

JOURNAL OF AVIAN BIOLOGY

Article

Acoustic, genetic, and morphological analyses of the Canarian common chaffinch complex *Fringilla coelebs* ssp. reveals cryptic diversification

Juan Carlos Illera, Juan Carlos Rando, Eduardo Rodriguez-Exposito, Mariano Hernández, Santiago Claramunt and Aurelio Martín

J. C. Illera (<http://orcid.org/0000-0002-4389-0264>) (illerajuan@uniovi.es), Research Unit of Biodiversity (UO-CSIC-PA), Oviedo Univ., Mieres, Asturias, Spain. – J. C. Rando, Abeque Association, Tenerife, Canary Islands, Spain. – E. Rodriguez-Exposito, Doñana Biological Station (EBD-CSIC), Dept of Ethology and Conservation of Biodiversity, Sevilla, Spain. – M. Hernández and ER-E, Depto de Bioquímica, Microbiología, Biología Celular y Genética, Inst. Universitario de Enfermedades Tropicales y Salud Pública de Canarias (IUETSPC), Univ. de la Laguna, Tenerife, Spain. – S. Claramunt, Royal Ontario Museum Dept of Natural History, Royal Ontario Museum, Toronto, ON, Canada. – A. Martín, Depto de Biología Animal, Edafología y Geología, Facultad de Ciencias, Univ. de La Laguna, Tenerife, Spain.

Journal of Avian Biology

2018: e01885

doi: 10.1111/jav.01885

Subject Editor: Theresa Burg

Editor-in-Chief: Thomas Alerstam

Accepted 6 October 2018

The common chaffinch *Fringilla coelebs* is the extant avian species with the highest level of differentiation across North Atlantic archipelagos. Such a degree of diversification has been traditionally recognised within the subspecies category, with one endemic subspecies occurring in Azores (*F. c. moreletti*), one in Madeira (*F. c. maderensis*), and three in the Canary Islands (*F. c. canariensis*, *F. c. palmae* and *F. c. ombriosa*). Recent genetic, acoustic, and sperm morphology studies informed us about the significant differentiation of the Gran Canaria population, which is traditionally included within *F. c. canariensis* subspecies. The goal of this study is to examine the similarity of the Canarian chaffinches, with the objective of determining if the Gran Canaria chaffinches represent an isolated and distinct population. In order to achieve this aim, we used a double approach: 1) we analysed new morphological and genetic data from the Canary Islands, and 2) we reviewed and synthesised the vast acoustic, morphological and genetic information available for these taxa in Macaronesia, with special emphasis on the Canary Islands. Genetic, acoustic, and sperm morphological data, and to a lesser extent phenotypic data, strongly support the existence of a cryptic taxon in Gran Canaria. Moreover, our findings also reveal an incipient speciation process on going in the Canary Islands, mostly driven by genetic differentiation. Overall, our synthesis suggests that individuals occurring in Gran Canaria should be considered as a novel taxon that we formally described as *Fringilla coelebs bakeri* ssp. nov.

Keywords: avian radiation, incipient speciation, integrative taxonomy



www.avianbiology.org

© 2018 The Authors. Journal of Avian Biology © 2018 Nordic Society Oikos

Introduction

Oceanic islands support high levels of speciation events due to the role of founder events, drift, mutation, limited gene flow, and selection acting on a small contingent of colonisers over time (Emerson 2002, Grant and Grant 2008). Such divergence events have produced a plethora of forms and colours that taxonomists have frequently described and classified as distinct taxa. Different types of information have been used to understand the origin and variation of biodiversity, for instance, biometry (Grant 1979a, b, Dennison and Baker 1991), acoustic (Lynch and Baker 1990, Päckert et al. 2006, Tietze et al. 2015), genetic (Alström et al. 2015, Stervander et al. 2015), or a combination of methods (Illera et al. 2014). However, cryptic differentiation, that is, species evolving similar morphologies, makes the correct identification of unique taxa difficult, which increases the risk of underestimating biodiversity (Padiál et al. 2010, Fišer et al. 2018).

The Canary Islands are an oceanic archipelago situated about 100 and 460 km from the African mainland. The archipelago consists of eight principal volcanic islands with a well studied variation of geological ages increasing towards the African continent. El Hierro appears as the youngest island (1 Mya) and Fuerteventura as the oldest (~ 20 Mya). The Canary Islands harbour a high number of terrestrial endemic species, making this archipelago one of the most important centres for biodiversity in the temperate region (Juan et al. 2000, Illera et al. 2012). As an example, the more than 150 native land vertebrate taxa inhabiting the archipelago, 21 (13%) are endemic (Arechavaleta et al. 2010). This value is even higher considering the plants where the endemic taxa (> 550 species) represent around 40% of the native flora (Francisco-Ortega et al. 2000). In relation to extant breeding birds, six species and more than 30 subspecies are endemics (Illera et al. 2012, 2016), while considering the extant and extinct species the number is much higher (Illera et al. 2012, 2016). Interestingly, the Canarian birds have recently provided several examples of cryptic differentiation. For instance, four subspecies of the Canarian blue tit *Cyanistes teneriffae* had traditionally been recognised in the Canary Islands based on morphology, plumage and song (Martín and Lorenzo 2001). However, Kvist et al. (2005) provided significant genetic divergences not only among the classical subspecies but also between Gran Canaria and the remaining populations. Such differences were used three years later to support the description of a new subspecies in Gran Canaria (Dietzen et al. 2008). Indeed, with such a level of differentiation in all Canarian blue tit subspecies have been suggested that each is treated as a full species (Sangster 2006, Illera et al. 2016). The goldcrest *Regulus regulus* provides another interesting case of cryptic differentiation. Päckert and colleagues (2006) studied the acoustic, morphology and genetics of the goldcrests in Macaronesia. They found an unforeseen colonisation pattern with two distinct lineages within the Canary Islands, suggesting two independent waves of colonisation

from the Iberian Peninsula. Such findings supported the description of a new subspecies (*R. r. ellenthalerae*), occurring in the western islands of La Palma and El Hierro, meanwhile the former subspecies (*R. regulus teneriffae*) inhabits the islands of Tenerife and La Gomera. In addition, similar scenarios have been documented to occur with the robin *Erithacus rubecula*, and the blue chaffinch *Fringilla teydea* in the Canary Islands (Dietzen et al. 2003, 2015, Liffield et al. 2016, Sangster et al. 2016). Overall, all these results show an interesting pattern at species level of independent but repeated bouts of colonisation from the continental areas to the Canaries, with subsequent processes of genetic isolation (and sometimes of extinction) producing new taxa over time. According to these results, it seems clear that the avian Canarian taxonomy needs to be reshuffled using unambiguous, diagnostic and independent traits (Illera et al. 2016).

The common chaffinch *Fringilla coelebs* has been one of the species most intensively studied using molecular tools in Macaronesia. The pioneer study carried out by Baker et al. (1990) using protein electrophoresis of 42 loci found support for two genetic groups within the Canary Islands. One of them would occur on the western islands of El Hierro and La Palma, and the other on Tenerife, La Gomera and Gran Canaria. Nonetheless, the first comprehensive phylogeographic study to understand the evolutionary history of this taxon in Macaronesia was performed by Marshall and Baker (1999). These authors using nucleotide sequences of four mitochondrial genes revealed an unforeseen colonisation pathway from north to south in a stepping stone mode starting in Azores and ending in Gran Canaria Island (Fig. 1). In addition, Marshall and Baker (1999) found a strong genetic structure among the three Macaronesian archipelagos where the common chaffinch occurs, suggesting long periods of isolation mostly without gene flow. This finding has been also confirmed in a subsequent multilocus approach using both mitochondrial and nuclear genes (Samarasin-Dissanayake 2010, Rodrigues et al. 2014). Recently, Suárez and co-workers (2009) studying the genetic structure of the common chaffinch in the Canary Islands found an unexpected result in Gran Canaria. These authors showed a strong genetic structure in Gran Canaria, which was compatible with a subspecific rank.

In addition to the molecular markers, the evolutionary biology of this passerine has been repeatedly analysed according to morphological, sperm length, and acoustic datasets (Grant 1979b, Dennison and Baker 1991, Lynch and Baker 1994, Marshall and Baker 1999, Rando et al. 2010, Stensrud 2012). Interesting, in a recent study analysing the loss of acoustic variability along the pathway of colonisation in Macaronesia, Lachlan et al. (2013) provided evidence of a significant loss of syllable sequencing within songs in the Gran Canaria chaffinches, which makes this song distinctive from any other Canarian chaffinch population. However, much of this information, and the interpretation of these findings, is tackled on individual traits, which limits the general understanding of the evolutionary consequences of

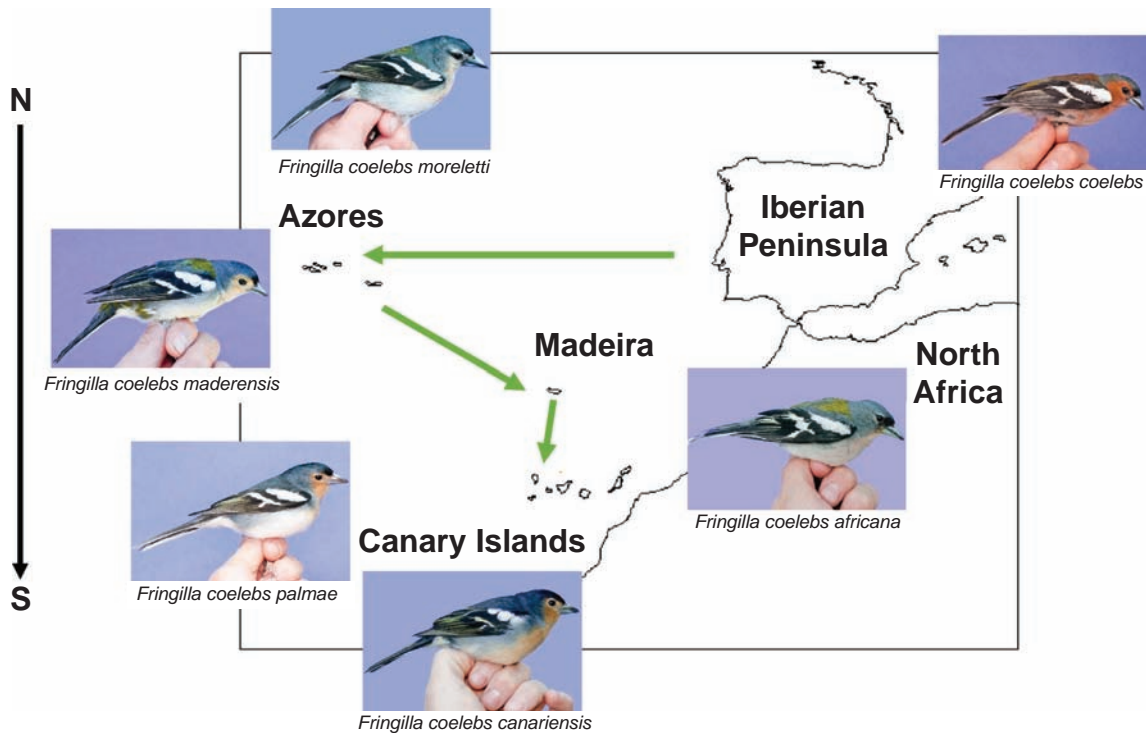


Figure 1. Distribution of the common chaffinch *Fringilla coelebs* in Macaronesia and nearby continental areas. Green lines depict pathway of colonisation of chaffinches in Macaronesia suggested by Marshall and Baker (1999).

experiencing long periods of isolation. In addition, there is mixed evidence of how morphology can be used to discriminate common chaffinches, and when the genetic divergence occurred within the Canary Islands. Such information is also necessary to reshuffle the taxonomy of this passerine within the Canary Islands. With these precedents, our main goal is to scrutinize whether the Gran Canarian birds can be characterised and identified by multiple traits. To achieve this aim we will use published information, but also new morphological and genetic data to re-analyse and re-evaluate the similarity of the Canarian common chaffinches. Our analysis will show that the common chaffinch in Gran Canaria is a distinguishable population from other Canarian populations from genetic and acoustic perspectives, and to a lesser extent from phenotypic characteristics, representing a new case of cryptic differentiation in the Canary Islands. Our final aim is to perform a formal taxonomic description of this novel taxon, and discuss the evolutionary implications of such a radiation in the Canary Islands.

Material and methods

The species

The common chaffinch with five subspecies described provides the best example of diversification within extant land birds in Macaronesia (Illera et al. 2016; Fig. 1). The species is distributed from Europe to the north of Africa, including

three Macaronesian archipelagos (Azores, Madeira and the Canary Islands). At present between 15 to 18 subspecies are recognised (Cramp and Perrins 1994, Clement 2018), with one endemic subspecies per Macaronesian archipelago, except in the Canary Islands where three endemic subspecies are traditionally recognised (Martín and Lorenzo 2001). Azorean populations show no significant morphological (Grant 1979b, Dennison and Baker 1991) or genetic (Baker et al. 1990, Samarasin-Dissanayake 2010, Rodrigues et al. 2014) differentiation among islands, and they are routinely grouped in a single subspecies *F. c. moreletti* Pucheran, 1859. Such a result is compatible with high levels of gene flow among populations (Rodrigues et al. 2014), which contrasts with the significant levels of mutation rates in the song memes found among populations (Lynch and Baker 1994). In Madeira the species only breeds on the Madeira Island with the exclusive subspecies *F. c. maderensis* Sharpe, 1888. Finally, in the Canary Islands the species occurs in the central and western islands being absent from the eastern islands (Lanzarote and Fuerteventura). Three Canarian subspecies were described according to their phenotypic differences: *F. c. palmae* Tristram, 1889 on La Palma, *F. c. ombriosa* Hartert, 1913 on El Hierro, and *F. c. canariensis* Vieillot, 1817 on Gran Canaria, Tenerife and La Gomera islands (Cramp and Perrins 1994, Martín and Lorenzo 2001).

Macaronesian chaffinches have in general shorter and rounded wings, and longer tarsus and bills than continental populations (Grant 1979b). Colour pattern also differs between mainland and oceanic island populations. Thus, like

in European populations, cheek front part is ochre, but it is still dark bluish on the side of the head and neck. Canary male chaffinches have an intense blue colour on the back. However, they show a variable extension of reddish-orange-pinkish colour on the breast, which differs from the greenish-brownish back of African chaffinches *F. c. africana/spodiogenys* (Corso et al. 2015; Fig. 1) and from the ochre-greyish back of European subspecies (*F. c. coelebs*) (Cramp and Perrins 1994, and references therein). White on tail and wings is less extensive, especially the lower wing bar, compared to *F. c. coelebs*, and the white wing-bars are less extensive, especially the lower bar (Fig. 1).

Morphological analyses

Skeletal measurements

Dennison and Baker (1991) studied morphological variances in the Macaronesian finches using skeletal measurements (after skeleton preparation) of fresh individuals. They found that Canary populations are morphologically less variable than Azorean finches, with no significant morphological differentiation within the Canary Islands. However, our own measurements obtained from live individuals caught in different ringing sessions across the five islands suggested conspicuous morphological differences among populations (Illera unpubl.). Thus, we decided to take morphological measurements from the same individuals (i.e. skeletons) used by Dennison and Baker (1991).

In total, we measured 110 adult male Canary chaffinches from 5 islands (El Hierro, La Palma, La Gomera, Tenerife and Gran Canaria) stored at Royal Ontario Museum (Supplementary material Appendix 1 Table A1). We took measurements from 10 skeletal traits (Table 1, Fig. 2). Bones were photographed with a Nikon 3200 digital camera on a

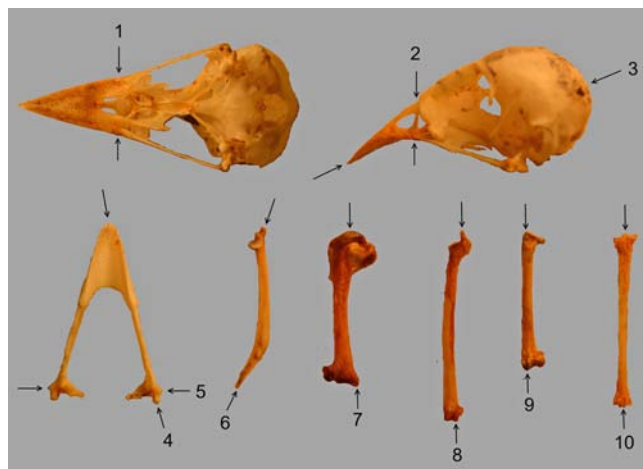


Figure 2. Morphological (cranial and post-cranial) traits measured on the Canary common chaffinches *Fringilla coelebs*. 1: premaxilla width, 2: premaxilla height, 3: skull length, 4: mandible length, 5: mandible width, 6: scapula length, 7: humerus length, 8: ulna length, 9: femur length, and 10: tarsometatarsus length.

graphic paper measured in millimetres, and measurements were scored using the program ImageJ ver. 1.45s (Rasband 1997). Bones were systematically placed in the same position on the graphic paper and photographed by the same person (JCI) in order to standardise the measurements taken.

Length differences among the Canary common chaffinches were analysed through two (cranial and postcranial variables) multivariate analysis of variance (MANOVA). In addition, we explored variation in the morphological traits performing two principal component analysis (PCA), one with cranial (i.e. head and bill) measurements (traits 1–5), and the other with postcranial lengths (traits 6–10). We

Table 1. Morphological measurements (mean \pm standard error) of extant *Fringilla coelebs* occurring in the Canary Islands. Sample size (in brackets) and range (in square brackets) are also provided. Numbers before morphological trait names correspond with the trait numbers used in the text.

	El Hierro	La Palma	La Gomera	Tenerife	Gran Canaria
¹ Bill width	7.3 \pm 0.2 (15) [6.8–7.6]	7.4 \pm 0.2 (14) [7.1–7.7]	7.3 \pm 0.3 (23) [6.6–7.8]	7.2 \pm 0.2 (20) [6.7–7.6]	7.3 \pm 0.3 (19) [6.8–7.7]
² Bill height	5.0 \pm 0.3 (13) [4.5–5.5]	5.0 \pm 0.2 (17) [4.6–5.4]	5.3 \pm 0.2 (22) [4.9–5.8]	4.9 \pm 0.3 (20) [4.2–5.6]	4.7 \pm 0.3 (22) [4.1–5.2]
³ Head length	32.5 \pm 0.5 (14) [31.7–33.6]	33.3 \pm 0.9 (17) [31.8–34.8]	34.4 \pm 1 (22) [32.1–36.1]	32 \pm 0.8 (18) [31–33.8]	32.8 \pm 1.1 (18) [30.6–34.6]
⁴ Mandible length	24.4 \pm 0.3 (10) [23.8–24.8]	24.9 \pm 0.4 (20) [24.1–25.9]	25.9 \pm 0.4 (19) [25.1–27]	24.3 \pm 0.5 (16) [23.6–25.1]	23.8 \pm 0.4 (22) [22.7–24.6]
⁵ Mandible width	14.5 \pm 0.3 (9) [14.1–14.9]	14.6 \pm 0.3 (19) [14–15.2]	15.4 \pm 0.4 (15) [14.9–16.1]	14.6 \pm 0.3 (17) [14–15]	14.1 \pm 0.2 (15) [13.7–14.5]
⁶ Scapula	21.5 \pm 0.5 (16) [20.6–22.3]	21.7 \pm 0.5 (18) [20.5–22.7]	21.8 \pm 0.4 (23) [21.2–22.5]	20.9 \pm 0.4 (17) [20.1–21.7]	20.7 \pm 0.5 (24) [19.8–21.5]
⁷ Humerus	20.4 \pm 0.3 (15) [19.7–21]	20.4 \pm 0.5 (24) [19.6–21.2]	20.5 \pm 0.4 (21) [19.8–21.1]	19.6 \pm 0.4 (19) [18.5–20.3]	19.1 \pm 0.4 (26) [18.3–19.8]
⁸ Ulna length	25.2 \pm 0.3 (12) [24.4–25.9]	25.1 \pm 0.5 (21) [24–26]	25.1 \pm 0.5 (21) [24.2–26]	24 \pm 0.6 (18) [22.6–25]	23.5 \pm 0.5 (25) [22.7–24.2]
⁹ Femur	18.1 \pm 0.4 (16) [17.3–19]	18.3 \pm 0.4 (24) [17.6–19.1]	18.7 \pm 0.4 (22) [18–19.4]	17.9 \pm 0.5 (21) [16.8–18.7]	17.8 \pm 0.4 (24) [17–18.5]
¹⁰ Tarsometatarsus	22.0 \pm 0.4 (15) [21.2–22.7]	22.1 \pm 0.6 (20) [20.9–22.9]	22.5 \pm 0.6 (21) [21.5–23.7]	21.5 \pm 0.7 (19) [20.1–22.8]	21.8 \pm 0.5 (21) [20.7–22.7]

performed the statistical analyses using the software SPSS, ver. 15.0.

Plumage characters

We roughly compared the external appearance of the Canarian common chaffinch males belonging to the same subspecies (*Fringilla coelebs canariensis*), that is, populations from Gran Canaria, Tenerife and La Gomera. We focused our analysis on the R4 tail feather because was the only tail feather with some kind of conspicuous variation for the white colour between some islands (Supplementary material Appendix 1 Fig. A1). We grouped individuals into two categories: 1) R4 with 0–3 mm tipped white, 2) R4 with ≥ 4 mm tipped white. We performed a contingency table analysis to investigate the association of each population to these categories.

Genetic differentiation

Rando et al. (2010) and Valente et al. (2017) estimated time of colonisation and diversification of common chaffinches in Macaronesia using mitochondrial DNA dating. However, these authors did not consider time of diversification within the Canarian subspecies. Thus, we estimated time of diversification of each subspecies and/or group of islands using the program BEAST ver. 1.8.1 (Drummond et al. 2012). We used the same alignment provided by Rando et al. (2010), adding six new sequences obtained from Gran Canaria (Genbank accession numbers: MH170890-5, Supplementary material Appendix 1 Table A2).

We extracted DNA from tissues stored at -80°C , following Malagó's et al. (2002) protocol. We carried out PCR reactions in a 12.5 μl volume, with a buffer consisting of 10 mM Tris-HCl pH 8.3, 2.5 mM MgCl_2 , 50 mM KCl, 0.2 mM dNTPs, 0.5 μM of the primers b1 (Kocher et al. 1989) and b6 (Morris-Pocock et al. 2010), and 0.25 U Taq polymerase (Invitrogen). We performed PCRs with an initial denaturation for 1 min at 94°C , followed by 36 cycles of 45 s at 94°C , 45 s at 52°C , 60 s at 72°C , and a final extension for 2 min at 72°C . PCR products were separated on 2% agarose gels. Amplicons were recovered from the agarose gel using pipet tip centrifugation (Dean and Greenwald 1995) and sequenced with the primers b1 and b6, as well as with a nested primer b3 (Morris-Pocock et al. 2010) using ABI BigDye v.3.1 chemistry. The sequenced products were run on an ABI 3730 Genetic Analyzer (Life Technologies).

We ran the Bayesian time-tree analyses only using common chaffinch sequences, that is, excluding all outgroups. We proceeded in this way because outgroups usually provide long branches and are less sampled than ingroups, which could bias the divergence time estimates (Drummond and Bouckaert 2015). We inferred the most appropriated nucleotide substitution model (HKY+G) from the program JModelTest ver. 2.1.4 (Darriba et al. 2012). We used a strict molecular clock, and defined the rate prior to have a mean of 0.01 and standard deviation of 0.0075 substitutions per site per million years (Illera et al. 2008). We used a Yule tree prior following the recommendation of Drummond and Bouckaert (2015),

since our analyses included sequences from populations with deep divergences. We conducted two independent MCMC analyses of 50 000 000 steps, with a burn-in of 5 000 000 steps. We assessed the convergence of MCMCs with Tracer ver. 1.6 (Rambaut et al. 2014).

We used the program MEGA ver. 7.0 (Kumar et al. 2016) to obtain the uncorrected pairwise genetic distances among populations. Finally, Suárez et al. (2009) inferred the genetic structure within the Canarian common chaffinches, but they did not consider the remaining Macaronesian and continental chaffinches. Thus, we built a haplotype network using Macaronesian and nearby continental cytochrome b sequences (Supplementary material Appendix 1 Table A2) to track the connections among and within common chaffinches using the software TCS ver. 1.21 (Clement et al. 2000). We performed the analysis fixing a limit of connection to 94%. Missing data or gaps were considered as a fifth state.

Data deposition

Data available from the National Center for Biotechnology Information: <<https://www.ncbi.nlm.nih.gov/nuccore/MH170890-5>> (Illera et al. 2018).

Results

Morphological differentiation

Cranial morphology

The MANOVA performed with skull and bill measurements (traits 1–5) identified significant morphological differences among the Canarian common chaffinches (Wilk's $\Lambda=0.11$; $df=20, 209$; $p < 0.001$). These differences were identified for all traits except premaxilla width (trait 1) ($F=1.33$; $p=0.27$). Significant differences found in premaxilla height were due to La Gomera chaffinches. This population showed the highest premaxilla height with all comparisons being significant ($p < 0.015$). However, there were no significant differences among the remaining populations ($p > 0.12$). In addition, the common chaffinches from La Gomera showed the longest head and mandible of all Canarian populations ($p < 0.002$ for all comparisons). We did not find any significant differences in any trait between Gran Canaria and Tenerife ($p > 0.1$ for all traits). Finally, La Palma and El Hierro showed significant differences only in the mandible length ($p=0.01$).

The PCA performed with skull and bill measurements (traits 1–5) produced two principal components explaining 76.5% of the total variance. PC1 explained 60.3%, and showed a high positive weighting for traits 2–5 (premaxilla height, skull length, mandible length and width), and a moderate positive weighting for premaxilla width (trait 1). PC2 explained 16.2% of the variance and showed a high positive weighting for premaxilla width, and a negative weighting for traits 2–5 (Fig. 3A). PC1 plot depicted all La Gomera individuals with values over zero being most of them segregated from other islands (Fig. 3A).

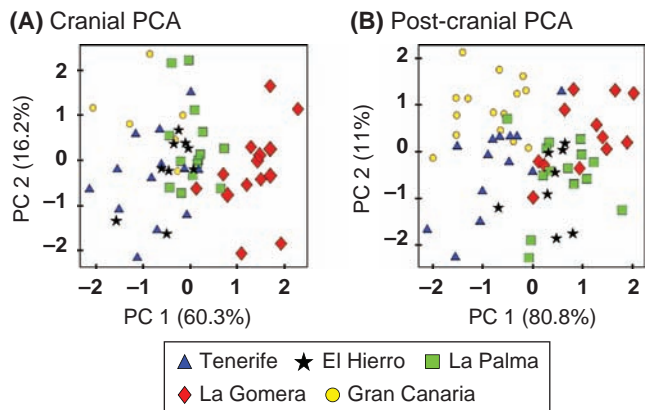


Figure 3. Principal component analysis (PCA) plots for the cranial (A) and post-cranial (B) traits. Cranial PCA (A) includes the following traits: bill width and height, head length, mandible length and width (traits 1–5). Post-cranial PCA (B): includes: scapula, humerus, ulna, femur and tarsometatarsus lengths (traits 6–10). Common chaffinches *Fringilla coelebs* from Gran Canaria (yellow circles), Tenerife (blue triangles), La Gomera (red rhombus), La Palma (green squares) and El Hierro (black stars).

Post-cranial morphology

The postcranial MANOVA (traits 6–10) showed significant differences in all traits among populations (Wilk's Lambda = 0.11; df = 20, 203; $p < 0.001$). Such a result was a consequence of significant differences found with any trait comparison between Tenerife and Gran Canaria with the remaining islands ($p < 0.005$). However, we did not find any significant differences between Tenerife and Gran Canaria ($p > 0.25$).

Postcranial PCA (traits 6–10) provided two principal components explaining 91% of the total variance. PC1 explained 80% of the total variance and showed a high positive weighting for all traits. PC2 explained the 11% of variance showing a negative weighting for scapula, humerus and ulna lengths (traits 6–8), a moderate positive weight for femur (trait 9) and a high positive weight for tarsometatarsus length (trait 10) (Fig. 3B). PC1 plot scored all Gran Canaria individuals and most from Tenerife under zero, whereas most birds from the remaining islands scored over zero. Thus, almost all birds of both groups appear segregated on this axis (Fig. 3B).

Plumage characters

The three populations of *Fringilla coelebs canariensis* (i.e. Gran Canaria, Tenerife and La Gomera) are in appearance

and size similar. However, significant differences are found at R4 tail feather. There is a highly significant association between the extension of tipped white at R4 and the island ($\chi^2 = 43.15$, $p < 0.01$). This result is explained because males on Gran Canaria show tiny white edges (81.5%, $n = 22$) or ≤ 3 mm white spots (18.5%, $n = 5$), whereas, Tenerife and La Gomera populations develop a clear tendency to show ≥ 4 mm extended white spots on R4 (Supplementary material Appendix 1 Fig. A1A). Such a pattern is especially strong on common chaffinch males occurring in Tenerife (85%, $n = 27$) than in La Gomera (65%, $n = 29$) (Supplementary material Appendix 1 Fig. A1B, A1C).

Dating and genetic differentiation

The sequence divergence (i.e. percentage of base differences between sequences) between Canarian common chaffinches subspecies, obtained from 46 sequences of 829 base pairs (bp) for the mtDNA cytochrome b (cyt-b) gene is as follows. *Fringilla coelebs bakeri* (new subspecies from Gran Canaria) and *F. c. canariensis* (Tenerife and La Gomera) differ between 0.72–1.21%. Meanwhile, the divergence between *F. c. bakeri* and *F. c. palmaelombriosa* (La Palma and El Hierro) ranged between 1.21–1.69% (Supplementary material Appendix 1 Table A3). The diagnostic characteristics (i.e. variable sites) in the mitochondrial sequences are shown in Table 2.

The haplotype network showed a clear differentiation among archipelagos and the continental areas (Fig. 4), which agrees with the pattern previously reported in Macaronesia (Marshall and Baker 1999, Rando et al. 2010, Rodrigues et al. 2014). Within the Canary Islands, our results also agree with the pattern found by Suárez et al. (2009), and support a genetic structure determined by three distinctive nodes. One node includes all Gran Canaria sequences; another node is grouping sequences from Tenerife and La Gomera and, finally, the third node clumps birds from La Palma and El Hierro (Fig. 4). Population connections between the Canarian chaffinches and their Macaronesian counterparts suggests a common ancestor to all of them. In addition, the central islands of Tenerife and La Gomera appear directly connected with the remaining common chaffinch populations.

Our dating shows slightly lower dates of colonisation and diversification of common chaffinches in Macaronesia than was previously reported (Rando et al. 2010, Valente et al. 2017). The age estimated for the colonisation of the extant common finches in Macaronesia suggests that this species arrived in the Azores during the middle Pleistocene

Table 2. Cytochrome b diagnostic bases (i.e. variable sites) for *Fringilla coelebs bakeri* in relation to the remaining Canarian common chaffinch subspecies. Pure cyt-b diagnostic bases for discriminating all *F. c. bakeri* individuals from other Canarian populations for cyt-b are shown in red. Numbers are according to the base position along a cyt-b fragment of 829 bp.

Position	293	299	305	374	390	443	503	659	707	785
<i>F. c. bakeri</i>	G	C	C	T	T	T	A	A	T	A
<i>F. c. canariensis</i>	G	T	T	C	T/C	C	C	A	C	A
<i>F. c. ombriosa</i>	A	T	T	C	C	C	C	T	C	G
<i>F. c. palmae</i>	A	T	T	C	C	C	C	T	C	G

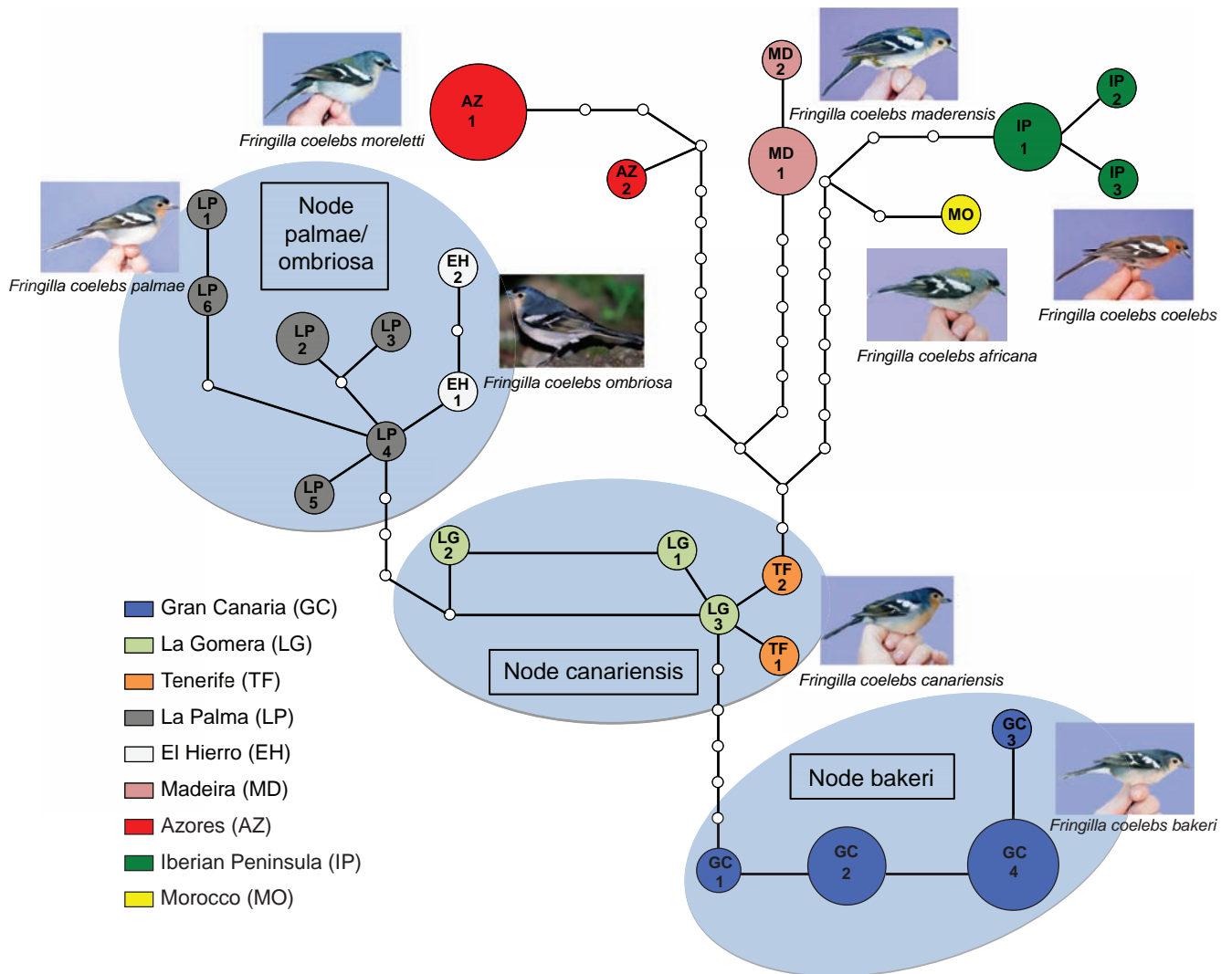


Figure 4. Parsimony network of the common chaffinch *Fringilla coelebs* in Macaronesia and the nearby continental areas (Iberian Peninsula and north Africa) based on the cytochrome b. Open small circles depict one-step mutation edge. The size of haplotypes (circles) represents its abundance, that is, the number of individuals sharing such a haplotype. The three groups (clusters) identified with the mitochondrial cytochrome b are shaded in blue.

(824 000 yr; 0.21–1.87 Mya, lower and upper 95% highest posterior density values, respectively). Shortly after this event, chaffinches colonised Madeira (708 000 yr; 0.18–1.62 Mya) and the Canary Islands (601 000 yr; 0.17–1.38 Mya). The Gran Canaria population diverged from the remaining Canary Islands approximately 493 000 yr (0.13–1.11 Mya) ago. Meanwhile, Tenerife, La Gomera, El Hierro and La Palma appear to have commenced their differentiation processes 383 000 (0.09–0.87 Mya) years ago.

Discussion

The family Fringillidae constitutes an iconic group for evolutionary biologists to study avian speciation because of the high number of species raised by adaptive radiation and hybridisation (Grant and Grant 2008, Price 2008,

Lamichhane et al. 2018). In Macaronesia, only the common chaffinch shows a moderate level of differentiation at the subspecies level, and it is not possible to state whether such a differentiation process is a consequence of selection (natural or sexual), or alternative evolutionary forces such as mutation, drift and founder effects (Spurgin et al. 2014, Illera et al. 2016, Van Doren et al. 2017). According to our results it is plausible to conclude that common chaffinches in Gran Canaria are isolated from the remaining Canarian populations, that is, there is no evidence of dispersal movements among islands. As result, Gran Canaria common chaffinches are characterised by multiple distinctive traits. For all the aforementioned reasons, we conclude that the common chaffinch lineage in Gran Canaria differs from other Canarian common chaffinches and should be ranked as a new taxon. The formal description is presented in the section taxonomic account.

Genetic and morphological differentiation

Delimiting a cryptic differentiation process is challenging because only few traits can experience visible changes. Thus, the limited skeletal differentiation found within the Canary Islands suggests that changes on other less conspicuous traits such as the genetic ones have been independently fixed and maintained on each population over time. The phenotypic similarities found among the Canarian populations could be a direct consequence of homoplasious evolution among lineages, perhaps because birds are experiencing similar environmental and sexual pressures across islands (Illera et al. 2014).

Our genetic results have provided robust evidence that, individuals from each archipelago consistently group together, which suggests long isolation processes with strong genetic differentiation on each archipelago. Strikingly, despite that Azores is composed by nine islands, which appear arranged along 600 km (i.e. furthest than the Canary Islands), our findings confirm that the genetic differentiation found in the Canary Islands is deeper than in Azores (Suárez et al. 2009, Rando et al. 2010, Rodrigues et al. 2014). Reasons to explain this pattern are unknown. However, it seems plausible to suggest that such circumstance is a direct consequence of contemporary gene flow, which would preclude genetic differentiation between the Azorean populations (Rodrigues et al. 2014). The high chaffinch abundances reported in the Azores in relation to the Canary Islands (Carrascal et al. 2008, Ceia et al. 2009) supports this hypothesis. Thus, in the Azores, there could be a recurrent density-dependent dispersal process, perhaps mediated by competition among individuals (Matthysen 2005). Under this scenario, common chaffinches inhabiting islands with high population densities could have developed a dispersal strategy to avoid competitive interactions. In contrast, the lower abundances of common chaffinches recorded in the Canary Islands could preclude a similar behaviour in this archipelago. The high genetic differentiation found among some of the Canarian populations provides evidence for the existence of limited gene flow.

Our findings support the pattern of three clades within the Canary Islands (Suárez et al. 2009), where common chaffinches first came to the central islands of Tenerife and/or La Gomera. This result suggests that both populations have served as the cradle of diversification of the Canarian common chaffinches and acted as source for the western and Gran Canaria islands. Our estimates of colonisation and diversification in the Canary Islands suggest that this process started 600 000 yr ago, with the longest period of isolation (> 490 000 yr) recorded for Gran Canaria. Previous studies reported the existence of strong genetic differentiation of some passerine species occurring in Gran Canaria in relation to their Canarian counterparts (Pestano et al. 2000, Dietzen et al. 2003, 2008, Kvist et al. 2005, Padilla et al. 2015). This recurrent pattern could be explained due to the geological age of Gran Canaria (\approx 14 my old), which makes it the third oldest island in the Canaries (Fuerteventura and

Lanzarote are the oldest ones). Therefore, the ancient age of Gran Canaria has favoured the genetic isolation and final differentiation in allopatry of many avian taxa there inhabiting (Illera et al. 2012).

Our genetic findings agrees with the results obtained by Lachlan et al. (2013) studying the acoustic differentiation within the common chaffinch, and Stensrud (2012) analysing the sperm morphology. Lachlan et al. (2013) tested the degree of differentiation between the populations of Gran Canaria and Tenerife with an experiment. They raised individuals from both islands in isolation conditions from birth, and exposed them to songs from both islands and the mainland. Results showed the highest responses when the call came from individuals belonging to the same island. Such a result highlights two main ideas: 1) the acoustic characteristics in the common finches were more inherited than learned, which is the reverse of patterns found in oscines where song has a strong cultural component (Grant and Grant 2008), and 2) Tenerife and Gran Canaria have a long history of isolation, which agrees with our estimate of divergence. On the other hand, Stensrud (2012) found that Gran Canarian finches showed the lowest sperm length on average, being significantly differentiated from the remaining Canarian populations analysed, although with a high variance. Again, Gran Canarian finches appeared clearly distinguishable from the remaining populations.

Interestingly, morphological differences between individuals from large (Tenerife and Gran Canaria) and small (La Gomera, El Hierro and La Palma) islands match with the co-existence or absence of other *Fringilla* extant species, whose individuals show the largest cranial and postcranial trait values (Rando et al. 2010). Thus, when common chaffinches co-exist in sympatry with the blue chaffinches in Tenerife (*F. teydea*) and Gran Canaria (*F. polatzeki*), they do not show significant morphological differences between them. However, when common chaffinches do not co-occur with other finch species (i.e. El Hierro, La Palma and La Gomera) they show larger scapula, humerus and ulna values (traits 6–9), than the common chaffinches from Tenerife and Gran Canaria ($p < 0.05$ in all the cases). In addition, individuals from these three islands (El Hierro, La Palma and La Gomera) show the highest morphological variation in skull traits and, overall, show longer hindlimb bones (Table 1). This morphological pattern suggests the existence of an ecological character displacement process driving morphological differentiation between big and small chaffinch species in Tenerife and Gran Canaria. Such a mechanism could explain how sympatric finch species minimise the competition for food resources in Tenerife (Grant and Grant 2006, 2010, Rando et al. 2010). In contrast, the biggest sizes and the highest morphological variation recorded in La Gomera, La Palma and El Hierro provide evidence for an expansion of their ecological niche, which is compatible with a competitive release phenomenon (Grant and Grant 2008). Although these phenomena are considered central to understand how species appear and multiply (Schluter 2000), alternative

explanations such as phenotypic plasticity or sexual selection cannot be rule out (Stuart and Losos 2013). Experimental approaches where the potential role of interspecific competition can be inferred through estimating the population growth in sympatry and allopatry (Germain et al. 2018) are now needed to comprehend the ultimate reasons behind the morphological pattern here found.

Taxonomic account

Genus: *Fringilla* Linnaeus 1758

Species: *Fringilla coelebs* Linnaeus 1758

Fringilla coelebs bakeri ssp. nove.

Diagnosis:

a) Appearance

Fringilla coelebs bakeri is in appearance and size similar to *F. c. canariensis* from Tenerife and La Gomera islands. However, *F. c. bakeri* males are different from *F. c. canariensis* in the pattern of tail feather R4. *F. c. bakeri* males show a tiny white edge or small white spot (≤ 3 mm), whereas, *F. c. canariensis* males develop a significant tendency to show conspicuous and extended white spot on R4 (≥ 4 mm) (Supplementary material Appendix 1 Fig. A1A).

b) Holotype

ROM 151158, adult male (skin and skeleton) from Fontanales (Gran Canaria Island, Canary Islands) collected by Michael D. Dennison 5 May 1985 (Fig. 5). Fresh measurements were taken by Michael D. Dennison on 1985, and bone measurements were taken by us for this study such as is described in Methods (Fig. 5).



Figure 5. *Fringilla coelebs bakeri*'s holotype. Frontal, back and right lateral views.

b.1) Genetics

The cytochrome b sequence of this specimen has been deposited in the National Center for Biotechnology Information (NCBI) gene bank database with the MH170895 accession number.

b.2) Holotype colour pattern:

Holotype skin shows dark bluish colour from crown to back. Rump is bright green. Upper tail-coverts and centre of tail are bluish-greyish tinged. Tail feathers are blackish-greyish except outer rectrices (R6-R5), which show a variable amount of white, and the internal rectrices (R1) which have pale green edges. Wing mostly black except for white median coverts and narrow white tips of greater coverts. Remiges are black with pale green edges. Face and underparts are pinkish, whitish on belly and under tail-coverts.

b.3) Holotype morphological measurements

b.3.1) Fresh

Data (all in millimetres except weight in grams) from the fresh specimen. Bill exposed (12.6); bill nasal (10.8); bill depth (7.8); bill width (6.6), tarsometatarsus (20.4), middle toe (11.2); wing length (not available); tail (not available), weight (22.5 g).

b.3.2) Bones

Bone measurements (in mm): premaxilla width (7.7); premaxilla height (5.2); head length (33.1); mandible length (23.8); mandible width (not available); scapula (20.9), humerus (19.4); ulna (23.9); femur (17.8); and tarsometatarsus (21.8).

c) Paratypes

Adult males (skins and skeletons): Paratype1 (ROM 151143), Paratype2 (ROM 151148), Paratype3 (ROM 151151), Paratype4 (ROM 151153), and Paratype5 (ROM 151157). All from the same locality as the holotype, collected between 3 and 5 May 1985, by Michael D. Dennison. Fresh measurements were taken by Michael D. Dennison on 1985, and bone measurements were taken by us for this study such as is described in Methods (Fig. 5).

c.1) Genetics

The cytochrome b region sequenced of these specimens have been deposited in the NCBI gene bank database with the following accession numbers: Paratype1 (MH170890); Paratype2 (MH170891); Paratype3 (MH170892); Paratype4 (MH170893); and Paratype5 (MH170894).

c.2) Paratype colour pattern

As holotype.

c.3) Paratype morphological measurements

In the same order of those of the Holotype. n.a.: not available measurement.

c.3.1) Fresh specimen measurements

All data in mm except weight in grams:

- 1) ROM 151143: 12.3; 10.9; 7.6; 6.9; n.a.; 10.7; 82.0; n.a.; 23.5 g
- 2) ROM 151148: 12.8; 11.1; 7.5; 6.5; 21.5; 10.8; n.a.; n.a.; 22.5 g

- 3) ROM 151151: 12.0; 10.4; 7.4; 6.5; 20.7; n.a.; 83.0; n.a.; 23.5 g
- 4) ROM 151153: 12.9; 11.1; 7.8; 7.0; n.a.; 10.6; 82.0; n.a.; 23.0 g
- 5) ROM 151157: 12.8; 10.8; 7.7; 6.5; 20.6; 11.0; n.a.; n.a.; 24.0 g

c.3.2) Bone measurements

All data in mm

- 1) ROM 151143: 7.2; 5.0; 34.6; 24.4; n.a.; n.a.; 19.5; n.a.; n.a.; n.a.
- 2) ROM 151148: 7.3; 4.8; n.a.; 24.3; 13.7; 20.9; 19.4; 23.7; 18.0; n.a.
- 3) ROM 151151: 7.3; n.a.; n.a.; 23.9; 14.5; 20.8; 19.7; 23.7; 18.1; n.a.
- 4) ROM 151153: 7.6; 4.5; 33.9; 24.1; n.a.; 19.8; 19.2; 23.5; 17.9; n.a.
- 5) ROM 151157: n.a.; 4.3; n.a.; 23.9; 14.2; n.a.; 19.1; 23.2; 17.8; 22.0 g

d) Institution housing material (holotype and paratypes):

Royal Ontario Museum (ROM), Toronto, Canada.

e) Status

Extant

f) Etymology:

The subspecies name is in honour of Professor Allan John Baker who contributed immensely to our understanding of genetic structure, acoustic, and phylogeography of common chaffinches in the Macaronesian islands and nearby continental areas.

g) Distribution

Gran Canaria Island (Canary Islands)

h) Habitat

This taxon is associated with ‘monteverde’ habitats, which represents both laurel forest and ‘fayal-brezal’ (*Myrica faya*–*Erica arborea*) woodlands. In addition, this taxon also occurs on chestnuts *Castanea sativa* and Canary pine *Pinus canariensis* forests. Furthermore, it extends its distribution on lower elevations exploiting the dense vegetation of willows *Salix canariensis* and reeds *Phragmites communis*, being able to be found in areas as low as 100 m above sea level (e.g. Barranco de Moya) (Martín and Lorenzo 2001).

Acknowledgements – Guillermo López provided chaffinches pictures of Fig. 1. Mark Peck selected the tissue of holotype and paratype specimens. Oliver Haddrath sequenced the cytochrome b gene from holotype and paratype specimens. Sarah Eglinton polished the language. The Royal Ontario Museum (Toronto, Canada) and the Museum of Nature and Man (Santa Cruz de Tenerife, Canary Islands, Spain) provided access to their chaffinch collections.

We thank two anonymous reviewers and Subject Editor for valuable comments and suggestions on our manuscript.

Funding – JCI was funded with an Oviedo Univ. and Banco de Santander mobility grant (ref.: 03.01.633B.481.60).

References

- Alström, P., Jönsson, K. A., Fjeldså, J., Ödeen, A., Ericson, P. G. P. and Irestedt, M. 2015. Dramatic niche shifts and morphological change in two insular bird species. – *R. Soc. Open Sci.* 2: 140364.
- Archavaleta, M., Rodríguez, S., Zurita, N. and García, A. 2010. Lista de especies silvestres de Canarias. Hongos, plantas y animales terrestres. 2009. – Gobierno de Canarias, Tenerife.
- Baker, A. J., Dennison, M. D., Lynch, A. and le Grand, G. 1990. Genetic divergence in peripherally isolated populations of chaffinches in the Atlantic islands. – *Evolution* 44: 981–999.
- Carrascal, L. M., Palomino, D. and Polo, V. 2008. Patrones de distribución, abundancia y riqueza de especies de la avifauna terrestre de la isla de La Palma (Islas Canarias). – *Graellsia* 64: 209–232.
- Ceia, R., Heleno, R. and Ramos, J. A. 2009. Summer abundance and ecological distribution of passerines in native and exotic forests in São Miguel, Azores. – *Ardeola* 56: 25–39.
- Clement, M., Posada, D. and Crandall, K. 2000. TCS: a computer program to estimate gene genealogies. – *Mol. Ecol.* 9: 1657–1660.
- Clement, P. 2018. Common chaffinch (*Fringilla coelebs*). – In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. A. and de Juana, E. (eds), *Handbook of the birds of the world alive*. Lynx Edicions, <www.hbw.com/node/61286> accessed 28 March 2018.
- Corso, A., Viganò, M. and Starnini, L. 2015. Identification of African chaffinch. – *Dutch Birding* 37: 392–402.
- Cramp, S. and Perrins, C. M. (eds) 1994. *Handbook of the birds of Europe, the Middle East, and north Africa: the birds of the western Palearctic*. Vol. VIII. Crows to finches. – Oxford Univ. Press.
- Darriba, D., Taboada, G. L., Doallo, R. and Posada, D. 2012. jModelTest 2: more models, new heuristics and parallel computing. – *Nat. Methods* 9: 772.
- Dean, A. D. and Greenwald, J. E. 1995. Use of filtered pipet tips to elute DNA from agarose gels. – *Biotechniques* 18: 980.
- Dennison, M. D. and Baker, A. J. 1991. Morphometric variability in continental and Atlantic island populations of chaffinches (*Fringilla coelebs*). – *Evolution* 45: 29–39.
- Dietzen, C., Witt, H.-H. and Wink, M. 2003. The phylogeographic differentiation of the European robin *Erithacus rubecula* on the Canary Islands revealed by mitochondrial DNA sequence data and morphometrics: evidence for a new robin taxon on Gran Canaria? – *Avian Sci.* 3: 115–132.
- Dietzen, C., García-del-Rey, E., Castro, G. D. and Wink, M. 2008. Phylogeography of the blue tit (*Parus teneriffae*-group) on the Canary Islands based on mitochondrial DNA sequence data and morphometrics. – *J. Ornithol.* 149: 1–12.
- Dietzen, C., Michels, J. P. and Wink, M. 2015. Formal description of a new subspecies of the European robin from Gran Canaria Island, Spain (Aves: Muscicapidae: *Erithacus rubecula marionae* subsp. nov.). – *Open Ornithol. J.* 8: 39–42.
- Drummond, A. J. and Bouckaert, R. R. 2015. Bayesian evolutionary analysis with BEAST. – Cambridge Univ. Press.

- Drummond, A. J., Suchard, M. A., Xie, D. and Rambaut, A. 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. – *Mol. Biol. Evol.* 29: 1969–1973.
- Emerson, B. C. 2002. Evolution on oceanic islands: molecular phylogenetic approaches to understanding pattern and process. – *Mol. Ecol.* 11: 951–966.
- Fišer, C., Robinson, C. T. and Malard, F. 2018. Cryptic species as a window into the paradigm shift of the species concept. – *Mol. Ecol.* 27: 613–635.
- Francisco-Ortega, J., Santos-Guerra, A., Kim, S.-C. and Crawford, D. J. 2000. Plant genetic diversity in the Canary Islands: a conservation perspective. – *Am. J. Bot.* 87: 909–919.
- Germain, R. M., Williams, J. L., Schluter, D. and Angert, A. L. 2018. Moving character displacement beyond characters using contemporary coexistence theory. – *Trends Ecol. Evol.* 33: 74–84.
- Grant, P. R. 1979a. Ecological and morphological variation of the Canary Island blue tits, *Parus caeruleus* (Aves: Paridae). – *Biol. J. Linn. Soc.* 11: 103–129.
- Grant, P. R. 1979b. Evolution of the chaffinch, *Fringilla coelebs*, on the Atlantic Islands. – *Biol. J. Linn. Soc.* 11: 301–332.
- Grant, P. R. and Grant, B. R. 2006. Evolution of character displacement in Darwin's finches. – *Science* 313: 224–226.
- Grant, P. R. and Grant, B. R. 2008. How and why species multiply: the radiation of Darwin's finches. – Princeton Univ. Press.
- Grant, P. R. and Grant, B. R. 2010. Songs of Darwin's finches diverge when a new species enters the community. – *Proc. Natl Acad. Sci. USA* 107: 20156–20163.
- Illera, J. C., Richardson, D. S., Helm, B., Atienza, J. C. and Emerson, B. C. 2008. Phylogenetic relationships, biogeography and speciation in the avian genus *Saxicola*. – *Mol. Phylogenet. Evol.* 48: 1145–1154.
- Illera, J. C., Rando, J. C., Richardson, D. S. and Emerson, B. C. 2012. Age, origin and extinctions of the avifauna of Macaronesia: a synthesis of phylogenetic and fossil information. – *Quat. Sci. Rev.* 50: 14–22.
- Illera, J. C., Palmero, A. M., Laiolo, P., Rodríguez, F., Moreno, A. C. and Navascués, M. 2014. Genetic, morphological, and acoustic evidence reveals lack of diversification in the colonisation process in an island bird. – *Evolution* 68: 2259–2274.
- Illera, J. C., Spurgin, L. G., Rodríguez-Exposito, E., Nogales, M. and Rando, J. C. 2016. What are we learning on speciation and extinction from the Canary Islands? – *Ardeola* 63: 15–33.
- Illera, J. C., Rando, J. C., Rodríguez-Exposito, E., Hernández, M., Claramunt, S. and Martín, A. 2018. Data from: Acoustic, genetic, and morphological analyses of the Canarian common chaffinch complex *Fringilla coelebs* ssp. reveals cryptic diversification. – National Center for Biotechnology Information, <<https://www.ncbi.nlm.nih.gov/nuccore/MH170890-5>>.
- Juan, C., Emerson, B.C., Oromí, P. and Hewitt, G. 2000. Colonization and diversification: towards a phylogeographic synthesis for the Canary Islands. – *Trends Ecol. Evol.* 15: 104–109.
- Kocher, T. D., Thomas, W. K., Meyer, A., Edwards, S. V., Pääbo, S., Villablanca, F. X. and Wilson, A. C. 1989. Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. – *Proc. Natl Acad. Sci. USA* 86: 6196.
- Kumar, S., Stecher, G. and Tamura, K. 2016. MEGA7: molecular evolutionary genetic analysis version 7.0 for bigger datasets. – *Mol. Biol. Evol.* 33: 1870–1874.
- Kvist, L., Broggi, J., Illera, J. C. and Koivula, K. 2005. Colonisation and diversification of the blue tits (*Parus caeruleus teneriffae*-group) in the Canary Islands. – *Mol. Phylogenet. Evol.* 34: 501–511.
- Lachlan, R. F., Verzijden, M. N., Bernard, C. S., Jonker, P.-P., Koese, B., Jaarsma, S., Spoor, W., Slater, P. J. B. and ten Cate, C. 2013. The progressive loss of syntactical structure in bird song along an island colonization chain. – *Curr. Biol.* 23: 1896–1901.
- Lamichhaney, S., Han, F., Webster, M. T., Andersson, L., Grant, B. R. and Grant, P. R. 2018. Rapid hybrid speciation in Darwin's finches. – *Science* 359: 224–228.
- Liffield, J. T., Anmarkrud, J. A., Calabuig, P., Cooper, J. E. J., Johannessen, L. E., Johnsen, A., Kearns, A. M., Lachlan, R. F., Laskemoen, T., Marthinsen, G., Stensrud, E. and García-del-Rey, E. 2016. Species-level divergences in multiple functional traits between the two endemic subspecies of blue chaffinches *Fringilla teydea* in Canary Islands. – *BMC Zool.* 1: 4.
- Lynch, A. and Baker, A. J. 1990. Increased vocal discrimination by learning in sympatry in two species of chaffinches. – *Behaviour* 116: 109–125.
- Lynch, A. and Baker, A. J. 1994. A population memetics approach to cultural evolution in chaffinch song: differentiation among populations. – *Evolution* 48: 351–359.
- Malagó Jr, W., Heitor, M. F., Matheucci Jr, E., Medaglia, A. and Henrique-Silva, F. 2002. Large scale sex typing of ostriches using DNA extracted from feathers. – *BMC Biotechnol.* 2: 19.
- Marshall, H. D. and Baker, A. J. 1999. Colonization history of Atlantic island common chaffinches (*Fringilla coelebs*) revealed by mitochondrial DNA. – *Mol. Phylogenet. Evol.* 11: 201–212.
- Martín, A. and Lorenzo, J. A. 2001. Aves del archipiélago canario. – Francisco Lemus Editor.
- Matthysen, E. 2005. Density-dependent dispersal in birds and mammals. – *Ecography* 28: 403–416.
- Morris-Pocock, J. A., Taylor, S. A., Birt, T. P. and Friesen, V. L. 2010. Concerted evolution of duplicated mitochondrial control region in three related sea birds. – *BMC Evol. Biol.* 10: 14.
- Päckert, M., Dietzen, C., Martens, J., Wink, M. and Kvist, L. 2006. Radiation of Atlantic goldcrests *Regulus regulus* spp.: evidence of a new taxon from the Canary Islands. – *J. Avian Biol.* 37: 364–380.
- Padial, J. M., Miralles, A., De la Riva, I. and Vences, M. 2010. The integrative future of taxonomy. – *Front. Zool* 7: 1–14.
- Padilla, D. P., Spurgin, L. G., Fairfield, E., Illera, J. C. and Richardson, D. S. 2015. Population history, gene flow and bottlenecks in island populations of a secondary seed disperser, the southern grey shrike (*Lanius meridionalis koenigi*). – *Ecol. Evol.* 5: 36–45.
- Pestano, J., Brown, R. P., Rodríguez, F. and Moreno, A. 2000. Mitochondrial DNA control region diversity in the endangered blue chaffinch, *Fringilla teydea*. – *Mol. Ecol.* 9: 1421–1425.
- Price, T. 2008. The speciation in birds. – Roberts and Company Publishers.
- Rambaut, A., Suchard, M. A., Xie, D. and Drummond, A. J. 2014. Tracer v1.6. – <<http://tree.bio.ed.ac.uk/software/tracer/>>.
- Rando, J. C., Alcover, J. A. and Illera, J. C. 2010. Disentangling ancient interactions: a new extinct passerine provides insights on character displacement among extinct and extant island finches. – *PLoS One* 5: e12956.
- Rasband, W. S. 1997. ImageJ. – U.S. National Inst. of Health, Bethesda, MD, USA, <<http://rsb.info.nih.gov/ij/>>.

- Rodrigues, P., Lopes, R. J., Reis, S., Resendes, R., Ramos, J. A. and Tristão da Cunha, R. 2014. Genetic diversity and morphological variation of the common chaffinch *Fringilla coelebs* in the Azores. – *J. Avian Biol.* 45: 167–178.
- Samarasin-Dissanayake, P. 2010. Population differentiation, historical demography and evolutionary relationships among widespread common chaffinch populations (*Fringilla coelebs* ssp.). – MS thesis, Univ. of Toronto.
- Sangster, G. 2006. The taxonomic status of “phylogroups” in the *Parus teneriffae* complex (Aves): comments on the paper by Kvist et al. (2005). – *Mol. Phylogenet. Evol.* 38: 288–289.
- Sangster, G., Rodríguez-Godoy, F., Roselaar, C. S., Robb, M. S. and Luksenburg, J. A. 2016. Integrative taxonomy reveals Europe’s rarest songbird species, the Gran Canaria blue chaffinch *Fringilla polatzeki*. – *J. Avian Biol.* 47: 159–166.
- Schluter, D. 2000. *The ecology of adaptive radiation*. – Oxford Univ. Press.
- Spurgin, L. G., Illera, J. C., Jorgensen, T. H., Dawson, D. A. and Richardson, D. S. 2014. Genetic and phenotypic divergence in an island bird: isolation by distance, by colonization or by adaptation? – *Mol. Ecol.* 23: 1028–1039.
- Stensrud, E. 2012. Allopatric speciation and multi-trait variation in the common chaffinch (*Fringilla coelebs*) complex. – MS thesis, Univ. of Oslo.
- Stervander, M., Illera, J. C., Kvist, L., Barbosa, P., Keehnen, N. P., Pruijscher, P., Bensch, S. and Hansson, B. 2015. Disentangling the complex evolutionary history of the Western Palearctic blue tits (*Cyanistes* spp.) – phylogenomic analyses suggest radiation by multiple colonization events and subsequent isolation. – *Mol. Ecol.* 24: 2477–2494.
- Stuart, Y. E. and Losos, J. B. 2013. Ecological character displacement: glass half full or half empty? – *Trends Ecol. Evol.* 28: 402–408.
- Suárez, N. M., Betancor, E., Klasert, T. E., Almeida, T., Hernández, M. and Pestano, J. J. 2009. Phylogeography and genetic structure of the Canarian common chaffinch (*Fringilla coelebs*) inferred with mtDNA and microsatellite loci. – *Mol. Phylogenet. Evol.* 53: 556–564.
- Tietze, D. T., Martens, J., Fischer, B. S., Y-Sun, H., Klusmann-Kolb, A. and Päckert, M. 2015. Evolution of leaf warbler songs (Aves: Phylloscopidae). – *Ecol. Evol.* 5: 781–798.
- Valente, L., Illera, J. C., Havenstein, K., Pallien, T., Etienne, R. S. and Tiedemann, R. 2017. Macroevolutionary dynamics in Atlantic island avifaunas support MacArthur and Wilson’s equilibrium prediction. – *Curr. Biol.* 27: 1660–1666.
- Van Doren, B. M., Campagna, L., Helm, B., Illera, J. C., Lovette, I. J. and Liedvogel, M. 2017. Correlated patterns of genetic diversity and differentiation across an avian family. – *Mol. Ecol.* 26: 3982–3997.

Supplementary material (JAV-01885 at <www.avianbiology.org/appendix/jav-01885>). Appendix 1.