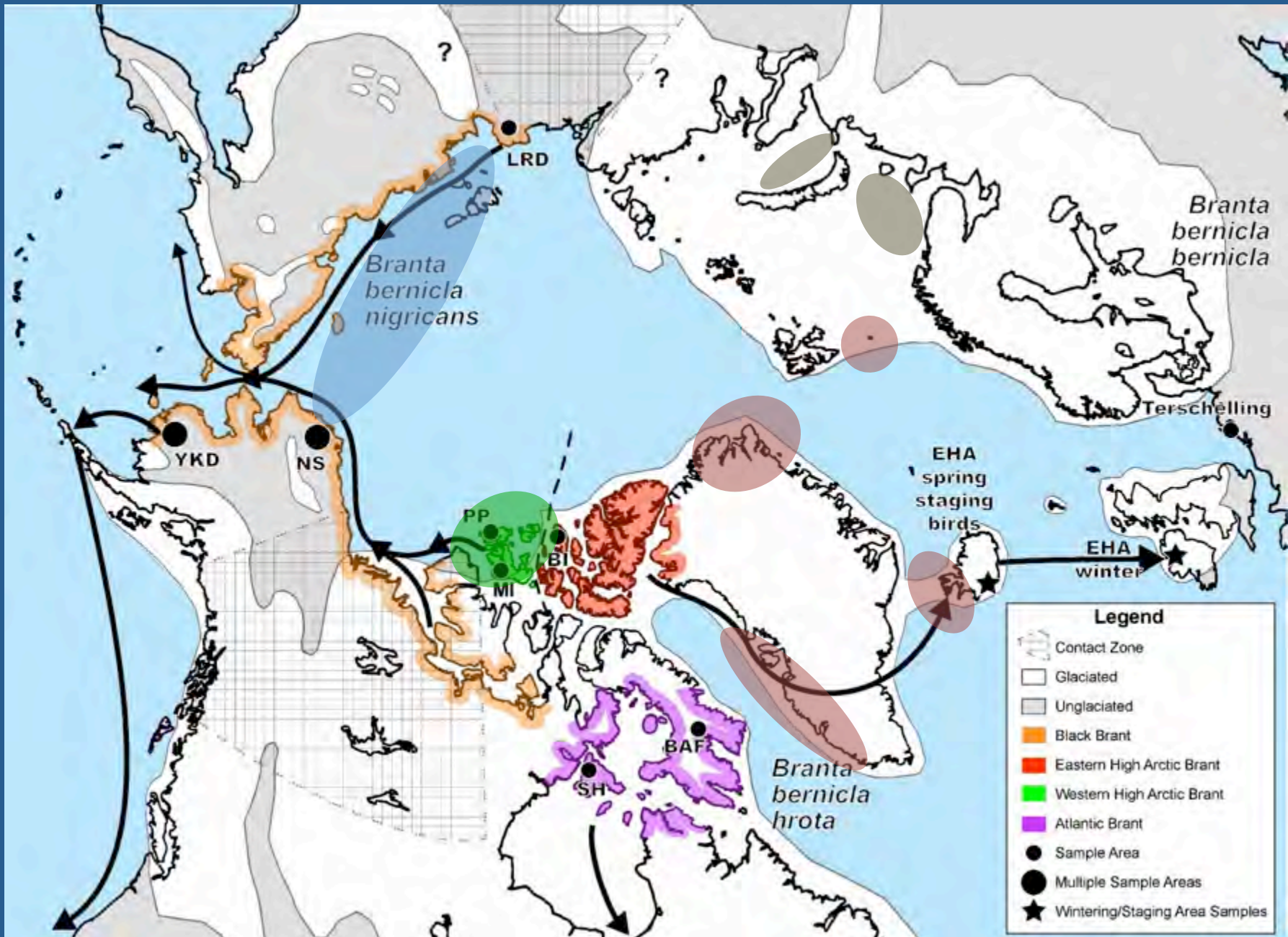


Bathurst Is. Canada

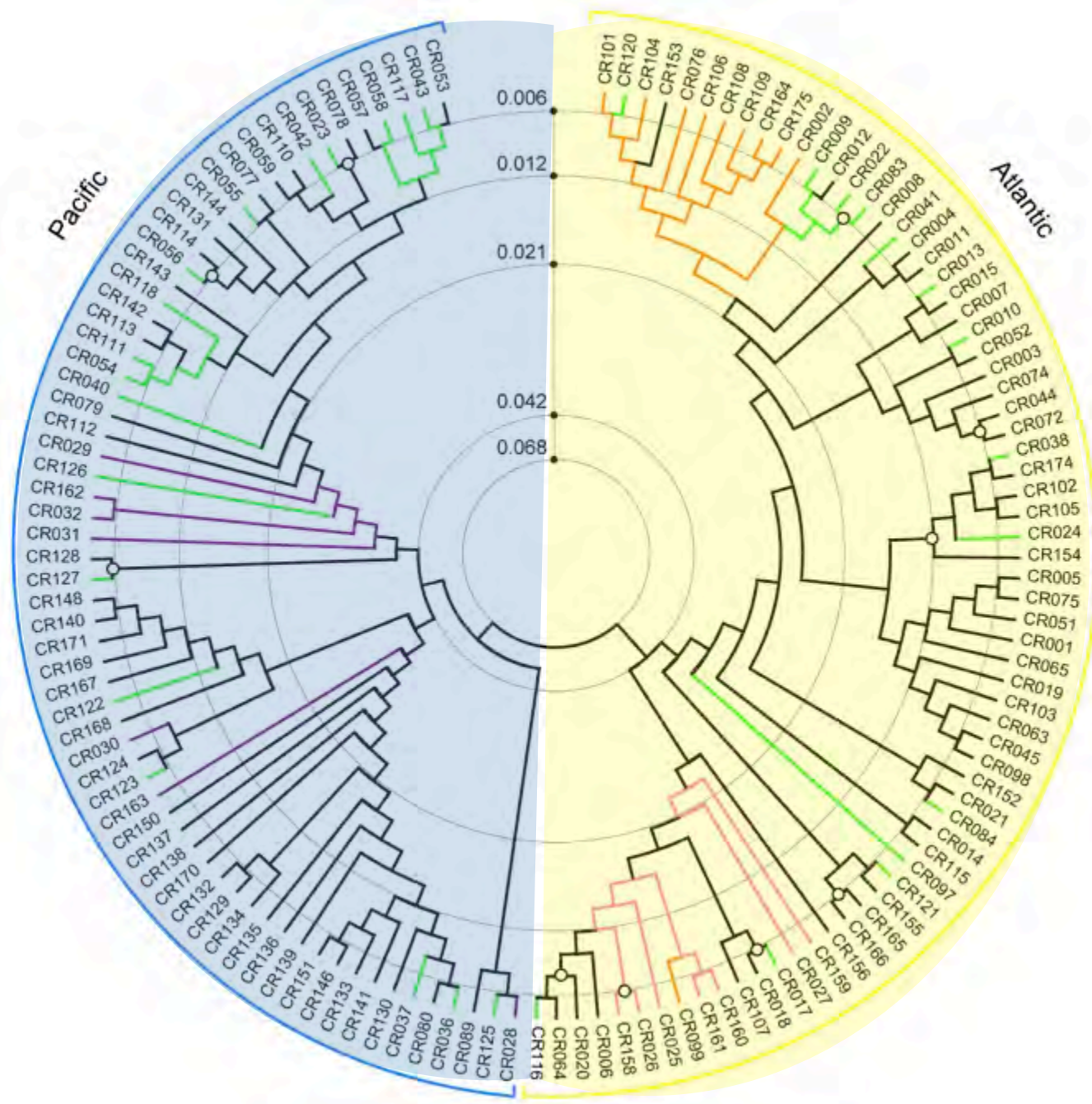
EHA (Light-belly) Brant



Bathurst Is. Canada



Maximum Likelihood
mtDNA control region
Branta bernicla

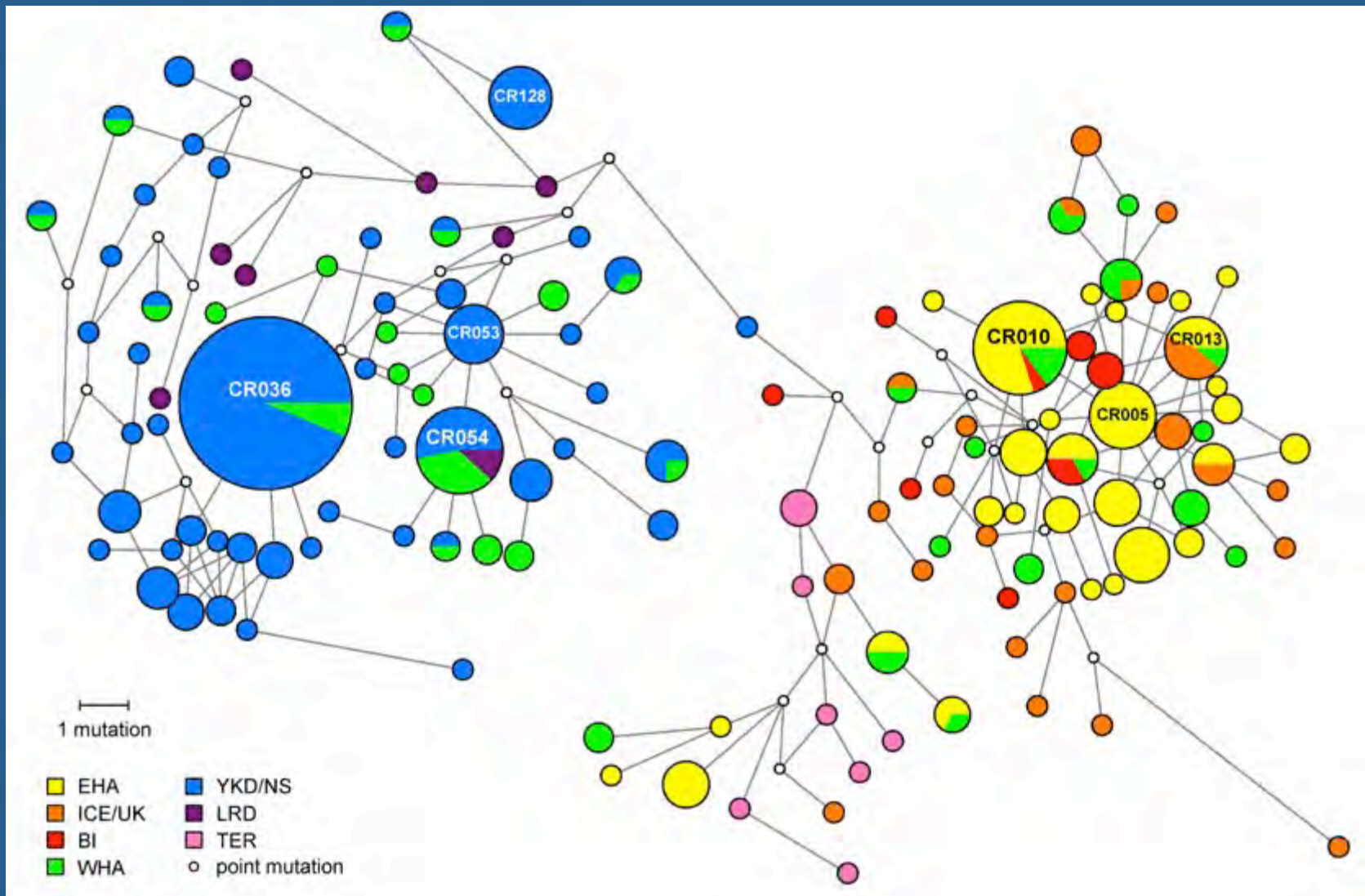


HKY+G_(0.17)+I_(0.49)
BIC = 5894.32
AIC = 3553.455

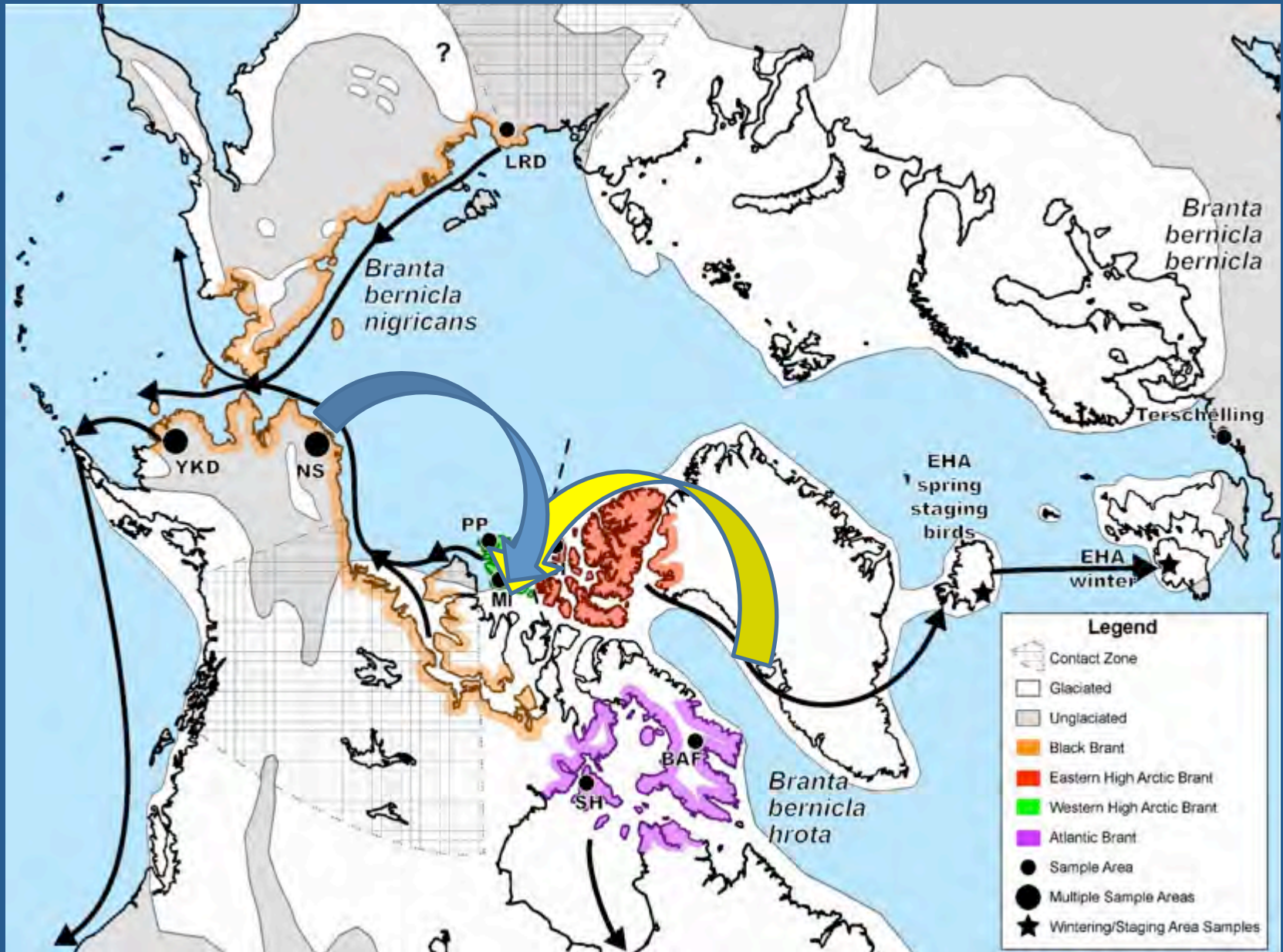
134 haplotypes

- WHA (PP/MEL)
- BI
- TER (*B. b. bernicla*)

Unrooted Network Brant mtDNA Control Region Haplotype Relationships



“MIGRATE” (Gene Flow) Analysis



Summary - Brant

- Brant in North America occur as 2 ancestral populations
 - likely held in two separate refugia, one in the Pacific, and one in the Atlantic.
- Clade divergence not yet timed but:
 - average distance among clades similar to Clades I and II Snow Goose (~7%), estimated divergence = 350,000 years ago (Quinn 1992)
- There is population-level substructuring within each clade, higher for mtDNA, and lower but still significant for microsatellite loci.
 - Gender bias in philopatry (female) and gene flow (male-mediated)

Summary - Brant

- Gene flow polarity analysis suggests populations within the Atlantic group are expanding westward, and within the Pacific group are expanding eastward, resulting in introgression between the two groups at WHA habitats (relationships to suture zone).
- Differentiation between WHA brant and populations on either side are not deep; fails to support the hypothesis that the ancestors of the WHA brant were held in a WHA refugium.