ResearchGate

See discussions, stats, and author profiles for this publication at: http://www.researchgate.net/publication/237067060

Large-scale population genetic structure in Bonelli's Eagle Aquila fasciata

ARTICLE *in* IBIS · JULY 2013

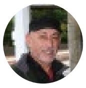
Impact Factor: 1.86 · DOI: 10.1111/ibi.12065

CITATION
1

DOWNLOADS
154

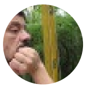
VIEWS
182

5 AUTHORS, INCLUDING:



Luis Palma
CIBIO Research Center in Biodiversity and …
29 PUBLICATIONS **269** CITATIONS
SEE PROFILE

M. Leonor Cancela
Universidade do Algarve
169 PUBLICATIONS **1,763** CITATIONS
SEE PROFILE



Pedro Beja
University of Porto
94 PUBLICATIONS **1,580** CITATIONS
SEE PROFILE

Available from: Pedro Beja
Retrieved on: 16 July 2015

Ibis (2013), 155, 485–498

Running head: Population genetic structure in Bonelli's Eagle

Large-scale population genetic structure in Bonelli's Eagle *Aquila fasciata*

Sara Mira,[1] Sophie Arnaud-Haond,[1,2] Luís Palma,[3] Maria Leonor Cancela [1,4] & Pedro Beja[3*]

[1]*Centro de Ciências do Mar, Universidade do Algarve, Campus de Gambelas, 8005-139 Faro, Portugal*

[2]*IFREMER, Centre de Brest, Department DEEP, BP70, 29280 Plouzané, France*

[3]*Centro de Investigação em Biodiversidade e Recursos Genéticos, Universidade do Porto, Campus Agrário de Vairão, 4485-661 Vairão, Portugal*

[4]*Department of Biomedical Sciences and Medicine, University of Algarve, Faro 8005-139 Faro, Portugal*

*Corresponding author.

Pedro Beja

E-mail: pbeja@mail.icav.up.pt

In bird species with high movement capacity, dispersal may connect local subpopulations over vast geographic regions, with important consequences for the design of conservation management strategies. Here we used a molecular approach to infer the patterns and rates of dispersal among eight Mediterranean subpopulations of the endangered Bonelli's Eagle, based on 245 individuals screened at 17 microsatellite loci. There was moderate genetic differentiation between subpopulations sampled in the western (Iberia and Morocco) and eastern Mediterranean (Cyprus), whereas differentiation among subpopulations in the former region was weak to moderate and followed a pattern of isolation-by-distance. Within the western Mediterranean, the small, peripheral and ecologically unique population of southwest Portugal had the lowest genetic diversity and the highest differentiation. The remaining subpopulations formed two loose clusters, including: (i) Morocco, and southwest and eastern Spain, and (ii) northeast Portugal, and western and central Spain. Few recent migrants were detected, and they originated primarily from adjacent subpopulations. Our findings suggest that western Mediterranean Bonelli's Eagles may have a large-scale metapopulation structure, with subpopulations connected to some extent by distance-dependent dispersal, probably influenced by natal philopatry and the geographical configuration of subpopulations. The matching of marked ecological and genetic divergence suggests that the peripheral subpopulation of southwest Portugal may be regarded as a distinct management unit.

Keywords: dispersal, ecological divergence, metapopulation, population fragmentation, philopatry

The spatial subdivision of once continuous populations due to human activity is considered one of the major contributors to species extinction (Fahrig 2003, Fischer & Lindenmayer 2007). Whereas subdivision may influence a population in diverse and complex ways, its long-term viability is often critically affected by dispersal among local subpopulations (Hanski 1999). Dispersal has direct demographic effects by influencing for instance, the probability of patch recolonization after local extinction, and the persistence of subpopulations through source-sink dynamics (Pulliam 1988, Hanski 1999). Further, dispersal influences long-term population viability through genetic effects, because restricted gene flow may lead to inbreeding depression and the loss of genetic diversity (Frankham *et al.* 2002).

In bird species with high movement capacity, dispersal has the potential to connect demographically and genetically local subpopulations separated by hundreds or even thousands of kilometres (e.g. Barlow *et al.* 2011, Geraci *et al.* 2012), with important consequences for the design of conservation management strategies (e.g. Martínez-Cruz *et al.* 2004, Alcaide *et al.* 2009). Quantifying dispersal in these species is challenging, however, often requiring large-scale and long-term studies based on laborious and expensive capture-recapture techniques (Stenseth & Lidicker 1992). To circumvent this problem, molecular approaches associated with powerful statistical techniques have increasingly provided a practical alternative with which to investigate dispersal (Broquet & Petit 2009). The spatial distribution of genetic diversity and differentiation among subpopulations has been used to infer the rates and patterns of historical gene flow, which in turn provide clues to understand how dispersal is affected by geographical, ecological and behavioural factors (Martínez-Cruz *et al.* 2004, Banks *et al.* 2005, Callens *et al.* 2011). Analyses based on individual multilocus genotypic data have also enabled estimation of contemporary migration rates, and the identification of migrants and their most likely origins (Taylor *et al.* 2007, Lancaster *et al.* 2011). Although all these approaches have some limitations because different population-level processes may result in similar genetic patterns (Broquet & Petit 2009), they may still provide useful information to support conservation management practices, particularly if genetic inferences are combined with life-history and demographic data (Banks *et al.* 2005, Alcaide *et al.* 2009, Callens *et al.* 2011).

Bonelli's Eagle *Aquila fasciata* is an endangered species in Europe (BirdLife International 2004), where it shows a marked pattern of large scale population subdivision (Ferguson-Lees & Christie 2001, Del Moral 2006), requiring improved information on dispersal patterns to guide ongoing conservation efforts (Soutullo et al. 2008, Hernández-Matías *et al.* 2010). In the Western Palaearctic, Bonelli's Eagles are mainly restricted to the Mediterranean region, with roughly 80% of European breeding pairs in the Iberian Peninsula (Del Moral 2006). The European population declined from the 1970s to the early 1990s, though at present the main subpopulations seem to be relatively stable or even increasing (Real & Mañosa 1997, Soutullo *et al.* 2008, Beja & Palma 2008, Carrascal & Seoane 2009a). In the Iberian Peninsula, Bonelli's Eagles appear to have a metapopulation structure (e.g. Soutullo *et al.* 2008), with a large proportion of breeding pairs in the core subpopulations of the Spanish Extremadura and Andalucia, surrounded by smaller and peripheral subpopulations in Portugal, and Eastern and Northern Spain (Del Moral 2006, Equipa Atlas 2008).

Connectivity among all subpopulations has often been assumed to be high (Soutullo *et al.* 2008), due to the large-scale dispersal capacity of individuals (Real & Mañosa 2001, Cadahía *et al.* 2010), and to the observation of territorial recruitment sometimes occurring hundreds of kilometres from an individual's place of birth (Cheylan *et al.* 1996, Cadahía *et al.* 2009, Hernández-Matías *et al.* 2010). However, dispersal may be behaviourally restricted because most individuals tend to breed close to their subpopulation of origin (i.e. exhibit natal philopatry; Greenwood & Harvey 1982), though females disperse farther than males (Cheylan *et al.* 1996, Hernández-Matías *et al.* 2010). Previous studies based on mtDNA showed no differentiation among Western Mediterranean subpopulations (Iberia and NW Africa), suggesting that the levels of gene flow may be sufficiently high to preclude the development of local genetic structure (Cadahía *et al.* 2007). However, the resolution of the study was limited because it used a single locus and the detected polymorphism was low (four haplotypes). Moreover, mitochondrial DNA is maternally inherited and thus it is only affected by female dispersal behaviour.

In this study we used 17 autosomal microsatellite loci in a variety of genetic analyses to test expectations regarding dispersal patterns among Bonelli's Eagle subpopulations in the Mediterranean region. If effective dispersal among all Bonelli's Eagle subpopulations is large and essentially unconstrained by distance, as assumed in earlier studies (Soutullo *et al.* 2008), then the entire population should be panmictic (Wright 1943, Kimura & Maruyama 1971). However, if dispersal is constrained by distance due for instance to philopatric behaviour, then geographical distance would be associated with a certain degree of local differentiation and there might be a pattern of isolation by distance (Wright 1943, Kimura &

Maruyama 1971). Furthermore, recent migrants detected in a population should be few and originate primarily from neighbouring populations. Finally, if effective dispersal and thus gene flow are very low, differentiation would be expected in the metapopulation system, and differences should be most pronounced in small and peripheral subpopulations (Eckert *et al.* 2008).

METHODS

Study species

The Bonelli's Eagle is a long-lived bird of prey (maximum age of reproduction: 25 years; Real & Mañosa 1997), with deferred maturity (age of first successful breeding: 4 years; Soutullo *et al.* 2008), relatively low fecundity (mean number of fledglings per breeding pair: 0.6-1.4; del Moral 2006), and high adult survival (annual adult survival rate: 87.1%-96.7%; Soutullo *et al.* 2008). Generation length varies across subpopulations, but is between about 9 and 13 years (estimated from demographic parameters in Real & Mañosa 1997, Soutullo *et al.* 2008). Breeding individuals are territorial, and show strong pair-bonding and high tenacity to the breeding territory within and between years (Bosch *et al.* 2010). However, after fledging there is a transient nomadic phase before territorial recruitment, during which individuals range widely over hundreds to thousands of kilometers (Balbontín & Ferrer 2009, Cadahía *et al* 2009, 2010). In a sample of Bonelli's Eagles marked as nestlings, territorial recruitment occurred primarily within or close to the natal subpopulation, with mean distance (±SD) from birthplace to the breeding territory of 136.9 ± 127.8km (23-430 km; n = 22) for females, and 72.6 ± 60.9 km (19-239 km; n = 19) for males (recalculated from Hernández-Matías *et al.* 2010).

Sampling and microsatellite genotyping

Blood samples from 245 Bonelli's Eagle nestlings were collected in the Iberian Peninsula, NW Africa (Morocco) and Cyprus (Table 1, Fig. 1). Samples within the Western Mediterranean were considered representative of seven subpopulations (Fig. 1), identified on the basis of regional clusters of breeding territories largely separated by distribution gaps (Del Moral 2006). Three of these (Western and Southwest Spain, and Morocco) contain the largest number of individuals, whereas the remaining subpopulations are much smaller and geographically peripheral to the core subpopulations. All these subpopulations were relatively close to each other (< 1000 km) and within the range of movements undertaken by immature Bonelli's Eagles during the transient nomadic phase (Balbontín & Ferrer 2009; Cadahía *et al.* 2009, 2010). In contrast, Cyprus was far from the Western Mediterranean populations (> 3000 km), with major discontinuities in the species distribution between the two localities (Ferguson-Lees & Christie 2001).

All samples were preserved in Queen's lysis buffer (Seutin *et al.* 1991) until DNA extraction and further laboratorial analysis. DNA was extracted using a blood extraction Kit from Amersham-Pharmacia. DNA was diluted to a final approximate concentration of 10 ng/µL. All individuals were genotyped for a total of 17 microsatellite loci, of which 14 were specifically developed for the Bonelli's Eagle (Mira *et al.* 2005) and three were designed for the Spanish Imperial Eagle *Aquila adalberti* (Martinez-Cruz *et al.* 2002). PCR-amplification was carried as described by Mira *et al.* (2005).

Genetic Variation

Bonelli's Eagle samples were obtained from 140 different breeding territories (Table 1), with some nests yielding up to two nestling samples in a given year, and some breeding territories yielding nestling samples over several years. The overall sample thus included an unknown proportion of siblings and half-siblings, which might bias the allele frequencies and consequently the statistical estimators (Ruzzante 1998). Because of this, instead of the overall sample (n = 245) we have used ten subsets of individuals from different territories, each with 140 individuals selected by randomly taking a single nestling from each breeding territory. Each genetic analysis was carried out independently for each of the ten subsets and results were then averaged across the ten subsets to obtain the overall estimates. Basing analysis on individuals from different territories was judged to overcome eventual bias due to kinship, as preliminary analysis using Queller and Goodnight's (1989) genetic estimate of relatedness, R, and the software SPAGeDI (Hardy & Vekemans 2002), indicated that within each population the mean relatedness between nestlings from different territories was negligible (mean $R < 0$ for all populations; Table S1), and thus we contend that our sampling scheme could be used for further genetic analyses.

Average allelic richness, average observed heterozygosity (H_O), and unbiased average expected heterozygosity (H_E; Nei 1978), were estimated within each subpopulation using

GENETIX 4.05 (Belkhir *et al.* 2004). Estimates of allelic richness using rarefaction were computed with HP-RARE 1.0 (Kalinowski 2005) for a rarefaction size equal to the minimum sample obtained (n = 6; Cyprus and Central Spain). Departure from Hardy-Weinberg equilibrium within each population was assessed with F_{IS}, estimated with f (Weir & Cockerham 1984), followed by a permutation test (10^4 permutations) of the null hypothesis of random mating (H_0: $F_{IS} = 0$) implemented in GENETIX (Belkhir *et al.* 2004). Linkage disequilibrium was also tested with GENETIX. To control for multiple comparisons, we used Storey and Tibshirani's (2003) *q*-value method for estimating the False Discovery Rates (FDR) from the distribution of *P*-values. To obtain a FDR of 5% in multiple testing, a *P*-value was considered significant at the 5% level only when the *q*-value was also ≤ 5% (Storey & Tibshirani's 2003).

Population genetic structure

The distribution of individuals among *a priori* subpopulations was first visualised with Factorial Correspondence Analysis (FCA) implemented in GENETIX. Levels of differentiation between subpopulations were then quantified with the widely used F_{ST} estimator θ (Weir & Cockerham 1984), and significant departures from H_0 of no differentiation were tested with the permutation (10^4 permutations) procedure implemented in GENETIX (Belkhir *et al.* 2004). In order to limit bias in this estimator due to a possible unbalanced distribution of polymorphism among populations, we also compared results with those obtained using the D_{est} (Jost 2008) estimator, corrected for the level of polymorphism, with statistical significance tested using the bootstrap resampling procedure ($2x10^4$) implemented in the package DEMEtics (Gerlach *et al.* 2010) for R (R Development Core Team 2012).

Isolation by distance (IBD) was assessed by correlating the pairwise estimates of $F_{\text{ST and}}$ D_{est} with geographical distances between subpopulations using the Mantel (1967) test implemented in GENETIX (10^4 randomizations). A similar analysis was carried out at the individual level using Queller and Goodnight's (1989) coefficient of relatedness, and relating pairwise relatedness to geographical distances with the permutation procedure (10^4) implemented in SPAGeDI (Hardy & Vekemans 2002). Because the exact location of many nests was unavailable, distances were always computed considering the geographical centre of each population. Cyprus was excluded from analyses since it was too far away from the remaining populations, whereas Morocco was excluded due to uncertain provenance of individuals.

To examine the extent to which *a priori* geographically defined subpopulations actually corresponded to genetic units, we used the Bayesian clustering method implemented in STRUCTURE 2.3.1 (Pritchard *et al.* 2000, Falush *et al.* 2003). Analysis assumed the admixture model with α inferred from the data, and correlated allele frequencies with $\lambda = 1$ (Falush *et al.* 2003, Pritchard & Wen 2004), and were based on Markov chain Monte Carlo (MCMC) sampling with 2×10^5 iterations, following a burn-in period of 10^5 iterations. Information on the geographical location of individuals was used as recommended by Hubisz *et al.* (2009), which allows structure to be detected at lower levels of divergence. Ten independent runs of STRUCTURE were performed for each *K*-value from one to nine. The optimal number of genetic units (*K*) was selected by considering for each value of *K* the log-likelihood given the number of clusters (Ln $P(X|K)$ and the standardized second order rate ΔK of change of Ln $P(X|K)$ (Evanno *et al.* 2005). Although the latter approach has been criticised, it may still provide useful estimates when populations deviate from the finite island model, as for instance in the case of hierarchically structured populations (Waples & Gaggiotti 2006).

STRUCTURE was also run using a hierarchical procedure, to investigate whether dominant genetic structure could be hiding fine scale genetic structure (Evanno *et al.* 2005). The procedure started by running a first round of STRUCTURE using the overall sample, and then selecting the optimal number of genetic units using the Δ*K* approach (Evanno *et al.* 2005). At this stage, subpopulations clustering as a single genetic unit with membership probability > 0.90 were excluded from further analysis, and a second run of STRUCTURE was performed on the individuals from each genetic unit including more than one subpopulation. The procedure was repeated until no further subpopulation could be identified as a distinct genetic unit. Outputs of STRUCTURE were visualised and the Evanno *et al.* (2005) method implemented using HARVESTER (Earl & vonHoldt 2012).

Recent dispersal

To estimate the recent exchange of individuals between genetic population units identified by STRUCTURE, we used assignment tests which allocate each individual to the population from which its multilocus genotypes was most likely to be derived (Waser & Strobeck 1998), using ARLEQUIN (Excoffier *et al.* 2005). As sampling was based on nestlings, the population of birth of each individual was known without error. Therefore, assignment of an individual to a population different from the one where it was sampled was taken to indicate a foreign origin of at least one of its parents.

Recent migration rates (last two generations) were also estimated using the Bayesian approach implemented in BAYESASS 3.0 (Wilson & Rannala 2003). The program was run using a large number of MCMC iterations (> 10^7), a burn-in of 10^6, and a sampling frequency of 10^3. To assure consistent and accurate estimates, several runs were started with different random number seeds, and MCMC chains were examined for evidence of convergence and mixing using TRACER (Rambaut & Drummond 2004). When there were inconsistent estimates or convergence problems, analysis were repeated using longer runs and by using different random seed numbers.

RESULTS

Properties of microsatellite loci

In total, 123 alleles were detected across 17 microsatellite markers and 245 birds genotyped (Table S2). The number of alleles per locus in the overall sample varied from two to 22, with an average of 7.2 alleles per locus. The observed and expected heterozygosities were the lowest for the populations from southwest Portugal and Cyprus (Table 1). Mean allelic richness was also the lowest for these two subpopulations after correcting for differences in sample size (Table 1).

Linkage disequilibrium tested on 136 pairs of loci at the level of each subpopulation, only indicated statistically significant departures from independent segregation after correcting for multiple comparisons (FDR < 0.05) in one and seven pairs of loci, for southwest Portugal and eastern Spain, respectively. Since the linked loci were inconsistent among populations, these findings suggest statistical rather than physical linkage, and thus all loci were used in subsequent analyses. The only inbreeding coefficient (F_{IS}) significantly different from zero at FDR < 0.05 was found for the population from western Spain (Table 1), suggesting a significant departure from Hardy-Weinberg equilibrium.

Population genetic structure

Factor correspondence analysis (FCA) highlighted strong differentiation between eastern (Cyprus) and western Mediterranean populations (Fig. 2). In a second analysis that excluded Cyprus, there was evidence for sharp differentiation of Bonelli's Eagles from southwest Portugal, with most individuals occurring in a cluster well separated from the other Iberian and North African populations (Fig. 2). Individuals from the remaining populations clustered close to each other, with some clinal variation apparent from north to south (Fig. 2).

The F_{ST} and D_{est} estimators were highly correlated (r= 0.96, $P < 0.001$), though D_{est}-values were consistently larger than F_{ST} -values (Table 2). Both estimators pointed out significant differentiation among all subpopulations after correcting for multiple comparisons (FDR < 0.05), particularly between the population from Cyprus and those sampled in the western Mediterranean (Table 2). The subpopulation of southwest Portugal also showed marked differentiation from the remainder, whereas differentiation among the other subpopulations was relatively low, albeit statistically significant for all pairwise comparisons (Table 2).

Genetic and geographical distances between populations were significantly correlated, for both F_{ST} (Mantel test: $r = 0.56$, $P = 0.005$) and D_{est} (Mantel test: $r = 0.43$, $P = 0.038$) estimators. However, differentiation observed in relation to the subpopulation of southwest Portugal showed consistent positive deviations from the isolation-by-distance trend lines, whereas the opposite was found for comparisons involving the other populations (Fig. 3; Fig. S1). When the population of southwest Portugal was removed from analysis there was an increase in the correlation between genetic and geographical distances for both F_{ST} (Mantel test: $r = 0.66$, $P = 0.008$) and D_{est} (Mantel test: $r = 0.56$, $P = 0.055$), though P-values were larger due to smaller sample sizes. In contrast to analyses at the population level, pairwise relatedness between individuals of different populations was not significantly related to geographic distance ($r = 0.054$, $P > 0.85$; Fig. S2).

In the first round of STRUCTURE, Ln $P(X|K)$ increased up to $K = 4$ and then levelled off, whereas ΔK peaked for $K = 2$, though showing a second, smaller peak for $K = 4$ (Fig. 4). At $K = 2$ the analysis separated nestlings from southwest Portugal (group membership probability = 0.954) from those of the other seven subpopulations (0.966). At $K = 4$, the analysis separated the subpopulations of Cyprus and southwest Portugal as clearly distinct genetic units (Fig. 1). The other two clusters were less clearly defined: one cluster included most of the individuals sampled from the coastal Mediterranean regions of Spain and North Africa (Morocco, and southwest and eastern Spain), and the other including most individuals sampled from the Central Iberian Peninsula (northern Portugal and western and central Spain) (Fig. 1). The Central Iberian group included about 20% of the genotypes from the coastal Mediterranean group, particularly from southwest and eastern Spain, but the reverse was not observed (Fig. 1). A second round of analyses excluding southwest Portugal returned $K = 3$ (Fig. S3), confirming the separation of Cyprus, central Iberian and coastal Mediterranean subpopulations. The third round of analysis excluding Cyprus returned $K = 2$, separating the central Iberian and coastal Mediterranean subpopulations (Fig. S4).

Recent dispersal

In assignment tests, all nestlings from southwest Portugal and Cyprus were assigned to their subpopulation of origin, thus indicating that their parents were also from the same subpopulations. Further, no nestling sampled from a different subpopulation was assigned to either southwest Portugal or Cyprus, thus pointing to few or no recent exchanges of individuals from these subpopulations with other subpopulations. In contrast, there was evidence of recent movements between the coastal Mediterranean and central Iberian populations, with 1.8% of the nestlings sampled in the former assigned to the latter, and 6.1% of those sampled in the latter assigned to the former. Foreign assignments were mostly recorded in the subpopulation from western Spain.

Inferences on recent migration rates using BAYEASS could not be drawn, as there were inconsistencies among runs and the analysis did not converge. Detailed analysis of the sampling of the MCMC chains using TRACER indicated that BAYEASS was particularly poor in resolving directional migration rates between coastal Mediterranean and central Iberian subpopulations, with posterior probability distributions often showing bimodality.

DISCUSSION

This study revealed moderate genetic differentiation between western and eastern Mediterranean subpopulations of the Bonelli's Eagle, that are separated by geographical distances well beyond the known dispersal range of individuals (Real & Mañosa 2001, Balbontín & Ferrer 2009, Cadahía *et al.* 2009, 2010). Within the western Mediterranean there was weak to moderate differentiation among subpopulations located relatively close to each other, which is inconsistent with earlier views that dispersal is pronounced and essentially unconstrained by distance (Soutullo *et al.* 2008). Instead, the observed levels of differentiation and the pattern of isolation-by-distance are consistent with the presence of distance-dependent dispersal**.** This is also supported by the detection of very few recent migrants, which originated primarily from neighbouring subpopulations. Although distance seemed to constrain dispersal, gene flow appeared to be sufficiently high to preclude major differentiation in the metapopulation system. Nonetheless, the pronounced differentiation of the southwest Portugal population is consistent with the expectation of particularly reduced gene flow in geographically peripheral subpopulations. Our findings are in line with other studies suggesting that population subdivision may have negative consequences, even for species with a very high dispersal capacity, which may be most pronounced in the case of small and geographically isolated subpopulations (Martínez-Cruz *et al.* 2004, Alcaide *et al.* 2009).

Spatial population structure: current versus historical processes

The current patterns of genetic structure observed in western Mediterranean Bonelli’s Eagles may be a consequence of a long-standing pattern of distance-dependent dispersal or may be due to recent anthropogenic habitat fragmentation coupled with demographic decline and genetic drift (e.g. Martínez-Cruz *et al.* 2007). Although there is at present little evidence to support either hypothesis, the information available suggests that historical rather than recent processes may underlie the patterns observed. First, although many Bonelli’s Eagle subpopulations suffered a marked demographic decline, those analysed in the present study showed no evidence for genetic bottlenecks (Mira 1996), probably because the population reduction was recent, the population size remained relatively high, and the species long generation time provided a buffer against the genetic effects of population fluctuations (Hailer *et al.* 2006, Brown *et al.* 2007). Second, there is no evidence for recent reductions in population connectivity, as no major changes in the range and spatial configuration of Bonelli’s Eagle subpopulations have been reported during the last decades (del Moral 2006). Third, in comparable long lived species, as for instance the Spanish Imperial Eagle *Aquila adalberti*, genetic structure resulting from anthropogenic processes was associated with demographic declines and fragmentation levels that were older and far more pronounced than those observed in the Bonelli’s Eagle (Martínez-Cruz *et al.* 2004, 2007). Despite this reasoning, it cannot be ruled out that recent anthropogenic processes affected contemporary genetic structure, particularly in small and peripheral populations that are prone to genetic drift (Martínez-Cruz *et al.* 2004, 2007, Alcaide *et al.* 2009). Clarifying these issues would require a more detailed analysis of the demographic trend and history of the Bonelli’s Eagle (e.g. Martínez-Cruz *et al.* 2007).

Distance dependent dispersal was inferred from the pattern of isolation-by-distance among Bonelli’s Eagle subpopulations, and by the observation that recent migrants were few in each subpopulation and originated primarily from neighbouring subpopulations. In contrast, pairwise relatedness between individuals sampled in different subpopulations was not correlated with distance, but this was probably because their true relatedness was inevitably low (they could at most be cousins, i.e. born from two brothers breeding in different subpopulations), and because kinship estimates based solely on genetic data are often imprecise (Van Horn *et al.* 2008). Taken together, these results are consistent with mark-recapture and satellite tracking studies pointing to natal philopatry in the Bonelli’s Eagle, with most individuals breeding within or close to their natal subpopulation (Cheylan *et al.* 1996, Hernández-Matías *et al.* 2010), despite the occurrence of a few recruitment events hundreds of kilometres from the individual's birthplace (Cheylan *et al.* 1996, Balbontín & Ferrer 2009, Cadahía *et al.* 2009, Hernández-Matías *et al.* 2010). These long-distance recruitments likely precluded strong divergence among subpopulations, though they were probably sufficiently rare to maintain the observed levels of genetic differentiation and isolation-by-distance (Wright 1943, Kimura & Maruyama 1971), as observed in other philopatric species with high mobility (Alcaide *et al.* 2009, Barlow *et al.* 2011).

The hypothesis of philopatry contributing to maintain small to moderate levels of genetic differentiation between spatially disjunct subpopulations is not incompatible with the apparent homogeneity of the mitochondrial control region in western Mediterranean Bonelli’s Eagles (Cadahía *et al.* 2007), as differences between the patterns derived from mtDNA and microsatellites are widespread in birds (e.g. Brito 2007, Hull *et al.* 2008b). Female-biased dispersal in the Bonelli's Eagle (Hernández-Matías *et al.* 2010), might have contributed to homogenize allele frequencies of maternally inherited mitochondrial markers over large geographical regions, while retaining the signature of distance-dependent dispersal in autosomal markers. It is more likely, however, that failure to detect spatial structure was due to the low diversity (four haplotypes) of this marker reducing the statistical power to detect genetic differentiation. As gene flow among populations appeared to be moderate, genetic structure was probably only detectable at the fine resolution allowed by a large number of microsatellites.

Geographical population configuration: effect on genetic diversity and gene flow

Geographical patterns of population configuration also seemed to play a role in the genetic patterns observed, probably because they resulted in some clusters of populations exchanging individuals more often among themselves than with other clusters. This was the case of subpopulations located along the Mediterranean coastal regions of the Iberian Peninsula (southwest and northeastern Spain) and northwestern Africa (Morocco), which are close to each other and emerged as a consistent genetic unit in the STRUCTURE analyses. This clustering suggests that there may be some exchange of individuals across the Mediterranean, though larger sample sizes from northwestern Africa would be needed to confirm this hypothesis. Although this exchange has not been directly observed (Cheylan *et al.* 1996, Real & Mañosa 2001, Balbontín & Ferrer 2009, Cadahía *et al.* 2009, 2010, Hernández-Matías *et al.* 2010), it should be expected given the close proximity of subpopulations on either side of the Strait of Gibraltar. Another genetic cluster emerging from the STRUCTURE analyses included most individuals from northeast Portugal, and western and central Spain. In this central Iberian cluster there was a significant representation of genotypes from the Mediterranean cluster, most pronounced in the populations of central and, to a much lesser extent, western Spain. This pattern is suggestive of an asymmetrical exchange of individuals between the two clusters. Asymmetrical migration was supported by assignment tests and it is in line with recent metapopulation models suggesting that the Bonelli's Eagle population in southwest Spain is a source of colonists for western and central Spain (A. Hernández-Matías, Pers. Comm.). Unfortunately, this pattern could not be further explored due to the unreliable estimates of recent migration rates provided by BAYESASS, possibly because the estimation method fails when genetic differentiation is too low and migration rates are too high (Faubet *et al.* 2007).

The geographical position of the small subpopulation of southwest Portugal (< 20 breeding females in 1990; Beja & Palma 2008) in the periphery of the core species range, probably contributed to its low genetic diversity and high divergence in relation to other subpopulations. In fact, these patterns are consistent with the expectations of increased genetic drift and reduced gene flow in small and peripheral subpopulations in a metapopulation system (Eckert *et al.* 2008), as already observed for other birds of prey with high movement capabilities (Martínez-Cruz *et al.* 2004, 2007, Alcaide *et al.* 2009). It is noteworthy, that similar patterns of high genetic divergence from the remaining populations of the Iberian Peninsula have been reported for a range of vertebrates inhabiting southwest Portugal, some of which have been recognised as highly circumscribed endemic taxa (e.g. Mesquita *et al.* 2005, Godinho *et al.* 2008, Gonçalves *et al.* 2009). Divergence of these populations is generally associated with the emergence of the Caldeirão

Mountains in the Lower Pliocene (3.4 to 5.3 Ma) (Gonçalves *et al.* 2009), which is probably much older than the process promoting genetic divergence of the Bonelli's Eagle subpopulations inhabiting the same region, as suggested by its lack of mtDNA differentiation (Cadahía *et al.* 2007). In both instances it may be argued that the remote geographical position of these mountains, located at the south-westernmost tip of the Iberian Peninsula and thus partially surrounded by the sea, and the relatively large habitat gap in relation to other mountain ranges with comparable environmental conditions, may be factors limiting gene flow and thus promoting genetic differentiation even in the case of a highly mobile species. Clearly, it would be interesting to investigate whether similar patterns of genetic differentiation occur in other bird species that also show rather isolated populations in the same region.

Together with the effects of small population size and peripheral geographical position, ecological divergence may also have played a role in the genetic pattern observed in Bonelli's Eagles from southwest Portugal, as suggested for other wide ranging species (Stenseth *et al.* 2004, Musiani *et al.* 2007, Sacks *et al.* 2008), including birds of prey (Hull *et al.* 2008a). The subpopulation of southwest Portugal is ecologically unique in that it is dominated by the behaviour of individuals nesting in trees (Palma *et al.* 2006), whereas individuals from the remaining subpopulations predominantly nest on cliffs (Carrascal & Seoane 2009b). In these circumstances, an eventual behavioural imprinting to the natal nest type might contribute to non-random dispersal (Davis & Stamps 2004), and thus to some reproductive isolation between ecotypes (Beltman & Metz 2005). Restricted dispersal between populations with contrasting nest-site selection patterns has long been hypothesised in birds of prey (Fox 1995), particularly in the case of cliff and tree-nesting Peregrine Falcons *Falco peregrinus* (e.g. Wegner *et al.* 2005). This hypothesis requires further testing, because in birds of prey the extent of imprinting to the fledging site may vary widely (e.g. Tordoff *et al.* 1998, Mannan *et al.* 2006, Rutz *et al.* 2008), and the information available to support a link between nesting habitat divergence and reproductive isolation remains scarce and ambiguous (Nesje *et al.* 2000, Hull *et al.* 2008a, Riegert *et al.* 2010).

Conservation implications

Despite recent positive trends in some subpopulations, the conservation of Bonelli's Eagle remains a high priority (Del Moral 2006). Findings from this study confirm the view that management of Bonelli's Eagles should assume a metapopulation structure (Real & Mañosa 1997, Soutullo *et al.* 2008), with distance-dependent dispersal between spatially discrete subpopulations, and occasional recruitment hundreds of kilometres from an individual's natal site (Cheylan *et al.* 1996, Cadahía *et al.* 2009, Hernández-Matías *et al.* 2010). Furthermore, the study suggests that the geographical scale of this metapopulation may be larger than usually assumed (Real & Mañosa 1997, Soutullo *et al.* 2008), given the possible exchange of individuals between the Iberian Peninsula and northwestern Africa. These results have fundamental consequences for the development of demographic models, and thus to the design of conservation management strategies. For instance, the assumption of an equal probability of individuals dispersing to any subpopulation, including the natal one, was incorporated into a recent metapopulation model for the Bonelli's Eagle, which suggested that pre-adult mortality plays a key role in determining overall population trends

(Soutullo *et al.* 2008). This result is in marked contrast to earlier demographic models that assumed local subpopulations to be isolated, concluding that adult mortality had the largest impact on population growth rate (Real & Mañosa 1997). The two results have distinct conservation implications, because adult and pre-adult Bonelli's Eagles often have disjunct spatial distributions and require distinct management actions (Real *et al.* 2001, Cadahía *et al.* 2010). New modelling exercises focusing on the entire Bonelli's Eagle metapopulation and accounting for distance-dependent dispersal are thus needed to strengthen conservation prescriptions.

The association of high genetic and ecological divergence in Bonelli's Eagles from southwest Portugal merits particular attention due to the conservation implications. This is one of the few subpopulations in western Europe that is increasing and expanding into neighbouring regions (Beja & Palma 2008), with preliminary mark-recapture and genetic data suggesting that individuals from this population are occupying forested and agricultural landscapes that would be unavailable to cliff-nesting individuals (L. Palma, P. Beja, R. Godinho & N. Ferrand, Unpubl. Data). Results thus suggest that this population may need to be regarded as a distinct management unit, though further research is still required to assess the extent to which ecological divergence is actually contributing to reduce gene flow with the remaining, cliff-nesting populations (Crandall *et al.* 2000, Fraser & Bernatchez 2001).

This study was partly supported by the Portuguese Science and Technology Foundation (FCT), through project PRAXIS/BIA/132/96 and a PhD grant to SM (SFRH/BD/3163/2000). Eagle nestlings were handled with permission from the authorities of each country. We grateful for the help with collecting Bonelli's Eagle samples by Bárbara Fráguas, Carlos de La Cruz, Ernesto Ferreiro, Juan Negro, Luis Cadahía, Savvas Iezequiel and Ursula Höfle, the help with data analysis by Mário Ferreira, and the critical reading of the manuscript by Joan Real, Christian Rutz, Benjamin Sacks, Hugo Rebelo, Rauri Bowie, Jérôme Fuchs, and three anonymous referees.

REFERENCES

Alcaide, M., Serrano, D., Tella, J.L. & Negro, J.J. 2009. Strong philopatry derived from capture–recapture records does not lead to fine-scale genetic differentiation in lesser kestrels. *J. Anim. Ecol.* **78**: 468-475.

Balbontín, J. & Ferrer, M. 2009. Movements of juvenile Bonelli's Eagles *Aquila fasciata* during dispersal. *Bird Study* **56**: 86-95.

Banks, S.C., Lindenmayer, D.B., Ward, S.J. & Taylor, A.C. 2005. The effects of habitat fragmentation via forestry plantation establishment on spatial genotypic structure in the small marsupial carnivore, *Antechinus agilis*. *Mol. Ecol.* **14**: 1667-1680.

Barlow, E.J., Daunt, F., Wanless, S., Álvarez, D.A., Reid, J.M. & Cavers, S. 2011. Weak large-scale population genetic structure in a philopatric seabird, the European Shag *Phalacrocorax aristotelis Ibis* **153**: 768-778.

Belkhir, K., Borsa, P., Chikhi, L., Raufaste, N. & Bonhomme, F. 2004. GENETIX 4.05, logiciel sous Windows TM pour la génétique des populations. Laboratoire Génome, Populations, Interactions, CNRS UMR 5000, Université de Montpellier II, Montpellier, France. Available at: http://www.genetix.univ-montp2.fr/genetix/intro.htm.

Beltman, J.B. & Metz, J.A.J. 2005. Speciation: more likely through a genetic or through a learned habitat preference? *Proc. Roy. Soc. Lond. B* **272**: 1455-1463.

Beja, P. & Palma, L. 2008. Limitations of methods to test density-dependent fecundity hypothesis. *J. Anim. Ecol.* **77**: 335-340.

BirdLife International 2004. *Birds in Europe: Population Estimates Trends and Conservation Status*. Cambridge: BirdLife International.

Bosch, R., Real, J., Tintó, A., Zozaya, E. & Castell, C. 2010. Home-ranges and patterns of spatial use in territorial Bonelli's Eagles *Aquila fasciata*. *Ibis* **152**: 105–117.

Brito, P.H. 2007. Contrasting patterns of mitochondrial and microsatellite genetic structure among Western European populations of tawny owls (*Strix aluco*). *Mol. Ecol*. **16**: 3423–3437.

Brown, J.W., Van Coeverden de Groot, P.J., Birt, T.P., Seutin, G., Boag, P.T. & Friesen, V.L. 2007. Appraisal of the consequences of the DDT-induced bottleneck on the level and geographic distribution of neutral genetic variation in Canadian peregrine falcons, *Falco peregrinus*. *Mol. Ecol.* **16**: 327–343.

Broquet, T. & Petit, E.J. 2009. Molecular estimation of dispersal for ecology and population genetics. *Annu. Rev. Ecol. Evol. Syst.* **40**: 193-216.

Cadahía, L., López-López, P., Urios, V. & Negro, J.J. 2010. Satellite telemetry reveals individual variation in juvenile Bonelli's eagle dispersal areas. *Eur. J. Wildlife Res.* **56**: 923-930.

Cadahía, L., López-López, P., Urios, V., Soutullo, A. & Negro, J.J. 2009. Natal dispersal and recruitment of two Bonelli's Eagles *Aquila fasciata*: a four-year satellite tracking study. *Acta Ornithol.* **44**: 193-198.

Cadahía, L., Negro, J.J. & Urios, V. 2007. Low mitochondrial DNA diversity in the endangered Bonelli's Eagle (*Hieraaetus fasciatus*) from SW Europe (Iberia) and NW Africa. *J. Ornithol.* **148**: 99-104.

Callens, T., Galbusera, P., Matthysen, E., Durand, E.Y., Githiru, M., Huyghe, J.R. & Lens, L. 2011. Genetic signature of population fragmentation varies with mobility in seven bird species of a fragmented Kenyan cloud forest. *Mol. Ecol.* **20**: 1829-1844.

Carrascal, L.M. & Seoane, J. 2009a. Linking density, productivity and trends of an endangered species: the Bonelli's eagle in Spain. *Acta Oecol.* **35**: 341-348.

Carrascal, L.M. & Seoane, J. 2009b. Factors affecting large-scale distribution of the Bonelli's eagle *Aquila fasciata* in Spain. *Ecol. Res.* **24**: 565-573.

Cheylan, G., Ravayrol, A., Cugnasse, J.-M., Billet, J.-M. & Joulot, C. 1996. Dispersion des Aigles de Bonelli *Hieraaetus fasciatus* juvéniles bagués en France. *Alauda* **64**: 413-419.

Crandall, K.A., Bininda-Emonds, O.R.P., Mace, G.M. & Wayne, R.K. 2000. Considering evolutionary processes in conservation biology. *Trends Ecol. Evol.* **15**: 290-295.

Del Moral, J. 2006. El águila Perdicera en Espanã. Población en 2005 y método de censo. SEO/BirdLife, Madrid, Spain.

Davis, J.M. & Stamps, J.A. 2004. The effect of natal experience on habitat preferences. *Trends Ecol. Evol.* **19**: 411-416.

Earl, D. A. & vonHoldt, B. M. 2012. STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. *Conservation Genet. Resour.* **4**: 359-361.

Eckert, C.G., Samis K.E. & Lougheed S.C. 2008. Genetic variation across species' geographical ranges: the central–marginal hypothesis and beyond. *Mol. Ecol.* **17**: 1170-1188.

Equipa Atlas 2008. Atlas das aves nidificantes em Portugal (1999-2005)., Lisboa: Assírio & Alvim.

Evanno, G., Regnaut, S & Goudet, J. 2005. Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. *Mol. Ecol.* **14**: 2611-2620.

Excoffier, L., Laval, G. & Schneider, S. 2005. Arlequin ver. 3.0: an integrated software package for population genetics data analysis. *Evol. Bioinform. Online* **1**: 47-50

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Ann. Rev. Ecol. Evol. Syst*. **34**: 487-515.

Falush, D., Stephens, M. & Pritchard, J. 2003. Inference of population structure using multilocus genotype data: linked loci and correlated allele frequencies. *Genetics* **164**: 1567-1587.

Ferguson-Lees, J. & Christie, D.A. 2001. *Raptors of the World*. Boston, Massachusetts: Houghton Mifflin Co.

Fischer, J. & Lindenmayer, D.B. 2007. Landscape modification and habitat fragmentation: a synthesis. *Global Ecol. Biogeogr.* **16**: 265-280.

Fox, N. 1995. *Understanding the Bird of Prey*. Surrey: Hancock House

Frankham, R., Ballou, J.D. & Briscoe, D.A. 2002. *Introduction to Conservation Genetics*. Cambridge: Cambridge University Press

Fraser, D.J. & Bernatchez, L. 2001. Adaptive evolutionary conservation: towards a unified concept for defining conservation units. *Mol. Ecol.* **10**: 2741-2752.

Geraci, J., Béchet, A., Cézilly, F., Ficheux, S., Baccetti, N., Samraoui, B. & Wattier, R. 2012. Greater flamingo colonies around the Mediterranean form a single interbreeding population and share a common history. *J. Avian Biol.* **43**: 341-354.

Gerlach, G., Jueterbock, A., Kraemer, P., Deppermann, J. & Harmand, P. 2010. Calculations of Gst and D: forget Gst but not all of statistics! *Mol. Ecol.* **19**: 3845–3852.

Godinho, R., Crespo, E.G., & Ferrand, N. 2008. The limits of mtDNA phylogeography: complex patterns of population history in a highly structured Iberian lizard are only revealed by the use of nuclear markers. *Mol. Ecol.* **17**: 4670–4683.

Goncalves, H., Martinez-Solano, I., Pereira, R. J., Carvalho, B., Garcia-Paris, M. & Ferrand, N. 2009. High levels of population subdivision in a morphologically conserved Mediterranean toad (*Alytes cisternasii*) result from recent, multiple refugia: evidence from mtDNA, microsatellites and nuclear genealogies. *Mol. Ecol.* **18**: 5143-5160.

Greenwood, P.J. & Harvey, P.H. 1982. The natal and breeding dispersal of birds. *Ann. Rev. Ecol. Evol. Syst*. **13**: 1-21.

Hailer, F., Helander, B., Folkestad, A.O., Ganusevich, S.A., Garstad, S., Hauff, P., Koren, C., Nygard, T., Volke, V., Vila, C. & Ellegren, H. 2006. Bottlenecked but long-lived: high genetic diversity retained in white-tailed eagles upon recovery from population decline. *Biol. Lett.* **2**: 316-319.

Hanski, I. 1999. *Metapopulation Ecology*. Oxford: Oxford University Press.

Hardy, O.J. & Vekemans, X. 2002. SPAGeDi: a versatile computer program to analyse spatial genetic structure at the individual or population levels. *Mol. Ecol. Notes* **2**: 618-620.

Hernández-Matías, A., Real, J., Pradel, R., Ravayrol, A., Vincent-Martin, N., Bosca, F. & Cheylan, G. 2010. Determinants of territorial recruitment in Bonelli's eagle (*Aquila fasciata*) populations. *Auk* **127**: 173-184.

Hubisz, M.J., Falush, D., Stephens, M. & Pritchard, J.K. 2009. Inferring weak population structure with the assistance of sample group information. *Mol. Ecol. Resour.* **9**: 1322-1332.

Hull, J.M., Anderson, R., Bradbury, M., Estep, J.A. & Ernest, H.B. 2008b. Population structure and genetic diversity in Swainson's Hawks (*Buteo swainsoni*): implications for conservation. *Conserv. Genet.* **9**: 305-316.

Hull, J.M., Hull, A.C., Sacks, B.N., Smith, J.P. & Ernest, H.B. 2008a. Landscape characteristics influence morphological and genetic differentiation in a widespread raptor (*Buteo jamaicensis*). *Mol. Ecol.* **17**: 810-824.

Jost, L. 2008. G_{ST} and its relatives do not measure differentiation. *Mol. Ecol*. **17**: 4015–4026.

Kalinowski, S.T. 2005. HP-RARE 1.0: a computer program for performing rarefaction on measures of allelic richness. *Mol. Ecol. Notes* **5**: 187–189.

Kimura, M., & Maruyama, T. 1971. Pattern of neutral polymorphism in a geographically structured population. *Genet. Res.* **18**: 125-131.

Lancaster, M.L., Taylor, A.C., Coopers, S.J.B. & Carthew, S.M. 2011. Limited ecological connectivity of an arboreal marsupial across a forest/plantation landscape despite apparent resilience to fragmentation. *Mol. Ecol.* **20**: 2258-2271.

Mannan, R.W., Mannan, R.N., Schmidt, C.A., Estes-Zumpf, W.A. & Boal, C.W. 2006. Influence of natal experience on nest-site selection by urban-nesting Cooper's hawks. *J. Wildl. Manage.* **71**: 64-68.

Mantel, N. 1967. Detection of disease clustering and a generalized regression approach. *Cancer Res.* **27**: 209-220.

Martí, R. & Del Moral, J.C. 2003. *Atlas de las aves reproductoras de España*. Madrid: Dirección General de la Conservación de la Naturaleza – Sociedad Española de Ornitología.

Martinez-Cruz, B., David, V.A., Godoy, J.A., Negro, J.J., O'Brien, S.J. & Johnson, W.E. 2002. Eighteen polymorphic microsatellite markers for the highly endangered Spanish imperial eagle (*Aquila adalberti*) and related species. *Mol. Ecol.* **2**: 323-326.

Martínez-Cruz, B., Godoy, J.A. & Negro, J.J. 2004. Population genetics after fragmentation: the case of the endangered Spanish imperial eagle (*Aquila adalberti*). *Mol. Ecol.* 13: 2243-2255.

Martínez-Cruz, B., Godoy, J.A. & Negro, J.J. 2007. Population fragmentation leads to spatial and temporal genetic structure in the endangered Spanish imperial eagle. *Mol. Ecol.* **16**: 477-486.

Mesquita, N., Hanfling, B., Carvalho, G.R., & Coelho, M.M. 2005. Phylogeography of the cyprinid *Squalius aradensis* and implications for conservation of the endemic freshwater fauna of southern Portugal. *Mol. Ecol.* **14**: 1939–1954.

Mira, S. 2006. Population genetics of an endangered species, the Bonelli's Eagle (*Hieraaetus fasciatus*). Ph.D. dissertation, Universidade do Algarve, Faro, Portugal.

Mira, S., Wolff, K., & Cancela, M.L. 2005. Isolation and Characterization of Microsatellite Markers in Bonelli's Eagle (*Hieraaetus fasciatus*). *Mol. Ecol. Notes* **5**: 493-495.

Musiani, M., Leonard, J.A., Cluff, H.D., Gates, C.C., Mariani, S., Paquet, P.C., Vilà, C. & Wayne, R.K. 2007. Differentiation of tundra/taiga and boreal coniferous forest wolves: genetics, coat colour and association with migratory caribou. *Mol. Ecol.* **16**: 4149-4170.

Nei M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals, *Genetics* **89**: 583-590.

Nesje, M., Røed, K.H., Bell, D.A., Lindberg, P. & Lifjeld, J.T. 2000. Microsatellite analysis of population structure and genetic variability in peregrine falcons (*Falco peregrinus*). *Anim. Conserv.* **3**: 267-275.

Palma, L., Beja, P., Pais, M. & Fonseca, L.C. 2006. Why do raptors take domestic prey? The case of Bonelli's eagles and pigeons. *J. Appl. Ecol.* **43**: 1075-1086.

Pritchard, J., Stephens, M. & Donnelly, P. 2000. Inference of population structure using multilocus genotype data. *Genetics* **155**: 945-959.

Pritchard, J.K. & Wen, W. 2004. *Documentation for* structure *Software* (version 2, p. Structure). Department of Human Genetics, University of Chicago, Chicago.

Pulliam, H.R. 1998. Sources, sinks and population regulation. *Am. Nat.* **132**: 652-661.

Queller, D.C. & Goodnight, K.F. 1989. Estimating relatedness using genetic markers. *Evolution* **43**: 258-275.

R Development Core Team 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Rambaut, A. & Drummond, A.J. 2004. *Tracer v1.3. 2004.* *http://evolve.zoo.ox.ac.uk/software.html.*(accessed 28 May 2012).

Real, J., Grande, J.M., Mañosa, S. & Sánchez-Zapata, J.A. 2001. Causes of death in different areas for Bonelli's Eagle *Hieraaetus fasciatus* in Spain. *Bird Study* **48**: 221-228.

Real, J. & Mañosa, S. 1997. Demography and conservation of western European Bonelli's Eagle *Hieraaetus fasciatus* populations. *Biol. Conserv.***79**: 59–66.

Real, J. & Mañosa, S. 2001. Dispersal of juvenile and immature Bonelli's Eagles in northeastern Spain. *J. Raptor Res.* **35**: 9-14.

Riegert, J., Fainová, D. & Bystřická, D. 2010. Genetic variability, body characteristics and reproductive parameters of neighbouring rural and urban common kestrel (*Falco tinnuculus*) populations. *Pop. Ecol.* **52**: 73-79.

Rutz, C. 2008. The establishment of an urban bird population. *J. Anim. Ecol.* **77**: 1008-1019.

Ruzzante, D.E. 1998. A comparison of several measures of genetic distance and population structure with microsatellite data: bias and sampling variance. *Can. J. Fish. Aquat. Sci.* **55**: 1-14.

Sacks, B.N., Bannasch, D.L., Chomel, B.B. & Ernest, H.B. 2008. Coyotes demonstrate how habitat specialization by individuals of a generalist species can diversify populations in a heterogeneous ecoregion. *Mol. Biol. Evol.* **25**: 1384-1394.

Seutin, G., White, B.N. & Boag, P.T. 1991. Preservation of avian blood and tissue samples for DNA analyses. *Can. J. Zool.* **69**: 82-90.

Soutullo, A., López-López, P. & Urios, V. 2008. Incorporating spatial structure and stochasticity in endangered Bonelli's eagle's population models: Implications for conservation and management. *Biol. Conserv.* **41**: 1013-1020.

Stenseth, N.C. & Lidicker, W. 1992. *Animal Dispersal*. London: Chapman & Hall.

Stenseth, N.C., Shabbar, A., Chan, K.-S., Boutin, S., Rueness, E.K., Ehrich, D., Hurrell, J.W., Lingjærde, O.C. & Jakobsen, K.S. 2004. Snow conditions may create an invisible barrier for lynx. *Proc. Natl. Acad. Sci. USA* **101**: 10632-10634.

Storey, J.D. & Tibshirani, R. 2003. Statistical significance for genomewide studies. *Proc. Natl. Acad. Sci. USA* **100**: 9440-9445.

Taylor, A.C., Tyndale-Biscoe, H. & Lindenmayer, D.B. 2007. Unexpected persistence on habitat islands: genetic signatures reveal dispersal of a eucalypt-dependent marsupial through a hostile pine matrix. *Mol. Ecol.* **16**: 2655-2666.

Tordoff, H.B., Martell, M.S. & Redig, P.T. 1998. Effects of fledge site on choice of nest site by Midwestern peregrine falcons. *Loon* **70**: 127–129.

Van Horn, R.C., Altmann, J. & Alberts, S.C. 2008. Can't get there from here: inferring kinship from pairwise genetic relatedness. *Anim. Behav.* **75**: 1173–1180.

Waples, R.S. & Gaggiotti, O.E. 2006. What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity. *Mol. Ecol.* **15**: 1419–1439.

Waser, P. & Strobeck, C. 1998. Genetic signatures of interpopulation dispersal. *Trends Ecol. Evol.* **13**: 43-44.

Wegner, P., Kleinstäuber, G., Baum, F. & Schilling, F. 2005. Long-term investigation of the degree of exposure of German peregrine falcons (*Falco peregrinus*) to damaging chemicals from the environment. *J. Ornithol.* **146**: 34-54.

Weir, B.S. & Cockerham, C.C. 1984. Estimating *F*-statistics for the analysis of population structure. *Evolution* **38**: 1358-70.

Wilson, G.A. & Rannala, B. 2003. Bayesian inference of recente migration rates using multilocus genotypes. *Genetics* **163**: 1177-1191.

Wright, S. 1943. Isolation by distance. *Genetics* **28**: 114-138

Table 1. Sample characteristics and summary genetic statistics for eight Bonelli's Eagle subpopulations genotyped for 17 microsatellite markers: sampling years (Years), number of genotyped individuals (N) and breeding territories (N_T), mean number of alleles per locus (A), mean allelic richness standardised for $N_T = 6$ (A_6), observed (H_O) and unbiased expected (H_E) heterozygosity, and coefficient of inbreeding (F_{IS}). Values of genetic statistics were averages (±SD) across 10 subsets of individuals from 140 breeding territories.

Population	Years	N	N_T	A	A_6	H_O	H_E	F_{IS}
Portugal								
Southwest Portugal (SWP)	1994-2000	79	19	3.19±0.12	2.59±0.05	0.43±0.01	0.45±0.01	0.02±0.04
Northeast Portugal (NEP)	1996-1999	34	19	4.86±0.11	3.63±0.04	0.55±0.01	0.58±0.01	0.04±0.02
Spain								
Southwest Spain (SWSP)	1998-2000	26	20	4.67±0.03	3.59±0.23	0.59±0.01	0.59±0.003	0.004±0.01
Western Spain (WSP)		74	50	5.67±0.09	3.64±0.14	0.57±0.003	0.60±0.003	0.06[a]±0.01
Central Spain (CSP)	1997-1998	6	6	3.59	3.59	0.57	0.61	0.07
Eastern Spain (ESP)	1999-2002	12	12	4.35	3.63±0.00	0.59	0.61	0.02
NW Africa								
Morocco (MOR)	1998	8	8	4.00	3.65±0.00	0.55	0.59	0.07
Eastern Mediterranean								
Cyprus (CYP)	1999	6	6	2.65	2.65	0.46	0.50	0.08

[a] Statistically significant at $P<0.05$ after controlling for False Discovery Rate.

Table 2. Pairwise genetic differentiation between subpopulations of Bonelli's Eagle in the Mediterranean region, estimated using D_{est} (upper diagonal) and F_{ST} (lower diagonal). Each row indicates mean (± SD) values obtained from analyses of 10 subsets of individuals from 140 breeding territories.

Population	SWP	NEP	SWSP	WSP	CSP	ESP	MOR	CYP
Southwest Portugal (SWP)		0.197[a]±0.008	0.196[a]±0.006	0.167[a]±0.007	0.184[a]±0.009	0.175[a]±0.005	0.175[a]±0.005	0.450[a]±0.012
Northeast Portugal (NEP)	0.125[a]±0.009		0.157[a]±0.012	0.066[a]±0.007	0.116[a]±0.008	0.147[a]±0.008	0.147[a]±0.008	0.436[a]±0.005
Southwest Spain (SWSP)	0.126[a]±0.007	0.088[a]±0.008		0.078[a]±0.004	0.113[a]±0.004	0.064[a]±0.004	0.082[a]±0.005	0.406[a]±0.007
Western Spain (WSP)	0.102[a]±0.005	0.047[a]±0.004	0.040[a]±0.003		0.095[a]±0.007	0.066[a]±0.005	0.099[a]±0.005	0.363[a]±0.006
Central Spain (CSP)	0.141[a]±0.010	0.070[a]±0.005	0.059[a]±0.003	0.043[a]±0.003		0.093[a]	0.070[a]	0.248[a]
Eastern Spain (ESP)	0.134[a]±0.006	0.104[a]±0.006	0.041[a]±0.002	0.040[a]±0.002	0.045[a]		0.152[a]	0.354[a]
Morocco (MOR)	0.133[a]±0.010	0.075[a]±0.005	0.032[a]±0.002	0.034[a]±0.003	0.062[a]	0.043[a]		0.393[a]
Cyprus (CYP)	0.355[a]±0.014	0.267[a]±0.004	0.260[a]±0.004	0.230[a]±0.003	0.224[a]	0.188[a]	0.250[a]	

[a] Statistically significant considering a False Discovery Rate < 0.05

Figure captions

Figure 1. Distribution of breeding subpopulations of Bonelli's Eagle sampled in this study. Dominant membership of subpopulations to the four genetic units identified by STRUCTURE is represented as coloured circles in the map of Europe (lower-right panel). Detailed results are presented for the Iberian Peninsula, where pie charts represent the proportions of population level membership to genetic units (upper-left panel). The shaded area represents the breeding range of Bonelli's Eagle in the western Palearctic (redrawn from Ferguson-Lees & Christie 2001) and in western Europe (redrawn from Martí & Del Moral 2003, Equipa Atlas 2008, Hernández-Matías *et al.* 2010). Subpopulation abbreviations are defined in Table 1.

Figure 2. Biplots of Factorial Correspondence Analyses (FCA) of Mediterranean (upper panel) and western Mediterranean (lower panel) subpopulations of Bonelli's Eagle, derived from allelic variation at 17 microsatellite loci. Points in each FCA biplot represent average scores for nestlings of each breeding territory, obtained from analyses of 10 subsets of individuals from 140 territories. Percentages of variation accounted for by FCA axes are provided in parentheses.

Figure 3. Average pairwise genetic distances (F_{ST}) plotted against geographical distances (Km) between six Bonelli's Eagle subpopulations in the Iberian Peninsula. Open squares represent comparisons involving the population of southwest Portugal, whereas black dots represent comparisons between the other populations. The fitted regression lines are

provided for the datasets with (solid line) and without (hatched line) the inclusion of the subpopulation from southwest Portugal.

Figure 4. Results of the first round of hierarchical STRUCTURE analyses for Bonelli's Eagles, showing variation in the estimated log-likelihood for the models (ln Pr (*X* | *K*)); solid line) and in the second order rate of change of the log-likelihood between successive models (Delta *K*; dashed line)*,* against the number of putative populations (*K*). Separate analyses were carried out for 10 subsets of unrelated individuals from 140 breeding territories, and results were then averaged across analyses.

Figure 1

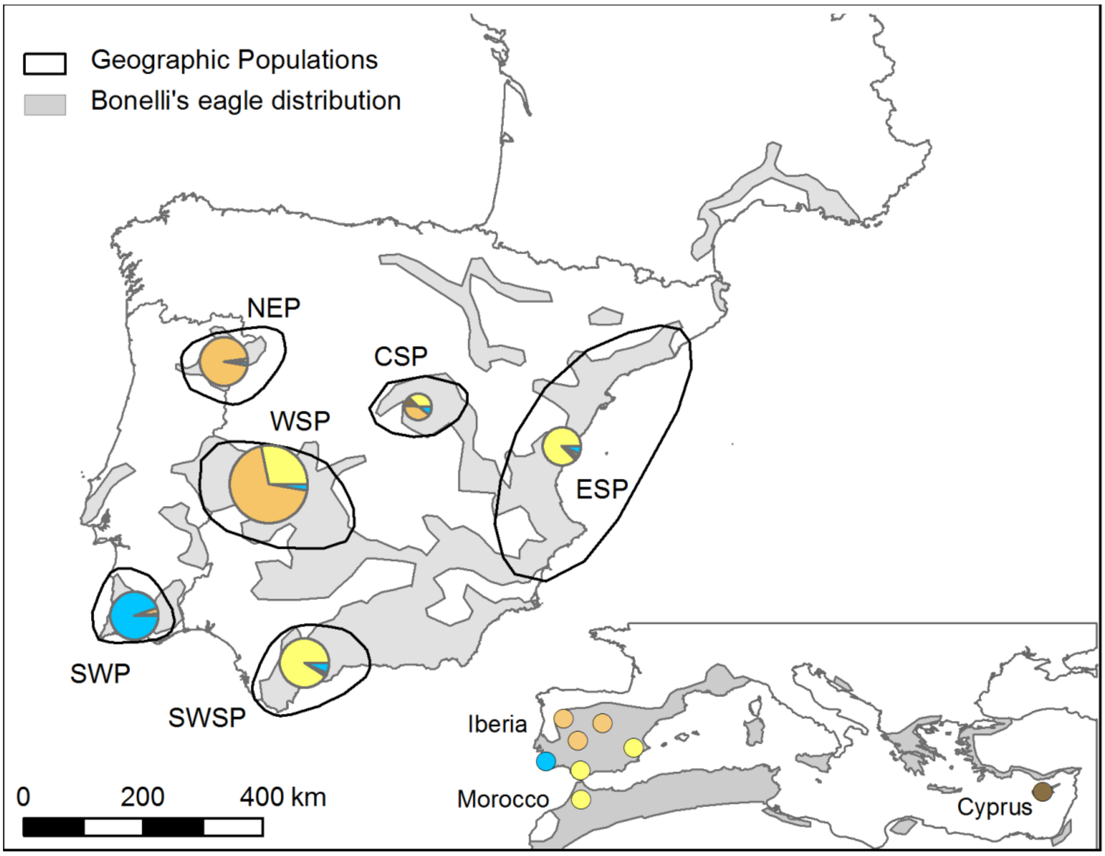
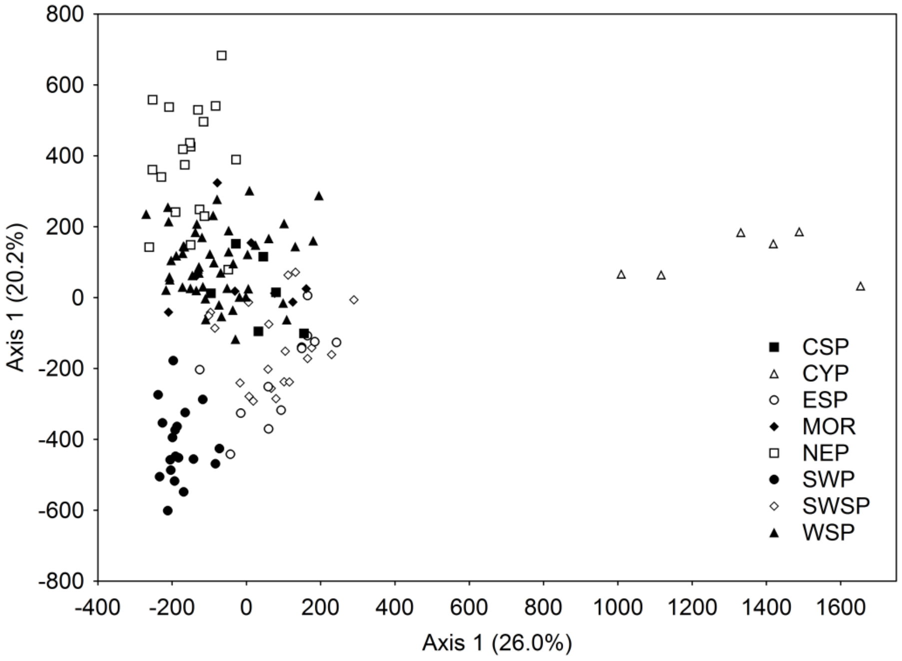

Geographic Populations
Bonelli's eagle distribution
NEP
CSP
WSP
ESP
SWP
SWSP
Iberia
Morocco
Cyprus
0
200
400 km

Figure 2


800
600
400
200
0
-200
-400
-600
-800
-400
-200
0
200
400
600
800
1000
1200
1400
1600
Axis 1 (20.2%)
Axis 1 (26.0%)
■ CSP
△ CYP
○ ESP
◆ MOR
□ NEP
● SWP
◇ SWSP
▲ WSP

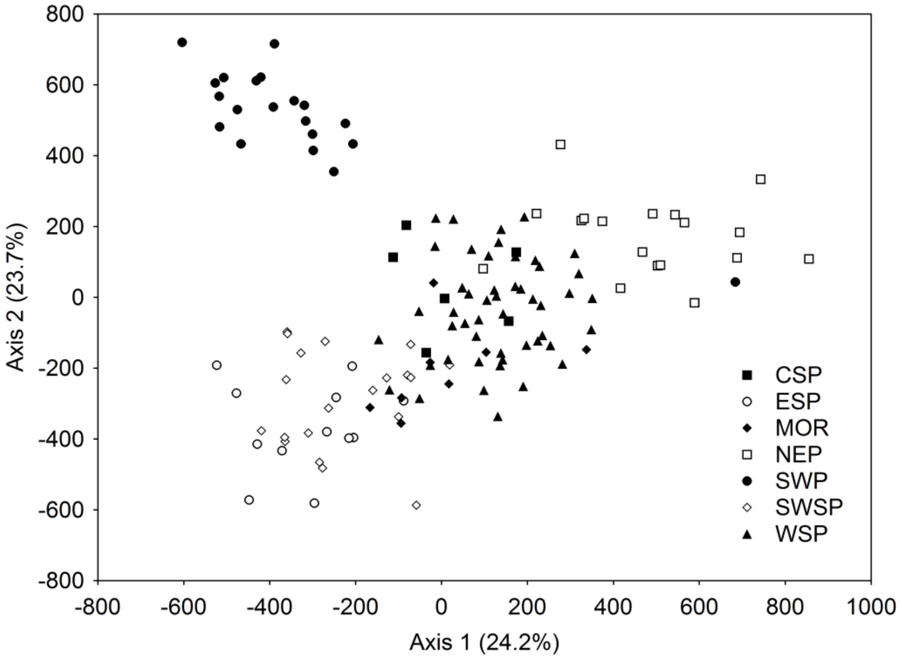

800
600
400
200
0
-200
-400
-600
-800
-800
-600
-400
-200
0
200
400
600
800
1000
Axis 2 (23.7%)
Axis 1 (24.2%)
■ CSP
○ ESP
◆ MOR
□ NEP
● SWP
◇ SWSP
▲ WSP

Figure 3

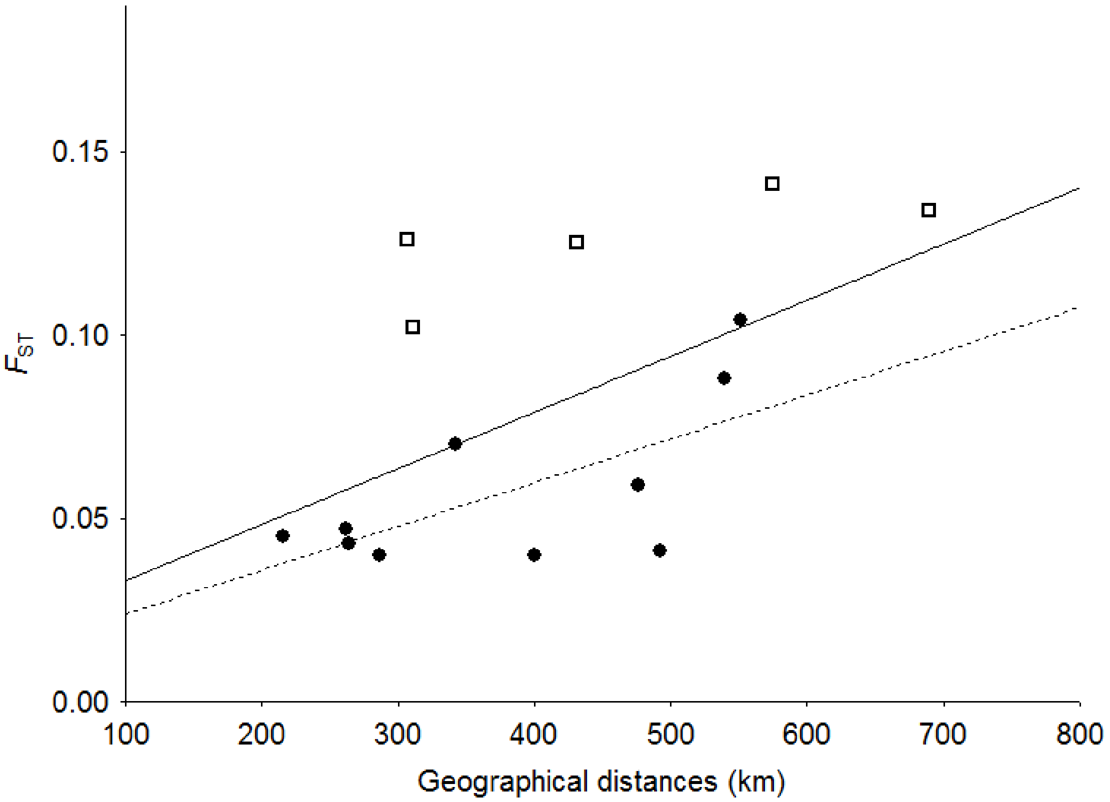
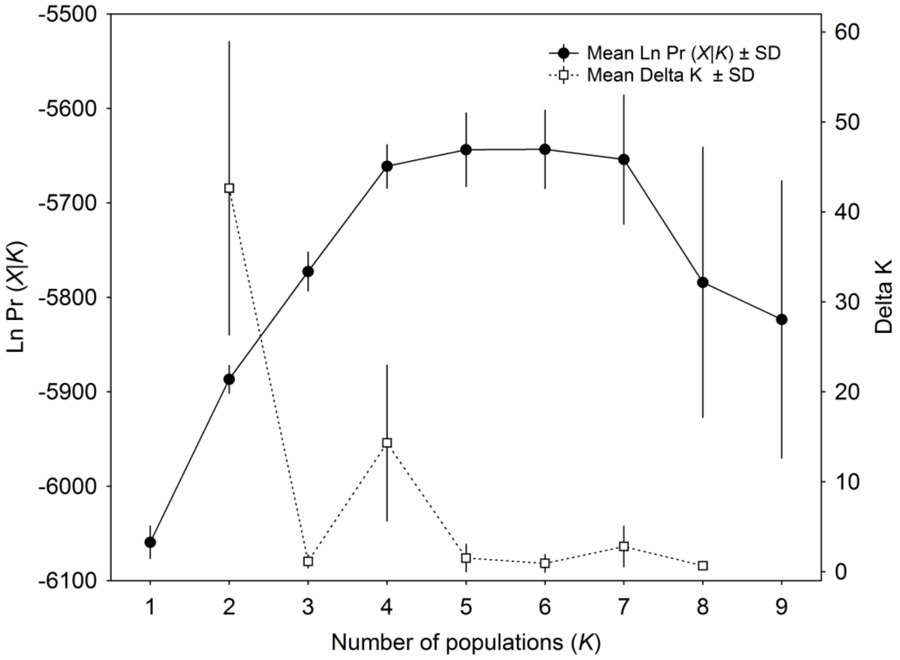

0.15
0.10
0.05
0.00
F_{ST}
100
200
300
400
500
600
700
800
Geographical distances (km)

Figure 4


-5500
-5600
-5700
-5800
-5900
-6000
-6100
Ln Pr (X|K)
60
50
40
30
20
10
0
Delta K
Mean Ln Pr (X|K) ± SD
Mean Delta K ± SD
1
2
3
4
5
6
7
8
9
Number of populations (K)

SUPPORTING INFORMATION

Figure S1. Average pairwise genetic distances (F_{ST}) plotted against geographical distances (Km) between six Bonelli's Eagle subpopulations in the Iberian Peninsula. Open squares represent pairwaise comparisons involving the subpopulation of Southwest Portugal, whereas black dots represent comparisons between the other subpopulations. The fitted regression lines are given for the datasets with (solid line) and without (hatched line) the population of Southwest Portugal.

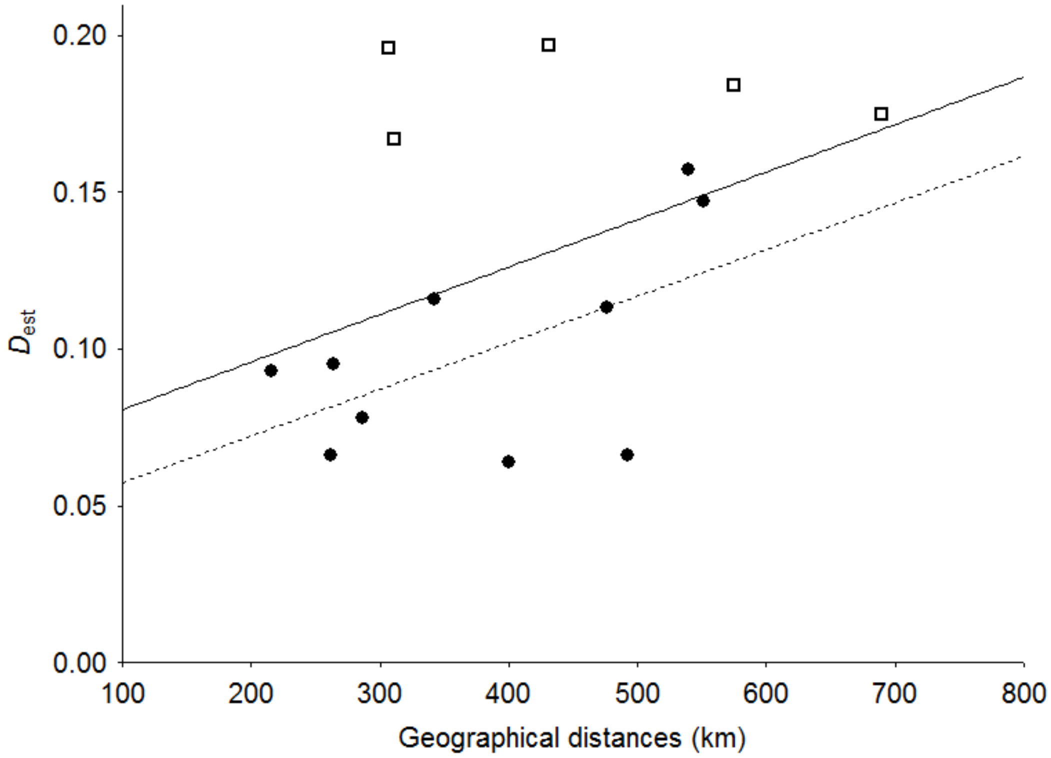


Figure S2. Pairwise genetic relatedness (R) plotted against geographical distances between individuals of six Bonelli's Eagle subpopulations in the Iberian Peninsula.

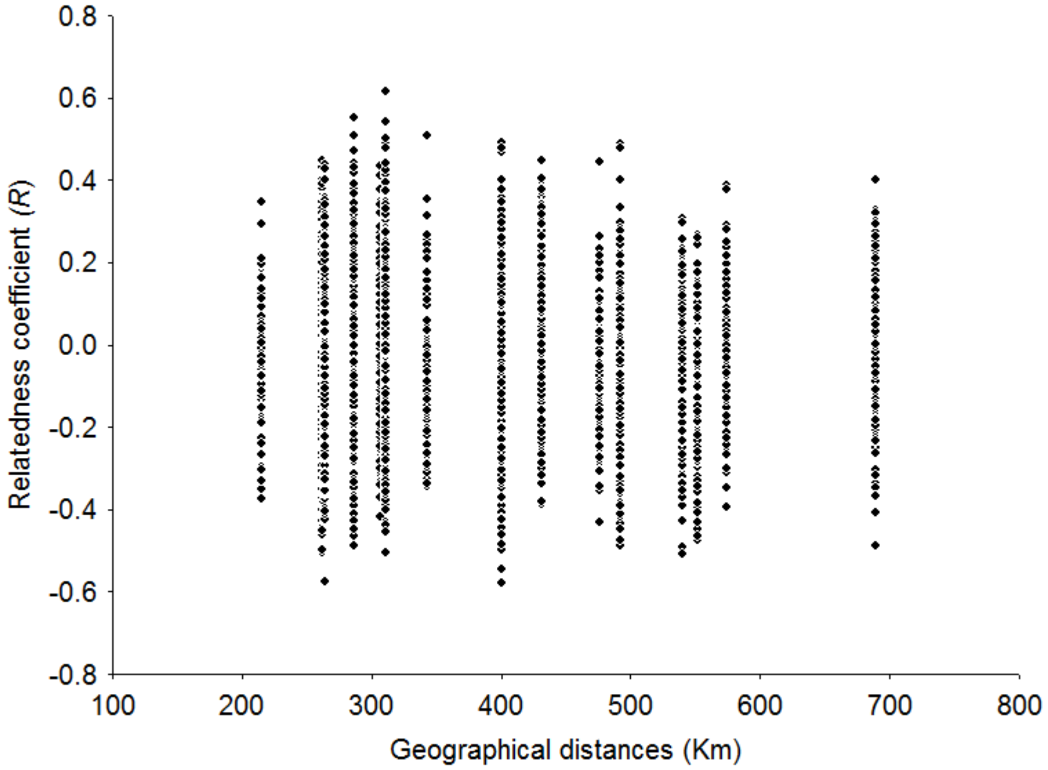


Figure S3. Results of the second round of hierarchical STRUCTURE analyses for Bonelli's eagles, showing variation in the estimated log-likelihood for the models (Ln Pr (*X* | *K*)); solid line) and in the second order rate of change of the log-likelihood between successive models (Delta *K*; dashed line), against the number of putative populations (*K*). Separate analyses were carried out for 10 subsets of unrelated individuals from 121 breeding territories (excluding SWP), and results were then averaged across analyses.

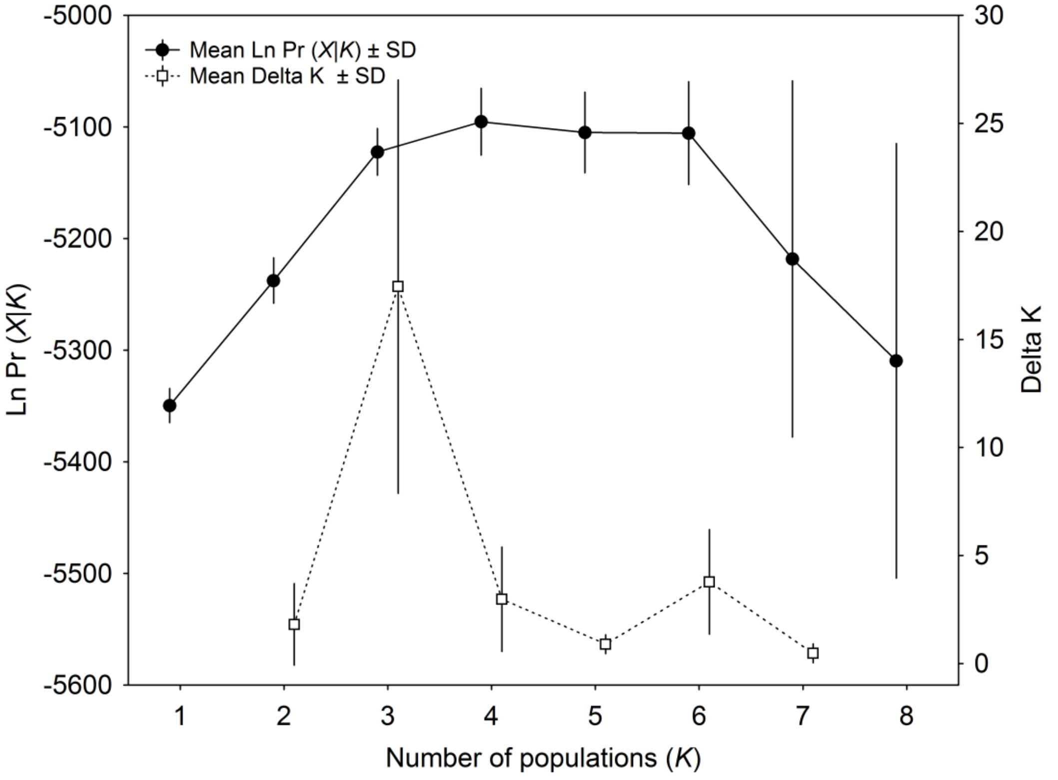


Figure S4. Results of the third round of hierarchical STRUCTURE analyses for Bonelli's eagles, showing variation in the estimated log-likelihood for the models (Ln Pr (*X* | *K*)); solid line) and in the second order rate of change of the log-likelihood between successive models (Delta *K*; dashed line), against the number of putative populations (*K*). Separate analyses were carried out for 10 subsets of unrelated individuals from 115 breeding territories (excluding SWP and CYP), and results were then averaged across analyses.

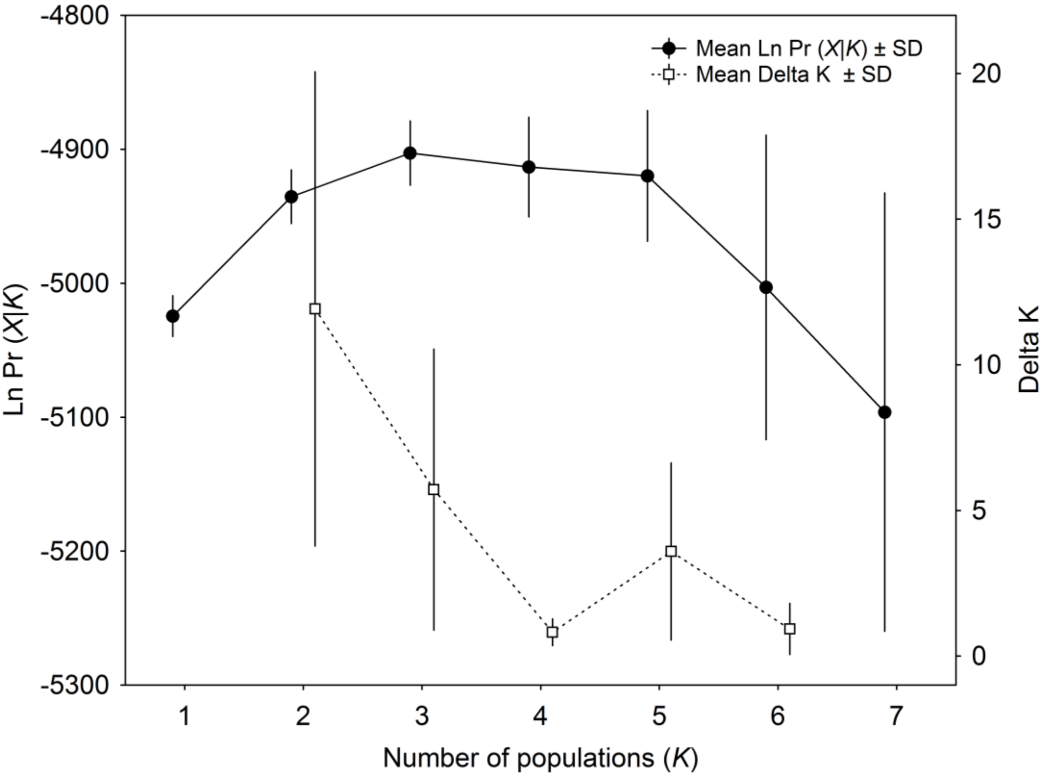


Table S1. Mean and Standard Error (SE) of pairwise relatedness among nestling Bonelli's Eagles from different territories within each subpopulation. Relatedness was estimated using Queller & Goodnight's (1989) *R*, and the software SPAGeDI (Hardy & Vekemans 2002). Mean and SE are jackknifed estimates over loci.

Population	**N**	**Mean**	**SE**
Southwest Portugal (SWP)	19	-0.059	0.003
Northeast Portugal (NEP)	19	-0.056	0.001
Southwest Spain (SWSP)	20	-0.059	0.003
Western Spain (WSP)	50	-0.020	0.001
Central Spain (CSP)	6	-0.202	0.002
Eastern Spain (ESP)	12	-0.093	0.002
Morocco (MOR)	8	-0.143	0.000
Cyprus (CYP)	6	-0.205	0.008

Table S2. Raw microsatellite genotypes for 245 individual Bonelli's Eagles from 8 breeding populations. The abbreviation of populations is given in Table S1.

n	Nest ID	Individual ID	Population	Aa02		HfC1E6		HfC1D10		Aa26		HfC7E1		Aa39		HfC4G1		HfP2E11		HfC7G4		HfC2D4		HfC5D4	
1	SWP1	A62	SWP	100	100	237	237	192	192	100	106	158	167	176	176	167	166	204	204	220	220	195	195	149	149
2	SWP1	A71	SWP	100	100	237	237	192	192	106	106	158	167	176	176	167	166	204	204	220	223	195	195	149	155
3	SWP1	A72	SWP	100	100	237	237	192	192	106	110	162	167	176	176	167	166	204	204	220	220	195	195	149	155
4	SWP2	A16	SWP	104	104	237	237	192	192	106	106	158	167	176	176	167	166	204	204	000	000	193	193	149	149
5	SWP2	A38	SWP	104	104	237	237	192	192	106	106	158	165	176	176	167	166	204	204	220	220	191	195	149	149
6	SWP2	A47	SWP	104	104	237	237	192	192	106	110	158	165	176	176	167	162	204	204	220	220	191	193	149	149
7	SWP2	A57	SWP	104	104	237	237	192	192	106	110	158	167	176	176	167	162	200	204	220	220	193	193	149	149
8	SWP2	A69	SWP	104	104	237	240	192	192	106	106	158	167	176	176	167	166	204	204	220	220	193	195	149	149
9	SWP2	A70	SWP	100	104	237	240	192	192	106	106	158	165	176	184	167	166	200	204	220	223	191	195	149	149
10	SWP3	A6	SWP	100	100	237	237	192	192	106	110	158	165	176	186	167	162	204	204	220	220	195	195	149	155
11	SWP3	A8	SWP	100	104	237	237	192	192	106	110	162	163	176	186	167	166	200	204	220	220	195	195	149	149
12	SWP3	A19	SWP	100	104	237	237	192	192	106	106	158	165	176	176	167	158	200	204	220	220	195	195	149	155
13	SWP3	A20	SWP	104	104	237	237	192	192	106	106	158	165	176	186	167	166	200	204	220	220	193	195	149	149
14	SWP3	A54	SWP	104	104	237	237	192	192	106	106	158	163	176	186	167	158	204	204	220	220	195	195	149	155
15	SWP4	A4	SWP	104	104	237	237	192	192	106	100	158	163	176	176	167	166	204	204	220	220	195	195	149	161
16	SWP4	A29	SWP	104	104	237	237	192	192	100	106	158	165	176	176	167	166	204	204	220	220	000	000	149	149
17	SWP4	A30	SWP	100	104	237	237	192	192	106	106	158	163	176	176	167	168	204	204	220	220	195	195	161	161
18	SWP4	A60	SWP	100	104	237	237	192	192	100	106	158	163	176	176	169	166	204	204	220	220	195	195	149	149
19	SWP4	A61	SWP	100	104	237	240	192	192	106	106	158	163	176	176	167	168	204	204	220	220	195	195	149	149
20	SWP5	A10	SWP	100	104	237	237	192	192	106	106	158	165	184	186	167	158	204	206	220	223	193	195	149	161
21	SWP5	A11	SWP	100	100	237	237	192	192	106	100	158	163	176	186	165	166	200	204	220	223	195	195	149	161
22	SWP5	A21	SWP	100	104	237	237	192	192	106	106	158	163	176	186	165	158	200	204	220	223	193	193	149	161
23	SWP5	A22	SWP	100	100	237	237	192	192	106	100	160	163	176	184	167	166	204	204	220	220	000	000	149	161
24	SWP5	A31	SWP	100	100	237	237	192	192	106	100	158	165	176	186	167	166	204	204	220	223	193	195	149	161
25	SWP5	A32	SWP	100	104	237	237	192	192	106	106	158	163	176	186	167	158	200	204	220	223	195	195	155	161
26	SWP5	A48	SWP	100	104	237	237	192	192	106	106	158	163	176	176	163	158	200	204	220	223	193	195	149	155
27	SWP5	A49	SWP	100	104	237	237	192	192	106	106	158	163	176	176	163	158	200	204	220	223	195	195	149	155
28	SWP5	A56	SWP	100	100	237	237	192	192	100	106	158	163	184	186	167	166	200	206	220	220	193	195	149	161
29	SWP5	A80	SWP	100	104	237	237	192	192	106	106	158	163	176	186	163	158	204	204	220	223	193	195	155	161
30	SWP6	A1	SWP	100	100	237	237	192	192	110	110	160	163	176	176	165	162	204	208	220	220	195	195	149	161
31	SWP6	A14	SWP	100	100	237	237	192	192	106	110	162	167	176	176	167	166	204	208	220	220	191	191	149	161
32	SWP7	A42	SWP	104	104	237	237	192	192	106	110	158	165	186	186	167	160	204	204	220	220	193	195	149	149
33	SWP7	A64	SWP	100	104	237	237	192	192	106	106	158	165	176	186	165	158	204	204	220	220	193	195	149	149
34	SWP8	A7	SWP	100	104	237	240	192	192	106	106	158	163	176	176	165	166	200	206	220	223	193	193	149	149
35	SWP8	A9	SWP	100	100	237	237	192	192	106	110	160	165	176	186	167	166	200	206	220	223	193	195	149	149
36	SWP8	A25	SWP	100	100	237	237	192	192	110	110	160	165	176	184	167	162	200	204	223	223	000	000	155	161
37	SWP8	A74	SWP	104	104	237	237	192	192	106	110	158	163	176	184	167	162	204	204	220	223	193	195	149	161
38	SWP8	A75	SWP	104	104	237	240	192	192	106	110	158	163	176	184	167	162	204	204	220	223	193	195	149	155
39	SWP9	A43	SWP	104	104	237	237	192	192	106	106	158	165	186	186	167	158	204	204	220	220	193	193	149	149
40	SWP9	A55	SWP	104	104	237	237	192	192	106	106	158	165	176	176	167	158	204	204	220	220	193	193	149	149
41	SWP9	A76	SWP	100	104	237	237	192	192	106	106	158	165	176	176	167	158	204	204	220	220	193	195	149	149

n	Nest ID	Individual ID	Population	Aa02		HfC1E6		HfC1D10		Aa26		HfC7E1		Aa39		HfC4G1		HfP2E11		HfC7G4		HfC2D4		HfC5D4	
42	SWP9	A77	SWP	104	104	237	237	192	192	106	106	158	167	176	176	167	158	204	204	220	220	193	193	149	149
43	SWP10	A12	SWP	100	100	237	237	192	192	110	110	162	163	176	176	167	162	200	204	220	220	195	195	149	149
44	SWP10	A23	SWP	100	104	000	000	192	192	106	110	162	163	176	186	167	166	200	204	220	220	191	195	149	155
45	SWP10	A24	SWP	100	100	000	000	192	192	110	110	162	163	176	186	167	162	200	200	220	220	191	191	155	155
46	SWP10	A40	SWP	100	104	237	237	192	192	106	110	164	167	176	184	171	162	204	204	220	223	193	195	149	161
47	SWP10	A41	SWP	100	104	237	237	192	192	106	110	162	167	176	176	167	166	204	204	220	220	193	195	149	155
48	SWP10	A52	SWP	100	104	237	237	192	192	106	110	162	167	176	176	171	166	200	204	220	220	191	193	149	149
49	SWP10	A67	SWP	104	104	237	237	192	195	100	106	166	167	176	176	171	168	200	204	220	220	193	193	149	161
50	SWP10	A68	SWP	104	104	237	237	192	192	106	106	164	167	176	184	171	166	200	204	220	223	193	193	149	149
51	SWP11	A53	SWP	100	104	237	240	192	192	106	106	160	165	176	176	167	166	204	204	220	223	193	195	149	149
52	SWP11	A63	SWP	104	104	237	237	192	192	106	106	158	163	176	176	167	160	200	204	220	223	000	000	149	149
53	SWP12	A35	SWP	100	100	237	237	192	192	106	106	158	163	174	176	167	160	204	204	220	220	191	191	149	161
54	SWP12	A36	SWP	100	104	237	237	192	192	106	106	158	163	176	176	167	160	204	204	220	220	193	195	149	155
55	SWP12	A44	SWP	100	100	237	237	192	192	106	106	158	163	174	186	165	160	204	204	220	220	191	195	149	155
56	SWP13	A5	SWP	100	104	237	237	192	192	106	106	158	165	176	176	167	166	200	204	220	220	195	195	149	161
57	SWP13	A15	SWP	100	104	237	237	192	192	106	110	160	165	176	176	167	166	200	204	220	223	195	195	149	149
58	SWP13	A39	SWP	104	104	237	237	192	192	106	106	160	165	176	176	167	166	200	204	220	220	195	195	149	161
59	SWP13	A50	SWP	100	100	237	237	192	192	106	110	158	165	176	176	167	160	200	204	220	220	195	195	149	149
60	SWP13	A51	SWP	100	100	237	237	192	192	106	110	160	165	176	176	167	166	204	204	220	223	195	195	149	161
61	SWP14	A2	SWP	104	104	237	237	192	192	106	100	158	163	176	176	165	166	000	000	220	223	195	195	149	155
62	SWP14	A3	SWP	100	104	237	237	192	192	106	100	160	163	176	176	167	166	200	204	220	220	195	195	161	161
63	SWP14	A26	SWP	100	104	237	237	192	192	106	100	160	163	176	176	167	166	204	204	220	223	195	195	161	161
64	SWP14	A27	SWP	100	104	237	237	192	192	106	110	160	163	176	176	167	160	204	204	220	220	195	195	149	161
65	SWP14	A28	SWP	104	104	237	237	192	192	100	106	158	163	176	176	165	166	200	204	220	223	195	195	149	161
66	SWP14	A58	SWP	100	104	237	237	192	192	100	106	160	163	176	176	165	166	204	204	220	223	193	195	161	161
67	SWP14	A59	SWP	104	104	237	237	192	192	106	110	158	163	176	176	167	160	200	200	220	220	195	195	149	155
68	SWP14	A78	SWP	100	100	237	237	192	192	106	110	158	163	176	176	165	160	204	204	220	220	195	195	149	155
69	SWP14	A79	SWP	100	100	237	237	192	192	106	110	160	163	176	176	167	160	204	204	220	220	195	195	155	161
70	SWP15	A13	SWP	100	104	237	237	192	192	106	106	158	163	176	184	167	160	200	204	220	220	195	195	149	155
71	SWP15	A17	SWP	100	104	237	237	192	192	106	106	158	163	176	184	167	160	200	204	220	220	195	195	149	161
72	SWP15	A18	SWP	100	100	237	237	192	192	106	100	160	163	176	184	167	166	204	204	220	220	195	195	149	161
73	SWP16	A65	SWP	100	104	237	237	192	192	106	110	162	165	176	176	167	166	204	204	220	220	191	191	149	155
74	SWP16	A66	SWP	100	104	237	237	192	192	106	106	166	165	176	176	167	166	204	204	220	220	195	195	149	155
75	SWP17	A33	SWP	100	104	237	237	192	192	106	110	158	165	176	186	167	160	204	204	220	220	193	195	149	161
76	SWP17	A34	SWP	104	104	237	237	192	192	106	110	158	163	176	186	167	160	204	204	220	220	193	195	149	161
77	SWP17	A45	SWP	100	104	240	240	192	192	106	110	158	165	176	184	167	162	204	204	220	223	193	193	149	161
78	SWP18	A73	SWP	104	104	237	237	192	192	106	106	158	167	176	176	167	166	204	204	220	223	193	193	149	149
79	SWP19	A37	SWP	100	100	237	237	192	192	106	110	158	167	174	176	167	160	204	204	220	220	193	195	149	149
80	NEP1	T1	NEP	100	104	237	237	192	195	100	110	164	171	176	184	171	170	204	216	220	220	193	193	149	155
81	NEP1	T2	NEP	100	104	234	237	192	195	100	106	164	163	176	184	187	170	204	204	220	220	193	193	149	155
82	NEP1	T13	NEP	100	104	234	240	192	195	100	100	168	163	184	184	171	170	204	216	220	220	193	195	149	155
83	NEP1	T14	NEP	100	104	234	240	192	195	106	110	164	163	176	184	171	164	204	216	220	220	193	195	149	149
84	NEP1	T31	NEP	100	104	234	240	192	195	100	110	164	171	176	184	171	170	204	204	220	220	193	193	149	149
85	NEP1	T32	NEP	100	104	234	240	192	195	100	100	170	171	176	184	171	170	204	204	220	220	193	193	149	155
86	NEP2	T3	NEP	100	100	237	240	192	192	100	106	158	171	176	184	189	158	204	204	220	220	193	193	155	161
87	NEP2	T4	NEP	100	104	237	237	192	192	100	106	168	163	184	184	189	170	204	204	220	220	193	193	149	149

n	Nest ID	Individual ID	Population	Aa02		HfC1E6		HfC1D10		Aa26		HfC7E1		Aa39		HfC4G1		HfP2E11		HfC7G4		HfC2D4		HfC5D4	
88	NEP3	T5	NEP	104	104	237	237	192	192	106	106	158	163	176	186	187	164	204	204	220	223	193	193	161	161
89	NEP3	T6	NEP	104	104	237	237	192	192	106	106	158	163	184	184	163	164	204	204	223	227	193	193	149	161
90	NEP3	T22	NEP	100	104	234	237	192	192	100	106	158	163	174	184	177	158	204	204	220	223	193	195	149	155
91	NEP3	T23	NEP	104	104	234	237	192	192	100	106	158	163	184	184	187	158	204	204	223	227	193	195	149	161
92	NEP3	T28	NEP	104	104	237	237	192	192	106	106	158	163	184	186	187	164	204	204	223	223	193	193	149	149
93	NEP3	T29	NEP	100	104	234	237	192	192	106	106	158	163	176	186	187	164	204	204	223	223	193	193	161	161
94	NEP4	T7	NEP	100	104	237	243	192	192	100	106	158	171	176	184	187	166	200	204	220	227	193	195	149	149
95	NEP5	T8	NEP	100	104	237	240	192	192	100	106	170	163	174	184	163	170	204	204	220	220	193	193	149	155
96	NEP5	T9	NEP	100	104	237	240	192	192	100	106	158	163	174	184	171	170	204	204	220	220	193	193	155	155
97	NEP6	T11	NEP	104	104	240	240	189	192	106	106	158	163	176	176	171	166	204	204	220	223	193	193	149	155
98	NEP6	T12	NEP	100	104	000	000	189	192	100	106	166	163	176	184	167	170	204	204	220	223	193	193	149	149
99	NEP7	T15	NEP	100	104	240	240	192	192	106	106	168	163	174	184	163	170	204	204	220	227	193	195	155	155
100	NEP8	T17	NEP	104	104	237	237	192	195	106	106	164	163	174	176	189	166	200	204	220	223	193	195	149	161
101	NEP8	T18	NEP	100	104	234	237	192	192	100	106	166	163	176	184	177	170	204	204	220	223	193	193	149	161
102	NEP9	T19	NEP	100	100	234	237	192	192	100	106	164	163	184	186	187	166	204	204	220	227	193	195	149	161
103	NEP10	T20	NEP	100	100	237	237	192	192	106	106	164	163	176	184	177	166	204	208	227	227	193	193	149	149
104	NEP11	T21	NEP	100	100	237	237	192	192	106	110	166	163	176	184	163	170	200	204	220	220	195	195	149	149
105	NEP12	T24	NEP	000	000	234	237	192	192	100	106	164	163	176	184	163	166	204	204	220	227	193	193	149	149
106	NEP13	T25	NEP	100	104	237	240	192	195	100	106	166	177	174	174	189	166	204	204	220	223	193	193	149	149
107	NEP13	T26	NEP	100	104	234	237	192	192	106	106	158	163	176	184	167	166	204	216	220	223	193	193	149	155
108	NEP14	T27	NEP	100	104	237	237	192	192	100	106	168	163	174	176	171	170	204	204	227	227	193	193	149	155
109	NEP15	T30	NEP	100	100	237	237	192	192	106	110	162	167	174	176	171	162	204	204	220	227	193	193	149	155
110	NEP16	T33	NEP	100	104	240	240	192	192	106	106	164	163	174	184	163	168	204	204	220	220	193	193	149	149
111	NEP17	T34	NEP	104	104	237	237	192	195	100	106	166	167	174	174	177	166	204	204	220	223	195	195	149	149
112	NEP18	T35	NEP	100	104	234	237	192	192	106	110	158	163	176	176	167	160	200	204	220	227	193	193	155	155
113	NEP19	T36	NEP	100	100	234	240	192	192	106	110	158	163	176	184	163	170	204	204	220	223	193	193	149	149
114	SWSP1	L12	SWSP	100	104	237	243	192	192	106	106	160	163	184	184	167	170	204	206	220	223	195	195	149	149
115	SWSP1	L13	SWSP	100	104	237	240	192	192	106	110	164	163	184	184	167	164	204	206	220	220	193	195	149	149
116	SWSP2	L15	SWSP	100	104	234	237	192	192	106	106	160	163	184	184	165	166	204	208	220	223	195	195	149	149
117	SWSP3	L16	SWSP	100	104	240	240	192	192	106	110	164	163	176	182	189	166	200	204	220	223	195	195	149	161
118	SWSP4	L17	SWSP	100	104	237	243	192	192	110	110	162	163	176	184	163	168	204	206	220	223	193	195	149	161
119	SWSP5	L18	SWSP	100	104	237	240	189	192	106	110	160	163	182	186	163	166	204	208	220	223	193	193	149	149
120	SWSP6	L19	SWSP	100	100	234	243	192	192	106	110	160	163	184	184	189	170	204	216	220	223	195	195	149	149
121	SWSP7	L20	SWSP	104	104	234	237	192	192	106	106	158	163	176	184	189	160	204	208	220	223	195	195	149	149
122	SWSP8	L21	SWSP	100	100	234	237	192	192	110	110	160	163	176	182	191	160	206	216	220	223	195	195	149	155
123	SWSP9	L22	SWSP	100	100	234	237	192	192	106	106	162	163	176	186	189	166	206	216	220	220	193	195	149	155
124	SWSP10	L23	SWSP	100	104	234	237	192	192	106	110	160	165	176	176	189	166	200	206	223	223	195	195	149	155
125	SWSP10	L24	SWSP	100	100	234	237	192	192	106	106	164	167	176	176	189	166	206	206	223	223	195	195	149	149
126	SWSP11	L25	SWSP	100	104	234	237	192	192	110	110	160	163	176	182	191	164	204	206	220	223	193	195	149	155
127	SWSP11	L26	SWSP	100	104	234	237	192	192	110	110	160	163	176	182	167	164	204	216	220	223	193	193	149	155
128	SWSP12	L27	SWSP	100	104	234	237	192	192	106	106	160	165	176	186	189	166	204	206	220	220	191	193	149	155
129	SWSP13	L28	SWSP	100	104	237	237	192	192	110	110	164	163	176	176	163	166	204	206	223	223	193	193	149	149
130	SWSP14	L29	SWSP	100	104	234	237	192	192	106	106	162	163	176	182	167	166	200	206	220	220	193	193	149	149
131	SWSP14	L30	SWSP	100	104	237	240	192	192	106	110	164	189	176	186	191	166	200	206	220	220	195	195	149	149
132	SWSP15	L33	SWSP	100	104	237	240	189	192	106	110	160	163	174	182	163	166	200	216	220	220	193	193	149	149
133	SWSP16	L34	SWSP	100	100	240	243	192	192	106	106	158	163	176	176	163	166	200	204	223	223	193	195	149	149

n	Nest ID	Individual ID	Population	Aa02		HfC1E6		HfC1D10		Aa26		HfC7E1		Aa39		HfC4G1		HfP2E11		HfC7G4		HfC2D4		HfC5D4	
134	SWSP17	L35	SWSP	100	100	234	237	192	192	110	110	164	163	176	182	167	166	200	206	220	220	195	195	149	149
135	SWSP18	L36	SWSP	100	100	240	243	192	192	106	106	164	163	176	182	163	166	204	204	220	220	195	195	149	149
136	SWSP18	L37	SWSP	100	100	240	243	192	192	106	106	160	163	176	186	189	166	204	206	220	223	195	195	149	149
137	SWSP19	L38	SWSP	100	100	237	237	192	192	106	110	158	163	184	184	165	160	200	208	223	223	195	195	149	149
138	SWSP20	L39	SWSP	104	104	237	237	192	192	106	106	160	167	176	184	189	164	204	206	220	220	195	195	149	155
139	SWSP20	L40	SWSP	104	104	234	237	192	192	106	106	164	167	176	184	189	166	206	206	220	220	195	195	149	149
140	WSP1	E4	WSP	100	104	234	240	192	192	110	110	166	163	176	182	179	166	204	216	223	223	193	193	149	149
141	WSP1	E5	WSP	104	104	234	240	192	192	106	110	158	163	182	184	163	166	204	206	223	223	193	193	149	149
142	WSP2	E7	WSP	100	100	234	237	192	195	106	106	164	163	176	176	189	168	200	204	223	223	195	195	149	161
143	WSP2	E8	WSP	100	100	234	237	195	195	106	106	166	165	176	182	189	170	204	216	220	223	195	195	149	155
144	WSP3	E22	WSP	100	100	237	237	192	192	106	106	000	167	176	184	187	000	200	200	223	227	195	195	149	149
145	WSP3	E23	WSP	100	104	234	237	192	192	106	110	000	167	176	184	171	000	204	204	220	223	195	195	149	149
146	WSP4	E43	WSP	104	104	237	240	192	192	106	106	158	163	176	176	163	166	200	204	220	223	191	193	149	149
147	WSP4	E44	WSP	104	104	237	240	189	192	106	110	162	163	176	176	167	164	204	204	223	227	191	193	149	149
148	WSP5	E48	WSP	104	104	237	240	192	192	106	110	166	163	176	184	163	170	204	216	220	223	193	193	149	149
149	WSP5	E49	WSP	104	104	237	240	192	195	106	110	164	163	176	176	163	170	204	204	223	223	191	193	149	149
150	WSP6	E55	WSP	100	104	237	261	192	195	106	110	160	163	174	176	167	160	204	204	220	220	191	193	149	155
151	WSP6	E56	WSP	100	104	237	261	192	192	106	106	166	163	174	176	167	166	200	204	220	223	191	193	149	149
152	WSP7	E57	WSP	104	104	237	237	192	201	106	110	164	163	174	176	167	166	204	204	223	223	195	195	149	161
153	WSP7	E58	WSP	100	104	237	237	192	192	106	106	166	163	174	184	167	166	204	204	223	223	195	195	149	149
154	WSP8	E62	WSP	100	104	234	240	192	192	106	106	160	163	174	184	167	164	204	204	220	223	195	195	149	149
155	WSP8	E63	WSP	100	104	237	240	192	192	106	110	160	163	174	182	167	166	204	216	220	220	191	193	149	149
156	WSP9	E65	WSP	100	104	240	240	189	192	106	106	164	167	174	174	167	170	204	206	220	223	193	195	149	155
157	WSP9	E66	WSP	100	104	240	240	192	192	106	106	160	167	174	176	167	166	204	204	223	227	191	193	155	161
158	WSP10	E67	WSP	104	104	237	240	189	192	106	110	162	165	176	182	167	166	200	204	223	223	193	193	149	149
159	WSP10	E68	WSP	104	104	237	240	189	192	106	110	162	163	174	184	167	166	204	204	223	223	191	193	155	155
160	WSP11	E69	WSP	100	104	234	237	192	201	110	110	160	163	182	184	165	160	204	216	220	223	195	195	149	161
161	WSP11	E70	WSP	104	104	234	237	192	192	106	110	158	163	184	186	163	160	204	216	223	223	191	193	149	149
162	WSP12	E71	WSP	104	104	237	237	192	192	106	110	160	163	176	184	165	166	204	216	220	223	195	195	149	155
163	WSP12	E72	WSP	104	104	240	240	000	000	106	110	158	163	176	184	165	170	204	204	220	223	191	193	155	155
164	WSP13	E73	WSP	104	104	234	237	189	189	106	110	160	163	182	184	167	160	204	216	220	223	193	193	149	149
165	WSP13	E74	WSP	104	104	237	237	189	201	106	106	164	163	182	184	163	166	204	216	220	223	193	195	149	149
166	WSP14	E75	WSP	100	100	234	240	192	195	106	106	166	163	176	182	189	170	200	204	220	223	195	195	149	161
167	WSP14	E76	WSP	100	104	237	237	195	195	106	106	164	165	176	182	189	168	204	216	220	223	195	195	149	149
168	WSP15	E77	WSP	100	104	240	240	189	201	106	110	158	163	174	174	163	166	204	204	223	227	191	193	149	149
169	WSP15	E78	WSP	100	104	237	240	192	201	110	110	158	163	174	174	165	166	204	204	223	227	193	195	149	149
170	WSP16	E81	WSP	104	104	234	243	192	195	110	110	160	163	174	184	167	164	204	216	220	223	193	195	149	149
171	WSP16	E82	WSP	104	104	234	243	192	195	106	106	166	163	176	186	165	166	204	216	220	223	193	195	149	161
172	WSP17	E83	WSP	100	104	237	240	192	192	106	110	164	187	176	184	189	170	200	200	223	227	193	195	149	149
173	WSP17	E84	WSP	100	104	237	240	192	192	106	106	158	171	176	184	189	164	204	204	223	227	193	195	149	149
174	WSP18	E85	WSP	100	104	237	237	192	192	106	106	164	177	184	184	177	166	204	204	223	223	191	193	149	161
175	WSP18	E86	WSP	100	104	234	237	192	192	106	106	166	163	176	184	163	168	204	204	223	223	193	193	149	161
176	WSP19	E89	WSP	100	104	237	240	192	192	100	106	166	163	174	186	165	168	200	204	223	223	193	193	149	149
177	WSP19	E90	WSP	100	100	237	240	192	192	106	110	160	163	176	186	165	162	204	204	223	223	191	193	149	149
178	WSP20	E91	WSP	100	104	237	240	189	192	106	106	164	163	176	184	165	164	200	216	220	223	193	195	149	155
179	WSP20	E92	WSP	104	104	237	240	189	192	106	106	162	165	176	176	181	166	204	216	220	220	195	195	149	149

n	Nest ID	Individual ID	Population	Aa02		HfC1E6		HfC1D10		Aa26		HfC7E1		Aa39		HfC4G1		HfP2E11		HfC7G4		HfC2D4		HfC5D4	
180	WSP21	E95	WSP	100	104	237	237	192	192	106	106	166	165	174	184	167	166	204	216	220	220	193	193	149	149
181	WSP21	E96	WSP	104	104	237	237	192	192	106	110	166	165	176	176	165	166	204	206	220	223	193	193	149	149
182	WSP22	E97	WSP	100	100	237	240	201	201	106	106	164	163	174	182	163	164	200	204	223	223	195	195	149	149
183	WSP22	E98	WSP	100	104	237	237	192	192	106	110	000	163	176	184	163	000	000	000	220	223	000	000	149	149
184	WSP23	E99	WSP	104	104	237	237	192	192	110	110	166	163	174	184	163	166	200	206	220	220	193	193	149	149
185	WSP23	E100	WSP	104	104	237	237	192	192	110	110	164	163	176	184	167	166	200	206	223	223	193	193	149	149
186	WSP24	E112	WSP	100	104	237	240	189	195	106	106	160	163	176	184	171	166	200	204	223	223	193	193	151	155
187	WSP24	E113	WSP	100	104	237	240	189	195	106	106	166	163	176	184	167	168	200	204	223	223	193	193	155	155
188	WSP25	E6	WSP	100	104	234	237	189	201	106	106	160	163	176	182	167	164	200	200	220	223	193	195	149	161
189	WSP26	E9	WSP	100	104	237	240	192	192	106	110	160	163	184	186	167	170	204	204	220	223	193	193	149	161
190	WSP27	E10	WSP	104	104	237	240	192	195	106	106	160	165	176	184	165	164	204	204	223	223	191	193	149	161
191	WSP28	E20	WSP	100	104	237	237	192	192	106	110	000	165	176	184	165	000	200	204	220	223	193	195	149	155
192	WSP29	E40	WSP	104	104	237	240	192	192	106	106	000	163	184	186	163	000	204	204	220	223	191	195	149	149
193	WSP30	E42	WSP	100	104	237	237	192	192	106	106	166	163	174	184	167	168	204	204	223	223	195	195	149	149
194	WSP31	E45	WSP	104	104	237	240	192	192	106	106	158	171	184	184	187	164	200	204	220	220	191	193	149	149
195	WSP32	E47	WSP	104	104	237	240	192	192	106	106	164	165	176	184	165	164	204	204	220	223	193	195	149	155
196	WSP33	E59	WSP	100	100	240	240	189	192	106	110	158	167	174	176	167	166	204	204	223	223	191	193	149	155
197	WSP34	E64	WSP	104	104	237	240	192	192	110	110	166	163	174	184	167	166	208	208	223	223	193	195	149	149
198	WSP35	E79	WSP	100	104	240	240	192	192	106	110	158	163	174	182	165	158	204	216	220	220	193	195	149	149
199	WSP36	E87	WSP	104	104	237	237	192	192	106	110	000	163	174	176	165	000	204	204	223	223	193	193	149	149
200	WSP37	E93	WSP	100	100	237	240	192	192	000	000	166	165	184	186	167	166	204	204	220	223	195	195	149	149
201	WSP38	E94	WSP	100	100	237	240	189	192	106	106	158	163	174	184	165	166	204	204	223	223	191	193	149	149
202	WSP39	E101	WSP	100	104	240	240	195	195	110	110	164	163	176	186	167	166	204	204	220	223	193	193	149	149
203	WSP40	E102	WSP	100	100	237	237	192	192	106	110	166	163	184	184	167	168	204	206	220	223	191	195	149	149
204	WSP41	E114	WSP	100	100	234	237	192	192	106	110	160	163	176	176	165	160	204	204	220	223	191	195	149	155
205	WSP42	E115	WSP	100	100	237	240	192	195	106	106	164	163	176	182	165	166	204	204	220	223	193	193	149	149
206	WSP43	E116	WSP	100	100	237	240	192	195	106	106	158	167	176	186	167	160	204	216	220	227	193	193	155	161
207	WSP44	E117	WSP	104	104	234	237	192	195	106	106	164	167	184	184	189	166	200	204	223	223	193	195	149	161
208	WSP45	E118	WSP	100	100	234	237	192	192	106	106	164	163	176	176	171	170	200	204	220	220	193	193	149	149
209	WSP46	E119	WSP	104	104	237	240	189	192	106	106	166	163	176	184	167	166	204	204	223	223	193	195	149	161
210	WSP47	E121	WSP	100	104	237	237	192	192	100	110	160	165	176	184	171	166	204	216	223	223	193	193	155	155
211	WSP48	E122	WSP	100	104	234	237	189	192	110	110	162	163	176	184	163	166	204	204	220	223	191	191	149	155
212	WSP49	E27	WSP	100	100	237	237	192	195	100	110	158	167	176	184	177	168	000	000	223	223	195	195	149	149
213	WSP50	E35	WSP	104	104	234	237	192	192	106	106	166	163	176	176	167	168	204	204	223	223	193	191	149	149
214	ESP1	L1	ESP	100	104	240	243	189	192	106	106	160	167	176	184	179	164	200	204	220	223	193	195	149	149
215	ESP2	L2	ESP	100	104	237	243	192	192	106	106	160	167	182	184	179	170	204	204	223	223	193	195	149	155
216	ESP3	L3	ESP	104	104	240	240	189	192	106	110	164	163	176	184	167	166	204	206	223	223	195	195	149	161
217	ESP4	L4	ESP	104	104	240	240	189	192	110	110	164	163	176	176	167	166	206	206	223	223	195	195	149	161
218	ESP5	L51	ESP	100	104	234	237	192	192	106	106	166	161	176	186	163	170	200	204	220	223	195	195	149	149
219	ESP6	L52	ESP	104	104	000	000	192	192	110	110	158	163	184	184	167	166	200	206	223	223	191	193	151	151
220	ESP7	L53	ESP	104	104	234	237	192	192	106	110	158	165	176	184	167	166	204	206	220	223	195	195	151	151
221	ESP8	L7	ESP	104	104	237	237	192	192	106	110	158	163	176	176	179	166	206	206	220	220	195	195	149	155
222	ESP9	L8	ESP	104	104	237	240	192	192	106	110	158	163	174	176	179	166	206	206	220	223	195	195	149	155
223	ESP10	L5	ESP	104	104	234	234	192	192	110	110	164	163	176	176	163	166	206	206	223	223	195	195	149	149
224	ESP11	L6	ESP	104	104	234	237	192	192	106	110	164	163	176	184	165	166	204	206	223	223	193	195	149	161
225	ESP12	L9	ESP	100	104	237	237	192	204	106	110	164	163	182	182	165	166	200	204	220	223	191	191	149	149

n	Nest ID	Individual ID	Population	Aa02		HfC1E6		HfC1D10		Aa26		HfC7E1		Aa39		HfC4G1		HfP2E11		HfC7G4		HfC2D4		HfC5D4	
226	CSP1	E12	CSP	104	104	234	240	192	192	106	110	158	163	176	186	165	164	204	216	223	223	191	193	149	149
227	CSP2	E50	CSP	100	104	234	237	192	192	106	110	158	163	184	184	163	166	204	216	220	220	193	195	149	155
228	CSP3	E51	CSP	104	104	237	240	192	192	106	110	160	163	184	184	163	168	204	204	220	223	193	195	151	155
229	CSP4	E52	CSP	100	100	234	237	192	195	106	110	160	163	182	186	163	172	200	200	223	223	193	195	149	149
230	CSP5	E53	CSP	104	104	237	237	192	192	100	106	000	163	176	184	163	000	206	214	220	223	193	193	161	161
231	CSP6	E54	CSP	104	104	237	237	192	192	100	100	160	163	182	184	171	170	200	206	220	220	193	193	149	161
232	MOR1	L43	MOR	100	104	237	237	192	192	106	106	158	163	182	184	169	164	204	214	223	223	193	193	149	149
233	MOR2	L44	MOR	100	100	237	240	192	192	106	110	160	167	176	184	169	160	200	214	220	223	193	193	149	149
234	MOR3	L45	MOR	100	104	237	237	192	195	106	106	158	163	174	182	167	162	204	204	223	227	193	195	149	149
235	MOR4	L46	MOR	104	104	237	240	192	192	106	110	162	163	176	176	163	170	204	216	220	220	191	195	149	149
236	MOR5	L47	MOR	100	104	237	237	192	192	110	110	160	163	184	184	163	166	200	216	223	223	195	195	149	149
237	MOR6	L48	MOR	100	100	237	237	192	192	110	110	164	163	184	184	167	166	204	214	223	223	193	195	161	161
238	MOR7	L49	MOR	100	100	237	240	192	192	106	110	166	167	176	184	189	170	200	214	223	223	191	193	149	149
239	MOR8	L50	MOR	100	104	240	240	192	192	106	110	160	163	176	184	171	160	200	216	227	227	193	195	149	149
240	CYP1	C1	CYP	100	104	234	234	192	192	110	110	160	163	182	182	167	168	204	204	223	223	193	195	155	155
241	CYP2	C2	CYP	104	104	234	240	189	192	100	110	164	165	182	184	167	166	204	216	223	223	193	193	155	155
242	CYP3	C3	CYP	104	104	237	243	189	189	100	110	164	165	182	182	167	166	204	216	223	223	193	193	155	155
243	CYP4	C4	CYP	104	104	234	243	189	189	110	110	160	163	182	182	165	166	204	208	220	220	000	000	155	155
244	CYP5	C5	CYP	100	104	240	243	189	192	110	110	160	163	182	182	163	168	200	204	223	223	000	000	155	155
245	CYP6	C6	CYP	100	100	240	243	192	192	110	110	160	163	182	184	165	160	200	204	223	223	000	000	146	155

n	Nest ID	Individual ID	Population	HfC8F4		HfC11D4		HfC1D2		HfC6C4		HfC3F2		HfP1A10	
1	SWP1	A62	SWP	244	248	247	247	161	175	173	173	179	193	273	279
2	SWP1	A71	SWP	244	244	247	247	161	161	167	173	179	179	279	279
3	SWP1	A72	SWP	248	248	247	247	161	175	167	173	179	193	273	279
4	SWP2	A16	SWP	244	248	245	247	161	175	165	173	193	193	279	279
5	SWP2	A38	SWP	244	248	245	247	161	161	165	173	179	179	279	279
6	SWP2	A47	SWP	244	248	245	247	161	175	165	173	179	193	279	279
7	SWP2	A57	SWP	244	248	245	247	161	161	165	173	179	193	279	279
8	SWP2	A69	SWP	244	248	245	247	161	175	165	173	193	193	279	279
9	SWP2	A70	SWP	244	248	247	247	161	161	165	173	179	193	279	279
10	SWP3	A6	SWP	244	248	243	245	161	161	173	173	179	179	249	277
11	SWP3	A8	SWP	244	248	245	245	161	175	173	173	179	193	249	273
12	SWP3	A19	SWP	244	248	247	247	161	161	171	173	179	179	273	279
13	SWP3	A20	SWP	244	244	245	247	161	161	167	171	179	179	249	277
14	SWP3	A54	SWP	244	248	245	247	161	161	167	167	179	179	277	279
15	SWP4	A4	SWP	244	248	247	247	161	161	167	173	179	179	273	279
16	SWP4	A29	SWP	244	248	247	247	161	161	173	197	179	187	273	279
17	SWP4	A30	SWP	248	248	243	245	161	161	167	173	179	187	273	279
18	SWP4	A60	SWP	248	248	247	247	161	161	173	197	179	179	273	273
19	SWP4	A61	SWP	248	248	247	247	161	175	173	197	187	193	273	279
20	SWP5	A10	SWP	244	244	247	247	161	175	173	183	179	193	275	277
21	SWP5	A11	SWP	244	244	245	245	175	175	173	183	179	181	277	279
22	SWP5	A21	SWP	244	244	245	247	161	175	173	183	179	193	279	279
23	SWP5	A22	SWP	248	248	245	245	161	175	173	197	179	193	279	279
24	SWP5	A31	SWP	244	244	245	245	161	175	173	173	179	193	279	279
25	SWP5	A32	SWP	244	244	245	247	175	175	165	173	179	193	275	277
26	SWP5	A48	SWP	244	244	247	247	175	175	173	173	179	193	277	279
27	SWP5	A49	SWP	244	244	247	247	175	175	173	173	179	193	277	279
28	SWP5	A56	SWP	244	244	247	247	161	175	173	173	179	181	275	277
29	SWP5	A80	SWP	244	244	245	247	175	175	173	183	179	193	279	279
30	SWP6	A1	SWP	244	244	245	245	161	161	167	173	179	187	279	279
31	SWP6	A14	SWP	244	248	245	247	161	171	173	173	179	191	279	279
32	SWP7	A42	SWP	244	244	245	245	161	161	167	173	179	179	277	279
33	SWP7	A64	SWP	244	244	245	245	161	161	167	173	179	193	273	279
34	SWP8	A7	SWP	244	244	247	247	161	161	165	183	179	179	279	279
35	SWP8	A9	SWP	244	244	245	245	161	181	167	167	175	179	279	279
36	SWP8	A25	SWP	244	244	245	245	161	181	165	167	175	179	279	279
37	SWP8	A74	SWP	244	248	247	247	161	161	165	173	179	179	273	279
38	SWP8	A75	SWP	244	248	247	247	161	181	165	173	175	179	279	279
39	SWP9	A43	SWP	244	248	245	247	161	161	167	173	179	179	279	279
40	SWP9	A55	SWP	244	244	245	247	161	175	167	173	179	193	273	279
41	SWP9	A76	SWP	244	248	245	247	161	175	173	183	179	193	279	279
42	SWP9	A77	SWP	244	244	245	245	161	175	167	167	179	193	279	279
43	SWP10	A12	SWP	244	248	245	245	161	175	165	173	179	193	279	279
44	SWP10	A23	SWP	244	244	245	247	161	175	165	173	179	193	277	279
45	SWP10	A24	SWP	244	244	245	245	161	175	165	173	179	193	279	279
46	SWP10	A40	SWP	244	244	245	247	161	175	165	197	193	193	279	279

n	Nest ID	Individual ID	Population	HfC8F4		HfC11D4		HfC1D2		HfC6C4		HfC3F2		HfP1A10	
47	SWP10	A41	SWP	244	244	245	247	161	161	165	197	179	193	279	279
48	SWP10	A52	SWP	244	244	245	247	161	175	165	197	193	193	279	279
49	SWP10	A67	SWP	244	244	247	247	175	175	171	197	181	181	249	279
50	SWP10	A68	SWP	244	244	247	247	161	161	167	197	193	196	279	279
51	SWP11	A53	SWP	244	248	247	247	161	161	167	173	179	179	279	279
52	SWP11	A63	SWP	244	248	247	247	161	161	173	173	179	179	279	279
53	SWP12	A35	SWP	244	244	245	247	161	161	171	183	179	179	273	279
54	SWP12	A36	SWP	244	244	245	245	161	161	165	183	179	179	273	279
55	SWP12	A44	SWP	244	244	245	247	161	161	165	167	179	179	277	279
56	SWP13	A5	SWP	248	248	245	245	161	175	167	171	179	193	273	279
57	SWP13	A15	SWP	244	248	245	245	161	175	167	173	179	193	273	279
58	SWP13	A39	SWP	244	248	245	245	161	175	167	171	179	193	273	279
59	SWP13	A50	SWP	248	248	245	245	161	175	167	167	179	193	279	279
60	SWP13	A51	SWP	244	244	247	247	161	175	173	173	179	193	273	279
61	SWP14	A2	SWP	244	248	247	247	161	161	173	173	179	179	279	279
62	SWP14	A3	SWP	248	248	245	245	161	175	173	173	179	193	279	279
63	SWP14	A26	SWP	244	244	247	247	161	175	173	173	179	193	279	279
64	SWP14	A27	SWP	244	244	247	247	161	161	173	183	179	179	279	279
65	SWP14	A28	SWP	244	248	247	247	161	175	173	183	179	193	279	279
66	SWP14	A58	SWP	248	248	247	247	161	175	173	173	179	193	279	279
67	SWP14	A59	SWP	244	244	247	247	161	161	173	173	179	179	279	279
68	SWP14	A78	SWP	244	248	247	247	161	161	173	183	179	179	279	279
69	SWP14	A79	SWP	244	248	247	247	161	161	173	183	179	179	279	279
70	SWP15	A13	SWP	248	248	247	247	161	175	165	173	193	193	273	279
71	SWP15	A17	SWP	244	248	247	247	161	175	165	197	179	193	279	279
72	SWP15	A18	SWP	248	248	247	247	161	175	173	197	179	193	279	279
73	SWP16	A65	SWP	244	244	245	247	161	161	165	173	179	179	277	279
74	SWP16	A66	SWP	244	244	245	247	161	175	165	171	179	193	249	279
75	SWP17	A33	SWP	244	244	245	247	161	161	167	167	179	179	279	279
76	SWP17	A34	SWP	244	244	245	247	161	181	167	173	175	179	279	279
77	SWP17	A45	SWP	244	248	245	247	161	181	167	167	175	179	279	279
78	SWP18	A73	SWP	244	248	247	247	161	175	167	183	179	179	279	279
79	SWP19	A37	SWP	244	244	245	247	175	175	165	173	193	193	275	277
80	NEP1	T1	NEP	244	248	247	247	175	175	165	165	179	181	269	289
81	NEP1	T2	NEP	244	244	247	247	163	175	159	169	179	193	269	285
82	NEP1	T13	NEP	244	244	247	247	161	175	165	165	181	196	269	285
83	NEP1	T14	NEP	244	244	245	247	161	163	159	201	193	196	269	285
84	NEP1	T31	NEP	244	248	245	245	161	173	165	171	179	197	245	275
85	NEP1	T32	NEP	244	248	245	245	161	173	159	171	179	181	269	275
86	NEP2	T3	NEP	244	244	245	247	161	175	159	197	193	193	279	279
87	NEP2	T4	NEP	244	244	247	247	161	175	165	165	193	193	275	279
88	NEP3	T5	NEP	244	244	245	245	161	161	167	199	187	193	279	279
89	NEP3	T6	NEP	244	244	245	247	161	161	159	199	187	196	279	279
90	NEP3	T22	NEP	244	244	245	247	175	181	165	195	179	191	279	281
91	NEP3	T23	NEP	244	244	245	247	175	175	165	195	179	191	279	281
92	NEP3	T28	NEP	244	244	245	247	175	175	165	167	175	179	273	277
93	NEP3	T29	NEP	244	244	245	245	171	175	197	197	179	191	279	279

n	Nest ID	Individual ID	Population	HfC8F4		HfC11D4		HfC1D2		HfC6C4		HfC3F2		HfP1A10	
94	NEP4	T7	NEP	244	244	245	245	175	181	179	199	179	181	279	279
95	NEP5	T8	NEP	244	244	245	247	175	175	159	199	179	181	249	279
96	NEP5	T9	NEP	244	244	247	247	161	175	197	199	179	196	275	279
97	NEP6	T11	NEP	244	252	245	247	161	175	199	201	181	189	249	279
98	NEP6	T12	NEP	244	252	247	247	175	175	179	201	175	181	249	279
99	NEP7	T15	NEP	244	244	245	245	175	175	159	199	179	181	275	279
100	NEP8	T17	NEP	244	252	247	247	175	181	171	193	175	179	271	277
101	NEP8	T18	NEP	244	244	247	247	173	181	165	191	179	197	279	279
102	NEP9	T19	NEP	244	244	245	245	173	181	191	197	179	196	279	279
103	NEP10	T20	NEP	244	248	245	245	161	173	167	191	181	181	279	289
104	NEP11	T21	NEP	244	246	245	247	175	175	169	193	175	193	279	279
105	NEP12	T24	NEP	244	246	245	247	173	181	171	193	175	179	245	249
106	NEP13	T25	NEP	244	252	245	245	173	181	165	165	175	179	245	279
107	NEP13	T26	NEP	244	244	245	245	175	181	171	191	181	196	263	277
108	NEP14	T27	NEP	244	244	245	247	161	173	165	201	179	179	245	279
109	NEP15	T30	NEP	244	244	245	245	161	173	167	175	179	179	277	277
110	NEP16	T33	NEP	244	252	243	245	175	175	193	195	197	197	245	279
111	NEP17	T34	NEP	244	252	245	245	175	175	165	197	179	193	245	273
112	NEP18	T35	NEP	244	244	243	245	173	175	159	197	179	179	263	277
113	NEP19	T36	NEP	244	244	243	243	175	175	165	165	181	197	245	277
114	SWSP1	L12	SWSP	244	244	245	247	173	173	159	165	179	193	249	271
115	SWSP1	L13	SWSP	244	244	247	247	161	173	165	165	179	196	279	279
116	SWSP2	L15	SWSP	244	244	245	247	161	175	165	197	179	196	263	269
117	SWSP3	L16	SWSP	244	244	245	245	161	175	169	171	193	198	245	279
118	SWSP4	L17	SWSP	248	248	247	247	173	175	173	197	179	195	249	289
119	SWSP5	L18	SWSP	244	246	247	247	161	181	167	179	175	196	271	273
120	SWSP6	L19	SWSP	244	244	245	247	175	181	165	203	196	196	249	269
121	SWSP7	L20	SWSP	244	244	247	249	161	181	171	173	196	196	279	279
122	SWSP8	L21	SWSP	244	244	247	247	161	187	165	165	197	197	279	289
123	SWSP9	L22	SWSP	244	244	247	249	161	175	165	171	196	196	273	277
124	SWSP10	L23	SWSP	248	252	247	247	161	175	165	203	179	196	249	277
125	SWSP10	L24	SWSP	248	252	247	247	161	175	165	203	179	196	249	277
126	SWSP11	L25	SWSP	244	244	247	247	161	187	165	165	196	196	279	289
127	SWSP11	L26	SWSP	244	244	247	247	181	187	165	165	195	195	279	289
128	SWSP12	L27	SWSP	244	244	247	247	161	173	183	203	196	196	273	277
129	SWSP13	L28	SWSP	244	244	247	249	173	181	173	197	179	196	249	263
130	SWSP14	L29	SWSP	244	244	247	249	161	187	165	171	179	196	273	277
131	SWSP14	L30	SWSP	244	244	247	249	161	187	165	171	179	195	277	277
132	SWSP15	L33	SWSP	244	248	247	247	161	181	167	171	175	196	249	277
133	SWSP16	L34	SWSP	244	248	245	247	163	175	171	173	193	195	263	269
134	SWSP17	L35	SWSP	244	244	247	247	161	175	167	171	196	196	271	273
135	SWSP18	L36	SWSP	246	248	245	247	161	175	197	203	196	196	249	273
136	SWSP18	L37	SWSP	244	244	245	247	161	175	197	203	196	196	273	273
137	SWSP19	L38	SWSP	244	244	247	247	175	175	165	193	179	179	263	289
138	SWSP20	L39	SWSP	244	248	245	247	161	175	167	203	179	196	269	277
139	SWSP20	L40	SWSP	248	252	245	247	161	175	167	171	179	196	269	279
140	WSP1	E4	WSP	244	244	247	247	175	175	165	197	179	193	245	273

n	Nest ID	Individual ID	Population	HfC8F4		HfC11D4		HfC1D2		HfC6C4		HfC3F2		HfP1A10	
141	WSP1	E5	WSP	244	244	247	247	175	175	193	195	196	196	245	279
142	WSP2	E7	WSP	248	248	247	247	175	175	165	191	196	196	263	289
143	WSP2	E8	WSP	244	248	247	247	175	175	165	191	175	196	263	263
144	WSP3	E22	WSP	244	244	245	247	161	161	201	201	196	196	279	279
145	WSP3	E23	WSP	244	244	245	247	161	161	159	201	196	196	249	279
146	WSP4	E43	WSP	244	244	245	247	161	175	167	199	181	193	279	279
147	WSP4	E44	WSP	244	244	245	245	161	161	159	197	187	187	249	285
148	WSP5	E48	WSP	244	248	247	247	161	175	159	167	181	196	275	279
149	WSP5	E49	WSP	244	244	247	247	173	181	171	193	175	179	271	277
150	WSP6	E55	WSP	244	244	245	247	161	175	159	167	181	196	275	279
151	WSP6	E56	WSP	244	248	245	247	175	175	165	191	179	196	279	287
152	WSP7	E57	WSP	244	244	245	245	161	177	159	191	191	193	279	279
153	WSP7	E58	WSP	244	244	245	247	175	181	165	191	175	179	271	277
154	WSP8	E62	WSP	244	252	247	247	161	175	165	187	179	193	245	269
155	WSP8	E63	WSP	244	244	247	247	161	175	165	187	175	196	245	263
156	WSP9	E65	WSP	244	252	245	247	173	181	201	203	179	196	279	279
157	WSP9	E66	WSP	244	252	245	247	175	181	183	197	179	196	279	279
158	WSP10	E67	WSP	244	244	247	247	161	187	169	197	196	196	273	289
159	WSP10	E68	WSP	244	244	247	247	161	175	165	169	175	196	279	289
160	WSP11	E69	WSP	244	244	245	247	175	181	193	199	196	196	245	279
161	WSP11	E70	WSP	244	244	245	247	181	181	193	197	181	191	273	279
162	WSP12	E71	WSP	244	244	245	247	173	181	165	165	179	179	277	281
163	WSP12	E72	WSP	244	248	247	247	173	175	165	165	191	196	273	281
164	WSP13	E73	WSP	244	244	247	247	175	181	165	199	181	195	273	279
165	WSP13	E74	WSP	244	252	247	247	175	181	193	199	181	181	279	279
166	WSP14	E75	WSP	244	248	247	247	161	173	159	165	179	181	245	275
167	WSP14	E76	WSP	244	246	247	247	161	173	165	171	179	181	245	269
168	WSP15	E77	WSP	244	248	247	247	161	181	167	201	179	179	279	279
169	WSP15	E78	WSP	244	248	247	247	161	181	165	171	179	179	263	279
170	WSP16	E81	WSP	244	252	247	247	175	175	195	201	179	195	263	289
171	WSP16	E82	WSP	244	252	247	247	175	181	195	201	179	195	279	289
172	WSP17	E83	WSP	244	248	245	245	161	181	159	199	175	179	249	279
173	WSP17	E84	WSP	244	244	245	247	161	161	199	201	179	196	249	279
174	WSP18	E85	WSP	244	248	245	247	175	175	165	191	179	179	263	269
175	WSP18	E86	WSP	244	248	247	247	175	175	167	167	179	179	269	279
176	WSP19	E89	WSP	244	244	247	247	175	181	171	203	179	196	245	249
177	WSP19	E90	WSP	244	244	245	247	175	181	171	201	179	196	245	249
178	WSP20	E91	WSP	244	244	245	247	173	181	165	197	175	179	279	289
179	WSP20	E92	WSP	244	244	245	247	175	181	165	165	175	179	245	279
180	WSP21	E95	WSP	244	244	245	247	175	175	159	165	181	195	279	279
181	WSP21	E96	WSP	244	244	247	247	175	181	159	197	179	195	279	279
182	WSP22	E97	WSP	244	248	247	247	161	181	191	201	179	196	279	279
183	WSP22	E98	WSP	244	244	247	247	173	181	165	165	179	196	245	249
184	WSP23	E99	WSP	244	244	245	245	175	175	165	199	179	195	277	277
185	WSP23	E100	WSP	244	244	245	245	173	175	165	199	179	195	277	289
186	WSP24	E112	WSP	244	248	247	247	161	181	191	201	179	191	269	279
187	WSP24	E113	WSP	244	248	247	247	161	161	191	201	179	187	263	279

n	Nest ID	Individual ID	Population	HfC8F4		HfC11D4		HfC1D2		HfC6C4		HfC3F2		HfP1A10	
188	WSP25	E6	WSP	244	252	247	247	175	175	165	165	179	198	273	277
189	WSP26	E9	WSP	244	244	245	247	175	181	165	197	179	179	245	289
190	WSP27	E10	WSP	244	244	245	247	161	175	171	199	181	187	279	279
191	WSP28	E20	WSP	244	244	247	247	181	181	171	201	171	201	249	279
192	WSP29	E40	WSP	248	252	247	247	173	181	165	171	179	191	263	279
193	WSP30	E42	WSP	244	244	247	247	161	161	167	199	187	193	279	279
194	WSP31	E45	WSP	244	244	247	247	161	175	199	199	196	196	275	279
195	WSP32	E47	WSP	244	244	247	247	161	161	159	191	179	193	279	279
196	WSP33	E59	WSP	244	252	245	247	181	187	197	201	196	196	263	279
197	WSP34	E64	WSP	244	244	247	247	175	175	165	165	179	198	245	273
198	WSP35	E79	WSP	248	252	245	247	175	181	171	191	179	179	263	277
199	WSP36	E87	WSP	244	244	245	245	175	181	167	171	175	179	245	277
200	WSP37	E93	WSP	244	244	245	245	175	175	165	191	175	179	245	279
201	WSP38	E94	WSP	244	244	247	247	175	181	171	201	175	179	249	279
202	WSP39	E101	WSP	244	248	245	247	175	181	165	193	175	181	263	279
203	WSP40	E102	WSP	244	244	247	247	173	175	197	201	179	179	263	279
204	WSP41	E114	WSP	244	244	247	247	175	181	165	197	196	196	279	289
205	WSP42	E115	WSP	244	244	247	247	161	161	159	167	196	196	277	279
206	WSP43	E116	WSP	244	244	245	247	161	175	177	201	179	195	263	279
207	WSP44	E117	WSP	244	244	245	247	161	175	191	191	175	193	279	279
208	WSP45	E118	WSP	244	248	247	247	175	181	165	201	181	191	277	279
209	WSP46	E119	WSP	244	244	247	247	161	175	165	197	179	196	279	279
210	WSP47	E121	WSP	244	244	247	247	177	181	171	171	175	191	263	263
211	WSP48	E122	WSP	244	244	247	247	173	181	165	171	179	196	279	289
212	WSP49	E27	WSP	244	248	247	247	161	181	167	197	179	196	249	279
213	WSP50	E35	WSP	244	248	245	247	161	175	167	201	179	193	245	279
214	ESP1	L1	ESP	248	252	245	245	175	175	165	179	179	198	271	279
215	ESP2	L2	ESP	244	248	245	247	161	175	165	165	179	198	279	279
216	ESP3	L3	ESP	244	246	245	247	161	175	165	181	179	179	279	281
217	ESP4	L4	ESP	244	244	247	247	161	161	165	181	175	179	271	277
218	ESP5	L51	ESP	244	244	245	247	175	187	167	171	179	195	287	289
219	ESP6	L52	ESP	244	244	245	245	163	175	165	197	191	193	273	279
220	ESP7	L53	ESP	244	252	247	247	161	175	165	197	193	196	273	279
221	ESP8	L7	ESP	244	244	245	247	161	175	167	197	179	193	269	289
222	ESP9	L8	ESP	244	244	247	247	161	175	165	197	179	193	269	269
223	ESP10	L5	ESP	244	244	247	249	173	173	165	165	193	196	279	279
224	ESP11	L6	ESP	244	244	245	249	173	175	165	191	193	196	279	279
225	ESP12	L9	ESP	244	248	247	247	161	161	167	179	175	196	245	275
226	CSP1	E12	CSP	244	248	245	247	175	175	169	197	181	181	279	289
227	CSP2	E50	CSP	244	248	247	247	161	161	167	199	187	193	279	279
228	CSP3	E51	CSP	248	248	247	247	161	161	167	199	187	193	279	279
229	CSP4	E52	CSP	244	248	247	247	175	181	159	165	179	193	279	289
230	CSP5	E53	CSP	244	244	245	247	161	175	167	175	193	196	279	289
231	CSP6	E54	CSP	244	244	245	247	161	161	159	165	193	193	249	275
232	MOR1	L43	MOR	244	248	245	247	161	161	197	207	179	179	271	291
233	MOR2	L44	MOR	244	248	247	249	175	189	159	159	179	196	273	273
234	MOR3	L45	MOR	244	244	247	249	161	175	159	189	196	196	249	277
235	MOR4	L46	MOR	244	244	245	247	161	161	169	193	179	179	275	287

n	Nest ID	Individual ID	Population	HfC8F4		HfC11D4		HfC1D2		HfC6C4		HfC3F2		HfP1A10	
236	MOR5	L47	MOR	244	244	245	247	161	175	171	185	179	196	249	277
237	MOR6	L48	MOR	244	248	245	247	161	161	175	195	179	195	269	277
238	MOR7	L49	MOR	244	244	245	247	161	161	179	199	179	196	279	291
239	MOR8	L50	MOR	244	252	247	247	175	175	159	189	179	179	249	279
240	CYP1	C1	CYP	248	248	249	249	175	175	203	203	179	181	273	279
241	CYP2	C2	CYP	248	248	249	249	161	161	167	195	193	193	279	279
242	CYP3	C3	CYP	246	252	249	249	161	161	167	195	175	193	279	279
243	CYP4	C4	CYP	246	246	249	249	161	175	185	203	179	193	279	279
244	CYP5	C5	CYP	248	252	249	249	000	000	000	000	000	000	000	000
245	CYP6	C6	CYP	248	252	249	249	161	175	167	195	181	181	273	279