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RESEARCH

Genetic assessment of subspecies composition in bean goose (*Anser fabalis*) harvest in Sweden, Finland and Estonia

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Abstract

Bean goose (*Anser fabalis)* harvest in Europe consists of two subspecies, whose conservation statuses are different. However, the proportions of each subspecies in hunting bags are unknown. We studied the subspecies composition among harvested bean geese in Sweden, Finland and Estonia by sequencing a short mitochondrial DNA (mtDNA) region (210 bp). The proportion of taiga bean geese (*A. f. fabalis*) over two hunting seasons was 94% in Sweden, but only 5.8% and 11% in Estonia and southeastern Finland, respectively. The majority of harvested bean geese in Estonia and southeastern Finland were tundra bean geese (*A. f. rossicus*), and hence the results show that the Finnish spatio-temporal harvest regulations have successfully managed to focus the harvest mostly to the abundant tundra bean goose. We also detected mitochondrial heteroplasmy, i.e. multiple mtDNA variants within some of the individuals. In addition, we discovered a few exceptional individuals with an mtDNA haplotype belonging to eastern taiga bean goose (*A. f. middendorffii*) or greater white-fronted goose (*A. albifrons*), which could be hybrids between bean goose subspecies or interspecific hybrids. Hybrid individuals are a problem to this type of method. We also noted that it was not possible to distinguish bean geese and pink-footed goose (*A. brachyrhynchus*). Our derived method is more cost-efficient than previously used molecular methods, and could be used to monitor bean goose hunting bag in the future.

Keywords Mitochondrial DNA · Control region · Heteroplasmy · Adaptive management · Harvest management

Introduction

Inadequacy of hunting bag statistics of European waterfowl has been pointed out on multiple occasions (Elmberg et al. 2006; Holopainen et al. 2018; Aubry et al. 2020). Although these studies mainly considered ducks, increasing the accuracy of harvest bag estimates has recently been recognised as one of the pressing needs to improve decision-making also in the international management of greylag goose (*Anser anser*) in Europe (Johnson and Koffijberg 2021). Despite the acknowledged need for better data on human offtake, only few actions have been taken to better estimate the quality (age, sex and population) and quantity of harvested waterfowl. Correct identification of harvested geese is often non-trivial, and hunters are known to make mistakes in identifying hunted waterfowl species (Christensen et al. 2017). Particularly challenging is identification of goose subspecies, such as within the bean goose clade.

The taiga bean goose (*Anser fabalis fabalis*) is a Palearctic goose species with international collaboration in management, but insufficient harvest data (Marjakangas et al.

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2015; Johnson et al. 2019). During the non-breeding season, taiga bean geese co-occur with tundra bean geese (*A. f. rossicus*) in many European countries (Fox and Leafloor 2018). Contrary to most other European goose populations, taiga bean goose population has declined throughout its range in recent decades (but note a recent increase in the Central Flyway, Jensen et al. 2023), whereas tundra bean goose population has been increasing at the same time (Fox and Leafloor 2018). The subspecies have different conservation statuses and thus, different needs for harvest management. They are both harvested in several countries throughout their ranges, but not separated in hunting bag statistics (Honka et al. 2017; Johnson et al. 2019). To safeguard the taiga bean geese from over-harvesting and to avoid unnecessary hunting restrictions for the abundant tundra bean geese, it is important to know where the different subspecies are harvested. With this information, the hunting can be spatially regulated to target mostly the tundra bean geese.

However, collecting subspecies-specific data on bean goose harvest is not a trivial task. Due to their morphological similarities, even expert identification from photographs of live specimen was shown to be unreliable (Solovyeva et al. 2022), and most morphological measurements overlap between the subspecies (de Jong 2019). As morphological identification performed by experts could leave cases in which the subspecies identification is uncertain, molecular genetics could provide a more accurate, but more laborious method for subspecies assignment. With molecular genetics, full mitochondrial (mtDNA) control region has been previously used to identify bean goose subspecies (Ruokonen et al. 2008; Honka et al. 2017). Ruokonen et al. (2008) showed that mitochondrial control region is suitable for bean goose subspecies identification by studying bean geese of known origin. However, using a short mtDNA control region fragment within the whole control region, as done with bean goose feathers in Honka et al. (2022), could provide a cheaper option compared the previous genetic subspecies identification method. We sequenced the most variable region of the mtDNA control region to assess the subspecies composition of bean goose harvest bag. We simplified the existing genetic subspecies composition determination method by using a much shorter sequence and thus cutting the costs of genetic analyses.

In this study, we assigned subspecies for bean geese hunted from Sweden, Finland and Estonia using a genetic method to produce information of harvest subspecies composition to support decision making in practical management. In addition, as hunting is currently spatially and temporally regulated in Finland to target mainly migrating tundra bean geese in Eastern Finland, we evaluated how effective the current hunting regulations are at targeting tundra bean geese. Last, we propose a workable solution for genetic subspecies monitoring of the hunting bag.

Materials and methods

We collected tissue samples from bean geese harvested in Sweden, Finland and Estonia, and used a short mitochondrial DNA fragment as in Honka et al. (2022) to assign the subspecies of the collected samples. Hunters voluntarily donated body parts (heads) of legally hunted bean geese during the hunting seasons of 2017/18 through 2019/20. From this sample pool, we extracted DNA from 625 bean geese harvested in Sweden, 36 in Finland and 125 in Estonia ($n = 786$).

DNA was extracted from muscle tissue samples stored in freezer in absolute ethanol using the E.Z.N.A. Tissue DNA Kit's (Omega Bio-Tek) Tissue protocol according to manufacturer's instructions, except that DNA was eluted first in 100 µl of Elution buffer and then a second time yielding a total of 200 µl of DNA extract. DNA concentrations were measured using a NanoDrop spectrophotometer (Thermo Fisher Scientific, Waltham, MA, USA) and if necessary, the extracts were diluted to 50 ng/µl. Concentrations below 50 ng/µl ($n = 16$) were left undiluted.

We amplified the most variable part of the mitochondrial (mtDNA) control region domain I (210 bp) using primers AdCR1F and AdCR2R (Honka et al. 2018), as in Honka et al. (2022) except the thermocycling conditions were: 98 °C for 30s, followed by 30 cycles of 98 °C for 10 s, 57 °C for 20 s and 72 °C for 15 s with a final extension at 72 °C for 7 min. Sequencing was performed in one direction with the primer AdCR1F using BigDye Terminator v.3.1 (Applied Biosystems, Waltham, MA, USA) and the sequencing reactions were run on an ABI3730.

The genetic subspecies determination method is derivative to Honka et al. (2017), originally tested and developed by Ruokonen et al. (2008) using bean goose subspecies of known origin, but instead of amplifying the whole mtDNA control region in two fragments and sequencing in both directions, we amplified a 210-base pair (bp) fragment, within the originally studied whole control region, and sequenced it in one direction, cutting costs of genetic analysis. Sequencing the DNA fragments in both directions allows to check the identity of the ambiguous bases from the other fragment, but we found that the sequence quality was very good which allowed sequencing for one direction due to high quality muscle tissue samples.

The program CodonCode Aligner v.4.0.4. (CodonCode Corporation, Centerville, MA, USA) was used to manually edit the sequences. In addition, we manually checked for the presence of heteroplasmies, i.e. the presence of multiple

mtDNA variants within a single individual (double-peaks in the sequence chromatograms). Mitochondrial DNA is maternally inherited, but due to germline or somatic mutations, or on some occasion trough paternal leakage, an individual can carry several different mtDNA types (Parakatselaki and Ladoukakis 2021). The mtDNA variants are called mtDNA haplotypes, because mtDNA is non-recombining and inherited as a single unit. A haplotype refers to physical grouping of genetic variants which are inherited together. The program BioEdit 7.2.5 (Hall 1999) was used to align the sequences with GenBank sequences of bean, pink-footed (*A. brachyrhynchus*) and greater white-fronted geese (*A. albifrons*). GenBank accession numbers of all the reference sequences are provided in Online Resource Table 1. Two GenBank sequences (MH491826 [Fa5] and MH491827 [Fa6]) had missing nucleotides which we replaced these with consensus data from other taiga bean goose sequences (invariable region), in order to check the presence of these haplotypes and thus avoiding describing new haplotypes.

We constructed median joining haplotype networks (Bandelt et al. 1999) using the program PopART with epsilon set to zero (Leigh and Bryant 2015). Haplotype networks are used to analyse and visualize DNA sequence relationships within populations or species, providing visual representations of the evolutionary relationships between studied individuals. We used the haplotype networks to assign specimens to subspecies with the aid of the reference sequences outlined above. A Numt (nuclear sequence of mitochondrial origin; GenBank accession number: AF159970), which is an insert of a copy of a mitochondrial DNA in the nucleus, was used as an outgroup to root the haplotype network (Bensasson et al. 2001). The Numt sequence was also used for quality control purposes to validate that we did not amplify any Numt sequences instead of mtDNA. Undescribed haplotypes (Fa9-Fa12 for taiga bean goose and Ro6-Ro7 for tundra bean goose; Fig. 1) were deposited in GenBank with accession numbers PP461004–PP461009. We observed cases of heteroplasmy, and to rule out pipetting errors and sample mix-ups, we re-extracted and/or re-sequenced some ($n=7$) of these samples, but the heteroplasmies remained. Numt can also cause the apparent presence of heteroplasmy (Bensasson et al. 2001; Parakatselaki and Ladoukakis 2021) and we compared our sequences with the known Numt sequence (Ruokonen et al. 2000), but the heteroplasmic sites did not correspond with the Numt. As the heteroplasmies do not allow all the haplotypes to be determined (two haplotypes per individual which would inflate the number of individuals), we constructed median-joining haplotype networks without heteroplasmic sequences in order to determine haplotypes and to assign subspecies, and with the heteroplasmies to assign subspecies for the heteroplasmic individuals. The studied fragment includes multiple diagnostic nucleotides which separate the taiga and tundra bean goose, and thus the heteroplasmic individuals could be assigned to subspecies.

Results

We obtained sequencing results from 779 out of 786 samples (the omitted seven samples failed in PCR). Twenty-three samples (3%) showed heteroplasmy, and only subspecies was assigned for these samples without haplotypic information as two haplotypes would be assigned to one sample, inflating the total number (Online Resource Figures S1). For the rest of the samples, we assigned both haplotype and subspecies (Fig. 1, Online Resource Figures S2–S4). The bean goose harvest in Sweden comprised of 93.1% taiga bean goose in the studied hunting seasons (2017/18–2018/19, Table 1; Fig. 2). Eight geese harvested in Sweden

Table 1 Total number and percentage of legally harvested bean geese (*Anser fabalis*) from Sweden ($n=622$), Finland ($n=36$) and Estonia ($n=121$) from hunting seasons 2017/18–2019/20 based on the subspecies determination relying on sequencing of the most variable part of mitochondrial DNA (mtDNA) control region (210 base pairs). Some geese had an mDNA of another species, either pink-footed Goose (*A. brachyrhynchus*) or greater white-fronted Goose (*A. albifrons*). All samples (including heteroplasmies) were included

Subspecies/mtDNA	Sweden			Finland			Estonia			All countries
	2017–2018	2018–2019	All years	2018–2019	2019–2020	All years	2018–2019	2019–2020	All years	All years
A. f. fabalis mtDNA	226 (96.2%)	353 (91.2%)	579 (93.1%)	2 (12.5%)	2 (10.0%)	4 (11.1%)	4 (7.8%)	3 (4.3%)	7 (5.8%)	590 (75.7%)
A. f. rossicus mtDNA	5 (2.1%)	29 (7.5%)	34 (5.5%)	14 (87.5%)	17 (85.0%)	31 (86.1%)	47 (92.2%)	66 (94.3%)	113 (93.4%)	178 (22.8%)
A. f. middendorffii mtDNA	0	0	0	0	1 (5.0%)	1 (2.8%)	0	0	0	1 (0.1%)
A. brachyrhynchus mtDNA	4 (1.7%)	4 (1.0%)	8 (1.3%)	0	0	0	0	0	0	8 (1.0%)
A. albifrons mtDNA	0	1 (0.3%)	1 (0.2%)	0	0	0	0	1 (1.4%)	1 (0.8%)	2 (0.3%)
All	**235 (100%)**	**387 (100%)**	**622 (100%)**	**16 (100%)**	**20 (100%)**	**36 (100%)**	**51 (100%)**	**70 (100%)**	**121 (100%)**	**779 (100%)**

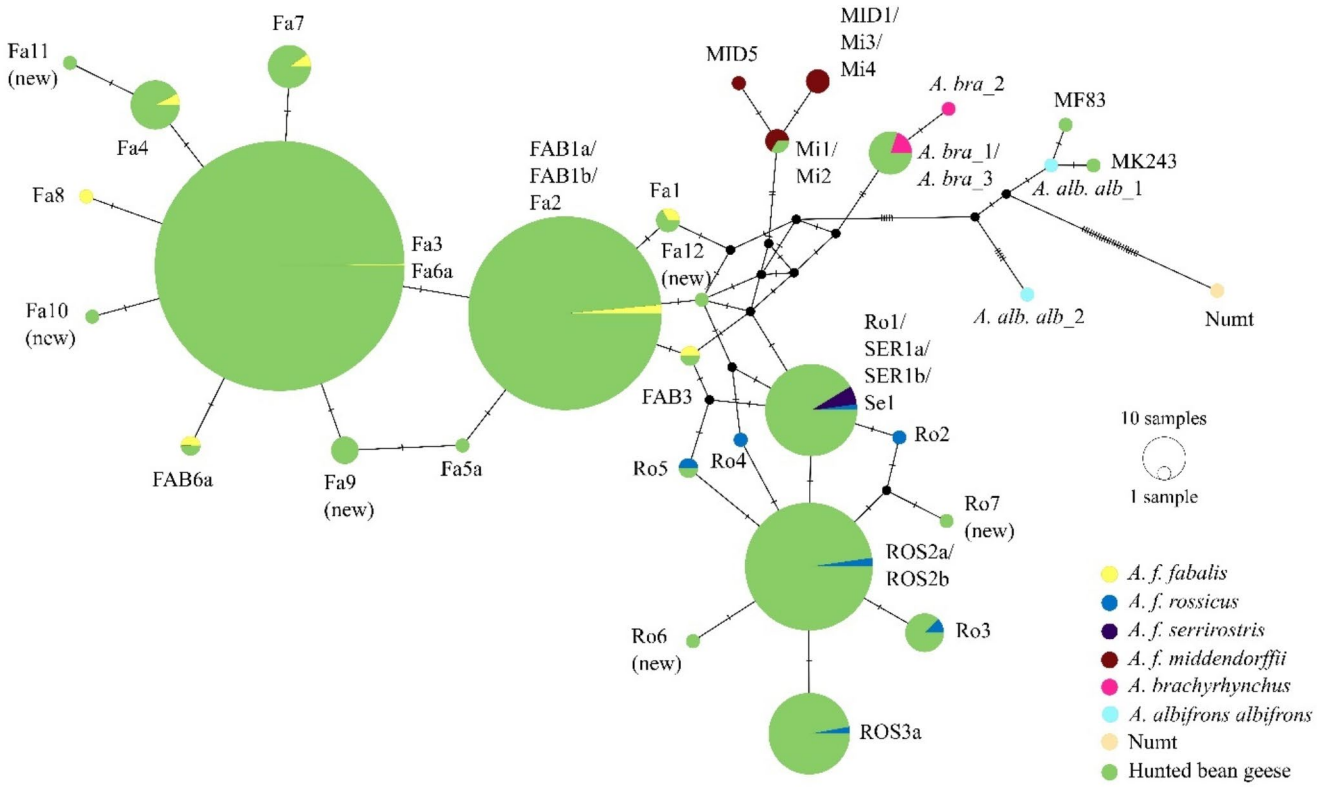

Fig. 1 A median joining haplotype network for harvested bean geese from Sweden, Finland and Estonia (hunting seasons 2017/18–2019/20; $n = 756$), bean goose subspecies (*Anser fabalis fabalis*, *A. f. rossicus*, *A. f. serrirostris* and *A. f. middendorffii*), pink-footed geese (*A. brachyrhynchus*) and greater white-fronted geese (*A. albifrons*) indicated by different colours. Individuals with heteroplasmy have been omitted from this haplotype level analysis ($n = 23$). To root the haplotype network a sequence of Numt (accession number: AF159970; nuclear sequence of mitochondrial origin) was used. The frequency of each haplotype is indicated with the size of the circle and the number of mutational differences is indicated with tick marks across branches. Black circles indicate unsampled haplotypes needed to construct the median haplotype network. Haplotypes which were identical in the studied DNA region but differ based on the whole control region sequence are indicated with forward slashes between haplotype names

had a pink-footed goose haplotype (Figs. 1 and 2, Fig. S2). As pink-footed goose haplotypes likely represent also taiga bean geese (see Discussion) and phenotypically none of the samples were pink-footed goose, which have a short pink bill (see example individual in Fig. 3a), the proportion of hunted taiga bean goose in Sweden raises to a total of 94.4%.

In Finland and Estonia, the percentage of hunted taiga bean geese was 11.1% and 5.8% in the hunting seasons of 2018/19 and 2019/20, respectively (Table 1; Fig. 2). Most harvested bean geese in Finland (86.1%) and Estonia (93.4%) were tundra bean geese (Table 1; Figs. 1 and 2).

We note that 44 samples clustered with a group including *A. f. rossicus* haplotype (Ro1) and eastern tundra bean goose (*A. f. serrirostris*) haplotypes, because the mtDNA control region is incapable of separating some western and eastern tundra bean goose sequences (Honka et al. 2017; Ruokonen et al. 2008). However, the eastern tundra bean goose is an Asian subspecies, and thus we classified these birds as *A. f. rossicus.* Furthermore, the phenotype of these birds did not match with the eastern tundra bean geese (Delacour 1954). In addition, we detected a few unexpected taxa: one goose from Finland with an mtDNA haplotype of eastern taiga bean goose (*A. f. middendorffii*, Table 1; Fig. 2, Fig. S3), presented in Fig. 3b, and two geese, with an mtDNA haplotype of greater white-fronted goose (Table 1; Fig. 2, Fig. S2, S4), presented in Fig. 3c and d.

Discussion

The vast majority (94%) of bean geese harvested in Sweden were taiga bean geese (including individuals with pink-footed goose haplotype). This is in par with estimates based on national counts and observation reports at 95% of taiga bean geese in October 2018 (Haas and Nilsson 2019) and 93% in October 2022 (Haas et al. 2023). Heinicke and de Jong (2013), on the other hand, reported 85% of taiga bean geese for 2009–2012 and demonstrated that subspecies proportions varied dramatically at local scale. However, Jensen et al. (2023) showed that the number of taiga bean geese in

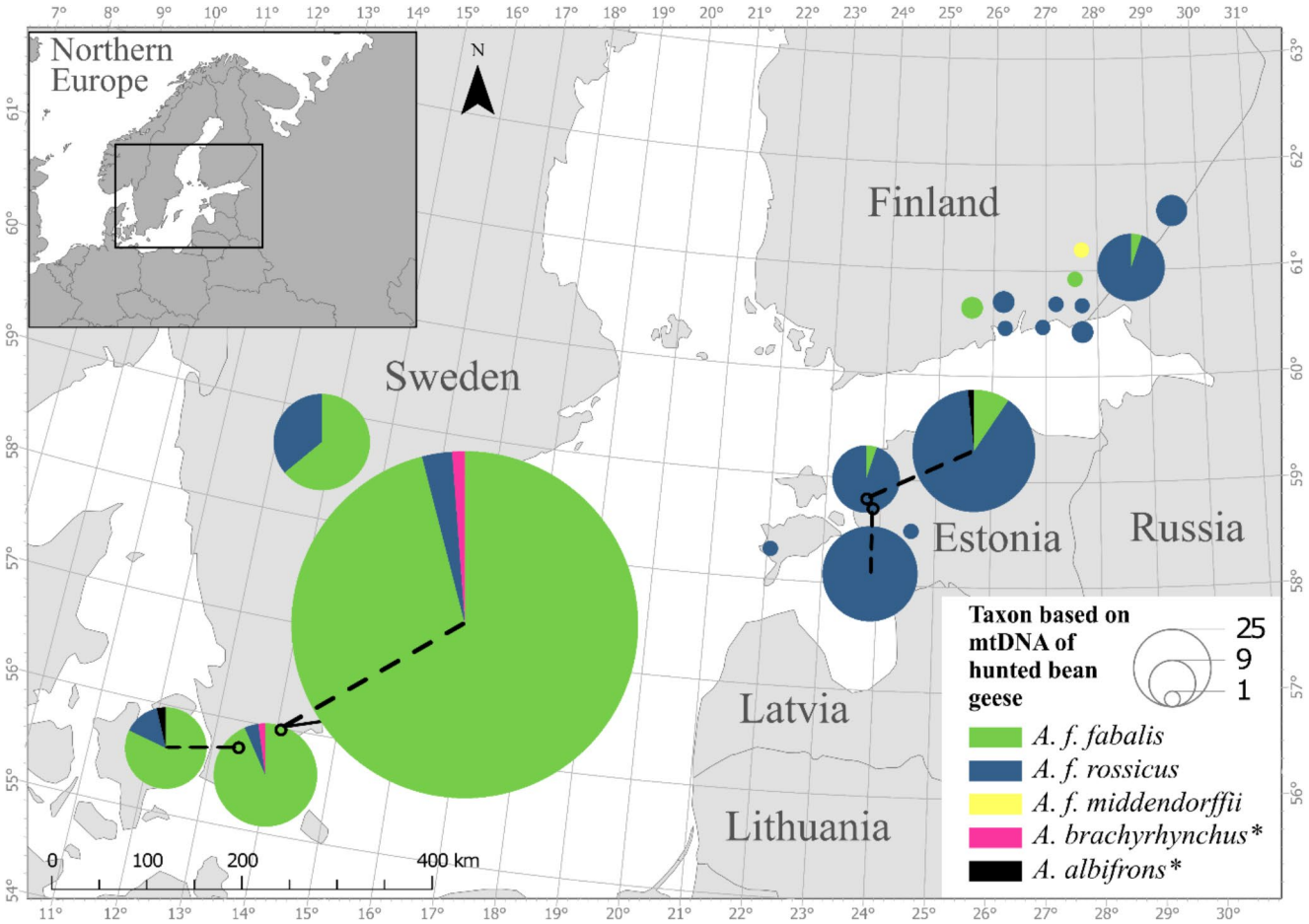

Fig. 2 Approximate harvest locations and taxa of bean goose samples used in this study ($n=779$) based on mitochondrial DNA sequencing from Sweden, Finland and Estonia. Taxa marked with an asterisk denote potential hybrid individuals or bean geese with a haplotype of another species. Size of the circles are proportional to the number of samples in each site. To avoid overlap of the circles, small open circles denote the sampling site and dashed line connects the sampling site and the corresponding pie chart. All samples (including heteroplasmies) were included

Sweden has increased since the sampling done by Heinicke and de Jong (2013), which could explain the high proportion of taiga bean geese in our sample. Most of the Swedish samples in our study (94%) were collected in Scania under the open hunting season (1 October – 31 December) and the rest (6.3%) in Västra Götaland under protective hunting regulations. Of the Scania samples, 84% were from a single estate (Trolle Ljungby). We note that the spatial coverage of the sampling for this study was limited and thus, may not be representative of the hunting bag in the whole country. This concerns especially the hunting for crop protection, which allows hunting also outside the (now former) open hunting season in Scania and Blekinge Counties.

At the time the Finnish samples were collected, bean goose hunting was only allowed in a restricted area in the south-eastern parts of the country in late autumn (1 October – 30 November), with the purpose to target harvest to tundra bean geese, which migrate over Finland later in the autumn than birds migrating from the moulting sites on Novaya Zemlya or breeding sites in the Arkhangelsk region (Piironen et al. 2021, 2022a, b). This target appears to be well met as 86% of the Finnish samples were tundra bean geese. Earlier in the season and northern and western parts of Finland, harvest consists mainly of taiga bean geese (Honka et al. 2017). Therefore, our results support the idea that bean goose harvest in Finland can be managed subspecies-specifically using spatial and temporal hunting regulations (Honka et al. 2017; Piironen et al. 2022).

In Estonia, 93% of the harvest consisted of tundra bean geese, which is roughly in line with the previous results of hunting bag composition based on images sent by hunters in the Baltic countries (Kampe-Persson and Boiko 2019). However, we note that Kampe-Persson and Boiko (2019) used different method to identify subspecies and hence, the results might not be fully comparable. No spatial hunting restrictions were in place in Estonia during our study period (harvest period: 1 October – 30 November). The origin of the taiga bean geese harvested in Estonia is interesting as

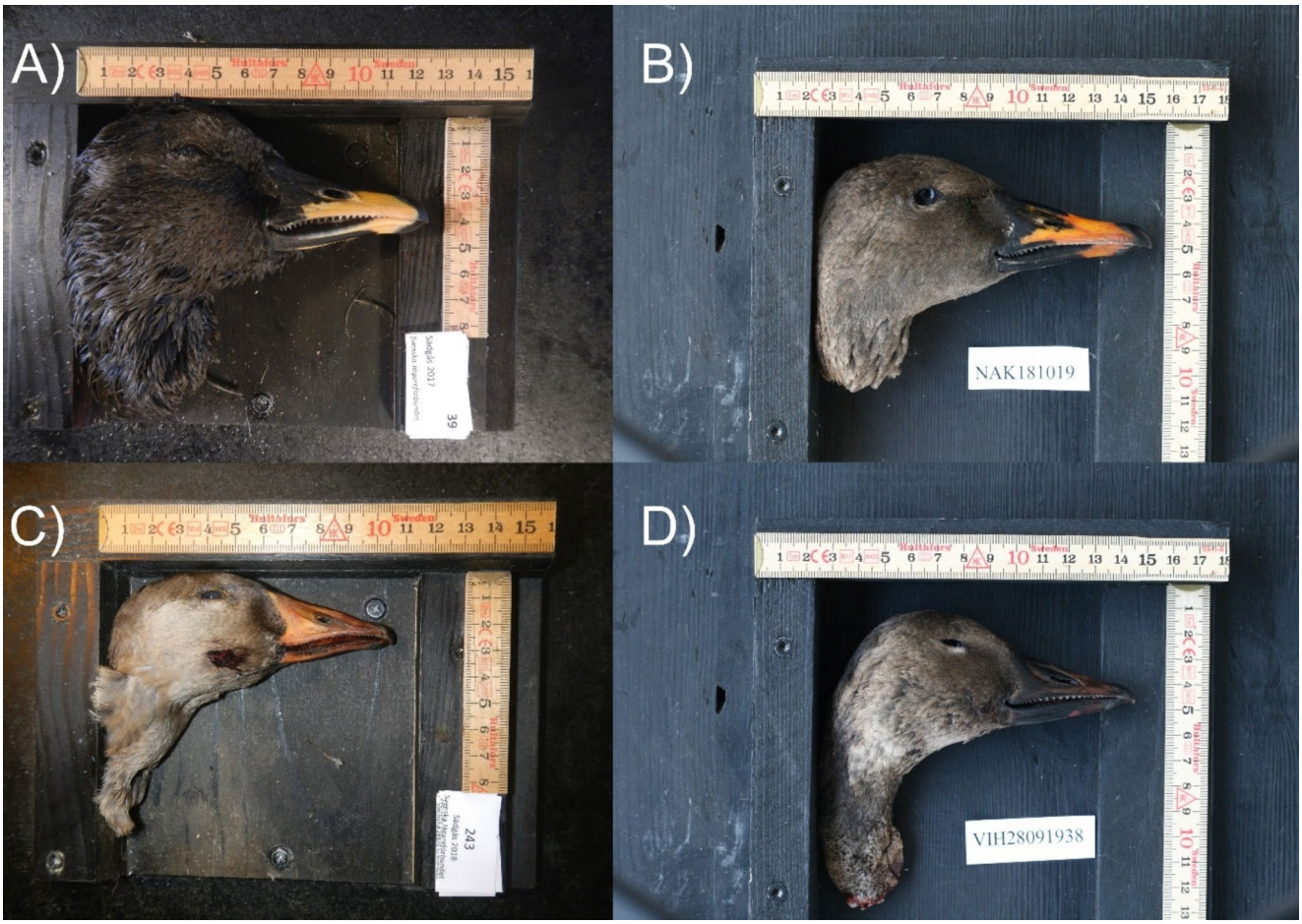

Fig. 3 Photos of bean goose (*Anser fabalis*) individuals with mtDNA haplotype other than western taiga bean goose (*A. f. fabalis*) or western tundra bean goose (*A. f. rossicus*). **A**) An individual with pink-footed goose haplotype (*A. brachyrhynchus*), though likely a normal variation for taiga bean geese, **B**) an individual with eastern taiga bean goose (*A. f. middendorffii*) haplotype, **C**) an individual with greater white-fronted goose (*A. albifrons*) haplotype from Sweden, and **D**) an individual with greater white-fronted goose haplotype from Estonia. In juvenile bean geese the orange/yellow colour of the beak has not yet fully developed, also juvenile greater white-fronted geese do not have white forefronts present in the adult plumage. Photos **A**) and **C**) the Swedish Hunter's Association and **B**) and **D**) Antti Piironen

the birds breeding around the Ural mountains appear to migrate south of Estonia (Rozenfeld et al. 2024), whereas birds breeding in Arkhangelsk region seem to migrate through Finland (Piironen et al. 2022b). Therefore, the origin of taiga bean geese migrating through Estonia should be further studied.

We note that taiga bean geese harbour an mtDNA haplotype typical for the pink-footed goose, although in low frequency (Honka et al. 2022). All geese in this study with the pink-footed goose haplotype ($n = 8$, 1% of the total sample size) were phenotypically bean geese (Fig. 3a) and we believe these individuals should be regarded as taiga bean geese, and hence the proportion of hunted taiga bean geese e.g. in Sweden is 94% instead of 93%. However, the haplotype sharing is a challenge for this method as also true pink-footed goose individuals could have been accidentally hunted, but the method would not distinguish them from taiga bean geese.

In addition, some of the tundra bean goose samples clustered in the haplotype network with both western and eastern tundra bean goose (*A. f. rossicus* and *A. f. serrirostris*) sequences. This is a problem in regions in which these two subspecies co-occur and sequencing of the whole mtDNA control region (Ruokonen et al. 2008; Honka et al. 2017) is advisable, although there is also a drawback that a few *A. f. rossicus* individuals have *A. f. serrirostris* haplotypes (Ruokonen et al. 2008).

We also note three exceptional individuals (0.4% of the total data). The first was an individual with a haplotype of Asian breeding eastern taiga bean goose (*A. f. middendorffii*, see Ruokonen et al. 2008) but a phenotype of the western taiga bean goose (*A. f. fabalis*, Delacour 1954; Fig. 3b). The eastern taiga bean geese have a very long and slender bill with black on the basal half of the bill, while the western taiga bean geese have shorter bills and typically orange colour extending over the nostrils (Delacour

1954). The breeding and wintering ranges are in East Asia (Li et al. 2020), thus this subspecies should not occur in Europe. The untypical phenotype could indicate hybridization between the two taiga bean goose subspecies. The two other exceptional individuals had an mtDNA of greater white-fronted goose, but their phenotype was not typical of a greater white-fronted goose (pers. comm. Kees Koffijberg and Gerard J.D.M. Müskens). The first goose (Fig. 3c) resembled a juvenile greater white-fronted goose with dark feathers around the bill and light plumage colour (the distinguishing white band above the beak appears only after the first moult), but the bill measurements were large for a greater white-fronted goose and completely orange bill is untypical. Bill colour of young greater white-fronted goose is duller than in adults which have pink bills, but some juveniles have been observed with orange bills. The other goose (Fig. 3d) was phenotypically and in beak size similar to a young western tundra bean goose. Like in greater white-fronted goose and in many geese species, in juvenile bean geese the beak colours are not fully developed and thus appear much duller than in adults. These exceptional geese could indicate cases of between subspecies and between species hybrids, which can only be detected in our method if the other subspecies or species served as the mother, due to maternal inheritance of mtDNA. Hybrid geese are a drawback to any genetic method but probably constitute a marginal number of hunted geese. In addition, besides difficulty with hybrid individuals and taiga bean geese with mtDNA typical of pink-footed goose, also eastern tundra bean geese would be drawback for this method as these could not be separated from the western tundra bean geese.

To our knowledge, we report the first incidence of mtDNA heteroplasmy in waterfowl. Heteroplasmy has been reported in many organisms and can originate from somatic mutations (and inherited to offspring if a mutation occurs in germ cells) or paternal mtDNA leakage (Parakatselaki and Ladoukakis 2021). The mtDNA has higher mutation rate than nuclear DNA and thus it is likely that within the individual multiple mtDNA variants exist (Parakatselaki and Ladoukakis 2021). In addition, cells harbour multiple mitochondria, thus the copy number is high. The heteroplasmies might remain undetected as in PCR and sequencing the major mtDNA variant might overrule the rare minor variants, and also the heteroplasmies might be in certain tissues, cells or even mitochondria (Parakatselaki and Ladoukakis 2021). Probably due to our large sample size ($n=779$) we were able to recover cases of heteroplasmy in which there were two more common mtDNA variants within the individual or the studied tissue.

Compared to previous results on hunting bag statistics using genetic methods (Honka et al. 2017), the sequencing of a shorter DNA region in this study provided cheaper and faster results. The difference in price and number of working hours is approximately half for the PCR-stage and approximately more than fourfold in the sequencing stage, meaning significant reductions to costs for monitoring purposes. In this study, we used tissue samples collected by hunters, but the genetic analyses can be applied to feather samples equally well. In future subspecies-assessment schemes, we propose that hunters could simply pull a feather from shot geese and send them by regular mail to an accredited laboratory as a part of subspecies composition surveillance. Although possible hybrids are a drawback to this method, these would be problematic in photography-based subspecies identification as well. In a recent study on North American geese, genetic subspecies identification method was used to refine the feather size ranges used in morphological identification of Canada (*Branta canadensis*) and cackling geese (*B. hutchinsii*) (Dooley et al. 2024), thus genetic methods can also be used to support morphology-based subspecies identification.

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Author contributions J.H., A.D.J, M.A. and A.P. conceptualised the study. Material preparation and data collection and analysis were performed by J.H., A.D.J, E.J. and A.P. The first draft of the manuscript was written by J.H. and A.P. and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Ethical approval No live animals were handled in this study, all samples were legally hunted.

Competing interests The authors declare no competing interests.

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