Lack of genetic structure in greylag goose (*Anser anser*) populations along the European Atlantic flyway

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Greylag goose populations are steadily increasing in north-western Europe. Although individuals breeding in the Netherlands have been considered mainly sedentary birds, those from Scandinavia or northern Germany fly towards their winter quarters, namely over France as far as Spain. This study aimed to determine the genetic structure of these birds, and to evaluate how goose populations mix. We used mitochondrial DNA and microsatellites from individuals distributed throughout the European Atlantic flyway, from breeding sites in Norway and the Netherlands to stopover and wintering sites in northern and south-western France. The mtDNA marker (CR1 D-Loop, 288 bp sequence, 151 ind.) showed 24 different haplotypes. The genetic distances amongst individuals sampled in Norway, northern France and the Netherlands were low (range 0.012-0.013). Individuals in south-western France showed a slightly higher genetic distance compared to all other sampling areas (ranges 0.016-0.017). The NJ tree does not show evidence of any single clades grouping together all individuals from the same geographic area. Besides, individuals from each site are found in different branches. Bayesian clustering procedures on 14 microsatellites (169 individuals) did not detect any geographically distinct cluster, and a high genetic admixture was recorded in all studied areas except for the individuals from the breeding sites in Norway, which were genetically very close. Estimation of migration rates through Bayesian inference confirms the scenario for the current mixing of goose populations.

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Introduction

The greylag goose (*Anser anser*) is widespread throughout the Palearctic. In Europe, the main breeding populations are located in central and northern countries, and the species rarely breeds in Mediterranean areas (Cramp, 1977; Hagemeijer & Blair, 1997; BirdLife International, 2004). European populations show different patterns of movement. Although individuals breeding in Scotland and the Netherlands are considered sedentary birds (Delany & Scott, 2006), those from Scandinavia or central Europe fly longer distances, namely over France to Spain, with some individuals reaching North Africa (Fox et al., 2010; Nilsson et al., 2013). Icelandic breeders winter in Ireland and Britain, and greylags from Russia reach the regions bordering the eastern Mediterranean, Black and Caspian seas. Individuals with morphological characters ascribed to the oriental subspecies *rubirostris* have been observed on rare occasions in western Europe (Cramp, 1977).

Widescale movement patterns have been studied through the recapture or resighting of marked birds (coloured neck collars and leg rings, see Nilsson et al., 2013). These methods gave valuable information about the origin of birds that were found in moulting areas (Nilsson, Kahlert & Persson, 2001), flying, or staging in winter quarters. Birds from Sweden and Norway fly to Denmark and/or the Netherlands (SOVON, 1987; Persson, 1993; Andersson et al., 2001). Recent monitoring of greylags tagged with GPS devices in Norway show that approximately 30-50% can stay in the Netherlands during the whole wintering season, whereas others migrate to France or Spain. These geese all return to their previous breeding sites, thus showing a high breeding site fidelity (Boos et al., 2012, Boos unpublished data). According to Ramo et al. (2012), an increasing number of greylag geese winter at higher latitude. A noticeable effect of climate changes probably explains this increasing tendency for geese to winter more closely to their breeding grounds.

The European Atlantic flyway covers a vast area stretching from northern France to Spain and Portugal, with arrivals from Scandinavia, Poland, Denmark and Germany (Fouquet et al., 2009). The situation in France is particularly complicated, because noticeable fluxes of

geese coming from Northern or Central Europe are found not only along the Atlantic flyway but also in other areas located in central and south-eastern France. The departure areas of these birds have yet to be been fully determined, and the timing of migration can probably differ depending on the origin of the populations (Fouquet, 1991; Comolet-Tirman, 2009). Furthermore, the relative proportion of geese travelling to France and originating from different countries may change over time (Pistorius, Follestad & Taylor, 2006; Pistorius et al., 2007). However, data from neck-collared or ringed geese can be skewed by variations in the marking and resighting efforts of the countries involved (Nilsson, 2007; Nilsson et al., 2013), and this makes it difficult to fully define the composition of goose subpopulations migrating south from observational data alone.

Genetics have become a useful tool in the study of migration and wintering patterns. Recent studies on Anseriforms examined spatial structure along the flyways or in wintering zones, then compared it to genetic data in breeding areas. In the king eider (*Somateria spectabilis*), strong site fidelity to wintering areas and pair formation at wintering quarters indicated a population structure defined by wintering rather than nest-site philopatry (Pearce et al., 2004). However, genetic analyses of mtDNA and microsatellite alleles showed a lack of spatial genetic structure, suggesting the possible existence of flows with homogenized gene frequencies. In the mallard *Anas platyrhynchos*, single nucleotide markers were used to investigate population structure on a continental scale throughout the northern hemisphere. This genetic analysis found a general panmixia, suggesting that mallards form a single large, interbreeding population (Kraus et al., 2013). The tufted duck (*Aythya fuligula*) shows high breeding site fidelity, but mtDNA and microsatellite markers revealed an extensive population admixture on the wintering ground (Liu et al., 2012, 2013). In the common pochard (*Aythya ferina*), genetic differentiation was observed among Eurasian breeding populations, but no evidence of genetic structure was detected for pochards sampled on European wintering grounds (Liu, Keller & Heckel, 2011).

Relatively few studies have investigated the genetic aspects of European geese of the genus *Anser,* and the subject has not been thoroughly investigated at all in the greylag goose.

Studies by Ruokonen (2004, 2005) examined the genetic variability in two species of conservation concern, the lesser white-fronted goose *Anser erythropus* and the pink-footed goose *Anser brachyrhynchus*, and investigated the phylogenetic relationship between seven *Anser* species (Ruokonen, Kvist & Lumme, 2000). A small amount of genetic differentiation between species has been observed in this genus (Ruokonen, Kvist & Lumme, 2000; Johnsen et al., 2010).

Actually, mitochondrial DNA showed the presence of highly fragmented populations in two species of conservation concern, the lesser white-fronted goose *Anser erythropus* (Ruokonen et al., 2004) and the pink-footed goose *Anser brachyrhynchus* (Ruokonen, Aarvak & Madsen, 2005).

However, population genetic among species of geese has not been investigated to date. Here we used both mitochondrial DNA and microsatellites to study the characteristics of greylag geese from two breeding areas (the Netherlands and north-western Norway) and two wintering zones (northern France and south-western France). This study investigates to what extent populations are genetically differentiated. Genetic structure could have been increased by the fragmentation of breeding geese in separated areas, or on the contrary, a limited genetic structure could have been developed by i) the widespread practice of amateur breeding and selling of geese (Hagemeijer & Blair, 1997; Wang et al., 2010), ii) the recent increase in the size of several populations (Klok et al., 2010), and iii) the habit of European geese to rest several times during their flight toward their winter quarters (Fouquet, Schricke & Fouque, 2009) at stopover sites where individuals from distant areas can admix and form pair bonds.

Knowledge of the genetic structure and diversity of greylag goose populations is a necessary scientific basis to manage this emblematic species (Lorenz, 1966) and decide on appropriate action for its conservation (Kampe-Persson, 2002) in the light of serious recent conflicts with agricultural and habitat protection interests in most North European countries (Klok et al., 2010).

Methods

Sample collection and DNA extraction

We analyzed feather samples from 174 greylag geese (Appendix 1) collected over the European Atlantic flyway (from two breeding grounds: in North and Western Norway, and six staging grounds: in the Netherlands, northern France and south-western France; see Table 1 and Fig. 1). One additional individual was collected in the Republic of Kalmykia in an area associated with the eastern *rubirostris* subspecies (Cramp, 1977). During the 2010/2011 and 2011/2012 (including 1-10 February) wintering seasons in France, goose feathers were obtained from greylag geese collected during the legal hunting period in natural areas by hunters collaborating with the study. Samples from the Netherlands were obtained on wild free-ranging geese collected in natural areas in the Zeeland region (near Rilland) by a local hunter before the 20th of September in 2011 and 2013, i.e. before the arrival of geese breeding in Norway or in Sweden (Nilsson, 2006, 2007; Boos pers. obs. based on GPS data). Samples from Norway were obtained from birds that were collected during the spring and summer legal hunting seasons, or from geese that were caught during the moulting period in 2010 and 2011 by A.F. for the Nordic Greylag Goose Project, which studies the ecology of the Norwegian breeding goose population (Nilsson, 2007). Feather calami were stored in ethanol at -20 °C, and total DNA was extracted using the commercial NucleoSpin®Tissue kit (Macherey-Nagel, Düren, Germany). After extraction, genomic DNA was stocked at -20 °C.

Mitochondrial DNA sequencing

Partial mitochondrial control region (CR1 D-Loop 288 bp) was amplified in 144 of the 174 individuals (Appendix 1) using L180 (5'TGGTTATGCATATTCGTGCATAGA'3) and H466 (5'TTTCACGTGAGGAGTACGAC TAAT'3) primers (Ruokonen et al., 2000). PCR amplifications were carried out in a Bio-Rad thermal cycler (Bio-Rad Laboratories Inc.; Hercules, California, USA). PCR reaction was performed in a final volume of 25 µl containing 0.4 µl dNTPs (10 mM), 1 µl MgCl2 (25 mM), 0.3 µl of each primer (25 pmol/µl), 2.5 µl 10× buffer,

129 0.4 µl Taq polymerase (5 unit/µl; QIAGEN), ddH2O and genomic DNA (20–100 ng/µl). The
130 selected cycling profile included a 4 min preliminary denaturation cycle at 94 °C followed by
131 32 denaturation, annealing and extension cycles (30 s at 94 °C, 30 s at 58 °C and 30 s at
132 72 °C, respectively) before a final extension of 7 min. Negative controls were included for
133 amplification procedures to detect contaminations.

134 The PCR product was purified using the EXO-SAP procedure with Exonuclease I
135 (Exo; Fermentas, Burlington, Canada) and Shrimp Alkaline Phosphatase (SAP; Fermentas,
136 Burlington, Canada). The purification cycle consisted of 30 min at 37 °C, then 15 min at 80
137 °C to deactivate the enzymes followed by a 10 min cooling-down step at 4 °C. DNA
138 concentration was determined after electrophoresis in 1.8% agarose gels (TBE 1%) stained
139 with ethidium bromide and visualized in a UV-trans illuminator Gel Doc XR (Bio-Rad
140 Laboratories Inc.; Hercules, California, USA) using the Molecular Imager ChemiDoc XRS
141 System and Quantity One software (Bio-Rad Laboratories Inc.; Hercules, California, USA).

142 Sequencing was carried out at Macrogen Laboratories (Amsterdam, The Netherlands)
143 in an ABI 3730xl Analyzer (Applied Biosystems).

144 Raw electropherograms were checked visually using FinchTV (Geospiza Inc.;
145 Seattle, WA, USA; http://www.geospiza.com), and sequences were aligned with ClustalW
146 algorithm in BioEdit 7.05 (Hall, 1999). The haplotype network was calculated in Network 4.6
147 (Fluxus Technology Ltd; Clare, Suffolk, England; fluxus-engineering.com) using the median
148 joining procedure (MJ: Bandelt et al., 1999). DNASP version 5 (Librado & Rozas, 2009) was
149 used to estimate mtDNA haplotype diversity (h), nucleotide diversity (π) and the mean
150 number of pairwise differences (k) in the sampled areas. Demographic and/or spatial
151 population expansion events were investigated using the mismatch distribution implemented
152 in DNASP v. 5. MEGA 5.0 (Tamura et al., 2011) was used to perform the neighbour-joining
153 method (NJ: Saitou and Nei, 1987), clustering pairwise Tamura-Nei's genetic distances
154 between haplotypes (TN93: Tamura and Nei, 1993). Support for the internodes in the NJ tree
155 was assessed by bootstrap percentages (BP: Felsenstein, 1988) after 1000 resampling steps.
156 One sequence of *Anser anser anser* (GenBank AF159962) from Finland and another of *Anser*

157 *anser rubrirostris* (GenBank AF159963) from Slimbridge Wetland Center, England, were
158 included as reference sequences in tree construction. A sequence of the lesser white-fronted
159 goose *Anser erythropus* (GenBank AY072580) and the bean goose *Anser fabalis* (GenBank
160 AB551534) were used as outgroups.

161 Maximum likelihood (ML) and maximum parsimony (MP) trees were obtained
162 through the DNAML, CONSENSE, DNAPARS programmes in PHYLIP 3.67 (Felsenstein,
163 2005). Bootstrap values were based on 1000 replicates, and the tree topologies were
164 visualized with FigTree 1.3.1 (Rambaut, 2008). The best substitution model for molecular
165 evolution was selected using the corrected Akaike Information Criterion (AICc, Burnham and
166 Anderson, 2004) in jModelTest (Posada, 2008). Maximum likelihood bootstrap supports were
167 estimated by performing 100 runs with 1000 bootstrap replicates.

168 The partition of mtDNA diversity within and among the sampled geographical
169 populations were investigated by running analyses of molecular variance (AMOVA,
170 Excoffier et al., 1992) using Arlequin 3.3 (Excoffier & Lischer, 2010).

171

172 **Microsatellite genotyping**

173 A total of 169 of the 174 samples (Appendix 1) were genotyped by PCR amplification at
174 fourteen microsatellite loci (Ans02, Ans04, Ans07, Ans13, Ans17, Ans18, Ans21, Ans24,
175 Ans25, Aalμ1b, Aph12b, Aph19b, Smo7b, Hhiμ1b) that had previously been isolated and
176 tested in *Anser anser* (Weiß et al., 2008). We used PCR reactions, thermal profiles,
177 fluorescent dye and multiplex sets, as indicated by Weiß et al. (2008). Microsatellite
178 genotyping was performed on an ABI Prism 3100 Genetic Analyzer (Applied Biosystems)
179 using the Macrogen Inc. GenScan service (Seoul, Korea). Negative controls were included for
180 amplification procedures. Results were analysed in GeneMapper v. 4.0 (Applied Biosystems,
181 Foster City, California).

182 Allele frequencies, standard diversity indices, observed heterozygosity (H_O) and
183 expected heterozygosity (H_E) for each locus and population were calculated in GENALEX v. 6
184 (Peakall & Smouse, 2006).

185 We performed a factorial correspondence analysis (FCA) of individual multilocus
186 scores in GENETIX 4.05 (Belkhir et al., 2004) to describe genetic clusters.
187 GENEPOP 3.4 (Raymond & Rousset, 1995; Rousset, 2008) was used to calculated
188 departures from the Hardy-Weinberg equilibrium at each locus and within each population.
189 Statistics were computed with Markov chain parameters at default settings.
190 We used ARLEQUIN 3.5 (Excoffier & Lischer, 2010) to estimate the genetic variance
191 within and between populations through a hierarchical Analysis of Molecular Variance
192 (AMOVA; Excoffier et al., 1992), and a Mantel test was performed with 1000 iterations to
193 determine the presence of isolation by distance.
194 The genetic structure of the sampled populations was computed using Bayesian
195 clustering procedures in STRUCTURE v. 2.3 (Pritchard, Stephens & Donnelly, 2000; Falush,
196 Stephens & Pritchard, 2003), without prior information about the origin and under
197 an admixed model. Analyses were performed where K=1-10 with $50x10^5$ iterations following
198 a burn-in period of $50x10^4$ iterations; all simulations were independently replicated four times
199 for each K. We explored the optimal value of K by plotting the average estimated LnP(D) (Ln
200 probability of the data) and using ΔK statistics (Evanno, Regnaut & Goudet, 2005) calculated
201 using STRUCTURE HARVESTER 0.6.93 (Earl & VonHoldt, 2012). CLUMPP v. 1.1.2 (Jakobsson
202 & Rosenberg, 2007) and DISTRUCT v. 1.1 (Rosenberg, 2003) were used to align the cluster
203 membership coefficients of the five STRUCTURE runs and display the results.
204 We investigated the presence of bottleneck events with BOTTLENECK v. 1.2.02
205 software (Cornuet & Luikart, 1996) for two models: the infinite alleles (IAM, Maruyama and
206 Fuerst, 1985) and the two-phase model (TPM, Di Rienzo et al., 1994).
207 Migration rate was estimated using the Bayesian inference approach implemented in
208 BAYESASS 3.0.3 (Wilson and Rannala 2003). We performed 10 runs of $9x10^6$ iterations with
209 a burn-in of 10%, and a sampling frequency of 200. Delta values were varied for all
210 parameters, and resulted in acceptance rates between 40% and 60% of the total iterations
211 (Wilson & Rannala, 2003).

Finally, isolation by distance was tested via Mantel tests with GENEPOP (Raymond & Rousset, 1995; Rousset, 2008); FST and geographic distance were compared using 1000 random permutations. The geographic distance connecting samples was represented by Euclidean (linear geographic) distances computed in QGis (QGIS Development Team, 2014).

Results

mtDNA

The mtDNA marker sequences (CR1 D-Loop 288 bp) showed 24 haplotypes defined by 10 polymorphic sites and distributed in 8 locations (Appendix 2). Among the 24 haplotypes found (GenBank accession numbers .....-.....), 14 haplotypes were shared by 2-47 individuals. According to the study areas, we found a total of eleven private haplotypes, the majority of which occurred in the Landes (SW France) population (Appendix 2). The diversity indices for mtDNA revealed moderate levels of genetic variation in the greylag goose in all sampled areas (Table 1). Haplotype diversity showed high values in all groups (range 0.798-0.949) except in breeding areas in Finnmark (0.564 ± 0.13 SD) and Vega, Norway (0.170 ± 0.10 SD).

The genetic distances recorded in Norway, Northern France and the Netherlands were low (range 0.012-0.013). A slightly higher genetic distance was observed in south-west France in comparison to all other sampling sites (ranges 0.018-0.022), while the two breeding sites in Norway were genetically very close (Table 2).

The NJ tree shows that clades are composed of a wide variety of different geese from different areas. Individuals from each site were present in different branches (Fig. 2). Besides, none of the clades grouped together individuals originating from the same areas. About half the individuals were grouped together with the GenBank reference sequence relating to the *anser* subspecies, while the remainder were either grouped with the sequence relating to the *rubrirostris* subspecies or differed clearly from both subspecies. Very similar topologies were obtained from trees generated with other tree-building methods (MP and ML; not shown).

240 The haplotype median-joining network (Fig. 2) was concordant with the phylogenetic
241 tree topology and did not reveal any geographic structures. The number of mutations
242 separating the different haplotypes was low (max = 10).
243 Whilst 88.85% of the total genetic variance shown in hierarchical AMOVA was
244 within populations, the remaining 11.15% occurred among populations. This indicates a small
245 differentiation between the sampled areas.
246 Non-significant raggedness indices indicated a good fit to a model of population
247 expansion in all sampled areas. Mismatch distribution results also suggested a population
248 expansion in all areas except the Gironde region (P = 0.044) and Finnmark (P = 0.042) (Fig.
249 3). Fu's FS value (Table 1) was only significantly negative for the Oise region, and was
250 consistent with a demographic expansion for all other areas.
251
252 ***Microsatellites***
253 Among the 15 microsatellites previously isolated by Weiß et al. (2008) only Ans26
254 was shown to be monomorphic in all investigated individuals. The remaining 14 polymorphic
255 microsatellite loci showed 2-12 different alleles per locus (*n* = 169 individuals; Table 3).
256 Observed and expected heterozygosities were moderate, with similar values in each
257 sampled population (H_o ranging from 0.374 to 0.484 and H_e from 0.433 to 0.549). Geese from
258 the Landes wintering area exhibited the highest number of private alleles (*n* = 3, Appendix 3).
259 Genetic structure was visualized using factorial correspondence analysis (FCA) in
260 each population (Fig. 4). The plot shows an absence of phylogeographic structure in the
261 different investigated areas: individuals from different areas overlap, with the exclusion of 4
262 samples from Nord, 1 sample from Finnmark, 1 from Oise and 1 from Gironde.
263 Significant departures from HWE, due to heterozygote deficit and related to positive
264 Fis values, were observed in all populations (Table 3, Appendix 3).
265 AMOVA analyses showed that 97.9% of the total genetic variance in geese was
266 significantly distributed within populations ($p < 0.001$), while only 2.1% was distributed

among populations. Overall fixation index FST from AMOVA was 0.02105, indicating a low differentiation between areas.

STRUCTURE analyses, performed without the use of prior information on sample locations, showed a maximum ΔK at K = 4, while likelihood values reached a plateau at K = 7 (Fig. 5). Graphs show no evidence of phylogeographic structure across sampled populations, whatever the K value. With K = 4, only 23 individuals with individual *qi* values were each assigned to a single cluster: two individuals from Finnmark, three from Vega and one from Gironde were attributed to cluster 1; one individual from Netherland, two from Finnmark, six from Vega, one from Charente Maritime, two from Gironde and one from Landes were attributed to cluster 2; two individuals from Oise and two from Landes were assigned to cluster 3. All other birds had a highly mixed genotype. In the case of K = 7, five other individuals, one from Finnmark, Charente Maritime and Gironde and two from Vega, were assigned to the same cluster with qi > 0.90.

Bottleneck events tested under IAM revealed a significant excess of heterozygotes (evidence of a recent bottleneck) in Nord, Landes and Oise populations (Wilcoxon sign-rank tests, all $P < 0.05$). Analysis under TPM only confirmed a recent bottleneck event for the Nord population ($P < 0.05$).

BAYESASS detected a low migration rate among localities and a high proportion of local individuals (> 68%, Table 4), suggesting that the flows among different areas were limited. Indeed, the analysis found a high proportion of local geese in six populations (> 90%). In two cases, gene flow appears to be strongly asymmetrical, with many birds moving from Charente Maritime to the Netherlands (20.7% ± 3.79 SD) and from Oise to Gironde (20.2% ± 3.44 SD), but not in the opposite direction (1.5% and 1.1% respectively).

The Mantel test calculated on geographic and genetic distances yielded a non-significant correlation coefficient ($P = 0.08$ n.s.), indicating that there is no relationship between geographic and genetic distances.

295 **Discussion**

296

297 In this study we used a pool of 14 microsatellites isolated by Weiß et al. (2008) for greylag
298 goose parentage in the long-established goose population at Konrad Lorenz Research Station,
299 Grünau, Austria (Lorenz, 1966; Hirschenhauser, Möstl & Kotrschal, 1999). We found that
300 these microsatellites can be successfully employed for geese sampled in a wide range of
301 localities along the European Atlantic flyway. This is the first large scale study showing a
302 moderate genetic variability of mtDNA and nuclear DNA in all French wintering areas and in
303 the Netherlands, with slightly lower mtDNA variability in the Norwegian breeding sites. A
304 moderate genetic variability in the greylag goose was already reported two decades ago by
305 Blaakmeer (1995), and has been found in other species of geese (*Anser erythropus*: Ruokonen
306 et al., 2004; Ruokonen et al., 2010; *Anser brachyrhynchus*: Ruokonen et al., 2005). Low
307 genetic variability also seems to be typical for other Anatidae species (*Aythya ferina*: Liu et
308 al., 2011; *Aythya fuligula*: Liu et al., 2012). Interestingly, our results show that the genotypes
309 deviated from Hardy-Weinberg expectation at 8 loci, and in all study areas, were due to
310 heterozygote deficiency. Besides, the deficit of heterozygotes matched with positive Fis
311 values. These results could be related to different factors, such as population substructuring or
312 recent population growth (Cornuet & Luikart, 1996).

313 Genetic distances between the different areas were low (0.012-0.017 range) and the
314 hierarchical AMOVA showed genetic variance to mainly occur within populations. These
315 findings could be explained by a small differentiation between the sampled areas and a
316 general admixture of greylag goose populations in our Western European study region.
317 However, it should be taken into account that genetic divergences in geese are
318 characteristically very low, with the lowest interspecies divergence reported here for avian
319 species (Ruokonen, Kvist & Lumme, 2000). The genetic tree shows that different branches
320 include individuals from each sampling area. No single branch exclusively grouped together
321 individuals originating from the same zone. Moreover, birds sampled in the western part of
322 the breeding range, traditionally ascribed to the *anser* subspecies, were not separated from

323 birds collected in the eastern part that were traditionally assigned to the *rubrirostris*
324 subspecies (Kampe-Persson, 2002). Birds from Iceland, Scotland and coastal Norway have
325 been sometimes separated as a race, *sylvestris*, classified in the *anser* group (Snow, Perrins &
326 Cramp, 1998). Although Icelandic and Scottish birds were absent from this study, individuals
327 from the Norwegian west coast did not appear to be clearly distinct from other European
328 geese. Our present results slightly differ from the findings of Blaakmeer's preliminary study
329 (1995), which reported genetic differences between breeders in two Dutch sites in comparison
330 to breeding sites in South Sweden and Norway. However, Blaakmeer's analyses (1995) show
331 significant differences for only one of six minisatellites, in only two of the three Dutch areas
332 studied.

333 Interestingly, the ANS19 sequence was recently found in the white Roman goose in
334 Taiwan. This race is widely bred for commercial purposes, and has been found to originate
335 from the European species *Anser anser* (Wang et al., 2010). Our data confirm the presence of
336 this sequence in Europe, particularly in the breeding population of the Norwegian west coast.

337 Haplotypes ANS02, ANS08, ANS11, ANS23 and ANS24 were only found during the
338 winter in France, and were absent in Norway and the Netherlands: this result could indicate
339 that some of the geese arriving in France came from areas we did not sample on the breeding
340 grounds. Ring recoveries and resighting records indicate that these birds probably originated
341 from North Germany, Poland, Denmark and Sweden (Nilsson et al., 2013).

342 The haplotype network confirmed the tree configuration. There was no geographic
343 pattern, and the number of mutations separating the different nodes was very low. This
344 confirms the low genetic distance between our studied populations in the large north-western
345 European population (as defined by Delany and Scott, 2006), and may reflect the rapid
346 population expansion (Aris-Brosou & Excoffier, 1996).

347 Data obtained from nuclear DNA by microsatellites were in accordance with findings
348 from mtDNA. As the mtDNA is uniparentally inherited whereas microsatellites are part of the
349 biparentally inherited nuclear DNA, a difference between the two genomes would have
350 indicated the presence of sex-biased dispersal (Fahey, Ricklefs & Dewoody, 2014). However,

351 sex-biased dispersal seems to be unlikely in greylag geese for three reasons: the family unit
352 remains together at least until autumn migration, the birds tend to pair before returning to the
353 breeding grounds, and males and females have long-term pair bonds (Rohwer & Anderson,
354 1988; Doherty et al., 2002). Sex-biased dispersal in birds is probably not a species constant
355 (Clarke et al., 1997). Within Anatidae in general, sex-biased dispersal was not detected in
356 several species (Doherty et al., 2002; Mabry et al., 2013), while it was found in some species
357 such as the white-fronted goose (*Anser erythropus,* Ruokonen et al., 2010), the common eider
358 (*Somateria mollissima,* Paulus & Tiedemann, 2003), and the spectacled eider (*Somateria*
359 *fisheri,* Scribner et al., 2001).

360 In our study of microsatellites, individuals from different geographic localities were
361 found to be combined in the Factorial Correspondence Analysis representation. Bayesian
362 structure analysis resulted in a best combination of four or seven groups, according to ΔK and
363 LnP(D) methods respectively. As seen in our previous analyses, no geographic clustering was
364 observed inside these STRUCTURE groups. Almost all individuals, with few exceptions,
365 showed admixed genotype regardless of the number of groups considered in the analysis.

366 The high mixing of genotypes and the lack of geographic structure among our studied
367 populations could be interpreted in the light of the data obtained through ringing activity and
368 the extensive neck-banding programme carried out in Scandinavia from 1984 to 2004
369 (Nilsson, 2007; Voslamber, Knecht & Kleijn, 2010). Ring recoveries and visual observations
370 showed that Scandinavian geese breeding in different zones can admix not only in the
371 moulting areas (Nilsson, Kahlert & Persson, 2001) but also along the European Atlantic
372 flyway, i.e. in the Netherlands (Voslamber, Knecht & Kleijn, 2010), France (Fouquet,
373 Schricke & Fouque, 2009; Nilsson et al., 2013) and Spain (Ramo et al., 2012) where they can
374 form pairbonds. Besides this Scandinavian data, the monitoring of collared and/or ringed
375 individuals performed in other European areas showed the presence of birds in France
376 originating from Germany, the Czech Republic and Poland. Populations that breed further
377 east do not seem to reach France in winter (Kampe-Persson, 2010). From these data it appears

that the greylag geese that cross France or winter there could result from a mixture of populations from different areas.

Our findings are somewhat unexpected if one assumes that the fragmentation of breeding populations into separate areas during the first part of the last century (Hagemeijer & Blair, 1997; Kampe-Persson, 2002), should have led to an increase in genetic structure. Moreover, birds breeding in the Netherlands have recently become highly sedentary (Fox et al., 2010), and this may also have contributed to the increase in genetic structure (Blaakmeer, 1995). However, a genetic panmixia could have been promoted by the widespread amateur breeding and selling of geese, and the recent increase and dispersal of several wild goose populations (Klok et al., 2010). In particular, geese with pink bills and legs, most probably *rubirostris* subspecies, have been spreading in Europe over the last few decades; their natural flyway toward wintering areas crosses other European countries (from Russia to Hungary, the Balkan States and Italy) but does not reach France.

The breeding of geese is a widespread practice among amateurs, who can easily obtain both goslings and adults with a grey wild appearance (B. and G. Vaschetti, pers. comm.). In some cases geese were released as part of assisted restoring projects and are now indistinguishable from the wild individuals (Kampe-Persson, 2010). Besides, birds with white plumage are common in breeding farms. In Asia, white geese are mostly descendants of the swan goose *Anser cygnoides*. Even if descendants of *Anser anser* can also be found there, they are usually farmed in Europe (Wang et al., 2010). Although the two species can hybridize in captivity, hybrids can be detected through karyotype (Shahin, Ata & Shnaf, 2014) or genotype examinations (Sun et al., 2014). The contribution of escaped white form geese to the admixture observed in wild populations is probably low given the high assortative mating of wild greylag geese, their long-term monogamous pair bonds, female-bonded clan structure, long parent-offspring relationships, and elaborate patterns of mutual social support (Hirschenhauser et al., 2000; Kotrschal, Scheiber & Hirschenhauser, 2010).

Our findings on the greylag goose genetic admixture are similar to those reported in the snow goose (*Chen caerulescens,* Avise et al., 1992) and the barnacle goose (*Branta*

406 *leucopsis,* Jonker et al., 2013). Despite the high rate of site philopatry seen in the snow goose,
407 which has also shown a high increase in population over the last decades, mtDNA markers
408 showed no clear distinctions between nesting populations across species range (Avise et al.,
409 1992). The barnacle goose recently changed its migratory traditions, and new populations
410 differing in migratory distance were observed. Genetic data showed an admixture between all
411 populations, despite the assumed traditions of migration within areas and the presence of a
412 newly established nonmigratory population in the Netherlands (Jonker et al., 2013). A lack of
413 genetic structure in wintering areas was also found in four species of Anatidae, namely the
414 common pochard, the mallard, the king eider and the tufted duck (Pearce et al., 2004; Liu,
415 Keller & Heckel, 2011, 2012; Kraus et al., 2013; Liu et al., 2013), and in the black-tailed
416 godwit (*Limosa limosa,* Lopes et al., 2013). The mixing of breeding populations in wintering
417 areas is believed to be a common phenomenon in birds, because the breeding ranges of most
418 species are considerably larger than their wintering ranges (Winker & Graves, 2008).
419 However, migratory populations vary in the degree to which individuals from distinct
420 breeding localities mix on different sites. Therefore, to understand population demographics
421 and genetic diversification, it is crucial to pinpoint which populations mix on breeding and
422 wintering grounds (Chabot et al., 2012).

423 Our DNA-based estimates of migration during the wintering period indicated a low
424 rate of exchange between our sampled areas. In five of eight areas the vast majority of
425 individuals (86-95%) did not switch among the different zones, and a moderate exchange
426 (about 20%) was only observed from Charente Maritime to the Netherlands and from Oise to
427 Gironde. These results seem to support the hypothesis that the French wintering birds arrive
428 from various areas, including zones that are not sampled here (i.e. Germany, Poland), while
429 the contribution of the Norwegian population represents only a portion of the whole
430 assemblage (Fouquet, Schricke & Fouque, 2009). This low exchange rate is also supported by
431 evidence of great changes in spatial ecology recorded in 28 GPS tagged western European
432 greylag geese, i.e. very low home ranges on wintering areas (<8.9±2.5 km²) compared to 2-5

433 fold values obtained in staging areas during migratory and premigratory periods (Boos
434 unpublished data).

435 Our data show evidence of genetic bottlenecks in just three groups under IAM, all
436 located along the same flyway (Nord, Oise and Landes), and in a single case (Nord) under
437 TPM. The discrepancy between IAM and TPM could be related to the different ability of the
438 mutation models to detect bottleneck events. Empirical data suggest that TPM is the most
439 appropriate model for microsatellite loci (Ellegren, 2000, 2004) while IAM results should be
440 interpreted with caution (Cornuet & Luikart, 1996). We did not observe any sign of
441 bottlenecks in the breeding populations: this indicates that greylag geese have never suffered
442 any severe demographic reduction, even at the beginning of the past century when the number
443 of breeding individuals was low in several European areas (Kampe-Persson, 2002).

444 Greylag goose populations are steadily increasing in North-Western Europe (Kampe-
445 Persson, 2002). The large number of geese in some areas is now in conflict with agricultural
446 interests, since geese not only forage in natural environments but also forage on crop fields.
447 The species is included in Annexes of the EU Birds Directive, Bern Convention and Bonn
448 Convention as a huntable species, but claims for a need to control the species are widespread
449 (Klok et al., 2010), and hunting and/or pressure on the authorities to reduce population levels
450 are becoming evident in some countries (Comolet-Tirman, 2009). Our data suggest that the
451 migratory geese shot over France show a relatively high diversity of origin, giving further
452 insight into the assumptions raised by Pistorius et al. (2006) who hypothesized that
453 demographic parameters for the Norwegian breeding population could be partly affected by
454 hunting-induced mortality or poor winter habitat quality in France and Spain. In addition to
455 recent data showing an increase in the Norwegian breeding population over the last decade
456 (Follestad pers. obs.), our results also suggest that hunting pressure in France (about 20000
457 geese/year, see Landry and Migot, 2000) does not specifically target or impact the Norwegian
458 breeding population or indeed any other, particulary in view of the fact that migration starts
459 after 10th February (based on GPS tagged geese, Boos 2014). Future studies could analyze
460 other European breeding and wintering areas; this could clarify the status of the different

populations and subspecies on the continent (the main *Anser anser anser* and *A. a. rubrirostris*, as well as the *sylvestris* forms from Iceland, Scotland and Norway), and help to build an effective international management strategy for this migratory species (Chabot et al., 2012).

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Supplemental Information

Appendix 1 - List of samples used in this study, with ID, population, sample provenance, collecting date, haplotype assignment and whether the sample was genotyped with microsatellites (STRs).

Appendix 2 - Table of mtDNA haplotypes found in *Anser anser* individuals.

Appendix 3 – Summary of genetic variation at 14 microsatellite loci in sampled populations. Na = No. of different alleles; Ne = No. of effective alleles. Ho = observed heterozygosity; He = expected heterozygosity; F = fixation index; HWE = Hardy-Weinberg equilibrium.

Figure Captions

Figure 1 – Main *Anser anser* flyways from breeding (yellow) to wintering (light blue) areas (modified from Comolet-Tirman 2009). Pie charts indicate the proportion of different haplotypes (mtDNA) found in each sampled population. Colours are identical to those used in the haplotype network (Fig. 2), and haplotypes found in one area alone are the same colour.

Figure 2 - Left: median-joining haplotype network. Areas of circles represent different sampled mtDNA haplotypes in proportion to their frequencies. Distances between haplotypes are proportional to the number of base differences. Colours match those utilized in Fig. 1, and haplotypes found in one area alone are the same colour. Right: Neighbour-joining tree based on 280 bp of CR1. Sampled areas are labelled with abbreviations: NF, Northern France (Oise and Nord); SWF, South-Western France (Gironde, Charente Maritime and Landes); Nor, Norway; Neth, Netherlands. Numbers below branches indicate bootstrap values; only values above 50% are shown, most of the clades are supported by low bootstrap values.

Figure 3 - Distributions of pairwise differences (Mismatch distribution) among mtDNA haplotypes for overall dataset and each sampled areas.

Figure 4 - Factorial Correspondence Analysis (FCA) of microsatellites data. Outliers concern individuals from Nord (4 ind.), Oise, Gironde and Finnmark (1 ind.) populations.

Figure 5 - Estimated population structure in Greylag Goose sampled populations. Each vertical line represents one individual and each colour represents a single cluster.

Table 1 - Genetic variability of mtDNA CR1 D-Loop. *h* = haplotype diversity, π = nucleotide diversity, D = Tajima's D, FS = Fu's FS. Standard errors are showed in brackets.

	Population	Season	N	Polymorphic sites	Hapl.	Private hapl.	*h*	π	K	D	FS
South Western France	Charente-Maritime	Autumn-winter	10	16	7	1	0.933 (0.06)	0.01790 (0.00254)	5.156	-0,409	-0,664
	Gironde	Autumn-winter	20	12	7	0	0.821 (0.06)	0.01519 (0.0012)	4.374	1.052	1.190
	Landes	Autumn-winter	36	19	13	5	0.798 (0.06)	0.0161 (0.0013)	4.633	0.0376	-0.360
North-France	Nord	Autumn-winter	17	10	6	0	0.833 (0.06)	0.01054 (0.0016)	3.025	0.014	0.433
	Oise	Autumn-winter	13	12	9		0.949 (0.042)	0.01309 (0.0020)	3.769	-0,103	-2,691*
North Europe	Norway Finnmark	Late spring	11	6	3	1	0.564 (0.13)	0.00947 (0.002)	2.727	1,31175	3,038
	Norway Vega	Late spring	23	7	3	1	0.170 (0.10)	0.0021 (0.0016)	0.609	-2,147*	0,270
	Netherlands	Autumn	14	11	8	2	0.890 (0.006)	0.01244 (0.0013)	3.571	0.541	-1.112
All Samples			144	20	24	-	0.823 (0.022)	0.01331 (0.0006)	3.819	-1,419	-4,515*

Table 2 – Tamura Nei genetic distance assessed by mtDNA.

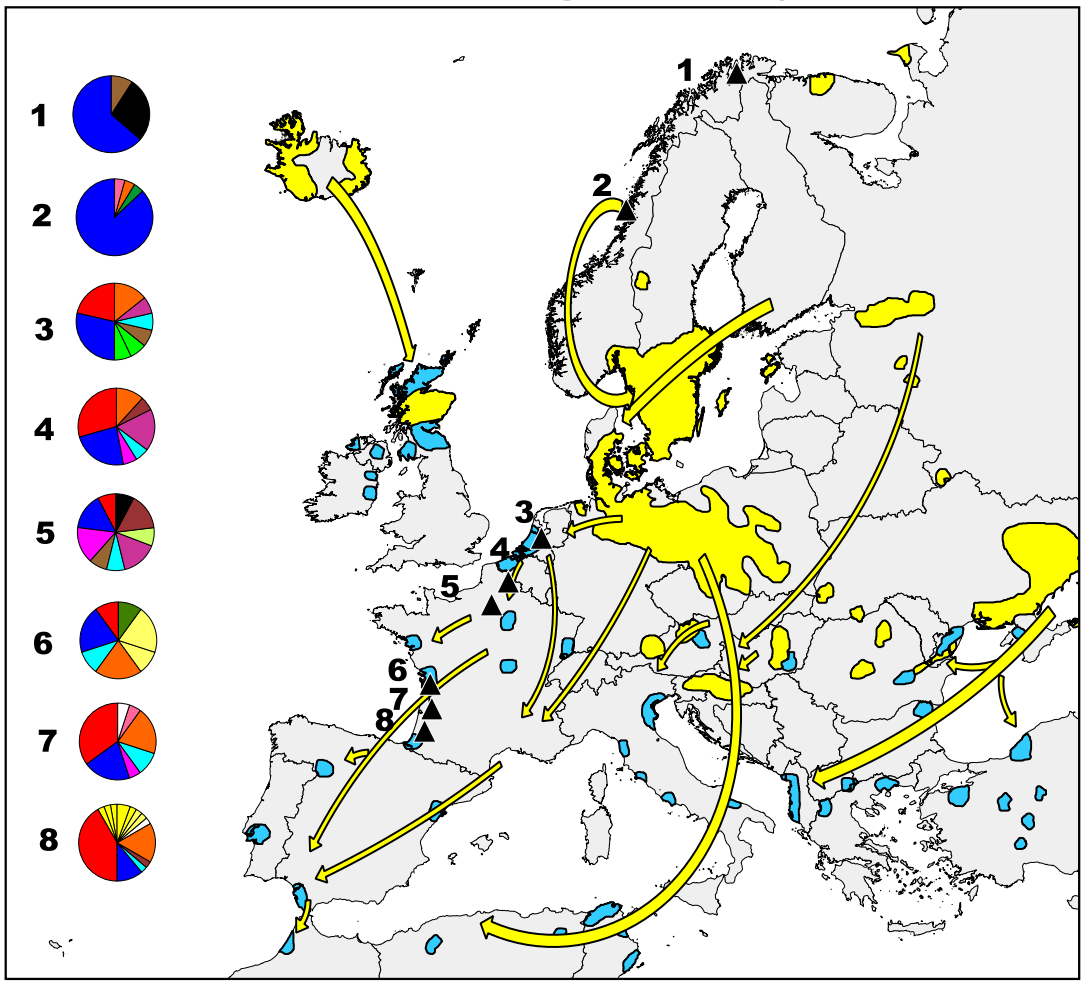
	SW France - Landes	SW France - Gironde	N France - Nord	N France Oise	Netherlands	Norway - Finnmark	Norway - Vega	SW France Charente M
SW France - Landes		0.004	0.004	0.004	0.004	0.005	0.006	0.005
SW France - Gironde	0.016		0.004	0.004	0.004	0.004	0.005	0.005
N France - Nord	0.015	0.014		0.004	0.004	0.004	0.004	0.005
N France Oise	0.016	0.015	0.013		0.004	0.004	0.004	0.005
Netherlands	0.015	0.014	0.013	0.013		0.004	0.004	0.005
Norway - Finnmark	0.018	0.016	0.014	0.013	0.014		0.003	0.006
Norway - Vega	0.017	0.014	0.012	0.012	0.012	0.008		0.006
SW France Charente M	0.020	0.019	0.019	0.018	0.018	0.022	0.019	

Table 3 - Summary of genetic variation at 14 microsatellite loci. N= number of individuals; Na = No. of different alleles; Ne = No. of effective alleles; Ho = observed heterozygosity; He = expected heterozygosity.

	Population	N	Na	Ne	Ho	He	HWE (P)
South Western France	Charente-Maritime	9	8.931 (0.071)	2.468 (0.340)	0.483 (0.082)	0.512 (0.051)	<0.001
	Gironde	24	4.286 (0.633)	2.575 (0.329)	0.462 (0.063)	0.504 (0.065)	<0.001
	Landes	45	4.643 (0.684)	2.625 (0.344)	0.484 (0.048)	0.542 (0.049)	<0.001
North- France	Nord	17	4.000 (0.584)	2.680 (0.332)	0.483 (0.072)	0.549 (0.056)	<0.001
	Oise	15	3.857 (0.573)	2.702 (0.403)	0.385 (0.061)	0.527 (0.063)	<0.001
North Europe	Norway Finnmark	11	3.357 (0.372)	2.137 (0.266)	0.374 (0.072)	0.433 (0.065)	<0.01
	Norway Vega	34	4.571 (0.661)	2.485 (0.312)	0.476 (0.060)	0.529 (0.048)	<0.001
	Netherlands	14	3.929 (0.549)	2.352 (0.305)	0.447 (0.063)	0.493 (0.052)	<0.001
All Samples		169	4.027 (0.200)	2.503 (0.115)	0.449 (0.023)	0.511 (0.020)	<0.001

Table 4 – Mean estimated number of migrants between breeding and wintering sites as calculated with BayesAss (standard deviations in parentheses).
Values on the diagonal (in bold) represent the estimated proportion of resident individuals in each population.

	Migration into							
Migration from	**Netherlands**	**NF-Nord**	**NF-Oise**	**NO-Finnmark**	**NO-Vega**	**SWF-Charente Maritime**	**SWF-Gironde**	**SWF-Land**
Netherlands	**0.8904** (0.0338)	0.0167 (0.0160)	0.0151 (0.0147)	0.0152 (0.0144)	0.0160 (0.0154)	0.0152 (0.0146)	0.0157 (0.0151)	0.0157 (0.0148)
NF- Nord	0.0145 (0.0139)	**0.9009** (0.0316)	0.0135 (0.0130)	0.0140 (0.0135)	0.0144 (0.0138)	0.0133 (0.0129)	0.0149 (0.0143)	0.0145 (0.0141)
NF- Oise	0.0142 (0.0135)	0.0460 (0.0238)	**0.6820** (0.0146)	0.0144 (0.0139)	0.0138 (0.0132)	0.0136 (0.0132)	0.2023 (0.0344)	0.0137 (0.0133)
NO-Finnmark	0.0191 (0.0183)	0.0212 (0.0198)	0.0174 (0.0165)	**0.8619** (0.0394)	0.0215 (0.0210)	0.0177 (0.0164)	0.0219 (0.0211)	0.0194 (0.0184)
NO-Vega	0.0085 (0.0081)	0.0078 (0.0078)	0.0078 (0.0078)	0.0081 (0.0079)	**0.9439** (0.0192)	0.0079 (0.0077)	0.0081 (0.0079)	0.0081 (0.0077)
SWF-Charente Maritime	0.2072 (0.0379)	0.0175 (0.0167)	0.0173 (0.0165)	0.0176 (0.0166)	0.0181 (0.0174)	**0.6872** (0.0192)	0.0177 (0.0168)	0.0174 (0.0166)
SWF-Gironde	0.0114 (0.0112)	0.0107 (0.0105)	0.0111 (0.0102)	0.0199 (0.0160)	0.0109 (0.0104)	0.0110 (0.0107)	**0.9142** (0.0270)	0.0109 (0.0105)
SWF- Land	0.0069 (0.0069)	0.0068 (0.0067)	0.0063 (0.0063)	0.0067 (0.0066)	0.0065 (0.0064)	0.0063 (0.0063)	0.0068 (0.0067)	**0.9538** (0.0164)


1
2
3
4
5
6
7
8
1
2
3
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5
6
7
8

Figure 2 – Left: median-joining haplotype network. Areas of circles represent different sampled haplotypes in proportion to their frequencies. Distances between haplotypes are proportional to the number of base differences. Colours match those utilized in Fig. 1, and haplotypes found in one area alone are the same colour. Right: Neighbour-joining tree based on 280 bp of CR1. Sampled areas are labelled with abbreviations: NF, Northern France (Oise and Nord); SWF, South-Western France (Gironde, Charente Maritime and Landes); Nor, Norway; Neth, Netherlands. Numbers below branches indicate bootstrap values; only values above 50% are shown, most of the clades are supported by low bootstrap values.

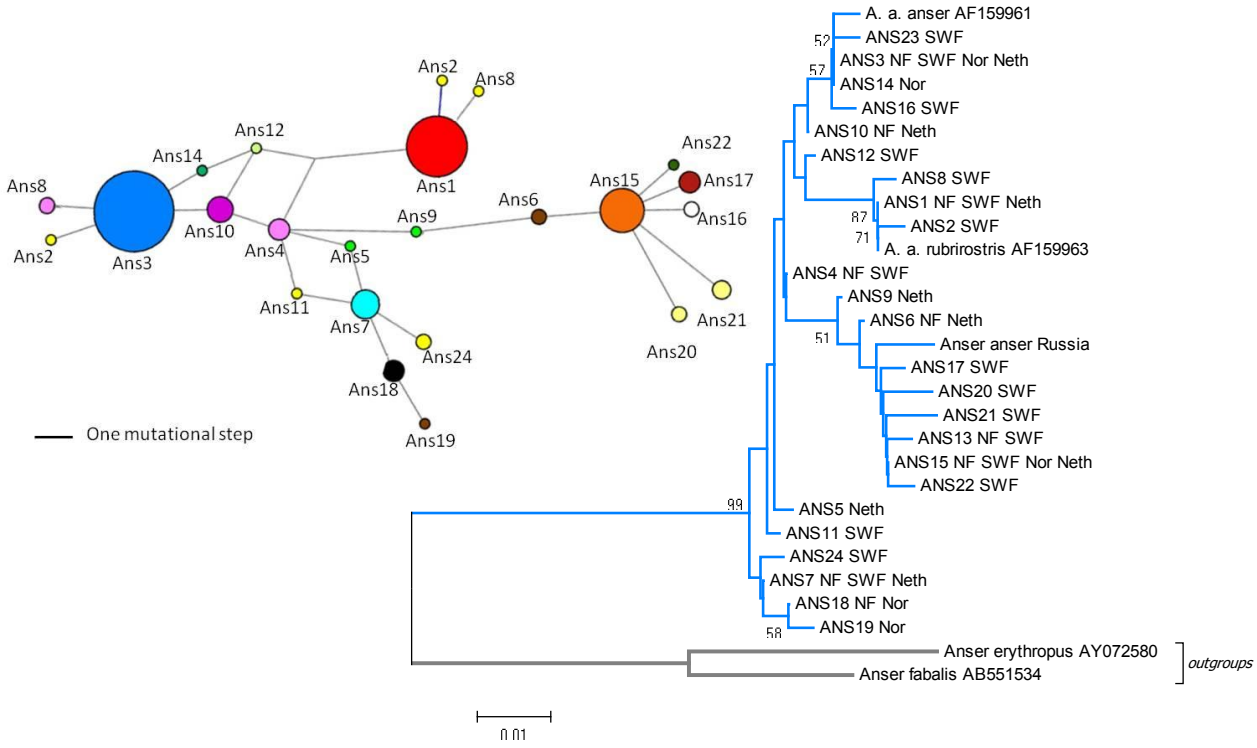
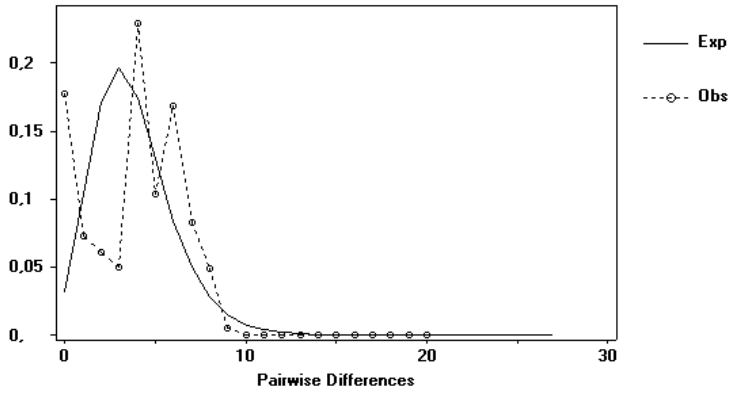
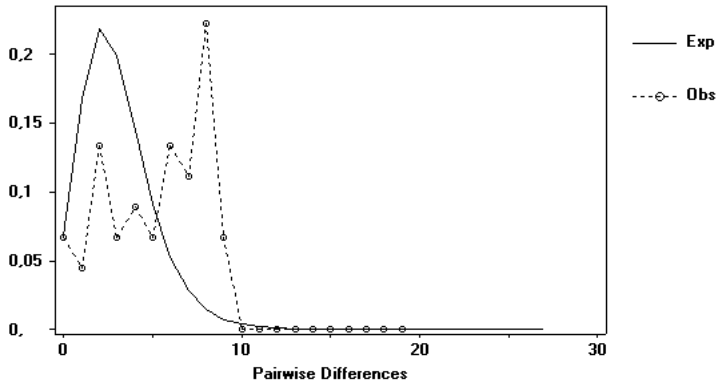


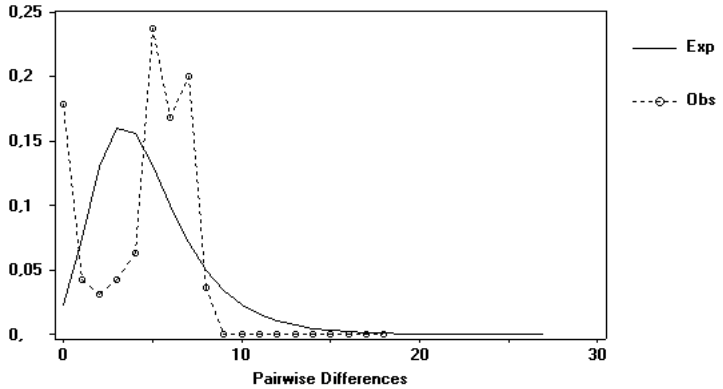
Figure 3 - Mismatch distribution calculated for all individuals and each population.



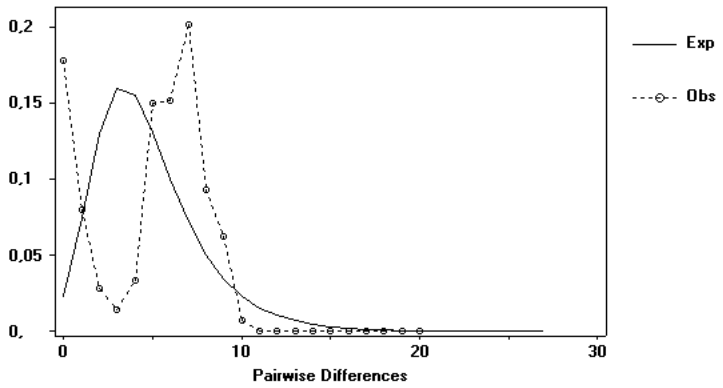
All Samples



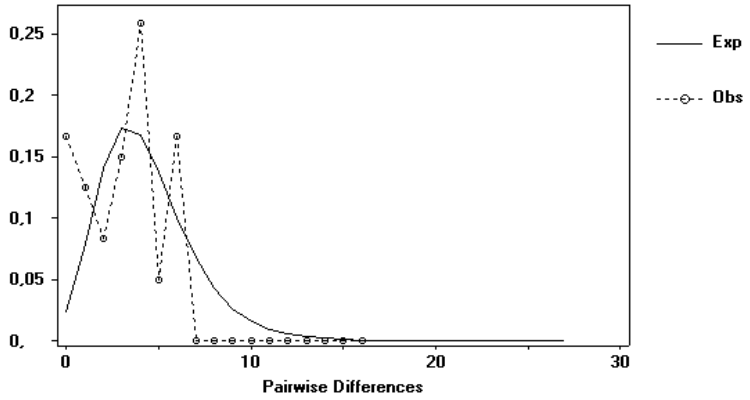
Charente Maritime



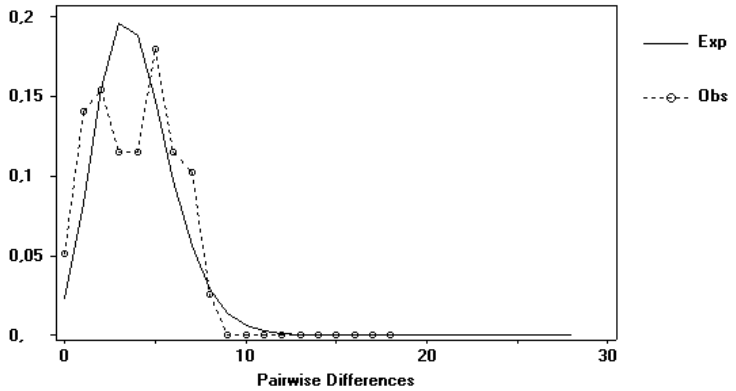
Gironde



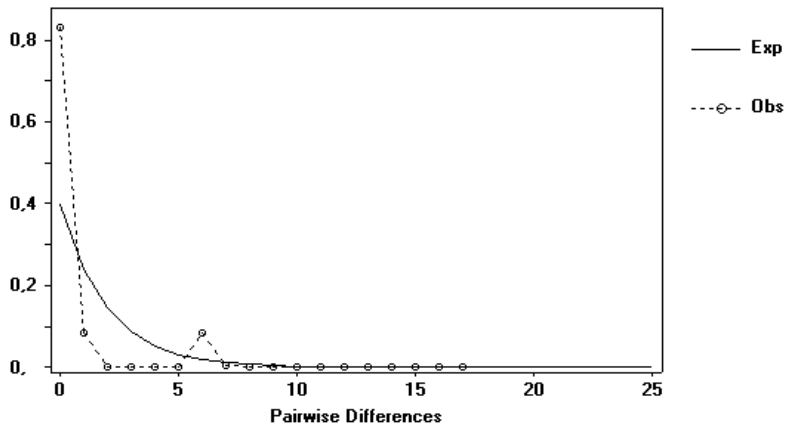
Landes



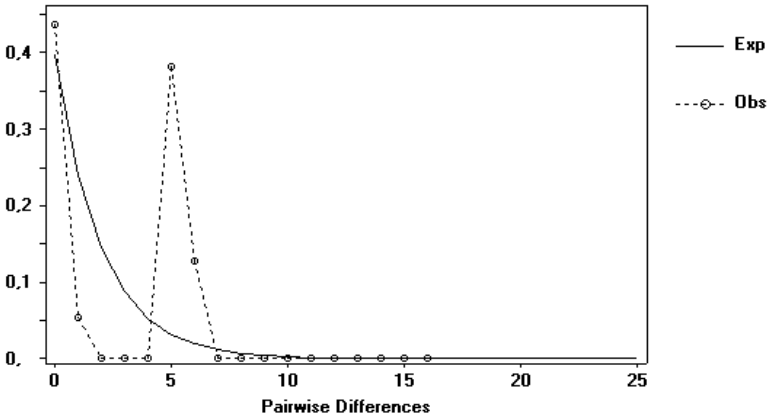
Nord



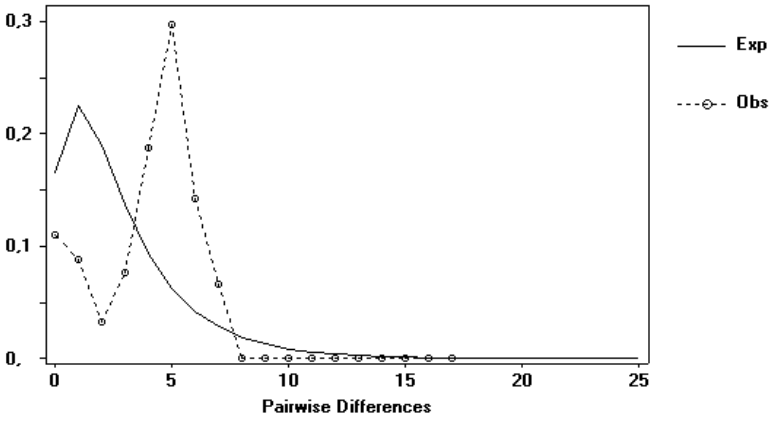
Oise



Norway Vega

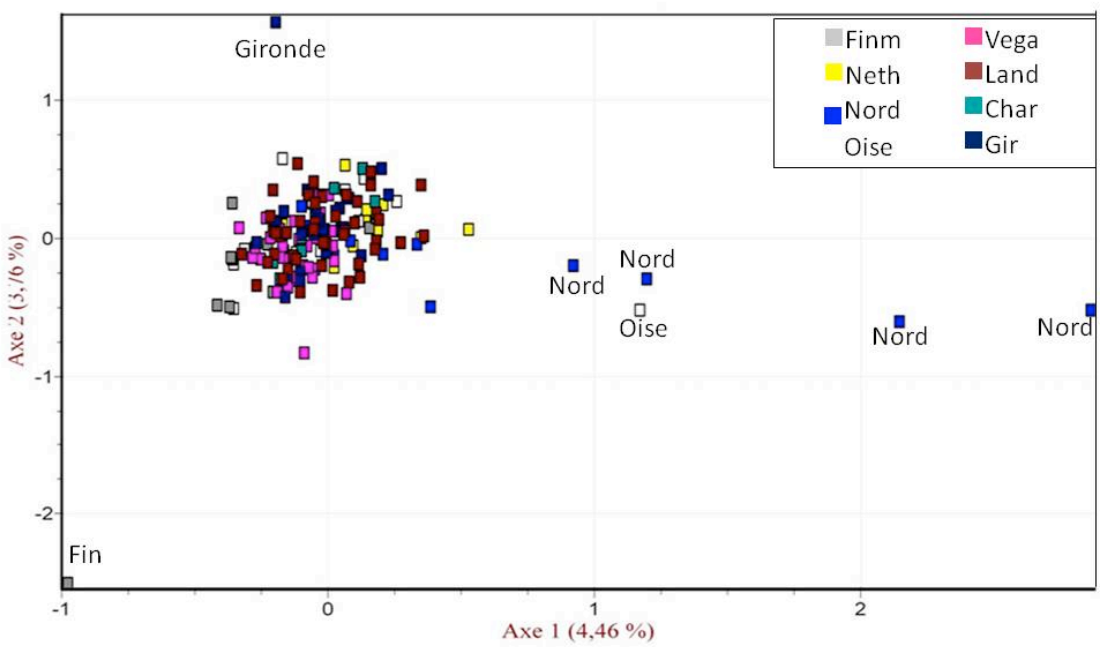


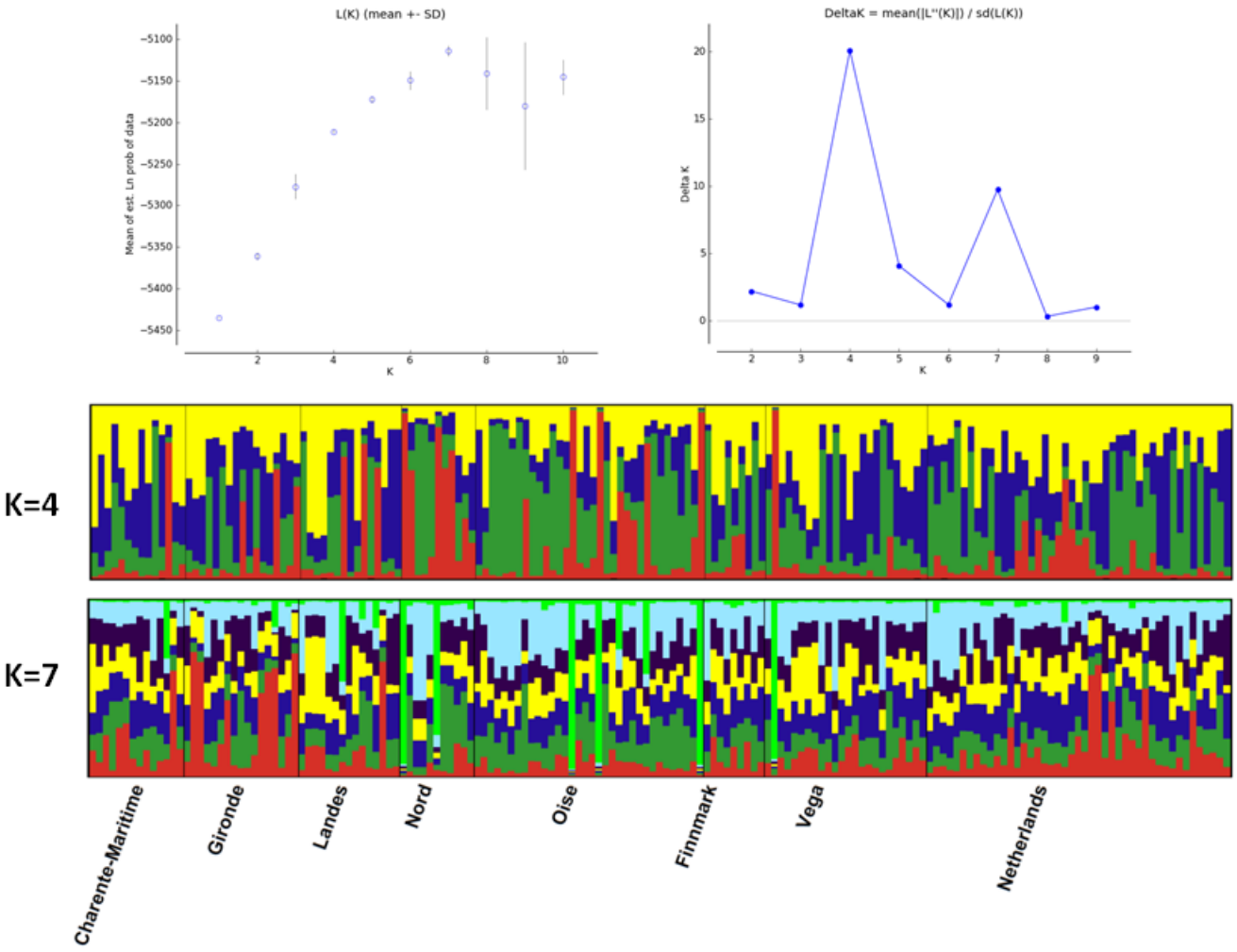
Norway Finnmark



Netherlands

Figure 4 - Factorial Correspondence Analysis (FCA) of microsatellites data. Outliers concern individuals from Nord (4 ind.), Oise, Gironde and Finnmark (1 ind.) populations.




L(K) (mean +- SD)
Mean of est. Ln prob of data
K
DeltaK = mean(|L''(K)|) / sd(L(K))
Delta K
K
K=4
K=7
Charente-Maritime
Gironde
Landes
Nord
Oise
Finnmark
Vega
Netherlands

Appendix 1 - List of samples used in this study, with ID, population, sample provenance, collecting date, haplotype assignment and whether the sample was genotyped with microsatellites (STRs).

Sample	ID	POP	pop_name	Country	Locality	Sampling date	MtDNA Haplotype	STRs
aa68	PB/87	NL	Netherlands	Netherlands	Netherlands	13/10/11	ANS15	
aa69	PB/80	NL	Netherlands	Netherlands	Netherlands	13/10/11	ANS5	x
aa70	PB/86	NL	Netherlands	Netherlands	Netherlands	30/09/11	ANS3	x
aa71	PB/75	NL	Netherlands	Netherlands	Netherlands	15/09/11	ANS15	x
aa72	PB/81	NL	Netherlands	Netherlands	Netherlands	30/09/11	ANS3	x
aa73	PB/79	NL	Netherlands	Netherlands	Netherlands	30/09/11	ANS6	x
aa74	PB/85	NL	Netherlands	Netherlands	Netherlands	13/10/11	ANS3	x
aa75	PB/76	NL	Netherlands	Netherlands	Netherlands	27/09/11	ANS1	x
aa76	PB/78	NL	Netherlands	Netherlands	Netherlands	27/09/11	ANS7	x
aa77	PB/82	NL	Netherlands	Netherlands	Netherlands	27/09/11	ANS1	x
aa78	PB/88	NL	Netherlands	Netherlands	Netherlands	27/09/11	ANS3	x
aa79	PB/77	NL	Netherlands	Netherlands	Netherlands	30/09/11	ANS10	x
aa80	PB/83	NL	Netherlands	Netherlands	Netherlands	20/09/11	ANS1	x
aa81	PB/74	NL	Netherlands	Netherlands	Netherlands	15/09/11		x
aa82	PB/84	NL	Netherlands	Netherlands	Netherlands	20/09/11	ANS9	x
aa26	59/33	59/62	Nord	Northern France	Nord	2011/2012	ANS1	x
aa37	59/40	59/62	Nord	Northern France	Nord	2011/2012	ANS13	x
aa41	59/44	59/62	Nord	Northern France	Nord	2011/2012		x
aa43	59/32	59/62	Nord	Northern France	Nord	2011/2012	ANS1	x
aa48	59/31	59/62	Nord	Northern France	Nord			x
aa53	59/45	59/62	Nord	Northern France	Nord		ANS1	
aa58	59/34	59/62	Nord	Northern France	Nord		ANS1	x
aa67	59/30	59/62	Nord	Northern France	Nord	end Jan 2012		x
aa103	59/89	59/62	Nord	Northern France	Nord	15/10/11	ANS4	x
aa104	59/90	59/62	Nord	Northern France	Nord		ANS15	
aa105	59/91	59/62	Nord	Northern France	Nord	15/10/11	ANS15	
aa106	59/92	59/62	Nord	Northern France	Nord		ANS1	x
aa107	59/93	59/62	Nord	Northern France	Nord	12/11/11	ANS3	x
aa108	59/94	59/62	Nord	Northern France	Nord	12/11/11	ANS3	x
aa109	59/95	59/62	Nord	Northern France	Nord	12/11/11	ANS10	x
aa110	59/96	59/62	Nord	Northern France	Nord	12/11/11	ANS3	x
aa111	59/97	59/62	Nord	Northern France	Nord	06/11/11	ANS3	x

aa112	59/98	59/62	Nord	Northern France	Nord	24/10/11	ANS10	x
aa113	59/99	59/62	Nord	Northern France	Nord	24/10/11	ANS10	x
aa49	60/43	60/76/80	Oise	Northern France	Oise		ANS3	x
aa93	60/60	60/76/80	Oise	Northern France	Oise	10/02/12		x
aa94	60/55	60/76/80	Oise	Northern France	Oise	10/02/12	ANS10	x
aa95	60/54	60/76/80	Oise	Northern France	Oise	10/02/12	ANS4	x
aa96	60/59	60/76/80	Oise	Northern France	Oise	04/02/12	ANS12	x
aa97	60/58	60/76/80	Oise	Northern France	Oise	10/02/12		x
aa98	60/56	60/76/80	Oise	Northern France	Oise	10/02/12	ANS4	x
aa114	60/151	60/76/80	Oise	Northern France	Oise		ANS7	x
aa115	60/152	60/76/80	Oise	Northern France	Oise		ANS1	x
aa116	60/153	60/76/80	Oise	Northern France	Oise		ANS18	x
aa117	60/154	60/76/80	Oise	Northern France	Oise	28/11/10	ANS13	x
aa118	60/155	60/76/80	Oise	Northern France	Oise	28/11/10	ANS13	x
aa56	62/35	59/62	Nord	Northern France	Pas-de-Calais			x
aa62	62/36	59/62	Nord	Northern France	Pas-de-Calais		ANS7	x
aa119	FRA124	60/**76**/80	Oise	Northern France	Seine-Maritime		ANS3	x
aa45	80/37	60/76/80	Oise	Northern France	Somme	2011/2012	ANS6	
aa51	80/38	60/76/80	Oise	Northern France	Somme		ANS10	x
aa120	Fin100	Finm	Finnmark	Norway	Finnmark	01/06/10	ANS3	x
aa121	Fin101	Finm	Finnmark	Norway	Finnmark	01/06/10	ANS3	x
aa122	Fin102	Finm	Finnmark	Norway	Finnmark	01/06/10	ANS3	x
aa123	Fin103	Finm	Finnmark	Norway	Finnmark	01/06/10	ANS3	x
aa124	Fin104	Finm	Finnmark	Norway	Finnmark	01/06/10	ANS18	X
aa126	Fin106	Finm	Finnmark	Norway	Finnmark	01/06/10	ANS3	x
aa127	Fin107	Finm	Finnmark	Norway	Finnmark	01/06/10	ANS3	x
aa128	Fin108	Finm	Finnmark	Norway	Finnmark	01/06/10	ANS3	x
aa129	Fin109	Finm	Finnmark	Norway	Finnmark	01/06/10	ANS19	x
aa130	Fin110	Finm	Finnmark	Norway	Finnmark	01/06/10	ANS18	x
aa131	Fin111	Finm	Finnmark	Norway	Finnmark	01/06/10	ANS18	x
aa132	Veg113	Norw	Vega	Norway	Vega	01/06/10	ANS3	x
aa133	Veg116	Norw	Vega	Norway	Vega	01/06/10	ANS3	x
aa134	Veg123	Norw	Vega	Norway	Vega	01/06/10	ANS3	x
aa135	Veg128	Norw	Vega	Norway	Vega	01/06/10	ANS3	x
aa136	Veg131	Norw	Vega	Norway	Vega	01/06/10	ANS3	x
aa137	Veg132	Norw	Vega	Norway	Vega	01/06/10	ANS3	x
aa138	Veg134	Norw	Vega	Norway	Vega	01/06/10	ANS3	x
aa139	Veg135	Norw	Vega	Norway	Vega	01/06/10		x

aa140	Veg137	Norw	Vega	Norway	Vega	01/06/10		x
aa141	Veg140	Norw	Vega	Norway	Vega	01/06/10	ANS3	x
aa142	Veg141	Norw	Vega	Norway	Vega	01/06/10	ANS3	x
aa143	Smo112	Norw	Vega	Norway	Vega	01/06/10		x
aa144	Smo114	Norw	Vega	Norway	Vega	01/06/10		x
aa145	Smo115	Norw	Vega	Norway	Vega	01/06/10		x
aa146	Smo117	Norw	Vega	Norway	Vega	01/06/10	ANS3	x
aa147	Smo118	Norw	Vega	Norway	Vega	01/06/10	ANS3	x
aa148	Smo119	Norw	Vega	Norway	Vega	01/06/10		x
aa149	Smo120	Norw	Vega	Norway	Vega	01/06/10	ANS3	x
aa150	Smo121	Norw	Vega	Norway	Vega	01/06/10		x
aa151	Smo122	Norw	Vega	Norway	Vega	01/06/10	ANS3	x
aa152	Smo125	Norw	Vega	Norway	Vega	01/06/10		x
aa153	Smo126	Norw	Vega	Norway	Vega	01/06/10		x
aa154	Smo127	Norw	Vega	Norway	Vega	01/06/10	ANS3	x
aa155	Smo129	Norw	Vega	Norway	Vega	01/06/10		x
aa156	Smo130	Norw	Vega	Norway	Vega	01/06/10	ANS3	x
aa157	Smo133	Norw	Vega	Norway	Vega	01/06/10	ANS3	x
aa158	Smo136	Norw	Vega	Norway	Vega	01/06/10	ANS3	x
aa159	Smo138	Norw	Vega	Norway	Vega	01/06/10	ANS3	x
aa160	Smo139	Norw	Vega	Norway	Vega	01/06/10	ANS14	x
aa161	Smo142	Norw	Vega	Norway	Vega	01/06/10		x
aa162	Smo146	Norw	Vega	Norway	Vega	01/06/10	ANS15	x
aa163	Smo147	Norw	Vega	Norway	Vega	01/06/10	ANS3	x
aa164	No143	Norw	Vega	Norway	Vega	01/06/10	ANS3	x
aa165	No149	Norw	Vega	Norway	Vega	01/06/10	ANS16	x
aa166	17/160	17	Charente Maritime	South-western France	Charente Maritime	10/02/12	ANS3	x
aa167	17/161	17	Charente Maritime	South-western France	Charente Maritime	07/02/12	ANS7	x
aa168	17/162	17	Charente Maritime	South-western France	Charente Maritime	10/02/12	ANS15	x
aa169	17/163	17	Charente Maritime	South-western France	Charente Maritime	07/02/12	ANS15	x
aa170	17/164	17	Charente Maritime	South-western France	Charente Maritime	07/02/12	ANS20	
aa171	17/165	17	Charente Maritime	South-western France	Charente Maritime	07/02/12	ANS21	x
aa172	17/166	17	Charente Maritime	South-western France	Charente Maritime	07/02/12	ANS21	x
aa173	17/167	17	Charente Maritime	South-western France	Charente Maritime	10/02/12	ANS1	x
aa174	17/168	17	Charente Maritime	South-western France	Charente Maritime	10/02/12	ANS22	x
aa175	17/169	17	Charente Maritime	South-western France	Charente Maritime	05/02/12	ANS3	x
aa16	33/09	33	Gironde	South-western France	Gironde	end Jan 2012	ANS4	x
aa17	33/05	33	Gironde	South-western France	Gironde	end Jan 2012		x

aa18	33/11	33	Gironde	South-western France	Gironde	end Jan 2012	ANS1	x
aa19	33/12	33	Gironde	South-western France	Gironde	end Jan 2012	ANS1	x
aa22	33/25	33	Gironde	South-western France	Gironde	end Jan 2012	ANS1	x
aa23	33/03	33	Gironde	South-western France	Gironde	end Jan 2012		x
aa25	33/18	33	Gironde	South-western France	Gironde	08/11/11	ANS15	
aa27	33/08	33	Gironde	South-western France	Gironde	end Jan 2012	ANS3	x
aa28	33/02	33	Gironde	South-western France	Gironde	end Jan 2012	ANS7	x
aa29	33/07	33	Gironde	South-western France	Gironde	end Jan 2012	ANS16	x
aa30	33/17	33	Gironde	South-western France	Gironde	end Jan 2012		x
aa31	33/04	33	Gironde	South-western France	Gironde	end Jan 2012	ANS1	x
aa32	33/19	33	Gironde	South-western France	Gironde	end Jan 2012	ANS1	x
aa33	33/06	33	Gironde	South-western France	Gironde	end Jan 2012	ANS1	x
aa36	33/14	33	Gironde	South-western France	Gironde	end Jan 2012	ANS3	x
aa38	33/13	33	Gironde	South-western France	Gironde	end Jan 2012	ANS7	x
aa39	33/20	33	Gironde	South-western France	Gironde	end Jan 2012	ANS17	x
aa40	33/26	33	Gironde	South-western France	Gironde	end Jan 2012	ANS15	x
aa42	33/27	33	Gironde	South-western France	Gironde	end Jan 2012	ANS1	x
aa44	33/21	33	Gironde	South-western France	Gironde	end Jan 2012	ANS3	x
aa59	33/29	33	Gironde	South-western France	Gironde	end Jan 2012		x
aa60	33/23	33	Gironde	South-western France	Gironde	end Jan 2012	ANS15	x
aa64	33/24	33	Gironde	South-western France	Gironde	end Jan 2012	ANS3	x
aa65	33/16	33	Gironde	South-western France	Gironde	end Jan 2012		x
aa66	33/22	33	Gironde	South-western France	Gironde	end Jan 2012	ANS15	x
aa24	40/47	40/64	Landes	South-western France	Landes	08/11/11	ANS15	x
aa34	X/53	40/64	Landes	South-western France	Landes	2011/2012	ANS17	x
aa35	X/50	40/64	Landes	South-western France	Landes	2011/2012	ANS1	x
aa46	40/46	40/64	Landes	South-western France	Landes	14/12/11	ANS3	x
aa52	X/39	40/64	Landes	South-western France	Landes	_		x
aa54	X/49	40/64	Landes	South-western France	Landes	_	ANS13	x
aa55	40/42	40/64	Landes	South-western France	Landes	_	ANS15	x
aa61	X/41	40/64	Landes	South-western France	Landes	_	ANS15	x
aa83	40/73	40/64	Landes	South-western France	Landes	16/11/11	ANS1	x
aa84	40/69	40/64	Landes	South-western France	Landes	16/11/11	ANS3	x
aa85	40/61	40/64	Landes	South-western France	Landes	29/01/12	ANS11	x
aa86	40/65	40/64	Landes	South-western France	Landes	16/11/11		x
aa87	40/71	40/64	Landes	South-western France	Landes	16/11/11		x
aa89	40/70	40/64	Landes	South-western France	Landes	16/11/11	ANS1	x
aa90	40/72	40/64	Landes	South-western France	Landes	16/11/11	ANS15	

aa91	40/67	40/64	Landes	South-western France	Landes	04/02/12		x
aa100	X/66	40/64	Landes	South-western France	Landes	_		x
aa101	X/62	40/64	Landes	South-western France	Landes	_		x
aa102	X/63	40/64	Landes	South-western France	Landes	_		x
aa176	40/170	40/64	Landes	South-western France	Landes	02/02/12	ANS21	x
aa178	40/172	40/64	Landes	South-western France	Landes	09/02/12	ANS1	x
aa180	40/174	40/64	Landes	South-western France	Landes	04/02/12	ANS23	x
aa181	40/175	40/64	Landes	South-western France	Landes	09/02/12	ANS15	x
aa182	40/176	40/64	Landes	South-western France	Landes	02/02/12	ANS1	x
aa183	40/177	40/64	Landes	South-western France	Landes	01/02/12	ANS3	x
aa184	40/178	40/64	Landes	South-western France	Landes	01/02/12	ANS1	x
aa185	40/179	40/64	Landes	South-western France	Landes	03/02/12	ANS1	x
aa186	40/180	40/64	Landes	South-western France	Landes	03/02/12	ANS24	x
aa187	40/181	40/64	Landes	South-western France	Landes	10/02/12	ANS20	x
aa188	40/182	40/64	Landes	South-western France	Landes	10/02/12	ANS7	x
aa189	40/183	40/64	Landes	South-western France	Landes	12/02/12	ANS24	x
aa190	40/184	40/64	Landes	South-western France	Landes	12/02/12	ANS1	x
aa40-1		40/64	Landes	South-western France	Landes	_	ANS1	*x*
aa40-2		40/64	Landes	South-western France	Landes	_	ANS1	x
aa40-3		40/64	Landes	South-western France	Landes	_	ANS1	x
aa40-4		40/64	Landes	South-western France	Landes	_	ANS2	x
aa40-5		40/64	Landes	South-western France	Landes	_	ANS8	x
aa40-6		40/64	Landes	South-western France	Landes	_	ANS1	X
aa40-7		40/64	Landes	South-western France	Landes	_	ANS1	X
aa40-8		40/64	Landes	South-western France	Landes	_	ANS1	X
aa47	64/52	40/64	Landes	South-western France	Pyrenee Atlantique	_	ANS15	x
aa50	64/48	40/64	Landes	South-western France	Pyrenee Atlantique	_	ANS1	x
aa57	64/51	40/64	Landes	South-western France	Pyrenee Atlantique	_	ANS3	x
rub1				Russia	Kalmykia		17	

Appendix 2 - Table of mtDNA haplotypes found in *Anser anser* individuals.

	France					North Europe			
	Charente Maritime	Gironde	Landes	Nord	Oise	Norway Finnmark	Norway Vega	Netherlands	Total
ANS1	1	7	15	5	1			3	32
ANS2			1						1
ANS3	2	4	4	4	2	7	20	4	47
ANS4		1		1	2				4
ANS5								1	1
ANS6					1			1	2
ANS7	1	2	1	1	1			1	7
ANS8			1						1
ANS9								1	1
ANS10				3	2			1	6
ANS11			1						1
ANS12					1				1
ANS13			1	1	2				4
ANS14							1		1
ANS15	2	4	6	2			1	2	17
ANS16		1					1		2
ANS17		1	1						2
ANS18					1	3			4
ANS19						1			1
ANS20	1		1						2
ANS21	2		1						3
ANS22	1								1
ANS23			1						1
ANS24			2						2
Total	10	20	36	17	13	11	23	14	144

Appendix 3 – Summary of genetic variation at 14 microsatellite loci in sampled populations. Na = No. of different alleles; Ne = No. of effective alleles. Ho = observed heterozygosity; He = expected heterozygosity; F = fixation index; HWE = Hardy-Weinberg equilibrium.

Pop	Locus	N	Na	Ne	Ho	He	F
Netherlands	**Ans02**	13	9.000	4.390	0.692	0.772	0.103
	Ans04	14	3.000	2.947	0.214	0.661	0.676
	Ans07	14	3.000	1.782	0.286	0.439	0.349
	Ans17	14	7.000	4.667	0.643	0.786	0.182
	Ans18	14	4.000	2.190	0.214	0.543	0.606
	Ans21	14	3.000	1.640	0.500	0.390	-0.281
	Ans24	14	3.000	1.338	0.286	0.253	-0.131
	Ans25	14	6.000	3.769	0.786	0.735	-0.069
	Aalu1b	14	4.000	2.190	0.429	0.543	0.211
	Aph12	14	2.000	1.600	0.214	0.375	0.429
	Aph19	14	2.000	1.774	0.500	0.436	-0.146
	Smo7	14	2.000	1.508	0.286	0.337	0.152
	Hhiu1b	14	3.000	1.156	0.929	0.135	-5.868
	Ans13	14	4.000	1.980	0.286	0.495	0.423
Nord	**Ans02**	16	8.000	3.606	0.750	0.723	-0.038
	Ans04	17	4.000	2.934	0.706	0.659	-0.071
	Ans07	17	3.000	2.181	0.294	0.542	0.457
	Ans17	17	8.000	5.026	0.706	0.801	0.119
	Ans18	16	3.000	1.724	0.125	0.420	0.702
	Ans21	17	3.000	1.847	0.235	0.458	0.487
	Ans24	17	1.000	1.000	0.000	0.000	-
	Ans25	17	7.000	4.983	0.882	0.799	-0.104
	Aalu1b	17	4.000	3.778	0.824	0.735	-0.120
	Aph12	15	3.000	2.103	0.533	0.524	-0.017
	Aph19	17	2.000	1.973	0.412	0.493	0.165
	Smo7	17	2.000	1.710	0.412	0.415	0.008
	Hhiu1b	17	4.000	1.889	0.529	0.471	-0.125
	Ans13	17	4.000	2.766	0.353	0.638	0.447
Oise	**Ans02**	14	9.000	6.759	0.857	0.852	-0.006
	Ans04	15	4.000	3.147	0.267	0.682	0.609
	Ans07	14	2.000	1.912	0.214	0.477	0.551
	Ans17	15	6.000	4.206	0.467	0.762	0.388
	Ans18	14	6.000	2.667	0.357	0.625	0.429
	Ans21	15	3.000	1.779	0.200	0.438	0.543
	Ans24	15	2.000	1.069	0.067	0.064	-0.034
	Ans25	15	6.000	3.947	0.600	0.747	0.196
	Aalu1b	14	4.000	2.947	0.643	0.661	0.027
	Aph12	14	3.000	2.074	0.286	0.518	0.448
	Aph19	15	2.000	1.867	0.333	0.464	0.282
	Smo7	15	2.000	1.642	0.533	0.391	-0.364
	Hhiu1b	15	2.000	1.069	0.067	0.064	-0.034
	Ans13	14	3.000	2.741	0.500	0.635	0.213

Finnmark	**Ans02**	9	6.000	3.857	0.778	0.741	-0.050
	Ans04	10	4.000	2.597	0.400	0.615	0.350
	Ans07	10	3.000	2.151	0.200	0.535	0.626
	Ans17	11	5.000	3.270	0.818	0.694	-0.179
	Ans18	8	2.000	1.280	0.250	0.219	-0.143
	Ans21	11	3.000	2.283	0.364	0.562	0.353
	Ans24	10	1.000	1.000	0.000	0.000	-
	Ans25	10	4.000	2.667	0.700	0.625	-0.120
	Aalu1b	11	4.000	1.330	0.182	0.248	0.267
	Aph12	11	3.000	1.582	0.455	0.368	-0.236
	Aph19	11	3.000	1.603	0.273	0.376	0.275
	Smo7	11	2.000	1.198	0.000	0.165	1.000
	Hhiu1b	11	2.000	1.198	0.182	0.165	-0.100
	Ans13	11	5.000	3.903	0.636	0.744	0.144
Vega	**Ans02**	31	11.000	3.979	0.774	0.749	-0.034
	Ans04	34	4.000	3.129	0.382	0.680	0.438
	Ans07	31	5.000	2.023	0.355	0.506	0.298
	Ans17	34	5.000	2.919	0.588	0.657	0.105
	Ans18	33	6.000	2.209	0.273	0.547	0.502
	Ans21	31	3.000	1.795	0.613	0.443	-0.384
	Ans24	30	3.000	1.224	0.067	0.183	0.635
	Ans25	34	8.000	5.639	0.882	0.823	-0.073
	Aalu1b	34	4.000	2.305	0.588	0.566	-0.039
	Aph12	34	3.000	2.070	0.412	0.517	0.203
	Aph19	34	2.000	1.895	0.588	0.472	-0.245
	Smo7	34	2.000	1.524	0.206	0.344	0.401
	Hhiu1b	34	3.000	1.433	0.353	0.302	-0.167
	Ans13	34	5.000	2.645	0.588	0.622	0.054
Charente-Maritime	**Ans02**	9	8.000	5.400	0.889	0.815	-0.091
	Ans04	9	4.000	2.746	0.111	0.636	0.825
	Ans07	9	3.000	1.588	0.000	0.370	1.000
	Ans17	9	5.000	3.057	0.444	0.673	0.339
	Ans18	9	3.000	2.793	0.222	0.642	0.654
	Ans21	9	3.000	1.976	0.667	0.494	-0.350
	Ans24	9	2.000	1.385	0.333	0.278	-0.200
	Ans25	8	6.000	4.923	0.875	0.797	-0.098
	Aalu1b	9	4.000	2.282	0.556	0.562	0.011
	Aph12	9	2.000	1.800	0.778	0.444	-0.750
	Aph19	9	2.000	1.800	0.222	0.444	0.500
	Smo7	9	2.000	1.385	0.889	0.278	-2.200
	Hhiu1b	9	3.000	1.256	0.222	0.204	-0.091
	Ans13	9	3.000	2.160	0.556	0.537	-0.034
Gironde	**Ans02**	23	9.000	5.186	0.826	0.807	-0.023
	Ans04	24	4.000	3.892	0.333	0.743	0.551
	Ans07	24	4.000	1.466	0.208	0.318	0.344
	Ans17	24	7.000	3.959	0.542	0.747	0.275
	Ans18	23	5.000	1.853	0.217	0.460	0.528
	Ans21	23	3.000	1.772	0.348	0.436	0.202
	Ans24	23	1.000	1.000	0.000	0.000	-

	Ans25	24	8.000	4.645	0.750	0.785	0.044
	Aalu1b	24	5.000	2.743	0.667	0.635	-0.049
	Aph12	24	2.000	1.946	0.667	0.486	-0.371
	Aph19	23	2.000	1.830	0.435	0.454	0.042
	Smo7	24	2.000	1.180	0.583	0.153	-2.818
	Hhiu1b	24	4.000	1.550	0.333	0.355	0.061
	Ans13	23	4.000	3.032	0.565	0.670	0.157
Landes	**Ans02**	45	11.000	4.500	0.756	0.778	0.029
	Ans04	44	4.000	3.741	0.477	0.733	0.349
	Ans07	44	3.000	1.955	0.227	0.488	0.535
	Ans17	45	7.000	4.787	0.689	0.791	0.129
	Ans18	45	6.000	1.777	0.333	0.437	0.238
	Ans21	45	3.000	1.874	0.467	0.466	-0.001
	Ans24	45	3.000	1.280	0.222	0.219	-0.015
	Ans25	45	8.000	4.350	0.800	0.770	-0.039
	Aalu1b	45	5.000	3.061	0.489	0.673	0.274
	Aph12	45	2.000	1.776	0.378	0.437	0.135
	Aph19	44	3.000	1.890	0.477	0.471	-0.014
	Smo7	45	2.000	1.557	0.556	0.358	-0.553
	Hhiu1b	45	4.000	1.529	0.356	0.346	-0.028
	Ans13	45	4.000	2.675	0.556	0.626	0.113

		N	**Na**	**Ne**	**Ho**	**He**	**F**	**HWE**	
								P-value	**(se)**
Mean for each locus (all populations confounded)	**Ans02**	20.000	8.875	4.710	0.790	0.780	-0,014	0.3783	(0.0209)
	Ans04	20.875	3.875	3.142	0.361	0.676	0,466	0.0000	(0.0000)
	Ans07	20.375	3.250	1.882	0.223	0.459	0,520	0.0000	(0.0000)
	Ans17	21.125	6.250	3.986	0.612	0.739	0,170	0.0000	(0.0000)
	Ans18	20.250	4.375	2.062	0.249	0.487	0,439	0.0000	(0.0000)
	Ans21	20.625	3.000	1.871	0.424	0.461	0,071	0.1042	(0.003)
	Ans24	20.375	2.000	1.162	0.122	0.125	0,051	0.0558	(0.0022)
	Ans25	20.875	6.625	4.365	0.784	0.760	-0,033	0.3506	(0.0153)
	Aalu1b	21.000	4.250	2.579	0.547	0.578	0,073	0.0218	(0.0022)
	Aph12	20.750	2.500	1.869	0.465	0.459	-0,020	0.0406	(0.0015)
	Aph19	20.875	2.250	1.829	0.405	0.451	0,107	0.1316	(0.0038)
	Smo7	21.125	2.000	1.463	0.433	0.305	-0,547	0.0003	(0.0001)
	Hhiu1b	21.125	3.125	1.385	0.371	0.255	-0,794	0.0707	(0.0034)
	Ans13	20.875	4.000	2.738	0.505	0.621	0,190	0.0004	(0.0002)