

Influence of game restocking on the migratory behaviour of the common quail, *Coturnix coturnix*

Ines Sanchez-Donoso¹, José Domingo Rodríguez-Teijeiro²,
Irene Quintanilla¹, Irene Jiménez-Blasco², Francesc Sardà-Palomera^{3,4},
Jesús Nadal⁵, Manel Puigcerver⁶ and Carles Vilà¹

¹Conservation and Evolutionary Genetics Group, Integrative Ecology Department, Estación Biológica de Doñana (EBD-CSIC), Seville, Spain, ²Department of Animal Biology, Faculty of Biology, University of Barcelona, Barcelona, Spain, ³Biodiversity and Animal Conservation Group, Forest Sciences Centre of Catalonia (CTFC), Solsona, Spain, ⁴Catalan Ornithological Institute (ICO), Barcelona, Spain, ⁵Department of Animal Production, ETSEA, University of Lleida, Lleida, Spain and ⁶Department of Experimental Sciences and Mathematics Didactics, Education Faculty, University of Barcelona, Barcelona, Spain

ABSTRACT

Background: The common quail, *Coturnix coturnix*, is a migratory bird hunted extensively across Europe. To satisfy this hunting interest, thousands of farm-reared birds are restocked every year. However, restocked individuals are not common quail but hybrids with domestic Japanese quail, *C. japonica*. Interbreeding between restocked and native birds in the wild allows the entry of alien alleles to the native populations, which could lead to the loss of adaptive phenotypes and behaviours, such as migratory drive. Sedentary individuals may face wintering conditions to which they are not adapted, suffering higher mortality. Some individuals have been observed to remain in northern latitudes during winter.

Question: Does game restocking contribute to the sedentarization of the common quail population?

Method: We sampled 42 quail during the autumn migration and 50 quail during winter in Spain. We genetically analysed them using a set of autosomal microsatellites and also sequenced a fragment of the mitochondrial DNA control region. We evaluated the proportion of admixed quail found and compared it with that previously found in a breeding population.

Results: None of the migratory quail were admixed individuals, although two of them showed introgression of Japanese mitochondrial DNA. Among wintering quail, only three individuals had a genetic composition compatible with a farm origin, while the rest were common quail. Thus, the proportion of admixed quail during winter was not higher than during the breeding season.

Conclusion: Restocking individuals with domestic Japanese quail ancestry is not directly associated with the presence of quail during winter in northern latitudes. The almost complete absence of individuals of farm origin among the migratory and wintering quail populations indicates that the vast majority of the restocked individuals probably die soon after release.

However, the genetic composition of the breeding population has already shown that some survive until the next breeding season and introgress their genes into the wild population.

Keywords: human-mediated changes, hybridization, introgression, migration, sedentarization, wintering.

INTRODUCTION

The common quail (*Coturnix coturnix*) is a small migratory Galliform species with an extensive Palaearctic distribution (Johnsgard, 1988; Del Hoyo *et al.*, 1994). It breeds mainly in cereal crops in Eurasia between March and August, and winters in herbaceous perennial vegetation in semi-arid regions of the sub-Saharan strip (Morel and Roux, 1966; Guyomarc'h, 1992). The common quail has a long tradition as a game species in Southern European countries. Due to its economic importance (Garrido, 2012) and in order to increase the number of individuals available for hunting, large-scale restocking of farm-reared quail is a common practice in some European countries. In Spain, which has Western Europe's largest breeding population (Rodríguez-Teijeiro *et al.*, 2006), restocking generally takes place from the end of the breeding season (around mid-August) to the beginning of the next breeding season. Intensive quail hunting areas have been created, where hunting and restocking are allowed throughout the year; however, these constitute a small proportion of the total land where hunting is allowed in Spain [1.2% in 2011 (MAGRAMA, 2011)]. The number of restocked quail is quite large: in Catalonia (Northeast Spain), where the breeding population is estimated to be between 5000 and 21,000 males (Rodríguez-Teijeiro *et al.*, 2004), more than 56,000 farm-reared quail have been restocked annually between 1990 and 2011 (data from intensive hunting areas; Catalan Department of Agriculture, Farming, Fisheries, Food and Environment), which means that the restocked population is from two to more than seven times larger than the breeding population.

Recent studies have shown that restocked quail are not common quail but hybrids with different degrees of admixture between common quail and domestic Japanese quail, *Coturnix japonica* (Barilani *et al.*, 2005; Amaral *et al.*, 2007; Sanchez-Donoso *et al.*, 2012). It has also been shown that Japanese quail of farm origin interbreed with common quail in the wild, resulting in the introgression of domestic Japanese quail alleles into the common quail gene pool (Sanchez-Donoso *et al.*, 2014). This interbreeding is considered one of the main threats to the conservation of common quail (Perennou, 2009) because it could introduce maladaptive alleles. Japanese quail evolved subject to different selective forces, and life in captivity may have led to a relaxation of natural selective forces while selecting for a completely different set of traits. Consequently, restocked birds are likely to have a genetic composition very different to native common quail.

Intercrossing common quail with restocked admixed farm-reared quail could lead to changes in the migratory behaviour of the local population. Japanese quail lack the migratory drive of common quail and hybrids partially inherit this trait (Derégnaucourt, 2000). Studies of quail in captivity have shown that migratory phenotypes are rare among hybrids (Derégnaucourt *et al.*, 2005a, 2005b). Sedentary quail may suffer reduced viability in the wild because sedentary individuals spend the winter in depleted habitat (harvested cereal cropland), with reduced food resources, increased predation risk, and adverse climatic conditions. Together, these could lead to a higher mortality rate and a potential decrease in quail population density (Rodríguez-Teijeiro *et al.*, 1992; Guyomarc'h, 2003).

Although the majority of the European common quail population migrates at the end of the breeding season, some individuals have been detected during the winter in Europe and North Africa (Caballero Pacho, 1957; Lack, 1986; Fontoura and Gonçalves, 1996; Thévenot *et al.*, 2003; Mur, 2009; Sardà-Palomera *et al.*, 2011). In this study, we wished to determine whether game restocking practices are contributing to the sedentarization of common quail. Using microsatellite genotyping and mitochondrial DNA (mtDNA) analyses, we studied the genetic origin of quail captured during the southward autumn migration to test whether individuals with some degree of admixture with domestic Japanese quail are part of the migratory population. We also analysed the genetic composition of quail hunted during winter in Spain to determine whether the wintering population had a larger proportion of individuals of admixed origin than the breeding population (Sanchez-Donoso *et al.*, 2014).

MATERIALS AND METHODS

Origin and collection of samples

We sampled a total of 92 quail. We captured 42 migratory individuals during the post-breeding migration (18 August to 24 October) of 2009 and 2012 in Garraf Natural Park (north-east Spain) using mist-nets and electronic decoys [for more information on sampling methods, see Rodríguez-Teijeiro *et al.* (2012)]. This park, which is protected, is located close to the Mediterranean coast and consists of native forests and scrublands where common quail do not breed. To determine the migratory status of the captured individuals, we measured the width of their subcutaneous pectoral lipid band with a calliper. The width of this band is a good indicator of the migratory state of common quail, since it is positively correlated with the level of migratory restlessness (Saint-Jalme, 1990) and total body fat content (Guyomarc'h *et al.*, 1990), which increases before migration. All individuals had a pectoral lipid band that was 13.6 ± 2.8 mm wide (range: 8.0–20.3 mm), which is larger than that measured during the breeding season (6.3 ± 2.8 mm, $N = 228$, personal observations). Several other factors indicated migratory status: quail do not breed in the sampling locality; they appeared during the night when quail do migrate (Guyomarc'h *et al.*, 1998); we sampled after the breeding season; and they did not show swollen cloacas [a clear indicator of inactive sexual status (Guyomarc'h and Belhamra, 1998)]. During the winters of 2003–2014 (from 6 October to 1 February), we also obtained samples of 50 wintering quail from 18 hunting areas distributed across Spain.

We took blood (100 μ L) or muscle tissue samples from each individual (from migratory and wintering quail, respectively) and stored them at -20°C in 95% ethanol until DNA was extracted using a DNeasy Blood & Tissue Kit (Qiagen) following the manufacturer's protocols.

Typing of microsatellite loci and analysis

Individuals were genotyped for 11 unlinked autosomal microsatellite loci originally developed for Japanese quail (Kayang *et al.*, 2002, 2004): GUJ0001, GUJ0017, GUJ0028, GUJ0039, GUJ0044, GUJ0057, GUJ0065, GUJ0074, GUJ0085, GUJ0093, and GUJ0097. Loci were amplified using the polymerase chain reaction (PCR). While some markers were successfully optimized for PCR-amplification in a multiplex, others were amplified separately and subsequently pooled before electrophoresis. (Detailed protocols are available

upon request.) All PCR products were electrophoresed on an ABI 3730 sequencer (Applied Biosystems) following the manufacturer's protocols. Alleles were sized and scored using the software GeneMapper v.3.5 (Applied Biosystems). Genotype data sets are available at: evolutionary-ecology.com/data/2942Appendix.pdf or consevol.org/resources.html.

To estimate overall genetic diversity, we calculated the average number of alleles per locus using FSTAT v.2.9.3.2 (Goudet, 1995). Observed (H_o) and expected (H_e , or gene diversity) heterozygosities (Nei, 1987), and the polymorphic information content [PIC (Botstein *et al.*, 1980)], which takes into account the number of alleles per locus and the frequency of these alleles, were calculated using the Excel Microsatellite Toolkit v.3.1.1 (Park, 2001).

Genotypes of migratory and wintering quail were analysed using the Bayesian clustering procedure implemented in STRUCTURE v.2.3.4 (Pritchard *et al.*, 2000). The genotype database analysed also included 38 pure common quail and 52 farm-reared quail intended for game restocking. We used these samples as reference for these two lineages, since they had previously been analysed in other quail hybridization studies in which their genetic origin had been assessed (Sanchez-Donoso *et al.*, 2012, 2014; Puigcerver *et al.*, 2014). For each individual, we estimated the proportion of its genotype that could be assigned to the farm cluster (q_{farm}) and its 90% probability interval. Analyses were performed in STRUCTURE for $K=2$, under the 'admixture model' (each individual may have ancestry in both parental populations), with correlated allele frequencies and without population or sampling location information (USEPOPINFO and LOCPRIOR inactive). Simulations were run for 100,000 steps following a burn-in period of 30,000 steps, and were replicated five times after verifying that results did not vary significantly with longer runs (Vähä and Primmer, 2006; Sanchez-Donoso *et al.*, 2012, 2014). Likelihood values converged during the runs.

We used Fisher's exact test to compare the proportion of individuals carrying alleles of farm origin with the proportion found in a breeding population sampled during 4 years in north-east Spain and constituting 283 individuals genotyped for the same set of loci (Sanchez-Donoso *et al.*, 2014).

Mitochondrial DNA sequencing and analysis

A 483-base-pair fragment of the 5' end of the mitochondrial DNA (mtDNA) control region was sequenced for the 92 quail under study. DNA samples were amplified via PCR using the primers PHDL and PH-H521 (Barilani *et al.*, 2005). Sequencing reactions were carried out using the same forward and reverse primers, and were run on an Applied 184 Biosystems 3730xl DNA Analyzer (Life Technologies) following the manufacturer's protocols. A consensus sequence was built for each sample using GENEIOUS v.8.0.5 (Biomatters Development Team, 2014). A GenBank BLAST search was done with the same software to identify any match to previously described haplotypes.

Mitochondrial DNA haplotypes were aligned with Muscle in GENEIOUS, together with 10 previously described common quail and 11 Japanese quail haplotypes downloaded from GenBank (Geer *et al.*, 2010) and used as a reference. We used MEGA v.6 (Tamura *et al.*, 2013) to compare all sequences, and for phylogenetic reconstruction, using the neighbor-joining (NJ) clustering method (Saitou and Nei, 1987) and adopting the Tamura-Nei model of sequence evolution (Tamura and Nei, 1993). Support for nodes was assessed with 500 bootstrap replicates. The main goal of the phylogenetic reconstruction was to separate common quail and Japanese quail sequence clades, not to represent accurately the evolutionary relationship among all haplotypes.

RESULTS

More than 95% of the wintering quail could be genotyped for nine or more loci (as well as more than 90% of the individuals used as reference in STRUCTURE analyses). The quality of DNA extracts for migratory quail was lower: 23% could be genotyped for nine or more loci, and all except three could be genotyped for six or more loci. The three migratory quail genotypes that did not reach six loci were excluded from further analyses. The lower quality of the genotypes probably caused wider confidence intervals of q_{farm} estimates for migratory quail (see below, Fig. 1). Genetic diversity was similar in migratory and wintering quail, and it was also similar to that of a breeding population in north-east Spain and genotyped for the same loci (Sanchez-Donoso *et al.*, 2014). Mean estimates (\pm standard deviation) for migratory ($N = 39$) and wintering quail ($N = 50$) were as follows: 14.5 ± 4.5 and 18.9 ± 5.5 alleles per locus, 0.91 ± 0.06 and 0.90 ± 0.06 for H_e , 0.81 ± 0.15 and 0.83 ± 0.10 for H_o , and 0.87 ± 0.05 and 0.88 ± 0.07 for PIC, respectively.

Results obtained with STRUCTURE showed that, as expected, common and farm quail reference samples were clearly differentiated (Fig. 1). Among the farm samples, some individuals showed admixed genotypes more similar to common quail than the rest of the farm quail. These results agree with previous findings about the nature of admixed quail reared in farms for game restocking purposes (Sanchez-Donoso *et al.*, 2012, 2014). All migratory quail analysed (39 individuals) showed genotypes compatible with a judgement that they are pure common quail. On the other hand, 47 of the 50 wintering quail analysed showed genotypes similar to pure common quail and three had genotypes similar to farm quail.

Forty-two mtDNA haplotypes were identified among the studied samples (GenBank accession numbers: KP797932 to KP797972), 13 of which matched shorter, previously described haplotypes (Fumihito *et al.*, 1996; Barilani *et al.*, 2005; Sanchez-Donoso *et al.*, 2014), while 29 haplotypes did not match any previously described haplotype. The low quality of one of the sequences forced us to exclude it from the phylogenetic tree (Fig. 2) but it clearly clustered with common quail sequences (analyses not shown).

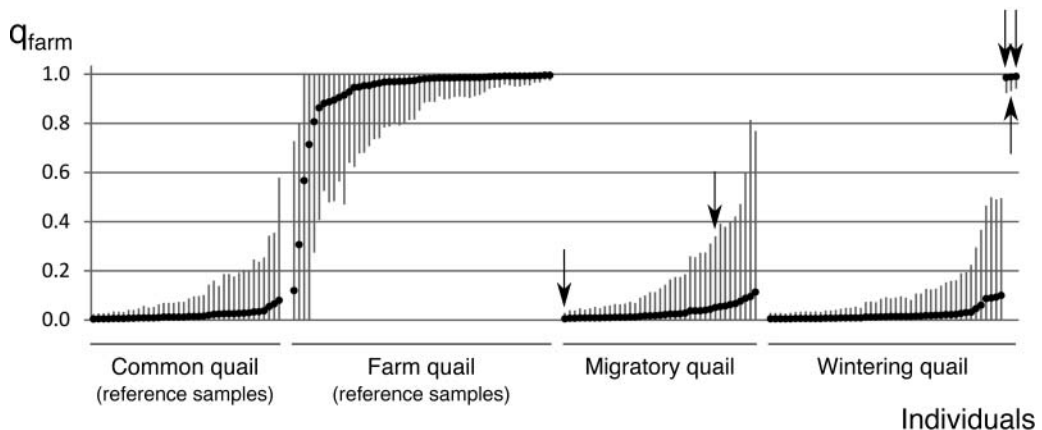


Fig. 1. Proportion of membership in the farm cluster (q_{farm}) based on STRUCTURE ($K = 2$) for common quail and farm-reared quail used as reference, and for migratory and wintering quail. Vertical lines are q_{farm} 90% probability intervals. Individuals are sorted by origin and q_{farm} value. Individuals of wild origin with a Japanese quail mtDNA haplotype (KP797932) are indicated by arrows (see text).

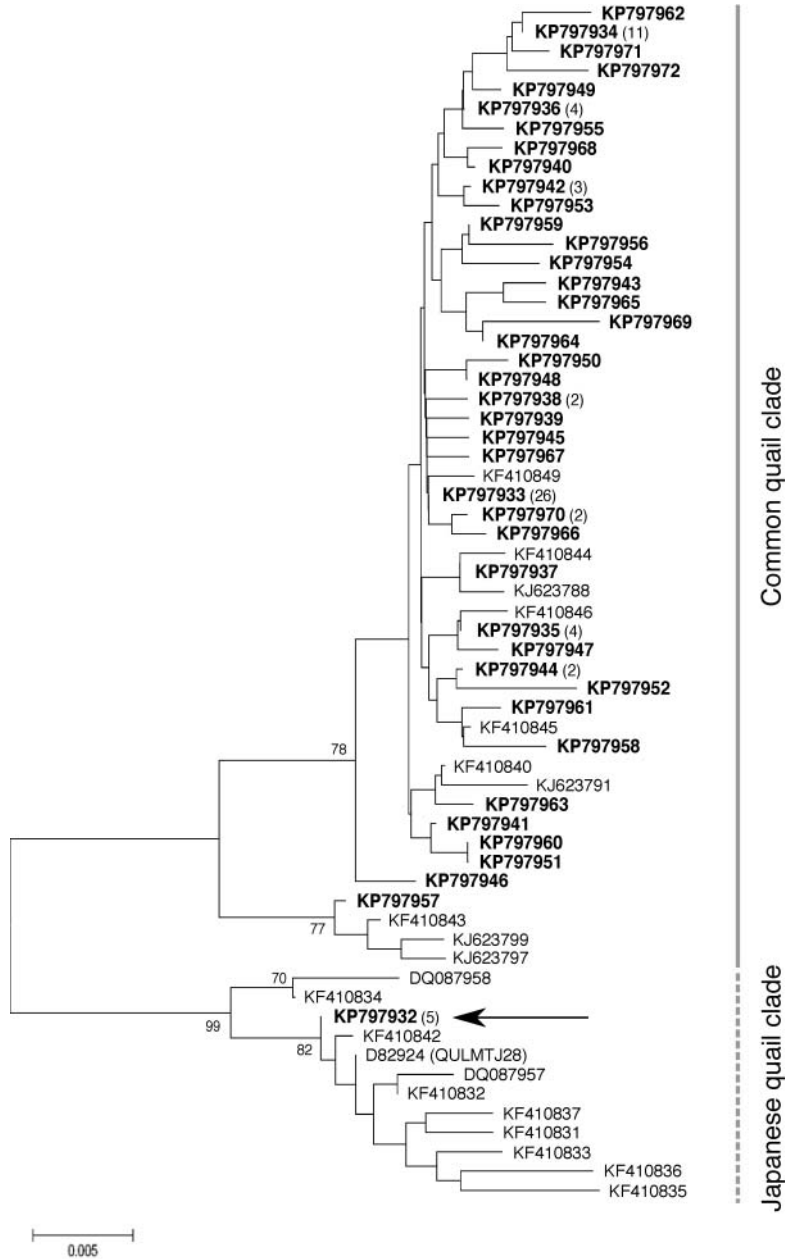


Fig. 2. Mid-point rooted neighbor-joining phylogenetic tree of mitochondrial control region haplotypes in migratory and wintering quail samples (**bold type**). Common quail (*Coturnix coturnix*) and Japanese quail (*C. japonica*) sequences obtained from GenBank are used as reference. Numbers of quail with each haplotype are shown in parentheses when more than one. Bootstrap support is indicated at the nodes when higher than 70%. Two clades were found, separating common quail from Japanese quail sequences with strong support. One Japanese quail haplotype (KP797932, marked with an arrow) was found in two migratory and three wintering quail. The remaining migratory and wintering quail showed common quail haplotypes.

The phylogenetic reconstruction using mtDNA sequences showed two clearly differentiated clades (Fig. 2), one constituted by common quail sequences and the other by Japanese quail sequences. All haplotypes from the study samples, except for one, were in the same clade, together with the previously described common quail haplotypes. The mismatched haplotype (GenBank accession number: KP797932) was in the Japanese quail clade and coincided with a previously identified Japanese quail haplotype that had already been described as the most common haplotype among Spanish farm-reared quail (Sanchez-Donoso *et al.*, 2014). Two migratory and three wintering quail showed this Japanese quail haplotype. These same three wintering individuals were the ones that showed genotypes compatible with a farm origin (Fig. 1).

None of the migratory quail showed evidence of recent admixture with domestic Japanese quail in their nuclear DNA, but two of them (5% of 39) showed evidence of farm quail ancestry in their mtDNA (Fig. 1). This implies that these individuals were descendants of older interbreeding events between farm quail and wild common quail that had been incorporated into the wild breeding population.

In contrast, three of the wintering quail (6% of 50) showed their mitochondrial and nuclear genotypes to be compatible with a farm origin (Figs. 1 and 2), probably representing restocked animals. This implies that the proportion of quail carrying alleles of farm origin was small and not different to the proportion observed during the breeding season in previous studies, i.e. about 9.9% of the breeding quail [Fisher's $P = 0.596$ (Sanchez-Donoso *et al.*, 2014)].

DISCUSSION

Our results show that migratory quail are mainly pure common quail. Since previous studies indicated that almost all farm-reared quail show some degree of admixture in their nuclear genome (Sanchez-Donoso *et al.*, 2014) but none of the migratory quail analysed showed evidence of nuclear admixture, we conclude that the migratory quail we studied were not individuals restocked from game farms or their immediate descendants. However, we found two migratory individuals with some sign of old Japanese ancestry. The presence of both the common quail nuclear genome and Japanese quail mitochondrial DNA in the same individual indicates introgression. Such individuals are the result of an old cross between a farm female [with domestic Japanese quail mtDNA (Barilani *et al.*, 2005; Amaral *et al.*, 2007; Sanchez-Donoso *et al.*, 2014)] and a wild common quail male whose female descendants had been repeatedly backcrossing with common quail males to the point that the nuclear DNA of the offspring became indistinguishable from that of common quail. Thus, although most domestic Japanese quail and their hybrids do not show migratory restlessness (Derégnaucourt, 2000; Derégnaucourt *et al.*, 2005a, 2000b), the offspring of old crosses with farm individuals could become part of the migrant population. Finding two introgressed quail among the migratory individuals also shows that farm restocked females breed in the wild and that, although their fitness is lower than that of common quail females (Puigcerver *et al.*, 2014), their offspring can reach maturity and be recruited into the wild population, perpetuating the introgression of domestic Japanese quail genes into the common quail gene pool. These results also emphasize the need to combine nuclear and mitochondrial genetic markers to fully assess the consequences of interbreeding. Without both kinds of information, the old introgression episodes would not have been detected.

The analysis of 50 quail sampled during winter – after most quail have long departed to their wintering grounds – indicated that quail wintering in northern latitudes are not mainly restocked individuals or their descendants, but pure common quail. Since previous analyses showed that farm-reared quail have Japanese mtDNA haplotypes (Barilani *et al.*, 2005; Amaral *et al.*, 2007; Sanchez-Donoso *et al.*, 2014), the three wintering individuals detected with a Japanese quail mtDNA haplotype and a farm-like genotype probably represent individuals raised in farms and released for hunting. Our results suggest that farm quail used for restocking experience marked mortality after their release, since they do not form a significant part of the migratory or wintering population. For other restocked game birds, like pheasants and partridges, mortality due to predation or low survival skills is very high (Parish and Sotherton, 2007; Buenestado *et al.*, 2009; Diaz-Fernández *et al.*, 2013; Mihaylov *et al.*, 2014). The mortality due to hunting should be added to this (Santilli and Bagliacca, 2008; Sevane *et al.*, 2011; Diaz-Fernández *et al.*, 2012), resulting in a very small proportion of the released animals contributing to local breeding stocks. For the quail, there are no data relating to the proportion of restocked individuals that are hunted. Since most restocking takes place immediately before hunting events, it is likely that most of them are killed soon after their release. The ones that survive hunting probably die during the following days owing to their poor adaptation to life in the wild under winter weather conditions, depleted habitats, and high predation rates (Puigcerver *et al.*, 2014). However, the detection of quail of farm origin among the wintering individuals together with their previously reported presence during the breeding season (Sanchez-Donoso *et al.*, 2014), well after most of the restocking has taken place, indicates that a fraction of the restocked admixed quail do survive hunting, winter weather, and are recruited to the breeding population during the next breeding season. As a result, domestic Japanese quail alleles introgress into the common quail gene pool (Sanchez-Donoso *et al.*, 2014).

Despite the presence of quail of farm origin in the wintering population, their frequency is low. Consequently, it is unlikely that restocking with farm quail is the main reason for the existence of this wintering population. Perennou (2009) claimed that the fraction of birds that do not migrate to the sub-Saharan strip but instead winter in the southern part of the breeding area has been increasing in recent decades, a trend that seems to have begun when restocking with captive-bred quail began. However, the tendency towards progressive sedentarization of the population has not been clearly demonstrated and needs to be further assessed (SEO/BirdLife, 2008–2015).

Over a longer timescale, rather than hybridization, climate change could be driving a selective reduction (perhaps due to relaxation of selective forces) of the quail restlessness drive, favouring an increase of sedentary phenotypes in traditionally non-wintering areas. Changes in the migratory phenology due to climate change have been observed in other bird species (Gordo *et al.*, 2005; Ward *et al.*, 2009; Møller *et al.*, 2010; Lehikoinen *et al.*, 2013; Martin *et al.*, 2014; Kullberg *et al.*, 2015). In the case of the common quail, first spring arrivals to northern Spain have been experiencing a shift towards earlier dates (data from 1983 to 2004), in line with an increase in mean temperature in the sub-Saharan strip where the main wintering grounds are located (Rodríguez-Teijeiro *et al.*, 2005). Also, some authors suggest a decrease in the number of long-distance migrants because of recurrent droughts in the Sahel since 1970 (Guyomarc'h, 1992). The effects of climate change on the quail's migratory phenology and any tendency to sedentarization should be investigated further.

Although hybridization with admixed quail restocked from farms for game purposes may not be affecting the migratory drive of the population, restocking admixed individuals presents other potential problems, such as the loss of the genetic identity of the species and

the introduction of maladaptive alleles (Ford, 2002), loss of genetic diversity (Ryman and Laikre, 1991; Laikre *et al.*, 2010), or the introduction of parasites and diseases into the natural population (Gortázar *et al.*, 2006; Peeler *et al.*, 2006). Consequently, we believe that the ban on restocking admixed quail should be strictly enforced.

ACKNOWLEDGEMENTS

This project was funded by the Catalan ‘Direcció General de la Recerca’ (2009SGR481 and 2014SGR1477), the Hunting Federation of the Basque Country, the Spanish Science Ministry (CGL2004-05308/BOS and CGL2007-63199/BOS), and the ‘Severo Ochoa micro-grants’ offered by the Doñana Biological Station (EBD-CSIC). The authors would like to thank the hunters who provided samples of winter quail. Thanks also to F. Granada for allowing the sampling of migratory quail on his property, and to the ‘Diputació de Barcelona’ and the secretary of the hunting estate, J. Feliu, which granted us permission to sample migratory quail. Thanks to Carolina Ponz, Xavier Larruy, Josep Anton Ferreres Oncins and his family, Ana Domínguez and all the fieldwork volunteers for technical assistance in the field; and J.A. Leonard for help in the design of laboratory protocols and the analysis of genetic data. Logistical support was provided by ‘Laboratorio de Ecología Molecular’ from Estación Biológica de Doñana-CSIC (LEM-EBD).

REFERENCES

- Amaral, A.J., Silva, A.B., Grosso, A.R., Chikhi, L., Bastos-Silveira, C. and Dias, D. 2007. Detection of hybridization and species identification in domesticated and wild quails using genetic markers. *Folia Zool.*, **56**: 285–300.
- Barilani, M., Derégnaucourt, S., Gallego, S., Galli, L., Mucci, N., Piombo, R. *et al.* 2005. Detecting hybridization in wild (*Coturnix c. coturnix*) and domesticated (*Coturnix c. japonica*) quail populations. *Biol. Conserv.*, **126**: 445–455.
- Biomatters Development Team. 2014. *Geneious* v.8.0.5. Auckland, NZ: Biomatters Ltd.
- Botstein, D., White, R.L., Skolnick, M. and Davis, R.W. 1980. Construction of a genetic linkage map in man using restriction fragment length polymorphisms. *Am. J. Human Genet.*, **32**: 314–331.
- Buenestado, F.J., Ferreras, P., Blanco-Aguilar, J.A., Tortosa, F.S. and Villafuerte, R. 2009. Survival and causes of mortality among wild Red-legged Partridges *Alectoris rufa* in southern Spain: implications for conservation. *Ibis*, **151**: 720–730.
- Caballero Pacho, O. (1957) Codornices invernantes en Galicia. *Ardeola*, **3**: 303.
- Del Hoyo, J., Elliot, A. and Sargatal, J., eds. 1994. *Handbook of the Birds of the World, Vol. 2: New Vultures to Guinea-fowl*. Barcelona: Lynx Editions.
- Derégnaucourt, S. 2000. Hybridization entre la caille des blés (*Coturnix c. coturnix*) et la caille japonaise (*Coturnix c. japonica*): Mise en évidence des risques de pollution génétique des populations naturelles par les cailles domestiques. PhD dissertation, Université Rennes I.
- Derégnaucourt, S., Guyomarc’h, J.C. and Belhamra, M. 2005a. Comparison of migratory tendency in European quail *Coturnix c. coturnix*, domestic Japanese quail *Coturnix c. japonica* and their hybrids. *Ibis*, **147**: 25–36.
- Derégnaucourt, S., Guyomarc’h, J.C. and Spano, S. 2005b. Behavioural evidence of hybridization (Japanese × European) in domestic quail released as game birds. *Appl. Anim. Behav. Sci.*, **94**: 303–318.
- Díaz-Fernández, S., Viñuela, J. and Arroyo, B. 2012. Harvest of red-legged partridge in central Spain. *J. Wildl. Manage.*, **76**: 1354–1363.
- Díaz-Fernández, S., Arroyo, B., Casas, F., Martínez-Haro, M. and Viñuela, J. 2013. Effect of game management on wild red-legged partridge abundance. *PLoS ONE*, **8**: e66671.

- Fontoura, A.P. and Gonçalves, D. 1996. Sedentariness of European quail (*Coturnix coturnix*) in Portugal. In *Proceedings of the XXII International Union of Game Biologists* (S. Golovatch and L. Penev, eds.), pp. 7–12. Sofia: Pensoft.
- Ford, M.J. 2002. Selection in captivity during supportive breeding may reduce fitness in the wild. *Conserv. Biol.*, **16**: 815–825.
- Fumihito, A., Miyake, T., Takada, M., Shingu, R., Endo, T., Gojobori, T. *et al.* 1996. Monophyletic origin and unique dispersal patterns of domestic fowls. *Proc. Natl. Acad. Sci. USA*, **93**: 6792–6795.
- Garrido, J.L. 2012. *La caza. Sector económico. Valoración por subsectores*. Madrid: FEDENCA-EEC.
- Geer, L.Y., Marchler-Bauer, A., Geer, R.C., Han, L., He, J., He, S. *et al.* 2010. The NCBI BioSystems database. Database issue of *Nucleic Acids Res.*, **38**: D492–D496.
- Gordo, O., Brotons, L., Ferrer, X. and Comas, P. 2005. Do changes in climate patterns in wintering areas affect the timing of the spring arrival of trans-Saharan migrant birds? *Global Change Biol.*, **11**: 12–21.
- Gortázar, C., Acevedo, P., Ruis-Fons, F. and Vincente, J. 2006. Disease risks and overabundance of game species. *Eur. J. Wildl. Res.*, **52**: 81–87.
- Goudet, J. 1995. FSTAT (version 1.2): a computer program to calculate *F*-statistics. *J. Hered.*, **86**: 485–486.
- Guyomarc'h, C., Guyomarc'h, J.C. and Saint-Jalme, M. 1990. Potentialités reproductrices chez les jeunes cailles des blés *Coturnix coturnix coturnix*. *Cah. Éthol. Appl.*, **10**: 125–142.
- Guyomarc'h, J.C. 1992. Structure, fonctionnement et microévolution des populations de cailles des blés (*Coturnix c. coturnix*) dans le Paléarctique occidental. In *Perdix VI: First International Symposium on Partridges, Quails and Francolins* (M. Birkan, G.R. Potts, N.J. Aebischer and S.D. Dowell, eds.), *Gibier Faune Sauvage*, **9**: 387–401.
- Guyomarc'h, J.C. 2003. Elements for a Common Quail *Coturnix c. coturnix* management plan. *Game Wildl. Sci.*, **20**: 1–92.
- Guyomarc'h, J.C. and Belhamra, M. 1998. Les effets de la sélection sur l'expression des tendances sexuelles et migratoires chez la caille des blés (*Coturnix c. coturnix*). *Cah. Éthol. Appl.*, **18**: 1–16.
- Guyomarc'h, J.C., Combreau, O., Puigcerver, M. 1998. *Coturnix coturnix* Quail. In *BWP Update: The Journal of Birds of the Western Palearctic*, Vol. 2, pp. 27–46. Oxford: Oxford University Press.
- Johnsgard, P.A. 1988. Genus *Coturnix* Bonnat 1791. In *The Quails, Partridges and Francolins of the World*, pp. 192–205. Oxford: Oxford University Press, Oxford.
- Kayang, B.B., Inoue-Murayama, M., Hoshi, T., Matsuo, K., Takahashi, H., Minezawa, M. *et al.* 2002. Microsatellite loci in Japanese quail and cross-species amplification in chicken and guinea fowl. *Genet. Select. Evol.*, **34**: 233–253.
- Kayang, B.B., Vignal, A., Inoue-Murayama, M., Miwa, M., Monvoisin, J.L., Ito, S. *et al.* 2004. A first-generation microsatellite linkage map of the Japanese quail. *Anim. Genet.*, **35**: 195–200.
- Kullberg, C., Fransson, T., Hedlund, J., Jonzén, N., Langvall, O., Nilsson, J. *et al.* 2015. Change in spring arrival of migratory birds under an era of climate change: Swedish data from the last 140 years. *Ambio*, **44** (suppl. 1): 69–77.
- Lack, P. 1986. *The Atlas of Wintering Birds in Britain and Ireland*. Calton, UK: T. & A.D. Poyser.
- Laikre, L., Schwartz, M.K., Waples, R.S., Ryman, N. and the GeM Working Group. 2010. Compromising genetic diversity in the wild: unmonitored large-scale release of plants and animals. *Trends Ecol. Evol.*, **25**: 520–529.
- Lehikoinen, A., Jaatinen, K., Vähätalo, A.V., Clausen, P., Crowe, O., Deceuninck, B. *et al.* 2013. Rapid climate driven shifts in wintering distributions of three common waterbird species. *Global Change Biol.*, **19**: 2071–2081.
- MAGRAMA, Ministerio de Agricultura, Alimentación y Medio Ambiente [Spanish Ministry of Agriculture, Food and Environment] (2011) *Estadística Anual de caza*. Madrid: MAGRAMA [http://www.magrama.gob.es/es/desarrollo-rural/estadisticas/est_anual_caza.aspx; accessed March 2015].

- Martín, B., Onrubia, A. and Ferrer, M.A. 2014. Effects of climate change on the migratory behavior of the common buzzard *Buteo buteo*. *Clim. Res.*, **60**: 187–197.
- Mihaylov, H., Gruychev, G. and Stoyanov, S. 2014. Survival of spring released, hand reared common pheasants (*Phasianus colchicus colchicus* L. 1758) and chukar partridges (*Alectoris chukar* J.E. Gray, 1830) in natural habitats in Bulgaria. *Balkan J. Wildl. Res.*, **1**: 55–61.
- Møller, A.P., Fiedler, W. and Berthold, P., eds. 2010. *Effects of Climate Change on Birds*. Oxford: Oxford University Press.
- Morel, G. and Roux, F. 1966. Les migrateurs paléarctiques au Sénégal. 1 – non passereaux. *Rev. Ecol. (Terre Vie)*, **1**: 95–123.
- Mur, P. 2009. L'hivernage de la caille des blés *Coturnix coturnix* en France. *Alauda*, **77**: 103–114.
- Nei, M. 1987. *Molecular Evolutionary Genetics*. New York: Columbia University Press.
- Parish, D.M.B. and Sotherton, N.W. 2007. The fate of released captive-reared grey partridges *Perdix perdix*: implications for reintroduction programmes. *Wildl. Biol.*, **13**: 140–149.
- Park, S.D.E. 2001. Trypanotolerance in West African cattle and the population genetic effects of selection. PhD dissertation, University of Dublin.
- Peeler, E., Thrush, M., Paisley, L. and Rodgers, C. 2006. An assessment of the risk of spreading the fish parasite *Gyrodactylus salaris* to uninfected territories in the European Union with the movement of live Atlantic salmon (*Salmo salar*) from coastal waters. *Aquaculture*, **258**: 187–197.
- Perennou, C. (2009) *European Union Management Plan 2009–2011. Common Quail, Coturnix coturnix*. Luxembourg: Office for Official Publications of the European Communities.
- Pritchard, J.K., Stephens, M. and Donnelly, P. 2000. Inference of population structure using multilocus genotype data. *Genetics*, **155**: 945–959.
- Puigcerver, M., Sanchez-Donoso, I., Vilà, C., Sardà-Palomera, F., García-Galea, E. and Rodríguez-Teijeiro, J.D. 2014. Decreased fitness of restocked hybrid quails prevents fast admixture with wild European quails. *Biol. Conserv.*, **171**: 74–81.
- Rodríguez-Teijeiro, J.D., Puigcerver, M. and Gallego, S. 1992. Mating strategy in the European Quail (*Coturnix c. coturnix*) revealed by male population density and sex ratio in Catalonia (Spain). *Gibier Faune Sauvage*, **9**: 377–386.
- Rodríguez-Teijeiro, J.D., Puigcerver, M. and Gallego, S. 2004. Guatlla *Coturnix coturnix*. In *Atles dels Ocells Nidificants de Catalunya, 1999–2002* (J. Estrada, V. Pedrocchi, L. Brotons and S. Herrando, eds.), pp. 112–113. Barcelona: ICO/Lynx Edicions.
- Rodríguez-Teijeiro, J.D., Gordo, O., Puigcerver, M., Gallego, S., Vinyoles, D. and Ferrer, X. 2005. African climate warming advances spring arrival of the Common quail *Coturnix coturnix*. *Ardeola*, **52**: 159–162.
- Rodríguez-Teijeiro, J.D., Barroso, A., Gallego, S., Puigcerver, M. and Vinyoles, D. 2006. Orientation-cage experiments with the European Quail during the breeding season and autumn migration. *Can. J. Zool.*, **894**: 887–894.
- Rodríguez-Teijeiro, J.D., Sardà-Palomera, F. and Puigcerver, M. 2012. Post-breeding movements and migration patterns of western populations of common quail (*Coturnix coturnix*): from knowledge to hunting management. *Anim. Biodivers. Conserv.*, **35**: 333–342.
- Ryman, N. and Laikre, L. 1991. Effects of supportive breeding on the genetically effective population size. *Conserv. Biol.*, **5**: 325–329.
- Saint-Jalme, M. 1990. La reproduction chez la caille des blés (*Coturnix c. coturnix*); études expérimentales des cycles saisonniers et de la variabilité interindividuelle. PhD dissertation, Université Rennes I.
- Saitou, N. and Nei, M. 1987. The neighbor-joining method: a new method for reconstructing phylogenetic trees. *Mol. Biol. Evol.*, **4**: 406–425.
- Sanchez-Donoso, I., Vilà, C., Puigcerver, M., Butkauskas, D., Caballero de la Calle, J.R., Morales-Rodríguez, P.A. et al. 2012. Are farm-reared quails for game restocking really common quails (*Coturnix coturnix*)? A genetic approach. *PLoS ONE*, **7**: e39031.

- Sanchez-Donoso, I., Huisman, J., Echegaray, J., Puigcerver, M., Rodríguez-Teijeiro, J.D., Hailer, F. *et al.* 2014. Detecting slow introgression of invasive alleles in an extensively restocked game bird. *Front. Ecol. Evol.*, **2**: 00015.
- Santilli, F. and Bagliacca, M. 2008. Factors influencing pheasant *Phasianus colchicus* harvesting in Tuscany, Italy. *Wildl. Biol.*, **14**: 281–287.
- Sardà-Palomera, F., Puigcerver, M., Sanchez-Donoso, I. and Rodríguez-Teijeiro, J.D. 2011. Guatlla *Coturnix coturnix*. In *Atles dels ocells de Catalunya a l'Hivern 2006–2009* (S. Herrando, L. Brotons, J. Estrada, S. Guallar and M. Anton, eds.), pp. 158–159. Barcelona: ICO/Lynx Edicions.
- SEO/BirdLife. 2008–2015. *Coturnix coturnix*. Programa SACRE en la temporada de invierno, Madrid [http://www.seguimientodeaves.org/sacin/subfConsultasGen.php?TIPO_CON = 1; accessed March 2015].
- Sevane, N., Dunner, S., García-Atance, M.A. and Cañon, J. 2011. Restocked and non-restocked populations genetic composition: a case study in red-legged partridge (*Alectoris rufa*). *J. Biol. Res.*, **16**: 266–273.
- Tamura, K. and Nei, M. 1993. Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. *Mol. Biol. Evol.*, **10**: 512–526.
- Tamura, K., Stecher, G., Peterson, D., Filipowski, A. and Kumar, S. 2013. MEGA6: Molecular Evolutionary Genetics Analysis version 6.0. *Mol. Biol. Evol.*, **30**: 2725–2729.
- Thévenot, M., Vernon, R. and Bergier, P. 2003. *The Birds of Morocco: An Annotated Checklist*. Tring, UK: British Ornithologists' Union.
- Vähä, J.P. and Primmer, C.R. 2006. Efficiency of model-based Bayesian methods for detecting hybrid individuals under different hybridization scenarios and with different numbers of loci. *Mol. Ecol.*, **15**: 63–72.
- Ward, D.H., Dau, C.P., Tibbitts, T.L., Sedinger, J.S., Anderson, B.A. and Hines, J.E. 2009. Change in abundance of Pacific brant wintering in Alaska: evidence of a climate warming effect? *Arctic*, **62**: 301–311.