# Iberian Hare *Lepus granatensis* Rosenhauer, 1856

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## Contents

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## Common Names

| | |
|---|---|
| English | Iberian hare |
| German | Iberischer Hase |
| French | Lièvre Ibérique |
| Spanish | Liebre Ibérica |
| Italian | Lepre iberica |
| Russian | иберийский заяц |

## Taxonomy, Systematics and Paleontology

The Iberian hare, *Lepus granatensis* Rosenhauer, 1856, was historically classified as a variety of the Cape hare, *Lepus capensis*, under subspecies *L. c. granatensis* (Chapman and Flux 1990), but morphological analyses confirmed the validity of the specific status of the Iberian hare, and the distinction from the Cape hare (Palacios 1983). When compared to the other hare species inhabiting the Iberian Peninsula, the interspecific morphological differences also allow their distinction (Palacios 1983). The Iberian hare shows specific characteristics, indicated by the weight, head, body, hind foot, and ear length ranges, being smallest in the Iberian hare, intermediate in the broom hare *L. castroviejoi*, and largest in the European hare *L. europaeus* (Palacios 1989). Also, *L. granatensis* shows a distinctive white pelage on the inner face of the legs, which extends to the upper side and reaches the tip of the toes. The distinction of this species has also been corroborated by molecular analyses based on an increasingly complex set of genetic markers along the years, such as allozymes (Bonhomme et al. 1986), mitochondrial DNA restriction fragment length polymorphisms (Pérez-Suárez et al. 1994), microsatellites (Estonba et al. 2006; Melo-Ferreira et al. 2014a; Sanz-Martín et al. 2014), single nucleotide polymorphisms (Melo-Ferreira et al. 2009), nuclear DNA sequences (Alves et al. 2003; Melo-Ferreira et al. 2012), whole exomes (Ferreira et al. 2021), and whole genomes (Seixas et al. 2018; Giska et al. 2019). Molecular estimates of species phylogenies based on high throughput DNA sequencing data, using both whole exomes with broad taxonomy coverage (Ferreira et al. 2021) and whole chromosome with more limited taxonomic coverage (Giska et al. 2019), suggested that a clade grouping the mountain hare (*L. timidus*) and the North American arctic hare (*L. arcticus*) and Alaskan hare (*L. othus*), and potentially the Manchurian hare (*L. mandshuricus*), comprise the closest living relatives of the Iberian hare among the analyzed taxa. Divergence time estimation based on full exome and genome sequence data suggested that the Iberian hare diverged from the closest relatives ~2 Mya (Giska et al. 2019; Ferreira et al. 2021).

Three subspecies of the Iberian hare have been proposed, based on morphological characteristics: *L. g. granatensis*, for all Iberian Peninsula, except the northwest; *L. g. gallaecius* Miller 1907, for Galicia and central Asturias, with measurements similar to *L. g. granatensis*, but darker coat coloration; and *L. g. solisi* Palacios and Fernandez 1992, for Mallorca Island on Balearic Archipelago (Spain), somewhat smaller than *L. g. granatensis* and the Anteroflexid of P3 may be absent (Alves and Nithammer 2003; Hoffmann and Smith 2007; Alves and Acevedo 2018). However, the subspecies classification has not been validated by genetic analyses (Seixas et al. 2014; Marques et al. 2017).

Despite difficulties in reconstructing the paleontological records of species of hares, due to overlap of morphological characters and persisting taxonomic uncertainties, the presence of the earliest paleontological records of the Iberian hare date from the Lower Pleistocene in the deposit of Huescar-1, in southern Spain (Mazo et al. 1985; Sesé 1994). An ancient DNA study identified *Lepus* spp. paleontological remains from Les Vautes, southern France (Forest 2003), as belonging to the Iberian hare, showing that the distribution of the species extended beyond the Pyrenees in the Neolithic (Lado et al. 2018). This work suggested that the current range of the species in the Iberian Peninsula, therefore, results from a postglacial retraction of an extended range, possibly due to the recent westwards invasion of *L. europaeus*.

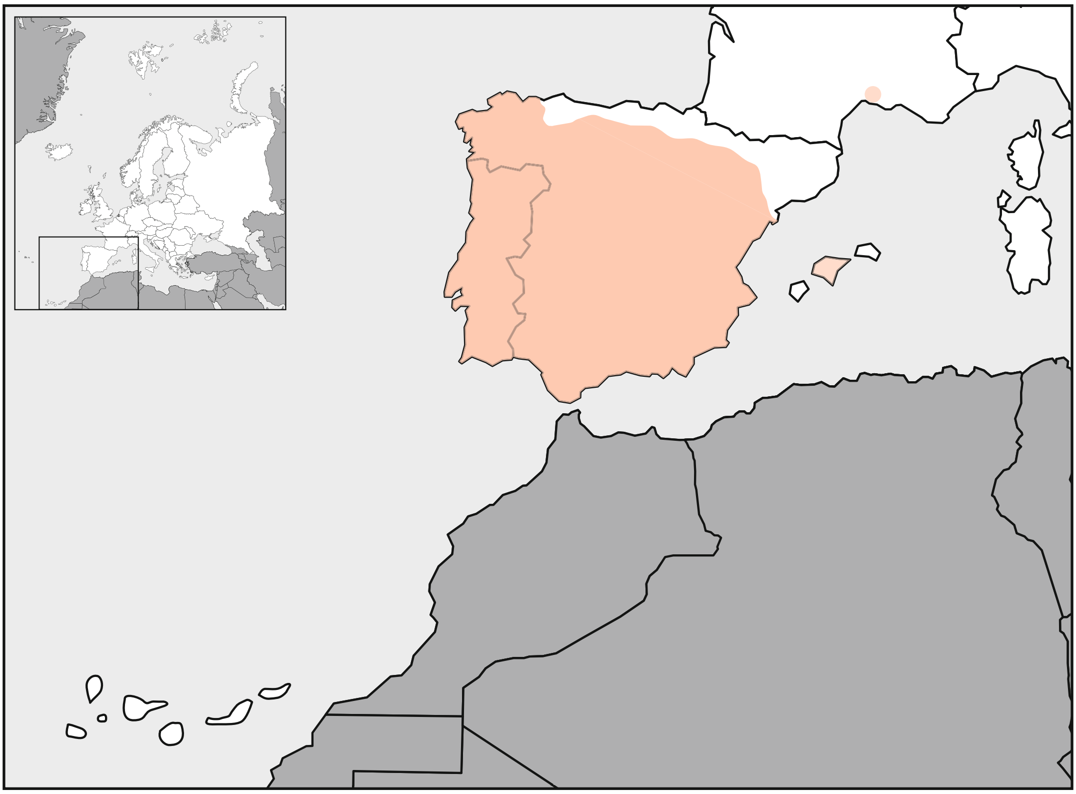
## Current Distribution

The Iberian hare is endemic to the Iberian Peninsula (Portugal and Spain). Cabrera (1914) indicated that the species was widely distributed in the Mediterranean areas south of the Ebro River, and also in Galicia, Asturias, and Mallorca Island (Balearic Archipelago, Spain). The following data on species' distribution dates from the 1960s, which maintained the range of the species the same, but some provinces, such as Palencia and Burgos (Northern Plateau) and Cáceres and Sevilla (Southern Plateau), were highlighted for their high population abundance (Ministerio de Agricultura 1968).

The current distribution range can be depicted from efforts to compile biodiversity data, both in Portugal and in Spain. Acevedo et al. (2012a) provided the first detailed map of the species range at 10x10km UTM squares using information from Carro and Soriguer (2007) as well as hunting bags data for Portugal (Almeida et al. 2004). Information for Portugal was recently updated in the Portuguese Mammal Atlas, revealing current absence in several locations in northwestern and central Portugal (Bencatel et al. 2019).

Overall, the Iberian hare naturally occupies most of the Mediterranean region in Iberia, from the Mediterranean coast, south of Ebro River to the Atlantic coast, and from Andalucía coast to the northern mountains of Leon, Palencia, Burgos, and the southern slopes of Navarra and Huesca (Fig. 1), where the broom and the European hare are present (parapatric ranges; see Acevedo et al. 2012b). The natural distribution range of the Iberian hare remain stable in the last decades; nevertheless, in some locations, it has been extirpated by humans, as mentioned for northwestern and central Portugal, namely near the Atlantic coast.

The Iberian hare was introduced in Mallorca Island (Balearic Archipelago, Spain) more than ~4000 years ago (Seixas et al. 2014), and traces of DNA from this species has been found in Corsica, predominantly as hybrids with the Apennine hare, thus most likely there are no pure individuals of Iberian hare in Corsica (Pietri et al. 2011). A more recent introduction (1980s) has been done in the French Pyrenees (Perpignan, southwestern France), for hunting purposes (Bordes et al. 2007). In the French Pyrenees, the Iberian hare is in sympatry with the European hare in some localities, and has been reaching high-density populations in some areas, according to the French Office for Biodiversity (unpub. data).



Map template: © Getty Images/iStockphoto

**Fig. 1** Distribution of the Iberian hare (*L. granatensis*) showing endemic area (apricot) and where it was introduced (light apricot). Raw data were obtained from Carro and Soriguer (2007) and Bencatel et al. (2019) for Spain and Portugal, respectively. (Map template: © Getty Images/iStockphoto)

## Description

In contrast to the general uniformity of the pelage pattern of the other hares in Europe, in the Iberian hare, the white ventral area is extensive, and there is a clear contrast between the ochraceous brown (gray-brown) color of the back and the white belly pelage that extends in a white strip to the forefeet and hindfeet (Fig. 2). It is the only species with white spots on the upper fore and hind feet. Pelage has an ochraceous brown tone with basically white long guard hairs as opposed to the gray hairs in the other two species occurring in the Iberian Peninsula. The external faces of the hips are bright reddish in contrast with the gray brown of the dorsal part of the back. The white coloration of the inner face of the legs is continued with the upper side of the legs and reaches to the tip of the toes. This pelage pattern is quite typical of *L. granatensis*, not occurring in the other hare species (Fig. 2). According to Palacios (1989), in spite of the color pelage uniformity, lightness differences are seen from one population to another, being darker in the northern range. The black area on the upper tail surface is never rounded posteriorly like in *L. europaeus*, but ends on the tip. The long guard hairs are very conspicuous, being white at the top and black at the base. The length of these guard hares range between 40 and 57 mm, and the longest whiskers range between 67 and 91 mm. No white stripes on the face, as in the *L. castroviejoi*.

The Iberian hare is smaller than the other two hare species that occur in Iberia, mean body weight ranging from 2.0 kg to 2.5 kg, and hind feet smaller than 130 mm (Table 1). However, independently of the body size, the Iberian hare

**Fig. 2** Iberian hare (*Lepus granatensis*). © J Jambas with kind permission

has the longest tail length of all hare species in Europe.

From the cranial characters (Fig. 3), *L. granatensis* is more similar to *L. europaeus* than to *L. castroviejoi*. It has a very developed posterior arm of the supraorbital process, which reaches the temporal tubercle. However, craniometrical measurements reflect the same size relationship as the body measurements, with *L. granatensis* being the smallest (Table 2). According to Palacios (1989), the aboral zygomatic width (AZW) was the only discriminating character found (of 46 cranial measurements) being significantly smaller than that observed in the other two hare species in Iberia (AZW: *L. granatensis* 38–43 mm, n = 155; *L. castroviejoi* 43.7–46.2 mm, n = 14; *L. europaeus* 43.5–48.4 mm, n = 23). The shape is similar to *L. europaeus,* but the posterior arm of the processus supraorbitalis does not diverge and the sutura coronalis is straight (Palacios 1977). Some skull indices described by Palacios (1983) allow the differentiation of the three species. Cranial dimensions of *L. granatensis* across the range show no important differences (Palacios 1989). The teeth are similar to *L. europaeus*, but the anterior fold of the first lower premolar (P3) is comparatively larger; see Palacios and Lopez-Martinez (1980) for detailed information on dental morphology. Regarding the postcranial skeletal, the relationship of the humerus length by femur length and of tibia to femur length is almost identical in the three species occurring in Iberia, but *L. granatensis* has the longer radius as related to the humerus.

There is no significant variation of measurements across diverse Spanish and Portuguese regions. Nevertheless, the ear length is somewhat greater in the south and hindfoot length is greater in the north. Iberian hares from Andalusia and the Guadalquivir valley are particularly lighter in color, whereas those from the Northwest, Coruña, are particularly darker. Thus, there is a geographical variation of coat color, with Iberian hares with the darkest coat found in areas with particularly high levels of annual precipitation, c. 2000 mm (Palacios 1989). Although there is no sexual dimorphism in the coloration pattern, females are in general heavier than males (average around 2.3 kg in males and 2.5 kg in females, Alves and Niethammer 2003, Table 1).

## Physiology

There are almost no studies focusing on aspects of the physiology of the Iberian hare, namely on metabolism, body condition, hormones, etc. However, a recent study has described the reference intervals for 22 hematological and serum biochemistry parameters for this species (Alves and Santos 2021). In general, the values are in accordance with those reported for European hares, except for higher number of white blood cells and urea concentration (Table 3). There are no differences when considering the scale mass index, despite differences among some parameters were observed between sex and age classes, as well between seasons.

**Table 1** Body measurementsof adult *Lepus granatensis* in the Iberian Peninsula (Adapted from Alves and Niethammer 2003). The numbers of specimens (within brackets), mean ± Standard deviation (SD) of each parameter are indicated

| | Spain[a,b] | | | | | | | Portugal[c] | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Leon | Burgos | Valladolid | Madrid | Toledo | Albacete | Granada | Pancas | Santarém | Idanha | Males[d] | Females[d] |
| Weight (g) | 2335 ± 238 (11) | 2541 ± 238 (11) | 2365 ± 315 (17) | 2189 ± 206 (9) | 2339 ± 317 (9) | 2060 ± 145 (8) | 2315 ± 277 (6) | 2417 ± 247 (157) | 2321 ± 226 (45) | 2269 ± 194 (9) | 2329 ± 200 (154) | 2554 ± 278 (57) |
| Head and body length (mm) | 462 ± 16 (9) | 465 ± 18 (9) | 459 ± 14 (16) | 456 ± 16 (7) | 461 ± 15 (9) | 446 ± 18 (6) | 470 ± 14 (4) | | | | | |
| Tail length (mm) | 102 ± 6.9 (10) | 102 ± 13 (7) | 100 ± 11 (15) | 105 ± 7.1 (8) | 103 ± 9.1 (10) | 104 ± 8.9 (7) | 109 ± 11 (4) | | | | | |
| Hind feet length (mm) | 116 ± 3.2 (16) | 117.9 ± 3.6 (12) | 117 ± 4.9 (24) | 117 ± 4.5 (14) | 114 ± 3.9 (13) | 114 ± 4.3 (11) | 114 ± 4.0 (8) | 121 ± 5.6 (215) | 124 ± 4.0 (57) | 120 ± 4.7 (13) | 122 ± 5.4 (160) | 122 ± 5.4 (125) |
| Ear length (mm) | 96 ± 3.6 (14) | 96.8 ± 4.9 (17) | 96 ± 5.0 (28) | 101 ± 3.2 (17) | 101 ± 4.6 (24) | 100 ± 5.2 (11) | 100 ± 4.4 (8) | 97.1 ± 4.9 (215) | 99 ± 3.5 (58) | 102.3 ± 4.7 (13) | 97.6 ± 5.1 (160) | 97.8 ± 4.5 (126) |
| Total length[e](mm) | 564 (9) | 567 (7) | 559 (15) | 561 (7) | 564 (9) | 550 (6) | 550 (4) | 551 ± 21.4 (130) | 556 ± 17.8 (58) | 547 ± 19.7 (13) | 545 ± 19.4 (110) | 560 ± 18.35 (91) |

[a] Palacios (1989)

[b] Names of the Spanish locations are the approximate cities of the region described by Palacios (1989)

[c] Alves and Niethammer (2003)

[d] Values for females and males were calculated with the data from the three Portuguese populations

[e] For the Spanish locals was calculated summing the head and body length with tail length

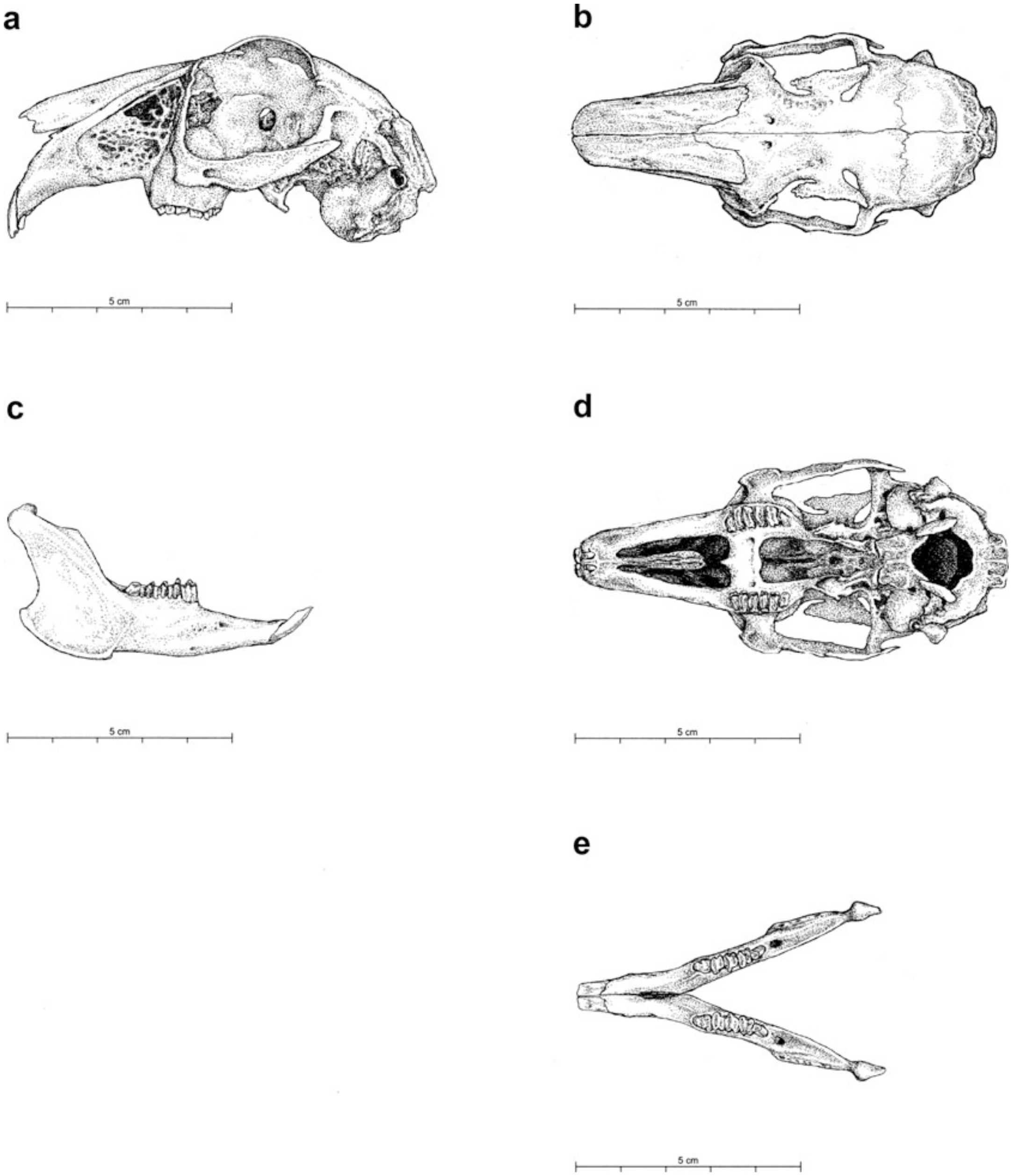


**Fig. 3** Skull of *Lepus granatensis*: (**a, b, d**) lateral, dorsal, and ventral view of skull; (**c**) lateral view of left mandible (view from outside), and (**e**) dorsal view of mandible. (© Franz Müller with kind permission)

**Table 2** Skull measurements (mm) of adult *Lepus granatensis, L. castroviejoi, and L. europaeus* in the Iberian Peninsula (Palacios 1983). The number of specimens (n), mean ± standard deviation (SD) are indicated

| | *L. granatensis* | | *L. castroviejoi* | | *L. europaeus* | |
|---|---|---|---|---|---|---|
| | *n* | *Mean ± SD* | *n* | *Mean ± SD* | *n* | *Mean ± SD* |
| Occipital length | 161 | 87.6 ± 2.7 | 13 | 95.0 ± 1.9 | 29 | 99.3 ± 3.1 |
| Total length | 158 | 88.7 ± 2.5 | 13 | 95.4 ± 2.1 | 30 | 96.6 ± 2.5 |
| Condylobasal length | 155 | 78.1 ± 2.3 | 13 | 84.6 ± 2.0 | 30 | 89.2 ± 2.2 |
| Palatal length | 161 | 35.5 ± 1.3 | 14 | 37.6 ± 0.9 | 30 | 48.8 ± 1.4 |
| Internal nasal length | 164 | 31.2 ± 1.9 | 14 | 32.0 ± 1.1 | 30 | 37.2 ± 2.3 |
| External nasal length | 168 | 39.2 ± 1.4 | 14 | 41.9 ± 0.9 | 30 | 44.7 ± 2.2 |
| Zygomatic width | 156 | 40.9 ± 1.1 | 14 | 45.0 ± 0.7 | 29 | 45.9 ± 1.0 |
| Upper dental series | 171 | 15.8 ± 0.6 | 14 | 17.4 ± 0.3 | 131 | 18.3 ± 0.6 |
| Alveolus height | 168 | 15.4 ± 0.7 | 14 | 15.3 ± 0.5 | 31 | 15.9 ± 0.8 |
| Width between supraorbital processes | 114 | 30.3 ± 1.5 | 12 | 31.7 ± 0.6 | 23 | 37.4 ± 1.7 |
| Postpalatal width | 158 | 9.7 ± 0.5 | 14 | 11.4 ± 0.5 | 31 | 11.2 ± 0.7 |
| Tympanic bulla length | 162 | 11.7 ± 0.5 | 13 | 11.3 ± 0.6 | 30 | 11.5 ± 0.6 |
| Vertical diameter of the foramen magnum | 148 | 11.9 ± 0.5 | 13 | 11.8 ± 0.5 | 27 | 12.7 ± 0.6 |
| Radius of incisors curvature | 50 | 10.2 ± 0.5 | 14 | 10.9 ± 0.3 | 27 | 10.1 ± 0.6 |

**Table 3** Hematology and serum biochemistry values for the Iberian hare, obtained in live animals (Adapted from Alves and Santos 2021). The number of specimens (n), mean ± standard deviation (SD), reference interval (using iterative processes for identifying the location of the median and values distribution), and range are indicated

| Parameter | Units | *n* | Median | SD | Reference interval | Minimum–maximum |
|---|---|---|---|---|---|---|
| WBC | $10^3$/μL | 100 | 6.73 | 2.66 | 2.76–13.29 | 2.28–16.90 |
| RBC | $10^6$/μL | 86 | 8.72 | 1.06 | 6.30–10.63 | 5.78–11.10 |
| HG | g/dL | 99 | 16.80 | 1.63 | 13.12–19.81 | 11.50–20.40 |
| HTC | % | 102 | 48.25 | 5.22 | 36.21–57.11 | 27.2–58.5 |
| MCV | fL | 100 | 55.25 | 3.85 | 49.49–63.98 | 48.80–65.70 |
| MCH | pg | 102 | 19.35 | 1.29 | 17.19–22.42 | 16.9–22.9 |
| MCHC | g/dL | 101 | 34.70 | 2.00 | 30.09–38.03 | 28.6–38.3 |
| PLAT | $10^3$/μL | 95 | 386.00 | 136.81 | 131.10–673.28 | 118.00–783.00 |
| TP | g/dL | 101 | 5.08 | 0.90 | 3.72–7.37 | 3.54–7.52 |
| ALB | g/dL | 99 | 2.85 | 0.30 | 2.30–3.47 | 2.17–3.64 |
| CREA | mg/dL | 103 | 1.17 | 0.80 | 0.83–2.19 | 0.80–2.95 |
| Urea | mg/dL | 100 | 45.00 | 11.18 | 25.69–69.89 | 21.00–81.00 |
| URIC | mg/dL | 98 | 1.20 | 1.46 | 0.22–5.59 | 0.20–7.90 |
| GLU | mg/dL | 101 | 223.00 | 76.47 | 99.39–493.00 | 77.00–459.00 |
| TRIG | mg/dL | 101 | 110.00 | 70.31 | 49.20–360.29 | 39.00–386.00 |
| CHOL | mg/dL | 101 | 20.00 | 5.79 | 12.32–37.63 | 10.00–43.00 |
| Ca | mmol/L | 96 | 2.97 | 0.22 | 2.55–3.46 | 2.33–3.40 |
| Na | mmol/L | 97 | 138.00 | 2.68 | 132.98–143.82 | 133.00–146.00 |
| K | mmol/L | 101 | 4.12 | 1.00 | 2.70–6.63 | 2.76–7.13 |
| Cl | mmol/L | 100 | 105.00 | 4.12 | 96.87–113.33 | 97.00–121.6 |
| Mg | mmol/L | 100 | 1.66 | 0.40 | 1.19–2.98 | 1.10–3.47 |
| P | mmol/L | 102 | 1.78 | 0.87 | 0.77–8.90 | 0.68–8.90 |

WBC = white blood cell count; RBC = red blood cell count; HG = hemoglobin concentration; HTC = hematocrit; MCV = mean corpuscular volume; MCH = mean corpuscular hemoglobin; MCHC = mean corpuscular hemoglobin concentration; PLAT = platelet count; TP = total protein; ALB = albumin; CREA = creatinine; URIC = uric acid; GLU = glucose; TRIG = triglycerides; CHOL = cholesterol; Ca = calcium; Na = sodium; K = potassium; Cl = chloride; Mg = magnesium; P = phosphorus.

## Genetics

Karyotype: 2n = 48 (assuming conservation across hares; Palacios 1979; Robinson et al. 1983).

Genetic and genomic analyses and ecological niche modelling suggest that the Iberian hare has colonized northern Iberia after the last glacial maximum, possibly from the southwest (Acevedo et al. 2012a, 2015; Marques et al. 2017; Seixas et al. 2018). Analyses of genetic variation showed that the species has relatively shallow population structure, and that the distribution of genetic variation is mostly determined by the demographic dynamics of the northwards range expansion (Melo-Ferreira et al. 2011; Marques et al. 2017; Seixas et al. 2018). The exception is the Northwest Iberia, where a genetic cluster has been found with single nucleotide polymorphism (SNP) data, suggesting that population might have escaped the expansion dynamics (Marques et al. 2017), and the Central and Northwest Iberia where an Iberian hare mitochondrial DNA (mtDNA) sublineage was found (Melo-Ferreira et al. 2011).

During the northwards postglacial expansion, the Iberian hare encountered and hybridized with Iberian populations of the mountain hare *L. timidus*, a species that was then present in the region, as attested by paleontological records (Altuna 1970). The Iberian hare replaced the mountain hare, and the latter species disappeared from the Iberian Peninsula. From these hybridization events, mtDNA haplotypes of *L. timidus* origin are now predominant in the northern range of the Iberian hare (Fig. 4), but are absent from the South (Melo-Ferreira et al. 2005; Alves et al. 2008; Acevedo et al. 2015). These ancient introgression events from *L. timidus* also affected *L. castroviejoi* and the Iberian populations of *L. europaeus*, where the introgressed mtDNA lineage is also found (Alves et al. 2003; Melo-Ferreira et al. 2005), explaining the high mtDNA diversity detected in *L. europaeus* from the Iberian Peninsula (Pérez-Suárez et al. 1994). Among the introgressed mtDNA variants of *L. timidus* origin, three sublineages were found in the Iberian hare, structured from Northeast to Northwest Iberia, which may represent a remnant of preexistent structure in the replaced *L. timidus* populations, and/or expansion of distinct haplotypes in different regions, "surfing" on the northwards expansion of the species (Melo-Ferreira et al. 2011). A study focused on patterns of evolution along the complete mtDNA sequence of several hare species showed that the variant of *L. timidus* may have evolved under positive selection, affecting several codons of mtDNA-encoded genes (Melo-Ferreira et al. 2014b). Whether the high frequencies of mtDNA introgression result from a selective advantage, from the demographic dynamics during and after the hybridization events, or both, remains being debated (Melo-Ferreira et al. 2011, 2014a, b; Seixas et al. 2018; Carpio et al. 2021). An ancient DNA study showed that the northwards expansion of the Iberian hare reached southern France in the Neolithic (Lado et al. 2018). These analyzed individuals carried the mitochondrial DNA haplotype of *L. timidus*, in keeping with the high proportion of introgression found in the northern Iberian populations.

The ancient hybridization between the Iberian and mountain hares also affected the nuclear genome, with inferences based on genome-wide data of 10 individuals suggesting that at least 1.3–2.4% of the Iberian hare genome is of mountain hare origin (Seixas et al. 2018). These analyses also proposed that the introgressive hybridization events occurred between 24 thousand years ago, based on identity by state tracts, and 7000 years ago, based on the introgressed tract length distribution. Nuclear introgression was found to be higher in the north but, contrary to mtDNA, also affects southern populations (Seixas et al. 2018). These patterns are compatible with a northwards range expansion of the species with hybridization and flow of introgressed variants towards the south, possibly driven by male-mediated dispersal. Introgressed fragments of *L. timidus* origin are less prevalent close to the center of the chromosomes and in the X-chromosome, which is consistent with an increased effect of low recombining regions and the X-chromosome in genomic incompatibilities between species. The inspection of the genome of

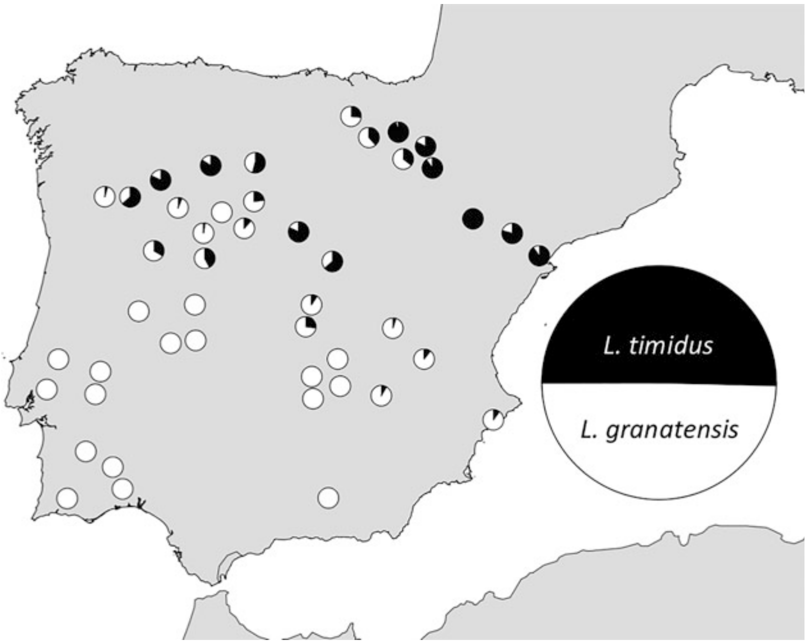


**Fig. 4** Distribution of mountain hare (*Lepus timidus*) mitochondrial DNA (mtDNA) introgression Into the Iberian hare (*L. granatensis*) populations. Pie charts show the proportion of analyzed Iberian hares with mountain hare mtDNA (in black) (Adapted from Acevedo et al. 2015)

the Iberian hare identified genomic regions with high frequencies of introgression that could not be predicted by a neutral model of demographic replacement with hybridization and are compatible with selection-driven introgression from *L. timidus* into *L. granatensis*. These genomic fragments include genes with immune functions and related with male fertility, suggesting that introgression in these cases was driven by adaptation to the environment or genomic conflicts (Seixas et al. 2018). Also, patterns of nuclear DNA introgression similar to the geographic distribution of mtDNA introgression affecting nuclear DNA-encoded genes with mtDNA functions suggest co-introgression and coevolution during and after the ancient hybridization events.

Given the presence of *L. granatensis* in southern France in the Neolithic (Lado et al. 2018), the natural current range of the species confined to the Iberian Peninsula may reflect a more recent retraction, possibly caused by the westward invasion of *L. europaeus* and interspecific competition (Acevedo et al. 2012a, b). SNP (Melo-Ferreira et al. 2009) and microsatellite data (Melo-Ferreira et al. 2014a) showed that the Iberian hare and the European hare hybridize in the area of contact in northern Iberia, but no traces of introgressed variants were found away from the contact zone, suggesting that genetic admixture between the species is rather limited (Melo-Ferreira et al. 2014a). Whole genome data estimates found that one Iberian hare from Navarra has 0.39% of the genome introgressed from *L. europaeus*, while for nine other individuals from the rest of the range the estimates varied between 0.01% and 0.03% (Seixas 2017). Analyses of genomic variation inferring the genomic tracts of introgression of different origins also suggested that the Iberian hare first contacted and hybridized with the mountain hare, and then more recently with the European hare (Seixas 2017). Minor traces of genetic admixture with the broom hare have been suggested from analyses of molecular variation (Melo-Ferreira et al. 2009, 2012). Also, a genetic variant originating from ancient hybridization with the Iberian hare has been found to cause a winter gray pelage in the mountain hare from Faroe Islands (Giska et al. 2019).

Studies comparing genetic diversity estimates in hare species from Europe show that levels of diversity are lower in the Iberian hare when compared to *L. timidus* and *L. europaeus* and larger than in *L. castroviejoi* (Estonba et al. 2006; Melo-Ferreira et al. 2009, 2014a; Seixas et al. 2018), in keeping with expected differences in effective population sizes across species. Estimates of long-term effective population size of *L. granatensis* vary between ~100,000 (Melo-Ferreira et al. 2012; Seixas et al. 2018) and 180,000 individuals (Giska et al. 2019), based on inferences using genetic variation data.

A study analyzing patterns of synonymous and non-synonymous substitutions in protein-coding genes based on transcriptome sequencing data, including the Iberian hare, other vertebrates and invertebrate species, suggested that the non-synonymous to synonymous ratio ($\pi_N/\pi_S$) did not differ significantly between vertebrates and invertebrates, contrary to expectations of higher adaptive rate in species with larger effective population sizes (Gayral et al. 2013). This study showed that even though neutral genetic diversity ($\pi_S$) is lower in the Iberian hare than in the European wild rabbit *Oryctolagus cuniculus*, $\pi_N/\pi_S$ is much higher in the Iberian hare, which is compatible with the hypothesis that smaller effective population sizes leads to a reduction in the efficiency of purifying selection.

The extensive studies using genetic information from the Iberian hare produced important genetic resources. These include partial mtDNA sequences (Alves et al. 2003; Melo-Ferreira et al. 2007, 2011), complete mtDNA sequences (Melo-Ferreira et al. 2014b), microsatellites (Estonba et al. 2006; Sanz-Martín et al. 2014; Melo-Ferreira et al. 2014a, b), SNPs (Marques et al. 2017), transcriptomes (Cahais et al. 2012; Gayral et al. 2013; Marques et al. 2017), exomes (Ferreira et al. 2021), and whole-genomes (Seixas et al. 2018). However, an Iberian hare reference genome assembly is currently lacking.

## Life History

The reproductive characteristics of the Iberian hare do not vary significantly among seasons, despite a lower activity observed in autumn, especially in males. This continuous pattern of breeding activity, without summer/autumn interruption, is different from the seasonal pattern reported in most populations of other hare species occurring in Europe (Palacios 1981; Lopez et al. 1996; Alves et al., 2002; Alves and Rocha 2003; Fernández et al. 2008, 2010), despite being in line with the observed in some hare species dwelling in the Mediterranean region, namely *L. europaeus* (Antoniou et al. 2008). Nevertheless, the peak of breeding occurs in spring. Mean litter size (based on embryo counts) observed in different populations from Portugal was 1.56 ± 0.10 (range between 1 and 4; Alves et al. 2002). However, higher average litter size (2.1) has been reported for Navarra and Granada (Farfán et al. 2004; Fernández et al. 2008). A maximum litter size of 7 was observed in Spain (Duarte 2000). Ovary mean weight 1.39gr ±0.08 (range between 0.64 and 2.20gr), mean testis weight 7.93gr ± 0.21 (range between 2.15 and 12.81gr), and epididymis weight 1.54gr ± 0.04 (range between 0.43 and 2.28gr) (Alves et al. 2002). The average daily sperm production and extra-gonadal sperm reserves was estimated as 353 x $10^6$ and 1762 x $10^6$ sperm cells, respectively, and the mean basal testosterone 7.28 ng/ml ± 1.08 (Alves et al. 2002). Evidence for precocious sexual maturity, pregnant females with 2307 g and males with descended testis with only 1811 g were detected in Portugal in March and June, respectively (Alves and Niethammer 2003). In Spain, males with 1.5 kg and females with 1.75 kg have been observed to be reproductively active (Fernández et al. 2010), suggesting reproduction in the year of birth. Prenatal mortality (due to loss of ova and/or resorption of embryos) in pregnant females was estimated as 21%, and the proportion of pregnant females with higher number of corpora lutea than visible embryos, as 26% (Alves et al. 2002). The gestation period is around 42 days. The annual potential production of young per adult female of 9.8 is in the range of values observed for other hare species (Alves et al. 2002). In Granada (southern Spain), the productivity of female per year has been estimated at 7.21 leverets, with an estimated average number of 3.48 litters per adult female and per year (Farfán et al. 2004). In Navarra (Northern Spain), a productivity of 6.2 litters per year was reported, indicating an average potential of 16.2

leverets per adult female and year (Fernández et al. 2008, 2010).

Mean weight of newborn leverets in captivity is 128.6gr ± 6.2 (n = 6, range between 123 and 140, litter size 1 leveret/female) (Alves and Niethammer 2003). However, smaller sizes of newborns (62 and 82gr) have been reported in Spain (Rodriguez et al. 1997). There are indications for superfetation as some observations of small embryos and fetuses in the final stage of the development in the uteri have been done (PC Alves unpublished data). It is also common to observe lactating pregnant females around all the year (Farfán et al. 2004). In general, females both being pregnant and lactating are heavier and bigger (Fernandez et al. 2010). The life span of the Iberian hare in captivity can reach at least 10 years (PC Alves unpublished data).

A study conducted in southern Spain (Doñana) estimated that the survival of the Iberian hare ranged from 38% (marshland) for a period of 141 days to 22% (ecotone) for a period of 220 days (Carro et al. 2002). It has been estimated in Granada a 27.91% minimum annual survival for leverets (Farfán et al. 2004). The age structure is not well known, but the existent data from Navarra suggest that the majority of the population is around 1 year of life and few specimens exceed that age (Fernández et al. 2010).

## Habitat and Diet

### Habitat

The Iberian hare occupies heterogeneous habitats in agroecosystems (Acevedo et al. 2012a). In general, the species prefers open landscapes and areas with sparse scrubland, avoiding close woodlands. However, in northern Iberia, it appears in humid mountains areas with oceanic climate (annual precipitation 1500–2000 mm), meadows, pastures, agricultural fields (wheat, etc.), and deciduous forests (Palacios and Meijide 1979; Duarte 2000; Tapia et al. 2010). In central Iberia (annual precipitation 300–800 mm), the species occupies mainly open areas of agricultural landscapes such as wheat, barley, oats, vineyards, and alfalfa. Calzada and Martínez (1994) described seasonal differences in the habitat preferences for this region, selecting agricultural fields in winter and fallows and alfalfa in summer. In southern Iberia, hares inhabit dry area (annual precipitation 300–600 mm, with some places lower than 200 mm) with olive groves, vineyards, wheat, barley, and natural scrubland vegetation (Duarte and Vargas 1998). Olive groves should be highlighted within the preferences of the species in southern range since the highest population densities are achieved in this woody crop (Duarte 2000). Farfán et al. (2012) described changes in the habitat preferences of the species between 1960s and 1990s in this region, selecting natural vegetation in the earlier period and agricultural lands in the latter one. Overall, this species is favored by patchy agrosystems within mosaics with well-developed natural vegetation giving a high structural diversity of the landscapes (Acevedo et al. 2012a; Farfán et al. 2012). Regarding resting site selection, hares mainly select uncultivated lands and pastures that are areas with a low rate of urban disturbance (Bartolomé et al. 2004; Sánchez-García et al. 2012). Hares are looking for sites with vegetation providing coverage (except in the front) that is characteristic of species in which hideout and scape is their antipredator mechanism. Other patterns of resting site selection were described in southern Iberia where the olive groves and neighboring agricultural fields are preferred (Duarte 2000).

In southern Iberia, marginally significant differences were reported for the home range size (90% minimum convex polygon) between VHF (very high frequency) radio-collared males (28 ha, n = 5) and females (24 ha, n = 9; Carro et al. 2011). Data from central Spain provided similar values to those reported in southern populations (35 and 19 ha, for 3 males and 3 females, respectively) using GPS (Global Positioning System) collars and 95% kernels for home range estimation (M. Martinez-Haro, unpublished data). In northern Iberian, the average home range size (95% minimum convex polygon) was 24 ha (Jaramillo-Fayad et al. 2015) and 39.6 ha (Sánchez-García et al. 2012), in Galicia (n = 14) and Valladolid (n = 23), respectively, from VHF radio-collared animals. Finally, Rodríguez et al. (1997) reported higher values (100–300 ha; 95% minimum convex polygon) in translocated VHF radio-collared individuals that can be not directly generalized to natural populations. In general, home range values for natural populations are equivalent to those reported for *L. europaeus*.

## Diet

Hares are herbivorous, mainly eating on grasses with spatiotemporal variations in diet depending on resources availability. Studies on Iberian hare feeding ecology are limited to Pauperio and Alves (2008) in central Iberia and to Carro and Soriguer (2010) in southern Iberia. These authors found a wide range of plant species in Iberian hare's diet (higher than reported for other hare species; see, e.g., Dingerkus and Montgomery 2001), being grasses the most represented ones. The species with higher rates of intake were *Anthoxanthum odoratum*, *Secale cereale*, and *Agrostis* spp. in central Iberia (Pauperio and Alves 2008), and *Cynodon dactylon*, *Hordeum* sp., *Aeluropus littoralis* and *Paspalum* sp. in southern Iberia (Carro and Soriguer 2010). In summer, when grass availability is lower, the ingestion of other groups increases, like shrubs, inflorescences (Pauperio and Alves 2008), and even cereal crops (Carro and Soriguer 2002), being generally associated with the higher nutritive value of alternative groups and reproductive plant parts. Overall, the information available for Iberian hare suggests that its diet did not differ substantially of that described for other hare species (Peroux 1995; Ballesteros 2003). According to Alves and Rocha (2003), the vegetation available for the Iberian hare in southern Portugal acquires a maximum protein content between January and April, where fiber reach the minimum value; on the contrary, from July to December, the trend is reversed and the protein content acquires its minimum (less than 10%) and that of fiber its maximum. The biomass of the vegetation acquires high values between January and April and its minimum between July and October.

## Behavior

In contrary to wild rabbits, hares do not use burrows for breeding neither to hide from predators. Usually they lay down in vegetation, making shelters and breeding sites (dens). Leverets born with open eyes and cover by hair, typical from nidifugous species. Parental care is limited (usually one or two visits a day when lactating), and leverets with 2 weeks are feeding grass and with 3 weeks do no longer depend of the mother's milk (Duarte 2000).

## Social Behavior

Iberian hares are generally solitary animals appearing sometimes in small groups to feed during the night, presumably as antipredator strategy. Social hierarchy is established by means of intimidating poses and pursuits. The hierarchy level is used for selecting feeding sites; dominant animals displace to subordinary ones to suboptimal areas (Rodríguez et al. 1997). Iberian hares are not territorial (Ballesteros 1998) but fights are frequent among males during the mating period. Fights are frequent when animals are maintained in captivity that limits the success of the intensive breeding programs. In particular, female seems to be more aggressive than males in captivity conditions.

## Activity

The activity patterns of Iberian hare were studied in Doñana National Park, southern Iberia (Carro and Soriguer 2010) and in Zamora, northern Iberia (Rodríguez et al. 1997). In general, these authors, both for southern and northern populations, reported that the Iberian hare is mainly nocturnal, spending most of the daytime in resting places and there is no substantial differences in the circadian rhythms between males and females. Males and females are mostly active slightly before dusk until a bit after dawn (sun rising), with slight interindividual variability. During its activity period (approx. 12 h), the hares search food resources and establish social relationships with conspecifics. Resting period starts earlier in the morning by entering forms. This period is only interrupted by short grooming periods. There are no robust data for assessing intra-annual variation in the activity pattern, but the activity in spring peaked in the sunset and is more variable during the night (Rodríguez et al. 1997).

## Parasites and Diseases

Health status is one the subject more broadly assessed in the Iberian hare, mainly in the last years and likely due to their potential relevance in the species' mortality, and as reservoir for zoonosis (Alzaga et al. 2008; Alzaga 2010; Carro and Soriguer 2010; Sánchez-García et al. 2012). For example, Alzaga (2010) studied the causes of mortality in 75 Iberian hares and found that bacterial diseases caused 45% of the total deaths (similar rate to traumatism), and parasites caused 8% of the deaths; no viral diseases were reported in this study.

Among bacterial diseases, tularemia (*Francisella tularensis*) is one of the most important, but other diseases such as pseudotuberculosis (*Yersinia pseudotuberculosis*), pasteurellosis (*Pasteurella multocida* and *P. haemolytica*), salmonellosis (*Salmonella typhimurium*), tuberculosis (*Mycobacterium tuberculosis* complex) were described (Rodríguez et al. 1997; García Pena et al. 1998; Aranaz et al. 2004; Carro and Soriguer 2010). But other bacterial diseases, namely caused by *Pseudomonas aeruginosa*, *Fusobacterium necrophorum*, *Streptococcus* sp., *Arcanobacterium pyogenes*, *Pseudomonas aeruginosa*, *Haemophilus* sp., *Clostridium perfringens*, *Staphylococcus aureus*, have been reported by Alzaga (2010).

Hares are considered to be very susceptible to tularemia, which may cause important epizootics, but they do not seem to be the usual reservoir. In Iberia Peninsula, tularemia has been related to common voles (*Microtus arvalis*; e.g., Rodríguez-Pastor et al. 2017), but it was suggested that Iberian hares can be associated in the transmission to humans (Luque-Larena et al. 2017).

Alzaga (2010) examined 170 Iberian hare sera widely distributed across the species range in Spain from 2003 to 2006, and no specific antibodies against *F. tularensis*, *Brucella* sp., and *Leptospira interrogans* were found. However, she found a high seroprevalence of *Toxoplasma gondii* (47%), a parasitic zoonosis, and concluded that Iberian hares could represent a relevant intermediate host for *T. gondii* in south-central Iberia. A moderate seroprevalence was also obtained in a posterior study in northern Iberia (Fernández-Aguilar et al. 2013). These authors studied the epidemiology of *T. gondii* and described evidence supporting that most juvenile seropositive hares did not survive as adults and/or there is a short-term humoral immune response against *T. gondii* in Iberian hares.

Iberian hare was described as an important reservoir for *Leishmania infantum*. In central Iberia, hares achieved high prevalence (74%) during an epidemic outbreak between 2009 and 2012 (Molina et al. 2012). In a retrospective study between 2004 and 2010, Ruiz-Fons et al. (2013) described a widespread presence of the parasite in Iberia and suggested that hares may have and unexpected role in the epidemiology of this zoonosis.

The parasite communities of the Iberian hare were studied by Alzaga (2010). Using more than 300 hunted animals widely distributed across the species range in Spain, this author described the parasite communities comparatively among the three hare species inhabiting the Iberian Peninsula (*L. castroviejoi* and *L. europaeus*, in addition to Iberian hare). In Table 4, a list of reported parasites is described for the Iberian hare (Sánchez-Covisa et al. 1999; García-Romero et al. 2001; Alzaga 2010; Segovia et al. 2014; Carvalho-Varela 1971; Cordero-del-Campillo 1994; Martínez et al. 2011; Rodríguez et al. 1973; Romero-Rodriguez 1976; Romero-Rodríguez et al. 1973; Vicente 1969).

The most well-known viral disease occurring in hares is provoked by the European brown hare syndrome virus (EBHSV), which causes the European brown hare syndrome (EBHS) in

**Table 4** Parasites reported in the Iberian hare (*Lepus granatensis*)

| | |
|---|---|
| Trematoda | *Dicrocoelium dendriticum* |
| | *Fasciola hepatica* |
| Nematoda | *Dermatoxys hispaniensis* |
| | *Graphidium strigosum* |
| | *Micipsella numidica* |
| | *Micipsella indica* |
| | *Nematodiroides zembrae* |
| | *Nematodirus* sp. |
| | *Passalurus ambiguus* |
| | *Passalurus nonanulatus* |
| | *Protostrongylus commutatus* |
| | *Protostrongylus terminalis* |
| | *Trichuris* sp. |
| | *Trichuris leporis* |
| | *Trichostrongylus retortaeformis* |
| | *Trichostrongylus colubriformis* |
| Cestoda | Multiceps *serialis* |
| | *Cittotaenia denticulata* |
| | *Leporidotaenia pseudowimerosa* |
| | *Taenia pisiformis* |
| | Anoplocephalidae |
| | *Mosgovoyia viscaciae* |
| | *Mosgovoyia pectinata* |
| | *Taenia pisiformis* |
| Protozoa | *Eimeria* sp. |
| | *Eimeria leporis* |
| | *Eimeria europaea* |
| | *Eimeria magna* |
| | *Eimeria media* |
| | *Eimeria septentrionalis* |
| | *Sarcocystis* sp. |
| | *Toxoplasma gondii* |
| | *Cryptosporidium parvum* |
| Ticks | *Rhipicephalus* sp. |
| | *Ixodes* sp. |
| | *Haemaphysalis* sp. |
| | *Dermacentor* sp. |
| | *Hyalomma* sp. |

brown and mountain hares. Despite causing severe deaths in those two species, interestingly it was never reported in the Iberian hare. Nevertheless, a virus from the same genus *Lagovirus* (family Caliciviridae), the rabbit hemorrhagic virus (RHDV), which is causing high mortalities in the European wild rabbit *Oryctolagus cuniculus*, have been detected in from dead Iberian hares collected in the 1990s in Portugal, where clinical signs were compatible with a *Lagovirus* infection (Lopes et al. 2014).

More recently, a new viral outbreak was detected in the Iberian hare. During 2018, widespread mortalities in the Iberian hare with myxomatosis-like clinical signs were reported in Portugal and Spain, which supported the potential species jump of the myxoma virus (MYXV) from the European rabbit to the Iberian hare (Águeda-Pinto et al. 2019; Dalton et al. 2019; García-Bocanegra et al. 2019; Carvalho et al. 2020). Molecular studies revealed that an insertion or recombination event with respect to the MYXV Lausanne reference strain may have been involved in the cross-species jump and increased virulence in its new host, the Iberian hare (Águeda-Pinto et al. 2019; Dalton et al. 2019). A comprehensive study between 2018 and 2020 in Spain demonstrates that spatial distribution of this viral disease is not homogeneous, with most outbreaks concentrated in the southern and central parts of this country. Nevertheless, consecutive outbreaks reported after 2018 suggest endemic circulation of this new emerging virus (García-Bocanegra et al. 2021). Moreover, a retrospective serological study shows that the Iberian hare may have been in contact with myxoma like virus between 1994 and 1999, since antibodies were detected in animals from that period (Abade dos Santos et al. 2022). The past contact of the Iberian hare with MYXV may have occurred with strains that circulated in wild rabbit, or unnoticed strains circulating in Iberian hare populations, suggesting the potential circulation of the MYXV (or similar virus) at least 20 years before the severe virus outbreaks observed in 2018. It should be noticed that hare myxomatosis outbreaks are causing severe mortalities in the Iberian hare, causing strong populations declines in Portugal and Spain.

Recently, a new leporid herpesvirus (LeHV-5) was detected in Iberian hares. Herpesvirus DNA was detected in hares with myxomatosis, where, in most cases, herpetic-like skin vesicles were present in the nostrils and lips along with necrosis of the genitalia, most evident in males affecting the penile glans but also observed in females (Abade dos Santos et al. 2020).

# Population Ecology

## Population Dynamics

The population abundance of the Iberian hare is widely variable in response to factors such as habitat quality, hunting pressure, natural predation, and diseases (Rodríguez et al. 1997; Gortázar et al. 2007; Lázaro et al. 2019). Available data on population density are scarce, old and mostly local, and results in diverse density estimates across regions (Table 5).

Studies on population age structure are very scarce in the Iberian hare, even considering them pivotal to understand population trends. In this species, the population trends are unclear. In the 1990s, numbers declined in northern Iberia (Duarte 2000) but increased in southern Iberia (Duarte and Vargas 1998). On the one hand, Gortázar et al. (2007) described significant interannual differences in abundance (period 1992–2002), both at local and regional scales, that produced a general positive trend suggesting that the species slightly increased in numbers during the study period in Aragón (northern Iberia). Carro and Soriguer (2017) showed that the species in Doñana National Park (southern Iberia) moderately declined between 1995 and 2012. Results from game bags in Spain (Garrido et al. 2019) suggest a 50% reduction between 2000 (1400.000) and 2017 (700.000). Moreover, from September 2018 populations are being affected by myxomatosis (Garcia-Bocanegra et al. 2019; see also section "Parasites and Diseases"). The MYXV is causing a high mortality and therefore is expected to contribute to hare population dynamics (but see Lázaro et al. 2019). More studies are needed to understand the current population trend of Iberian hare at both local and global scales, as well as to evaluate the impact of recent hare myxomatosis outbreaks on population dynamics.

## Competition with other Leporids

Parapatry is a biogeographical term used to refer to species whose distribution ranges do not overlap but are immediately adjacent to each other. No environmental barriers usually exist in the contact zones between the Iberian hare and the other hare species occurring in Iberia, hence competitive exclusion is advocated as a main factor that modulates species ranges (Bull and Possingham 1995). Thus, the Iberian hare distribution range (see section "Current Distribution") might be explained by occurrence of the *Lepus* species inhabiting the Iberia (Acevedo et al. 2012a, b), representing, therefore, a clear example of parapatry. The Iberian hare seems to have advantage over *L. europaeus*, as their contact zone is more favorable for the former (Acevedo et al. 2012b). This result is consistent with positive population trends described for *L. granatensis* and negative trends for *L. europaeus* in a region where the species coexist in northern Spain (Gortázar et al. 2007). Similarly, a macroecological study showed the existence of some areas with a high environmental potential for *L. castroviejoi,* but unoccupied by this species, that are currently within the area currently occupied by Iberian hare (Acevedo et al. 2014). This result

**Table 5** Summary of the values of population density reported for Iberian hare (*Lepus granatensis*)

| Region | Density (ind/km$^2$) | References |
|---|---|---|
| Navarra | 5.8 | Carro and Soriguer (2010) |
| León | 13 | Calzada and Martínez (1994) |
| León | 22.1 | López et al. (1996) |
| Zamora | 2–10 | Rodríguez et al. (1997) |
| Valladolid | 11–15.3 | Sánchez-García et al. (2012) |
| Castilla-La Mancha | 1.1–2.7 | Herranz (2000) |
| Castilla-La Mancha | 7.6 | Lázaro et al. (2019) |
| Évora | 13.7–37.4 | Batista and Cruz de Carvalho (1996) |
| Granada | 32 | Palomares and Ruiz-Martinez (1994) |
| Huelva | 1–31 | Carro and Soriguer (2010) |

suggests that competition with the Iberian hare could be an important factor constraining the expansion process of *L. castroviejoi* to these favorable territories (Ballesteros et al. 1986). Summarizing, the Iberian hare seems to have adaptive advantages for the possible interspecific relationships that could be established with the other hare species inhabiting Iberia.

## Effects of Global Change

The effects of land use changes on the Iberian hare were studied by Farfán et al. (2012). These authors showed that the requirement of the species changed substantially from a highly association with natural vegetation in the 1960s to one linked to cultivated lands in the 1990s. In this case, changes in land use did not suppose relevant shifts in the species distribution range but in the habitat availability for the species. The Iberian hare has benefited from new habitat since the cultivated areas provide year-round cover and food. Regarding climate change, Acevedo et al. (2012a) forecasted an increase in the species distribution range in a close future. According to these authors, it is predicted a higher probability of occurrence of the species in its current range, and a northward expansion (see also Araujo et al. 2011). Moreover, results from the previous study suggested favorable conditions for the Iberian hare presence in southern France, a region where there are paleontological evidence suggesting its presence since 5.5–7.5 thousand years before present (Lado et al. 2018), and where it has been recently distributed (Bordes et al. 2007). Overall, and despite the current negative population trend (namely due to diseases and change in habitat use), given the ecological requirements of the species, climate change is not expected to be a relevant threat for the species.

## Conservation Status

It is considered *Least Concern* in the IUCN Red List of Threatened Species (Soriguer and Carro 2019). It is also considered *Least Concern* in the regional IUCN red list assessments of Portugal (Cabral et al. 2005) and Spain (Palomo et al. 2007). Nevertheless, it is possible that the new information on population trends might change this status, due to the population decline observed in the last years, which has been dramatically accelerated by hare myxomatosis outbreaks since 2018.

## Management

The Iberian hare is highly associated with open agricultural landscapes. Nevertheless, it is fundamental to have shelters for refugee, namely for avian predators, namely Spanish imperial eagle (*Aquila adalberti*), golden eagle (*Aquila chrysaetos*), Bonelli's eagle (*Aquila fasciata*), booted eagle (*Hieraaetus pennatus*), red kite (*Milvus milvus*), black kite (*Milvus migrans*), common buzzard (*Buteo buteo*), goshawk (*Accipiter gentilis*), and the Eurasian eagle-owl (*Bubo bubo*). The red fox (*Vulpes vulpes*) is the main mammal predator, namely for juveniles. The Iberian hare is an important small game species in Portugal and Spain. It represents an important social, cultural, and economic value for rural areas. The main hunting activities are done traditional by shooting, but dog hare coursing is also very popular in some regions of Portugal and Spain. Hunting is only allowed in hunting estates, and the open season is between September and December (in some regions may go to end of February). A limited number of animals are allowed per hunter. Translocations are common, namely for hare dog coursing, although they are not recommended by the national entities, and in several regions are not allowed. In some regions, the Iberian hare can cause agricultural damages (crops, vineyards, etc.) and need to be controlled when densities are high, or the fields be protected using fences. Nevertheless, hare control may be also done when cases of zoonosis outbreaks are detected, as it happened last decade in Madrid region, Spain. Leishmaniasis was detected in 2009 and, by December 2012, human infections had increased significantly in several cities of this region (Carrillo et al. 2013). While dogs are the main reservoir host, the Iberian hare were suspected as a potential reservoir for *Leishmania* infections (Molina et al. 2012), and thus Iberian hare populations were controlled by the authorities and/or hunted.

The main factors affecting the Iberian hares are: loss of habitat due to the disappearance of traditional crops and intensification of farming (Palacios and Ramos 1979; Carro and Soriguer 2007); transformation of Mediterranean landscapes, with the abandonment of traditional agricultural practices, associated with the scrub and forest regeneration, which has increased the abundance of the wild boar (*Sus scrofa*), and thus reducing the Iberian hare namely in mountain areas, as well as the implementation of intensive crops (Delibes-Mateos et al. 2009); unsustainable hunting management (Palacios and Ramos 1979; Carro and Soriguer 2007); abusive and indiscriminate use of phytosanitary products (Rodríguez et al. 1997; Carro and Soriguer 2007) and rodenticides in agricultural areas (Olea et al. 2009); poaching (Palacios and Ramos 1979; Carro and Soriguer 2007); death by run over on roads; increase in opportunistic predators (Herranz 2000; Carro and Soriguer 2007; Ballesteros 2003); and, last but not least, emerging diseases (Molina et al. 2012; García-Bocanegra et al. 2021).

## Future Challenges for Research and Management

The Iberian hare is endemic in the Iberian Peninsula, and its populations have the ancestral footprints of past hybridization with the mountain hare, already extinct in the region: a ghost of a hybrid past. The several genetic and genomic studies conducted in the Iberian hare make the reticulate evolutionary history of this species a textbook example in evolutionary biology (Arnold 2015). The patterns of ancient introgression from the mountain hare and more recent introgression from the brown hare show that the range shifts since the last glacial maximum promoted contacts between species and hybridization. Thus, the presence of portions of genetic variation originating from other species, in particular the mountain hare and affecting massively mtDNA and some parts of the nuclear genome, make the Iberian hare a particularly suited model to study the impact of animal hybridization in the evolutionary trajectories of species. Research has shown that possibly a combination of demographic circumstances and natural selection contributed to the current admixed gene pool of the species. Further research is needed to clarify the physiological and ecological impacts of introgression in the Iberian hare populations.

Moreover, despite the increasing knowledge in the evolutionary history of the Iberian hare, basic ecological and physiological studies are still very scarce. The population dynamics of the Iberian hare is poorly known, and there is no information on the body metabolism and hormone function of this species. Finally, this species has recently been affected by a virus jump from the wild rabbit, and so far the consequences of the recent outbreaks caused by the myxoma virus are still not well known, thought the observed population decline and extirpation of populations in some regions is a main concern for conservation of this endemic species. The absence of management and conservation programs in Spain and Portugal for this species, associated with the fact that is an important game and simultaneously prey species, elevated the concern regarding its threatened status. Definitely, more attention should be given for preserving the natural populations of the Iberian hare.

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