

1 Bottlenecks, remoteness and admixture shape genetic variation in island populations of Atlantic
2 and Mediterranean common kestrels (*Falco tinnunculus*)

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17 ABSTRACT

18 We studied genetic diversity and differentiation in island and nearby continental populations of a bird of
19 prey, the common kestrel (*Falco tinnunculus*). We sampled 11 islands in the Eastern North Atlantic ([Madeira](#)
20 [and Canary Islands](#)) and Western Mediterranean archipelagos ([Balearic Islands](#)) and two continental sites
21 ([Iberian Peninsula and North-West Africa](#)). We used microsatellite (9 loci, N = 470) and mitochondrial data
22 (cytochrome b sequences, N = 244) and applied Bayesian clustering, multivariate frequentist statistics and
23 coalescence analyses. We revealed two main genetic clusters; the first including populations from the
24 Atlantic islands and the second comprising populations from the Balearic Islands, the Iberian Peninsula and
25 North-West Africa, with additional finer scale structuring. The highest levels of genetic variation were found
26 in Iberian Peninsula, North-[West Africa](#) and Lanzarote island. The lowest diversity was detected in La Palma,
27 the most north-westerly island of the Canary Islands. The lowest levels of haplotype and nucleotide diversity
28 were observed in Madeira and Gran Canaria and the highest in Menorca. We found evidence of decreasing
29 genetic diversity with increasing severity of a past population bottleneck and, to some extent, with increasing
30 geographic distance from the continent. The two Canary Island subspecies, *F. t. dacotiae* and *F. t. canariensis*,
31 have diverged from each other to some degree and from the continental and Balearic conspecifics of *F. t.*
32 *tinnunculus*. Samples from Madeira, representing *F. t. canariensis*, indicated affinities to both Canary Islands
33 and Mediterranean clusters, depending on the marker and methods applied. Our results suggest stronger
34 gene flow between close islands than between distant islands. The genetic structure of an endemic
35 subspecies *F. t. dacotiae* in the easternmost Canary Islands is suggested to have an origin in a past
36 hybridization between continental *F. t. tinnunculus* and insular *F. t. canariensis*.

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40 INTRODUCTION

41 Island phylogeography has been intensively studied during the last decades, especially on oceanic
42 archipelagos such as Hawaii, Galapagos and those of the Macaronesian region (Shaw and Gillespie 2016).
43 This is because islands often show simpler patterns of evolutionary processes than those observed in
44 continental sites and therefore offer more explicit study systems. Furthermore, oceanic islands form clear
45 areal boundaries. Many of them are geographically small and isolated and their geological ages and histories
46 are rather well known. Thus, biological phenomena, such as colonizations and evolutionary radiations, can
47 often be connected with historical events, e.g. the emergence of islands, catastrophes or changes in habitats
48 (Emerson 2002).

49 According to the Theory of Island Biogeography (MacArthur and Wilson 1967), extinctions and
50 colonizations of islands depend on the distance and size of an island. Islands that are small-sized and distant
51 from the continent have less species than islands that are larger and closer to the continent. This original
52 theory can be modified to other levels of biodiversity and species diversity replaced with genetic diversity,
53 because it has been shown to correlate well with genetic diversity in island habitats (Vellend and Geber 2005).
54 Consequently, the theory would predict that genetic diversity correlates negatively with the distance to the
55 continent and positively with the island size. Island populations lose genetic variation through founder
56 effect and by genetic drift due to small population sizes. In fact, they have commonly been found to harbour
57 less genetic variation than their continental counterparts (Frankham 1997). However, gene flow can
58 effectively counteract the loss of variation as well as hinder genetic differentiation between populations
59 overtime. Gene flow results from dispersal, which in turn is affected by the spatial location of islands, winds
60 and ocean currents and the dispersal capacity, ecological requirements and biotic interactions of the taxa
61 considered (Whittaker 1998, Juan et al. 2000, Algar et al. 2013).

62 The Macaronesian Islands in the Atlantic Ocean and the Balearic Islands in the Mediterranean Sea are
63 located some 100–1300 km from the African and European continents and most of their terrestrial biota
64 originates from one or both continents. Further on, we describe in more detail the islands sampled in this

65 study. The Canary Islands are a group of volcanic islands, with the easternmost islands only about 100 km off
66 the coast of Morocco, North Africa. Their ages vary from the youngest, westernmost island of El Hierro (1.2
67 million years (My)) to the oldest, easternmost islands of Lanzarote (15.5 My) and Fuerteventura (22 My;
68 Coello et al. 1992). The Madeira Islands, volcanic as well, are located about 500 km north from Canary Islands
69 and about 700 km off the coast of Morocco. The oldest island, Porto Santo is estimated to be 11.1 – 14.3 My
70 old, the three small Desertas Islands 3.2– 3.6 My and the largest island, Madeira 4.6 – 0.18 My old
71 (Geldmacher et al. 2000). The Canary Islands particularly, have suffered several periods of volcanic activity
72 since their formation, except La Gomera (Juan et al. 2000). Though the Pleistocene glaciations did not reach
73 these islands, changes in sea level, ocean currents, trade winds and temperature (Rognon and Coudé-
74 Gausson 1995) caused repeated changes in the habitats (Rijsdijk et al. 2014).

75 Many of the extant bird species inhabiting these islands have colonized them in relatively recent times
76 (some 100 000 – 500 000 years ago). However, older colonization events have occurred, especially in extant
77 endemic species (up to 8,54 million years ago (Mya); Illera et al. 2012, Illera et al. 2016, Valente et al. 2017).
78 The Canary Islands and Madeira have been mostly colonized from Iberia and North-West Africa, due to their
79 proximity, prevailing winds and ocean currents (Juan et al. 2000). Phylogeographic studies have revealed a
80 complex series of colonizations, extinctions and contemporary gene flow in their biota, including strong
81 genetic differentiation among islands or no differentiation at all (Illera et al. 2012). The level of endemism in
82 this region is high; about 50% of the terrestrial invertebrates are endemic (Juan et al. 2000). Several endemic
83 species and subspecies of birds are presently recognized on the islands and many previously recognized
84 subspecies have recently been upgraded to species level due to their genetic, morphological and acoustic
85 distinctiveness (e.g. Helbig et al. 1996, Dietzen et al. 2003, Kvist et al. 2005, Päckert et al. 2006, Illera et al.
86 2007, Barrientos et al. 2009, González et al. 2009, Illera et al. 2011, Sangster et al. [2016](#), Illera et al. 2016).

87 Despite being situated in the Mediterranean, the Balearic Islands have been considered ‘ocean-like’
88 islands (Alcover et al. 1992) due to their long-distance to the mainland (about 100-200 km from the coast of
89 Spain). The Balearic Islands are remnants of an old mountain chain located between Iberia and southern

90 Europe until the early Oligocene (30 Mya), when the western Mediterranean basin began to form. During the
91 late Eocene, the access from the Mediterranean Sea to the Atlantic Ocean closed, leading to the Messinian
92 Salinity Crisis (MSC), desiccation of most of the Mediterranean Sea during Miocene. This ended, when the
93 present Gibraltar Strait opened some 5.3 Mya (García-Castellanos et al. 2009). In the Pleistocene, the region
94 was impacted by consecutive periods of cooling and warming of the climate due to the glacial cycles.

95 The present native fauna of the Balearic Islands is suggested to have arrived after the MSC (Bover et
96 al. 2008) and over time, the geographic isolation led to evolution of distinct faunal compositions in this area.
97 The distribution of the extant bird fauna does not seem to be related with the paleogeographic relationships
98 between the islands (Palmer et al. 1999). The Pleistocene bird communities were much the same as at
99 present, although there was more endemic avifauna in Middle and Late Pleistocene than today (Alcover et
100 al. 1992, Seguí and Alcover 1999) and changes in habitats after human colonization have had a profound
101 effect (Palmer et al. 1999). At present, there are only two endemic breeding bird species (The IUCN Red List
102 of Threatened Species, 2016), but several regional endemic subspecies have been recognized (GOB Grup
103 Balear d'Ornitologia I Defensa de la Naturalesa 2009).

104 The common kestrel (*Falco tinnunculus*, Linnaeus 1758; hereafter kestrel) is a small-sized diurnal bird
105 of prey inhabiting the Palaearctic, Afrotropic and Indo-Malay ecoregions. North-eastern populations in
106 Eurasia exhibit low philopatry and are migratory or partially migratory, whereas southern populations are
107 highly philopatric, resident or partially migratory. The migratory intensity of populations seems, therefore,
108 to increase with latitude (Village 1990). Canarian kestrel populations are considered sedentary (Carrillo
109 2007), with juveniles dispersing all over the island from their [natal territories](#) (Carrillo unpubl.). Natal
110 dispersal has been estimated to be longer in the north-east than in the southern Europe (average 277 and
111 146 km, respectively; Newton 2007) and has been shown to be female-biased, at least in the [North](#) (Vasko et
112 al. 2011). The populations sampled for this study are suggested to be sedentary or nomadic (Village 1990).
113 The species inhabits a wide range of open or partly forested habitats and breeds in rocky cavities, tree holes,
114 old nests of other birds and in nest boxes (Village 1990). Boyce and White (1987) suggested the origin of the

115 kestrel group to be in Africa because the majority of this group inhabits this continent and genetic data place
116 its origin in the Old World (Groombridge et al. 2002). The subspecies defined to specific regions differ slightly
117 by size and plumage coloration (Vaurie 1961). We studied three subspecies of the kestrel that inhabit
118 Madeira, central and western Canary Islands (*F. t. canariensis*), eastern Canary Islands (*F. t. dacotiae*) and
119 Balearic Islands, Iberian Peninsula and Northern Africa (*F.t. tinnunculus*). The current conservation status of
120 the kestrel is 'least concern' according to the IUCN (IUCN Red List of Threatened Species 2016). *F. t. dacotiae*
121 was classified as 'vulnerable' by the Spanish Ornithological Society / BirdLife (Carrillo 2004).

122 As the kestrel inhabits most of the Macaronesian (excluding the Azores) and the Balearic Islands and
123 the close continents, the species provides an excellent model to study colonization patterns, genetic
124 diversification and gene flow in these regions. Many studies of passerine birds of these regions have revealed
125 complex evolutionary histories and present day genetic patterns, but there is still scarce information about
126 the birds of prey that are generally able to travel larger distances than passerines. Present and past dispersal
127 has been connected with a lack of phylogeographic structure over large geographic scales (e.g. peregrine
128 falcon *Falco peregrinus* Bell et al. 2014) and with a longitudinal clinal change of haplotype frequencies (e.g.
129 white-tailed sea-eagle *Haliaeetus albicilla* Hailer et al. 2007). Still, several studies have shown differentiation
130 in raptor populations of the same region as this study (genetic differentiation in the osprey *Pandion haliaetus*,
131 Monti et al. 2018; morphological differentiation in the peregrine falcon, Rodríguez et al. 2011).

132 The kestrel populations have been shown to be genetically structured on the Cape Verde Islands,
133 between Cape Verde and Europe (Hille et al. 2003) and between Europe and Canary Islands (Alcaide et al.
134 2009). Genetic differentiation of the two Canary subspecies (Groombridge et al. 2002, Alcaide et al. 2009)
135 provided support to the initial description of these taxa by morphologic and plumage coloration (*F.t.*
136 *canariensis*, Koenig 1890; *F. t. dacotiae*, Hartert 1912-21). Previous genetic studies have shown a decrease of
137 genetic variation in Canary Island populations compared to the continental populations. For instance, Alcaide
138 et al. (2009) found a loss of genetic variation and increase in inbreeding and Alcaide et al. (2010) detected a
139 noteworthy reduction in microsatellite diversity and a smaller and more divergent set of the major

140 histocompatibility complex alleles than in continental *F.t. tinnunculus*. Here, we used mitochondrial and
141 nuclear microsatellite markers to study population genetics of the kestrel in the Canary, Madeira and Balearic
142 Islands, Iberian Peninsula and North-Africa. As these markers have different types of inheritance (maternal
143 mitochondria and biparental microsatellites) and mutation rates, they may reveal different past and present
144 events that are behind the current genetic patterns. We wanted to find out I) if there is genetic differentiation
145 between the island populations and among the island and continental populations. We assumed that we
146 would find some clustering of the populations according to the subspecies defined for each region. In
147 addition, we hypothesized that II) genetic diversity in the island populations is lower than in continental ones
148 and it decreases with a greater distance from the continent, as suggested by the Theory of Island
149 Biogeography. Also, we studied III) the founder effects or bottleneck processes, commonly found in island
150 populations. Finally, we modelled the evolutionary history of the three subspecies inhabiting the study
151 region. We were particularly interested in assessing the genetic distinctiveness and effective population size
152 of the endemic *F. t. dacotiae* in the eastern Canary Islands.

153

154 MATERIALS AND METHODS

155 *Sampling*

156 Samples of kestrels were obtained from Balearic islands (*F. t. tinnunculus*, Mallorca N = 33; Ibiza N = 19 and
157 Menorca N = 13), Canary Islands (*F. t. canariensis*, La Palma N = 31, Tenerife N = 79, Gran Canaria N = 82, La
158 Gomera N = 33, El Hierro N = 23; *F. t. dacotiae*, Fuerteventura N = 37, Lanzarote N = 36), Madeira (*F. t.*
159 *canariensis*, Madeira N = 21, Porto Santo N = 1), Iberian Peninsula (*F. t. tinnunculus*, Spain N = 38, Portugal N
160 = 5) and North-western Africa (*F. t. tinnunculus*, Ceuta, Spain N = 13; Morocco, Atlas Mountains N = 6)
161 between the years 1998 and 2014. Detailed information of samples and sampling can be found from
162 Appendix 1 (Supplementary material Appendix 1 and Table A1).

163 *Microsatellites*

164 Altogether nine polymorphic microsatellite markers were amplified in three multiplex PCRs with fluorescein
165 labelled forward primers. Variation in the nuclear microsatellite loci was studied by calculating expected (H_E)
166 and observed heterozygosities (H_O) and allelic richness (AR) using programs GENETIX v. 4.05.2 (Belkhir et al.
167 2004) and HP-RARE (Kalinowski 2005). Linkage disequilibrium, deviations from Hardy-Weinberg equilibrium
168 and inbreeding coefficients (F_{IS}) were estimated and tested with GENEPOP v. 4.2 (Raymond and Rousset
169 1995) and GENETIX (see Supplementary material Appendix 2 for details).

170 For the genetic population structure, pairwise F_{ST} -values between the sampling locations and analyses
171 of molecular variance (AMOVA) were calculated with ARLEQUIN v.3.5.1.3 (Excoffier and Lischer 2010). For
172 AMOVA, the sampling sites were grouped according to geographical locations (Table A2 in Appendix S2). In
173 addition, a Mantel test between Slatkin's linearized F_{ST} s and logarithms of geographic distances among
174 sampling sites was performed and correlations between the level of genetic variation (H_E , H_O and AR) of the
175 island populations and their geographic distances to the closest continental coastline and the sizes of the
176 islands were estimated. The microsatellite data were further examined with Bayesian clustering programs
177 STRUCTURE v.2.2 (Pritchard et al. 2000, Falush et al. 2003) and TESS v.2.3 (Chen et al. 2007, Durand et al.
178 2009) as well as the multivariate Discriminant Analysis of Principal Components (DAPC) implemented in the
179 package adegenet (Jombart 2008, Jombart et al. 2008) in R (R Development Core Team 2011) to search for
180 the best number of genetic clusters (Supplementary material Appendix 2).

181 *Cytochrome b sequences*

182 A part of the mitochondrial cytochrome b gene was amplified from 229 randomly selected individuals from
183 each population (11-22 individuals per population; Supplementary material Appendix 1 and 2). To estimate
184 mitochondrial genetic diversity, we calculated number of variable sites, nucleotide diversity (π), the
185 Watterson estimator from number of segregating sites (θ), haplotype diversity (H_d) and number of
186 haplotypes using program DNASP v.5 (Librado and Rozas 2009). The correlations of cytochrome b gene
187 diversity (π , θ and H_d) of the island populations to the distance to the closest mainland coastline and the
188 island size were estimated and a Mantel test between Slatkin's linearized Φ_{ST} s and logarithms of geographic

189 distances was performed with ARLEQUIN. In addition, ARLEQUIN was used to calculate Tajima's D and Fu's
190 F, pairwise Φ_{ST} -values and AMOVA, for which the populations were grouped according to different scenarios
191 (Supplementary material Appendix 2, Table A2). Finally, a parsimony network of the haplotypes was
192 constructed with TCS v. 1.21 (Clement et al. 2000).

193 *Demographic history and effective population sizes*

194 For the detection of possible past population bottlenecks, we performed the heterozygosity excess test and
195 the mode shift test for allele frequency distribution implemented in BOTTLENECK v. 1.2.02 (Cornuet and
196 Luikart 1996) with the microsatellite data (Supplementary material Appendix 2). As a comparative method,
197 we estimated the modified Garza-Williamson index (M-ratio; Garza and Williamson 2001) using ARLEQUIN.
198 We also estimated correlations between the microsatellite diversity (H_E , H_O and AR) and M-ratio.

199 In addition, we applied a coalescent analysis of population history using DIYABC v. 2.0.4 (Cornuet et al.
200 2014). We divided the microsatellite data according to the three subspecies described for each location (*F. t.*
201 *canariensis*, Madeira and western Canary Islands; *F. t. dacotiae*, eastern Canary Islands; *F. t. tinnunculus*,
202 Iberia, Balearic Islands and North Africa) and designed four scenarios to be tested: 1) *F. t. canariensis* and *F.*
203 *t. tinnunculus* diverged at time t2 and *F. t. dacotiae* appears as an admixture population between these two
204 at time t1, this scenario was constructed for testing if *F. t. dacotiae* could have arisen as a mixture of the two
205 subspecies with ranges close by; 2) *F. t. tinnunculus* and *F. t. dacotiae* diverged at time t2 and *F. t. canariensis*
206 diverged from *F. t. tinnunculus* at t1; 3) *F. t. tinnunculus* and *F. t. canariensis* diverged at time t2 and *F. t.*
207 *dacotiae* diverged from *F. t. tinnunculus* at t1 and 4) *F. t. tinnunculus* and *F. t. canariensis* diverged at time t2
208 and *F. t. dacotiae* diverged from *F. t. canariensis* at t1 (Appendix S2). Then, we applied the scenario that best
209 explained the data to estimate divergence times, effective population sizes (N_e) and admixture rate. N_e s were
210 calculated also by applying the linkage equilibrium method in program NEESTIMATOR v. 2.01 (Do et al. 2013).
211 We also estimated pairwise net mean Tamura-Nei distances among the three subspecies with MEGA v.6
212 (Tamura et al. 2013), and transformed the distances into divergence times between the subspecies. To detect
213 genetic signs of past changes in population size (bottlenecks and demographic expansions) from the

214 mitochondrial data, we estimated Ramons-Onsins and Rozas R2, raggedness index (r), the time since the
215 expansion (τ), Tajima's D and Fu's Fs values using DNASP and constructed Bayesian skyline plots with program
216 BEAST v. 1.8.0 (Drummond et al. 2012). Further details can be found in Supplementary material Appendix 2.

217

218 RESULTS

219 *Genetic variation and structure, microsatellites*

220 The highest levels of genetic variation were found in the two continental populations Iberia, North-western
221 Africa and Lanzarote, the second easternmost island of the Canaries. The lowest diversity, in turn, was
222 detected in La Palma, the most north-westerly island of the Canary Islands (Table 1). There was a significant
223 negative correlation between H_E and AR and the distance to the nearest continent ($r = -0.694$, $R^2 = 0.481$, p
224 $= 0.018$, $r = -0.686$, $R^2 = 0.471$, $p = 0.020$, respectively). The correlation between H_O and the distance to
225 continent was also negative, though not significantly ($r = -0.593$, $R^2 = 0.351$, $p = 0.055$). Correlations between
226 the diversity values and island sizes were positive, but not significantly (H_E : $r = 0.422$, $R^2 = 0.179$, H_O : $r = 0.416$,
227 $R^2 = 0.173$, AR: 0.312 , $R^2 = 0.097$). Mantel test between geographic distances and F_{ST} -values was significant (r
228 $= 0.566$, $p < 0.01$). Results of data quality checking and linkage disequilibrium can be found from
229 Supplementary material Appendix 3.

230 Pairwise F_{ST} -values were low, but still significant, with an overall F_{ST} of 0.0837 ($p < 0.01$; Supplementary
231 material Appendix 3) and in AMOVA, the grouping of sampling sites into two groups was the best supported
232 alternative with an F_{CT} of 0.0819 (Supplementary material Appendix 2, Table A2; Group 1). Both Bayesian
233 methods, STRUCTURE and TESS divided the data similarly to AMOVA, showing a clear genetic division
234 between the Atlantic (Canary Islands and Madeira) and Mediterranean (Iberia, North Africa and Balearic
235 Islands) sampling sites (Figs 1a and b, Supplementary material Appendix 3). This was also seen in DAPC
236 analyses with $K = 2$ (Fig. 1c), with an additional cluster detected in the Canary Islands when $K = 3$
237 (Supplementary material Appendix 3, Fig. A4). The greatest differences between the alternative analyses

238 were seen in the level and spatial distribution of genetic admixture they discovered with $K=2$. Details of the
239 microsatellite results can be found from Supplementary material Appendix 3.

240 *Genetic variation and structure, cytochrome b sequences*

241 Description of the sequence alignment can be found in Appendix S3. The lowest levels of haplotype and
242 nucleotide diversity were observed in Madeira ($H_d = 0.271$, $\pi = 0.00081$) and Gran Canaria ($H_d = 0.419$, $\pi =$
243 0.00086) and the highest in Menorca ($H_d = 1.000$, $\pi = 0.00756$; Table 2). The level of genetic variation of the
244 island populations decreased with increasing distance from the continent, but not significantly (H_d : $r = -0.457$,
245 $R^2 = 0.209$, $p = 0.159$; π : $r = -0.336$, $R^2 = 0.113$, $p = 0.312$; θ : $r = -0.379$, $R^2 = 0.143$, $p = 0.252$). Correlations
246 between haplotype diversity and θ and island sizes were slightly positive and non-significant (H_d : $r = 0.019$,
247 $R^2 = 0.000$; θ : $r = 0.100$, $R^2 = 0.009$) and the correlation between π and island sizes was slightly negative ($r = -$
248 0.029 , $R^2 = 0.000$). Likewise, the correlation between the logarithms of the geographic distances and Slatkin's
249 linearized F_{ST} -values was not significant ($r = 0.146$, $p = 0.155$).

250 Pairwise Φ_{ST} -values showed clear divergence between most of the sampling sites, with a mean overall
251 Φ_{ST} of 0.2009 ($p < 0.01$) and AMOVA supported three clusters as the best grouping (Supplementary material
252 Appendix 2, Table A2 and Appendix 3). The haplotype network (Fig. 2) showed two most abundant
253 haplotypes, which differentiated from each other only by one substitution. The first one of the two (Ca I; Fig.
254 2 and Supplementary material Appendix 3, Table A4) is dominating in the Eastern Canary Islands, whereas
255 the other was found in all study populations (Co I; Fig. 2 and Supplementary material Appendix 3, Table A4).
256 Two further haplotypes shared by several individuals were found only in the Canary Islands and Madeira (Ca
257 II and Ca III; Fig. 2 and Supplementary material Appendix 3, Table A4) and three other haplotypes shared by
258 several individuals were found only in the Balearic Islands (Me I, Me III and Me IV; Fig. 2 and Supplementary
259 material Appendix 3, Table A4). However, there is a large amount of singleton haplotypes that did not group
260 based on their sampling locations.

261 *Demographic history and effective population sizes*

262 The DIYABC analyses with the microsatellite data suggested the scenario number 1 to be the most suitable
263 one of the four alternatives. This scenario included a split of *F. t. canariensis* and *F. t. tinnunculus* at time t_2
264 and later admixture of these two at time t_1 , forming *F. t. dacotiae* (Supplementary material Appendix 3). The
265 divergence of *F. t. tinnunculus* from *F. t. canariensis* (t_2) was estimated to have occurred only 633 (95% HPD
266 211 – 5 170) generations ago, and the emergence of *F. t. dacotiae* only 78.9 (95% HPD 23.5 – 382) generations
267 ago. With a generation length of 5.4 years (BirdLife International 2017), this would transform to only about
268 3 400 years ago for the split between *F. t. tinnunculus* and *F. t. canariensis* and 426 years ago for the
269 emergence of *F. t. dacotiae*. The admixture rate was estimated to be 0.263 per generation (95% HPD 0.025
270 – 0.856). Using the cytochrome b sequences, the estimates of divergence times were 25-100 times higher;
271 the net mean distances among the subspecies transformed to years were 75 600 years ago for the split
272 between *F. t. tinnunculus* and *F. t. canariensis*/*F. t. dacotiae* (net distance = 0.000204) and 62 200 years ago
273 between *F. t. canariensis* and *F. t. dacotiae* (net distance = 0.000168).

274 The effective population sizes estimated with DIYABC based on microsatellites were 9 090 (95% HPD 4
275 800 – 9 920) for *F. t. tinnunculus*, 5 560 (95% HPD 2 330 – 9 480) for *F. t. canariensis* and 3 780 (95% HPD 1
276 310 – 9 560) for *F. t. dacotiae*. The linkage disequilibrium approach resulted in smaller estimates: 726.0 (95%
277 CI 393.8 – 2 994.3) for *F. t. tinnunculus*, 717.5 (95% CI 419.9 – 1 774.4) for *F. t. canariensis* and 198.0 (95% CI
278 121.3 – 441.2) for *F. t. dacotiae*. The effective population sizes for each sampling location are shown in Table
279 1. The Wilcoxon tests for heterozygote excess were significant for Lanzarote, Iberia and North-western Africa,
280 but only when the IAM was applied. Additionally, a shifted allele frequency distribution was found in
281 Menorca. The modified Garza-Williamson indices were below the threshold of 0.68 for all populations, except
282 for Iberia, implying a past bottleneck. At the subspecies level, there were indications of past bottlenecks in
283 *F. t. dacotiae*, indicated by both significant heterozygote excess and a small G-W index and in *F. t. tinnunculus*,
284 based on significant heterozygote excess. Correlations of H_E , H_O and AR with the M-ratio were positive ($r = 0.$
285 0.671 , $R^2 = 0.450$, $p = 0.024$, $r = 0.542$, $R^2 = 0.294$, $p = 0.085$, $r = 0.577$, $R^2 = 0.333$, $p = 0.063$, respectively).
286 Population size expansions predating the declines were suggested by the mitochondrial DNA, especially for
287 *F. t. tinnunculus* (Table 2).

288 The female effective population sizes estimated from the Bayesian skyline plots were large, varying
289 from 652 000 in Gran Canaria to 28.6 million in Menorca, with wide 95 % posterior density intervals (Fig. A5
290 in Appendix S3). These sizes undoubtedly reflected the large amount of variation detected in the cytochrome
291 b gene. However, the skyline plots showed signs of decreasing effective population sizes for all the Canary
292 Island populations, except for Gran Canaria and for Ibiza, Mallorca and North Africa. The time for the onset
293 of the decrease was dated to around 95 000 years ago (ya) for Fuerteventura, 80 000 ya for Tenerife, 50 000
294 ya for La Palma, 40 000 ya for Mallorca, 30 000 ya for Lanzarote, La Gomera and El Hierro, and 10 000 ya for
295 North Africa. The oldest dates estimated are older than the split between *F. t. tinnunculus* and *F. t.*
296 *canariensis*/*F. t. dacotiae*, reflecting the wide 95% posterior density intervals.

297 DISCUSSION

298 We found that kestrels of the Madeira and Canary Islands are genetically distinct from their conspecifics
299 around the Mediterranean Sea. Individuals from the easternmost Canary Islands, Fuerteventura and
300 Lanzarote, may have mixed ancestry, as they clustered variably with the Mediterranean birds or with the
301 western Canary Islands and Madeiran birds. The kestrels in the Balearic Islands do not differ from each other,
302 nor from the continental populations, based on microsatellites. In addition, we observed signs of decreasing
303 microsatellite genetic diversity with increasing geographic distance from the continent and with increasing
304 severity of a past population bottleneck in the Canary Island populations.

305 Genetic differentiation among some populations and subspecies of kestrels has already been
306 discovered. Groombridge et al. (2002) found that the South African rock kestrel (*F. rupicolus*), previously
307 considered a subspecies of the kestrel, is a sister clade to the remaining subspecies of the common kestrel,
308 leading to an upgrade of the rock kestrel to a species level (e.g. [IOC World Bird List Version 2.0 2009](#); [Gill and](#)
309 [Donsker 2018](#)). Later, two focal subspecies in Cape Verde, *F. t. neglectus* and *F. t. alexandri*, were shown to
310 be genetically different (Hille et al. 2003) and differentiation between Canarian and European birds was
311 detected ([Alcaide et al. 2009](#)). Our data supported the existence of at least two different genetic clusters, but
312 they differed slightly depending on alternate methods.

313 With the mitochondrial DNA, the birds from Madeira were somewhat loosely grouped with the
314 'Mediterranean' kestrels and birds from the Canary Islands formed a separate group. With the microsatellite
315 data, the birds from Madeira clustered with the birds from the Canary Islands forming an 'Atlantic' group.
316 The remaining populations formed a 'Mediterranean' cluster, with some indications of mixed ancestry as
317 well. The variable placement of Madeiran birds (Figure 1 and 2) might reflect a different timing of gene flow
318 and isolation and incomplete lineage sorting. Such examples exist also from other birds of the region. For
319 example, in the spectacled warbler *Sylvia conspicillata*, two genetic clusters were found with microsatellites,
320 whereas mitochondrial DNA showed no structuring (Illera et al. 2014). In the blackcaps *Sylvia atricapilla*, no
321 geographic structure was found with mitochondrial DNA (Pérez-Tris et al. 2004). As the mutation rate of the
322 mitochondrial markers is slower than that of the microsatellites, these markers reflect different time scales
323 and thus different events in the past history; the mitochondrial markers indicate older events than the
324 microsatellite markers. The differentiation was stronger in cytochrome b sequences than in microsatellites,
325 as reflected by larger F_{ST} -values of mitochondrial sequences compared to those of microsatellites
326 (Supplementary material Appendix 3, Table A3). This can result from the smaller effective population size of
327 the mitochondrial markers compared to the nuclear markers. The mitochondrial DNA has an effective
328 population size of only a quarter of the nuclear microsatellites due to its haploidy and maternal inheritance.
329 This leads to a stronger effect of genetic drift in mitochondrial than in nuclear markers and thus, stronger
330 differentiation.

331 The fact that Madeiran birds were clustered with Mediterranean birds using mitochondrial data, but
332 with Canary Island birds using microsatellite data, might also indicate differential dispersal distances between
333 males and females. Indeed, at least in the northern populations, the female dispersal distances are larger
334 (152 km for males and 194 km for females; Vasko et al. 2011). Thus, one explanation for the affinity of
335 Madeiran birds to Mediterranean cluster in female-inherited mitochondrial data can be that females tend to
336 travel larger distances every now and then. Males, on the other hand, if they disperse for shorter distances,
337 are then creating the affinity of the Madeiran birds to the Atlantic cluster seen in the microsatellite data. The
338 strong affinity to Canary Islands, revealed by the TESS analysis, suggests that the more common source is

339 anyhow the Canary Islands rather than the Iberian Peninsula. This is supported by the classification of the
340 Madeiran kestrels to the same subspecies with kestrels from the western Canary Islands, *F. t. canariensis*.

341 The Madeira Islands are in general poor in terrestrial vertebrate species diversity; there are only four
342 endemic bird species (Madeira laurel pigeon, *Columba trocaz*; Madeira petrel, *Pterodroma madeira*; Desertas
343 petrel, *Pterodroma deserta* and Madeira firecrest, *Regulus madeirensis*; Câmara 1997, del Hoyo and Collar
344 2014) and another endemic vertebrate (the lizard *Lacerta dugesii*, Brehm et al. 2003). Many species, birds as
345 well, show genetic and morphological differentiation in their Madeiran populations (e.g. the Berthelot's pipit
346 *Anthus berthelotii*, Illera et al. 2007, Spurgin et al. 2014 and the canary *Serinus canaria*, Dietzen et al. 2006).
347 This scarce number of terrestrial vertebrates and differentiation of Madeiran populations is very likely due
348 to the isolation of the islands in the Atlantic Ocean and thus, rare successful colonizations resulting from
349 sweepstakes dispersal.

350 Our microsatellite data, [despite supporting](#) the existence of at least two different genetic clusters, also
351 showed ambiguous results in the easternmost Canary Islands, Fuerteventura and Lanzarote. The individuals
352 from those islands, *F. t. dacotiae*, showed mixed ancestry or were clustered variably to either of the two
353 clusters, which was also demonstrated as elevated levels of genetic variation in the latter island. This, and
354 the support from the coalescent analyses for admixed ancestry together with an excess of homozygotes that
355 can be caused by the Wahlund effect, suggest that *F. t. dacotiae* could originate from the hybridization of *F. t.*
356 *tinnunculus* and *F. t. canariensis*. However, there was no linkage disequilibrium, which is expected after
357 mixing two diverged lineages. On the other hand, it is possible that the admixture occurred so long ago that
358 linkage disequilibrium has already disappeared. The coalescent analyses suggest that *F. t. dacotiae* originated
359 only about 426 years ago, but it should be noted that the confidence interval for the estimate was large, and
360 the hybridization could have occurred even around ten times earlier. The affinity of the eastern Canary Island
361 populations to the African continent was also detected in other species. For example, the subspecies of the
362 Canary Island blue tit (*Cyanistes teneriffae*) of Lanzarote and Fuerteventura (ssp. *degener*, also considered as
363 full species *Cyanistes degener* by Illera et al. 2016) are similar in appearance and only slightly genetically

364 different from North African subspecies (ssp. *ultramarinus*; Illera et al. 2011, Stervander et al. 2015) and the
365 Canary Island subspecies of the southern grey shrike *Lanius meridionalis koenigi* is polyphyletic with *L.*
366 *meridionalis elegans* from North Africa and have colonized the Canary Islands from North Africa multiple
367 times (Klassert et al. 2008, Olsson et al. 2010).

368 Our results suggest stronger gene flow between close islands than between distant islands. Mantels
369 tests detected isolation-by-distance pattern in the microsatellite data and the same trend was observed also
370 in the cytochrome b data. Previous studies have often found isolation-by-distance in the same region in other
371 avian species as well, for example in the stone-curlew *Burhinus oedicephalus* (Mori et al. 2017), in the southern
372 grey shrike *Lanius meridionalis koenigi* (Padilla et al. 2014) and in the kestrel population from Cape Verde
373 (Hille et al. 2003). However, no isolation-by-distance patterns have also been reported e.g. in the Berthelot's
374 pipit *Anthus berthelotii* (Spurgin et al. 2014) and in the trumpeter finch *Bucanetes githagineus* (Barrientos et
375 al. 2014). There were also significant negative correlations between genetic diversity of island kestrels and
376 geographic distance to the continent in the microsatellite data. Correlations were negative as well for the
377 different diversity parameters from mitochondrial sequences, but they remained non-significant.
378 Surprisingly, the continental populations showed less cytochrome b sequence variation than many of the
379 island populations (Table 2). As birds are able to traverse large distances, the negative correlations between
380 diversity and geographical distance expected based on the Theory of Island Biogeography (MacArthur and
381 Wilson 1967), are not always true. For example, two species of white-eyes, *Zosterops lateralis* and *Z.*
382 *flavifrons*, in Vanuatu Archipelago showed contrasting patterns between genetic diversity, geographic
383 distance and island area (Clegg and Phillimore 2010). Additionally, Wang et al. (2014) found that time spent
384 in isolation played a much larger role in explaining genetic diversity than distance to the continent or island
385 area in pond frogs (*Pelophylax nigromaculatus*) of the Zhoushan Archipelago. However, studies on island
386 phylogeography or population genetics of island species commonly have not reported correlations between
387 the genetic variation within islands and distance to the continent; it has been more common to correlate
388 genetic and geographic distances between islands.

389 Frankham (1997) noted that genetic diversity in island populations is commonly smaller than in
390 continental populations and this occurs in many populations in the Canary Islands as well (see Illera et al.
391 2016 for a review), yet it does not always seem to be the case. For example, James et al. (2016) found that
392 this pattern appeared to be true only in bottlenecked species. When these species were excluded, island and
393 continental species showed similar levels of genetic diversity. Spurgin et al. (2014), in turn, found that in
394 Berthelot's pipit (*Anthus berthelotii*), the divergence between islands was dependent on bottleneck severity
395 during the founding of new island populations, while geographic distance did not seem to play any role. We
396 found past bottlenecks for all the island kestrel populations, especially in terms of low M-ratios. Additionally,
397 the positive correlations between M-ratios and the amount of genetic diversity suggests that the severity of
398 a bottleneck had an effect on the genetic variation in kestrels.

399 The mitochondrial data showed signs of a past demographic expansion in almost all populations. The
400 estimates of effective population sizes varied a lot depending on the data and method used. N_e estimates
401 from Bayesian skyline plots varied from hundreds of thousands to millions. Estimates using microsatellite
402 data for *F. t. dacotiae* were considerably smaller, varying from thousands to only 198 (Table 1). This
403 discrepancy could have arisen due to different evolutionary rates and patterns of inheritance of the used
404 markers, which should lead to four times faster lineage sorting for mitochondrial markers than for nuclear
405 markers. This has not occurred in the island populations of the kestrel, since they show a significant variation
406 in cytochrome b sequences, as a likely result of retaining ancestral polymorphism, spanning perhaps from a
407 past demographic expansion of the ancestral population. This large variation can now be seen as large
408 mitochondrial N_e estimates. However, the microsatellite data correlate better with the present situation. As
409 an example, the rough estimates of the census population sizes for *F. t. canariensis* are around 7100 – 8800
410 pairs (Carrillo 2007) and less than 500 pairs for *F. t. dacotiae* (Carrillo 2004), which are close to the estimates
411 from the microsatellite data.

412 To summarize, we found evidence of at least two separate genetic clusters, significant isolation-by-
413 distance and decreasing genetic diversity with increasing geographic distance from the continents and with

414 increasing severity of population bottlenecks, suggesting differentiation among the island populations. The
415 two Canary Island subspecies, *F. t. dacotiae* and *F. t. canariensis*, have diverged from each other to some
416 degree and from the continental and Balearic conspecifics of *F. t. tinnunculus*. Samples from Madeira,
417 representing *F. t. canariensis*, indicated affinities to both Canary Islands and Mediterranean clusters,
418 depending on the marker and methods applied. *F. t. dacotiae* showed signs of being a hybrid population
419 between *F. t. canariensis* and *F. t. tinnunculus*. Whether *F. t. dacotiae* actually fills the criteria of a different
420 subspecies or an evolutionary significant unit can be debated, especially because the definitions for both
421 terms are still vague (see discussion e.g. in Fraser and Bernatchez 2001, Waples and Gaggiotti 2006,
422 Frankham 2010). We suggest that populations in Fuerteventura and Lanzarote should be treated as a
423 management unit by the 'precautionary principle' used in conservation, considering the level of divergence,
424 the small census and effective sizes and seemingly special history of *F. t. dacotiae*.

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Table 1. Genetic variation detected by microsatellites. N = number of samples, H_E = expected heterozygosity, H_O = observed heterozygosity, AR = allelic richness and F_{IS} = inbreeding coefficient with 95% confidence interval in parentheses, IAM = Wilcoxon test for genetic bottleneck (p for heterozygosity excess) using the infinite allele model, TPM = Wilcoxon test for genetic bottleneck (p for heterozygosity excess) using the two-phase model, MS = Mode shift test. M ratio = modified Garza-Williamson index, N_e = effective population size based on linkage equilibrium, NS = non-significant, SM = shifted mode, NA = not applicable.

Population	N	H_E	H_O	AR	F_{IS} (95% CI)	IAM	TPM	MS	M-ratio	N_e
La Palma	31	0.497	0.403	3.24	0.207 (0.057 – 0.317)	NS	NS	NS	0.4275	105.5 (42.1–Infinite)
Tenerife	79	0.599	0.488	3.77	0.191 (0.125 – 0.243)	NS	NS	NS	0.6472	8 583.9 (375.0–Infinite)
Gran Canaria	82	0.629	0.551	4.04	0.139 (0.081 – 0.189)	NS	NS	NS	0.6193	385.6 (179.2– 9858.0)
La Gomera	33	0.572	0.486	3.56	0.167 (0.059 – 0.250)	NS	NS	NS	0.4905	127.2 (59.5–1 277.2)
El Hierro	23	0.514	0.434	3.48	0.183 (0.038 – 0.257)	NS	NS	NS	0.4180	52.4 (22.5–1 319.6)
Madeira	22	0.577	0.532	3.69	0.108 (-0.078 – 0.219)	NS	NS	NS	0.4849	195.6 (49.2–Infinite)
<i>F. t. canariensis</i>	270	0.611	0.497	3.86	0.189 (0.154 – 0.223)	NS	NS	NS	0.8421	717.5 (419.9–1 774.4)
Fuerteventura	37	0.635	0.581	4.06	0.100 (-0.004 – 0.160)	NS	NS	NS	0.5299	73.5 (44.8–155.2)

Lanzarote	36	0.733	0.583	5.24	0.225	P <	NS	NS	0.6516	342.4
					(0.108 – 0.298)	0.05				(87.4–Infinite)
<i>F. t. dacotiae</i>	73	0.690	0.587	4.65	0.157	P <	NS	NS	0.6862	198.0
					(0.086 – 0.208)	0.01				(121.3–441.2)
Mallorca	33	0.684	0.580	4.64	0.170	NS	NS	NS	0.6141	242.8
					(0.054 – 0.247)					(91.7–Infinite)
Ibiza	19	0.652	0.567	4.57	0.162	NS	NS	NS	0.5068	137.6
					(0.032 – 0.224)					(43.5–Infinite)
Menorca	13	0.646	0.548	4.28	0.195	NS	NS	SM	0.4291	28.7
					(0.026 – 0.243)					(13.9–113.8)
Iberia	43	0.736	0.639	5.26	0.145	P <	NS	NS	0.7267	Infinite
					(0.066 – 0.194)	0.05				(294.2–Infinite)
North-western Africa	19	0.708	0.654	5.06	0.105	P <	NS	NS	0.5756	Infinite
					(-0.037 – 0.202)	0.05				(108.8–Infinite)
<i>F. t. tinnunculus</i>	127	0.720	0.604	5.11	0.165	P <	NS	NS	0.8623	726.0
					(0.122 – 0.203)	0.01				(393.8–2 994.3)
Total	470	0.682	0.738	4.53	NA	NA	NA	NA	NA	NA

Table 2. Variation in cytochrome b sequences. N = number of sequenced samples, #H = number of haplotypes, Hd = haplotype diversity, π = nucleotide diversity, θ = mutation parameter from the number of segregating sites, R2 = the Ramos-Onsins and Rozas R2 statistic r = raggedness index and τ = represents the time since expansion. Standard deviations for Hd, π and θ are given in parentheses. p-values for Tajima's D and Fu's F are shown below the values and significant values are highlighted in bold, NS = non-significant, NA = not applicable.

Population	N	#H	Hd	π	θ	Tajima's D	Fu's F	R2	r	τ
La Palma	20	14	0.953 (0.033)	0.00420 (0.00084)	0.00527 (0.00218)	-0.7457 p = 0.237	-7.6305 p = 0.000	0.1180 P = 0.352	0.0329 NS	1.698 P = 0.137
						NS				
Tenerife	15	8	0.829 (0.085)	0.00432 (0.00095)	0.00460 (0.00207)	-0.2363 p = 0.478	-1.2472 p = 0.249	0.1304 NS	0.0724 NS	1.477 p = 0.326
						NS				
Gran Canaria	17	4	0.419 (0.141)	0.00086 (0.00040)	0.00184 (0.00100)	-1.7187 p = 0.030	-1.0077 p = 0.137	0.1477 NS	0.173 NS	6.036 P = 0.599
La Gomera	19	11	0.883 (0.055)	0.00354 (0.00063)	0.00356 (0.00161)	-0.0236 p = 0.552	-4.4326 p = 0.015	0.1387 P = 0.557	0.0263 NS	1.786 P = 0.042
						NS				
El Hierro	17	9	0.794 (0.078)	0.00220 (0.00051)	0.00332 (0.00155)	-1.2151 p = 0.099	-1.9566 p = 0.083	0.1058 NS	0.0251 NS	1.247 P = 0.029
						NS				
Madeira	21	4	0.271 (0.124)	0.00081 (0.00044)	0.00173 (0.00093)	-1.6096 p = 0.027	-0.9400 p = 0.143	0.1001 NS	0.4338 NS	0.000 0.882
<i>F. t. canariensis</i>	109	33	0.810 (0.027)	0.00289 (0.00034)	0.00473 (0.00152)	-1.1244	-28.6020 P = 0.000	0.0568 0.124	0.0265 NS	0.739 P = 0.153

P = 0.141

NS

Fuerteventura	18	11	0.908	0.00429	0.00398	0.2812	-3.7970	0.1447	0.0272	2.608
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			0.051)	(0.00060)	(0.00177)	p = 0.666	p = 0.022	p = 0.601 NS	p = 0.044	
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NS

Lanzarote	17	6	0.647	0.00251	0.00405	-1.4130	-0.5501	0.1397	0.1627	0.000
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			(0.120)	(0.00102)	(0.00182)	p = 0.061	p = 0.386 NS	P = 0.522 NS	P = 0.779 NS	
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NS

<i>F. t. dacotiae</i>	35	14	0.827	0.00356	0.00484	-0.8721	-4.935	0.0861	0.0129	1.121
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			(0.051)	(0.00062)	(0.00184)	P = 0.212	P = 0.036	P = 0.194 NS	P = 0.012	
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NS

Mallorca	18	10	0.850	0.00306	0.00507	-1.4909	-4.0840	0.0781	0.0583	0.806
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			(0.077)	(0.00081)	(0.00216)	p = 0.053	p = 0.007	P = 0.013	P = 0.257 NS	
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NS

Ibiza	19	8	0.865	0.00316	0.00428	-0.9489	-1.5232	0.0963	0.0724	1.949
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			(0.046)	(0.00051)	(0.00186)	p = 0.191	p = 0.182 NS	P = 0.120 NS	P = 0.408 NS	
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NS

Menorca	11	11	1.000	0.00756	0.00765	-0.0534	-6.1198	0.1401	0.0331	4.248
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			(0.039)	(0.00127)	(0.00342)	p = 0.515	p = 0.003	P = 0.342 NS	P = 0.075 NS	
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NS

Iberia ¹	26	8	0.526	0.00140	0.00359	-2.0286	-3.7943	0.0740	0.0767	0.188
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			(0.118)	(0.00045)	(0.00153)	p = 0.011	p = 0.005	p = 0.045	p = 0.439 NS	
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	17	7	0.596	0.00196	0.00332	-1.4740	-2.3273	0.1212	0.0703	0.000
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			(0.139)	(0.00094)	(0.00155)	p = 0.062	p = 0.044	P = 0.313 NS	P = 0.317 NS	
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NS

<i>F. t.</i>	91	31	0.779	0.00315	0.00662	-1.5920	-24.934	0.0461	0.0276	0.408
<i>tinnunculus</i>			(0.045)	(0.00047)	(0.00203)	P = 0.025	P = 0.000	P = 0.017	p = 0.049	
Sub-Saharan	6	4	0.867	0.00523	0.00654	NA	NA	NA	NA	NA
Africa			(0.129)	(0.00211)	(0.00349)					
Asia	3	3	1.000	0.00415	0.00415	NA	NA	NA	NA	NA
			(0.272)	(0.00130)	(0.00289)					
Total ²	244	75	0.833	0.00358	0.00995	-0.9214	-2.5738	0.0300	0.0198	0.645
			(0.021)	(0.00030)	(0.00242)	p = 0.260	p = 0.143	NS P = 0.006	P = 0.365	NS
										NS

¹ includes sequences from UK (N = 2), Greece (N = 1) and Norway (N = 1)

² all sequences included, also those originating from populations for which some parameters were not estimated due to a small sample size

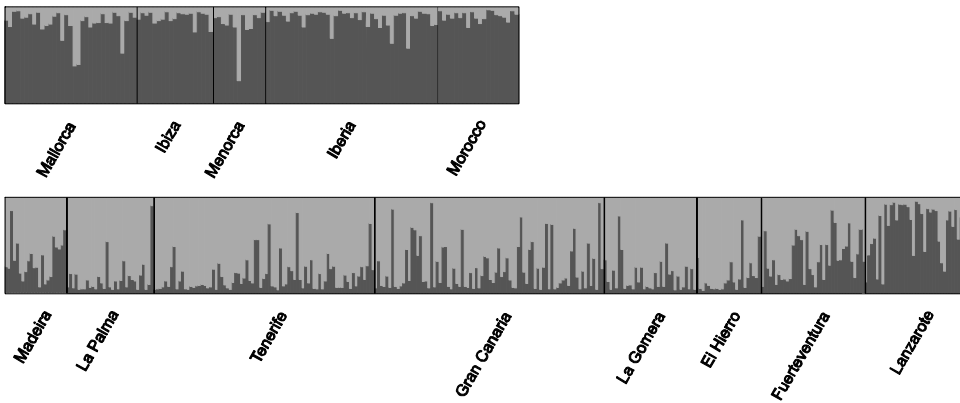
FIGURE LEGENDS

Figure 1. Genetic clustering of the common kestrel study populations based on STRUCTURE, TESS and DAPC analyses. (a) Proportion of individuals assigned to either of the genetic clusters detected by STRUCTURE, when $K = 2$; one bar represents one individual. (b) Proportion of individuals assigned to either of the genetic clusters detected by TESS, when $K = 2$, placed on a map. (c) Proportion of individuals of a sampling site assigned to the two genetic clusters detected by DAPC (represented as the two columns of squares). The sizes of the squares represent the proportion of the individuals with the scale below the figure.

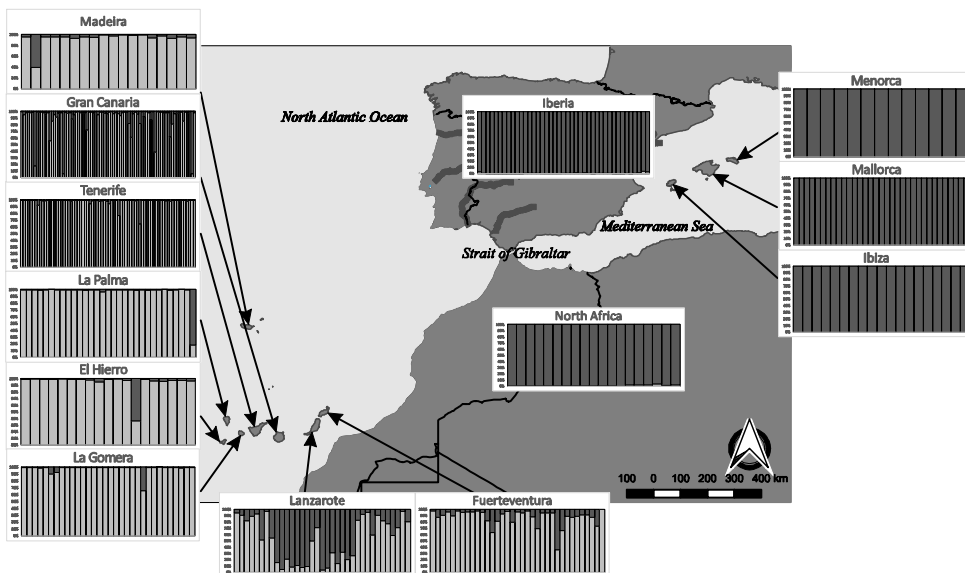
Figure 2. Minimum spanning haplotype network of the cytochrome b sequences of the studied common kestrels. The sizes of the circles are proportional to the number of individuals sharing the haplotype. Study sites are depicted by different colors. Co = Common, Me = Mediterranean, Ca = Canary Islands, SA = Sub-Saharan Africa. Details of the haplotype distribution can be found also from Supplementary material Appendix 3, Table A4.

Figure 1

(a)



(b)



(c)

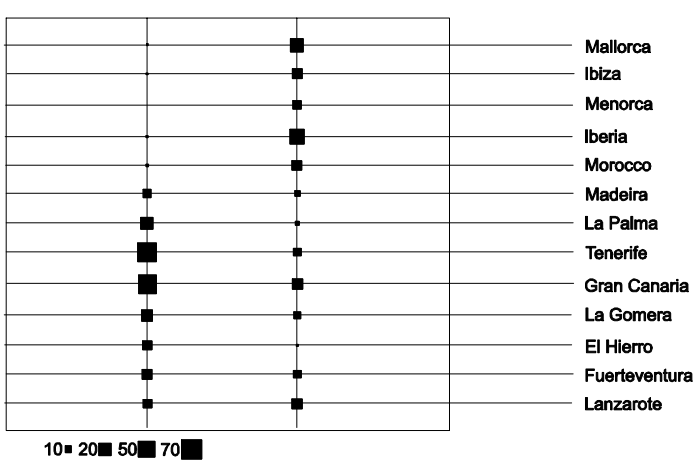


Figure 2

