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Birds of different feather flock together - genetic structure of Taiga Bean Goose in Central Scandinavia

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Summary

During their flightless summer moult, Taiga Bean Geese *Anser fabalis fabalis* gather at communal moulting sites. Individuals from the Nord-Trøndelag breeding area in Norway have been observed to join with local individuals on moulting sites in Vilhelmina Municipality, Sweden. These two groups show distinct features in breeding habitat and migratory behaviour, but are they also genetically distinct? We used 12 microsatellite loci for genotyping 109 blood, feather and faecal samples from three sampling areas (Røyrvik in Norway and Stalon and Nästansjö in Sweden) to examine genetic diversity and structure. Clustering and Principal Coordinate analyses of all samples unveiled at least two distinct clusters, which were unevenly distributed over the sampling sites. Grouped by sampling sites, AMOVA and F_{ST} analyses showed that samples from the three sites differed genetically. These differences were larger between Røyrvik and Nästansjö than between Stalon and the other two. Relatedness was high among the Røyrvik samples. From our results we conclude that one of the clusters describes the Røyrvik breeding subpopulation, while the other(s) breed mainly in Sweden. Although these subpopulations simultaneously use the same moulting area in Vilhelmina, they appear to be ecologically, behaviourally and genetically distinct, in particular the Røyrvik sub-population. For goose conservation and management, we suggest that the Nord-Trøndelag (Røyrvik) subpopulation is considered a separate flyway management unit. Unravelling the Swedish sub-populations will need further study. For bird conservation is general, we suggest active genetic sampling for detailed population structure analyses and subsequent differentiated conservation and/or management schemes.

Introduction

Many years have passed since the publications of *Systema Naturae* (Linnaeus 1735) and *On the Origin of Species* (Darwin 1859), but consensus about the species concept remains elusive (de Queiroz 2007, Hausdorf 2011, Barrowclough *et al.* 2016, Burfield *et al.* 2017). Nevertheless, species level taxonomy dominates conservation and management policy and practice, e.g. the US Endangered Species Act (U.S. Fish & Wildlife Service 1973), the Birds Directive of the EU (EU 2009) and the IUCN Red List of Threatened Species (IUCN 2017). Even with a pragmatic approach, agreeing on "valid" species can be problematic, especially when novel technologies keep changing the resolution of the taxonomic landscape (Sites and Marshall 2004, Goldstein *et al.* 2005, Johnson *et al.* 2005, Tobias *et al.* 2010, Baetu 2012). Also, strict species-level policies ignore within-species population structures, which are potentially significant for biodiversity conservation (Sullivan *et al.* 2014, Coetzer *et al.* 2015, Peters *et al.* 2016). Increasingly though, below species-level

population units are recognised in conservation and management, e.g. the "distinct population segments" of the Endangered Species Act and "flyway management units" of the African-Eurasian Waterbird Agreement (UNEP/AEWA) (Marjakangas *et al.* 2015). We expect this trend to continue and spread, and, thus, the need for in-depth knowledge of population structures to increase.

After several decades of unprecedented increase in large avian herbivore numbers across the northern hemisphere (Ankney 1996, Fox *et al.* 2010), their management has become an urgent topic (Hake *et al.* 2010, Madsen *et al.* 2015). Large avian herbivores, e.g. geese, deliver a wide range of ecosystem services (Green and Elmberg 2014), but can also cause damage and nuisance (Owen 1990, Jefferies and Rockwell 2002). Outside the breeding season, they frequently mix in multi-species gatherings, making species-level monitoring and impact evaluations, and thus, evidence-based control and management programmes, difficult to implement (MacMillan *et al.* 2004). Species with unfavourable conservation status run an obvious risk of paying a devastating toll in harvesting and crop-protection schemes targeting these avian herbivore communities at large, e.g. when protected geese are shot unintentionally during hunts of geese with similar appearance or in scaring off mixed species flocks. A similar situation occurs when species contain multiple subpopulations with different sizes and trends, and thus, conservation status. If these subpopulations are not treated separately, units with poor conservation status risk to be harmed by species-level policies, e.g. under the Birds Directive of the EU (EU 2009) or national hunting regulations. Loss of below species-level biodiversity could very well reduce ecosystem services and resilience (Ryder 1986, Zink 2003, Díaz *et al.* 2006).

Outside the breeding season, the Bean Goose *Anser fabalis* is found in multi-species assemblies on agricultural land in temperate Eurasia (del Hoyo *et al.* 1992). Unlike most of its guild members, Bean Goose numbers have decreased in recent times (Fox *et al.* 2010, IUCN 2017). In many European countries it is still a hunted species, and it is also subject of crop-protection measures through scaring and shooting (Fox and Madsen 1997, Hake *et al.* 2010, Månsson *et al.* 2015, Fox *et al.* 2016a). Throughout its huge range, the Bean Goose exhibits a high level of variation in breeding habitat, migration routes, morphology and genetics. For these reasons, the Bean Goose is a challenging species for evidence-based conservation and management at the combined multi-species, species and subspecies levels ("pan-taxonomic level").

The taxonomy of the Bean Goose and its relationship to nearby species has long been debated (Delacour 1951, Sangster and Oreel 1996, Sangster *et al.* 1999, Ruokonen and Aarvak 2011, Honka *et al.* 2017). The Pink-footed Goose *Anser brachyrhynchus* is now considered to be genetically distinct from *A. fabalis* (Ruokonen *et al.* 2008, but see Delacour 1951), although recently, Ottenburghs *et al.* (2016) placed *A. brachyrhynchus* as a sister species of the (split off) Tundra Bean Goose *A. serrirostris*. Other *Anser* geese are also considered closely related to the Bean Goose (Ruokonen *et al.* 2000). Clearly, taxonomic revision is ongoing in this genus.

Below species level, the number of proposed subspecies has varied over time (Ruokonen and Aarvak 2011 for a review), but currently a system of four subspecies is most commonly accepted: two tundra forms (Eastern *A. f. serrirostris* and Western *A. f. rossicus*) and two taiga forms (Eastern *A. f. middendorffii* and Western *A. f. fabalis*). Meanwhile, species status has been suggested for most of these subspecies, either alone or in combination with others (Burgers *et al.* 1991, Sangster and Oreel 1996, Ruokonen *et al.* 2008, Ottenburghs *et al.* 2016). Given the status of 'species' in national and international legislation and agreements, this situation is unsatisfactory. UNEP/AEWA avoided much of this controversy by agreeing on an International Single Species Action Plan (ISSAP) for the (Western) Taiga Bean Goose, yet accepting the subspecies status of this taxon (Marjakangas *et al.* 2015, see also Madsen and Williams 2012).

This Taiga Bean Goose ISSAP preliminarily recognizes three flyway units in Europe (Western, Central and Eastern I), thus further differentiating the population structure (Marjakangas *et al.* 2015). The ISSAP also points at an urgent need for evidence to support the delineation of these flyway units. Fox *et al.* (2016b) used multi-element feather stable isotope analyses to support the delineation of these flyway units, but genetic support is still missing. Also, there is no evidence to

support that the proposed level of population structure, expressed by separate flyways, is the optimal level for conservation and management. On the contrary, neckband sightings and location data from GPS/GSM-tagged individuals suggest that further refinement is needed (de Jong and Nilsson 2016, Kroglund and Østnes 2016, Mitchell *et al.* 2016).

Taiga Bean Geese perform annual migrations over thousands of kilometres and, across its range, in diverse directions (Nilsson *et al.* 2009, Marjakangas *et al.* 2015). During these movements, individuals from across the breeding range regularly use the same areas for staging or wintering (Nilsson 2013, Arzel *et al.* 2006). Strong pair bonds are commonplace in geese, but unfortunately the timing of pair formation, and thus its role in gene flow and population structuring in Taiga Bean Goose, is unknown. Well-known are the strong family bonds (the young stay with their parents for almost a full annual cycle) and the social structure of goose flocks (Prevett and MacInnes 1980, Ely 1993). In these social networks, experience is gathered and shared to form traditions, e.g. in movement patterns and phenology (Raveling 1979). When different assemblies develop different patterns, this could lead to population structuring. Taiga Bean Geese are flightless for a few weeks during the moulting period in June-August. Adults with chicks moult in their breeding territories, but the rest gather at specific moulting sites (Salomonsen 1968, Nilsson *et al.* 2008, 2010, de Jong 2013). If geese from various breeding regions meet at those moulting sites, genetic admixture could occur. In summary, over the course of their life cycle, there are life history traits that could promote small-scale genetic structure and other traits that could counteract this.

In this study, we examine genetic diversity and structure in Central Scandinavian Taiga Bean Goose, representing a subset of the Western Flyway Unit (Marjakangas *et al.* 2015). The aim is to add knowledge about fine-scale genetic variation in the light of pan-taxonomic conservation and management of geese. The role of fine-scale genetic variation is probably important for many bird species, particularly those in need of conservation measures.

Materials and methods

Study population

The Taiga Bean Goose breeds across a discontinuous range in the northern boreal zone, from Scandinavia into the West-Siberian Lowlands (Fox *et al.* 2010). Within this range, four flyway units have been preliminarily accepted, of which three occur in Europe (Marjakangas *et al.* 2015). With an estimated population size of 1,500 individuals, the Western Flyway Unit (WFU) is the least numerous of these units. Its breeding range spans from Dalarna County northward through western Sweden and adjacent parts of Norway, but in most of this range, the occupancy appears to be patchy (Svensson *et al.* 1999, Marjakangas *et al.* 2015). Breeding Taiga Bean Geese have been studied in Nord-Trøndelag County in Norway (Kroglund and Østnes 2016) and Södra Lappland region in Sweden (Parslow-Otsu 1991, Parslow-Otsu and Kjeldsen 1992, Svensson *et al.* 1999, Nilsson *et al.* 2008). Although these areas are geographically close by, the Scandic Mountain Range splits the distribution into two ecologically separated clusters. Recent work in these areas, e.g. with GPS/GSM neck-collars, has shown that individuals from these clusters share wintering and moulting areas, but that their migration routes and staging sites differ (de Jong and Nilsson 2016, Kroglund and Østnes 2016).

Sample collection and DNA extraction

Blood, feather and faecal samples were collected during spring and summer at three locations from 2010 to 2016 (Table 1). Geese were caught with cannon nets at spring staging sites in Røyrvik municipality in 2010 and 2013 and by herding flightless moulting flocks (> 70 to > 300 individuals) into standing nets at the Stalon and Nästansjö sites in 2012 and 2015. These catching sites were chosen on the basis of known occurrences (Nilsson *et al.* 2008, Kroglund and Østnes 2016), but without prior knowledge of potential population structure. In addition to sampling live birds, shed feathers

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Table 1. Distribution of the $N = 109$ unique DNA samples over sites, years and sample types.

Site	Period	Sample type	*n*
Røyrvik	2010	blood	2
Røyrvik	2013	pulled feather	2
Røyrvik	2013-2016	shed feather	16
Røyrvik	2016	dropping	3
Stalon	2012	blood	4
Stalon	2015	pulled feather	9
Stalon	2013-2016	shed feather	24
Nästansjö	2012	blood	33
Nästansjö	2015	pulled feather	16

and droppings were collected opportunistically during scouting trips within breeding and moulting areas. In six cases, subsequent analyses showed that individual geese had been sampled in the Røyrvik breeding area and the Stalon moulting site. These individuals were geographically assigned to their breeding area. The location of the settlements Røyrvik, Stalon and Nästansjö are 64.89°N/13.56°E, 64.93°N/15.88°E and 64.79°N/16.52°E respectively, but we keep the exact locations of the nearby breeding and moulting sites secret in order to reduce the risk of human disturbance.

Genomic DNA was extracted from feathers using the Maxwell® 16 Research System (Promega, Madison, WI, USA) and the Maxwell 16 tissue DNA Purification Kit. Genomic DNA from blood samples was extracted with either the method above or using Qiagen's Blood and Tissue Kit (Qiagen, Hilden, Germany). Genomic DNA from faecal samples was extracted using FastDNA Spin Kit for Soil (MP Biomedicals, Santa Ana, CA, USA).

Microsatellite genotyping

All samples were genotyped at 13 autosomal microsatellite loci and one sex-typing marker. The autosomal loci used included one locus previously developed from the Greater White-fronted Goose *Anser albifrons* (Aalμ1; Fields and Scribner 1997) and 12 loci previously developed from the Bean Goose (Kleven *et al.* 2016). The Z-002A marker (Dawson 2007) was added to sex the samples. Loci were PCR-amplified with fluorescent-labelled forward primers (Applied Biosystems, Foster City, CA, USA) in two multiplexes as described in Kleven *et al.* (2016), and Aalμ1 (VIC labelled) was added to multiplex set b (see Table 2 in Kleven *et al.* 2016). Multiplexing was performed with a Multiplex PCR Kit (Qiagen) following the manufacturer's protocol, but using 8.4 μL reaction volume. PCR products (0.8 μL) were mixed with GeneScan 500 LIZ (Applied Biosystems) size standard (0.14 μL) and Hi-Di formamide (6.16 μL). PCR products were separated on an ABI 3130xl Genetic Analyzer and allele sizes assigned using GeneMapper software (Applied Biosystems).

Moulted feathers and faecal samples, like other types of non-invasively collected material, commonly have relatively low amounts and/or quality of DNA, which may result in genotyping errors such as the failure to amplify an allele (allelic dropout) or PCR-generated amplification of false alleles (Taberlet and Luikart 1999, Pompanon *et al.* 2005). To reduce the probability of genotyping errors, DNA from each moulted feather and faecal sample was analysed in three (or more if required) independent PCR replicates. We used ConGenR (Lonsinger and Waits 2015) to check for false alleles (FA rate = 0 in all loci) and allelic dropout rates. Based on the independent replicates, a locus-level consensus genotype was constructed using the following criteria: heterozygosity was accepted when at least two of the independent PCR-replicates showed heterozygosity, whereas homozygosity was only accepted when this was expressed in three independent PCRs. Samples that did not meet these requirements were omitted from the dataset. Samples with a consensus genotype containing at least 10 loci were used for individual identification with R-package Allelematch 2.5 (Galpern *et al.* 2012). The final dataset came to include 109 unique Taiga Bean Geese individuals,

19 of them represented by multiple consensus samples (17 from Røyrvik). Finally, we controlled the dataset for these 109 individuals for evidence of null alleles with Microchecker (Van Oosterhout *et al.* 2004).

Statistical analyses

First, we checked for global heterozygosity deficiency with Hardy-Weinberg U-test in Genepop 4.5.2 (Rousset 2008) and compared expected and observed heterozygosity with Arlequin 3.5.2.2 (Excoffier and Lischer 2010). Fstat 2.9.3.2 (Goudet 2001) was used to estimate allelic richness within sampling sites. Secondly, we analysed genetic distances between sampling sites by pairwise F_{ST} tests and AMOVA (in both cases using 99,999 permutations in Arlequin 3.5.2.2).

Thirdly, we explored the genetic structure among the samples. We used Structure 2.3.4 (Pritchard *et al.* 2000) with an admixture model (initial Alpha = 1.0) and independent allele frequencies and applied 100,000 burn-in steps, 1,000,000 repeats and 20 iterations. Test runs had shown that LnLikelihood stabilised within < 100,000 iterations and log(Alpha) showed weak levels of white noise across the range of repeats. We then used Structure Harvester Web 0.6.94 (Earl and vonHoldt 2012) to evaluate the number of clusters, and Clumpak (Kopelman *et al.* 2015) to barplot averaged probabilities of cluster assignments. Supplementary to Structure, we used R package adegenet 2.0.1 (Jombart 2008, Jombart and Ahmed 2011) for cluster analyses and assignments. In addition to Bayesian clustering methods, we used GenAlEx 6.5 (Peakall and Smouse 2012) for Principal Coordinate Analysis (PCoA). Finally, we calculated relatedness within and between sampling populations with ML-Relate (Kalinowski *et al.* 2006).

Results

There was no evidence of false alleles for any of the 13 loci, and allelic dropout was observed in only three loci and at low rates (Afa02 = 0.0075, Afa25 = 0.0310 and Afa34 = 0.0074). Locus Afa18 showed evidence for a null allele and even failed to pass the global Hardy Weinberg equilibrium test. Consequently this marker was excluded from further analyses.

The Global Hardy-Weinberg U-test across all 12 loci and all samples (n = 109) showed no significant deficit of heterozygosity ($P > 0.05$). Across loci averaged observed heterozygosity (H_o) did not differ significantly from expected heterozygosity (H_e) for neither of the sampling sites (Table 2). Allelic richness was slightly lower among the Røyrvik samples compared with the Stalon and Nästansjö samples (Table 2).

Pairwise F_{ST} between sampling sites showed a higher level of differentiation between the Røyrvik and Nästansjö samples (F_{ST} = 0.034, $P < 0.001$) than between the Røyrvik and Stalon samples (F_{ST} = 0.014, $P < 0.01$) and between the Nästansjö and Stalon samples (F_{ST} = 0.004, $P > 0.05$). Global AMOVA showed that 2% of the variation resulted from differences between populations and 98% from within populations (F_{ST} = 0.015, $P < 0.001$).

The results of the Structure analysis unveiled two or three genetic clusters among the 109 samples (Figure 1), with ΔK values favouring a split into two clusters (see Evanno *et al.* 2005) (Figure 2). Adgenet results showed the lowest BIC values for three genetic clusters (Figure 3) and the sampled individuals were well separated in a scatterplot for these three clusters (Figure 4).

Table 2. Measurements of genetic variation at 12 loci for samples from the three sampling sites: number of samples per site (n), observed average heterozygosity (H_O), expected average heterozygosity (H_E) and allelic richness ± SD (AR).

Sampling area	n	H_O	H_E	AR
Røyrvik	23	0.793	0.738	6.66 ± 1.85
Stalon	37	0.723	0.757	7.45 ± 2.12
Nästanjö	49	0.741	0.750	7.19 ± 1.91

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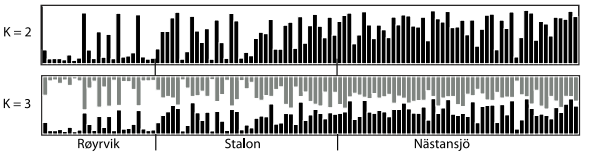

Figure 1. Assignment probability for individual Taiga Bean Geese on one of two (K = 2) or three (K = 3) clusters from Structure models.

Assigned against these three clusters, the individuals were non-randomly distributed over the sampling sites ($\chi^2_{3,3}$ $P < 0.001$). Cluster 1 dominated among the Røyrvik samples and cluster 3 among the Nästansjö samples, while cluster 2 was more evenly spread among the sampling sites (Table 3). A complex distribution of subpopulations across the sampling sites was also expressed in the results of the PCoA. Although the first three axes explained 19.6% of the overall variation, the sampling sites were not clearly separated when plotted against any pair of these three axes (Figure 5).

Within sampling sites, family relationships were more frequent among the Røyrvik samples than among the Stalon and Nästansjö samples (Table 4). Between sampling sites, family relationships were more common between Røyrvik and Stalon than between Røyrvik and Nästansjö (Table 4). The levels of relatedness within and between the Stalon and Nästansjö samples were similar (Table 4).

Discussion

Genotyping errors were unlikely to have significantly influenced the results and the elimination of the poorly behaving Afa18 locus ensured that the HWE requirements were not violated. The H_o to H_e ratios and allelic richness for the three sampling sites were indicative of modest levels of genetic variation within the overall pool of samples.

Although the L(K) output of Structure showed very similar levels for K = 2 and K = 3 (Figure 2A), Structure Harvester suggested only two clusters in accordance with Evanno *et al.* (2005) (Figure 2B). Structure and Structure Harvester have been criticised for overemphasising K = 2, though (Janes *et al.* 2016). Based on Bayesian Information Criterion (BIC) levels, R program adegenet suggested three clusters (Figures 3 and 4). Until further data are available, we can only conclude that at least two subpopulations occur within this very restricted part of the Taiga Bean Goose range.

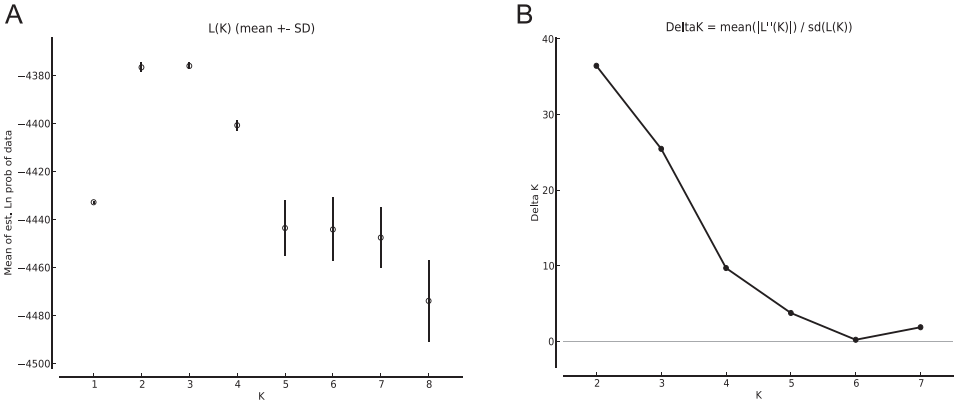

Figure 2. Means of estimated Ln probabilities (A) and ΔK (B) across the number of Structure clusters (K).

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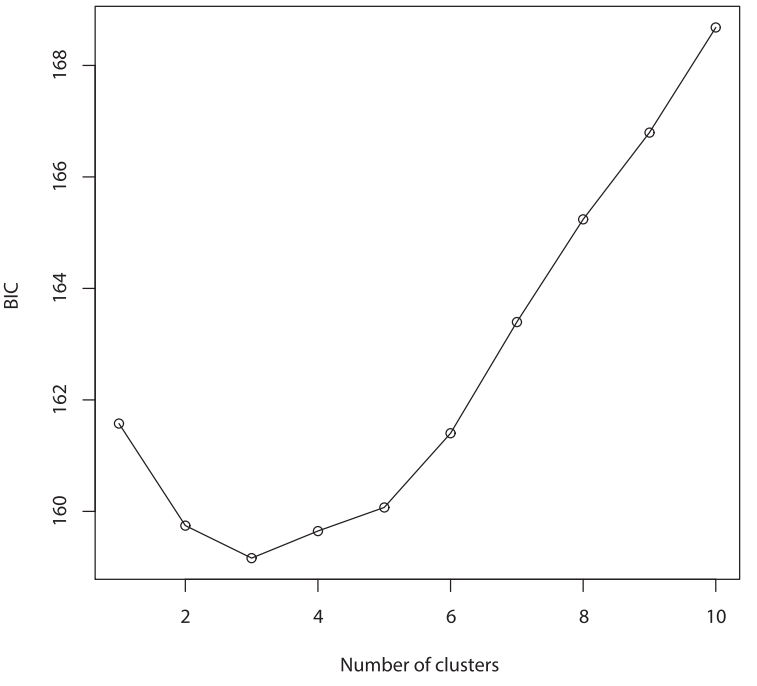

Figure 3. Values of Bayesian Information Criterion (BIC) for 1 – 10 adegenet clusters on 40 retained Principal Components.

Individuals assigned to these clusters were unevenly distributed over the three sampling sites (Figure 1, Table 3), but the PCoA results showed that the samples from these three sites are not clearly separated (Figure 5). Viewed from a sampling site point of view, the genetic distance between the samples from Røyrvik and Nästansjö was larger than between those from Røyrvik and Stalon. The genetic distance between Stalon and Nästansjö was small. The AMOVA results showed that the samples from the three sites were significantly different, but that site contributed with only 2% of the overall genetic variation.

Our interpretation of these findings is that two or more subpopulations come together in the Stalon-Nästansjö moulting region. One of these subpopulations originates mainly from the Røyrvik breeding area and prefers the Stalon site. The link between Røyrvik and Stalon is confirmed by six cases of duplicate sampling and by the positions of four individuals tagged with GPS devices. These tagged individuals moved between the Røyrvik breeding area and the Stalon moulting site during multiple years (Kroglund and Østnes 2016, A. de Jong unpubl. data). Other individuals (n = 16) tagged with GPS devices at the Stalon and Nästansjö moulting sites proved to be Swedish residents and never visited Norway (A. de Jong unpubl. data).

Despite the incomplete sorting of subpopulations (clusters) between sampling areas, the genetic distance between the samples from Røyrvik and Nästansjö was in the same order of magnitude as those found between e.g. salmon populations of different rivers, differentiation levels commonly warranting genetic management units (Banks *et al.* 2000, Ayllon *et al.* 2006, Olafsson *et al.* 2014). Similar levels of F_{ST} values are also reported by Ely *et al.* (2017) for Greater White-fronted Goose populations along the Pacific Flyway and by Kvist *et al.* (2011) for three European subspecies of Reed Bunting *Emberiza schoeniclus*. We predict that, once the subpopulations found in our study can be properly assigned to breeding ranges, the genetic distances between these breeding populations will become important to consider in conservation and management policies.

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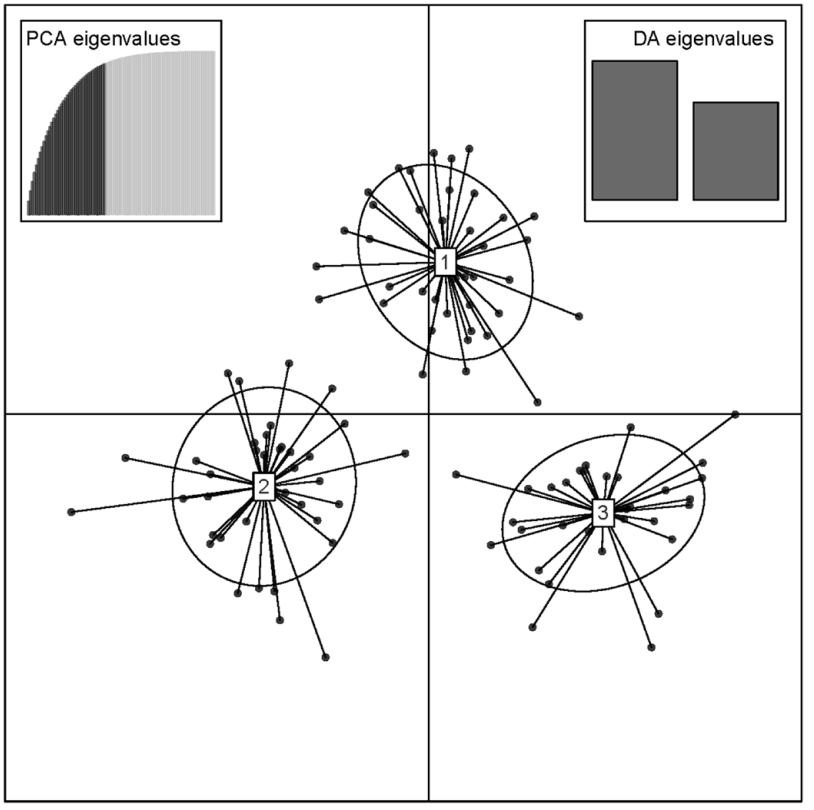

Figure 4. Scatterplot of individuals in the three clusters from the discriminant analysis of principal components (DAPC) analysis in adgenet. Retained Principal Components and Eigenvalues depicted in the insets.

Relatedness among individuals from the Røyrvik breeding area was high. Feathers and droppings (83% of the included Røyrvik samples) from family groups may have been sampled simultaneously, but even geographically and temporally separated samples were related. Our interpretation is that the observed level of relatedness mainly derived from the small population size of the Røyrvik group. This interpretation is supported by observational evidence, with a maximum of only 33 individuals observed within the pre-breeding staging area during recent years (Kroglund and Østnes 2016, J. E. Østnes unpubl. data).

High levels of relatedness can influence statistical analyses of genetic data (Palsbøl *et al.* 2010, Iacchei *et al.* 2013, Putman and Carbone 2014). Preferably, the dataset should have been weeded for redundant family members, but our limited sample size did not allow this. Consequently, the results of our statistical analyses should be interpreted with this level of relatedness in mind. Meanwhile, for fine-scale genetic structure in a species with strong family bonds, relatedness is

Table 3. Number of individuals assigned to adegenet clusters 1, 2 and 3 across sampling sites.

	Cluster 1	Cluster 2	Cluster 3
Røyrvik (n = 23)	14	9	0
Stalon (n = 37)	13	16	8
Nästansjö (n = 49)	8	16	25

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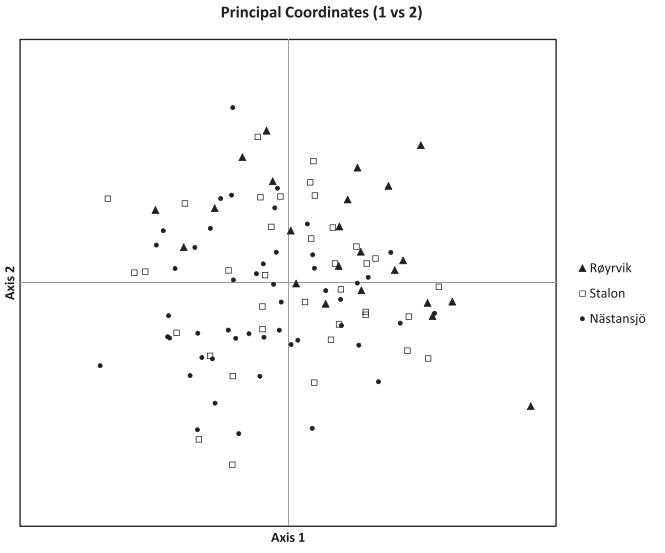

Figure 5. PCoA plot of the individuals from the three sampling sites.

an unavoidable aspect. Relatedness and pedigree can also be used in further studies of the genetic structure and population size in Bean Goose and other bird species that are difficult to study during the breeding season (Økland *et al.* 2009, Creel and Rosenblatt 2013). Our study has shown that non-invasive sampling (collection of faeces and feathers) can be used in this context.

Goose conservation and management deals with multi-species, multi-population systems, in which (genetic) management units can be game, pest or red-listed; sometimes all at once. They may also be trans-border migrants, and their ecology and demography poorly understood. The task is truly challenging, but possible to fulfil (Tuvendal and Elmberg 2015). Currently, 'species' are the main unit of policy making and implementation, and goose count results are the main input into the decision-making process. Instead, we suggest that conservationists and managers combine information from counts, migration studies and analyses of stable isotope and genetic samples in the design and implementation of their pan-taxonomic effort. Low- or non-invasive methods for intensive, range-wide sampling and genotyping (e.g. sampling of shed feathers and eDNA) are available to facilitate the data input for fine-tuned biodiversity conservation and management.

For conservation ecology at large, the recognition of fine-scale genetic structures within species raises the question whether or not the appointed sub-populations are "evolutionarily significant units" (*sensu* Ryder 1986). Considering the difficulties in predicting the long-term significance of any genetic "unit", we suggest that even fine-scale genetic variation, especially when supported by differences in ecological and behavioural traits, is viewed as an important aspect of biodiversity, meriting conservation effort and careful management.

Table 4. Average relatedness (a) and relationship assignments (b) based on 12 microsatellite data within (bold) and between sampling areas: Røyrvik = R, Stalon = S and Nästansjö = N. Total number of pairs = 5,886.

		RxR	RxS	RxN	SxS	SxN	NxN
a	Average relatedness	**0.141**	0.068	0.037	**0.060**	0.050	**0.062**
b	Parent-offspring (%)	**7.9**	1.4	0.0	**0.5**	0.2	**0.5**
	Full sibling (%)	**6.3**	1.3	0.2	**0.5**	0.4	**0.8**
	Half sibling (%)	**22.9**	13.4	8.8	**13.8**	11.9	**14.6**
	Unrelated (%)	**62.8**	83.9	91.0	**85.3**	87.5	**84.1**
	Number of pairs	253	851	1127	666	1813	1176

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