1 **Long-term reciprocal gene flow in wild and domestic geese reveals complex domestication history**

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Abstract

Hybridization has frequently been observed between wild and domestic species and can substantially impact genetic diversity of both counterparts. Geese show some of the highest levels of interspecific hybridization across all bird orders, and two of the goose species in the genus *Anser* have been domesticated providing an excellent opportunity for a joint study of domestication and hybridization. Until now, knowledge of the details of the goose domestication process has come from archaeological findings and historical writings supplemented with a few studies based on mitochondrial DNA. Here, we used genome-wide markers to make the first genome-based inference of the timing of European goose domestication. We also analyzed the impact of hybridization on the genome-wide genetic variation in current populations of the European domestic goose and its wild progenitor: the graylag goose (*Anser anser*). Our dataset consisted of 58 wild graylags sampled around Eurasia and 75 domestic geese representing 14 breeds genotyped for 33,527 single nucleotide polymorphisms. Demographic reconstruction and clustering analysis suggested that divergence between wild and domestic geese around 5,300 generations ago was followed by long-term genetic exchange, and that graylag populations have 3.2–58.0% admixture proportions with domestic geese, with distinct geographic patterns. Surprisingly, many modern European breeds share considerable (> 10%) ancestry with the Chinese domestic geese that is derived from the swan goose *Anser cygnoid*. We show that the domestication process can progress despite continued and pervasive gene flow from the wild form.

64   **1.   Introduction**

65   Reproductive isolation is a defining feature of speciation and yet hybridization between species is an

66   important general phenomenon in evolution (Arnold 2004; Abbott *et al.* 2013). Among birds, the

67   Anseriformes (ducks, geese, and swans) show particularly pervasive hybridization, 41.6% to > 60% of

68   species hybridizing with each other (Grant and Grant 1992; Ottenburghs *et al.* 2016a). Domestication

69   generates differentiated gene pools and reproductive isolation between domestics and their wild

70   progenitor, but hybridization between domestic and wild forms has been well demonstrated in both

71   plants (Arnold 2004; Janzen *et al.* 2019) and animals (Godinho *et al.* 2011; Frantz *et al.* 2015). The

72   impacts include genetic and trait enrichment of domestics, for instance, in chicken the acquisition of a

73   yellow skin phenotype is a result of past mating between red junglefowl and grey junglefowl (Eriksson

74   *et al.* 2008). In geese, a high tendency for hybridization between wild and domestic forms has also

75   been suggested (Kuijken and Devos 1996; Heikkinen *et al.* 2015), creating an exciting opportunity to

76   study the complex dynamics of hybridization and domestication.

77   The domestic geese of the world (European and Chinese forms) are derived from two different

78   wild species: the graylag (*Anser anser*) and the swan goose (*Anser cygnoid*), respectively (Delacour

79   1954; Shi *et al.* 2006). *A. anser* and *A. cygnoid* shared a common ancestor about 3.4 Mya

80   (Ottenburghs *et al.* 2016b) but are still able to hybridize (Ottenburghs *et al.* 2016a), and some

81   domestic breeds are reportedly hybrid (Buckland and Guy 2002). The graylag has been divided into

82   the western, nominate subspecies *A. a. anser* (Linnaeus, 1758) with a European breeding range and

83   the eastern subspecies *A. a. rubrirostris* (Swinhoe, 1871) breeding further east, although the

84   subspecific boundary is not well defined, and mitochondrial DNA has not been found to distinguish

85   them (Heikkinen *et al.* 2015). Of these subspecies, *rubrirostris* is larger and lighter colored than *anser*

86   (Cramp and Simmons 1977) and has a pink bill and cold pink legs in contrast to the orange bill and

87   flesh-colored legs of *anser*, the bill color used as primary evidence in favor of the original

88   domestication of *rubrirostris* (Kear 1990). As with all domesticates, domestic geese varieties are

89   morphologically more diverse than their wild counterparts, particularly in plumage and body size

90   (Buckland and Guy 2002).

91   The current knowledge about goose domestication relies largely on ancient texts and

92   archaeological evidence. Questions about where and when domestication took place, the genetic

93   changes associated with it and the later history of domestic geese, however, remain largely

94   unresolved (Heikkinen *et al.* 2015). There are depictions from the New Kingdom of Egypt that suggest

95   geese were already fully domesticated by the 18th Dynasty (1450-1341 BCE). The earliest reliable

96   reference to domestic geese in western Eurasia is Homer's Odyssey (first half of 8th century BCE) and

97   geese were certainly well-established poultry by Roman times (Albarella 2005).

98   Genetic diversity in the mitochondrial DNA (mtDNA) of graylag and European domestic geese

99   showed reduced diversity in the domestics (Heikkinen *et al.* 2015) which may result from an early

100   domestication bottleneck or, alternatively, later breed formation. There is a particular mitochondrial

101   haplogroup common in the domestics (Heikkinen *et al.* 2015), and archaeological domestic goose

102   bones from the High Medieval (11th-13th century CE) of Russia belonged to that haplogroup (Honka *et*

103   *al.* 2018).

104   MtDNA relationships between extant Chinese and European domestic goose breeds confirm

105   that the former, excluding one breed, have swan goose ancestry, whereas European domestic goose

106   and the Chinese Yili breed have graylag ancestry (Shi *et al.* 2006; Sun *et al.* 2013; Ren *et al.* 2016).

107   However, Chinese mtDNA haplotypes may occasionally occur in European domestics, and vice versa

108   (Sun *et al.* 2013; Heikkinen *et al.* 2015).

109 Genomic data can be much more powerful than mtDNA in terms of inference about

110 hybridization. For instance, New World cattle, along with their taurine ancestry have been shown

111 genomically to have a greater proportion of indicine ancestry than previously assumed (McTavish *et*

112 *al.* 2013) and genomic studies of domestic pigs have shown them to have received genetic input from

113 wild boars (Frantz *et al.* 2015). Genomic studies of modern dog breeds also show an ancestry that can

114 only be explained by gene flow from multiple regional wolf populations (Skoglund *et al.* 2015). Plant

115 varieties are often shown to be the product of hybridization by genomic studies, for example maize

116 (Hufford *et al.* 2013). Interpretation of genomic data is still challenging and for the study of domestic

117 species and their interactions with their wild progenitors, it is best to apply genomics to infer jointly

118 the genetic impact of initial domestication and subsequent hybridization of wild and domestic

119 populations, as the latter can obscure domestic-wild genetic relationships and may also give a false

120 impression of the location and number of times a species has been domesticated (van Heerwaarden

121 *et al.* 2011; Marshall *et al.* 2014; Larson and Fuller 2014).

122 Here we investigate goose domestication history using genome-wide single nucleotide

123 polymorphism (SNP) data from thousands of loci, obtained by genotyping-by-sequencing (GBS). We

124 used 56 and 50 samples of graylag and domestic geese from a previous mtDNA study (Heikkinen *et al.*

125 2015), together with 2 new Turkish graylag and 25 new domestic specimens. We studied the interplay

126 between domestication and hybridization by addressing the following questions: i) what is the extent

127 of genetic differentiation amongst wild and domestic geese? ii) what is the approximate time of

128 domestication? and iii) what is the role of intra- and interspecific hybridization in goose domestication

129 history and iv) how does hybridization affect the genetic composition of modern populations?

130 **2. Materials and methods**

131 a) Sampling

132 The wild-collected graylag samples derive widely from Eurasia (Figure 1, Supplementary File 1, Table

133 S1) representing both subspecies. As no morphological data were available, we could not discriminate

134 the samples between eastern and western subspecies. However, based on their sampling and the

135 known geographic distribution of the populations, we can be confident that the Iranian and

136 Kazakhstani samples belonged to the eastern subspecies *rubrirostris*. The European domestic goose

137 samples represented 14 different breeds (Supplementary File 1, Table S1) together with individuals

138 unattributed to a recognized breed or which were presumptive hybrids between European and

139 Chinese domestic geese. Some specimens were reported to be Chinese domestic geese. The domestic

140 samples were obtained from local breeders in Denmark, Sweden, and the UK, and those from Turkey

141 were collected directly by the authors.

142 b)   DNA extraction and GBS library construction

143 GBS (Elshire *et al.* 2011) libraries were constructed at the Cornell Biotechnology Resource Center

144 (BRC) following DNA extraction with the DNeasy Blood and Tissue Kit (QIAGEN) with RNase treatment.

145 Each individual DNA sample and an adaptor with a unique barcode were combined in a 96-well plate

146 along with a common adaptor. Samples were treated with the EcoT-22I (ATGCAT) restriction enzyme

147 to create fragmented DNA. Barcoded adapters and common adapters with matching sticky ends were

148 ligated to each sample with T4 DNA ligase. The samples were pooled and purified with a QIAquick PCR

149 Purification Kit (QIAGEN). PCR amplification of the library used primers complementary to barcoded

150 and common adapters with products purified as above, and the samples were 100 bp SE-sequenced

151 with Illumina HiSeq 2000/2500 at the BRC.

152 c)   GBS pipeline and SNP calling

153   Raw sequence reads were run through the Command Line Interface of the Tassel 5 GBS v2 Discovery

154   and Production pipelines (Glaubitz *et al.* 2014). Details about the pipelines and SNP calling are in the

155   Supplementary File 1 (see Figure S1 for quick outline of the workflow). Good quality reads were

156   recorded as tags and aligned to the *A. cygnoid domesticus* GenBank assembly

157   (AnsCyg_PRJNA183603_v1.0 GCF_000971095.1) (Lu *et al.* 2015) using the Burrows-Wheeler Aligner

158   with default settings (Li and Durbin 2009). After running the raw data through the pipelines, 69,865

159   SNPs were obtained.

160   The SNPs were subjected to additional filtering using VCFtools (Danecek *et al.* 2011). We

161   removed indels, loci with more than two alleles and invariant loci. However, loci that were within-

162   species invariant but divergent from the reference were retained for phylogenetics, informing about

163   graylag-swan goose divergence. After preliminary analyses loci with observed heterozygosity over

164   0.75 were removed as potential paralogs. Individuals with more than 20% missing data across loci

165   were removed. The final dataset consisted of 33,527 biallelic SNPs and 133 individuals (58 wild and 75

166   domestic).

167   d)   The estimation of genetic diversity

168   Genetic diversity and pairwise F_{ST} values were investigated with the hierfstat R package (Goudet

169   2005). Expected heterozygosity (H_E) was calculated for each locus and population and averaged across

170   loci. Difference in average H_E between graylags and European domestics was tested with a two-

171   sample t-test with the Welch correction for non-homogeneity of variance (Welch 1938). For

172   comparing the genetic diversity among wild and domestics, only pure graylag populations (defined as

173   having < 10% admixture with domestic geese) and pure European domestic geese (defined as having <

174   10% admixture with Chinese domestic geese) were used to avoid hybridization effects on the

175   estimates. The admixture proportions were obtained from STRUCTURE.

176   The variance components across loci for hierarchical F-statistics for pure graylags and pure

177   European domestics were estimated using locus-by-locus analysis of molecular variance (AMOVA)

178   implemented in Arlequin 3.5.2.1 (Excoffier and Lischer 2010). The significance was tested with 16 000

179   permutations.

180   e)   Population structure analyses

181   Population clustering and structure was analyzed with STRUCTURE 2.3.4 (Pritchard *et al.* 2000) and

182   Principal Component Analysis (PCA) (Patterson *et al.* 2006). For the whole dataset, STRUCTURE was

183   run with 1000 burn-in steps followed by 10 000 iterations of MCMC for data collection for K = 1-10

184   allowing admixture with five replicates of each run to reach convergence. For the STRUCTURE

185   analyses done separately on graylags and European domestic geese, see Supplementary File 1. An

186   admixture model with correlated allele frequencies among populations (Falush *et al.* 2003) was used

187   in all STRUCTURE analyses and the iterations were automated with StrAuto 1.0 (Chhatre and Emerson

188   2017). We applied both likelihood of K and Evanno's ΔK (Evanno *et al.* 2005) of successive K values to

189   determine the optimal number of clusters, using STRUCTURE HARVESTER (Earl and VonHoldt 2012).

190   CLUMPP 1.1.2 (Jakobsson and Rosenberg 2007) was used to align the assignments from different

191   replicates of K and DISTRUCT 1.1 (Rosenberg 2003) for visualization. A PCA was performed with the

192   prcomp function in R (R Core Team 2017) and the significance of eigenvalues determined based on

193   the Tracy-Widom distribution (Patterson *et al.* 2006; van Heerwaarden *et al.* 2011).

194   A neighbor-joining tree was constructed for phylogenetic analysis, with pairwise distance

195   between individuals obtained with the R package ape (Paradis *et al.* 2004) based on 40,191 loci. The

196   *A. cygnoid* reference genome and the invariant sites that differed from it were included in the tree

197   construction.

198   f)   Tests for admixture and simulations of demographic history

199   The history of admixture was tested with a 3-Population test f_3(C; A, B) implemented in AdmixTools

200   4.1 (Patterson *et al.* 2012). This method offers a formal test to explain observed patterns of admixture

201   in a target population without an outgroup. For identification of admixture between Chinese and

202   European domestics, Grey and White Chinese were combined to represent the Chinese, and the

203   Landes breed that had minimum indication of admixture in STRUCTURE was chosen to represent the

204   European domestic source population. In addition, we tested several combinations of graylag geese,

205   European domestic geese, and Chinese domestic geese as source populations to detect possible

206   admixture in populations and breeds that implied admixture in STRUCTURE. See also Supplementary

207   File 1 for further information.

208   Different models of demographic history were tested with fastsimcoal2 ver 2.6 (Excoffier *et al.*

209   2013). Fastsimcoal2 uses coalescent simulations to estimate the likelihood of a demographic model

210   and the probabilities obtained from simulations are then used to compute the composite likelihood of

211   the model. The likelihood is maximized with a conditional maximization algorithm (ECM). We

212   excluded all SNPs that had missing data within the whole data set and executed the analyses with a

213   site frequency spectrum (SFS) based on 6,229 SNPs (Supplementary File 1, Figure S2). As there are no

214   estimates of the genetic diversity per base pair for graylags, we estimated the proportions of variable

215   and monomorphic sites in the data as we needed the information about the invariant sites for the

216   fastsimcoal2 analysis. From the BAM file with –depth option in SAMtools 1.7 (Li *et al.* 2009), we

217   estimated 9,801,382 bp covered with GBS tags. We then mimicked the filtering steps done for the

218   biallelic SNPs to reduce the total number of sites in equivalent proportions. We removed the same

219   number of sites that corresponded to the number of SNPs that were removed because they were

220   indels, had more than 2 alleles or had heterozygosity over 0.75. Since some of the SNPs were

221 removed from this analysis due to missing data in some individuals, we removed an equal proportion

222 of sites from the total number of sites as well. The final folded SFS had 1,681,316 sites of which

223 1,675,087 were monomorphic and 6,229 polymorphic.

224   To infer the demographic history, we chose a subset of individuals from both wild-collected

225 graylags and domestic geese to represent the genetic variation in both groups. Therefore, 11 graylags

226 with > 90.8% of graylag ancestry and 15 domestic geese with > 91.4% of European domestic goose

227 ancestry were selected for the analysis. The mutation rate for the simulations was $1.38 \cdot 10^{-7}$ per

228 generation (Pujolar *et al.* 2018). The parameter estimation for each model tested involved 100,000

229 simulations and 40 conditional maximization (ECM) cycles. The parameters for each model were

230 estimated with 100 independent runs to obtain the global maximum. The models tested were i)

231 simple divergence of two populations with no gene flow, ii) divergence of two populations with

232 continuous gene flow and iii) divergence of two populations with changing gene flow patterns (Figure

233 2, Figure S3-S4). The best model was selected based on Akaike's weight of evidence as in Excoffier *et*

234 *al.* (2013). For parametric bootstrapping 100 SFS were simulated with the parameter estimates

235 obtained from the real SFS, followed by maximum likelihood estimation with 50 independent runs for

236 each bootstrap SFS. The 95% confidence intervals were obtained from the bootstrap data for each

237 estimated parameter.

238 **Data availability**

239 The Supplementary File 1 that contains extended Materials and Methods, and Results including

240 supplementary figures and tables, and Supplementary File 2 containing commands for the Tassel

241 pipeline and vcftools are stored in figshare along with the VCF file containing the filtered genotypes.

242 The raw sequence reads are available in NCBI's Sequence Read Archive (SRA) under BioProject

243 PRJNA634849.

3.   Results

a)   Population structure

There was clear genetic differentiation between graylags and domestic geese according to
STRUCTURE and PCA (Figure 3A-B). STRUCTURE aims to find the optimal number of ancestral
populations (K) from the given data and the subdivision was clear in our data. At K = 2,
populations/breeds are clustered based on their status (wild or domestic) and, at K = 3, domestic
geese are further separated into European and Chinese. At K = 4, the fourth cluster is within graylag
populations but none of the individuals are unanimously assigned to that cluster. The likelihood was
highest for K = 3. These results were supported by PCA as the first two PCs out of 14 significant PCs (p
< 0.05) were enough to separate the three groups (wild, European domestic, Chinese domestic) from
each other (Figure 3A). Overall, the graylag populations showed 3.2% - 23.5% admixture proportions
with European domestic geese when K = 3 (Table S1). In contrast, not all European domestic geese
showed admixture with graylags and the admixture percentages ranged from 0.0 to 8.4%. At K = 3
many European domestic goose breeds showed mixed ancestry with Chinese domestic geese (0.0 -
27.1%).

        The neighbor-joining tree repeated the major patterns observed with STRUCTURE and PCA,
revealing a star shaped phylogeny and confirming that the domestic and graylag geese largely form
different clades (Figure S5). Surprisingly, the Chinese domestic geese were closer to European
domestic geese and graylags, than to the swan goose reference genome. In addition, one graylag
from Turkey was more closely related to the Chinese domestic geese than other graylags, also
indicated by admixture proportions from STRUCTURE. Further, two Crested Faroese individuals and
four domestics from the USA (2 unknown and 2 Toulouse crosses) were closer to Chinese than

266   European domestic geese. These six individuals also showed high proportions of admixture with

267   Chinese domestics in the STRUCTURE analysis.

268   Unequal sample sizes did not have a large effect on the results (Supplementary File 1, Figure S6-

269   S11). Some further population structure was observed within both graylags and domestic geese,

270   when analyzed separately with STRUCTURE and PCA. Geographically, graylags differentiated by

271   subspecies (Supplementary File 1, Figure S12-S13). STRUCTURE indicated little differentiation among

272   European domestic geese, but the PCA revealed separation between the European breeds and the

273   Turkish domestic geese (Supplementary File 1, Figure S14-S15).

274   b)   Genetic diversity

275   An AMOVA was used to partition genetic diversity among graylag vs. domestic (group level), and

276   among populations (graylag) and among breeds (domestic), and within population levels (Table 1).

277   The fixation index between graylag and domestic geese was 0.158 and there was also significant

278   differentiation among graylag populations/domestic breeds (Table 1). The average pairwise F_{ST}

279   between graylag populations and domestic breeds was 0.197, among graylag populations 0.088 and

280   among domestic breeds 0.174 (Supplementary File 1, Table S2).

281   The genetic diversity measured as average H_E was higher in pure graylags (0.146) than in pure

282   European domestic geese (0.096) (Welch's t-test, degrees of freedom (df) = 10.594, p = 3.91×10^{-5}, see

283   also Supplementary File 1, Figure S16). The average H_E ranged from 0.140 (Denmark) to 0.150

284   (Kazakhstan) in pure graylags and from 0.047 (Landes) to 0.123 (Domestic N-Turkey) in pure European

285   domestics. The difference in average H_E remained when non-pure graylag and non-pure European

286   domestics were included in the comparison (0.156 vs. 0.107; Welch's t-test, df = 19.28, p = 0.000418).

287   The average H_E was higher in admixed populations compared to non-admixed populations in both

288   graylag and domestic populations (Supplementary File 1; Table S1, Figure S16).

289   c)   Admixture and the time of domestication

290   STRUCTURE implied considerable mixed ancestry from multiple genetic clusters for Dutch and Turkish

291   graylags, but the f_3 analysis did not confirm admixture for the Dutch population even though multiple

292   source populations of graylag and domestic goose were tested (Table S3). However, the Turkish

293   population is more complicated as they obtained negative f_3 when analyzed together with multiple

294   combinations of source populations indicating admixture with Chinese domestic goose but not with

295   European domestic goose. This signal appeared consistently when several graylag and European

296   domestic goose populations were used as source populations with Chinese domestic geese. However,

297   as the Turkish graylags appeared genetically very dissimilar, we analyzed them separately which

298   resulted in neither of them obtaining negative f_3 (Table S3). The two Turkish graylag samples came

299   from the same area as our NW-Turkish domestic population, which among Turkish domestic geese

300   showed highest admixture with graylags (2.2%), but admixture was not confirmed with the f_3 test

301   (Table S4). We did not obtain negative Z-scores to any of the other graylag populations either (Table

302   S5-S6).

303   The f_3 analysis confirmed admixture of domestic geese in line with the STRUCTURE results. Most

304   notably, the African breed is a hybrid between European and Chinese domestic geese (Z-score -

305   6.399), unexpected as this breed has been assumed to have originated solely from swan goose. The

306   European-Chinese hybrid status of the Kholmogory and Steinbacher breeds was also confirmed (Z-

307   scores of -8.933 and -5.349, respectively). The Kholmogory breed also fell halfway between European

308   and domestic geese both in STRUCTURE and PCA, whereas the Steinbacher was genetically closer to

309   European domestic geese in the PCA. However, the Diepholzer breed, which reportedly is also a

310   hybrid, was not confirmed as such in our analysis. Other domestic breeds/groups with admixture

311   status in STRUCTURE were also confirmed to have a European-Chinese admixture when a Z-score

312 threshold of -3 (roughly corresponding to $p < 0.01$) was used: Sebastopol, Toulouse cross, Domestic

313 NY, Embden, Tufted Roman (Figure 3C, Supplementary File 1, Table S5). These breeds also gave a

314 similar signal when other combinations of European domestic goose breeds and Chinese domestic

315 geese were used as source populations (Table S7). The Crested Faroese breed gave indication of

316 admixture based on STRUCTURE analysis and the f_3 test supported this (Z-score of -2.228, p < 0.05).

317 Surprisingly, the Northern Turkish domestic population was not admixed with Chinese domestic geese

318 in STRUCTURE but f_3 analysis gave a contrasting signal (Z-score -2.459, p < 0.05).

319 The demographic model that best fit our data suggested divergence of graylag and domestic

320 geese with a recent migration rate change (Table 2, Supplementary File 1, Table S8). The model

321 suggested divergence around 5319 generations ago (95% confidence intervals (CI): 2014-6503) with

322 asymmetric but close to equal migration rates from graylags to domestic geese following divergence.

323 About 159 (88-476) generations ago, there was a change in the gene flow patterns, suggesting higher

324 gene flow (m) from graylag geese to domestic geese towards modern times. However, translated to

325 actual number of migrants ($N_e m$), the numbers suggest that the gene flow has been higher from

326 domestic geese to graylag geese across domestication history, (0.41 graylag geese vs. 1.34 domestic

327 geese migrating per generation following the domestication event, and 1.65 graylag geese vs. 1.67

328 domestic geese per generation migrating after the gene flow pattern changed). Given an estimated

329 generation time for these geese of about 3 years, the numbers suggest divergence about 14 000 BCE

330 and gene flow shift about 480 years ago.

331 **4.   Discussion**

332 We studied the dynamics of domestication and hybridization in grey (*Anser*) geese using genome-

333 wide SNP data. The results demonstrated genetic divergence between Eurasian wild graylag and

334 European domestic geese with long-term genetic exchange between them. We also inferred temporal

335   changes in the direction of gene flow. The degree of hybridization between graylag and domestic

336   geese also varied geographically. Surprisingly, several domestic goose breeds also showed a

337   substantial genetic contribution of Chinese domestic geese. We also provide insights about the origin

338   and the timing of goose domestication.

339   a)   Genetic diversity and differentiation of graylag and European domestic geese

340   Domestic species often show reduced genetic diversity compared to their wild ancestor, attributable

341   to genetic drift during population bottlenecks of initial domestication, combined with subsequent

342   artificial selection associated with breed formation (Moyers *et al.* 2018). Domestic geese appear to

343   follow the same trend. We found European domestic geese to have lower H_E than wild graylags. In

344   general, graylag populations were much more uniform in their level of genetic diversity whereas

345   domestic populations showed more variance, which is likely to reflect the human influence on breed

346   formation.

347   European domestic geese are genetically distinct from their wild progenitor but no more so

348   than for other domestic birds. The average pairwise F_{ST} values between graylag populations and

349   domestic goose breeds were lower than between red junglefowl and domestic chicken populations

350   (Kanginakudru *et al.* 2008), and domestic geese are less distinctive than domestic pigeons (Stringham

351   *et al.* 2012). Among domestic geese, the Turkish are particularly interesting. From mtDNA, the Turkish

352   domestic geese stand out as the most genetically variable group (Heikkinen *et al.* 2015), and although

353   this is less evident from GBS, among the pure European domestic geese the Northern Turkish showed

354   the highest average H_E. The f_3 analysis indicates a history of admixture with Chinese domestics for this

355   population, which may explain its high genetic diversity.

356   We found a genetic separation between European and Near Eastern populations of graylags

357   that aligned with the western and eastern subspecies (*A. a. anser* and *A. a. rubrirostris*) (Scott and

358   Rose 1996), a distinction which could not be made based on mtDNA (Heikkinen *et al.* 2015).

359   Hybridization between the western and eastern subspecies is suggested from admixture in Dutch and

360   Danish graylags in STRUCTURE as there is a genetic component that is more prevalent in the eastern

361   populations. There is historical evidence for the introduction of *rubrirostris* to Belgium in 1954 and to

362   Netherlands in 1960s (Rooth 1971; Kuijken and Devos 1996); thus, *rubrirostris* genes may have

363   originated from the recently introduced gene pool spreading to Denmark.

364   b)   When and where were geese domesticated?

365   Traditional views on goose domestication claim it first occurred in the eastern Mediterranean

366   (possibly Egypt) around the 3rd Millennium BCE (Zeuner 1963; Albarella 2005). Domestication of

367   chicken and perhaps pigeon took place earlier, but domestication of duck later, at least in Europe

368   (Larson and Fuller 2014). Demographic modelling suggests that the wild graylag and related domestic

369   lineages split approximately 5,300 generations ago placing domestication origins at 14 000 BCE

370   assuming a 3-year generation time (Cramp and Simmons 1977). This estimated genetic divergence

371   time is, admittedly, considerably earlier than any evidence for animal domestication except dog. It is

372   important to note that the estimated divergence times have large confidence intervals and merely

373   indicates the split between the ancestors of contemporary wild and domestic lineages. It is most likely

374   that our demographic modelling reflects the early divergence of different lineages of graylags, only

375   one of which contributed to later domestication. The subsequent reduction or even disappearance of

376   that wild lineage means that, despite wide geographical sampling, the possible modern wild

377   population(s) of the graylag progenitor to domestic geese was not sampled in this study. It is also

378   worth remembering that using *A. cygnoid* reference genome may have caused a mapping bias of *A.*

379   *anser* alleles failing to map on the reference genome due to sequence divergence. This would have

380   affected the subsequent SNP calling by reducing the number of rare, derived *A. anser* alleles, which in

381   turn could cause our divergence time estimate to be an underestimate. Another thing to bear in mind

382   is the uncertainty about the mutation rate. The estimate we used by Pujolar *et al.* (2018) was

383   estimated for pink-footed goose which is a closely related to graylag goose and was supported by

384   Ottenburghs *et al.* (2016b) who obtained a similar substitution rate for geese. However, both

385   estimates are about two orders of magnitude higher than that estimated for collared flycatcher using

386   pedigree data (Smeds *et al.* 2016). It is possible that this is a taxon-related difference but in case the

387   substitution rate for graylag goose is actually closer to that of collared flycatcher, the mutation rate

388   we used here would be too high and our estimate of the domestication time would have to be pushed

389   even further back. Therefore, the estimated divergence time should be considered as a guideline for

390   future studies and not as an absolute truth. Future studies would benefit from whole genome

391   sequencing of graylag goose in resolving the questions about both mapping bias and the substitution

392   rate.

393   Given that genetic diversity would be expected to be highest in the 'domestication center' and

394   reduce with increasing distance from there, the high mtDNA diversity of Turkish domestic geese

395   means the eastern Mediterranean cannot be ruled out as a candidate for the origin of goose

396   domestication. However, as we have shown, hybridization between wild and domestic geese can also

397   generate high genetic diversity both within and outside the original domestication location. More

398   thorough sampling of the graylag population around the Black Sea would be beneficial in resolving the

399   role of eastern Mediterranean region in the domestication history of goose as this population was not

400   well represented in our study. Additionally, the progenitor of domestic geese could be sought by

401   ancient DNA approaches.

402   c)   The role of intra- and interspecific hybridization in goose domestication history

403   i.   Evidence of current hybridization

404 Domestic animals and their wild relatives are often observed to interbreed, and this is also true for

405 geese. Both field observations and mtDNA results (Kuijken and Devos 1996; Heikkinen *et al.* 2015)

406 suggested some current hybridization between domestic and graylag geese. Genome-wide analysis

407 covering multiple graylag populations and domestic breeds revealed a considerable impact of

408 hybridization on genetic diversity of both wild and domestic geese.

409   Hybridization is particularly prevalent in certain geographical regions. Dutch and especially

410 Turkish wild graylag samples had more shared genetic affiliation with domestics than Scandinavian

411 and Finnish graylag populations (Figure 3B). Some regions may offer more hybridization

412 opportunities, e.g. climate may allow graylags to be sedentary year-round and be favorable for

413 keeping domestic geese. The Netherlands, for instance, lies on the Atlantic flyway offering breeding,

414 staging, and wintering areas for graylags (Madsen *et al.* 1999; Andersson *et al.* 2001). Since pair-

415 bonding of geese generally occurs on wintering grounds (Rohwer and Anderson 1988), hubs for

416 migrating geese such as the Netherlands may permit population mingling. Nevertheless, the f_3 test did

417 not support a simple history of admixture for the Netherlands. Patterson *et al.* (2012) have stated that

418 population-specific drift may mask the signal of admixture in such analyses, leading to a non-negative

419 f_3. The f_3 model is relatively simple, with only two sources, and may not catch the signal of admixture

420 in the Dutch graylag population because of the previous contribution of *rubrirostris*, which was not

421 included in the model.

422   Based on ringing data most graylag populations in Scandinavia follow the Atlantic flyway - some

423 of the geese wintering in the Netherlands and others in southwest Spain. However, Finnish graylags

424 favor the Central European flyway and winter in North Africa, with a minority of Finnish graylags using

425 the Atlantic Flyway (Madsen *et al.* 1999; Andersson *et al.* 2001). The Finnish populations of graylag

426 showed the lowest admixture proportions with domestic geese (S-Finland 3.2% domestic goose, N-

427 Finland 3.3% domestic geese) among graylag populations. Rearing geese is not a popular practice in

428 Finland, and they constituted less than 5% of poultry kept in Finland in 2014 ("Official Statistics of

429 Finland (OSF): Number of livestock [e-publication]. Helsinki: Natural Resources Institute Finland

430 [referred: 17.12.2016]. Access method: http://www.stat.fi/til/klm/index_en.html" 2016). The

431 Norwegian populations showed only slightly higher admixture proportions with domestic geese,

432 although the domestic mtDNA haplotype ANS19 was detected from a wild graylag collected in

433 Finnmark, Norway (Pellegrino *et al.* 2015). This haplotype is a partial sequence of the D5 haplotype

434 identified by Heikkinen *et al.* (2015), and identical to that found in White Roman domestic geese

435 (Wang *et al.* 2010).

436   Inferring the hybridization patterns in the Turkish graylags is more complicated, as Turkish

437 graylags indicate hybridization with both Chinese and European domestics. Both graylags sampled in

438 Turkey showed considerable admixture with domestic geese. One of them appeared genetically as a

439 hybrid of European and Chinese domestic goose with only a small proportion of graylag ancestry,

440 whereas the other one was a more equal mix of European domestic goose and graylag supplemented

441 by a considerable Chinese domestic goose ancestry. However, what appears as a hybridization

442 between European and Chinese domestic geese may also be related to ancestral variation, and result

443 from close relatedness of the Turkish graylags to the graylag population that was domesticated,

444 reinforced by a gene flow from the Chinese domestic goose. There is some indication of hybridization

445 between graylags and domestic geese within that area as the domestic geese sampled from the same

446 area showed some admixture with graylags, but this was not confirmed with f_3 analysis. These results

447 may reflect a local practice of keeping captive graylags within a flock of domestic geese as several

448 sources state that it has been a common practice to collect wild eggs and goslings in many places

449 across Eurasia (Gray 1871; Honka *et al.* 2018). Another possibility is that the Turkish graylags have

450   hybridized with some unsampled distinct graylag population and simply appear genetically like

451   domestic geese due to lack of representation of the unsampled wild population. The graylag

452   population breeding and wintering in the Black Sea region is not well monitored (Fox *et al.* 2010).

453   ii.   Long-term hybridization

454   Domestication can be seen as an analogy of speciation where an animal population transforms to an

455   ecotype that is adapted to the human niche (Larson and Fuller 2014) and at later stages of

456   domestication is perpetuated with reproductive isolation in the form of selection managed by

457   humans (Zeder 2012). However, this reproductive isolation may not be complete (Frantz *et al.* 2015).

458   While the genetic divergence of the graylag and its domestic descendant is evident, our results

459   suggest extensive long-term genetic exchange between them. In addition, the demographic modelling

460   suggests that the gene flow patterns have changed over time.

461   Initially, gene flow was greater from domestic geese to graylag geese. It is unlikely that the early

462   stages of goose domestication were rigorously managed, allowing matings outside the domestic gene

463   pool. It is in the farmers' interest to keep the domestic geese and wild geese reproductively isolated

464   to keep control over the traits that are being selected, but artificial selection of traits would have

465   become possible only after the domestic gene pool had been established. After that, it may

466   occasionally be beneficial to restock the flock to maintain enough genetic diversity. Several sources

467   have suggested that it has been a common practice to collect goose eggs from the wild and raise

468   them in captivity. The natural tendency for imprinting in geese facilitates this practice. Goose-keeping

469   became well-established in the Medieval period (Albarella 2005) and the rise in number of domestic

470   geese may have allowed an increase in domestic goose escapees resulting in increased gene flow

471   ($N_e m$) from domestic geese back to graylags towards modern times.

472   Furthermore, not only have domestic geese admixed with wild graylags but also European and

473   Chinese domestic geese have hybridized. Hybridization with ancestral species or closely related

474   species is frequent in domestic species, e.g., the genetic composition of chicken derives from multiple

475   different species of *Gallus* (Eriksson *et al.* 2008). Similarly, the genetic composition of domestic geese

476   seems to derive from two closely related species. This hybridization with Chinese domestic geese may

477   have introduced some traits not present in graylags to European domestic geese and vice versa.

478   **5.   Conclusion**

479   This study is the first attempt to answer questions related to goose domestication history using

480   population genetic approach with genome-wide data. We have shown that hybridization has played

481   and continues to play a significant role in shaping the wild and domestic graylag populations.

482   Admittedly, the demographic models we used here were quite simple and they are unlikely to capture

483   every nuance of the population history, but they offer a starting point for future studies which may

484   include more elaborate analyses of demographic history, for example changes in effective population

485   size associated with population bottlenecks during domestication. Selection scans could be used to

486   identify introgressed alleles that have been under selection during domestication. The use of whole

487   genome sequencing would be advantageous in aforementioned analyses and would also enable

488   assessment of runs of homozygosity (ROH) in goose genome.

489   **Authors' contributions.**

490   MEH conceived the study, contributed to data collection, analyzed the data, and drafted the

491   manuscript. MR acquired the funding, conceived the study, and contributed to data collection. TAW

492   contributed to data collection and participated to data analysis. MMA and İG contributed to data

493   collection. KMD, JA, JBS and TP conceived the study and contributed to writing and interpretation of

data, with TP also participating in data analysis. All authors, excluding MR, reviewed, improved, and

approved the manuscript.

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Table 1. Hierarchical analysis of molecular variance (AMOVA) of graylags and their domestic descendants, considering pure populations of graylags (first group) and pure breeds of European domestic geese (second group).

| SOURCE OF VARIATION	SUM OF SQUARES	VARIANCE COMPONENTS	PERCENTAGE VARIATION	FIXATION INDICES
Among groups	47565.119	431.4291	15.8	$F_{CT} = 0.158^{**}$
Among populations and breeds within groups	82960.489	302.51404	11.1	$F_{SC} = 0.131^{**}$
Within populations and breeds	345889.821	2003.45893	73.2	$F_{ST} = 0.268^{**}$
Total	476415.429	2737.40207		

** $p < 0.001$

686 **Table 2.** Maximum likelihood estimates (MLE) for the parameters of the preferred demographic model for goose

687 domestication history (see text) with their 95% confidence intervals (CI).

| MODEL	PARAMETER	MLE	95% CI
Divergence with changing gene flow patterns	ANCSIZE	1112	378.95 - 7990.65
	T_1	5319	2014.45 - 6503.75
	$M1_{WD}$	4.25×10^{-4}	1.21×10^{-7} - 6.28×10^{-4}
	$M1_{DW}$	5.35×10^{-4}	2.88×10^{-4} - 6.45×10^{-4}
	T_2	159	88.9 - 476.25
	$M2_{WD}$	1.72×10^{-3}	1.30×10^{-3} - 2.23×10^{-3}
	$M2_{DW}$	6.69×10^{-4}	4.17×10^{-4} - 8.00×10^{-4}
	N_{WILD}	2504	2352.4 - 2680.25
	N_{DOM}	959	833.95 - 1040.55

ANCSIZE, effective population size of ancestral population; T_1, time of divergence in generations;

N_{DOM}, effective population size for domestic geese; N_{WILD}, effective population size for graylags; T_2,

estimate of time in generations when the migration matrix switched; $M1_{WD}$ migration rate from wild to

domestic following T_1; $M1_{DW}$ migration rate from domestic to wild following T_1; $M2_{WD}$ migration rate

from wild to domestic following T_2; $M2_{DW}$ migration rate from domestic to wild following T_2.

688
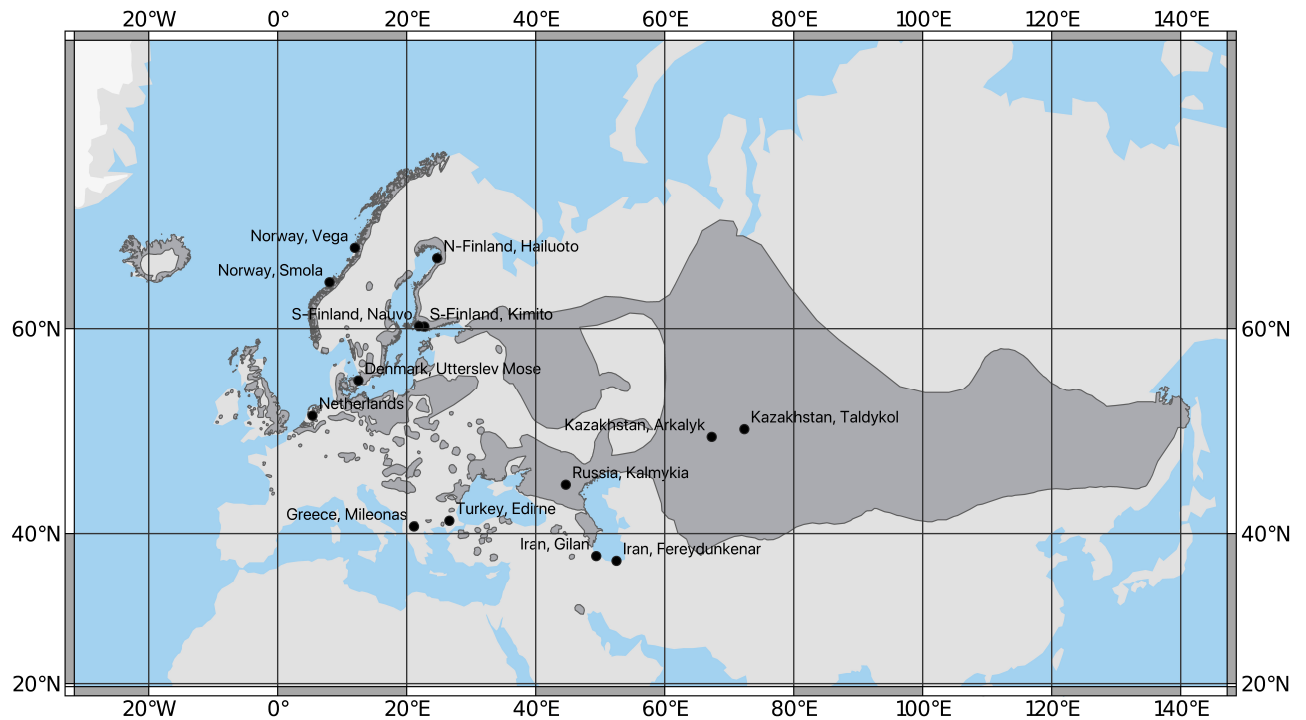
Figure 1. Map showing the sampling sites for wild graylags used in this study. The breeding area of the species is shown on darker grey. The sampling sites in Kazakhstan were combined for analyses (one sample per location) and the sampling sites in Southern Finland included combined samples from the geographically close sites of Västanfjärd, Nauvo (shown) and Kimito (shown). The Iranian samples were collected during the wintering season. Map modified from IUCN ("BirdLife International and Handbook of the Birds of the World (2016) 2016. *Anser anser*. The IUCN Red List of Threatened Species. Version 2018-1").

698
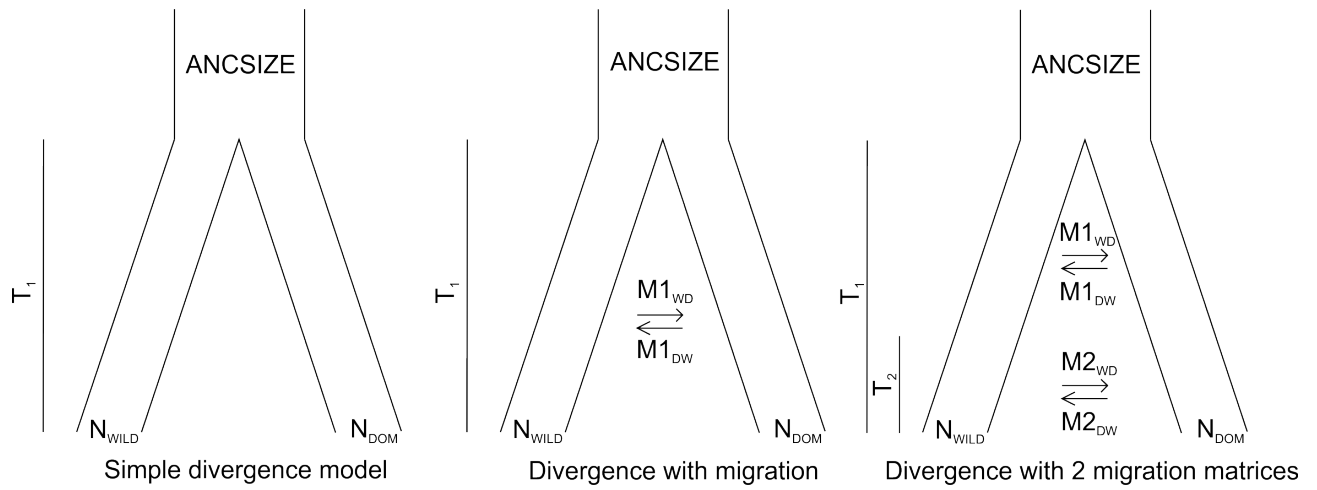
Figure 2. Demographic histories of goose domestication as tested with fastsimcoal2.

700
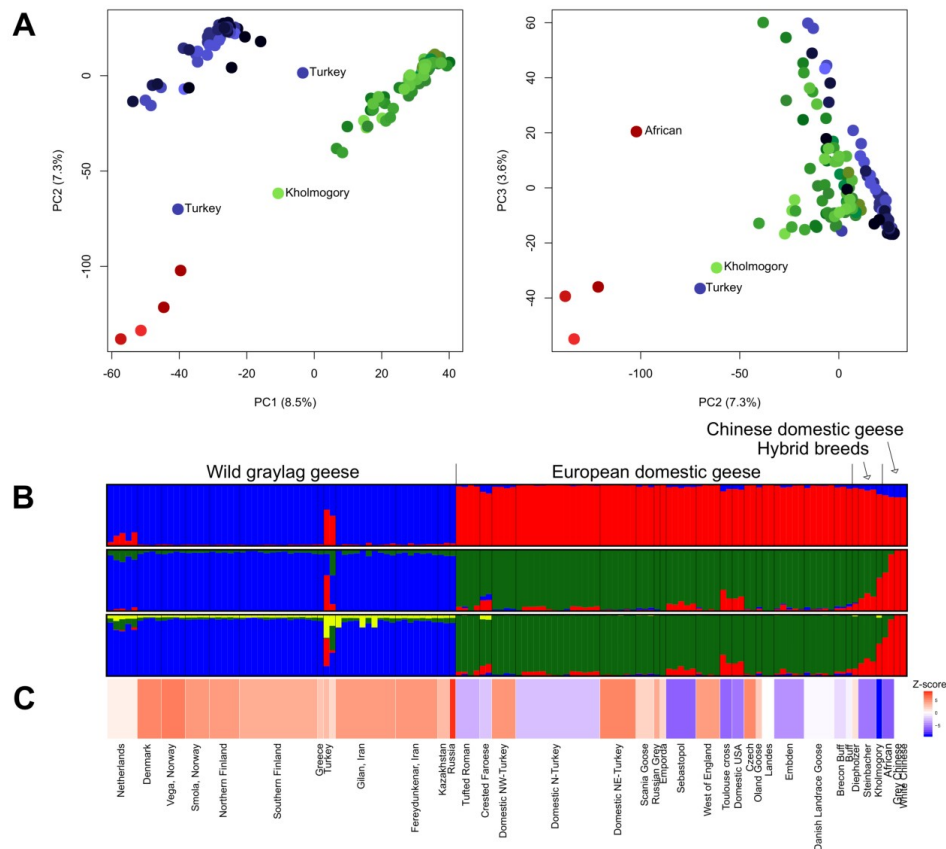
Figure 3. The genetic divergence and hybridization patterns in graylag and domestic geese. Population

status and names labelled as in Supplementary File 1, Table S1. The colors in A) and B) are associated

to different groups as follows: graylags (blue), European domestics (green) and Chinese domestics

(red). A) The first three principal components summarizing the genetic variation in geese (percentage

explained by each PC is shown). Different shades refer to different populations. B) STRUCTURE

assignment plots for $K = 2$, $K = 3$, and $K = 4$. Each vertical bar represents one individual with K number

of colors indicating proportion of ancestry from the inferred clusters, and populations/breeds are

separated by black vertical line. C) Plot relating to the f_3 (Supplementary File 1, Table S5) values

obtained for each population. Turkey refers to two adjacent bars in the plot since the Turkish graylags

were analyzed as two separate individuals. The more negative the f_3, the more significant is Z-score in

favor of admixture. The f_3 values were not calculated for Landes and the Chinese geese, as they were

used as source populations, thus they were given an f_3 value of 0.