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RESEARCH ARTICLE

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Human decimation caused bottleneck effect, genetic drift, and inbreeding in the Canarian houbara bustard

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Abstract

An endangered subspecies of the African houbara bustard, the Canarian houbara (*Chlamydotis undulata fuertaventurae*), is endemic to the Canary Islands off southern Morocco (Lanzarote, Fuerteventura, and La Graciosa islands). This population decreased over the last centuries because of hunting and egg collection, and was close to extinction in Lanzarote around the middle of last century. Later, the species recovered because of hunting bans, but in Fuerteventura a significant decline has again occurred in the last decades and houbaras are on the brink of extirpation on that island. We describe the genetic characteristics and recent evolutionary history of this subspecies to provide essential information for the evaluation of the conservation actions implemented and for the development of new measures to prevent further declines and local extirpations. We amplified microsatellite loci to infer genetic variability, population structure, and gene flow. The subspecies exhibited relatively high genetic variability but reduced heterozygosity. In spite of high gene flow among locations and islands, we identified 2 genetic units: 1 comprising La Graciosa and Fuerteventura islands, and the other restricted to Lanzarote. We detected genetic bottlenecks and subsequent inbreeding in both units, with a reduced effective number of

alleles in Lanzarote compared to Fuerteventura-La Graciosa. This genetic structure may be explained by human-induced historical population declines and an associated bottleneck effect, particularly in Lanzarote. Conservation measures should aim to recover the houbara population of Fuerteventura, improving survival of adults and juvenile productivity, and to ensure that genetic flow continues among breeding locations and islands to recover the original population structure (an unique genetic unit over the range of the species) and prevent further genetic deterioration, which could lead to extirpation of this endemic subspecies.

KEYWORDS

bottleneck effect, Canary Islands, *Chlamydotis undulata fuertaventurae*, gene drift, inbreeding, islands, population genetics

Endemic species are typically prone to extinction because of attributes that may hinder their ability to adapt to the environment, such as limited geographic range, small population size, and reduced genetic diversity (Işik 2011). Genetic diversity is the basis for evolutionary change because it allows populations to evolve in response to environmental changes (Frankel and Soulé 1981), so any reduction in genetic diversity may threaten the survival of a population. This may be particularly important for species living on islands because they have higher extinction rates when their genetic variability is reduced (Frankham 1998). Genetic variability is the result of mutation rate, selection, genetic drift, and gene flow (Bohonak 1999), and the study of genetic variability and gene flow among populations is important for the conservation of a species (Cassin-Sackett et al. 2019), especially in the case of island endemics (Kearns et al. 2022).

The Canarian subspecies of African houbara bustard (*Chlamydotis undulata fuertaventurae*; bustard) is endemic to the Canary Islands, with distribution limited to the eastern islands (Fuerteventura, Lanzarote, and La Graciosa) and an occasional occurrence in Lobos (Martín and Lorenzo 2001). In the past it was also present in Gran Canaria (Meade-Waldo 1893, Martín and Lorenzo 2001) and there is evidence indicating that it inhabited Tenerife (Collar 1983, Rando 1995). Following paleontological evidence, the Canarian archipelago was colonized by Moroccan houbara bustards (*C. u. undulata*) >130,000–170,000 years ago (Ancochea et al. 1990, Rando 1995), although according to mitochondrial DNA analysis, both African subspecies diverged genetically around 20,000–25,000 years ago (Idaghdour et al. 2004). The Moroccan houbara bustard is in northern Africa, from Mauritania to the Nile Valley, whereas the MacQueen's bustard (*C. macqueenii*) is distributed between the eastern part of the Nile Valley and Mongolia (del Hoyo et al. 2018, BirdLife International 2021). Like other species of the bustard family, houbaras breed in leks, with males displaying at their territories and females visiting them for mating (Hingrat and Saint Jalme 2005). Once the breeding season is over, more than one third of males and females perform seasonal movements within each island (Abril-Colón et al. 2022), and fly between islands, which could represent natal dispersal movements (Alonso et al. 2022*a*). The Canarian houbara bustard is classified as globally endangered (BirdLife International 2021), after a population decline over the nineteenth and twentieth centuries due to hunting and egg collection (Webb et al. 1842, Meade-Waldo 1889, Cabrera y Diaz 1893, Collar 1983), and more recently due to habitat destruction caused by human activities and mortality from collisions with power lines, aerial telephone lines, and roadkills (Lorenzo 2004, Ucero et al. 2021). In Fuerteventura, where a significant reduction in houbara numbers has occurred in the last decades (Schuster et al. 2012, Ucero et al. 2021), habitat loss has been estimated at around 13% for 1996–2011, and a predicted additional 20–28% loss by 2025 (Banos-González et al. 2016). Lanzarote, in

contrast, represents the subspecies' stronghold, with approximately 80% of the population (Alonso et al. 2020, Ucero et al. 2021).

Following the bustard hunting ban in 1971, several conservation measures were proposed to prevent further demographic declines (Lorenzo 2004). But no studies on the bustards' genetic diversity and structure, gene flow, and other relevant parameters of population genetics have been conducted. The scarce genetic data that have been published were framed within studies focusing on the Moroccan bustard or the MacQueen's bustard and were limited to phylogenetic contexts (Idaghdour et al. 2004, Pitra et al. 2004, Lesobre et al. 2010, Korrida et al. 2012).

We describe the population genetic structure of the houbara subspecies endemic to the Canary Islands. Previous studies in this area showed genetic differentiation among islands in other bird species (Illera et al. 2020), but potential genetic relationships between Lanzarote and Fuerteventura islands have been detected (Kvist et al. 2005). In relation to the genetic population structure, we tried to capture the signal of gene flow, as it determines such structure (Mapel et al. 2021). Canarian houbara bustards have the ability to fly between islands (Alonso et al. 2022*a*), but the question arises as to whether there is genetic exchange between island populations. Our objective was to provide genetic information necessary for the management and conservation of this endangered subspecies. This includes a description of its genetic variability including inbreeding and past bottleneck presence, structure, and gene flow.

STUDY AREA

This study was carried out in 2016–2021, and included the whole distribution of the Canarian subspecies of the African houbara bustard, which covers the 3 easternmost islands of the Canary archipelago (Lanzarote, Fuerteventura, and La Graciosa; Figure 1). The Canary Islands belong politically to Spain, but they are located in the Atlantic Ocean, 140 km west of the northwestern coast of Africa. Lanzarote has a surface of 846 km^2. The climate is subtropical-desert (Köppen climate classification; Köppen 1918) but softened by the influence of the cold Canary Current of the ocean, and the almost permanent trade winds from the northeast. The average rainfall is approximately 110 mm/year, concentrated in 15–20 precipitation days typically in December–February. Summers are dry, with <1 mm of precipitation in June–August. Average temperatures are 18°C in winter (Dec–Mar) and 25°C in summer (Jun–Sep), with intermediate values in autumn and spring. The island has a volcanic origin, with abrupt relief including the maximum altitude of 671 m in the Famara massif in the north, and deep ravines and cliffs in Ajaches, a second mountain massif in the south. The last eruption of Timanfaya (1730–1736) covered some 200 km^2 with lava in the west. The other half of the island, where houbaras occur, shows a weathered relief and smoothed topography, with some sand semi-desert areas southwest of the Famara massif, which consist on sandy or stony terrain. The dominant vegetation consists of xerophytic shrubs (gorse [*Launaea arborescens*], saltwort [*Salsola vermiculata*], box-thorn [*Lycium intricatum*], seablite [*Suaeda* spp.], spurge [*Euphorbia* spp.]), partly modified by goat grazing and farming activities in some areas of the islands. The dominant fauna includes steppe birds such as the cream-colored courser (*Cursorius cursor*), stone curlew (*Burhinus oedicnemus insularum*), Berthelot's pipit (*Anthus bertelottii*), and Barbary partridge (*Alectoris barbara koenigi*), reptiles such as the Atlantic lizard (*Gallotia atlantica*) and Canary wall gecko (*Tarentola angustimentalis*), and few mammals such as the Canarian shrew (*Crocidura canariensis*). La Graciosa, an island located 1 km north of Lanzarote, has a surface area of 29 km^2 and physiographic and relief characteristics, and flora and fauna similar to those of Lanzarote. The environmental management of this island is the responsibility of the National Parks Autonomous Organization. The island of Fuerteventura is located 11 km south of Lanzarote and 97 km from the African coast. With a surface area of 1,660 km^2, it is the largest of these islands and the second largest in the Canary archipelago. The climate is drier and its aridity index is higher than Lanzarote's, with 98 mm annual rainfall and an mean annual temperature of 21.1°C. It is also under the influence of the trade winds, which are strongest in spring and summer. It is the oldest island of the archipelago, and is characterized by the presence of extensive plains caused by erosive processes. In the central area is the Betancuria massif, with a maximum altitude of 762 m, and to the south is the Jandía peninsula, with a maximum altitude of

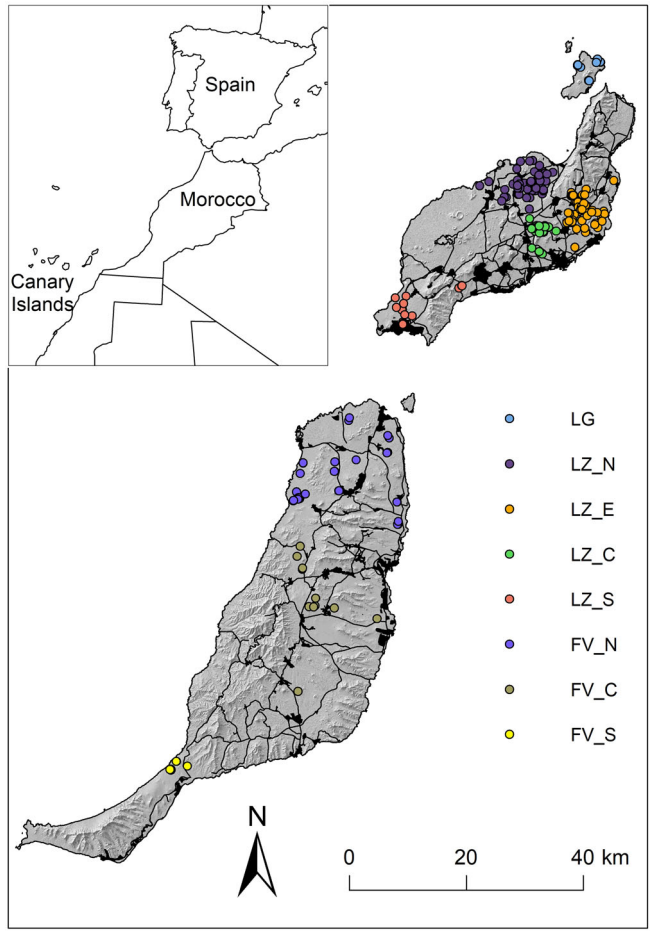

FIGURE 1 African houbara bustard sampling sites, Canary Islands, Spain, 2016–2021, and the 8 sampling locations defined in the study (La Graciosa [LG], Lanzarote [LZ], Fuerteventura [FV]). N = North, C = Center, E = East, S = South. Black lines are roads.

813 m. The vegetation is very sparse, with the most common species being gorse, Canary Island candle plant (*Kleinia neriifolia*), balsam spurge (*Euphorbia balsamifera*), and Canarian spurge (*E. canariensis*). Cereal and vegetable farming, which in the past represented the economic base of these islands, now occupies only a few small areas, with some fields under irrigation, particularly in the center of Lanzarote. Large parts of the 3 islands are now protected areas. Urban areas and infrastructure are mainly located on the eastern coast of the islands.

METHODS

Sample collection

Between November 2016 and January 2021, we collected 214 samples (108 feathers and 106 feces) from all sites where houbaras were spotted during surveys of the breeding populations on the islands (Alonso et al. 2020, Ucero et al. 2021). We collected samples immediately after observing the birds. Because we collected nearly all samples during the breeding season without repeating collection sites in different years, and both sexes are very faithful to their display and nesting

sites within and between years (Abril-Colón et al. 2022), the chances of collecting repeated samples from the same individuals were negligible. To be sure that we minimized repeated samples of the same birds, we searched for matching genotypes and discarded 5 samples from Fuerteventura. We collected the samples as fresh as possible, discarding excessively dry or degraded samples, and placed them in individual plastic bags, which we then conserved in a freezer (−20°C) for genetic analysis. Before collection, we sexed individuals using their distinctive plumage (Glutz et al. 1973, Cramp and Simmons 1977) and then confirmed sex through molecular analyses. In addition to the samples collected from the ground, we plucked contour feathers from birds captured for radio-tracking (33 males, 21 females). We collected 268 samples: 194 in Lanzarote, 60 in Fuerteventura, and 14 in La Graciosa (Table S1, available in Supporting Information). To calculate genetic parameters at a more detailed geographical scale, and based on a visual inspection of the aggregation of all samples and on the species' distribution (Alonso et al. 2020, Ucero et al. 2021), we divided the sample into 8 locations based on discontinuities in the species' distribution, such as the sea straits between the islands, mountains, volcanic landscapes not used by the species, or urban areas with infrastructures acting as dividers between patches used by houbaras (Figure 1). Sample sizes for these 8 locations varied between 11 (Fuerteventura South) and 64 individuals (Lanzarote North; Table 1, Table S1).

DNA extraction and microsatellite amplification

We extracted DNA from samples using the commercial kit Blood and Tissue DNeasy (Qiagen, Düsseldorf, Germany). In the case of the feathers, we followed the kit protocol except for AL buffer and EtOH (i.e., we employed 300 µl instead 200 µl); we used 50 µl of AE buffer for the final elution. In the case of feces, we used an improved method for extracting degraded DNA samples from birds (Alda et al. 2007), using the columns and buffers of the above-mentioned kit. We employed flow cabins, filter pipette tips, and separate rooms and equipment depending on work (i.e., pre- and post- polymerase chain reaction [PCR] experiments) for laboratory tasks, following the protocols of the molecular laboratory of the National Museum of Natural Sciences, Madrid, Spain, where DNA analytical work is successfully done by highly qualified technicians.

We amplified 22 microsatellite loci originally designed for Moroccan bustards (Chbel et al. 2002). The PCR reaction mixtures (including positive and negative controls) followed original MyTaq DNA Polymerase kit (Bioline – Ecogen, Madrid, Spain) protocols, and PCR conditions included 94°C for 2 minutes followed by 40 cycles at 94°C for 20 seconds, annealing temperature for 20 seconds (we kept 9 microsatellite loci for analyses; Table S2, available in Supporting Information), 72°C for 60 seconds, and a final extension of 72°C for 10 minutes. We amplified each microsatellite individually (no multiplexing). We visualized PCR amplifications in 2% agarose gels (SYBR^{TM} Safe, Thermo Fisher, Waltham, MA, USA) and sequenced PCR products using an ABI PRISM 3130 sequencer (Secugen S.L., Madrid, Spain). We then genotyped microsatellite peaks with GeneMapper 4.0 (Applied Biosystems, Waltham, MA, USA) and binned alleles with Tandem 1.09 (Matschiner and Salzburger 2009). We independently repeated all samples after extraction 3 times and read genotypes 2 independent times in each of those repetitions.

We determined sex for all individuals with the P2 and P8 primers (Griffiths et al. 1998). We used the same PCR templates as those of microsatellite loci; PCR conditions were 94°C for 4 minutes followed by 40 cycles of 94°C for 20 seconds, 53°C for 30 seconds, and 72°C for 45 seconds, with a final extension of 72°C for 7 minutes. We ran PCR products in a 2% agarose gel for 75 minutes (100 V), which led to different band patterns for males and females (validated with known-sex individuals).

Statistical analyses

We tested the presence of null alleles and large allele dropout in the dataset with Microchecker version 2.2.3 (van Oosterhout et al. 2004). We also tested linkage disequilibrium among loci, using Genepop (Raymond and Rousset

TABLE 1 Number of alleles per locus (Na), effective number of alleles per locus (Eff_Na), and observed (H_O) and expected heterozygosity (H_E) of the 9 amplified microsatellite loci studied in the Canarian houbara, in the 8 sampling locations (LG = La Graciosa, LZ = Lanzarote, FV = Fuerteventura; N = North, C = Center, E = East, S = South) defined in the Canary Islands, Spain, 2016–2021. An asterisk (*) indicates departure from Hardy–Weinberg Equilibrium at a significant *P*-value after sequential Bonferroni correction for multiple testing (Rice 1996).

		Microsatellite locus												
Location	***n***	**BusA18**	**BusA22**	**BusA29**	**BusA113a**	**BusA120**	**BusA210**	**BusD117**	**BusD118**	**BusD119**	**Na**	**Eff_Na**	**H_O**	**H_E**
All	263	10	24	13	30	20	25	17	15	12	18.44	3.34	0.46	0.70
LG	14	5	8	6*	5	3	6	5	5	3	5.11	4.01	0.59	0.72
LZ_N	64	6	10*	5	16*	14*	13	9*	7*	7	9.67	3.47	0.44	0.64
LZ_C	32	4	5*	4	11*	12*	6	4	7	6	6.56	3.54	0.46	0.61
LZ_E	66	5	13*	5	16*	15*	8	9*	9*	7	9.67	3.58	0.44	0.65
LZ_S	27	4	6*	4	11*	7	8	7	6	6	6.56	2.89	0.50	0.61
FV_N	36	8	15*	10*	9	11	17*	8	11	6	10.56	4.99	0.49	0.78
FV_C	13	5	5	6	4	6	7	4	6*	4	5.22	3.37	0.39	0.68
FV_S	11	6	4	3	4	5	7	6	6	5	5.11	3.63	0.53	0.71

1995). We measured the genetic variability as the number of alleles per locus (Na), the effective number of alleles per locus (Eff_Na), the observed and expected heterozygosities (H_O and H_E, respectively), and the inbreeding coefficients (F_{IS}) with GenoDive 2.0b25 (Meirmans and van Tienderen 2004). We also used the same software for calculating deviations from Hardy–Weinberg equilibrium, and fixation indexes (F_{ST}), with their associated *P*-values after sequential Bonferroni correction for multiple testing (Rice 1996).

We inferred the population structure with a Bayesian probability test using the program STRUCTURE version 2.3.4 (Falush et al. 2003) with the following settings: a model of admixture and independent allele frequencies, 10 different runs of 10^5 steps (10% burn-in) for each number of genetic units (*K*; from 1 to 8 because 8 locations were sampled in the 3 islands). We determined the number of genetic units (*K*) present in the dataset with Structure Selector (Li and Liu 2018) using the 2 available methodologies: Puechmaille (2016) and Evanno et al. (2005). With the first methodology (Puechmaille 2016), we analyzed all the 4 estimators available (MedMedK, MedMeaK, MaxMedK, MaxMeaK) using a threshold value of 0.8 because the larger the threshold value (between 0.5 and 0.8), the more stringent the definition of a spurious cluster is and the larger the differentiation between 2 subpopulations needs to be for them to be considered to belong to different clusters. With the Evanno et al. (2005) methodology, deltaK values detect the level of structure in the dataset, which is based on the rate of change in the log probability of data between successive *K* values. In addition, as unbalanced sampling can potentially affect STRUCTURE results (Puechmaille 2016, Meirmans 2019), we repeated analyses by subsampling the largest samples by dividing the 2 largest sampling locations (Lanzarote North and Lanzarote East; Table 1) into 4 new locations with half of the samples in each of them.

We measured gene flow as the number of migrants per generation (*Nm*) among locations and among genetic units with Genepop (Raymond and Rousset 1995). We tested the potential for drastic reductions in population sizes to produce genetic bottlenecks with Bottleneck version 1.2.02 (Piry et al. 1999); we adjusted settings for microsatellite loci as proposed by Piry et al. (1999): 2-phase model (TPM; variance = 12, proportion of stepwise mutation model = 95%) and Wilcoxon signed-rank test (10,000 iterations). Significant *P*-values (<0.05) in these analyses indicate the presence of recent bottlenecks.

RESULTS

Of the 22 microsatellite loci developed for houbara bustard by Chbel et al. (2002), we analyzed 9 after PCR amplification (Table 1): BusA18, BusA22, BusA29, BusA113a, BusA120, BusA210, BusD117, BusD118, and BusD119 (BusA101 and BusA112 did not amplify, and the rest resulted in bad or inconsistent peak patterns). Genotyping success on these loci was 90.92% in feathers and 73.31% in feces (Table S3, available in Supporting Information) and we did not find large allele dropout in the dataset, but the presence of null alleles was suggested by Microchecker software for 7 of the 9 loci (all but BusA18 and BusD119). Between both sample

TABLE 2 Genetic variability of males and females, and of feather and feces samples of Canarian houbara collected in the Canary Islands, Spain, 2016–2021. *n* = number of individuals, Na = mean number of alleles per locus, Eff_Na = effective number of alleles per locus, H_O = observed heterozygosity, and H_E = expected heterozygosity.

Population	*n*	Na	Eff_Na	H_O	H_E
Females	68	9.78	3.65	0.50	0.66
Males	133	12.78	3.69	0.44	0.67
Feathers	161	13.56	3.87	0.47	0.68
Feces	102	12.88	3.59	0.41	0.70

types (Table 2), the number of alleles per locus ($t = -0.31$, $P = 0.76$), the effective number of alleles per locus ($t = -0.37$, $P = 0.71$), the observed heterozygosity ($t = -0.56$, $P = 0.58$), and the expected heterozygosity ($t = 0.38$, $P = 0.71$) were similar, so we dismissed potential errors caused by sample type. We identified matching genotypes in 3 individuals of Fuerteventura (5 samples); thus, in these cases we used only 1 sample/bird in analyses, which reduced our sample from 268 to 263 (161 feathers and 102 feces): 189 from Lanzarote, 60 from Fuerteventura, and 14 from La Graciosa. We only found l linkage disequilibrium in 2 cases: BusA22/BusD117 and BusA18/BusA113a. Two of the loci (Table 1) were not in Hardy–Weinberg equilibrium in ≥50% of the locations (BusA22 in 5 locations, BusA113a in 4 locations). Thus, we deleted these loci from additional analyses in 2 different additional datasets, 1 of them comprising 8 loci (the 9 loci of the dataset except BusA22) and another comprising 7 loci (the 9 loci of the dataset except BusA22 and BusA113a). As BusA22 and BusA113a were loci affected by the above-mentioned linkage disequilibrium, these 7- and 8-microsatellite loci datasets did not include any locus affected by linkage disequilibrium. Results were similar with all 3 datasets (Tables S4–S9, available in Supporting Information); thus, we only present and discuss the dataset including 9 microsatellite loci.

The mean number of alleles per locus was between 5.11 (La Graciosa) and 10.56 (Fuerteventura North) and effective number per allele was between 2.89 (Lanzarote South) and 4.99 (Fuerteventura North; Table 1). The observed heterozygosity was smaller than expected in all sampling locations (analysis of variance, $F = 19.17$, $P < 0.01$).

We could determine the sex by molecular procedures in all captured birds plus a number of feathers and feces, totaling 201 individuals (76.4% of all samples; 133 males, 68 females). In all cases, genetic sex corresponded with sex determined morphologically. The genetic variabilities calculated for males and females were similar (Table 2), with no differences in Eff_Na ($t = 0.04$, $P = 0.98$), H_O ($t = 0.51$, $P = 0.61$), or H_E ($t = 0.17$, $P = 0.87$).

Fixation index values (F_{ST}; Table 3) indicated genetic population differentiation between La Graciosa island and all locations of Lanzarote (F_{ST} values ranged between 0.053 and 0.093). In contrast, they did not show genetic differences between La Graciosa and any Fuerteventura population (F_{ST} values ranged between −0.006 and 0.015). Genetic differentiation was also significant between all locations of Lanzarote and 2 Fuerteventura locations (Fuerteventura North and Fuerteventura Center) but not compared with the southern population of Fuerteventura (Fuerteventura South). Within islands, there was no genetic differentiation among locations (F_{ST} values ranged

TABLE 3 Fixation indexes (F_{ST}; above diagonal) and number of migrants per generation (*Nm*; below diagonal) among sampling locations of Canarian houbara (LG = La Graciosa, LZ = Lanzarote, FV = Fuerteventura; N = North, C = Center, E = East, S = South) in Spain, 2016–2021. An asterisk (*) indicates a significant *P*-value after sequential Bonferroni correction for multiple testing (Rice 1996).

	Location							
Location	**LG**	**LZ_N**	**LZ_C**	**LZ_E**	**LZ_S**	**FV_N**	**FV_C**	**FV_S**
LG		0.066*	0.093*	0.061*	0.053*	0.015	0.008	−0.006
LZ_N	2.599		0.008	0	0.007	0.088*	0.055*	0.028
LZ_C	1.252	7.072		0.003	0.02	0.085*	0.047*	0.053
LZ_E	1.939	9.406	6.872		0.01	0.074*	0.046*	0.023
LZ_S	1.671	6.876	4.408	7.488		0.106*	0.079*	0.033
FV_N	2.484	4.034	2.544	3.918	2.603		0.015	0.019
FV_C	0.623	2.014	1.360	1.492	1.163	2.169		−0.009
FV_S	1.004	2.964	1.504	2.926	2.623	2.098	1.135	

between −0.009 and 0.008). We detected >1 migrant per generation among all population pairs in all comparisons except between La Graciosa and Fuerteventura Center (Table 3).

According to these F_{ST} results among locations, STRUCTURE software inferred the presence of 2 genetic units in the dataset, one of them comprising La Graciosa and Fuerteventura islands, and the other covering Lanzarote (Figure 2; Figures S1, S2, available in Supporting Information). The presence of these 2 units was confirmed following Puechmaille (2016) and Evanno et al. (2005) criteria, and was not affected by unbalanced sampling (Figures S3–S5, available in Supporting Information). When considering these 2 genetic units, F_{ST} values showed high genetic differentiation among them ($F_{ST} = 0.069$, $P < 0.01$), and the number of migrants among these units was high ($Nm = 7.37$). The genetic variability of the inferred genetic units in terms of observed (and reduced) heterozygosity was similar between them (Table 4), but the effective number of alleles per locus was smaller in Lanzarote than in the genetic unit composed by La Graciosa and Fuerteventura

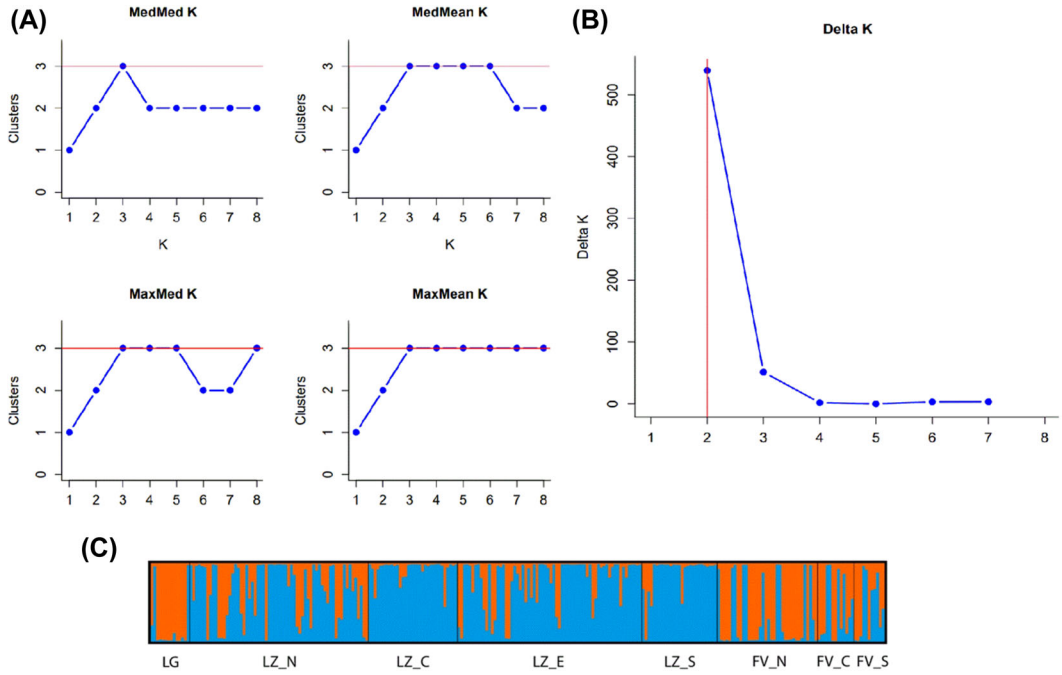

FIGURE 2 Identification of the genetic units (*K*) including the 8 different Canarian houbara sampling locations from La Graciosa (LG), Lanzarote (LZ), and Fuerteventura (FV), Spain, 2016–2021, and 9 microsatellite loci: A) Puechmaille (2016) estimators (MedMedK, MedMeaK, MaxMedK, and MaxMeaK), B) Evanno et al. (2005) deltaK values, C) STRUCTURE output showing 2 genetic units. N = North, C = Center, E = East, S = South.

TABLE 4 Genetic bottleneck presence (B = *P*-value for Bottleneck version 1.2.02 software) and inbreeding coefficients (F_{IS}, $^*P < 0.05$) of the 2 genetic units inferred for Canarian houbaras in the Canary Islands, Spain, 2016–2021. Na = mean number of alleles per locus, Eff_Na = effective number of alleles per locus, H_O = observed heterozygosity, and H_E = expected heterozygosity.

Population	Na	Eff_Na	Ho	He	B	F_{IS}
LG + FV	13.00	5.19	0.49	0.80	0.002*	0.39*
LZ	14.00	3.58	0.45	0.65	0.002*	0.31*

($t = -2.05$, $P = 0.057$). We detected the presence of genetic bottlenecks and inbreeding in both genetic units (Table 4).

DISCUSSION

This study describes the genetic structure and dynamics of the insular subspecies of African houbara, which is endemic to the Canary Islands. The number of samples used ($n = 263$) represents nearly half of the estimated population of this endangered subspecies and covered its entire geographic range (Palacín and Alonso 2020, Ucero et al. 2021), so our sampling should have captured most of its current genetic diversity. There was similar genetic variability in both sexes, which suggests that this parameter was not influenced by the lek mating system (Hingrat and Saint Jalme 2005), or any possible sex-differential dispersal movements, despite the skewed sex ratio in the population (Alonso et al. 2020). The genetic variability was relatively high, reaching values similar to those reported for the Moroccan bustard (Lesobre et al. 2010) and the MacQueen's bustard (Pitra et al. 2004). It was also similar to values in other species of the bustard family (e.g., various bustard populations in Spain and central Europe; Horreo et al. 2014, 2016). This is a relevant and positive finding from a conservation point of view because erosion of genetic variability represents a serious threat for the survival of species (Amos and Balmford 2001).

From STRUCTURE analyses and from fixation indexes (FST) among sampling locations and between STRUCTURE-derived clusters, we inferred the presence of 2 different genetic units: 1 composed of birds from La Graciosa and Fuerteventura, and 1 in Lanzarote. This led us to disregard genetic differences produced by local adaptation because habitat conditions in La Graciosa are more similar to those found in some areas of Lanzarote than to those found in Fuerteventura. We did not detect genetic differences among sampling locations within the same island, in agreement with the high gene flow among them, which was a lot higher than 1 migrant/generation and could be considered enough for population homogenization (Wang 2004). The presence of genetic differences between both genetic units (Lanzarote vs. Fuerteventura-La Graciosa) is striking, given the high gene flow between them (Table 3). Such gene flow between both genetic units inferred from genetic data was supported by an observation of a radio-tagged male flying from La Graciosa to Fuerteventura in what we interpreted might have been a natal dispersal movement if that individual had not died after the displacement (Alonso et al. 2022*a*). There are 2 possible explanations for these apparently contradictory results. First, the contemporary gene flow between genetic units has not lasted long enough to dilute past genetic differences. This would imply that, as differences do exist between genetic units, gene flow among them must have been limited in the past. The possible barrier effect of sea straits between islands existed over many thousands of years, but the genetic unit of Lanzarote is geographically located in the middle of the 2 islands comprising the other genetic unit (La Graciosa-Fuerteventura). Nothing points to recent changes in gene flow patterns among the 3 islands as the cause of the genetic pattern found here.

The second explanation to genetic differences (despite high gene flow among genetic units) could be the presence of an initially unique genetic unit over all 3 islands, and a subsequent appearance of the second genetic unit in Lanzarote through genetic drift and a bottleneck effect. This could have occurred because of reductions in population size, as explained below. This would agree with previous studies on Moroccan bustards where genetic drift was proposed as a possibility in the Canarian subspecies (Idaghdour et al. 2004, Korrida and Schweizer 2014) and occurred in other endemic island birds (Shultz et al. 2016). Small populations are prone to suffer genetic drift and bottleneck effects (Masel 2011), and this could be the cause of current genetic differences between Lanzarote and the other 2 islands. Several facts support this interpretation. First, the reduced effective number of alleles in Lanzarote in comparison with the other genetic unit (La Graciosa-Fuerteventura) supports a more pronounced bottleneck in Lanzarote. Second, the reduced heterozygosity and inbreeding values in Lanzarote are clear signs of a bottleneck effect (de Meeûs 2018), and could be explained by independent genetic drift in subpopulations (Garnier-Géré and Chikhi 2013). Third, the lack of a positive correlation between genetic and geographic distances

(Lanzarote represents an independent genetic unit, in spite of being located between La Graciosa and Fuerteventura), is a sign of genetic drift (Jordan and Snell 2008). And finally, historical records of the abundance of houbaras in the islands also support the interpretation that current genetic differences between Lanzarote and the other 2 islands could have been caused by genetic drift and bottleneck effects following a drastic population reduction in Lanzarote. While available chronicles of the conquerors of the Canary Islands in the fifteenth century report abundant bustards in the eastern islands of the archipelago (P. Bontier and J. Le Verrier 1402–1404, cited in Collar 1983), most ornithological literature from the nineteenth and early twentieth centuries report a much higher abundance of the species in Fuerteventura than in Lanzarote where it was seen in much smaller numbers mostly in the south (Webb et al. 1842; Meade-Waldo 1889, 1890; von Thanner 1905; Polatzek 1909; Bannerman 1914). These authors also reported on houbara hunting, female capture at nest with snares, and egg collection as regular activities, the latter apparently being the most frequent. For example, the species had been decimated in the recent past as a consequence of egg collection (>100 eggs in a single season; von Thanner 1905, Polatzek 1909). Moreover, the higher human population in Lanzarote could have been a possible cause of the lower density of houbaras there compared to Fuerteventura (Polatzek 1909). By the mid-twentieth century, houbaras were already rare on both islands but still seen in Lanzarote (Hemmingsen 1958, Hüe and Etchécopar 1958, Bannerman 1963), where the population could have even started to increase in the 1960s (Trotter 1970). The International Council for Bird Preservation 1979 expedition to the Canaries confirmed the scarcity of the species, and the lower numbers in Lanzarote (only 7 birds counted, ~20 estimated) compared to Fuerteventura (42 birds seen, ~80–100 estimated; Lack 1983). The expedition participants suggested that numbers had possibly not varied much since the early years of the twentieth century.

The ornithological literature summarized above makes it quite clear that the Canarian houbara bustard population in Lanzarote must have been close to extirpation, probably because of human overexploitation at the turn of the twentieth century, when it likely collapsed to a few birds, causing the genetic bottleneck and consequent reduced variability identified in this study. As for Fuerteventura, the larger size of this island and its lower human population prevented such a dramatic reduction, and houbara numbers probably did not decline to <100 individuals because of refugia far from human habitations (Collar 1983, Lack 1983). The demographic recovery was boosted by the bustard hunting ban in 1971, and in Lanzarote the population increased to 440–452 birds (Alonso et al. 2020). In Fuerteventura, the much more arid, almost desert-like conditions and the progressive abandonment of traditional agriculture probably represented 2 of the main factors preventing a demographic recovery similar to that of Lanzarote and the species is now seriously threatened with extirpation on that island, with only 100 birds (Ucero et al. 2021). Surveys in the last 6 years confirm that juvenile productivity in Fuerteventura is significantly lower than in Lanzarote, and below the minimum for population sustainability (Alonso et al. 2022*b*).

The reduced heterozygosity in the genetic datasets is relatively common in endangered endemic island birds (Callicrate et al. 2014, Campana et al. 2020). It could be produced either by a bottleneck effect as proposed above, or by different methodological factors, such as the used of feces, sampling errors, or presence of null alleles. In this case, all of the methodological factors were rejected as the origin of the mentioned reduced heterozygosity (Text S1, available in Supporting Information).

In summary, the Canarian houbara bustard shows a relatively high genetic variability with 2 genetic units: 1 in La Graciosa and Fuerteventura islands and the other in Lanzarote. Genetic analyses suggest that there are 7 migrants/generation, which should guarantee a homogenization of both units into a single one in the not too distant future. This genetic structure is likely the result of past demographic reductions, especially in Lanzarote where the species was on the brink of extinction around the turn of the twentieth century, followed by genetic drift or a bottleneck effect on that island. Owing to such population reductions, Canarian houbara bustards suffered genetic bottlenecks and subsequent inbreeding on both main islands (Lanzarote and Fuerteventura), though these were more marked in Lanzarote, where there were fewer birds by 1980 after human decimation. Among other factors (Ucero et al. 2021), differences in habitat quality between both islands must have been a key factor explaining their different demographic evolution after these bottlenecks. Fuerteventura is a much more arid island and does not

have the irrigated farmland areas of Lanzarote in mosaic with shrubland where houbaras aggregate to look for food in summer, the most critical season of the year (Abril-Colón et al. 2022).

Moreover, the traditional farming system designed to retain rainfall and run-off water in Fuerteventura, which provided important food resources for houbaras in summer, has gradually ceased to be cultivated since the 1970s and is almost completely abandoned (González-Morales 1986, Medina 1999). All this has led to a continuous demographic decline in Fuerteventura and houbaras are now on the brink of extirpation on that island.

MANAGEMENT IMPLICATIONS

The disappearance of the houbara population on Fuerteventura (La Graciosa-Fuerteventura) would represent an irreversible loss of genetic diversity and would leave the subspecies with only the genetic unit with the lowest current genetic variability (Lanzarote). It is thus urgent to promote the survival and enhance the breeding condition of adults by conserving gorse shrubland. It would be advisable to plant alfalfa plots, and restore traditional agricultural fields to provide food for houbaras in summer. Second, it would be necessary to guarantee protection against human disturbances and nest or chick predators in the main reproductive nuclei of Canarian houbara on this island. Third, measures are needed to guarantee connectivity among breeding locations within and between islands, such as preventing further fragmentation of the habitat and burying at least the most dangerous aerial power and telephone lines to reduce collision mortality of migrating and dispersing birds.

If all recommended conservation measures are implemented, the current high gene flow among breeding nuclei within islands and between the 2 genetic units should continue, without losing further genetic diversity and even increasing it on Lanzarote. These measures would potentially lead to a genetic homogenization over the whole range of the species in all 3 islands, thus recovering what was probably the original population structure of Canarian houbara bustards. We therefore propose the management of this subspecies as a single elemental conservation unit. To check that these measures are effective, and to follow the dynamics of this endangered subspecies to ensure its conservation, new genetic sampling is recommended in future years to study changes on its genetic structure and variability and act accordingly.

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CONFLICTS OF INTEREST

The authors declare that there are no conflicts of interest

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the authors but restrictions apply to the availability of these data, which were used under license from the Government of the Canary Islands for the current study, and so are not publicly available. Data will however be available from the authors when the current genetic studies are finished, upon reasonable request and with permission of the Government of the Canary Islands.

ETHICS STATEMENT

Capture and handling of Canarian houbara bustards for radio-tracking purposes and genetic sample collection were authorized and conducted under permissions issued by regional authorities (Viceconsejería de Medio Ambiente, Gobierno de Canarias, license 2015/10584). The methods used comply with the Spanish guidelines for ethical use in animal research (Spanish RD 53/2013). The study adheres to the standard guidelines for the treatment of animals in wildlife research (European directive 2010/63/UE).

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