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Genomic diversity and signals of selection processes in wild and farm-reared red-legged partridges (*Alectoris rufa*)

R. Ros-Freixedes [a], R.N. Pena [a], C. Richart [b,c,**], J. Nadal [a,*]

[a] Department of Animal Science, University of Lleida, Lleida, Spain
[b] Departament de Medicina i Cirurgia, Universitat Rovira i Virgili, Tarragona, Spain
[c] Fundación Universitat Rovira i Virgili, Tarragona, Spain

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ABSTRACT

The genetic dynamics of wild populations with releases of farm-reared reinforcements are very complex. These releases can endanger wild populations through genetic swamping or by displacing them. We assessed the genomic differences between wild and farm-reared red-legged partridges (*Alectoris rufa*) and described differential selection signals between both populations. We sequenced the whole genome of 30 wild and 30 farm-reared partridges. Both partridges had similar nucleotide diversity (π). Farm-reared partridges had a more negative Tajima's D and more and longer regions of extended haplotype homozygosity than wild partridges. We observed higher inbreeding coefficients (F_{IS} and F_{ROH}) in wild partridges. Selective sweeps (Rsb) were enriched with genes that contribute to the reproductive, skin and feather colouring, and behavioural differences between wild and farm-reared partridges. The analysis of genomic diversity should inform future decisions for the preservation of wild populations.

1. Introduction

Commercial hunting and the development of hunting tourism have boosted the economy and infrastructure development of some rural areas. For instance, the revenue of partridge hunting each year in Spain is estimated to be 4.95 M € [1]. The increasing demand of game birds for commercial hunting has led to the rearing of game birds on farms, which are then released massively into the wild and can hybridize with wild populations or displace them [2,3]. Therefore, there is a need to analyse the genetic diversity of game bird populations in order to guide future decisions for the preservation of wild populations and the appropriate management of the released farm-reared partridges, leading towards a sustainable balance between wild and farm-reared game bird populations [4,5].

Genetic dynamics of wild populations with releases of farm-reared reinforcements are very complex [6,7]. Wild populations undergo natural selection, a process that promotes heritable traits that increase fitness while removing or restraining undesirable traits. Natural selection favours distinct adaptations to diverse habitats and, together with sexual selection, drives the evolution of wild populations [8,9]. While natural selection is expected to occur, human hunting of individuals with the most desirable phenotypic traits can affect the mating system through reduced availability of well-fitted breeding individuals and, as a consequence, affect sexual selection. This can generate a process of selection against desirable phenotypes and ultimately reduce fitness and viability of the population, which has been termed 'unnatural selection' [10].

On the other hand, captive populations are typically founded by a small number of individuals. Such population bottlenecks lead to large coefficients of inbreeding and low effective population sizes [11,12], resulting in inbreeding depression [13]. In extreme situations, severe inbreeding can reduce the reproductive success by 87–90% [14]. Outcrossed and crossbred animals are bred in some species to ameliorate inbreeding depression or achieve hybrid vigour. Moreover, captive populations undergo artificial selection, for instance by selective breeding, which aims to develop traits controlled by the breeder, or by adaptation to the captivity environment [15–17]. Selection for tameness and adaptation to captive environments also makes the animals less fitted to live in the wild [18]. As a consequence, captive-born individuals frequently have reduced fitness when released into the wild, resulting in negative effects on natural reproduction in the wild [14,19–22].

Understanding the impact that the selection processes have at the

* Correspondence to: Jesús Nadal, Department of Animal Science, University of Lleida, 191 Rovira Roure Ave, Lleida 25198, Spain.
** Correspondence to: Cristobal Richart, Departament de Medicina i Cirurgia, Universitat Rovira i Virgili, 21 Sant Llorenç St, Reus Tarragona 43201, Spain.
E-mail addresses: cristobalmanuel.richart@urv.cat (C. Richart), jesus.nadal@udl.cat (J. Nadal).

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genetic, physiological, morphological, and behavioural levels is key to improve the management and conservation of wild animal populations. The bird species in which the selection processes have been studied the most is the chicken. The red junglefowl, the ancestor of domestic chicken, possesses higher genetic diversity and effective population number, and lower linkage disequilibrium decay and homozygosity than domestic chicken breeds [23]. Within modern chicken breeds, genetic diversity is uneven: gamecock (fighting) breeds present higher genetic variation than commercial and indigenous breeds [24]. The red junglefowl also constitutes a modern-day example of introgression between domesticated animals and their wild counterparts [25]. Continual gene flow between domestic and wild populations has compromised the red junglefowl gene pool, especially since the last century, when habitat loss of the red junglefowl and human expansion led to more contact opportunities with domestic specimens [26]. A similar situation has been observed in wild duck populations, for which the introgression with domestic ducks is recognised [27–29], and in other wild game birds such as quails and partridges [30,31].

The wild red-legged partridge (*Alectoris rufa*) is distributed naturally in South-West Europe, although it has been introduced in all continents. Natural selection favoured wild partridges with high foraging efficiency and anti-predator behaviour, so that they take advantage of many different habitat resources that requires constant trial-and-error learning [32–35]. Food search and predator avoidance require a combination of traits related to instinctual behaviour, the learning about habitat structure, and the identification of diverse food resources and up to 82 species of predators [36,37]. Socialization in wild populations is complex and dynamic, including the phases of family, supra-family, and autumn and winter coveys. All these complex functions require the development of specific brain regions and of the nervous system. The immune and digestive systems of wild partridges are also highly specialized for different habitats [38]. In contrast, farm-reared partridges are artificially selected for their tameness, reduced mobility and curiosity, greater egg laying, size and spurs, which can negatively affect their ability for food search, habitat selection, escape reaction, socialization, learning and overall fitness. The immune system and digestive tract of farm-reared partridges are highly specialized for captivity [39,40].

In central Spain there are suitable habitat conditions for a high density of wild red-legged partridges (>50 individuals/100 ha) despite that a density decline of 51% was observed between years 2010 and 2017 [41,42]. The aim of this study was to reveal the molecular genomic variation between wild and farm-reared red-legged partridges in central Spain. The objectives of this study were to assess whether there are genomic differences between wild and farm-reared partridges and to identify which are the differential selection signals between wild and farm-reared partridges.

2. Material and methods

2.1. Biological sampling

Two populations of red-legged partridges were sampled (Table S1). The first population was a wild population from Ciudad Real (central Spain; 38°39′ N, 3°13′ W; 790–840 m a.s.l.) in "Las Ensanchas", a small game hunting state where there are no releases of farm-reared partridge population reinforcements. A total of 30 samples of muscle were obtained by researchers from bagged birds [43] in years 2006 to 2009. The second population was farm-reared. Another 30 samples of muscle were collected from slaughtered partridges from an integrated farm that has >20,000 breeding pairs and sells partridges for hunting in the province of Ciudad Real. This population of farm-reared partridges was founded in 1978 using individuals from breeding farms in France and Spain and, since then, this population has been selected for reproductive performance and feathering development. Since the foundation of this farm-reared population, there have been introductions of captive individuals from other breeding farms, as well as, occasional introductions of wild partridges from populations with farm-reared partridge population reinforcements [44]. Biological tissues were immersed in a 1.5 ml tube with absolute ethanol and stored at −20 °C.

The study was conducted in full compliance with Spanish laws and regulations, including the licence of "Las Ensanchas" for sampling shot partridges. The protocol was approved by the Committee on the Ethics of Animal Experiments of the University of Lleida (Ref. 1998–2012/05).

2.2. DNA isolation

DNA was isolated following a standard phenol-chloroform extraction [45]. DNA samples were quantified in a Qubit fluorometer (Life Technologies, Waltham, MA USA), the purity was assessed in a Nanodrop-100 spectrophotometer (Thermo Fisher Scientific, Wilmington, DE, USA) and the integrity checked by electrophoresis in agarose gels. DNA was stored at −20 °C until analysis.

2.3. Whole-genome sequencing

The short-insert paired-end libraries for the whole-genome sequencing were prepared with PCR-free protocol using KAPA HyperPrep kit (Roche, Basel, Switzerland) with some modifications. In short, depending on the material availability, 0.4–1.0 μg of genomic DNA was sheared on a Covaris™ LE220-Plus (Covaris, Brighton, UK) in order to reach the fragment size of ~400 bp. The fragmented DNA was size-selected for the fragment size of 220–550 bp with AMPure XP beads (Agencourt, Beckman Coulter, Nyon, Switzerland). The size selected genomic DNA fragments were end-repaired, adenylated and Illumina platform compatible adaptors with unique dual indexes and unique molecular identifiers (Integrated DNA Technologies, Leuven, Belgium) were ligated. The libraries were quality controlled on an Agilent 2100 Bioanalyzer with the DNA 7500 assay (Agilent, Madrid, Spain) for size and quantified by Kapa Library Quantification Kit for Illumina platforms (Roche).

The libraries were sequenced on NovaSeq6000 (Illumina, San Diego, CA, USA) in paired-end mode with a read length of $2 \times 151 + 17 + 8$ bp following the manufacturer's protocol for dual indexing. Image analysis, base calling and quality scoring of the run were processed using the manufacturer's software Real Time Analysis (RTA 3.4.4, Illumina) and followed by generation of FASTQ sequence files. For each sample, a minimum of 20 Gb of sequencing data was generated, which represents a sequencing depth of ~20× of the partridge genome.

DNA sequence reads were pre-processed using Trimmomatic [46] to remove adapter sequences from the reads. Because an annotated reference genome for *A. rufa* was not yet available, we mapped the reads to the genome of the closest species available, which was the Japanese quail (*Coturnix japonica*; reference genome version: 2.1; GenBank accession: GCA_001577835.2) using the BWA-MEM algorithm [47]. Duplicates were marked with Picard (http://broadinstitute.github.io/picard). Single nucleotide polymorphisms (SNPs) and short insertions and deletions (indels) were identified with the variant caller GATK HaplotypeCaller (GATK 3.8.0) [48,49] using default settings. Variant discovery with GATK HaplotypeCaller was performed separately for each individual and then a variant set for the whole population was obtained by jointly genotyping all individuals at the variant sites with GATK GenotypeGVCFs. We retained all biallelic variants for further analyses with VCFtools [50].

Variants were annotated using Ensembl Variant Effect Predictor (Ensembl VEP; version 104, September 2021) [51] using the RefSeq transcript databases. For variants with multiple predicted consequence types (e.g., in the case of multiple transcripts), the variant was annotated with the most severe predicted consequence type. Stop-gain, start-loss, stop-loss, splice donor, splice acceptor, and frameshift indel variants were classified as loss-of-function variants. Loss-of-function variants together with in-frame indels and missense variants were considered as

putatively deleterious.

2.4. Genetic variation

For the analysis of the transitions-to-transversions ratio (Ti/Tv), nucleotide diversity (π) and Tajima's D [52] we used all called variants to avoid biases caused by the alteration of the allele frequency spectrum. These parameters were calculated using VCFtools using non-overlapping windows of 10 kb for π and Tajima's D. We calculated the fixation index (F_{ST}) between both populations using Weir and Cockerham's weighted estimator [53] in the same 10-kb windows.

2.5. LD decay, inbreeding and runs of homozygosity

We estimated the linkage disequilibrium (LD) decay in each population using PopLDdecay software (https://github.com/hewm2008/PopLDdecay; [54]) with default settings. We estimated the heterozygosity and inbreeding coefficient (F_{IS}) [55] based on the homozygosity rate of each individual, using the method-of-moments implemented in the *--het* function in PLINK 1.9 [56]. For the detection of runs of homozygosity (ROH) we only used variants with minor allele frequency (MAF) $\geq$ 0.05 across both populations because the extremely high variant density and the large number of rare variants that arise from whole-genome sequencing hinder the detection of ROH. In these analyses, we used the *--homozyg* function in PLINK 1.9 with the parameters to define the ROH segments as proposed by Ceballos et al. [57] for whole-genome sequence data; that is: *--homozyg-snp 50 --homozyg-kb 300 --homozyg-density 50 --homozyg-gap 1000 --homozyg-window-snp 50 --homozyg-window-het 5 --homozyg-window-missing 5 --homozyg-window-threshold 0.05*. Ceballos et al. [57] demonstrated that for ROH analysis to produce similar results with whole-genome sequence data than in marker arrays, a larger number of heterozygous sites must be allowed. With *--homozyg-window-het 5* (as recommended by Ceballos et al. [57]), we observed no ROH. This is likely caused by a much greater density of heterozygous variants in our population (1 per 0.55 kb) than in Ceballos et al. [57] (1 per 1.1 kb in whole-genome sequence data, as opposed to 1 per 7.1 kb in marker array data). Thus, we allowed for an even greater number of heterozygous sites by setting *--homozyg-window-het 10* or *15*. Given the limitation in defining ROH in a standard way with whole-genome sequence data, we considered the ROH-based metrics as relative measures to compare both populations rather than absolute measures. Inbreeding based on the ROH (F_{ROH}) was calculated as the sum of the lengths of ROH relative to the total length of the genome.

2.6. Population structure

For ease of performing and interpreting the analyses of the population structure, we preselected a subset of variants that could be similar to the high-density marker arrays that are available in other avian species. We filtered out variants with MAF $<$ 0.05 across both populations and we pruned variants based on LD with a restrictive threshold set to $r^2 =$ 0.25 using the *--indep-pairwise* function in PLINK 1.9 [56] with windows of 10 Mb to account for long-range linkage disequilibrium shifted by 2000 variants in each step. A total of 473,991 variants remained.

To investigate the population structure, we performed a principal component analysis (PCA) with the *--pca* function in PLINK 1.9 [56]. The scores of the samples for the first principal components, together with the eigenvalues of the principal components, were computed. We also performed an analysis of individual ancestry using the software Admixture 1.3.0 [58]. We considered a number of subpopulations of K = 2. We identified the most appropriate number of subpopulations by calculating the cross-validation error with different values of K.

2.7. Detection of selective sweeps

The extended haplotype homozygosity (EHH) measures the reduction in haplotype diversity as the probability that two extended haplotypes around a given locus are identical given that they have the same allele at the locus. The EHH statistic can be used to recognize signals of positive selection from polymorphism data [59]. We phased the genotype for each population separately using fastPHASE software [60] with default settings, using 4,490,694 variants that were retained after LD-based pruning with a threshold of $r^2 = 0.8$ (with windows of 10 Mb shifted by 2000 variants in each step as described above). We then used the *rehh* R package [61] to calculate the change in site-specific EHH between the wild and farm-reared populations as a standardized score of the ratio of integrated normalized site-specific EHH (Rsb) [62,63]. The Rsb test assumes that a selective sweep occurred in only one of the two compared populations. A positive Rsb value is indicative of a higher level of site-specific EHH in the wild compared to the farm-reared population, whereas a negative value represents decreased site-specific EHH in the wild compared to the farm-reared population. We performed these analyses with the default parameters of the *rehh* package. We considered values of Rsb with an associated *p*-value $\leq 10^{-8}$ as significant, which corresponded to values of approximately $|\text{Rsb}| \geq$ 5.7. Genomic regions that included flanks of 100 kb around each significant variant were considered and searched for candidate genes. Any overlapping genomic regions that arose from individual significant variants were merged. Genomic regions with multiple variants with significant Rsb (minimum with 15 variants spanning 300 kb, including the 100-kb flanks) were prioritized for the analysis of their functional annotation.

2.8. Functional annotation of genes in relevant regions

The Ensembl release 108 database was used to investigate candidate genes in relevant genomic regions. For this, the BioMart tool was used to extract annotated genes in the Japanese quail and chicken reference genomes (coturnix_japonica_2.0 and GRCg7b, respectively). The list of gene symbols was used to catalogue the genes according to their annotated functionality. Gene ontology (GO), KEGG pathway and gene expression network enrichment was assessed with DAVID Bioinformatics Resources 6.8 (https://david.ncifcrf.gov/; [64]), KOBAS (http://kobas.cbi.pku.edu.cn/kobas3; [65]) and Enrichr (https://maayanlab.cloud/Enrichr/; [66]).

3. Results

3.1. Sequencing data and genetic variation

After removing duplicate reads, whole-genome sequencing of the 60 partridges produced an average of 109.24 M (33.37 M SD) read-pairs per individual. After alignment, an average of 71.61% (2.92% SD) of bases were aligned to the reference genome of the Japanese quail and passed quality filters (see Table S1 for details), which resulted in an average depth of 18.4× (4.3× SD; range: 12.7 to 28.0×). Sequencing depth did not differ between wild and farm-reared partridge samples. Individual statistics for each of the 60 partridge samples sequenced are shown in Table S1.

We identified a very large number of biallelic variants across the two populations, adding up to a total of 13,845,259 SNPs and 4,600,748 indels in the sequenced individuals. The Ti/Tv ratio was 2.35. The average nucleotide diversity π was very similar in both populations (wild: 0.0024; farm-reared: 0.0025; Fig. 1A). However, the average Tajima's D was lower in the farm-reared population than in the wild population (wild: −0.06; farm-reared: −0.44; Fig. 1B). The weighted F_{ST} between both populations was on average 0.05 (0.04 SD) (Fig. 1C). Some 10-kb windows at the extremes of the chromosomes showed much higher F_{ST} values than the rest of the genome. This was likely due to inaccuracies in the assembly of the chromosome extremes. Except for this, we did not find evidence of 10-kb windows deviating significantly from the average per-window π, Tajima's D or F_{ST} along the genome.

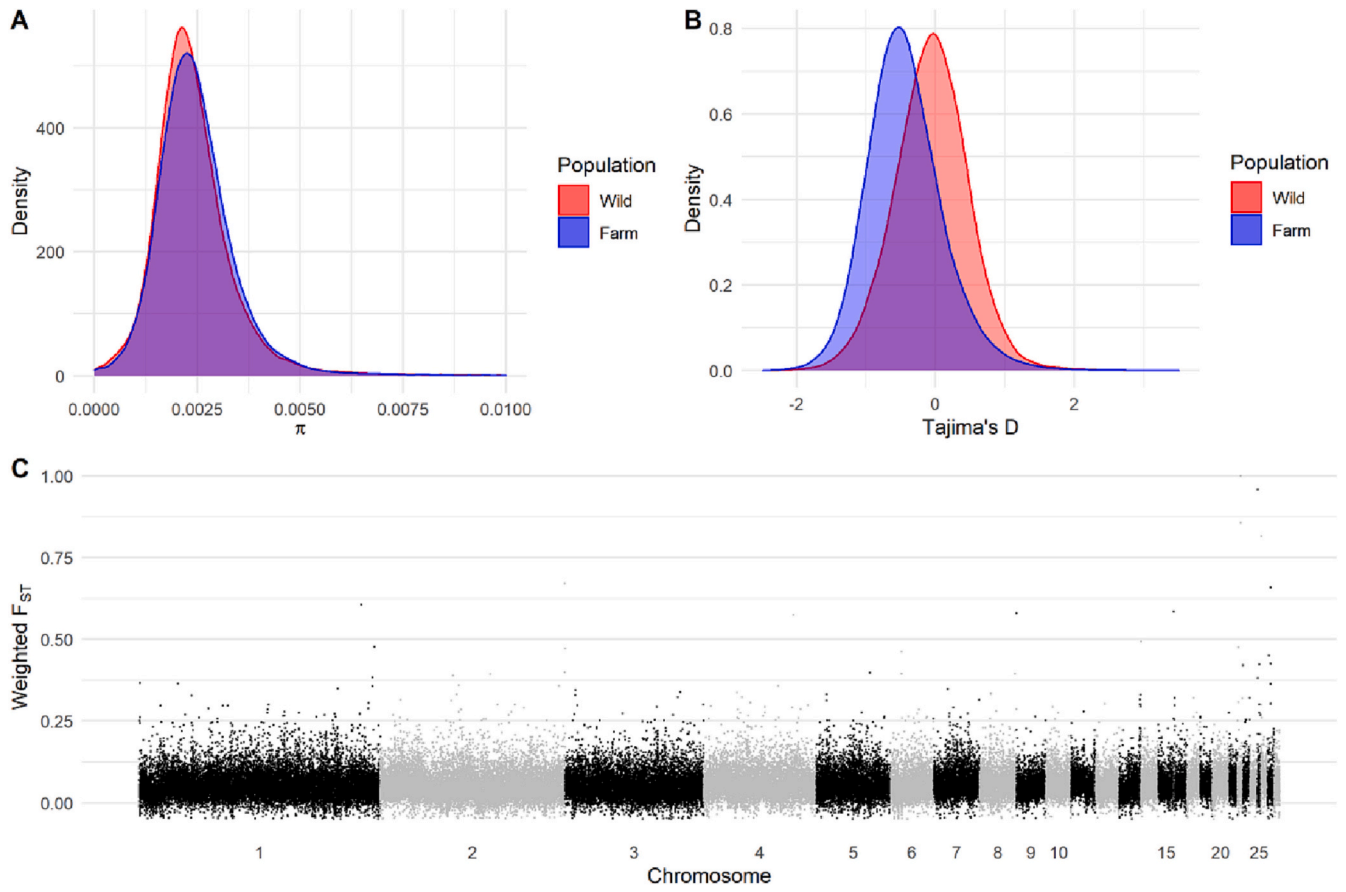

Fig. 1. Distribution of (A) nucleotide diversity (π) and (B) Tajima's D estimates; and (C) weighted F_{ST} between wild and farm-reared populations. In panel C, the alternation of black and grey colours indicates the transition between chromosomes (shorter chromosomes may be unlabelled).

We also identified a large number of common variants, as 6,095,574 SNPs and 2,297,758 indels had MAF $\geq$ 0.05 across the two populations. Of these, we identified 5,605,893 SNPs and 2,085,602 indels in the wild population and 5,740,946 SNPs and 2,136,834 indels in the farm-reared population. A large proportion of the common variants were identified in both populations (5,251,265 SNPs and 1,924,678 indels) and the rest were found to be population-specific (wild: 354,628 SNPs and 160,924 indels; farm-reared: 489,681 SNPs and 212,156 indels). Most variants were either intergenic or intronic. The farm-reared population had a larger fraction of exonic SNPs, particularly with missense and splicing consequences (Table 1), but also synonymous SNPs or in potentially regulatory regions, such as untranslated regions (UTR). In contrast, the fractions of loss-of-function variants, including frameshift indels, and in-frame indels was very similar in both populations.

3.2. LD decay, inbreeding and runs of homozygosity

The wild population had lower LD levels and faster LD decay than the farm-reared population (Fig. 2). Both populations had similar heterozygosity rate estimates but the wild population was significantly more inbred than the farm-reared population (higher F_{IS}; Welch's *t*-test: $p < 0.001$; Table 2). The detection of ROH was very sensitive to the number of heterozygous sites that were allowed within a ROH segment [57]. When 10 heterozygous sites were allowed, a few ROH segments were detected in the farm-reared population but almost none in the wild population. However, when 15 heterozygous sites were allowed, the wild population had more ROH segments than the farm-reared population (Welch's *t*-test: $p < 0.001$; Table 2), although of a similar average length ($p = 0.143$). This resulted in a greater F_{ROH} for the wild population compared to the farm-reared population ($p < 0.001$). Thus, F_{ROH} and F_{IS} consistently showed higher inbreeding in the wild population than in the farm-reared population, although F_{ROH} estimated from the ROH segments was of much lower magnitude than the F_{IS} estimated from the heterozygosity rate. In addition to the number of heterozygous sites allowed per ROH segment, the detection of ROH segments is very sensitive to the parameters used to define them and to the filtering of variants based on MAF or linkage disequilibrium [67,68]. This makes ROH detection challenging in whole-genome sequencing data. Our ROH estimates from whole-genome sequence data, which used all called variants with MAF $\geq$ 0.05, should be interpreted with caution due to the lack of reference values.

3.3. Population structure

The wild and farm-reared populations could be clearly distinguished at the genetic level. Principal component analysis results are shown in Fig. 3. The first principal component (PC1; 3.0% of variance) captured variation between the wild and farm-reared populations in a way that PC1 scores allowed the correct clustering of samples of each population. The second principal component (PC2; 1.8% of variance) captured mostly variation within the populations, mainly the wild population.

Admixture analysis confirmed the findings from PCA. When the number of subpopulations was defined as K = 2, all samples were correctly assigned to the cluster that corresponded to their population of origin (Fig. 4). Admixture analysis showed little common ancestry between the wild and farm-reared populations. The contribution of common ancestry between wild and farm-reared populations was very variable across individuals, but on average it was larger in the farm-reared partridges, reaching 0.47 in one sample. The number of subpopulations was supported by the observation that the minimum cross-

Table 1
Main predicted consequences of the variants called in wild and farm-reared red-legged partridge populations.

Predicted consequence	Wild population		Farm-reared population	
	Number of variants	Percentage of variants (%)	Number of variants	Percentage of variants (%)
Loss-of-function	11,085	0.144	11,307	0.144
Splice acceptor/ donor	1372	0.018	1394	0.018
Stop-gain	921	0.012	940	0.012
Stop-loss	80	0.001	82	0.001
Start-loss	192	0.002	192	0.002
Frameshift indels	8520	0.111	8699	0.110
In-frame indels	2395	0.031	2421	0.031
Missense	33,564	0.436	34,793	0.442
Protein-altering variant	299	0.004	298	0.004
Splice region	13,533	0.176	14,146	0.180
Stop retained	55	0.001	56	0.001
Synonymous	51,695	0.672	53,791	0.683
Coding sequence variant	51	0.001	54	0.001
Untranslated regions (UTR)	38,843	0.505	40,141	0.510
5' UTR	25,283	0.329	26,271	0.333
3' UTR	13,560	0.176	13,870	0.176
Non-coding transcript exon	44,742	0.582	45,827	0.582
Intronic	3,885,935	50.522	3,989,906	50.648
Upstream	573,112	7.451	588,666	7.472
Downstream	421,295	5.451	432,383	5.489
Intergenic	2,614,891	33.997	2,663,991	33.817
Total	7,691,495	–	7,877,780	–

validation errors were achieved with K = 1 (0.89) and K = 2 (0.90). Increasing the number of subpopulations did not reflect any stratification within populations and increased cross-validation error (K = 3: 1.09; K = 4: 1.28).

3.4. Selective sweeps

We identified 4621 variants with an Rsb with an associated *p*-value lower than 10^{-8} (equivalent to Rsb scores with absolute value from 5.7 to 19.0; Fig. 5). These variants belonged to 1053 distinct genomic regions (Table S2). There were more genomic regions with negative Rsb (839 regions) than with positive Rsb (214 regions). That is, increased site-specific EHH in the farm-reared compared to the wild population was more common than increased site-specific EHH in the wild compared to the farm-reared population. This imbalance suggests stronger directional selection in the farm-reared population than in the wild population.

To investigate genes potentially affected by selection due to captivity, we selected 13 genomic regions (516 variants) that contained at least 15 variants with significant Rsb spanning at least 300 kb (including flanks). All these genomic regions had negative Rsb and contained at least one variant with Rsb < -8.2 and $-\log(p\text{-value}) > 15.8$ (Table 3). In three instances, genomic regions that were very closely located were manually merged into 3 genomic regions, resulting in a total of 7 genomic regions for further analyses. The region with the largest number of SNPs was on chromosome 2 (72.9–75.4 Mb) and held 218 variants. The median nucleotide diversity π was lower in the genomic regions with extreme Rsb values (wild: 0.0021; farm-reared: 0.0021) than in the rest of the genome (wild: 0.0023; farm-reared: 0.0024).

A total of 92 gene features were identified across the 7 genomic regions. However, gene names were only annotated for 69 of these gene features using Japanese quail or chicken genome information (Table S3 and S4). First, in order to have a general vision of the genes in the relevant genomic regions, clusters of genes from common families, functions or protein domains were generated with DAVID (Table S5). From the 11 clusters of genes generated with our data, it is worth highlighting clusters related to brain development (annotation cluster 1); calcium transport (annotation cluster 2); mitochondrial respiratory complex and function (annotation cluster 4); and extracellular space signalling (annotation cluster 9) and structure (annotation cluster 7). The study of GO terms helped us identify genes related to additional processes related to brain development, including sleep, and signalling members of extracellular exosomes (Table S6). When the representation of KEGG pathways was tested, several clusters of pathways showed to be affected by the genes on the Rsb region (Fig. S1; Table S7), related to carbohydrate and protein metabolism, mineral absorption, immune response and cytochrome P450 activity. In addition, as anticipated by GO results, the cell adherence junctions and citrate cycle pathways were also identified.

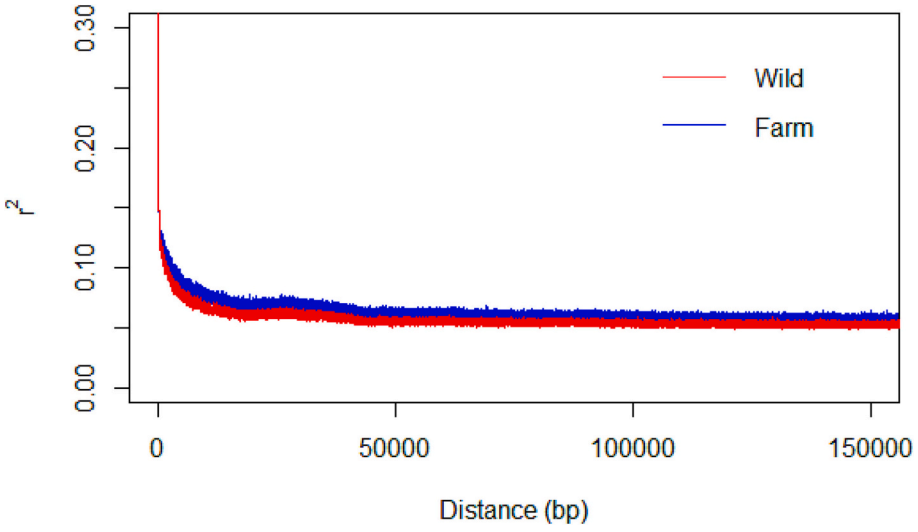

Fig. 2. Linkage disequilibrium (r^2) decay in wild and farm-reared populations.

Table 2
Heterozygosity and inbreeding coefficients based on homozygosity (F_{IS}) or runs of homozygosity (F_{ROH}).

Parameter	Population		Welch's *t*-test *p*-value
	Wild	Farm-reared	
Heterozygosity	0.211 (0.002)	0.214 (0.003)	<0.001
F_{IS}	0.378 (0.006)	0.370 (0.009)	<0.001
ROH with *--homozyg-window-het 10*			
F_{ROH}	0.000 (0.000)	0.003 (0.002)	<0.001
Number of segments	0.1 (0.3)	6.8 (4.8)	<0.001
Segment length (kb)	40.5 (124.3)	373.4 (33.3)	<0.001
ROH with *--homozyg-window-het 15*			
F_{ROH}	0.056 (0.015)	0.034 (0.010)	<0.001
Number of segments	118.6 (29.6)	71.3 (19.5)	<0.001
Segment length (kb)	392.3 (13.7)	398.1 (16.5)	0.143

Standard deviation (SD) is shown in parentheses.

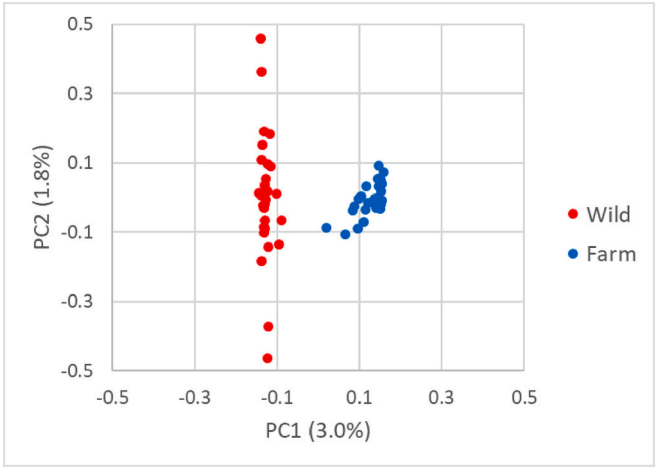

Fig. 3. Population structure according to principal component analysis. Within parenthesis, percentage of variance accounted by the first two principal components (PC1 and PC2).

4. Discussion

Our study examined the genome of wild and farm-reared red-legged partridges to assess the genomic diversity and inbreeding of wild and farm-reared populations and to reveal molecular signals of selection processes.

4.1. Origin and management of the farm-reared partridges

Four species of the *Alectoris* genus coexist in the Mediterranean region [69,70]. The first farm-reared red-legged partridges were originated through crosses between various species of *Alectoris* by French and Italian breeders, mainly by crossing the red-legged partridge (*A. rufa*) with the chukar partridge (*A. chukar*), which was domesticated in China [7,71–73]. The farm-reared population that we studied was founded in 1978 with approximately 100 breeding pairs derived from those hybrid partridges and accumulates approximately 60 generations of breeding.

Farm-reared partridges had a more negative Tajima's D than wild partridges [74], which is compatible with directional selection, purifying selection or population expansion after a bottleneck. Farm-reared partridges also had more and longer regions of EHH than wild partridges, which is also compatible with directional artificial selection. In contrast, despite the different demographic histories of the wild and farm-reared populations, both populations had a similar nucleotide diversity and we observed higher inbreeding coefficients in wild partridges. Thus, the demographic bottleneck and artificial selection reflected by selective sweeps did not result in an apparent loss of genetic diversity in these farm-reared partridges.

The lack of loss of genetic diversity in these farm-reared partridges is not straightforward to reconcile with expectations from a captive population that has suffered a severe bottleneck and artificial directional selection. However, our hypothesis is that this observation in farm-reared partridges is caused by the interplay of low selection intensity [75,76], the expansion in number of breeding pairs since foundation of

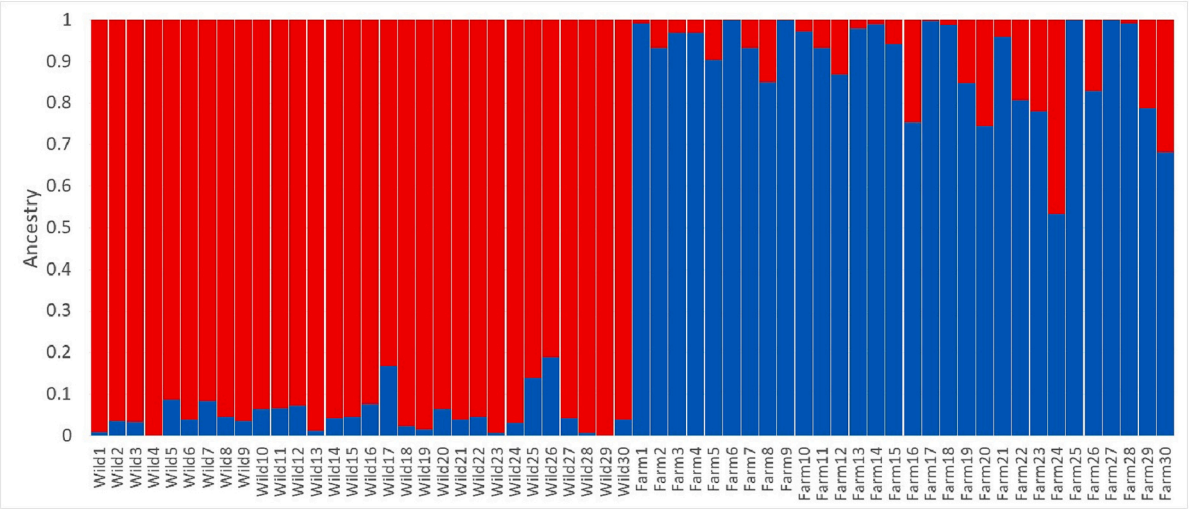

Fig. 4. Population structure according to admixture analysis (K = 2).

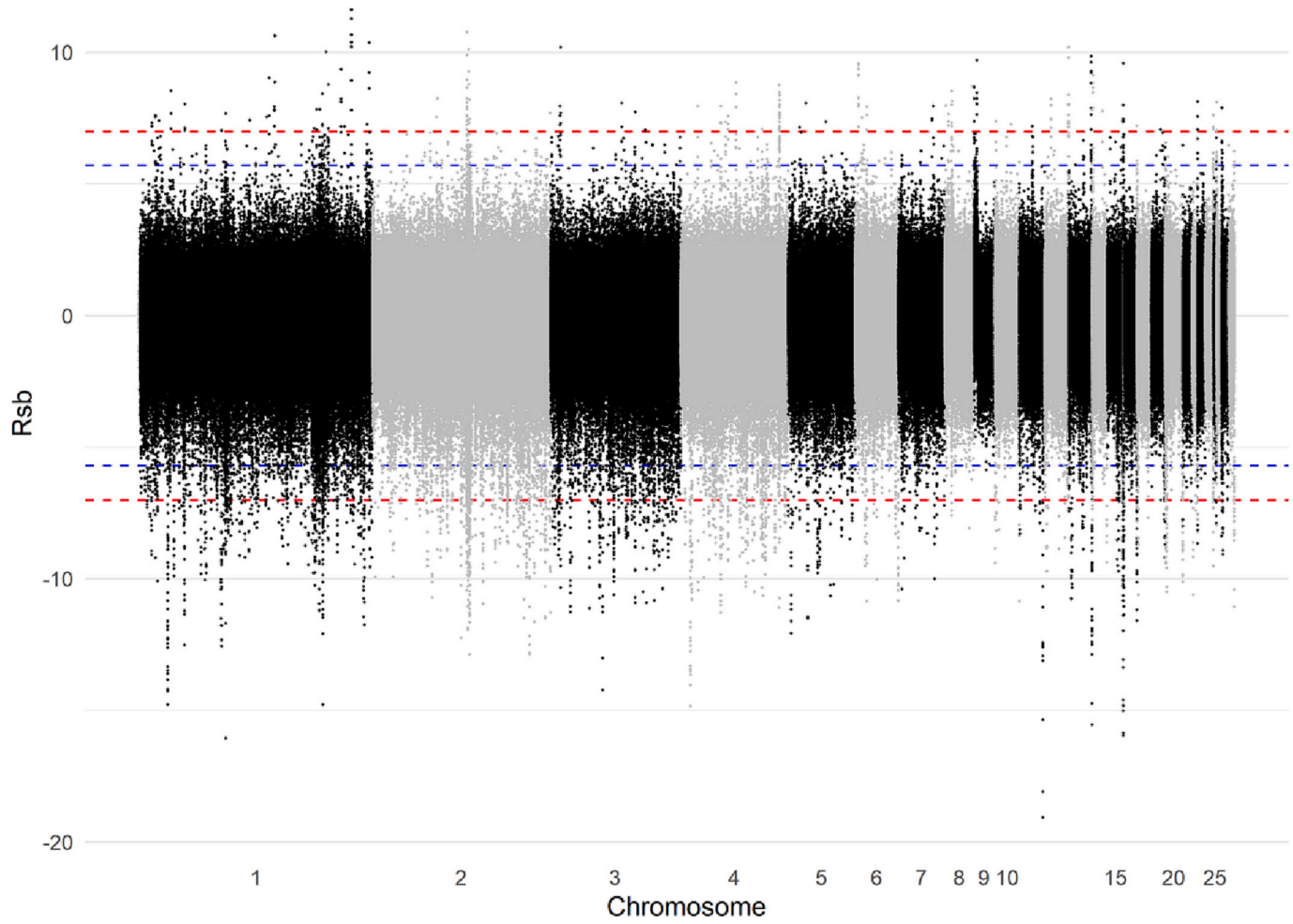

Fig. 5. Rsb estimates across the partridge genome. Blue and red dashed lines indicate |Rsb| scores of 5.7 (p-value $\leq 10^{-8}$) and 7.0 (p-value $\leq 10^{-9}$), respectively. The alternation of black and grey colours indicates the transition between chromosomes (shorter chromosomes may be unlabelled). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3
Relevant genomic regions according to the number of significant SNP variants, most extreme Rsb value and its significance level (−log(p-value)).

Region	Chromosome	Start position (bp)	End position (bp)	Length (bp)	Number of significant SNPs	Most extreme Rsb value	–log(p-value)
1a	1	67,563,742	67,908,277	344,535	24	−9.0	18.6
1b	1	67,843,659	68,318,362	474,703	22	−16.0	57.2
1c	1	69,849,036	70,158,960	309,924	18	−8.3	15.8
2a	1	139,203,197	139,852,206	649,009	40	−11.2	28.4
2b	1	141,703,524	142,081,857	378,333	25	−8.5	16.8
2c	1	142,145,766	142,629,451	483,685	43	−14.8	48.7
3a	2	72,942,670	73,359,094	416,424	31	−10.4	24.8
3b	2	73,931,050	74,361,175	430,125	29	−11.9	32.1
3c	2	74,512,615	75,358,021	845,406	158	−12.9	37.2
4	15	11,244,425	11,697,260	452,835	53	−16.0	56.6
5	19	8,386,010	8,760,791	374,781	23	−9.2	19.4
6	20	1,163,156	1,561,436	398,280	31	−9.4	20.3
7	24	5,106,090	5,425,660	319,570	19	−9.5	20.7

the population (to >20,000 breeding pairs) [77–79], and the contribution of crosses from diverse gene pools [80]. In the farm, the replacement cycle lasts 3 years and 40% of males and 25% of females are replaced in every cycle. Nonetheless, selection intensity is low. Females are removed mainly because of reduced egg laying, while males are removed mainly because of lack of spurs or aggressive behaviour. The replacements are derived from crosses between farm-reared females and males that are captured from wild populations that have received farm-reared partridge population reinforcements, and selected based on body size and feathering condition. Additionally, there have been recurrent introductions of individuals from other captive populations (20–30% of breeding pairs every replacement cycle) and occasional introductions of wild males (1% of breeding pairs every 1 or 2 replacement cycles, with a selection intensity of 70%) and, rarely, wild females. Theoretical models indicate that continually introducing wild individuals into captive populations does not eliminate the negative effect that releasing farm-reared individuals has on the fitness of wild populations [19,81]. In contrast, the estimated number of breeding pairs in the studied wild

population is of <1000 [43].

4.2. Genomic diversity and inbreeding

The Ti/Tv ratio was close to the generally expected values for whole-genome sequencing assuming spontaneous and neutral mutations [82]. We included 13,845,259 SNPs and 4,600,748 indels to calculate nucleotide diversity (π), which was similar in both populations, albeit slightly higher in farm-reared than in wild partridges. Conversely, wild Japanese quails have a higher π than domestic populations [30]. In mallards, π is higher [27,83] or even doubles [29,84] that of farm-reared ducks. The higher π values in wild species with respect to domestic populations seems to be a common feature in vertebrate species (red jungle fowl vs indigenous chickens and broilers [24,85–87]; wild vs domestic mice [88]; wild boars vs domestic pig [89]; wild vs farm-reared wels catfish [90]). Our π estimates (wild: 0.0024; farm-reared: 0.0025) were similar to those reported in *A. chukar* (range: 0.0010–0.0033; [6]) and *Perdix perdix* (range: 0–0.003; [91]) using mitochondrial markers, but much lower than reported in other modern *A. rufa* populations (range: 0.09–0.71; [92]), also using mitochondrial markers. This marked difference may arise from the use of whole-genome sequencing and the large proportion of rare variants in such data. It has been pointed out that estimation of π using whole-genome sequence data from VCF files can result in substantial downward bias if missing genotypes are considered as homozygous for the reference allele [88,93]. However, although this could affect our π estimates, the bias should equally affect the wild and farm-reared populations and the comparison between both populations should be valid.

Our results showed that wild and farm-reared partridges differ at the genomic level. The PCA and the admixture analysis confirmed the structure between the two groups, similarly to results found when comparing populations of wild red jungle fowl [86], bobwhite [81], pheasant [94], Guinea fowl [95] and mallard [84] with individuals bred in captivity. These analyses have also made it possible to differentiate between wild and domestic roosters [23], wild and domestic ducks [83], and between different lineages of domestic bird and mammal species. Wild partridges showed lower proportions of ancestry from farm-reared partridges than farm-reared partridges did from wild partridges. Two wild partridges (6.6%) and five farm-reared partridges (16.6%) did not show common ancestry with the opposite group. These results are consistent with the observations by Forcina et al. [69] using 168,000 genetic markers across samples of *A. rufa* and *A. chukar* from diverse geographical locations, which showed little loss of genetic diversity in *A. rufa* and limited and spatially uneven introgression from chukar partridges.

Tajima's D was close to neutrality in wild partridges and negative in farm-reared partridges. Tajima's D values of zero indicate that a population is in mutation-drift equilibrium, while positive values indicate a scarcity of rare alleles compatible with balancing selection or sudden population contraction, and negative values indicate an excess of rare alleles compatible with directional selection, purifying selection or population expansion after a bottleneck [52]. Tajima's D values reported in other wild and domestic bird species are very variable, from large differences between red jungle fowl (mostly positive values; [86]) and domestic indigenous chicken breeds (mixed negative and positive values; [86,96]), but opposite results in wild (negative values) and domestic (positive values) quails [30]. Positive values have also been detected for other wild bird populations, with its magnitude being larger for populations in decline, such as brown eared pheasants (2.3), than for stable populations, such as blue eared pheasants (0.7) [97]. Our Tajima's D estimates, which were more negative Tajima's D in the farm-reared (−0.44) than in the wild population (−0.06), are compatible with directional selection in the farm-reared population. The more neutral value for the wild population would indicate stability for the wild population and temper the concerns about their possible decline [43].

Farm-reared partridges showed more sequence variants than wild partridges. In farm-reared partridges, we detected 1477 more variants with predicted deleterious consequences in coded proteins (loss-of-function, in-frame indels and missense variants; Table 1) than in wild partridges. In this context, “deleterious” could mean “not generally tolerated in the wild” but these variants could otherwise be beneficial (and therefore favoured by selection processes) in a domesticated setting [98]. In domestic livestock populations, the average number of deleterious alleles carried per individual has been reported to be greater than in wild populations [99]. Similar results have been reported in chickens and pigs [98], yaks [100], dogs [101], as well as in crop species such as rice [102] and sunflower [103]. The accumulation of predicted deleterious variants in the domestic partridges is consistent with the ‘cost of domestication’ hypothesis [104] but also with the multiple crosses between diverse gene pools between the farm-reared partridges [75].

Despite being bred in captivity, farm-reared partridges also had lower inbreeding estimates, both F_{IS} and F_{ROH}, than wild partridges. Fewer ROH segments in farm-reared partridges than in wild partridges confirm the absence of recent inbreeding in the farm-reared partridges and reflect the contribution of multiple gene pools to the genome of farm-reared partridges and the larger number of breeding pairs in the farm-reared population [105].

We advise caution when interpreting population genetic parameters using high-density whole-genome sequence data. The population genetic parameters are very sensitive to data structure (e.g., allele frequency spectrum biased towards rare variants) and pitfalls can arise for some population genetic parameters, such as π [88,93] or ROH [57] as pinpointed here, if they are calculated without suitable adjustments in their assumptions and settings or filtering of variants, which are not well-established yet.

4.3. Selective sweeps

Selection has imprinted genetic signals that are distinct between the two partridge populations in the form of selective sweeps [106]. While F_{ST}, which targets differences in allele frequencies between populations, did not capture any noticeable selective sweep in our study, Rsb, which incorporates linkage information and targets differences in haplotype frequencies, was a more successful approach. We observed a higher number and longer regions with negative Rsb than with positive Rsb, which indicates more and longer regions of EHH in the farm-reared than in the wild partridges. This result is consistent with a greater selection pressure in the farm-reared partridges than in the wild partridges as a consequence of artificial selection. The Rsb patterns across the genome reflected how artificial selection in farm-reared partridges has putatively acted on a different set of genes [107–109].

The largest selective sweep was detected in chromosome 2 at 72.9–75.3 Mb. This genomic region held a large number of variants with negative Rsb (218 variants). Two genes in this region (*IGFBP1* and *IGFBP3*) have been associated with embryonic, post-hatch growth [110] and body weight at 10 weeks of age [111] in broilers. Variants in a third gene in this region have been related to patterns of vocal learning in songbirds [112], mice, and humans (*CNTNAP2*). The role of these three genes is consistent with the less developed motor function of farm-reared partridges and the behavioural differences between farm-reared and wild populations.

Several genes located close to or within the region of chromosome 1 at 67.6–70.2 Mb are related to reproductive success, with functions related to egg development and mineralisation (*PTHLH* and *TRPV6*) or sperm capacitation (*TRPV6*) [113,114] For instance, the parathyroid hormone-like hormone (*PTHLH*) gene is a potent calcium regulator that stimulates the proliferation of follicular granulosa and theca cells and the production of progesterone in pre-hierarchal follicles. In hens, variants in this gene lower the age at first laying and increase the number of eggs laid at 32 weeks [115]. Also of interest are several genes related to feather budding (*PCDH19* [116] in region 2) and colour dilution like *ASIP* [117], in region 6, and *BCO2* [118] in region 7. The latter encodes

for a beta-carotene oxigenase whose activity also colours the skin and bill of different birds. Evolution of pigmentation traits from wild to domestic type is one of the most striking changes during domestication. In chicken, this gene represents a well-characterised genetic sweep occurring during the domestication process and that is responsible for the white skin of most modern breeds [85]. Feather colouring is a vital part of adaptation to the environment, as it is visual sharpness and adequate taste buds. In this sense, mutations in *PITPNM3* (region 5) cause retinal con dystrophy in several species. The action of the bitter taste receptors, such as *TAS2R40* in region 1, is essential for diet selection as many toxins are characterised by a bitter taste. Selective breeding has changed the bitter taste receptor repertoire in modern chicken breeds [119].

4.4. Conclusion

The demographic histories and selection processes have imprinted different genomic signals in the wild and farm-reared partridges. The demographic bottleneck and artificial selection reflected by selective sweeps did not result in an apparent loss of genetic diversity in the farm-reared partridges. The wild partridges are genetically distinct from the farm-reared partridges and although our results temper the concerns about their possible decline, we advise to remain wary of the loss of genetic diversity and increased inbreeding in the Spanish autochthonous wild red-legged partridge populations. The release of even slightly less fitted captive-born individuals to reinforce wild populations typically results in reductions of population sizes and of genetic load, which leads to a reduction of fitness in the long term and can result in the loss of the autochthonous gene pool. The technology to study the signals of selection processes at the genomic level is now more available and affordable than ever. This technology could allow the design of marker panels to genetically characterise populations and guide future decisions for the preservation of wild populations and the appropriate management of the released farm-reared partridges.

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Author statement

R. Ros-Freixedes: Conceptualization, Methodology, Software, Resources, Writing – original draft, Writing - review & editing. **R.N. Pena:** Conceptualization, Methodology, Investigation, Resources, Writing – original draft, Writing - review & editing. **C. Richart:** Funding acquisition. **J. Nadal:** Conceptualization, Methodology, Investigation, Resources, Writing – original draft, Writing - review & editing, Funding acquisition.

Data availability

Sequence reads are available from the Sequence Read Archive of NCBI with accession number PRJNA824288.

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