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ORIGINAL ARTICLE

Colonization patterns and genetic structure of peripheral populations of the trumpeter finch (*Bucanetes githagineus*) from Northwest Africa, the Canary Islands and the Iberian Peninsula

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ABSTRACT

Aim This paper has three aims: (1) to reconstruct the colonization history of two peripheral populations of the trumpeter finch (*Bucanetes githagineus*) presumably originating from the same source, one the result of an ancient expansion process and the other recently established and still expanding; (2) to estimate the importance of key events, such as past and current gene flow and bottlenecks, in both expansion processes and their contribution to the present population structure and genetic diversity; and (3) to find out whether two peripheral populations that established at widely differing times also differ in terms of genetic diversity.

Location Northwest Africa (assumed source population), Canary Islands (long-established peripheral) and south-eastern Iberian Peninsula (recently established peripheral).

Methods Bayesian analysis of population structure, individual assignment tests, *F*-statistics, maximum likelihood migration estimates, genetic diversity indices and bottleneck tests were calculated with microsatellite data from 194 trumpeter finches from five breeding and two seasonal non-breeding sites.

Results Our data support the existence of two subpopulations (Canary Island and Ibero-African) as the most likely population structure. Seasonal sites in the Iberian Peninsula had the highest percentage of birds assigned to other, mainly Iberian, sites. Pairwise F_{ST} values showed that the Canary Island localities were very similar to each other, but differed from the rest. Gene flow estimates within subpopulations were only slightly higher in the Canary Island population than in the Ibero-African one. Gene diversity indices were similar at all localities. Canary Island sites show evidence of bottlenecks, whereas the Ibero-African sites do not.

Main conclusions Our data show that, at present, birds from the Canary Islands are genetically differentiated from those in North Africa and continental Spain. We could not unequivocally confirm the African origin of Canary populations because the contrary is also plausible. The Iberian Peninsula seems to have repeatedly received individuals from North Africa, which would have led to the relatively high genetic diversity found in these recently established localities and prevented bottlenecks. Movements of individuals towards sites outside their current range during the non-breeding season are likely to precede the establishment of new breeding sites at the periphery of the distribution range.

Keywords

Assignment testing, birds, bottleneck, dispersal, *F*-statistics, gene flow, microsatellite, nomadic, peripheral population, range expansion.

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INTRODUCTION

Range expansions are recurrent phenomena in the history of many species. The rapid range expansion of a species commonly results in a homogeneous genetic structure and low diversity at the range periphery, as the colonizing populations typically experience a series of consecutive bottlenecks. This process may also result in rapid differentiation from the source owing to genetic drift. This phenomenon is known as the 'leading edge' hypothesis (Hewitt, 1999) and is reinforced by a founder effect when early peripheral populations are made up of just a few individuals (Beebee & Rowe, 2004). In this sense, even though recently established populations are not expected to fit gene flow–mutation–drift equilibrium, the few studies that have attempted to reconstruct the colonization history of contemporary expanding species show that, the more recent the colonization event, the lower the genetic diversity of the population (Estoup *et al.*, 2004; Herborg *et al.*, 2007). However, the existence of a contemporary gene flow is a key factor that can prevent genetic differentiation of peripheral populations (Kirkpatrick & Barton, 1997) and also allow the recovery of genetic diversity after a recent genetic bottleneck (Hansson *et al.*, 2000; Keller *et al.*, 2001; Ortego *et al.*, 2007). Estoup *et al.* (2004) and Herborg *et al.* (2007) studied invasive species in the absence of current gene flow from the original source population (i.e. in the absence of successive invasions), finding pronounced genetic impoverishment in peripheral localities. Although similar patterns of genetic diversity are expected for naturally expanding populations, this topic has been little explored to date (but see Fabbri *et al.*, 2007), possibly because the existence of current gene flow diffuses these patterns. Both genetic reconstruction of the colonization history and study of the ongoing spread of a population are important questions in gaining an understanding of the evolutionary aspects of such range expansion (Herborg *et al.*, 2007).

The trumpeter finch (*Bucanetes githagineus*, Lichtenstein, 1823) is a granivorous fringillid distributed throughout the arid regions of the Western Palaeartic, from the Middle East to Western Sahara (Cramp & Perrins, 1994). Whereas this species has been present in the easternmost Canary Islands (Fuerteventura and Lanzarote) for at least 7000 years (Castillo *et al.*, 2001), it was recorded breeding in the Iberian Peninsula for the first time as recently as in 1971 (García, 1972). Since then, the species has expanded throughout south-eastern Spain (Carrillo *et al.*, 2007). Although the Northwest African population is expected to be the source of both the Iberian and the Canary Island populations, the fact is that, at present, the origin of birds breeding in these regions and the exchange of individuals among populations are unknown. On the basis of plumage coloration and body measures, Cramp & Perrins (1994) proposed the existence of a different race in the Canaries than in Northwest Africa and Europe. However, genetic or detailed morphological studies are lacking. This unique situation offers an excellent opportunity to study the colonization patterns and genetic structure in different populations of the same species established at different times, one of them currently in expansion probably as an effect of climate change (Carrillo *et al.*, 2007).

The specific aims of our study are to investigate: (1) whether the North African population of the trumpeter finch is the source of both the Canary Island and the Iberian population; (2) the importance of two key processes in the colonization of these two peripheral populations, namely the occurrence of continuous gene flow (which could prevent the genetic differentiation of peripheral populations) and the occurrence of a founder effect (i.e. a small number of colonizers from the source population leading to genetic differentiation); and (3) considering the hypothetical scenario that North Africa is the common source of both populations, to study whether two peripheral populations differing widely in establishment age also differ in genetic diversity, with the oldest being genetically more diverse, as has been found for invasive species (Estoup *et al.*, 2004; Herborg *et al.*, 2007).

MATERIALS AND METHODS

Study area, sample collection and laboratory protocol

We collected samples from three regions in the westernmost area of the current range of the trumpeter finch (Fig. 1; see also Table 1 for exact coordinates): the Canary Islands, Northwest Africa and the Iberian Peninsula. Birds were sampled on two of the Canary Islands, Lanzarote and Fuerteventura. These islands are located *c.* 100 km from the African coast, and have rich populations of the study species (Martín & Lorenzo, 2001). One locality, Errachidia, which was sampled as being representative of the population in North Africa, is located south of the Middle Atlas Mountains and north of the Sahara Desert, more than 900 km from the Canary Islands and more than 350 km from the Mediterranean coast of Morocco. The arid landscape around Errachidia is representative of the typical breeding habitat of the trumpeter finch, which is an abundant breeding species in the numerous wadis of the region (R. Barrientos, C. Carrillo, L. García, J. Benzal and F. Valera, personal observation). In the Iberian Peninsula, two breeding localities (Tabernas and Monnegre) and two seasonal, non-breeding sites (Gorafe and Cabo de Gata) were sampled. Tabernas is the richest and seemingly most stable breeding population (Manrique *et al.*, 2003), whereas Monnegre (250 km north in inland Alicante Province) is the northernmost recently confirmed breeding locality (year 2000), and undergoes strong interannual fluctuations (0–40 breeding pairs, López-Iborra *et al.*, 2006). Owing to the marked seasonality of their trumpeter finch populations, there are two further localities in the south-eastern Iberian Peninsula of special interest: Gorafe and Cabo de Gata. Birds (mainly juveniles, Fernández-Ordóñez & Pérez-Contreras, 2006) are known to spend the summer in large numbers in Gorafe (100 km from Tabernas), where a small breeding nucleus has recently been found (year 2005, Pérez-Contreras & Fernández-Ordóñez, 2006). Although trumpeter finches also breed in

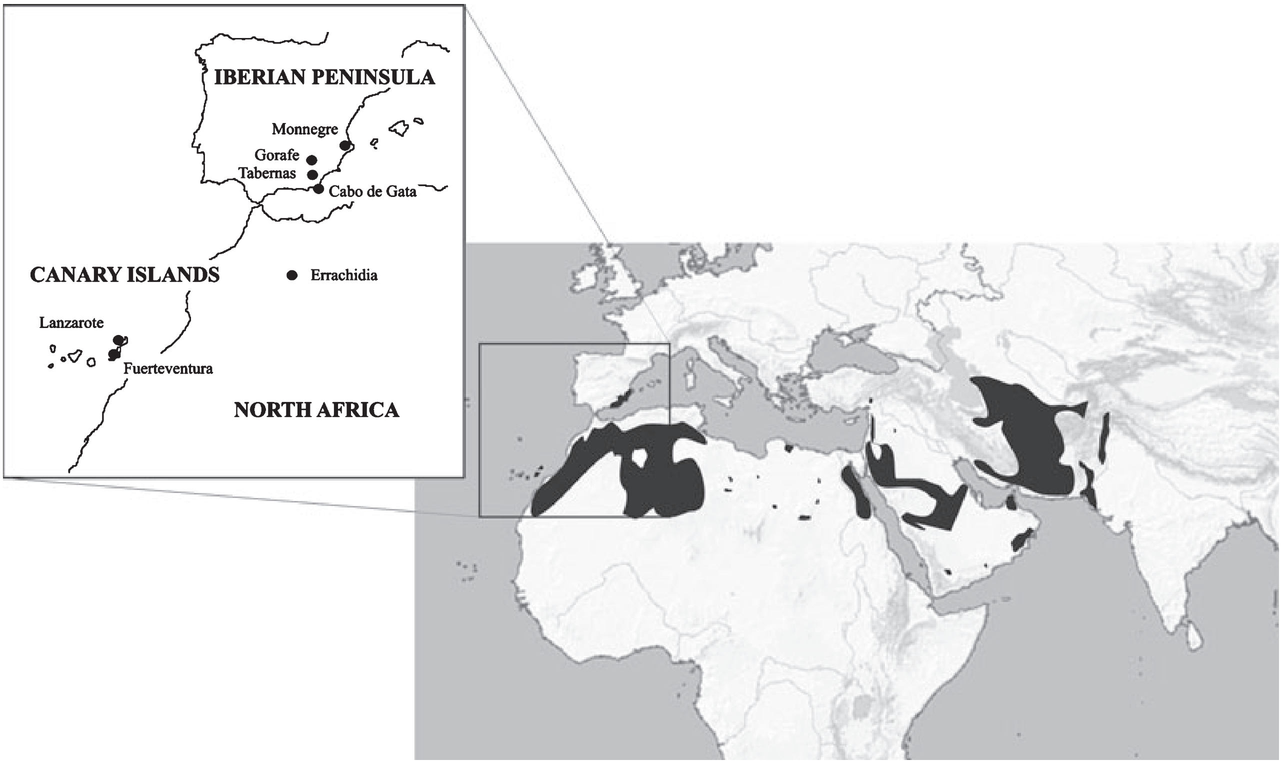

Figure 1 Worldwide breeding range of the trumpeter finch (*Bucanetes githagineus*) (black areas) (based on Cramp & Perrins, 1994), with sampling sites highlighted in the upper left corner.

Table 1 Locations and biogeographical regions of trumpeter finch (*Bucanetes githagineus*) sampling sites. Sample size refers to the number of birds analysed. Years and months refer to the date when birds were trapped.

Location	Coordinates	Region	Sample size	Years	Months
Fuerteventura	28°35′ N, 13°58′ W	Canary Islands	26	2004, 2005	II–IV
Lanzarote	28°54′ N, 13°46 W	Canary Islands	25	2004, 2005	III–IV
Monnegre	38°30′ N, 00°30′ W	Iberian Peninsula	15	2006	VI–VII
Cabo de Gata	36°38′ N, 02°14′ W	Iberian Peninsula	22	2004	I–II
Gorafe	37°29′ N, 03°02′ W	Iberian Peninsula	26	2003–2005	VII–VIII
Tabernas	37°02′ N, 02°30′ W	Iberian Peninsula	51	2002–2005	V–IX
Errachidia	31°56′ N, 04°25′ W	North Africa	29	2003, 2006	VI–VII, X

Cabo de Gata (50 km from Tabernas) this is mainly an overwintering area where birds aggregate in flocks during the winter (authors, unpublished data). Ringing studies have shown that birds from Tabernas and Gorafe move to Cabo de Gata in autumn and winter (authors, unpublished data).

We trapped trumpeter finches in the study locations by mist-netting, and, in some cases (33% of the samples from Monnegre and 27% from Fuerteventura), by sampling one chick per brood. Most birds in the Canary Islands, Tabernas, Monnegre and Errachidia were trapped during the breeding season [from January to May in the Canary Islands (Martín & Lorenzo, 2001), February to July in continental Spain (López-Iborra *et al.*, 2006; Barrientos *et al.*, 2007), and February to June in Morocco (Thévenot *et al.*, 2003)], although in some cases some captures were in the non-breeding season (Table 1), when immigrants are also potentially present. In contrast, birds in Gorafe and Cabo de Gata were sampled during the peak out-of-breeding concentrations, that is, during summer at the first site and during winter at the second (Table 1). It is thus very likely that trapped birds originated in other breeding populations rather than at the sampling site. We took blood samples by brachial venipuncture using 70 × 1.5 mm heparinised capillary tubes. Samples were immediately stored in a vial with 1 mL of 96° ethanol until laboratory analysis. Birds were released after sampling.

DNA was extracted from blood samples following the standard phenol/chloroform procedure (Sambrook & Russell, 2001). We chose to use highly variable nuclear DNA microsatellite markers, as these have proved useful for studying the effects of recent demographic events and range expansion (e.g. Beebee & Rowe, 2004; Spaulding *et al.*, 2006; Herborg *et al.*, 2007; Kvist *et al.*, 2007). Specifically, we selected seven polymorphic microsatellites, namely three developed for the Scottish crossbill, *Loxia scotica* (Piertney *et al.*, 1998; Lox1, Lox2 and Lox8), one for the magpie, *Pica pica* (Martínez *et al.*, 1999; Ppi2), one for the crowned leaf warbler, *Phylloscopus occipitalis* (Bensch *et al.*, 1997; Pocc6), one for the house sparrow, *Passer domesticus* (Griffith *et al.*, 1999; Pdo5) and one for the blue tit, *Parus caeruleus* (GenBank accession no. AF041466; Pk12).

Polymerase chain reactions (PCRs) were performed in 10-μL volumes containing 50 ng of template DNA, 0.4 μM of each primer, 0.1 mM of each dNTP, 1 μL of 10× PCR buffer (2.5 mM $MgCl_2$) and 0.16 units of Dynazyme (Finnzymes, Espoo, Finland). The PCR protocol for the crossbill primers was 94°C for 2 min followed by 35 cycles of 94°C for 30 s, 52°C for 45 s (Lox1) or 53°C for 30 s (Lox2) or 52°C for 30 s (Lox8) and 72°C for 30 s, with a final extension of 72°C for 5 min. For Ppi2 the protocol was 94°C for 2 min followed by 35 cycles of 94°C for 30 s, 50°C for 45 s and 72°C for 45 s, with a final extension of 72°C for 10 min. For Pocc6 the protocol was identical to that for Ppi2, but with an annealing temperature of 53°C for 30 s. The PCR cycling conditions for Pdo5 consisted of 94°C for 90 s, a touchdown of 94°C for 45 s, 55°C /53°C /51°C for 45 s, 72°C for 45 s followed by 35 cycles of 45 s at 94°C, 45 s at 50°C and 45 s at 72°C, ending with a final extension of 72°C for 10 min. Finally, conditions for Pk12 were identical to those for Pdo5, except that we used a touchdown profile, starting with annealing temperatures of 50°C /49°C /47°C and finally 45°C for 35 cycles. PCR products were run on an ABI 3730 automatic DNA sequencer and alleles were scored with GENEMAPPER ver. 3.7 (Applied Biosystems, Foster City, CA, USA).

Statistical analyses

Null alleles and allelic dropouts were diagnosed with MICRO-CHECKER ver. 2.2.3 (Van Oosterhout *et al.*, 2004) because null alleles could interfere in the population structure and inbreeding analyses. Testing for linkage disequilibrium between pairs of loci within each population was performed using a chi-square test (at the 0.05 level) with ARLEQUIN ver. 3.1 (Excoffier *et al.*, 1992). We used the Bayesian approach to analyse population genetic structure with STRUCTURE ver. 2.0 (Pritchard *et al.*, 2000). The likelihood of the data and following probabilities for the different number of subpopulations were calculated with *K* (1–7), where *K* is the different number of subpopulations, running the Markov chain Monte Carlo (MCMC) for 1,000,000 iterations after burn-in periods of 100,000 iterations. To check the consistency of the results, we performed two replicate runs for each *K*. We used GENECLASS ver. 2 (Piry *et al.*, 2004) to detect first-generation migrants and assign them to one of the sampled populations. ARLEQUIN was used to estimate pairwise F_{ST} between the localities, and F_{ST} *P*-values were corrected with the Bonferroni step-down correction (Holm, 1979). Maximum likelihood migration (i.e. bidirectional asymmetric gene flow) rates were estimated with MIGRATE ver. 2.1.3 (Beerli, 2004), which was used to build a full migration matrix model with a Brownian motion approximation to the stepwise mutation model. As suggested by the programme author, Markov chain parameters were set as short chains = 10 (10,000 genealogies sampled) and long chains = 3 (100,000 genealogies sampled). After discarding loci with possible allelic dropouts or null alleles, the inbreeding coefficient (F_{IS}) for each sampled locality (Weir & Cockerham, 1984) as well as gene diversity and allelic richness were calculated using FSTAT ver. 2.9.3.2 (Goudet, 2001). Mean expected and observed heterozygosity were calculated with MSA ver. 3.12 (Dieringer & Schlötterer, 2003).

The Cornuet & Luikart (1996) test in BOTTLENECK ver. 1.2.02 (Piry *et al.*, 1999) was used to assess the strength of bottlenecks following the recommendations of Piry *et al.* (1999), using the two-phase model (TPM) for microsatellite data with 5% multiple-step changes, and the results were evaluated using the sign, standardized difference and one-tailed Wilcoxon tests.

RESULTS

We found linkage disequilibrium in only five tests, including four distinct pairs of loci. Physical linkage can therefore be discarded. Population subdivision was analysed using STRUCTURE. The lnP(D), where lnP(D) is the probability of every *K*, (−5833.2 and −5832.9, in the two replications, respectively) identified two subpopulations as the most likely structure. These subpopulations are the Canary (Fuerteventura and Lanzarote) and the Ibero-African (the rest of localities) ones.

GENECLASS assignment tests for first-generation migrants (Table 2) confirmed this structure, as the two island localities had the highest percentages assigned to the sampling site. At

Table 2 Results of the assignment tests for first-generation migrants of the trumpeter finch (*Bucanetes githagineus*) as the percentage of individuals from the sampling site assigned to every location.

	Assigned to (%)						
Sampled in	Fuerteventura	Lanzarote	Monnegre	Cabo de Gata	Gorafe	Tabernas	Errachidia
Fuerteventura	57.8	23.1	3.8	0.0	3.8	7.7	3.8
Lanzarote	28.0	60.0	0.0	0.0	0.0	8.0	4.0
Monnegre	0.0	0.0	40.0	6.7	13.3	33.3	6.7
Cabo de Gata	0.0	0.0	18.4	18.4	4.6	40.2	18.4
Gorafe	7.7	3.8	7.7	7.7	34.6	30.8	7.7
Tabernas	3.9	5.9	5.9	17.6	13.7	47.1	5.9
Errachidia	3.4	6.9	3.4	27.6	6.9	6.9	44.9

these sites, assignments to non-Canary localities were only 19.1% in Fuerteventura and 12.0% in Lanzarote. In the Ibero-African subpopulation, the samples with the lowest assignment to sampling sites were those for which the population size increases during the non-breeding season (i.e. Cabo de Gata and Gorafe), indicating that the bulk of these birds come from other sites. In Cabo de Gata, most individuals were assigned to Tabernas (40.2%). In Gorafe, Tabernas was again an important source, assignment percentages to Tabernas being just slightly below those found for Gorafe itself (30.8% vs. 34.6%). In the recently established population in Monnegre, a large proportion of individuals was again assigned to Tabernas, although a lower proportion than that assigned to Monnegre (33.3% vs. 40.0%). In Tabernas and Errachidia (south-eastern Morocco) most finches were assigned to the site at which they were sampled, although in both cases at least one individual was assigned to one of the other localities.

Genetic differentiation among localities was quantified by F_{ST} values (Table 3). The results confirmed our previous findings, as the two Canary Island localities were very similar to each other, but differed from the rest. Surprisingly, Errachidia, the site included in the expected source region, was statistically different from Tabernas and Gorafe. All the Iberian pairwise F_{ST} values were non-significant. However, the differences among these Iberian sites were smaller than those between Iberian and Canary Island localities (Table 3).

Gene flow estimates among localities (Table 4) give no clear evidence for differential gene flow among the populations. Nevertheless, several flows, such as Lanzarote towards Errachidia, Tabernas towards Lanzarote, Fuerteventura towards Lanzarote, and Lanzarote towards Fuerteventura, are high (above $N_m = 8.45$, where N_m is the average number of successfully reproducing migrants per generation). On the other hand, they are low (below $N_m = 2.52$) for Fuerteventura towards Monnegre, Monnegre towards Lanzarote, and Monnegre towards Errachidia, which suggests that some situations are more likely than others. In order to find the gene flow between subpopulations based on the genetic structure found with STRUCTURE, the average N_m was calculated from Table 4. It seems that gene flow is higher among Canary Island subpopulation sites than among Ibero-African sites ($N_m = 8.48$ and 5.38, respectively). Average gene flow between localities belonging to different subpopulations is 5.77, which is lower than that within the Canary Islands and similar to that within Ibero-Africa.

MICRO-CHECKER indicated the existence of null alleles in two loci, Lox8 and Pk12, which were removed from inbreeding coefficient calculations (Table 5). Gene diversity and allelic richness were fairly similar at the various localities (Table 5), although, overall, they were slightly higher in Errachidia (the site sampled in the likely source area). Theta values were also similar at different localities (Table 5), and therefore our interpretation of genetic diversity based on these results must be taken with some caution. F_{IS} values were the lowest in the Canary Islands, medium in Errachidia and highest in the Iberian Peninsula, suggesting reasonably strong inbreeding or a Wahlund effect in the Iberian localities.

Finally, bottleneck tests showed that the Canary Island birds probably underwent a founder effect as inferred from sign (Fuerteventura $P = 0.02$; Lanzarote $P = 0.02$), standardized (Fuerteventura $P = 0.03$; Lanzarote $P < 0.01$) and Wilcoxon (Fuerteventura $P < 0.01$; Lanzarote $P < 0.01$) tests. There was no evidence of a bottleneck at any of the Iberian sites ($P > 0.10$ in all the tests).

Table 3 Genetic structure of the trumpeter finch (*Bucanetes githagineus*) in the westernmost Palaeartic. Pairwise F_{ST} values are shown below the diagonal and their uncorrected P-values above the diagonal. When appropriate, the significance levels of these P-values after Bonferroni step-down correction are marked with * for $P < 0.05$ and with ** for $P < 0.01$.

Site	Fuerteventura	Lanzarote	Monnegre	Cabo de Gata	Gorafe	Tabernas	Errachidia
Fuerteventura		0.63	< 0.01*	< 0.01*	< 0.01**	< 0.01*	< 0.01**
Lanzarote	0.00038		< 0.01**	< 0.01*	< 0.01**	< 0.01*	< 0.01**
Monnegre	0.04001	0.04386		0.70	0.01	0.20	0.03
Cabo de Gata	0.02568	0.02422	0.00109		0.20	0.70	0.10
Gorafe	0.03159	0.02971	0.03381	0.00919		0.02	< 0.01*
Tabernas	0.02040	0.01963	0.00991	0.00088	0.01417		< 0.01*
Errachidia	0.03348	0.02516	0.01824	0.00977	0.02114	0.02186	

Table 4 Gene flow (average number of successfully reproducing migrants per generation, N_m) estimates for breeding localities of the trumpeter finch (*Bucanetes githagineus*). We excluded seasonal populations from Gorafe and Cabo de Gata from these analyses because, according to assignment tests (Table 2), they are made up mainly of birds from other localities.

	Place of origin (N_m)				
Destination	Fuerteventura	Lanzarote	Monnegre	Tabernas	Errachidia
Fuerteventura		8.46	6.59	6.05	4.90
Lanzarote	8.50		2.07	9.14	7.26
Monnegre	2.51	5.26		5.91	5.17
Tabernas	4.62	5.76	7.06		5.96
Errachidia	4.92	10.14	2.06	6.12	

Table 5 Average observed (H_o) and expected (H_e) heterozygosity, inbreeding coefficient (F_{IS}), theta (θ), gene diversity and allele richness (N_{AR}) calculated for the seven loci (except for F_{IS}, which was calculated excluding Lox8 and Pk12), together with sample sizes (N) in the localities where trumpeter finches (*Bucanetes githagineus*) were sampled.

Site	Mean H_o	Mean H_e	Mean F_{IS}	θ	Gene diversity	Mean N_{AR}	N
Fuerteventura	0.5442	0.7169	−0.006	1.9537	8.3948	0.7219	26
Lanzarote	0.4939	0.6667	0.024	2.0097	7.8811	0.7256	25
Monnegre	0.5668	0.7213	0.212	1.9439	8.2095	0.7223	15
Cabo de Gata	0.5526	0.7131	0.115	1.9871	8.8398	0.7235	22
Gorafe	0.6145	0.7148	0.165	1.7502	7.5461	0.6726	26
Tabernas	0.6246	0.7253	0.139	1.9638	8.4307	0.7205	51
Errachidia	0.6076	0.7253	0.098	2.0094	10.0658	0.7311	29

DISCUSSION

Colonization patterns

Analysis of the genetic population structure and F_{ST} genetic distances shows that, at present, birds in the Canary Islands are genetically differentiated from those in North Africa and continental Spain. Bottlenecks in the island populations probably caused their genetic differentiation by genetic drift, which is seemingly supported by morphological data (Cramp & Perrins, 1994; R. Barrientos *et al.*, unpublished data).

In contrast, our results do not allow us to confirm the African origin of Canary Island populations because: (1) the strongest gene flow is from Lanzarote to Errachidia, and (2) even though gene diversity is slightly higher in Errachidia, other measures of diversity are very similar. Moreover, from our results, we cannot reject the Canary Islands as the source from which the species spread eastwards to colonize and expand through North Africa. However, it should be emphasized that the gene flow estimates suggest that there are common genetic features in the populations studied, which may be the result of past histories of the populations, not necessarily of present birds flying from one locality to another. On the other hand, bottleneck traces found in Canary Island populations could support both situations mentioned above. We cannot discard the possibility that these bottlenecks may have occurred as a result of a population decrease during a certain period, for instance if the islands acted as a refugium. Such bottlenecks may also have been the result of the arrival of a small number of past colonizers from the continent, causing a founder effect in the island populations. This latter scenario coincides with the general pattern of colonization in the Canary Islands, where the common pattern found is one or a few, rather than many, colonization events. For example, the common European chaffinch (*Fringilla coelebs*) colonized them in a single wave via the Azores and Madeira (Marshall & Baker, 1999), Canary robins (*Erithacus rubecula*) probably arrived in two or three colonization events (Dietzen *et al.*, 2003), and goldcrests (*Regulus regulus*) coming directly from Europe colonized them in two independent major events (Päckert *et al.*, 2006). This absence of many major Canary Island colonization events, despite the short distance to the mainland (*c.* 100–125 km), could be explained, at least partly, by the fact that the prevailing winds in Northwest Africa are from the north-east (e.g. Freudenthal *et al.*, 2002), whereas the wind direction that would have facilitated colonization by nomadic displacement from Africa is south-east. The fact that the Canaries have a large number of endemic species and subspecies of birds despite the short distance to the mainland (e.g. Pestano *et al.*, 2000; García-del-Rey & Cresswell, 2005; Kvist *et al.*, 2005; Illera *et al.*, 2006, 2007; Päckert *et al.*, 2006) seems to support the low number of colonization events.

Considering the possibility that the trumpeter finch colonized the Canary Islands from North Africa, we can first reject colonization facilitated by humans, as trumpeter finches were present in these islands at least 7000 yr BP (Castillo *et al.*, 2001) and humans arrived in the Canary Islands much later, *c.* 3000 yr BP (Onrubia-Pintado, 1987). On the other hand, the history of colonization and speciation in the Canary Islands shows that most colonizers arrived from North Africa and the Iberian Peninsula by means of a stepwise colonization sequence from older to younger islands; that is, from eastern (Fuerteventura and Lanzarote) to western (Tenerife, La Palma, La Gomera or El Hierro) islands (Juan *et al.*, 2000), although some exceptions can be found as in the case of the blue tit (*Parus caeruleus teneriffae*) (Kvist *et al.*, 2005). Diversification and expansion from the Canary Islands to the continents is not the usual pattern in arid-land species either. For instance, the appearance of an ecologically close species, the houbara bustard (*Chlamydotis undulata*), which has an endemic Canary subspecies (*Ch. u. fuertaventurae*) as in the case of the trumpeter finch, is explained by colonization from North Africa (Idaghdour *et al.*, 2004). Trumpeter finches are present in large numbers in Fuerteventura and Lanzarote, the older and easternmost islands, whereas their numbers decrease in the other, younger islands, such as Tenerife and La Gomera, and the species only recently colonized the youngest island of El Hierro (Martín *et al.*, 1990). This fits the stepwise colonization pattern from eastern to western islands mentioned above. Although our results do not allow assignment of the North African population as the unequivocal source of the Canary populations, the similarity of the colonization patterns to those of other species from North Africa seems to support such a scenario.

Our results support the existence of an Ibero-African population but they do not allow us to determine whether the North African population is the source of the Iberian one. It could even be speculated that the Iberian population is the source of the Canary finches. However, the distribution of the species from the Middle East to the Western Sahara (Cramp & Perrins, 1994), the recent spread to the north of Morocco (Cramp & Perrins, 1994), the subsequent, ongoing colonization of the Iberian Peninsula (Carrillo *et al.*, 2007) and the general patterns of colonization of the Canary Islands (see above) suggest that the Iberian Peninsula was not the source of the Canary Island and African populations.

Our data show no evidence of bottlenecks in any Ibero-African locality, and therefore there must have been and must still be a strong gene flow from Africa towards the Iberian localities. This constant gene flow may be the reason for the similar genetic structures found in African and Iberian sites. However, the F_{ST} values suggest incipient genetic differentiation between Tabernas (the oldest and largest breeding site in Iberia; Carrillo *et al.*, 2007) and Errachidia. Assignment tests point out a highly dynamic scenario in the Ibero-African subpopulation, with the strong exchange of birds resulting in little genetic differentiation among sites. Such results are in agreement with those found by Godoy *et al.* (2004) and Guillaumet *et al.* (2006). However, strong gene flow and low genetic differentiation seem to be uncommon when comparing populations between North Africa and the Iberian Peninsula, as the Strait of Gibraltar constitutes a major barrier to gene flow even in flying species such as birds (Saetre *et al.*, 2001; Salzburger *et al.*, 2002; Broderick *et al.*, 2003) and bats (Castella *et al.*, 2000; Juste *et al.*, 2004).

Assignment tests, as well as gene flow estimates, show that Tabernas is the main source of exchange of birds in the Iberian Peninsula. It has been suggested that the spread of the trumpeter finch in the Iberian Peninsula may have been favoured by the current climate change in the Mediterranean region (Carrillo *et al.*, 2007). Considering the increase in temperature and decreased precipitation forecast for the Mediterranean (IPCC, 2007), the spread of the trumpeter finch through the Iberian Peninsula could be favoured further in the near future.

Genetic structure of Iberian peripheral localities

Previous studies have found that source localities have the highest values of genetic diversity, whereas newly colonized populations retain only a part of the total diversity of the source [e.g. greenfinch, *Carduelis chloris* (Merilä *et al.*, 1997); great reed warbler, *Acrocephalus arundinaceus* (Bensch & Hasselquist, 1999)]. It is often assumed that these differences in genetic variability are related to differences in population size (Amos & Harwood, 1998). However, in view of the recent colonization of the Iberian Peninsula, our results only partly fit such expectations. Although the locality sampled within the range of the most likely source population (i.e. Errachidia) had the greatest genetic diversity in most of the estimated parameters, the differences were slight. Thus, in contrast to the predictions made from studies of invasive species by Estoup *et al.* (2004) and Herborg *et al.* (2007), for example, recently established Iberian localities did not have unambiguously lower genetic diversity than the long-established populations in the Canary Islands or North Africa. Therefore, our results show that the maintenance of a continuous gene flow from North African to Iberian populations prevents the decrease of genetic diversity levels in recently established localities (i.e. Iberian sites).

On the other hand, the northernmost breeding locality (Monnegre) exchanges individuals with the rest of the sites studied (less than half of the birds trapped there were assigned to Monnegre) and undergoes wide yearly fluctuations and even temporary extinctions (López-Iborra *et al.*, 2006). These results seem to fit a pattern of local extinctions and recolonizations from neighbouring localities in which a metapopulation system is maintaining Monnegre over time (Hanski, 1998). High inbreeding coefficients at Iberian sites might be the result either of a metapopulation structure, or of having sampled individuals at one sampling site originating from several different populations. Differentiation patterns should vary over time as a consequence of repeated extinctions and recolonizations (Hanski, 1998; Beebee & Rowe, 2004). Therefore, long-term monitoring of gene flow and more detailed reproductive information are necessary to confirm the existence of a metapopulation structure.

Seasonal movement among Ibero-African localities

The assignment tests made from our genetic data show that birds from the rest of the Ibero-African sites strongly contribute to the two out-of-breeding concentrations of trumpeter finches studied here (i.e. Gorafe and Cabo de Gata). Cabo de Gata is a wintering area receiving individuals from other Iberian localities (mostly from the largest breeding population in Tabernas) as well as from Africa. Carrillo *et al.* (2007) have suggested a parallel between the creation of new winter quarters and the advance of breeding areas. Thus, the establishment of birds in new winter quarters in south-eastern Spain could have enhanced trumpeter finch expansion in the Iberian Peninsula, as described for some other expanding bird species [penduline tit, *Remiz pendulinus* (Valera *et al.*, 1993); great cormorant, *Phalacrocorax carbo* (Volponi, 1999)]. A similar process, that is, previous, sporadic occurrence of birds out of the breeding season in new areas preceding breeding in those areas (Valera *et al.*, 1993), could account for the founding of new breeding places in the Iberian Peninsula. For instance, Gorafe, where breeding has only recently been recorded, is a common summer locality for juveniles (Fernández-Ordóñez & Pérez-Contreras, 2006). Natal dispersal is more common than that of adults (Greenwood & Harvey, 1982), and finally settling in a permanent breeding area often takes place during the juvenile period (especially in short-lived birds, for example Van den Bosch *et al.*, 1992). Therefore, we suggest that the current Ibero-African (mostly Iberian) breeding localities contribute to the out-of-breeding summer juvenile concentrations, which gradually turn into new breeding sites, and this could well be the process behind trumpeter finch breeding range expansion in the Iberian Peninsula. The pattern of movements supported by our data for this species could also be representative of some other North African species expanding northwards. Such expansion may become frequent in the present scenario of climate change (Parmesan *et al.*, 1999; Valiela & Bowen, 2003).

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