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Discrimination among Similarly Colored Goose Species in Federal Harvest Surveys

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Discrimination among similarly colored goose species in federal harvest surveys

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Abstract

Each year in the United States, fall-winter (sport) harvests of goose species are estimated from federal surveys coordinated by the United States Fish and Wildlife Service, including the Migratory Bird Harvest Survey to estimate total goose harvest and the Parts Collection Survey (PCS) to estimate the species and age composition. For the PCS, randomly selected hunters collect tail and wing feathers of each goose shot during the hunting season, and then biologists determine the age class and species of each sample at organized events (Wingbees) in each of the 4 flyways (Pacific, Central, Mississippi, and Atlantic). For similarly colored goose species, cackling (Branta hutchinsii) versus Canada (B. canadensis) geese (dark geese) and Ross's (Anser rossii) versus snow (A. caerulescens) geese (light geese), different protocols evolved among Wingbees to differentiate samples into groupings of management interest, leading to difficulties in estimating species-level harvests among the 4 flyways or nationally. We conducted a study among the United States flyways during 2019-2022 to derive thresholds of central tail feather length to discriminate between dark geese and between light geese. We compared morphological- and genetic-based approaches. There was support for 2 distinct mitochondrial DNA (mtDNA) clades in dark and light geese, but only dark goose clades corresponded with central tail feather lengths (morphological size and species identification). Derived thresholds for central tail feather lengths of dark geese in the 3 westernmost flyways using genetic-based species' discrimination were 145 mm for adults and 134 mm for juveniles, approximately 13 mm and 9 mm less, respectively, than thresholds using morphological-based species' discrimination. There was limited ability to discriminate light geese based on either mtDNA or central tail feather lengths. We suggest managers use our derived thresholds based on genetic-based species' discrimination to classify dark goose PCS samples. More advanced genome analyses should be conducted before changing current Wingbee protocols for light geese. Lastly, we encourage more studies to incorporate genetic analyses to complement morphological discrimination.

KEYWORDS

cackling goose, Canada goose, discrimination, genetics, harvest, harvest survey, Ross's goose, snow goose

Harvest is an important metric for monitoring status and trends, efficacy of harvest regulations, and, in conjunction with band-recovery data, abundance of many North American goose populations via Lincoln estimates (Lincoln 1930, Alisauskas et al. 2009, U.S. Fish and Wildlife Service [USFWS] 2023, Canadian Wildlife Service Waterfowl [CWS] Committee 2023). Since 1962, the USFWS has annually conducted a cooperative Migratory Bird Harvest Survey to estimate the total fall-winter (sport) harvests of ducks and geese in the United States and a Parts Collection Survey (PCS) to estimate the species and age composition (Raftovich et al. 2023). Similarly, since 1967, the CWS has annually conducted a cooperative Harvest Questionnaire Survey and Species Composition Survey to estimate waterfowl harvests in Canada (Smith et al. 2022). For all states, excluding Hawaii, the Migratory Bird Harvest Survey and PCS provide total fall-winter harvest estimates for 6 goose species: greater white-fronted goose (Anser albifrons), brant (Branta bernicla), snow goose (A. caerulescens), Ross's goose (A. rossii), Canada goose (B. canadensis), and cackling goose (B. hutchinsii; sample sizes are too small for emperor geese [A. canagicus]). Each year the USFWS selects a random sample of hunters to participate in the PCS. Participating hunters remove the tail feathers and primary wing feather tips from each goose shot during the hunting season and mail their samples in pre-assigned envelopes to the USFWS (Raftovich et al. 2023). Biologists then determine the species and age class (juvenile [hatch-year] or adult [after-hatch-year]) of each goose sample based on feather coloration and characteristics at annual organized events (Wingbees), which occur in the 4 United States flyways (Pacific, Central, Mississippi, and Atlantic).

Biologists have used size, specifically tail feather length, and flyway-specific Wingbee protocols to discriminate species of geese with similarly colored tail and wing feathers. The intent was to separate Ross's geese from snow geese (light geese) and various management populations of cackling and Canada geese (dark geese). The Flyway Councils and USFWS currently recognize 20 management populations of light (*n* = 5) and dark (*n* = 15) geese (USFWS 2023). For dark geese, biologists developed flyway-specific protocols to try to differentiate the harvests of the 7 subspecies that occur in the Pacific Flyway (Johnson et al. 1979, Trost 1997, Pearce and Bollinger 2003), small Canada geese from large, or temperate-nesting, Canada geese in the Central Flyway (Johnson et al. 2004, Central Flyway Council 2013), and sub-Arctic-nesting Canada geese from giant, or temperate-nesting, Canada geese in the Mississippi Flyway (Moser and Rolley 1990, Merendino et al. 1994, Leafloor and Rusch 1997, Thompson et al. 1999, Mississippi Flyway Council 2017). For light geese, biologists developed separate protocols based on flyway-specific analyses (Johnson et al. 2004, Oldenburger et al. 2011). Wingbee protocols in the Atlantic Flyway did not involve discrimination of these species groupings or measuring feathers because distribution and harvests of

Ross's and cackling goose that far eastward were presumed to be negligible (Baldassarre 2014, Jónsson et al. 2020, Mowbray et al. 2020*a*).

Past methods to estimate goose harvests from the PCS have limitations. Flyway-specific Wingbee protocols allowed for separation of specific populations of management interest for each flyway but hindered a uniform approach to estimate species-level harvests in a similar manner among flyways or nationally. This complicated the estimation of national harvests of cackling and Canada geese, which recently became a management priority. In April 2020, the USFWS updated its List of Migratory Birds (50 CFR 10.13) and distinguished cackling goose and Canada goose as separate species (85 FR 21286). Previously, cackling goose was included within the Canada goose listing and combined Canada and cackling goose harvests were reported as Canada goose in the annual USFWS harvest report (Raftovich et al. 2023). Assessing status and harvests of game species listed in 50 CFR 10.13 (cackling goose now separated from Canada goose) is a priority of the USFWS and a primary objective of federal harvest surveys (Raftovich et al. 2023). Another limitation of past protocols was that biologists classified and recorded data differently among flyways, limiting post hoc or comprehensive analyses. Additionally, many of the Wingbee species' discrimination thresholds to classify species and populations were based on analyses conducted 20-30 years ago. Managers have expressed concern that the body size of some species may have changed during this time, particularly for Ross's geese and the midcontinent population of lesser snow geese (A. c. caerulescens), in which there is evidence of recent population declines and effects of density dependence (Alisauskas et al. 2022, Baldwin et al. 2022, Weegman et al. 2022). Lastly, Wingbee species' discrimination thresholds were based only on morphological analyses, whereas genetic-based approaches may provide more accurate discrimination (Inman et al. 2003. Shorev et al. 2007).

No comprehensive study to compare morphological- and genetic-based approaches for classifying goose PCS samples has been conducted. Genetic studies reported distinct separation of cackling goose and Canada goose (these species were not sister taxa; Quinn et al. 1991, Paxinos et al. 2002, Scribner et al. 2003, Leafloor et al. 2013, Ottenburghs et al. 2016). This underpinned the American Ornithologists' Union decision to include cackling goose as a separate species from Canada goose (American Ornithologists' Union 2004) and subsequently the USFWS followed this designation (85 FR 21286). Fewer genetic studies on light geese have been undertaken. Researchers reported limited genetic separation of light geese and 2 divergent mitochondrial DNA (mtDNA) clades; however, these mtDNA clades were not associated with current species' taxonomic identification (Avise et al. 1992, Quinn 1992, Weckstein et al. 2002, Shorey 2005, Ottenburghs et al. 2016).

Managers have raised concerns about the inconsistency of goose Wingbee protocols among flyways and potential inaccuracy of goose harvest estimates, which could bias Lincoln estimates and assessment of population status and trends. We conducted a study during 2019–2022 with data from all 4 United States flyway Wingbees to evaluate central tail feather length thresholds to discriminate species using morphological- and genetic-based approaches. Our objective was to develop standardized United States Wingbee and PCS protocols to accurately estimate the harvests of dark geese and light geese. We predicted that there would be similarity between species' discrimination thresholds using genetic- and morphological-based methods because central tail feather lengths should correspond to genetic species' identification, species' discrimination thresholds would differ by age class and flyway because these variables were important in past PCS analyses and protocols, and discrimination between cackling geese and Canada geese would be more evident than between Ross's geese and snow geese, given greater separation in central tail feather lengths and genetic differentiation based on past studies.

STUDY AREA

Hunters selected for the PCS were from all states in the United States (except Hawaii), an area that encompassed nearly all ecotypes in North America (Commission for Environmental Cooperation 1997, Omernik and Griffith 2014). Data for our study were provided by hunters that participated in the PCS during the 2018–2019 to 2021–2022

hunting seasons. Hunters harvested geese during waterfowl hunting seasons in each state (88 FR 56489), primarily during September–March. During the 2021–2022 hunting season, there were an estimated 2,647,600 geese harvested by 545,400 active goose hunters in the United States, and the number of active goose hunters varied by flyway (Pacific = 17%; Central = 25%; Mississippi = 42%; Atlantic = 17%; Raftovich et al. 2023). Biologists examined the hunter-harvested PCS samples at the 4 Wingbees, which occurred in Redding, California; Hartford, Kansas; Carbondale, Illinois; and Laurel, Maryland.

METHODS

We implemented the same data collection protocols at all 4 United States flyway Wingbees during 2019–2022 with each year representing the previous hunting season (e.g., the 2019 Wingbee included samples from the 2018–2019 hunting season, spanning approximately Sep 2018 to Mar 2019). We did not include data from Canada in our study because of funding limitations and because the federal harvest surveys of each country are administered separately. The CWS also recently updated their Species Composition Survey species' discrimination thresholds for dark geese based on genetic analyses (M. Gendron, CWS, unpublished data). Biologists classified species and age class of each PCS goose sample based on feather coloration and characteristics (Hanson 1967, Tacha et al. 1989, Johnson et al. 2004, https://www.fws.gov/lab/featheratlas/; accessed 15 Apr 2023) and measured the central tail feather length of all measurable dark and light goose samples. If the central tail feather length could not be measured (missing, molted, or not fully developed), biologists classified samples to small (cackling, Ross's) or large (Canada, snow) species only. Biologists recorded central tail feather length data for dark goose samples during the first 3 years of the study (2018–2019 to 2020–2021 hunting seasons) and light goose samples during all 4 years (2018–2019 to 2021–2022 hunting seasons) to further increase sample size.

For our genetic analyses, we collected a random subsample of PCS juvenile and adult dark and light goose feathers during the first 2 years of the study (2018-2019 to 2019-2020 hunting seasons) from all harvest states, months, and ranges of central tail feather length. To ensure that we obtained sufficient sample sizes for analyses, we used prior PCS data to determine the distribution of central tail feather lengths of the 4 species and age class groupings of interest (juvenile dark geese, adult dark geese, juvenile light geese, adult light geese). We then divided the distribution into 8 equal intervals between the minimum and maximum quantiles. We collected up to 25 feather samples in each of the 8 measurement intervals (n = 200 samples [25×8]), when possible, for each species and age class grouping in each flyway (n = 16 groups: 2 species groupings × 2 age classes × 4 flyways). We included 3 feathers from each PCS sample in an envelope labeled with the record information and shipped all envelopes to the United States Department of Agriculture Animal and Plant Health Inspection Service Wildlife Services National Wildlife Research Center in Fort Collins, Colorado, USA, for genetic analyses.

Genetic analyses

For dark geese, we conducted simulations to determine the number of samples to select for genetic analyses and deriving species' discrimination thresholds using logistic models fit to genetic species' classifications. We used available PCS measurement data and finite mixture models (see below) to estimate an approximate measurement threshold that presumably discriminated between species. We evaluated how sample size and the concentration of selected samples near the presumed threshold (e.g., ± 1 SD, ± 0.25 SD) affected the bias and precision of the estimated species' discrimination threshold using logistic models (50% probability value; see below). To minimize bias and precision of the 50% probability value, our final sampling scheme involved randomly selecting at least 50 samples from each species grouping, age class, and flyway. We selected most samples (>75%) from \pm 0.75 standard deviation of the presumed species' discrimination threshold and fewer samples (<25%) from the lower and upper

quantiles of data (samples with the smallest and largest central tail lengths, respectively). Because most cackling geese occur in the Pacific and Central flyways, we increased our sample sizes in these 2 flyways to approximately 100 adults and 60 juveniles (Table 1).

For light geese, we focused our analyses on adults and randomly selected approximately 50 samples from the Pacific, Central, and Mississippi flyways and 30 samples from the Atlantic Flyway (Table 1). We selected fewer samples from the Atlantic Flyway because of a limited sample size of smaller central tail feather lengths and because Ross's geese were presumed to not frequently occur that far eastward. We selected half of the samples from the

TABLE 1 Number of cackling and Canada goose (dark goose) and Ross's and snow goose (light goose) samples submitted to the United States Fish and Wildlife Service Parts Collection Survey (PCS) during the 2018–2019 to 2021–2022 hunting seasons. Samples sizes are shown by category as determined by biologists at the United States flyway Wingbees where they measured central tail feather length, classified samples to small species (cackling or Ross's) or large species (Canada or snow), or did not measure or classify samples. Of these samples, we collected a subset for genetic analyses and tested a smaller subset, of which most samples provided sufficient mitochondrial DNA (mtDNA) amplification. We present summaries by flyway (Atlantic, Mississippi, Central, Pacific) and age class (Ad = adult, Juv = juvenile). To conserve space, we did not include 680 unknown age samples.

		Atlantic		Mississippi		Central		Pacific		
Data set		Ad	Juv	Ad	Juv	Ad	Juv	Ad	Juv	Total
Cackling-Canada goose (dark goose)										
PCS ^a	Measured	6,961	806	4,895	460	6,367	528	4,604	900	25,521
	Classified, small	0	23	7	43	45	172	37	150	477
	Classified, large	1,942	2,447	1,314	1,693	732	1,860	360	839	11,187
	Not measured or classified	14	1	73	16	4	2	0	0	110
	Total	8,917	3,277	6,289	2,212	7,148	2,562	5,001	1,889	37,295
Genetic ^b	Collected	386	171	230	190	449	204	453	275	2,358
	Tested	57	43	55	50	107	59	107	68	546
	Sufficient amplification	54	43	53	47	98	53	94	57	499
	% (sufficient/tested)	95%	100%	96%	94%	92%	90%	88%	84%	91%
Ross's-snow goose (light goose)										
PCS ^c	Measured	266	86	270	66	768	255	2,056	1,374	5,141
	Classified, small	0	0	0	6	2	2	1	4	15
	Classified, large	15	22	32	26	47	18	95	219	474
	Not measured or classified	70	38	155	60	791	275	86	57	1,532
	Total	351	146	457	158	1,608	550	2,238	1,654	7,162
Genetic ^b	Collected	53	22	114	35	242	104	232	220	1,022
	Tested	31		50		50		57		188
	Sufficient amplification	22		27		45		38		132
	% (sufficient/tested)	71%		54%		90%		67%		70%

^aTotals were the number of PCS samples submitted during the 2018-2019 to 2020-2021 hunting seasons.

^bTotals were the number of PCS samples collected for genetic analyses during the 2018–2019 to 2019–2020 hunting seasons.

^cTotals were the number of PCS samples submitted during the 2018-2019 to 2021-2022 hunting seasons.

lower quantiles of central tail feather lengths and half of the samples from the upper quantiles. Because past studies indicated light geese had less genetic differentiation than dark geese, we believed our sampling scheme for light geese would increase the likelihood that we would classify the most samples to a genetic clade, rather than selecting most samples near the presumed species' discrimination threshold (intermediate central tail feather lengths) as we did for dark geese.

We extracted genomic DNA from selected feather samples using Qiagen DNeasy Blood and Tissue extraction kits following a manufacturer's protocol for feather extractions, which included 1,4-dithiothreitol to aid in feather digestion and cell lysis (Qiagen 2020). We amplified an approximate 400-base-pair fragment of the mtDNA control region using C1 and C1R primers as described in Sorenson and Fleischer (1996). The 20-µL polymerase chain reaction (PCR) contained 1 µL extracted DNA template, 2 µL AmpliTaq Gold 10X Buffer II (Applied Biosystems, Foster City, CA, USA), 1 µL 25-mM MgCl₂ (Applied Biosystems), 1.6 µL 10-mM dNTP mix (2.5 mM each dNTP; Invitrogen, Waltham, MA, USA), 1 μL each 10-μM primer, 0.1 μL 10-mg/mL Bovine Serum Albumin (Thermo Fisher Scientific, Waltham, MA, USA), 0.5 µL AmpliTaq Gold DNA Polymerase (Applied Biosystems), and 11.8 µL molecular grade H₂O. Thermocycling conditions were an initial denaturation at 95°C for 10 minutes, followed by 40 cycles of 95°C for 45 seconds of denaturation, annealing at 60°C for 1 minute, extension at 72°C for 1 minute, and a final extension at 72°C for 7 minutes. We purified PCR products using ExoSAP-IT (Thermo Fisher Scientific). We performed cycle sequencing reactions in 10- μ L reactions with 1 μ L of purified PCR product, 1 μ M of primer, 0.25 µL of BigDye Terminator version 3.1, and 2.275 µL of 5x sequencing buffer (Thermo Fisher Scientific). We conducted sequencing on an ABI 3500xl genetic analyzer (Thermo Fisher Scientific). We visualized, edited, and aligned DNA fragments using Sequencher version 5.4.6 (Gene Codes Corporation, Ann Arbor, MI, USA). We removed redundant haplotypes using PAUP* version 4.0a169 (Swofford 2003).

To identify Anser and Branta clades based on previous genomic work (Ottenburghs et al. 2016, 2017), we added an emperor goose and other Branta species haplotypes from the National Center for Biotechnology Information's GenBank (Benson et al. 2015; AY112973, KJ680301 brant; AY072568, AY072570 nene [B. sandvicensis]; AY112976 red-breasted goose [B. ruficollis]; FJ688136, FJ688137, FJ688138, FJ688139, FJ688140, FJ688141, FJ688142, FJ688143, FJ688144, FJ688145 cackling goose; AY112974, AY072575 barnacle goose [B. leucopsis]; NC007011, JQ036310 Canada goose; AY072583 emperor goose). We did not use any GenBank sequences for light geese because it would not help elucidate relationships in our phylogenetic tree, as there were shared haplotypes between the species (Weckstein et al. 2002). We performed maximum likelihood (ML) tree generation using the evolutionary model that best fit our sequence data. For model selection, we used Akaike's Information Criterion corrected for small sample size (AIC_c; Burnham and Anderson 2002) with jMODELTEST (Posada 2008) and applied the estimated model parameters to the likelihood settings in PAUP* version 4.0a169 (Swofford 2003). For the model test, we chose 11 substitution schemes, and we tested for among-site rate variation and equal rates in invariable sites, gamma, and both. We used an outgroup root of emperor goose, brant, and red-breasted goose because phylogenetic relationships of Anserinae were well defined and Anser and Branta were sister taxa (Donne-Goussé et al. 2002, Sun et al. 2017). We generated ML trees starting from a neighbor-joining tree with a tree-bisection reconnection that had a reconnection limit of 8 and an unlimited number of MaxTrees. We assessed branch support by bootstrapping with 1,000 replicates of fast stepwise-addition and retaining groups with >50% frequency (Felsenstein 1985) in PAUP*.

Species' discrimination thresholds

For genetic-based methods, we fit logistic models in SAS (SAS Institute 2015) to the mtDNA species' classifications to derive thresholds for central tail feather lengths to discriminate species. We created models that included additive effects and main effect interactions of central tail feather length, age class, and harvest flyway. We evaluated model fit and effect significance using AIC_c (Burnham and Anderson 2002). We presented the coefficient values and 95%

confidence intervals from the top model to further evaluate effect size and significance (log of the odds ratio, with 0 indicating the explanatory variable has no directional influence on the response variable). We calculated the species' discrimination threshold as the central tail feather length where the probability of species' assignment was equal (50% probability) and used the delta method to calculate the variance (Powell 2007). We selected the 50% probability because it is the value that minimizes overall species' classification error when estimating proportions from samples obtained from 2 overlapping normal distributions. We focused our analyses on dark geese harvested in the Pacific and Central flyways because we had very few or no samples of genetically classified cackling geese in the Mississippi and Atlantic flyways and poor genetic species' classification and model fit for light geese.

For morphological-based methods, we fit finite mixture models using package mixR (Yu 2022) in Program R (R Core Team 2022) to the distribution of central tail feather lengths from each species' grouping and age class of all PCS samples to estimate means and variances of the underlying component distributions. We specified 2 component distributions and modeled these as being normally distributed with unequal variances. We calculated the species' discrimination threshold as the central tail feather length where the upper portion (right tail) of the small species' distribution (cackling and Ross's geese) equaled the lower portion (left tail) of the large species' distribution (Canada and snow geese). We did this by numerically solving and minimizing to zero the squared value of the difference between the areas in the 2 distribution tails. We focused our analyses on dark geese harvested in the Pacific and Central flyways to directly compare to our genetic results. We also fit finite mixture models to central tail feather length data of light geese harvested in the Pacific and Central flyways to directly compare to evaluate the ability to potentially discriminate greater (A. c. atlantica) and lesser snow geese.

Species' harvests by state and county

We derived the harvest proportions of cackling geese and Canada geese in each state and counties of Washington, Oregon, and California using all PCS samples submitted by hunters during the 2018–2019 to 2020–2021 hunting seasons. We used the state- and year-specific harvest values derived from the Migratory Bird Harvest Survey and associated PCS sample sizes (Raftovich et al. 2023). For example, if the goose harvest in North Dakota in 2020 was 150,000 geese based on the Migratory Bird Harvest Survey and 1,000 goose PCS samples were received from North Dakota in 2020, then each PCS sample represented 150 geese in the harvest $\left(\frac{150,000harvest}{1,000PCS samples}\right)$. If 100 of the 1,000 PCS samples were classified as cackling geese, then the cackling goose harvest in North Dakota in 2022 was 15,000 (150 × 100 PCS samples).

We first assigned all measured juvenile and adult PCS samples as cackling or Canada goose using the discrimination thresholds for juveniles and adults derived from our logistic model analyses of mtDNA classifications (4 groups: juvenile cackling goose, adult cackling goose, juvenile Canada goose, adult Canada goose). Next, we added to these 4 groups all the juvenile and adult PCS samples that were classified to species but could not be measured for central tail feather length. We then proportionally assigned all the PCS samples that did not have age class or measurement information to the 4 groups equal to the observed proportions of all the samples that did have information. Lastly, we multiplied the number of parts in each group by the applicable state- and year-specific harvest values to derive the total harvests for each group. Our analyses at the county level used the same approach, except that we summarized harvest proportions for each county within a state rather than in aggregate for the entire state.

RESULTS

We received 37,295 dark goose and 7,162 light goose PCS samples of which biologists measured the central tail feather length of 25,521 and 5,141 of these samples, respectively (Table 1). Sample sizes among flyways of measured dark goose samples ranged from 4,604 to 6,961 for adults and 460 to 900 for juveniles. Samples sizes

among flyways of measured light goose samples ranged from 266 to 2,056 for adults and 66 to 1,374 for juveniles, with most samples obtained from the Pacific and Central flyways. Most (92%) samples that could not be measured were classified as Canada geese (Table 1). This was primarily because of the large numbers of temperate-nesting Canada geese, particularly juveniles, that had unmeasurable central tail feather lengths because they were undergoing feather molt during the hunting season. This results from the earlier and prolonged breeding period of temperate-nesting Canada geese relative to the 3 sub-Arctic- and Arctic-nesting goose species, which principally breed during June and July.

We collected 2,358 dark goose and 1,022 light goose PCS samples to consider for genetic analyses (Table 1). A high proportion of the feather samples had sufficient mtDNA amplification for analyses, especially dark geese, similar to Inman et al. (2003) and Shorey et al. (2007). We randomly selected 326 adult and 220 juvenile dark goose samples for genetic analyses, of which 91% (499 of 546) had sufficient mtDNA amplification. Seventy percent (132 of 188) of our randomly selected adult light goose samples produced sufficient mtDNA for analyses.

The DNA sequencing methods produced 499 bi-directional sequences for dark geese (cackling [n = 176] and Canada geese [n = 323]) and 132 for light geese. We reduced the dataset so haplotypes were represented by a single DNA sequence (non-redundant haplotypes), which resulted in 143 DNA sequences (GenBank [n = 20], cackling [n = 35], Canada [n = 62], light geese [n = 26]) with 388 base pairs. To construct the ML tree, we attempted 52,100,000 rearrangements and generated 20,769 trees. Our top-ranked ML tree (Jukes Cantor model ΔAIC_c of 1,859.53 from the next possible model) had statistical support for a distinct clade of cackling geese (99% bootstrap support) and a distinct clade of Canada geese (71% bootstrap support; Figure 1). Support also existed for 2 distinct clades that contained both Ross's and snow goose samples (97% and 62% bootstrap support). The emperor goose sequence from Genbank grouped within 1 of these clades with a very long branch length, showing high genetic distance. The 2 dark goose clades corresponded with central tail feather lengths (morphological size) and presumed species identification. The 2 light goose clades contained samples of both species and had no pattern in central tail feather lengths (Figures 1 and 2). We labeled the light goose clades A and B corresponding to Quinn (1992) and Weckstein et al. (2002).

Haplotypes within the cackling goose clade differed from haplotypes within the Canada goose clade by an average of about 31 base-pair single nucleotide polymorphisms (SNPs), while the 2 light goose clades differed by about 15 SNPs. Some light goose samples of drastically different central tail feather lengths that were harvested in different flyways had the same mtDNA haplotype or occurred in the same clade. Within the light goose clade B, some of the unresolved branches (closely related mtDNA sequences) contained mostly geese that were harvested in northwest Washington, presumably Wrangel Island lesser snow geese, or the Atlantic Flyway, presumably greater snow geese. Two samples in the cackling goose clade more closely associated with GenBank sequences for barnacle goose than cackling goose.

Based on mtDNA classification, cackling geese generally had smaller central tail feather lengths than Canada geese, with some overlap in species' classifications between 130–160 mm for adults and 120–145 mm for juveniles (Figure 2). No juvenile or adult samples were genetically classified as cackling geese from the Atlantic Flyway, and no juvenile samples were genetically classified as cackling geese from the Mississippi Flyway. In contrast to dark geese, adult light goose samples classified to clade A or clade B spanned the entire range of central tail feather lengths, and both clades were present in all 4 flyways in relatively equal proportions (47–63% of samples in each flyway were classified to clade A).

Species' discrimination thresholds

Logistic model selection results for genetic classification indicated that age class was an important variable for estimating species' probabilities from central tail feather lengths and harvest flyway was equivocal. Inclusion of age class in models as an additive (age + length) or interaction (age × length) effect decreased AIC_c values by



FIGURE 1 Maximum likelihood tree constructed from our genetic samples of Ross's, snow, cackling, and Canada geese (n_h = number of haplotypes; n_i = number of individual samples) submitted to the United States Fish and Wildlife Service Parts Collection Survey during the 2018–2019 to 2019–2020 hunting seasons and reference sequences downloaded from GenBank (emperor, Canada, cackling, barnacle, red-breasted, Hawaiian goose, and brant). We included bootstrap branch supports on branches with support >50%. For Canada and cackling geese (dark geese), there were 2 distinct clades, 1 with all Canada goose samples and 1 with all cackling goose samples plus 2 reference samples labeled as barnacle goose. For Ross's and snow geese (light geese), there were also 2 clades, but each clade contained both species. We labeled the clades A and B corresponding to Quinn (1992) and Weckstein et al. (2002). We included summary statistics of central tail feather lengths of our genetic samples within each clade (mean [mu], standard deviation [SD], and range).



FIGURE 2 Classification based on mitochondrial DNA (mtDNA) for A) adult and juvenile cackling and Canada goose (dark goose) and B) adult Ross's and snow goose (light goose) samples submitted to the United States Fish and Wildlife Service Parts Collection Survey during the 2018–2019 to 2019–2020 hunting seasons and selected for genetic analyses, shown by harvest flyway and central tail feather length.

23.69–25.28 units compared to a model without these effects (length; Table 2). Inclusion of harvest flyway increased AIC_c values by 0.18 units when modeled as an additive effect (age + flyway + length) and decreased AIC_c values by 3.29 units when modeled as an interaction effect (age × flyway + length) compared to a model without these effects (age + length). Based on the top model (age × flyway + length), age class had the greatest effect size, with adults being larger than juveniles (coefficient value [for adults] = 1.19 [95% CI = 0.69–1.70]). There was little directional influence of harvest flyway (Central Flyway = -0.35 [-0.76-0.05]) and minor, directional influence of the age × flyway interaction (0.48 [0.07-0.88]). Central tail feather length was also an important predictor variable (-0.22 [-0.27--0.16]; we defined success as cackling goose, and Canada geese have larger central tail feather lengths). Based on the top model, there was a 1-mm difference for adult dark geese in the species' discrimination threshold between the Pacific and Central flyways (≤144 mm and ≤145 mm, respectively) and a 7-mm difference for juveniles (≤137 mm and ≤130 mm, respectively; Table 2; Figure 3). When we combined data between flyways (age + length), the species' discrimination thresholds for dark geese were ≤145 mm for adults and ≤134 mm for juveniles.

For morphological classification methods, finite mixture models fit to PCS central tail feather length data performed well for dark geese but relatively poorly for light geese, particularly juveniles. Estimated species' discrimination thresholds from finite mixture models were greater than those estimated from the genetic-based approach. Central tail feather lengths of dark geese harvested in the Pacific and Central flyways had a bimodal distribution, and species' discrimination thresholds from finite mixture models from finite mixture models were 158 mm for adults and 143 mm

TABLE 2 Model results using Akaike's Information Criterion corrected for small sample size (AIC_c) for logistic models fit to mitochondrial DNA (mtDNA) species' classifications of cackling and Canada goose samples submitted to the United States Fish and Wildlife Service Parts Collection survey from the Pacific and Central flyways during the 2018–2019 to 2019–2020 hunting seasons. We modeled species' classifications as a function of age class (juvenile and adult), harvest flyway (Pacific and Central), and central tail feather length (length), as additive effects (+) or main effect interactions (×). We derived the species' discrimination threshold as the central tail feather length where the probability of species' assignment was equal (50% probability).

						Central tail feather length threshold (mm)			
				Number of		Adult		Juvenile	
Model	AIC _c	ΔAIC_{c}	AIC _c weight	parameters	Flyway	Mean	SE	Mean	SE
age × flyway + length	173.52	0.00	0.58	5	Central	145	1.6	130	2.0
					Pacific	144	1.8	137	2.1
age × flyway × length	176.20 2.68		0.15	8	Central	146	1.8	130	2.1
					Pacific	144	1.5	137	2.3
age + ngth	176.81	3.29	0.11	3	Both	145	1.2	134	1.5
age + flyway + length	176.99	3.47	0.10	4	Central	144	1.4	132	1.7
					Pacific	146	1.6	135	1.7
age × length	178.40	4.88	0.05	4	Both	145	1.2	134	1.6
length	202.09	28.57	0.00	2	Both	141	1.1	141	1.1



FIGURE 3 Probability of being a cackling goose for a given central tail feather length based on logistic models (left = age × flyway + length; right = age + length) fit to mitochondrial DNA (mtDNA) species' classifications for juvenile and adult cackling and Canada goose samples submitted to the United States Fish and Wildlife Service Parts Collection Survey from the Pacific and Central flyways during the 2018–2019 to 2019–2020 hunting seasons. The probability of being a Canada goose is 1 minus the probability of being a cackling goose.

for juveniles (Figure 4), approximately 13 mm and 9 mm greater, respectively, than the genetic-based thresholds. In contrast, central tail feather length distributions of light geese were rather unimodal. A finite mixture model fit to central tail feather length data of adult light geese from the Pacific and Central flyways estimated the component distributions shifted from each other, with a resulting species' discrimination threshold of 142 mm. For juveniles, there was no separation in the estimated component distributions, and each component distribution spanned nearly all central tail feather lengths. Thus, the derived juvenile species' discrimination thresholds were not diagnostically meaningful. Similarly, finite mixture models did not provide meaningful results when fit to central tail feather length



FIGURE 4 Finite mixture models using normal distributions and unequal variances (k = 2 component distributions) fit to juvenile (left) and adult (right) central tail feather lengths of samples submitted to the United States Fish and Wildlife Service Parts Collection Survey for A) cackling and Canada geese (dark geese) harvested during the 2018–2019 to 2020–2021 hunting seasons in the Pacific and Central flyways and B) Ross' and snow goose geese (light geese) harvested during the 2018–2019 to 2020–2021 hunting the 2018–2019 to 2021–2022 hunting seasons in the Pacific and Central flyways and C) in the Atlantic Flyway (grey bars = histogram of data; black line = density of the combined 2-species distribution; blue and orange lines = density of each component distribution). We included the estimated proportion (pi), mean (x; mm), and standard deviation (sd) for each component distribution, and the calculated species' discrimination threshold (mm) between the 2 component distributions.

data of juvenile or adult light geese from the Atlantic Flyway. Ross's geese do not readily occur in the Atlantic Flyway, but greater and lesser snow geese do, suggesting little ability to discriminate between lesser and greater snow geese using central tail feather lengths.

Species' harvests by state and county

Estimated state and county harvest proportions of cackling and Canada geese were consistent with species' distributions (Baldassarre 2014, Mowbray et al. 2020*a*). States with the highest proportions of cackling goose harvest were coastal states in the Pacific Flyway and southern states in the Central Flyway (Figure 5). Midcontinent cackling geese (*B. h. hutchinsii*) primarily occur in the Central and Mississippi flyways. Counties in Washington, Oregon, and California with higher proportions of cackling goose harvest were consistent with the distributions of the 3 cackling goose subspecies that occur in the Pacific Flyway: Aleutian cackling geese (*B. h. leucopareia*) concentrate in the San Joaquin and northwest coastal areas of California; minima cackling geese (*B. h. minima*) primarily occur in northwest Oregon and southwest Washington and throughout the Willamette Valley and Puget Trough; and Taverner's cackling geese (*B. h. taverneri*) display a more eastward distribution, primarily east of the Cascade Mountains, with concentrations in counties in eastern Oregon and Washington along the Columbia River.

DISCUSSION

As predicted, we found a greater ability to discriminate between cackling and Canada geese than between Ross's and snow geese (Figures 1, 2, and 4). Like past studies, mtDNA effectively classified cackling and Canada geese into 2 distinct clades that were associated with morphological size (Quinn et al. 1991, Pearce et al. 2000, Paxinos et al. 2002,



FIGURE 5 Proportion of cackling goose harvest (juveniles and adults) of the total cackling and Canada goose harvest estimated during the 2018–2019 to 2020–2021 hunting seasons for states in the Pacific, Central, and Mississippi flyways and counties within Washington, Oregon, and California, USA. We used a species' discrimination threshold of ≤134 mm and ≤145 mm for juvenile and adult central tail feather lengths, respectively, to classify United States Fish and Wildlife Service Parts Collection Survey samples. Counties colored white did not have sufficient data.

Scribner et al. 2003, Leafloor et al. 2013). Cackling and Canada geese diverged about 2.9 million years ago (Ottenburghs et al. 2016). These species were likely separated during past glaciation events, with cackling geese nesting in sub-Arctic and Arctic refugia areas and most Canada geese nesting south of the ice sheets (Ploeger 1968). Hybridization between the 2 species occurred primarily within limited contact zones around the tundra and taiga boundary relatively recently (Scribner et al. 2003, Leafloor et al. 2013, Ottenburghs et al. 2017, 2020). For the 2 samples that more closely associated with reference sequences of barnacle geese, either these truly were barnacle geese (or descendant hybrids) or the reference sequences for barnacle geese were incorrectly assigned. Barnacle geese and cackling geese are sister taxa and have close genetic association (Ottenburghs et al. 2016), and vagrant barnacle geese, and captive-reared birds, occur in the United States (Silcock and Jorgensen 2020). Similarly, 2 of approximately 1,000 presumed cackling goose samples collected in eastern Canada were more closely associated with a reference barnacle goese mtDNA sequence than cackling goose mtDNA sequences (Silcock and Jorgensen 2020).

Like past studies (Avise et al. 1992, Quinn 1992, Weckstein et al. 2002), we report support for 2 divergent mtDNA clades in light geese. These clades did not have an associated pattern with morphological size (presumed species; Figures 1 and 2). Many factors likely contributed to light geese having less genetic differentiation than dark geese. Ross's and snow geese diverged more recently (around 2.1 million years ago) than cackling and Canada geese (Ottenburghs et al. 2016), and Ross's and snow geese likely nested together in Arctic refugia during past glaciation events (Ploeger 1968). Compared to dark geese, the biology of light geese favors greater degrees of genetic interchange: sympatric nesting in large colonies (Kerbes et al. 1983), mate pairing in winter when geese from various breeding areas intermix (Ganter et al. 2005), frequent hybridization and production of fertile offspring (Trauger et al. 1971, Weckstein et al. 2002, Ottenburghs et al. 2017), and large-scale distributional shifts and intermixing among populations during recent decades (Johnson and Troy 1987, Cooke et al. 1988, Jónsson et al. 2020, Alisauskas et al. 2022, Sliwinski et al. 2023). Additionally, both species groups exhibit asymmetric sex-mediated gene flow and size-based sexual selection, which can complicate the understanding of evolutionary histories. In light geese, males have less site fidelity than females, primarily pairing in winter and following females to natal grounds (Alisauskas et al. 2022), and paired males are typically larger than females (Ankney 1977). Thus, mtDNA, which is maternally inherited, may not reflect the higher levels of genetic interchange of males or sex- and sizebased directional hybridization patterns that can be better deciphered from broader genome analyses (Kulikova et al. 2004, Zink and Barrowclough 2008, Ely et al. 2017, Wilson et al. 2018).

Contrary to our prediction, genetic-based species' discrimination thresholds were smaller than morphological-based thresholds using comparable data (dark geese harvested in the Pacific and Central flyways; Figures 3 and 4; Table 2). Relative to the morphologically derived thresholds, more samples were genetically classified as Canada goose that had smaller central tail feather lengths than samples genetically classified as cackling geese that had larger central tail feather lengths. The same result was found by Leafloor et al. (2013) for dark geese sampled along the western coast of Hudson Bay. They suggested that the persistence of Canada goose mtDNA in phenotypic cackling geese was the result of historical hybridization events that occurred during a warmer climactic period, when the Arctic and sub-Arctic ecotone was located farther north. In contrast to our study, Leafloor et al. (2013) measured hard structural parts (skull, tarsus, culmen). Hard structural parts are preferred for quantifying morphological traits (Dzubin and Cooch 1992), but such parts cannot be mailed for the PCS because of putrefaction and an undue time burden on participants to collect samples. Our similar findings to Leafloor et al. (2013) suggested that central tail feather lengths served as a good, quantifiable characteristic of morphology for dark geese, and our results were not likely due to measurement errors (systematically under-measuring central tail feather lengths of samples genetically classified as Canada geese).

Convergent evolution in sub-Arctic-nesting Canada geese, namely selection for small morphological characteristics for long distance migrations, may have contributed to mtDNA-classified Canada geese that had shorter central tail feather lengths. Asymmetric introgression of the maternally inherited mtDNA cackling goose lineage into phenotypic Canada geese (offspring with cackling goose mtDNA but larger morphologies) would be more likely based on biology, although our study and Leafloor et al. (2013) reported the opposite. In dark geese, the male is typically larger than the female (Mowbray et al. 2020*a*, 2020*b*), and Canada geese more commonly occur in

cackling goose nesting areas (Luukkonen et al. 2008, Dieter et al. 2010, Dooley et al. 2019) than vice versa (Jantunen et al. 2015). A larger male Canada goose breeding with a smaller female cackling goose would be the more likely cross-species pairing. Thus, past hybridization events may not fully explain the observed genetic and morphological patterns, as suggested by Leafloor et al. (2013). Short-tailed avian species were found to migrate greater distances than medium- and long-tailed avian species, suggesting there was natural selection for aerodynamically efficient flight in which shorter tail lengths decreased drag (Fitzpatrick 1999). This could explain how genetically pure Canada geese that breed in sub-Arctic areas and migrate long distances evolved smaller tail lengths (selection pressure rather than past hybridization).

The relative abundance of dark goose populations and their availability to hunters also contributed to the morphological-based species' discrimination thresholds being larger than the genetic-based thresholds. Participating hunters in the PCS were randomly selected, and their harvests should be generally proportional to the abundance and availability of various populations during the hunting season (USFWS 2023). Temperate-nesting Canada geese (those with shorter migration distances and thus longer tail lengths) composed most of the Canada geese harvested in the United States (sub-Arctic-nesting Canada geese composed the minority; Mississippi Flyway Council 2017). The PCS data and respective feather length distributions, which were proportionally dominated by relatively large-tailed temperate-nesting Canada geese, resulted in the upper distribution being skewed toward large-tailed samples. In contrast, our genetic-based approach more equally represented all goose morphologies, as we randomly selected samples among all central tail feather lengths. The PCS data and resulting feather length distributions generally represented the dark goose morphologies available to hunters, not the direct relationship between mtDNA species' classification and central tail feather length. Also, morphological-based species' discrimination thresholds just using Central Flyway PCS data and finite mixture models (≤ 138 and ≤157 mm for juveniles and adults, respectively; not shown in Figure 4) were similar to the current Central Flyway Wingbee thresholds that were based on morphological analyses of Central Flyway data in the early 2000s (≤137 and ≤155 mm; Johnson et al. 2004). This result implied that there has not been a major change in central tail feather lengths of harvested dark goose PCS samples in the Central Flyway during the past 20 years.

In partial support of our prediction, age class was an important variable for discriminating between dark geese using central tail feather length (juvenile thresholds were smaller than adults), but differences in species' discrimination thresholds were minimal between the Pacific and Central flyways (Figure 3; Table 2). However, detection of species based on mtDNA classification differed by harvest flyway. We did not genetically classify any samples as cackling geese in the Atlantic Flyway or any juvenile samples as cackling geese in the Mississippi Flyway, even though we tested many samples that had central tail feather lengths less than the derived species' discrimination thresholds based on Pacific and Central flyway data (\leq 134 mm for juveniles and \leq 145 mm for adults; Figures 2 and 3). Logistic models cannot be fit if all or nearly all items were the same classification, which was why we focused analyses on data from the Pacific and Central flyways. Our result of few or no cackling geese harvested in the Mississippi and Atlantic flyways was consistent with band-recovery data (Mississippi Flyway Council 2013, 2017) and this species' distribution being limited in the eastern United States (Baldassarre 2014, Mowbray et al. 2020*a*).

Sampling issues, including small sample size in general and the low production of cackling geese in the central and eastern Arctic during our study (USFWS 2018), likely contributed to the lack of juvenile samples genetically classified as cackling goose in the Mississippi Flyway. Sampling and environmental conditions may have also contributed to the slight difference (7 mm) in the derived juvenile species' discrimination thresholds between the Pacific and Central flyways, as essentially no difference was detected for adults (1 mm; Table 2). The smaller juvenile cackling goose species' discrimination threshold for the Central Flyway than the Pacific Flyway was opposite of expectation. Minima cackling geese, the smallest subspecies, occur in the Pacific Flyway (Mowbray et al. 2020*a*). Thus, we expected the Pacific Flyway threshold to be smaller than the Central Flyway threshold. For Arctic-nesting geese, gosling body size is dependent on spring phenology. Later spring phenology translates to later nesting dates, reduced plant growth, and consequently smaller gosling size (Lepage et al. 1998, Gauthier et al. 2006, Richman et al. 2015). The shorter central tail feather lengths of genetically classified juvenile cackling geese from

the Central Flyway to those from the Pacific Flyway could have been due to later spring phenology in corresponding Arctic breeding areas during our study (USFWS 2018). Regardless, a difference of 3-4 mm in the juvenile species' classification threshold (flyway-specific [130 mm and 137 mm] vs. both flyways combined [134 mm]; Table 2) would have minimal influence on resulting species-specific harvest estimates because <1% (Figure 4) of the 9,940 (Table 1) juvenile dark goose PCS samples occurred within those measurement ranges.

Our species' discrimination thresholds for dark geese based on mtDNA classifications and central tail feather lengths (≤134 mm for juveniles and ≤145 mm for adults) provide an improved and more defensible approach for estimating harvests of these species in the United States than past or alternative methods. Species' harvest proportions based on our thresholds (Figure 5) coincided with the known wintering distributions and use areas of the 4 cackling goose subspecies (Baldassarre 2014, Mowbray et al. 2020*a*), suggesting future utility of our approach to separately monitor harvests of these subspecies. The feather length thresholds we calculated were similar to the genetic-based thresholds recently developed by the CWS to discriminate between dark goose samples harvested in prairie Canada (Alberta, Saskatchewan, and Manitoba) for the Species Composition Survey (M. Gendron, CWS, unpublished data; 139 mm [range = 130–145 mm] for juveniles and 146 mm [142–149 mm] for adults). Thus, adoption of our thresholds for the PCS would create a more uniform harvest estimation approach for dark geese throughout North American than any time in the past.

We had limited ability to discriminate between Ross's and snow geese and between lesser and greater snow geese based on either mtDNA (Figures 1 and 2) or central tail feather lengths (Figure 4). However, we did obtain reasonable results from the finite mixture models fit to central tail feather length data of adult light geese from the Pacific and Central flyways (Figure 4). Our derived species' discrimination threshold (< 142 mm) was identical to the currently used threshold at the Pacific Flyway Wingbee (S. Olson, USFWS, unpublished data), which was based on analyses from Oldenburger et al. (2011; using California-harvested samples). This result also implied that there has not been a major change in the size of light goose PCS samples during the past 15 years. We are cautious of this species' discrimination threshold, given the disparity that we found between genetic- and morphological-based species' discrimination thresholds for dark geese. Support for 2 mtDNA clades within snow geese was found by Humphries et al. (2009), similar to our results and previous studies (Avise et al. 1992, Quinn 1992, Weckstein et al. 2002), but they also found mtDNA differentiation between lesser and greater snow geese in the Atlantic Flyway. Although we did not find statistical support in our top selected ML tree for the differentiation of lesser and greater snow geese, we did find some nonsignificant differentiation in clade B from a cluster of samples harvested in the Atlantic Flyway (Figure 1). Our inability to discriminate lesser and greater snow geese in the Atlantic Flyway using central tail feather length contrasted with Sliwinski et al. (2023), who classified lesser and greater snow geese with 95.5% accuracy using head measurements. However, their classification accuracy was based on an initial classification of samples to subspecies from head and culmen length measurements described in Humphries et al. (2009), not genetic classification. Central tail feather lengths may be less diagnostic for light geese compared to other, hard structural parts. Light geese nest in the Artic and sub-Arctic and are long-distance migrants. Thus, convergent selection pressure for similar central tail feather lengths may be greater for light geese than dark geese. Although our study provided rather ambiguous results for discriminating light geese, we believe that greater resolution may be achieved using next-generation genomic sequencing approaches (double-digest restriction-associated digest sequence). These techniques have shown promise in resolving genetic relationships of closely related waterfowl species and sub-species of geese (Lavretsky et al. 2019, Wilson et al. 2022), and preliminary analyses indicated their ability to successfully discriminate among Ross's geese, lesser and greater snow geese, and putative hybrids (R. Wilson, University of Nebraska-Lincoln, unpublished data).

MANAGEMENT IMPLICATIONS

Our study demonstrated a discrepancy between genetic- and morphological-based species' discrimination thresholds. We encourage more studies to incorporate genetic analyses to complement morphological discrimination. Practitioners should also consider using feathers for genetic analyses, as such parts provided sufficient DNA without requiring special storage buffers or deep freezers and can have some other advantages over tissue or blood sampling (less invasive to the bird, no medium or cooling needed in the field). Our genetic-based species' discrimination thresholds for dark geese provide a defensible and uniform approach for estimating harvests of these species from federal harvest surveys in the United States, an important component of status monitoring and assessment for game species listed on the USFWS List of Migratory Birds. We suggest managers use the genetic-based species' discrimination thresholds from this study to differentiate juvenile (\leq 134 mm) and adult (\leq 145 mm) dark goose PCS samples in the 3 westernmost flyways (Pacific, Central, and Mississippi), where we detected cackling geese based on mtDNA. We also suggest that combined statelevel harvests in the Central and Mississippi flyways and combined county-level harvests for spatial areas in the Pacific Flyway may provide reasonable indices to separately monitor harvests of the 4 cackling goose subspecies. In the Atlantic Flyway, we suggest classifying all PCS samples as Canada geese because we did not detect any cackling geese based on mtDNA and use of our derived species' discrimination thresholds would incorrectly classify many mtDNA Canada geese with smaller central tail feather lengths as cackling geese. We encourage more genetic assessments in the Atlantic Flyway, particularly sampling geese with small central tail feather lengths, to first confirm presence of cackling geese in this flyway before attempting discrimination of dark goose PCS samples. Similarly, for light geese, we encourage more advanced genome analyses in conjunction with similar analyses of central tail feather lengths before modifying current Wingbee protocols.

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CONFLICTS OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

Goose parts were voluntarily collected by hunters during legal hunting seasons per applicable hunting regulations. Selection of participants for federal harvest surveys followed ethical and legal standards per federal law (88 FR 85906, 50 CFR 20.20, 44 USC 3501).

DATA AVAILABILITY STATEMENT

The mtDNA sequences are uploaded to GenBank (accession numbers: PP690651–PP690773). Summaries and estimates of federal harvest survey data can be found at https://www.fws.gov/harvestsurvey/ and are available upon request to the USFWS Division of Migratory Bird Management Branch of Monitoring and Data Management.

ORCID

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