Is it time for genetic reinforcement of French Iberian ibex populations?

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Highlights

- The Iberian ibex became extinct in the Pyrenees in 2000.
- During the period 2014-2017, 204 Iberian ibex from the Sierra de Guadarrama National Park (central Spain) were released in the French Pyrenees.
- All founders came from the same donor population.
- Despite the high number of founders, the reintroduced populations have low genetic variability.
- Future management actions aimed to reinforce genetic variability in these populations are discussed here.

Abstract

An evolutionary significant unit of the Iberian ibex (*Capra pyrenaica*), the Pyrenean ibex or “bucardo” (*Capra pyrenaica pyrenaica*) became extinct in its natural range, the Pyrenees, at the beginning of the twentieth-first century. Several years later (2014-2021) more than 250 specimens (*C. p. victoriae*) coming from the same donor population from central Spain were released in four localities of the French Pyrenees. Despite an initial fast demographic increase, the genetic variability of these populations remains low. Moreover, it is expected that genetic variability continues to decline due to genetic drift and that inbreeding accumulates. Here we revise options for genetic rescue or reinforcement of these populations involving future

release of animals from different extant Spanish populations, mainly those belonging to the subpecies *C. p. hispanica*. The future hybridization between both phenotypes or "subspecies" may occur anyways in the next years, since currently there is a natural expansion of *C. P. hispanica* populations from the southern Pyrenees (Spanish side).

Keywords: *Capra pyrenaica*, conservation, genetic diversity, management, reintroductions

1. Introduction: the effects of reintroductions in animal genetics

Translocation is a management tool involving the deliberate movement of organisms from one site in another one with the aim to establish self-sustaining populations and/or to improve the conservation status of a population, species or ecosystem. Such actions include both reinforcement and reintroduction within a species or subspecies' indigenous range, and introductions outside indigenous range (IUCN/SSC, 2013). Inbreeding and genetic drift are two processes particularly relevant in reintroduction events because all reintroduced populations experience one or some periods with small population size (bottlenecks) (Keller et al., 2012; Grossen et al., 2018).

Inbreeding depression is caused by mating between relatives leading to a reduction in fitness, survival and resistance to diseases, among other negative consequences. It involves mutations generating deleterious recessive alleles, and is highly variable between species and populations (Keller et al., 2002), traits (Keller et al., 2006), life cycle stages (Husband and Schemske, 1996), environmental conditions (Szulkin and Sheldon, 2007), or even among founder lineages of the same population, since such deleterious recessive alleles seem to be unevenly distributed among individuals (Lacy et al., 1996; Keller et al., 2012).

Random sampling of the gene pool from generation to generation is a source of evolutionary stochasticity. Diverse factors, such as uneven sex-ratios, variation in family size, non-random mating, and inbreeding may result in non-random representation of genomes across generations (Lych et al., 2011). Random genetic drift is the main process involved in loss of genetic variation in small populations (Allendorf and Luikart, 2007; Frankham, 2008; Keller et al., 2012). Genetic drift operates in finite populations and leads to random changes in allele frequencies over generations as each parental allele has a probability of 50% to be passed on the offspring each time it is produced (Frankham et al., 2002). This random variation increases with decreasing population size (Keller et al., 2012) and, in the long term, some alleles may be completely lost. As these changes occur randomly, we can expect that different populations will lose different alleles. Consequently, genetic drift generates loss of genetic variation within populations and increases genetic divergence among populations (Gaggiotti and Couvet, 2004).

To summarise, genetic drift is one of the main drivers of loss of genetic variation and inbreeding can potentially reduce population growth rate and increase the risk of extinction (O’Grady et al., 2006) and, therefore, reintroduction programs have to take into account the effects of both processes. The effective population size (N_e) is the size of an idealized population that would give rise to a similar variance in allele frequencies and inbreeding rate as the studied population (Keller et al., 2012). The magnitude of drift is generally defined by the inverse of the the effective number of gametes sampled per generation - $2Ne$ (Lynch et al., 2011).

Ungulates have been moved around mainly for food and hunting since historic times (Lever, 1985). Translocation and reintroduction programs were carried out worldwide to improve the conservation status of a number of wild Caprinae, which experienced a general decline during last centuries due mainly to over-exploitation and habitat destruction and fragmentation

(Randi, 2005; de Jong et al., 2020). Therefore, the documented consequences of such conservation actions should be taken into account in future projects.

Translocations for restoring extirpated populations may favour the establishment of contact (hybridization) zones between subspecies, as was reported for the northern chamois (*Rupicapra rupicapra*) in the Alps and the Balkan Mountains (Crestanello et al., 2009; Sprem and Buzan, 2016). On the other hand, reintroductions may retain and magnify rare components of genetic diversity. This is the case of a pronghorn antelope (*Antilocapra americana*) population derived from 17 reintroduced specimens in Oregon in 1969. By the beginning of the 21th century, 2 rare alleles of the source population were frequently found in the translocated population (Stephen et al., 2005). Rapid intervention (e.g., population supplementation or reinforcement through translocation) following demographic bottleneck allows genetic restoration of ungulate populations (Poirier et al., 2019). Moreover, translocation management has successfully contributed to the reestablishment of populations not only without diminishing genetic diversity, but also leading to increased allelic richness and heterozygosity compared with indigenous source populations, as reported for bighorn sheep (*Ovis canadensis*) in Arizona (Gille et al., 2019).

Some authors consider that bottlenecks and founder events may be used as synonyms because they produce similar genetic consequences (Maudet et al., 2002; Biebach and Keller, 2009). They evidenced how contemporary Swiss Alpine ibex (*Capra ibex*) populations have lower genetic variation than the ancestral Italian population used for reintroduction and detected genetic drift with each bottleneck event. However, according to these authors, if ibex populations continue to grow and expand, gene flow may increase and override the genetic patterns caused by bottlenecks or founder events.

Translocations of captive-reproduced ungulates are of concern for conserving gene pools of indigenous populations, as captive breeding often includes non-indigenous individuals and/or may produce artificial hybrids (Storfer, 1999; Randi, 2005).

2. The distribution of *Capra pyrenaica* in the Iberian Peninsula over time

Paleontological, archaeozoological and cave paintings evidence the presence of the Iberian ibex throughout the Iberian Peninsula during thousands of years and through the Middle Ages, when they remained abundant. A reconstruction of its range during the XVIth century can be made on the basis of a series of systematic questionnaries implemented in Spain during the reign of Philip II (Ortega Rubio, 1919; Viana et al., 2022) (Figure 1a). During the XIXth and early XXth centuries, the ibex distribution became more and more fragmented (Madoz, 1845-1850; Cabrera, 1911) (Figures 1b-c), mainly as a result of a prolonged hunting pressure and habitat deterioration.

The creation of the Ordesa National Park (nowadays Ordesa y Monte Perdido National Park, Huesca, Spanish Pyrenees) is supposed to be one of the first conservation action involving *C. pyrenaica*, and an opportunity to preserve the Pyrenean ibex or “bucardo”, *C. p. pyrenaica*. But its range and numbers continued to reduce to a point that in mid-1990s several national game reserves particularly focused to this species were created. The creation of these reserves could not prevent the extinction of bucardo, but this fact, together with the increase of vigilance, the absence of predators, a massive human abandonment and forest management favoured the natural expansion of the other ibex “subspecies” during last decades. However, as happened with many other game species, human translocations have strongly influenced the current distribution and status of *C. pyrenaica* (Fandos et al., 2022).

During last years, size of most Iberian ibex populations has increased and, consequently, expanded their range (Figure 1d). In southern Spain this species has colonized new areas (i.e., without previous records of its presence) in Sevilla and Córdoba provinces, and currently occupies a number of available habitats from the sea level to high mountain ranges. The population from the Serranía de Ronda is an exception, as its number has recently decreased because of the impact of sarcoptic mange and the strategy implemented to manage it, based on the elimination of animals ("sanitary vacuum"). Less than 1000 individuals currently inhabit this mountain range, from which Iberian ibex expanded towards the west (Grazalema and Líjar mountain ranges) and the east, occupying the whole mountainous area of the Malaga province. To our knowledge, the population from Tejeda-Almijara has not suffered sarcoptic mange outbreaks and currently has around 2500 effectives. The Sierra Nevada Natural Space (SNNS) harbours the largest population of the southern Iberian Peninsula (Granados et al., 2001) and the most genetically diverse ibex population (Márquez et al., 2020), with a current size near 15000 animals which also extend over adjacent areas (e.g., Sierras de Huétor Natural Park, Sierra de Lújar, Sierra de la Contraviesa, Sierra Alhamilla, Sierra de Gádor, or Desierto de Tabernas, among others). It has been monitored during last 25 years within the context of the Sierra Nevada Global Change Observatory Program, aimed to diagnose the level of exposure and adaptation of its ecosystems and to develop appropriate management solutions (Granados et al., 2020). The nucleus from the Sierras de Cazorla, Segura y Las Villas Natural Park (SCSVNP) was the source of Ibex inhabiting the adjacent mountain ranges of Albacete and Murcia provinces, Sierra Mágina Natural Park, or eastern Sierra Morena, among others, in the Granada and Jaén provinces. After experiencing a severe demographic decline caused by a Sarcoptic mange outbreak in 1985-1988, the SCSVNP actually harbours a stable population ranging from 1800 to 2100 ibex.

Animals from central Sierra Morena expanded to adjacent areas of Jaén and Ciudad Real provinces both naturally and by translocation. This population is very fragmented and mostly reclused in closed (fenced) private terrains (Granados et al., 2001) and currently includes near 1500 animals. The Iberian ibex extends also over most of the mountain ranges of the southeastern Iberian Peninsula, reaching the Sierra de Alcaraz and the Maestrazgo. Some of these nuclei (e.g., Muela de Cortes National Game Reserve) are now affected by the Sarcoptic mange.

From the Tortosa y Beceite National Game Reserve ibex expanded through wide areas of Tarragona, Teruel, and Castellón provinces and, currently, is present in most of the Sistema Ibérico, the whole estimated population over 50000 specimens (García-González et al., 2022). Recently, Antón and Román (2022) reported the presence of ibex in Burgos province. Reintroductions carried out during the 1970s allowed consolidating the ibex population from the Serranía de Cuenca, which became extinct at the beginning of the XXth century. Nowadays, near 500 animals occupy this and surrounding mountain ranges.

The historic presence of the Iberian ibex in the Sierra de Gredos mountain range is known. Animals from this national game reserve were reintroduced in other areas: Batuecas National Game Reserve in 1973 (currently with more than 2000 animals), Riaño since 1991 (over 600 specimens), Posada de Valdeón, or Sierra de Ancares in 1999, or Sierra de Guadarrama National Park, among others.

The Gerês-Xures massif (northern Potugal-southern Galicia, Spain) was the last redoubt for the Cabrera's subspecies *C. p. lusitanica*. The last known individuals disappeared in 1890, but this mountain range was recolonized by 1998 after reintroducing animals from Sierra de Gredos National Game Reserve (*C. p. victoriae*) in Invernadeiro Natural Park, southern Galicia, Spain (Moço et al., 2006). By 2017 near 680 specimens were distributed in 3 nuclei: Serra do Gerês, Serra Amarela and Castro Laboreiro (Fonseca et al., 2017).

Other examples of recent translocations are: Montserrat (actually ca 200 ibex) where 10-20 animals coming from the TBNGR were released during 1995-1996; Cabañeros National Park in which ibex from the SGNGR were introduced in 1995. Ibex coming from SCSVNP were introduced in Bastaras (Huesca province) in 1970. Some individuals escaped from this enclosure and recolonized the Sierra de Guara, near the Pyrenees (Herrero et al., 2013). Also during the 1970s the Montgri massif, near of the coast of Gerona province (northeastern Spain) also received animals from SCSVNP (Table 1). The geographic location of the main populations referred in this section is included in Figure 2.

3. Phylogeny of genus *Capra* and the genetic variability and taxonomy of *C. pyrenaica*

3. 1. Phylogeny of genus Capra

The taxonomy of genus *Capra* is complex and controversial (Manceau et al., 1999b). This is due, at least in part, to the fact that all extant *Capra* species share the same diploid number (2n = 60) and are capable to hybridize each other producing fertile offspring (Schaller, 1977). Groves and Grubb (2011) distinguished three phenetic groups within genus *Capra*: (i) true goats, with sickle-shaped horns, relatively narrow skull, facial profile strongly concave and narrow basicranium, among other features; (ii) markhor, with no precornual convexity, facial profile not markedly concave, broad basicranium and spiral horns; and (iii) ibex, with no spiralled horns, horn base without convexity, or ethmoid fissure narrow, as main morphological characteristics.

Presumably there is only one wild species in the first group: *Capra aegagrus*, and a single species of markhor: *Capra falconeri* (Groves and Grubb, 2011). Some authors (e.g., Ellerman and Morrison-Scott, 1951) assigned all ibex species except the Iberian ibex, *Capra pyrenaica*, and the Daghestan tur, *Capra caucasica*, to a single species: *Capra ibex*. Other authors follow classification of Heptner et al. (1961), who distinguished up to seven species within the ibex group: *C. pyrenaica*, *C. ibex*, *C. cylindricornis*, *C. caucasica*, *C. sibirica*, *C. nubiana* and *C. walie*. Recent classifications (i.e., Corbet, 1978; Valdez, 1985) include *C. sibirica*, *C. nubiana* and *C. walie* into *C. ibex*.

Phylogenetic analysis of two nuclear genes located in the Y-chromosome and cytochrome b sequences revealed two well-defined clades: one of these including the domestic goat (*C. hircus*), the bezoar (*C. aegagrus*) and the markhor (*C. falconeri*), and the other one comprising the remaining wild species (Pidancier et al., 2006). Phylogenetic trees based on the complete mitochondrial genome evidence that *C. pyrenaica* and *C. ibex* are close to each other (Manceau et al., 1999b; Pidancier et al., 2006; Kazanskaya et al., 2007). Ureña et al. (2018) suggested a monophyletic origin of the Alpine ibex and the Iberian ibex, and highlighted the distinctiveness of the bucardo from the remaining Iberian ibex. These authors considered *C. p. pyrenaica* as one of the major clades of wild *Capra* species in western Europe.

We have obtained a maximum likelihood tree (Saitou and Nei, 1987) using the complete mitochondrial sequences from different *Capra* species available in the GenBank® and from *Ammotragus lervia* as outgroup (Figure 3). The best-fit nucleotide substitution model with the lowest BIC (Bayesian Information Criterion) value was chosen using MEGA version 10 (Kumar et al., 2018). Overall, the genetic relationships fitted the species grouping based on morphological features: *Capra hircus* and *C. aegagrus*, as “true” goats, are closely related each other and the same happens with most of the wild species (“ibex”) (Groves and Grubb, 2011). Note that the sequence used for *C. pyrenaica* comes from a specimen from Sierra Nevada Natural Space.

It has been hypothesized that *Capra pyrenaica* evolved from an ancestor related to *C. caucasica* (namely *C. caucasica praepyrenaica*) during the second half of the Upper Pleistocene (Crégut-Bonnoure, 1992). This ancestor would have been originated in the Middle East and, eventually, arrived to the Pyrenees during the Würm III/IV transition (20000-18000 years bp), and differed from and did not have contact with the Alpine ibex (*C. ibex*) (Crégut-Bonnoure, 2009). If there is evidence that the common ancestor of wild goats arose from interspecific hybridization (Ropiquet and Hassanin, 2006), some authors (e.g., Manceau et al., 1999b) suggest that *C. pyrenaica* and *C. ibex* share a monophyletic origin.

3. 2. Genetic variability and taxonomy of C. pyrenaica

Up to five subspecies of *Capra pyrenaica* Schinz, 1838 have been proposed, mainly on the basis on horn size and shape, and fur colour pattern. Cabrera (1911) described *C. pyrenaica lusitanica* Schlegel, 1872 from northern Portugal (now extinct), *C. p. pyrenaica* Schinz, 1838 (from the Pyrenees, also extinct), *C. p. victoriae* Cabrera, 1911 from the Sierra de Gredos, and *C. p. hispanica* Schimper, 1848 from several Mediterranean mountain ranges. Few years later, Camerano (1917) described *C. p. cabrerae* from Sierra Morena. Since one specimen from the Pyrenees was included in the stock used for describing *C. p. hispanica*, Wyrwoll (1999) proposed replacing the name of this subspecies by *C. p. nowaki*.

The four subspecies described by Cabrera were officially recognized by the IUCN (Shackleton, 1997). Nevertheless, such infraspecific classification is not supported by genetic data, instead, different evolutionary significant units (ESUs) (Manceau et al., 1999a; Ureña et al., 2018), and management units (MUs) (Márquez et al., 2020; Barros et al., 2022) were identified. The former *C. p. pyrenaica* (bucardo) population is considered as an ESU (Manceau et al., 1999a; Ureña et al., 2018). Several MUs have been identified; 3 in Andalucía (southern Spain): (i) western, including Sierra de las Nieves NP, Sierra de Grazalema NP and Torcal de Antequera NP, (ii) eastern, including SCSLVNP and SMNP, and (iii) central, including the remaining ones (Márquez et al., 2020). In Cataluña (northeastern Spain) two MUs were identified: (i) TBNGR and Montserrat, and (ii) Montgrí (Barros et al., 2022).

Microsatellite analyses revealed that, at an infraspecific level, genetic divergence (F_{ST}) between *C. p. victoriae* and *C.p. hispanica* ranges between 0.39 and 0.47, evidencing that they are quite different. Moreover, the genetic differences within different *C. p. hispanica* populations reach similar values (Angelone-Alasaad et al., 2017). Practically all the extant Iberian ibex populations, but that from the Sierra Nevada Natural Space (SNNS) evidence recent bottleneck events (Angelone-Alasaad et al., 2017).

Mitochondrial markers (particularly, cytochrome b) have been characterized for a number of Iberian ibex populations (Manceau et al., 1999; Márquez et al., 2020; Granados et al., 2022; Barros et al., 2022). More than 30 haplotypes have been described (Table 2) and the SNNS population harbouring 50% of them shows the highest diversity. Recently, Barros et al. (2022) found up to 14 cyt-b haplotypes in several ibex populations from Cataluña (northeastern Spain). Nevertheless, as they used longer sequences (1140 bp) it is not easy to relate these haplotypes with those described in former studies (Table 2). Diverse cyt-b sequences from *C. pyrenaica* and other wild *Capra* species and *Ammotragus lervia* were obtained from the GenBank® and used to construct a phylogenetic tree (Figure 4). Curiously, the Alpine ibex, *C. ibex*, was closer to *C. p. hispanica* than to the bucardo, but, overall, sequences from both *C. pyrenaica* “subspecies” were clearly separated. The control region (mtDNA) of Iberian ibex coming from a number of Spanish populations was also studied (Manceau et al., 1999). No geographic structuration between the populations analysed was found, and these authors suggested that the proximity of haplotypes does not reflect recent gene flow between populations. Again, the sequences of the bucardo and the Alpine ibex were very close.

Regarding the major histocompatibility complex (MHC), up to seven DRB1 haplotypes have been described, being the SNNS, together with La Sierra National Game Reserve (LSNGR) (*C. p. victoriae*), harbouring up to 4 haplotypes, the populations showing greater diversity. Figure 5 groups the different populations analysed according to the haplotypes they present. Adaptive genes, such as those included in the MHC may better to guide conservation management than neutral markers do (Manlik et al., 2019). Microsatellites have also been studied in *C. pyrenaica*, not only to obtain values of heterozygosity or allelic richness, to quantify genetic distinctiveness, or to find evidence of genetic flow between populations (e.g., Angelone-

Alasaad, 2017; Angelone et al., 2018; Barros et al., 2022), but also to infer DRB1 gene haplotypes of the major histocompatibility complex (Alasaad et al., 2012). We must take into account that one of the consequences of hybridization in the evolutionary past of genus *Capra* is that mtDNA and nuclear genes do not coevolve and acquire different evolutionary histories (Healy and Burton, 2020).

4. The extinction, reintroduction and current status of the Iberian ibex in the French range

The Iberian ibex population inhabiting the Pyrenees, whose specimens were called "bucardos", experienced a demographic expansion approximately 20000 years ago, after which different factors (e.g., exploitation and diseases, among others) led to its decline (Forcina et al., 2021). Numerous remains of *C. p. pyrenaica* dated between the Late Pleistocene and the Holocene (ca. 11700 yr bp) were found, mainly, in southern France and the northern Pyrenees (García-González, 2012). Mainly due to overhuntinhg, but also to high levels of homozygosity, diseases and interspecific competence (García-González and Herrero, 1999),the Iberian ibex disappeared from the French Pyrenees during the mid-19th century, but remained until late 20th century in the Spanish side of the Pyrenees, and became extinct in January 2000 when the last known female died (Pérez et al., 2002). No captive population of the extinct subspecies exists, but cells from skin biopsies of this animal (obtained before it died) were used for cloning this extinct taxon. One morphologically normal bucardo female (genetically identical to the donor cells) was obtained, but died a few minutes after birth (Folch et al., 2009).

In the late 1990s, the re-colonization of the southern Pyrenees (Spanish side) by Iberian ibex (*C. p. hispanica*) began when several specimens escaped from an enclosure in the Sierra y Cañones de Guara Natural Park (SCGNP), northern Spain (Herrero et al., 2013).

Between 2014 and 2021 a total of 254 Iberian ibex were released in five locations of the French Pyrenees: Cauterets, Gèdres and Accous, Pyrenees National Park (PNP), and Cagateille and Massat in the Ariège Regional Natural Park (ARNP) (Garnier et al., 2021) (Figures 6-10). The animals released (belonging to *C. p. victoriae*) came from the Sierra de Guadarrama National Park (SGNP) (central Spain). This population began with the introduction in this site of 67 animals (41 females and 26 males) coming from Gredos National Game Reserve (GNGR) and Batuecas National Game Reserve (BNGR), between 1990 and 1992 (Refoyo et al., 2015). Currently, there are around 540 individuals in the French Pyrenees (340 in PNP and 200 in ARNP).

5. Managing reintroduced populations

Despite genetic issues strongly influences the outcome of translocation actions, we must consider that they interact with other factors which potentially may cause a demographic decline (e.g., habitat loss, poaching, diseases, competence or predation, among others) and that, often, genetic problems arise as a secondary consequence of such primary factors causing this decline (Jamieson and Lacy, 2012).

When planning genetic management of a translocated population we must take into account the sensitivity of methods used for measuring genetic diversity, among other factors, and establish criteria for selecting individuals for translocation (e.g., those with low inbreeding coefficient and high or unique genetic variability), the number of individuals and subsequent translocations needed to assure long-term viability of the population (Groombridge et al., 2012). The choice of individuals is important in determining both the short- and longer-term genetic consequences of a translocation and, therefore, the success of such management actions. Thus, genetic assessment of the founder population is only the first step of a genetic monitoring program to guide future translocations and management of reintroduced populations (El Alqamy et al., 2012).

Small natural populations, and translocated ones as well, may be “genetically rescued” by introducing novel genetic material (e.g., from unrelated individuals from another population) with the aim to mitigate the detrimental effects of inbreeding (Madsen et al., 1999). Despite genetic rescue has evident positive effects leading to an increase of the fitness and viability of the translocated population, it also may produce detrimental effects: swamping of local genetic variation and traits, which would result in genetic replacement of the population, or reduction of the effective population size (N_e), among others (Hedrick and Fedrickson, 2010).

Despite translocated populations may experiment a short-term demographic increase and and this may be coupled with considerable loss of genetic diversity during the establishment phase and beyond, depending on the founder size and population growth rate. Overall, the development of long-term strategies and guidelines would be consistent with a goal of minimizing inbreeding and maintaining genetic diversity in reintroduced populations (Jamieson and Lacy, 2012).

Genetic rescue may also lead to an artificial admixture of evolutionary lineages and/or to homogenize existing diversity and biogeographic patterns, even with detrimental effects on the viability of the endangered population (i.e., outbreeding depression) (Gippoliti et al., 2018). This was the case of a program aimed to “recover” Alpine ibex in the High Tatra mountain range after its local extinction at the end of the nineteenth century. Both Bezoar goats (*Capra hircus*) and Nubian ibex (*Capra nubiana*) were used for restocking such population. Bezoar goats came from Asia minor and it is not clear whether these animals were domestic or wild. This management action led the production of hybrids with intermediate phenotypic features, but their rut period moved to the end of the summer, with the consequent birth of offspring in winter involving their death (Turcek, 1951). The predicted probability of outbreeding depression in crosses between two populations is elevated when populations belong to distinct species, show fixed chromosomal differences, did not exchange genes within the last 500 yr, or inhabit different environments. On the contrary, such probability is low when populations share the same karyotype (belong to the same species) or occupied similar environments (Frankham et al., 2011). In our case, since translocated animals are similar in phenotype, ecology and behaviour to the extinct form (Garnier et al., 2021) this translocation may be considered as an ecological replacement (IUCN/SSC, 2013)

Genetic analyses of all Iberian ibex founders translocated in France were performed (Brambilla et al. 2022). Results show that the four reintroduced nuclei have a low genetic variability (He = 0,345 to 0,353, Ar = 2,383 to 0,353). However, this variability is comparable to that of the source population of individuals transferred (Guadarrama). Despite the current inbreeding rates of the two French nuclei are not alarming, it is susceptible to increase suddenly. This can be avoided by increasing the effective population size ($N_e > 50$) (Quéméré, 2016). In our case, taking into account the genetic structure of Iberian ibex populations, several authors proposed reintroducing animals from the most polymorphic populations or from diverse origins and even “subspecies” to re-establish an ibex population in the French Pyrenees (Manceau et al., 1999; Angelone-Alasaad et al., 2017; Angelone et al., 2018). So, different potential sources become available, since most of the genetically analysed populations have allelic diversity (N_a) and observed heterozygosity (H_o) greater than those shown by the two French nuclei (Table 3). Within this context, animals coming from Tortosa and Beceite National Game Reserve (TBNGR), Maestrazgo and Sierra Nevada would be excellent candidates to achieve it.

Population managers should consider some risks in reinforcement programs. First, diseases not only can compromise the success of reintroductions but also pose a risk to native fauna (Kock et al., 2010). Among the multiple pathogens that ibex can harbour (Pérez et al., 2006), the mite *Sarcoptes scabiei* (which causes sarcoptic mange) raises significant concern because of the potential high mortality rates it can produce in ibex populations (Fandos, 1991).

Second, the risk of gene introgression from the domestic goat is of particular concern since it supposes a threat to the genetic integrity of wild species (Cardoso et al., 2021; Moroni et al., 2022). Finally, taken into account the potential geographic expansion (both natural and unnatural) of ibex, it would be recommended to avoid that *C. pyrenaica* and *C. ibex* become sympatric in the medium-long term in order to prevent hybridization between both species.

6. Conclusions

The bucardo, *Capra pyrenaica pyrenaica*, became extinct from its natural range (i.e., the Pyrenees) in 2000. This meant the disappearance of much more than one "subspecies", since a unique evolutionary significant unit was lost. Recently, the Iberian ibex has re-colonized this mountain range due to both natural and unnatural (translocations) expansion of this species. Since all the animals reintroduced in the French Pyrenees came from the same donor population, the current levels of genetic diversity of these populations are low. Moreover, such levels likely will decrease because of processes such as inbreeding and random genetic drift. If both a genetic restoration program is launched or a natural expansion of ibex from southern Pyrenees (Spanish side) occurs, we expect an hybridization process involving the so called *C. p. victoriae* and *C. p. hispanica* at short-medium term. Such event could allow increasing genetic diversity at short term and produce changes in phenotypic and fitness-related traits of hybrids, but its consequences in terms of adaptation, life history, and evolutionary potential are unknown (Iacolina et al., 2018).

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Figure captions

Figure 1. Historic distribution of *Capra pyrenaica* in the Iberian Peninsula. A: distribution according the topographic reports by the king Philip II between 1574 and 1582 (Ortega Rubio 1918; Viana et al., 2022). B: map based on the Spanish Geographic, Statistics and Historic Dictionary (Madoz, 1845-1850). C: ibex populations reported by Cabrera (1911). D: current distribution (adapted from Castillo-Contreras and Fuentes-Rodríguez, 2022).

Figure 2. Map of the Iberian Peninsula showing the location of the main Iberian ibex populations reported in section 2. BLSX-PGNP: Baixa Limia do Xures Natural Park-Peneda-Gêres National Park; PENP: Picos de Europa National Park; BNGR: Batuecas National Game Reserve; GNGR: Gredos National Game Reserve; SGNP: Sierra de Guadarrama National Park; CNP: Cabañeros National Park; MSM: Sierra Madrona-Sierra Morena; SIN: Sierra de las Nieves; TA: Tejeda-Almijara; SLO: Sierra de Loja; SCON: Sierra de la Contraviesa; SNNS; Sierra Nevada Natural Space; SMNP: Sierra Mágina Natural Park; SCSVNP: Sierras de Cazorla, Segura y Las Villas Natural Park; MCNGR: Muela de Cortes National Game Reserve; SCNP: Serranía de Cuenca Natural Park; ATPN: Alto Tajo Natural Park; TBNGR: Tortosa y Beceite National Game Reserve; PNP: Pyrenees National Park; ARNP: Ariège Reginal Natural Park. In grey, the current distribution of *Capra pyrenaica*.

Figure 3. Maximum likelihood tree using the complete mitochondrial sequence available in GenBank® from different *Capra* species, and *Ammotragus lervia* as outgroup. Nodes indicate Bootstrap values supported by 1000 replicates.

Figure 4. Maximum likelihood tree using the cytochrome b sequences available in GenBank® from different species of the genus *Capra*, and *Ammotragus lervia* as outgroup. Nodes indicate Bootstrap values supported by 1000 replicates.

Figure 5. Similarity of the studied Iberian ibex (*Capra pyrenaica*) populations according to the MHC haplotypes they present (Angelone et al., 2018). B-SF: Batuecas National Game Reserve-Sierra de Francia; LSNGR: La Sierra National Game Reserve; SS: Sierra de Segura; SCSVNP: Sierras de Cazorla, Segura y Las Villas Natural Park; SCNP: Serranía de Cuenca Natural Park; SM: Sierra del Mencal; CNP: Cabañeros National Park; SCON: Sierra de la Contraviesa; ATNP: Alto Tajo Natural Park; SHNP: Sierra de Huétor Natural Park; SL: Sierra de Loja; SNNS: Sierra Nevada Natural Space; STANP: Sierras de Tejeda y Almijara Natural Park; PTBNGR: Puertos de Tortosa y Beceite National Game Reserve. B-SF and LSNGR belong to the so-called *C. p. victoriae*.

Figure 6. Procedence of the animals from the Sierra de Guadarrama National Park (SGNP) used to reintroduction of the species in the French Pyrénées. BNGR: Batuecas National Game Reserve; GNGR: Gredos National Game Reserve; SCGNP: Sierra y Cañones de Guara Natural Park; PNP: Parc National des Pyrénées; ARNP: Ariège Regional Natural Park.

Figure 7. Release of a radio-collared adult male in Cauterets (PNP). Photo by P. Llanes, Parc National des Pyrénées.

Figure 8. Release of marked females and young males in Cauterets (PNP). Photo by P. Llanes, Parc National des Pyrénées.

Figure 9. Group of females and kids acclimatized to their new habitat. Photo by Alexandre Garnier.

Figure 10. Group of males acclimatized to their new habitat. Oldest males show the typical phenotype of *Capra pyrenaica* victoriae, with a large proportion of fur black-coloured. Photo by Alexandre Garnier.

Origin	Destination	Reference	Year	Number and sex of animals
GNGR SCSVNP	PENP	Arenzana, 1964	1957-1962	14
GNGR	Pyrenees	Fandos et al., 2022	≈1960	12
GNGR	BNGR	Fandos et al., 2022	1974-1979	9 ♂♂, 28 ♀♀, 1 kid
GNGR	Riaño	Fandos et al., 2022	≈1980	
GNGR-BNGR	La Pedriza	Fandos et al., 2022	1989-1992	
GNGR	SGNP	Fandos et al., 2022	≈1990	12
BNGR	Invernadeiro	Fandos et al., 2022	1992	30
GNGR	Montes de Toledo	Acevedo et al., 2011	1990-1995	
Riaño	Ancares (León)	Fandos et al., 2022	1992-1995	39
Invernadeiro BL-SXNP	Ancares (Galicia)	Prada and Herrero, 2013	1992-1995	
Riaño	Mampodre	Fandos et al., 2022		
SGNP	PNP ANP	Garnier et al., 2022	2014-2017	58 ♂♂, 91 ♀♀ 39 ♂♂, 56 ♀♀
SGNP	Valle de Arán		2015	11
SGNP	Bajo Pallards	Fandos et al, 2011	2022	
SCSVNP	Madrid Zoo	Fandos et al., 2022	1969 1975	2 2 ♂♂, 4 ♀♀
SCSVNP	Serranía de Cuenca	Fandos et al., 2022	1972 1979	3 ♂♂, 2 ♀♀ 9 ♂♂, 15 ♀♀
SCSVNP	Private properties (Albacete)	Fandos et al., 2022	1974 1975 1979	1 ♂, 2 ♀♀ 7 1 ♂, 1 ♀
SCSVNP	MCNGR	Fandos et al., 2022	1974 1975	52
SCSVNP	Almoraima (Cádiz)	Fandos et al., 2022	1975	16
SCSVNP	Private property (Guadalajara)	Fandos et al., 2022	1975	4
SCSVNP	La Garganta (Ciudad Real)	Fandos et al., 2022	1976	6 ♂♂, 10 ♀♀
SCSVNP	Private properties (Toledo)	Fandos et al., 2022	1976 1976 1977 1977 1980	2 ♀♀ 2 ♂♂, 4 ♀♀ 1 6 ♂♂, 3 ♀♀ 3 ♀♀
SCSVNP	Private properties (Ciudad Real)	Fandos et al., 2022	1976 1978 1979 1979 1980 1980	6 ♂♂, 4 ♀♀ 2 20 ♂♂, 9 ♀♀ 6 1 ♂,3 ♀♀ 4 ♀♀

SCSVNP	Private property (Madrid)	Fandos et al., 2022	1976	1 ♂; 1 ♀
SCSVNP	Bastaras (Huesca)	Fandos et al., 2022	1977 1979 1980	12 ♂♂, 5 ♀♀ 6 ♂♂ 4 ♀♀
SCSVNP	Almonacid Sierra (Zaragoza)	Fandos et al., 2022	1977 1980	4 ♂♂, 2 ♀♀ 4 ♀♀
SCSVNP	Pamplona Zoo	Fandos et al., 2022	1977	3
SCSVNP	San Pedro de Alcántara (Málaga)	Fandos et al., 2022	1978	16
SCSVNP	Montes de Toledo	Fandos et al., 2022	1979	6 ♂♂, 2??
SCSVNP	Private property (Valencia)	Fandos et al., 2022	1979	2 ♂♂, 2 ♀♀
SCSVNP	Montgrí	Fandos et al., 2022		
SNNS	Serranía de Ronda	Fandos et al., 2022	1979	
SNNS	Sierra de Baza	Fandos et al., 2022		
SNNS	SMNP	Fandos et al., 2022	1994	10 ♂♂, 10 ♀♀
SNNS	lmuñécar Zoo	Fandos et al., 2022	1997	1 ♂, 1 ♀
SNNS	Garcipollera (Huesca)	Fandos et al., 2022	1995	2 ♂♂, 1 ♀
SNNS	Cumbres Mayores (Huelva)	Fandos et al., 2022	1995-1997	3
SNNS	Sierra Harana (Granada)	Fandos et al., 2022	1994-1995	5 ♂♂, 1 ♀
SNNS	Sierras de la Región de Murcia	Fandos et al., 2022	2003 2011	19 3 ♂♂; 6 ♀♀
SNNS	Orce	Fandos et al., 2022	2011	3 ♂♂; 6 ♀♀
TBNGR	Monserrat	Fandos et al., 2022	1995-1996	10-20

Table 1. A synopsis of *Capra pyrenaica* translocations events in the Iberian Peninsula. When kown, the number and sex of released animals is incuded. ANP: Ariège Natural Park; BL-SXNP: Baixa Limia-Serra do Xurés Natural Park; BNGR: Batuecas National Game Reserve; GNGR: Gredos National Game Reserve; MCNGR: Muela de Cortes National Game Reserve; PENP: Picos de Europa National Park; PNP: Pyrenees National Park; SGNP: Sierra de Guadarrama National Park; SCSVNP: Sierras de Cazorla, Segura y Las Villas Natural Park; SMNP: Sierra Mágina Natural Park; SNNS: Sierra Nevada Natural Space; TBNGR: Tortosa y Beceite National Game Reserve.

Haplotype	SNI	TA	SNE	SLO	CM	MAE	GBG	MC	MSM
H-1	1	1	1	1	1	1	1	1	1
H-2			1						
H-3			1						
H-4			1						
H-5			1						
H-6			1						
H-7	1								
H-8			1						
H-9			1						
H-10			1						
H-11			1						
H-12			1						
H-13			1						
H-14			1						
H-15			1						
H-16				1					
H-17			1						
H-18			1						
H-19			1						
H-20	1								
H-21	1	1							
H-22	1								
H-23					1				1
H-24					1				
H-25					1				
H-26									1
H-27						1	1		
H-28							1	1	
H-29							1		
H-30							1		
H-31							1	1	
H-32								1	
H-33								1	
H-34							1	1	1
TOTAL	5	2	17	2	4	2	7	6	4

Table 2. Presence of the cytochrome b haplotypes in the Iberian Ibex (*Capra pyrenaica*) populations studied, according to Márquez et al. (2020) and Granados et al. (2022). SIN: Sierra de las Nieves; TA: Tejeda-Almijara; SNE: Sierra Nevada; SLO: Sierra de Loja; CM: Cazorla – Mágina; MAE: Maestrazgo; GBG: Gredos, Batuecas, Guadarrama; MC: Muela de Cortes; MSM: Sierra Madrona, Sierra Morena. Populations of the so-called *C. p. victoriae* remarked in grey.

Population	**n**	**k**	**N_a**	**H_o**	**H_e**	**N_e**	**Reference**
Cautererts (PNP)	48	25	2.56		0.34	38.9	Quéméré, 2016
Ustou (ARNP)	54	25	2.60		0.35	38.9	Quéméré, 2016
TBNGR	102	14	5	0.63	0.57		Barros et al., 2022
Montserrat	21	14	4	0.63	0.63		Barros et al., 2022
Montgrí	8	14	3	0.49	0.35		Barros et al., 2022
GNGR	26	30	2.39	0.36	0.35		Angelone-Alasaad et al., 2017
Maestrazgo	69	30	2.68	0.41	0.43		Angelone-Alasaad et al., 2017
SNNS	238	30	3.25	0.37	0.39		Angelone-Alasaad et al., 2017

Table 3. Data on genetic diversity of different Iberian Ibex populations derived from microsatellites analysis. K: number of loci (microsatellites) characterized; n: number of samples analyzed; N_a: average number of alleles per analyzed locus; H_0: observed heterozigosity; H_e: expected heterozigosity; N_e: population efective number; GNGR: Gredos National Game Reserve, PNP: Pyrenees National Park; ARNP: Ariege Regional Natural Park; SNNS: Sierra Nevada Natural Space; TBNGR: Tortosa y Beceite National Game Reserve.