Lepus europaeus (Lagomorpha: Leporidae)

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Abstract: *Lepus europaeus* Pallas, 1778, commonly called the European hare, is one of 32 species of *Lepus*. It is widely distributed in Europe and Asia where it was not native but introduced by humans for sport. *L. europaeus* does not burrow, nor hibernate, and gives birth to precocial young (leverets). It prefers open grassland, fields, agricultural farmland, and pastures with hedgerows and bushes. Declining populations in several countries since the 1960s led to increased research to investigate the reasons; *L. europaeus* is considered threatened in several countries, but of “Least Concern” by the International Union for Conservation of Nature and Natural Resources.

Key words: declining population, European brown hare, game animal, lagomorph, leporid, worldwide distribution

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Lepus europaeus Pallas, 1778

European Hare

- Lepus (Eulagos) europaeus europaeus* Pallas, 1778:30. Type locality not stated; restricted to “southern Poland” by Trouessart (1910); further restricted to southwestern Poland by Ognev (1940:140).
- Lepus t[imidus]. albus* Bechstein, 1801:1096. Type locality “Thuringia, Germany.”
- Lepus t[imidus]. flavus* Bechstein, 1801:1096. Type locality “Thuringia, Germany.”
- Lepus t[imidus]. niger* Bechstein, 1801:1096. Type locality “Thuringia, Germany.”
- Lepus medius* Nilsson, 1820:224. Type locality “Zealand, Denmark.”
- Lepus hybridus* Desmarest, 1822:349. Type locality “certain cantons of Siberia and Russia.”
- Lepus syriacus* Hemprich and Ehrenberg, 1832: pt. 2, sig. u, fig. XIV, II. Type locality “Mount Lebanon.”
- Lepus caspicus* Hemprich and Ehrenberg, 1832: pt. 2, sig. y. Type locality “Astrachan [=Asktrakhan, Russia].”
- Lepus aquilonius* Blasius, 1842:89. Type locality “hauptsächlich den Gegenden zwischen dem 56.° und 63.° N. Br.,” central Russia.
- Lepus timidus* var. *hymenalis* Tumac Eversmann, 1850:201. Type locality “Kazan.”

- Lepus campicola* Gervais, 1859:47. Nomen nudum.
- Lepus meridionalis* Gervais, 1859:47. Nomen nudum.
- Eulagos Judeae* Gray, 1867:222. Type locality “The Holy Land;” restricted to Ain Fashkha, Palestine by Qumsiyeh (1996:314).
- Lepus timidus coronatus* Fitzinger, 1867:161. Nomen nudum.
- Lepus timidus rufus* Fitzinger, 1867:161. Nomen nudum.
- Lepus timidus cinereus* Fitzinger, 1867:161. Nomen nudum.
- Lepus timidus nigricans* Fitzinger, 1867:161. Nomen nudum.
- Lepus timidus maculatus* Fitzinger, 1867:161. Nomen nudum.
- Lepus campestris* Bogdanov, 1871:175. Name preoccupied, not *L. campestris* Bachman, 1837.
- Lepus timidus* var. *argenteo-grisea* König-Warthaussen, 1875:277. Type locality “Ulm,” Württemberg, Germany.
- Lepus timidus* var. *tumac* Tichomirov and Korchagin, 1889:31. First suitable name for *tumac* Eversmann, 1850.
- Lepus transsylvanicus* Matschie, 1901:236. Type locality “von Taslau in Rumänien.”
- Lepus creticus* Barrett-Hamilton, 1903:126. Type locality “Crete.”
- Lepus cypricus* Barrett-Hamilton, 1903:127. Type locality “Cyprus.”
- Lepus parnassius* Miller, 1903:145. Type locality “Agorianni, north side of Lyakura (Parnassus) Mts., Greece.”
- Lepus cyrensis* Satunin, 1905:60. Type locality “Village Barda, Djevanshirski county, Elisavetpolski province of Russia.”
- Lepus e[uropaeus]. pyrenaicus* Hilzheimer, 1906:512. Type locality “(Bagnères), Pyrenäen.”

- Lepus e[uropaeus]. transsylvaticus* Hilzheimer, 1906:512. Incorrect subsequent spelling of *transsylvanicus* Matschie, 1901.
- Lepus e[uropaeus]. meridiei* Hilzheimer, 1906:512. Type locality “(Aveyron), Sudfrankreich [=southern France].”
- Lepus dayanus conneri* Robinson, 1918:15. Type locality “between Ahwaz and Mohammerah, Karun R. [=Karun River], Persia.”
- Lepus europaeus tesquorum* Ognev (in Ognev and Worobiev, 1923), 1923:115. Type locality “Dokuchaevskaya Experimental Station.”
- Lepus europaeus ghigi* de Beaux, 1927:2. Type locality “Stampalia, Island, Aegean Sea” vide Ellerman and Morrison-Scott (1966:437).
- Lepus europaeus caucasicus* Ognev, 1929:75. Type locality “Umgebung von Wladikawkas [=vicinity of Vladikavkaz, North Ossetia].”
- L[epus]. e[uropaeus]. caucasicus* nato *ponticus* Ognev, 1929:75. Type locality “Ansiedlung Beta, Tschernomorski-Gouvernement,” Black Sea Coast.
- L[epus]. e[uropaeus]. caspicus* nato *kalmykorum* Ognev, 1929:75. Type locality “Sangegend [= sand zone of] Akima Ikizochura, Kalmyken-Steppe.”
- Lepus europaeus carpathous* de Beaux, 1929:144. Type locality “a Scarpanto [=in Karpathos].”
- Lepus europaeus iranensis* Goodwin, 1939:4. Type locality “Teheran, Iran; alt about 3500 feet.”
- Lepus europaeus niethermeri* Wettstein, 1943:282. Type locality “Vytina, 1000m altitude, Peloponnese,” southern Greece.
- Lepus europaeus borealis* Kuznetsov, 1944:271. Type locality “Northern Bashkiria,” Bashkortostan Republic of Russia.
- Lepus europaeus biarmicus* Heptner, 1948:709. Replacement name for *Lepus europaeus borealis* Kuznetsov, 1944.
- Lepus cyanotus* Blanchard, 1957:30. Type locality “Lanslebourg, Savoie, France, 2600 m.”
- Lepus capensis astaricus* Baloutch, 1978:444. Type locality “dans la forêt d’Astara à 30 km de la Mer Caspienne.”

CONTEXT AND CONTENT. Order Lagomorpha, family Leporidae, genus *Lepus*. Sixteen subspecies are currently recognized (Schai-Braun and Hackländer 2016):

- L. e. caspicus* Hemprich and Ehrenberg, 1832. See above; *kalmykorum* Ognev is a synonym.
- L. e. conneri* Robinson, 1918. See above; *astaricus* Baloutch and *iranensis* Goodwin are synonyms.
- L. e. creticus* Barrett-Hamilton, 1903. See above.
- L. e. cyprius* Barrett-Hamilton, 1903. See above.
- L. e. cyrensis* Satunin, 1905. See above; *caucasicus* Ognev, *ghigi* de Beaux, are synonyms.
- L. e. europaeus* Pallas, 1778. See above; *albus* Bechstein, *aregenteogrisea* König-Warthaussen, *cyanotus* Blanchard, *flavus* Bechstein, *niger* Bechstein, and *pyrenaicus* Hilzheimer are synonyms.
- L. e. hybridus* Desmarest, 1822. See above; *aquilonius* Blasius, *biarmicus* Heptner, *borealis* Kuznetsov, *campestris*

- Bogdanov, *hyemalis* Eversmann, *tesquorum* Ognev and Worobiev, *tumac* Tichomirov and Kortchagin are synonyms.
- L. e. judeae* (Gray, 1867). See above.
- L. e. karpatorum* Hilzheimer, 1906:512. Type locality “Karpathen [=Carpathian Mountains].”
- L. e. medius* Nilsson, 1820. See above.
- L. e. occidentalis* de Winton, 1898:152. Type locality “Herefordshire,” England.
- L. e. parnassius* Miller, 1903. See above; *niethermeri* Wettstein is a synonym.
- L. e. ponticus* Ognev, 1929. See above.
- L. e. rhodius* Festa, 1914:9. Type locality “Island of Rhodes.”
- L. e. syriacus* Hemprich and Ehrenberg, 1832. See above.
- L. e. transsylvanicus* Matschie, 1901. See above; *campicola* Gervais, *cinereus* Fitzinger, *coronatus* Fitzinger, *maculatus* Fitzinger, *meridiei* Hilzheimer, *meridionalis* Gervais, *nigricans* Fitzinger, *rufus* Fitzinger, and *transsylvaticus* Hilzheimer are synonyms.

NOMENCLATURE NOTES. The vernacular names of *Lepus europaeus* are European brown hare, European hare, brown hare, and field hare. In Germany field hare (Feldhase) is most commonly used throughout the country. Petter (1961) placed *L. europaeus* into *L. capensis* as a polytypic species which ranges from North East Africa eastward across the North Arabian Peninsula and the Middle East, and northward through Israel to Turkey, Russia, and China. He argued that body size, dental characters, and pelage color depend on climatic and ecological variation among habitats. This was accepted until further morphological studies argued the converse. Sludski and Strautmann (1980) stated the “large *L. europaeus*” and “small *L. capensis*” (= *L. tolai*) in Kazakhstan were sympatric species without evidence of hybridization and interpreted it as overlapping ends of a Rassenkreis (ring of populations). Also results of reanalysis by Angermann (1983) indicated a marked discontinuity between both species running from the eastern Mediterranean coast (central Israel) through Iran, and on this basis separated *L. europaeus* from *L. capensis* and *L. tolai* (Hoffmann and Smith 2005). Recent research (Slimen et al. 2005, 2006, 2008) support Petter’s hypothesis that *L. europaeus* and *L. capensis* are conspecific. However, until conclusive evidence is available, most taxonomists retain *L. europaeus* and *L. capensis* as valid species (Hackländer and Schai-Braun 2018).

DIAGNOSIS

Lepus europaeus (Fig. 1) and the sympatric *Lepus timidus* (mountain hare) in the northern hemisphere are very similar in size. Although some arctic subspecies of *L. timidus* may be as large as, or even larger, than the largest *L. europaeus*, *L. europaeus* is generally heavier at 3.5–5.0 kg (*L. timidus* averages from 2.4 kg in the Alps to 3.4 kg in Siberia—Angerbjörn 2018). Head-body length of *L. europaeus* is 550–650 mm (460–560 mm in *L. timidus*). The ears are longer from notch 110–140 mm

Fig. 1.—Adult *Lepus europaeus*, gender unknown, industrial area near Hamburg, Germany, July 2017. Photograph by A. Bock.

and when bent forward they are longer than forehead (versus 67–106 mm in *L. timidus*, ears when bent forward are equal in length to forehead); the tail is also longer at 75–140 mm (mean 95 mm) compared with 53–70 mm in *L. timidus*; length of hind foot is 130–164 mm (mean 147 mm) which is shorter than in *L. timidus* (145–172 mm—[Krapp 2003](#); [Angerbjorn 2018](#)).

The length of the skull (from the most rostral to the most caudal point of the occipital) averages 97.1 mm in *L. europaeus* (*L. timidus* averages 90 mm). The facial region of the skull is extended with markedly raised nasalia ([Fig. 2](#)) compared to a shorter facial and a more concave frontal region in *L. timidus*. Dentale is softer, processus condyloideus is inclined more posteriorly than in *L. timidus*. Diastema relatively long (average 31.2 mm), and at over 80% of lower tooththrow, longer than in *L. timidus*, corpus mandibulae with incisivus (I) inclined anteroventrally (anterodorsal in *L. timidus*). Incisivus 1 (I1) of *L. europaeus* are rectangular in section; ratio of length to width 0.74:0.80 compared to the more quadratic dimension in *L. timidus* of 0.84:0.95; incisors are additionally more curved than in *L. timidus*. Root of I1 far anterior of sutura premaxillo-maxillaris with a frequency of 78.3–100% compared to 98.6–100% in *L. timidus*. Zygomatic length (34.7–41.8 mm) and zygomatic width (44–49 mm) are longer than in *L. timidus* (length = 33.4–37.9; width = 42.5–45.6 mm). Front and rear wings of supraorbital appendix are well developed and mostly free (not as well developed in *L. timidus*), osseous palate shorter (compared to *L. timidus*), choanae wide. Coat color of *L. europaeus* does not change to white in winter as in *L. timidus*, although animals in the northern latitudes may

Fig. 2.—Dorsal, ventral, and lateral views of skull and lateral view of mandible of an adult male of *Lepus europaeus*, collection locality Schwarzenbek, Germany, 02.12.1997, specimen number 8933 (468), Zoological Museum, University of Hamburg, greatest length of skull 95 mm. Photograph by A. Bock.

turn slightly lighter. Teat formula $2p + 4a = 6$ compared to $2p + 6a = 8$ for *L. timidus* ([Krapp 2003](#)).

Although similar in appearance to *L. europaeus*, *Lepus capensis* (Cape hare) is overall smaller and lighter (with ear length 97–114 mm; skull length 27.5–30 mm; length of hind foot 93–103 mm, weight 1.5–2.5 kg). When compared to the sympatric *Oryctolagus cuniculus* (European rabbit) the difference is obvious. The European rabbit is smaller (body weight 0.9–1.8 kg, head–body length 375 [female] and 406 [male] mm), and has a more compact shape. The European rabbit burrows and its leverets are born nidicolous (altricial) compared to the *L. europaeus* which lives aboveground with nidifugous (precocial) leverets. Ears are shorter (when bent

forward they do not extend to the nose) and have no black tips. Furthermore, the eyes do not have a light-brown iris but look black and the pelage has more grayish than yellowish base hair and longer guard hair with black ends (Zörner 1981; Krapp 2003).

GENERAL CHARACTERS

Lepus europaeus is the largest species of *Lepus* in Europe with a head–body length of 550–650 mm. The weight ranges from 3.5 to 5 kg and varies in both males and females during the course of the year, due to food supply and reproductive cycle. Length of cranium is 96–104 mm, width of zygomatic arch 44–51 mm, width of cranium 28.9–35.1 mm, cranium height 26.1–29.7 mm, length of lower toothrow 19–21 mm, and length of upper toothrow 17–19 mm. Depending on geographical location and seasonal changes, the pelage color of *L. europaeus* ranges from tawny-brown to grayish-brown, with a beige-white venter. The face is brown with beige eye rings. Eyes are large with black pupils and light-brown iris. Molting occurs twice a year, one starting around February the other starting in July. The winter coat may be slightly lighter toward yellowish-gray, especially in northern regions of its distribution. The tail (75–140 mm) is V-shaped, black above and white below. Length of hind foot is 130–150 mm. Ears with black tips are 110–140 mm, longer than the forehead when bent forward. External sexual dimorphism is lacking;

thus, sex determination is only possible by examining genitalia (Zörner 1981; Krapp 2003).

DISTRIBUTION

During the last Ice Age (about 12,000 years ago) *Lepus europaeus* was forced into southern Europe, only *L. timidus* could survive in more northern habitats due to its adaptations to colder conditions. After that *L. europaeus* recolonized the postglacial steppe landscape and later adapted well to agricultural farmland (Fickel 2003).

Lepus europaeus is native in Albania, Austria, Belarus, Belgium, Bosnia and Herzegovina, Bulgaria, Croatia, Czech Republic, Denmark, Estonia, Finland, France, Germany, Greece, Hungary, Islamic Republic of Iran, Iraq, Israel, Italy, Latvia, Liechtenstein, Lithuania, Luxembourg, Macedonia, Moldavia, Montenegro, Netherlands, Poland, Romania, Russian Federation, Serbia, Slovakia, Slovenia, Spain, Switzerland, Syrian Arab Republic, Turkey, and Ukraine. *L. europaeus* was introduced in Argentina, Australia and Tasmania, Barbados, Brazil, Canada, Chile, Crete, Falkland Islands (Malvinas), Ireland, New Zealand, Réunion, Sweden, United Kingdom, United States, and Uruguay (Fig. 3; Hackländer and Schai-Braun 2019).

Masseti (2012) gives a broad overview of several *Lepus* taxa of the Ionian and Aegean Islands. He lists *L. e. creticus*, from Cephalonia, Crete, and several small islets of Crete, including Gavdhos, Gavdhopoula,

Fig. 3.—Distribution of *Lepus europaeus*. Subspecies shown are 1), *L. e. europaeus* original distribution = yellow areas, introduced = orange areas; 2) *L. e. occidentalis*; 3) *L. e. creticus*; 4) *L. e. cyprius*; 5) *L. e. hybridus*; 6) *L. e. parnassius*; 7) *L. e. rhodius*; 8) *L. e. syriacus*; 9) *L. e. transsylvanicus*. Possible subspecies of Greece (*L. e. caspicus*, *L. e. connori*, *L. e. cyrensis*, *L. e. judeae*, *L. e. karpathorum*, *L. e. medius*, *L. e. ponticus*, see text for details) are not on map. Map modeled in Quantum GIS 2.4 (Chugiak) by A. Bock (2015), based on information and maps from Chapman and Flux (1990), Slimen et al. (2008), Krapp (2003), Masseti (2012), Reid (2011), Thulin et al. (2006).

Gaidouronisi (Chrysi), Koufonisi, and the Archipelago of the Dionysades. Furthermore, *L. e. ghigii*, from Astypalaia, *L. e. carpathous*, from Karpathos, *L. e. rhodius*, from Rhodos, and *L. e. cyrensis*, from the island of Kos. Subspecies of *L. europaeus* of Paximada (Dionysades Islands) and Koufonisi are smaller than those of Crete; however, they fit the typical morphology of *Lepus europaeus europaeus*, and not *L. capensis* (Niethammer 1992). Distinction of insular subspecies was based on coat coloration, body, and skull measurements, and they can be regarded more as ecophenotypic varieties than true geographical subspecies. Nonetheless, Mamuris et al. (2001) found high mtDNA variability and detected haplotypes from the Greek hares that were different from those of Central Europe. Based on this, Suchentrunk et al. (2003) analyzed the multilocus allozyme variability of Greek hares with regard to the occurrence of indigenous alleles due to the late Pleistocene refuge (see “Genetics”). In summary, Greek hares differ from Bulgarian hares, but within Greek hares the gene pool diversity is slight, thus favoring the hypothesis of a late Pleistocene refugial population in the southern Balkans, with little genetic differentiation among Greek subspecies to support earlier descriptions. A clear difference can be made between Anatolian and European brown hares. In Turkey, Demirbaş and Albayrak (2014) compared morphometric data and pelage color of *L. e. europaeus* subspecies, namely, *L. e. transsylvanicus*, *L. e. cyrensis*, *L. e. caucasicus*, and *L. e. syriacus*, and concluded that Anatolian hares belong to the subspecies *L. e. syriacus*.

In Canada, *L. e. hybridus* was introduced and established in Ontario around the Great Lakes and south of the Canadian Shield. Nine individuals escaped from captivity near Brantford, Ontario, in 1912, slowly spreading in southern Ontario north of Lake Erie (St. Thomas and Woodstock), west and north of Lake Ontario (Toronto) to Goodrich on the east side of Lake Huron. However, it has failed to spread further north (Reynolds and Stinson 1959; Whitaker and Hamilton 1998). In the United States *L. e. hybridus* was introduced into Dutchess County, New York, in 1893. Importations continued through 1911 to provide a game species. *L. e. hybridus* was introduced and established in New York and Connecticut (Hall 1951; Whitaker and Hamilton 1998).

In Australia *L. europaeus* was introduced and became established on the shores of Westernport Bay, Victoria in 1862. Another colony was set up in 1863 on Phillip Island by the Acclimatization Society of Victoria where it thrived and became a source for distribution to many parts, for example, Tasmania and New Zealand (Myers et al. 1989). In Australia *L. europaeus* now occupies about 700,000 km² in the east and south (Stott 2003). In New Zealand the first *L. europaeus* introduction was in 1851 from Britain but it died out, the second introduction of six *L. europaeus* came also from Britain via Australia in 1863 and established a stable population (up to

200 in 1865). Compared to European rabbits introduced at around the same time it did not become a pest (Flux 1990).

For South America, Grigera and Rapoport (1983) and Bonino et al. (2010) give detailed but somewhat conflicting information about *L. europaeus* (considering it conspecific with *L. capensis*). Thirty-six *L. europaeus* were imported from Germany in 1888 at “Estancia La Hansa” near the town of Cañada de Gomez, Province of Santa Fe, Argentina. From France *L. europaeus* was introduced in 1897 near Tandil, Province of Buenos Aires, Argentina, and nine *L. europaeus* were liberated in the Province of Santa Cruz, southern Argentina in 1930. In the 1980s, *L. europaeus* occupied large parts of Argentina, Chile, Uruguay, Paraguay, and southern parts of Bolivia and Brazil. Since then it spread further north and, probably coming from Bolivia, now also inhabits parts of Peru (Bonino et al. 2010). Additional recorded introductions of *L. europaeus* as a game animal are documented by Flux (1990).

FOSSIL RECORD

It is supposed that *Lepus europaeus* derived from *L. capensis*, the oldest known Old World hare of the genus *Lepus* probably in the Middle East. There the complex of *L. europaeus* and *L. capensis* led to a ring of subspecies, for example, *L. e. cyrensis* and *L. e. caucasicus* (Kraupp 2003).

The oldest reliable fossils of *L. europaeus* date back from early to middle Pleistocene (1.8 million–126,000 years ago). In the late Pleistocene a now-extinct subspecies *L. e. gureevi* (126,000–11,784 years ago) lived in the Caucasus; another extinct subspecies *L. e. euxinicus* lived in the Crimea and possibly Moldavia (Benecke 1999). More than 60 fossil sites have been reported for *L. europaeus* in the south of Europe and Asia, including Spain, Italy, France, Yugoslavia, Hungary, Ukraine, European Russia, Caucasus, and Kazakhstan (Kraupp 2003).

The first reliably identified *L. europaeus* fossils north of the Alps appear about 8,000 years ago, thus post-Pleistocene (Musil 1985; Döhle 1999 [not seen, cited in Fickel et al. 2008]). A study by Baryshnikov (2003) on the Mammoth (*Mammuthus primigenius*) found *L. europaeus* in one of three caves in the Caucasus and two of four caves in the Crimea. Holocene (~12,000 years ago) fossils of *L. europaeus* have been found in more than 120 sites in Switzerland, Austria, Poland, Yugoslavia, Hungary, Israel, Moldavia, Ukraine, Crimea, Caucasus, and Ural. Both the Pleistocene and Holocene fossils lay within the range of the recent distribution of *L. europaeus*. Investigation of skeletal remains of animal density at Psede near Malchin, Germany includes *L. europaeus* and dates back to the Holocene corresponding to reforestation after the last Ice Age. However, the determination of *Lepus* species and subspecies based on fossil skulls is difficult, and the above statements should be accepted with caution (Fischer and Heinrich 1983).

FORM AND FUNCTION

Form.—The joint of the nasal bone of *Lepus europaeus* is almost as long as the suture of the frontal bones. Width of the choanae gap exceeds that of the hard palate and does not narrow caudally. Nasal bones are wide and clearly stand out from the outer rim of the premaxillare which itself exceeds its length. Entrance to nasal cavity is wide, rear protrusion of zygomatic arch is short and front and rear wings of processus supraorbitalis are well developed and mostly free (Krapp 2003).

Teeth are covered on all sides with enamel, thicker and harder on the labial than on the lingual side; thus on the lingual it wears quicker and teeth stay sharp. Rootless teeth grow continuously; however, molar milk teeth (premolars) of young *L. europaeus* have roots and are low crowned. The dental formula is: i 2/1, c 0/0, p 3/2, m 3/3, total 28. General designation of teeth are for upper jaw I¹, I², P², P³, P⁴, M¹, M², M³ in lower jaw: I₁, P₃, P₄, M₁, M₂, M₃. The vertebral column of *L. europaeus* consists of 7 C, 12 T, 7 L, 4 S, 15–17 C, total 45–47. The clavicle is rudimentary with no connection to scapula and sternum. Compared to *Oryctolagus* and all other genera of rabbits, the muscles of *L. europaeus* are dark with long fibers, characteristic of a long-distance runner (Krapp 2003). The mean heart weight at 1% of the body weight is relatively large (0.72–1.27%). The liver is large, 2.8% of the body weight. The uterus shows a labyrinth-like hemoendothelial placenta; females have 3–5 pairs of mammae, two pairs thoracic, three pairs ventral (Zörner 1981).

The stomach of *L. europaeus* is pouch-like with the esophagus joining in its middle. One side is bulged, the other narrows to merge with the intestinal tract. The stomach has a storage capacity of about 350 ml. The small intestine consists of 8–10 Peyer's patches and merges into a well-developed and folded cecum, with an inner spiral; total length of cecum longer than the whole body. Its capacity is many times that of the stomach (Zörner 1981).

Function.—The digestive processes of the small and large intestine are comparable to other vertebrates. However, the physiology in the cecum differs markedly in *Lepus europaeus* and other *Lepus* species. Feces are either hard (normal) or soft. Soft feces originate from the fermented materials in the cecum and are reingested to obtain vitamins and microbial proteins (Hirakawa 2001). The reingestion process and function were first described in a tame *L. europaeus* by Drane (1895) and the timing, 0600–1600 h, was confirmed in wild *L. europaeus* by Watson and Taylor (1955). Individual *L. europaeus* in New Zealand reingested soft feces about 10 times from 0840 to 1530 h; hard feces, composed mostly of poorly digestible large food particles, were normally discarded at night but also eaten in times of food shortage (Flux 1981).

Leporids prevented from eating feces show signs of malnutrition. *Lepus brachyurus* (Japanese hare) and *Lepus timidus* ingest hard feces for the first hour of resting in the morning, then soft feces until the early afternoon, and then again hard feces until dusk when they leave the form to start nighttime activity.

For further details, see the comprehensive review by Hirakawa (2001).

In *L. europaeus*, hormonal production is influenced by the photoperiod. Caillol et al. (1986, 1992) investigated seasonal variation in the pituitary response in *L. europaeus* from October 1983 to September 1984. Production of the luteinizing hormone in the pituitary gland is regulated by luteinizing hormone-releasing hormone. The study showed that both luteinizing hormone and the pituitary response to luteinizing hormone-releasing hormone injection rose in spring with increasing day length. By April full reproductive activity was reached with almost all females pregnant; ovulation continued until July. Thereupon the testicular testosterone production and ovulation decrease (Lincoln 1974; Flux 1987). An analysis of apoptosis and proliferation of testes found active testosterone-producing Leydig cells to appear in the middle of November along with the start of the breeding season at winter solstice in December (Leydig cells were absent in September—Štrbenc and Bavdek 2001).

Lepus europaeus has several glands important for communication, recognition, and reproduction: the submandibular gland, the chest gland, and the Harderian gland (eye gland) on the head; and the inguinal gland (on both sides of the genitalia) and the anal gland. Knowledge of the putative nose gland is still lacking. However, it is known that submandibular glands are more prominent in males than in females. Glands on the head transfer scents to body and feet during grooming, at the same time marking the environment with an individual footprint. *L. europaeus* marks stones and twigs thus emphasizing its home range. In females the inguinal gland is more prominent than in males. It is supposed that secretion, indicated by a yellow crusting in the inguinal region, promotes sexual attraction. Anal glands are the same size in both sexes and might serve to mark feces, thus important environmental areas. Latrine marking as known from the European rabbit has not been observed in *L. europaeus*. However, urine marking of the environment and conspecifics is common (Krapp 2003).

The resting metabolic rate (mean $\pm$ SD) of five adult *L. europaeus* from Southern France was 0.54 ± 0.071 ml O₂ g⁻¹ h⁻¹ (Kronfeld and Shkolnik 1996). Hackländer et al. (2002a, 2002b) analyzed the metabolic rate of leverets by measuring the rectal temperature and found that the resting metabolic rate depended on ambient temperature and body weight (thus energy uptake). Basal metabolic rate of leverets declined from 0.54 W kg⁻¹°C⁻¹ in week 1 to 0.21 W kg⁻¹°C⁻¹ in weeks 3–5 (Hackländer et al. 2002a).

Valencak et al. (2010) examined the maximum sustained metabolic rate and its correlation to possible limited heat dissipation. They hypothesized that heat dissipation limitation would constrain energy turnover in lactating European hares. The metabolizable intake of females was measured during lactation at different ambient temperatures (mean $\pm$ SEM): In group 1 females and their litters were both exposed to $22 \pm 2^\circ\text{C}$, in group 2 both were exposed to $5 \pm 2^\circ\text{C}$, whereas in group 3 females were exposed to $22 \pm 2^\circ\text{C}$ while their litters were exposed to $5 \pm 2^\circ\text{C}$.

The metabolizable energy intake (MEI) reflected heat production at all times as stored body energy was released rather than retained. Energy from food was largely transferred to milk, and as soon as solid food intake of leverets began during lactation the MEI of the females decreased. Compared to other animals this result suggests that none of the lactating females encountered an actual physiological limitation as heat load seemed not to be a physiological constraint determining lactational performance (Valencak et al. 2010).

Lepus europaeus body temperature averages 38.3°C (38.0–38.6°C—Paci et al. 2006), and a tame *L. europaeus*, normally recorded at 36.7°C, reached 41.1°C while hyperventilating (Drane 1895). The large ears regulate temperature, not only by dissipating heat on hot summer days but also by retaining warmth in winter by reducing blood flow. Kronfeld and Shkolnik (1996) found that the water turnover (mean $\pm$ SD) was 336.8 ± 22.9 ml day⁻¹ Bm^{-0.82} (with Bm = body mass). Normally, *L. europaeus* covers water needs by food uptake. However, when green grass and other water-containing food are scarce, *L. europaeus* drinks or eats snow (Zörner 1981).

In *L. europaeus* the average heart rate is 102 min⁻¹ and the average respiratory rate is between 40 in a tame individual (Drane 1895) and 71 min⁻¹ in laboratory animals (Noszczyk-Nowak et al. 2009; Paci et al. 2006). *L. europaeus* is a typical flight animal, with its lateral eyes giving a 360° field of vision. However, the disadvantage is that only moving objects can be located. Binocular vision is available where fields of vision overlap; 10° forward and 9° backward (Kovacs and Heltay 1985). It often waits until the very last moment and then escapes at high speed. Large ears indicate a good sense of hearing for distant noises and sounds. *L. europaeus* reacts to the slightest difference in background noise level, raising its body and trying to locate the origin of the sound to prepare to escape. *L. europaeus* also has a sense of touch with tactile bristle hairs on forehead and upper lip (Zörner 1981). The olfactory sense is very well developed as behavior studies show; a male crossing the trail of a female that passed 10 min earlier knew immediately which direction she had taken (Flux 1981). During my long-term observations I have observed individuals intensively “checking the wind” to identify sources of danger, to locate familiar places, or to recognize conspecifics, especially during the breeding season. The sense of taste probably plays an important role in food selection (Zörner 1981; Krapp 2003).

ONTOGENY AND REPRODUCTION

Ontogeny.—Living embryos can be detected by ultrasound at day 11 of gestation (Roellig et al. 2010). Leverets of *Lepus europaeus* are precocial, born with eyes open and fully furred in the same pelage color as the adults. The first molt in leverets occurs at a weight of 1.25–1.75 kg, regardless of time of year and the second molt to winter pelage is at the same time as in adults (Flux 1990).

The average head–body length of a newborn is about 178 mm, length of hind foot 42 mm, ear length 35 mm, and tail length 36 mm; weight 123 g, range 100–165 g (Zörner 1981; Flux 1990). For captive *L. europaeus* fed the same diet, weight at birth (mean $\pm$ SEM) varies with season and litter size (January–March: 114.3 ± 7.7 g in litters of 1 [$n = 23$] and 88.34 ± 5.7 g in litters of 4 [$n = 12$]; April–October: 124.3 ± 7.0 g in litters of 1 [$n = 20$] and 107.4 ± 4.6 g in litters of 4 [$n = 48$ —Martinet et al. 1970]). Postpartum parental care of litters is short. Lactation length until weaning is on average 35 days; nursing occurs only once a day, primarily after sunset. Leverets are fed milk with a high fat content of 23.01% (Schneider 1979; Zörner 1981). After 10 days small amounts of solid food are consumed. Then leverets lose their milk teeth, and the female shows aggressive behavior toward them (Fig. 4). From birth to weaning leverets increase their weight (mean $\pm$ SD) 8.5-fold from 121 ± 3 g to $1,031 \pm 26$ g (Hackländer et al. 2002b). Reproductive maturity of both male and female is reached after 4–8 months. To determine the age of young *L. europaeus* Stroh’s tubercle palpation (Stroh 1931) is a useful method based on ossification of the epiphyseal cartilage of the ulna. In young *L. europaeus* the epiphyseal cartilage can be palpated in the forelegs for 6–8 months (Broekhuizen and Maaskamp 1979). Another widely used method, the dry weight of eye lenses, classifies categories of <6 months, 6–12 months, 1–3 years, and >3 years. Over 3 years there is too much individual variation (Andersen and Jensen 1972).

Fig. 4.—Juvenile *Lepus europaeus* born in early 2020, gender unknown, industrial area near Hamburg, Germany, May 2020. Photograph by A. Bock.

Reproduction.—The start of sexual activity in the breeding season is the result of a complex system involving photoperiod and resulting production of hormones in the hypothalamus and pituitary gland, climatic conditions, and individual nutritional status (Nelson et al. 1990; Krapp 2003). *Lepus europaeus* is a polyestrous seasonal breeder with a reproduction period of about 215–256 days. Generally, breeding season starts in mid-winter (December–February) in males followed by females about a month later (Zörner 1981; Caillol et al. 1986). In New Zealand and other places south of the equator, breeding season starts soon after the shortest day of year in June and in New Zealand over 90% of adult females are pregnant from August to February (Flux 1990).

In males from the northern hemisphere, inhibition of spermatogenesis starts in September and lasts to mid-December; in October and November gonads are entirely inactive (April–May in New Zealand—Flux 1990). Testes are relocated into the inguinal region, and their weight reaches a minimum for the year. Production of sexual hormones testosterone and luteinizing is low. At the end of December testes relocate to the scrotum, becoming visible. Their weight increases rapidly and spermatogenesis probably starts at a weight of 5 g (Zörner 1981).

In females, the cycle of gonad development starts in January, about a month later than in males; lowest weight of ovaries ranges from November to December. As *L. europaeus* is a strictly induced ovulator, stimulation by copulation is considered a necessity. These cycles depend on climatic conditions, and in a warm winter the hormonal resting period might be shorter (Roellig et al. 2010).

Considered to be an r-selected species with early maturity and relatively short life span, reproduction within the breeding season can be increased if a new conception overlaps an ongoing pregnancy (superfetation). Thus, the normally 42- to 43-day gestation period can be reduced to only 38 days. However, this can be seen mainly in captive hares (Flux 1990). Ultrasonography revealed a new set of corpora lutea near the active corpora lutea of the current pregnancy up to 2 days before delivery. Prepartum conception shortens the reproductive cycle, increasing the average number of litters within the breeding season, thus enhancing reproductive success (Roellig et al. 2010).

A female gives birth to on average eight leverets per year. If conditions are good, 11 leverets are possible; unfavorable conditions can lead to a remarkable decrease in offspring due to embryonic resorption before mid-term (embryo about 25 mm in length—Roellig et al. 2010). Maximum reproductive performance was 12 in Denmark (Hansen 1992 [not seen, cited in Krapp 2003]) and 20 in the South of France (Bray 1998).

Females that do not take part in reproduction show changes in the uterus that lead to sterility more frequently in old females (Krapp 2003). In the northern hemisphere young females born at the beginning of the breeding season normally do not reproduce in the same year; however, young females in Argentina and New Zealand may breed in their year of birth. This can be explained

by the food which is available and of good quality (high protein content) year-round (Dietrich 1985).

Number of litters during one breeding season averages 3 (range 1–4), and average litter size is 3 (range 1–5). Prenatal mortality determines the litter size; the highest death rate is in spring and autumn (23.4–58% and 30–55.6%, respectively), the lowest in summer (12.8–28%—Zörner 1981; Krapp 2003). Observations of parturition in free-ranging *L. europaeus* are rare. If not disturbed the female gives birth to the leverets at one site. If disturbed, she might split places for parturition. However, dispersal of the litter is induced by the leverets themselves after about 3 days, probably a precaution against predation on the whole litter (Zörner 1981).

ECOLOGY

Population characteristics.—Estimates of population density depend on the method of data acquisition and the time of year (see “Miscellaneous”). According to Pikula et al. (2004) the highest mean densities can be reached in warm and dry or moderately dry districts with mild winters and shorter duration of sunshine. Densities of *Lepus europaeus* vary with availability of food and shelter and number of predators. Optimal conditions can lead to densities up to 100 individuals/km² (Klansek 1996) but also densities of 1 individual/km² are viable. High densities in Austria can exceed 100 individuals/km²; but in Switzerland (adjacent to Austria) densities reach only 6–19 individuals/km² (Pfister et al. 2002). On islands with almost no predation pressure, for example, Illumø in Denmark, density reached 339 individuals/100 ha without hunting (Abildgård et al. 1972). Nevertheless, even with hunting, density is higher on predator-free islands than in areas where predators exist (e.g., island Ven, South Sweden—Frylestam 1979). In Germany densities fluctuated from 5 to 26 individuals/km² averaging 11 individuals/km² in 2013 (Wildtier-Informationssystem der Länder Deutschlands [WILD], <https://www.jagdverband.de/forschung-aufklaerung/wild-monitoring>). In Argentina *L. europaeus* reached densities of 100 individuals/km² (Dietrich 1985) compared to only 20–30 individuals/km² in New Zealand (Flux 1990). Densities vary depending on landscape, climate, predation, and diseases. Survival and mortality are influenced by a complex of interacting factors including climate and geographic area, diseases, predators, and anthropogenic factors like agriculture, hunting, or traffic. Generally, mortality is high in leverets; about 75% of them die within the first 8 months. Average adult mortality is about 38% (Broekhuizen and Maaskamp 1979; Gehle 2002).

Despite high leveret mortality young *L. europaeus* dominate the population with about 55%, varying from 30% to 70% depending on conditions. *L. europaeus* that are 1–3 years of age form about 30% of the population, and those 3 years and older about 14% (Zörner 1981; Krapp 2003).

Lepus europaeus can reach an age of 8–13 years. A mark-recapture analysis revealed that females outnumber males when

older; thus, females have a higher life expectancy than males. Generally, *L. europaeus* that dominate and effectively contribute to the population are 8 months to 5 years of age. The sex ratio can vary with annual climatic and ecological conditions, and changes in population dynamics. However, overall it is close to 1:1 (Zörner 1981; Dietrich 1985; Flux 1990; Krapp 2003).

Space use.—Originally, *Lepus europaeus* inhabited temperate savanna or grassland. After forest clearance and reclamation of wetlands for cultivation and agriculture *L. europaeus* followed to take advantage of the food supply. In this situation, *L. europaeus* prefers open fields and pastures bordered by hedgerows and woodlots (Fig. 5). Investigation of movements of radiotracked *L. europaeus* in England and Germany found a preference for low-growing crops, different areas used for feeding during night and sheltering during day, preference for woodlands and hedges and shifting activity according to crop development (Tapper and Barnes 1986; Rühle and Hohmann 2004). *L. europaeus* favors high diversity of plants with different crops, vegetables, and high-energy weeds like clover and corn poppy to cover physiological and reproductive needs (Jennings et al. 2006; Reichlin et al. 2006). Studies by Tapper and Barnes (1986) and Rühle and Hohmann (2004) found that night ranges were larger than day ranges and ranges increased as the number of habitats increased. The home range of *L. europaeus* is about 21–190 ha (Rühle and Hohmann 2004; Flux 2009). Males have larger home ranges than females but once a home range is established *L. europaeus* shows high site fidelity (Bray et al. 2007). In Australia, *L. europaeus* home ranges averaged 149 ha, compared to 10 ha for the European rabbit. *L. europaeus* can show extraordinary homing and sense of direction. In two relocation projects in Poland two of 500 and two of 300 *L. europaeus* returned “back home” over a distance of 229 km and 464 km, respectively (Zörner 1981). *L. europaeus* has great mobility that enables it to travel 20 km in a night and hundreds of kilometers in heavy snow or drought to look for food (Angermann et al. 1990). Also, if densities

are high, it moves to find other suitable habitats, even up to elevations of 2,000 m (Flux 1990).

Lepus europaeus lives aboveground year-round, exposed to all climatic conditions. Even when giving birth, females do not build nests but choose dry and sheltered places. It scratches shallow “forms” in places that meet its requirements, for example, exposed to sunlight (in winter), dry elevations in wetlands or in places that provide enough cover. The size of the form equals the size of the resting *L. europaeus* (Zörner 1981).

Diet.—*Lepus europaeus* is exclusively herbivorous and generally the diet depends on what is available. The diet consists of a variety of sweet grass (*Poaceae*), weeds (*Asteraceae*, *Brassicaceae*, *Fabaceae*, *Plantaginaceae*), crops like rye (*Secale cereale*), wheat (*Triticum vulgare*), barley (*Hordeum*), and oat (*Avena sativa*); however, weeds and wild grasses are selected over crops when available (Reichlin 2006). A study of *L. europaeus* in southern Sweden revealed that rape, widely represented in agriculture, was less eaten in mixed farmland. It was only selected in rape monocultures; however, *L. europaeus* avoided it in late autumn possibly due to its content of glucosinolates (Frylestam 1986). The autumn diet in Hungarian *L. europaeus* included 24 species, among the cultivated species mainly wheat, *Triticum aestivum*, but grasses and shrubs (and a high consumption of elderberry, *Sambucus*) were also important food components in every area (Katona et al. 2010). Generally, food intake shifts to bark, young branches, and buds when weeds and crops are scarce in winter; thus, *L. europaeus* can damage reforestation or fruit-growing areas. In winter, *L. europaeus* generally prefers crops over weeds and also feeds on sugar beet and carrots if provided by hunters (Zörner 1981; Reichlin et al. 2006). In late autumn and winter, foraging takes place at night, dusk, or dawn; with increasing day length and vegetation growth, and the onset of breeding season, foraging extends to daytime. Food in other parts of the world, for example, alpine grassland in New Zealand, may comprise species never previously encountered such as *Aristotelia fruticosa*, *Celmisia allanii*, *Celmisia coriacea*, *Chionochloa rubra*, *C. pallens*, *C. flavescens*, *Dracophyllum uniflorum*, *Hymenanthera alpina*, *Poa colensoi*, and *Schoenus pauciflorus* (Flux 1990).

In captivity *L. europaeus* drinks water on a regular basis; the amount of food (hay, hare pellets) intake is approximately 500 g. If temperature decreases food intake increases (Zörner 1981).

Diseases and parasites.—*Lepus europaeus* is sensitive to diseases, and due to its decreasing population size it is an important research topic (Frölich et al. 2001; Wibbelt and Frölich 2005). Diseases caused by bacteria and parasites dominate; virus infections play a minor, yet threatening role. Spread and extent of infections exacerbate with cool and damp weather. The European brown hare syndrome (EBHS) is a highly contagious and fatal disease. The calicivirus (genus *Lagovirus*, family *Caliciviridae*) affects the inner organs, for example, kidney, spleen, and liver, eventually causing death. EBHS was first described in Sweden in 1980 by Gavier-Widen and Mörner

Fig. 5.—*Lepus europaeus* in typical habitat near Hamburg, Germany. Photograph by A. Bock.

but it has been reported from all over the world (Wibbelt and Frölich 2005; Paci et al. 2011).

Rabbit hemorrhagic disease virus (RHDV), a calicivirus affecting only European rabbits (*Oryctolagus cuniculus*), was first reported in China in 1984. In 2010 a new strain of this calicivirus, RHDV2, emerged in France and has been recently reported to cause widespread epidemics in France not only in European rabbits but also in *L. europaeus*. Symptoms are similar to those of the EBHS, for example, hyperemic trachea, hepatitis necrosis, and splenomegaly (Le Gall-Recule 2017). Myxomatosis caused by the myxoma virus is very rare but occasionally transferred to *L. europaeus* by bloodsucking insects or contact with infected rabbits. In *L. europaeus* the disease is protracted; pathoanatomical findings include nodular swellings of skin and subcutaneous tissues on back and limbs. Papillomatosis can be found only occasionally; symptoms caused by the virus are tissue proliferation of skin and mucous membranes (Frölich et al. 2001).

Among bacterial infections, pseudotuberculosis (*Yersinia pseudotuberculosis*) is one of the most important diseases in *L. europaeus*. It occurs year-round sometimes with a plague-like spread and high mortality. Impact is higher under cool and damp weather conditions. Infection occurs via oral uptake of infected food. Symptoms are diarrhea, respiratory problems, ataxia, and paralysis. Most *L. europaeus* become weak, lose weight, and die after 8–10 days or some weeks due to organ failure of liver and spleen, or acute enteritis and swelling of intestinal lymph nodes (Frölich et al. 2001). Pasteurellosis caused by *Pasteurella multocida* is a widespread pathogen also known as hemorrhagic septicemia. This disease occurs mainly in spring and winter, following cool, damp weather, food shortage, and a higher parasite burden, with a mortality of up to 80%. Infection occurs either by *P. multocida* already present in the respiratory system spreading into the bloodstream or by ingestion of contaminated food. Symptoms are hemorrhagic laryngotracheitis, petechial subserosal bleeding, and swelling of liver and spleen. Acute cases result in death within 24–48 h; rarer subacute cases the animal may live for days or weeks before death occurs. Brucellosis (*Brucella suis*) is restricted to limited geographical areas as *L. europaeus* is not highly affected. However, chronic septicemia may extend over a year or longer; at first, symptomless but then the infected individual loses weight, weakens, and develops yellow-gray purulent and necrotizing nodular tissue affecting genitals, liver, spleen, lung, and lymph nodes. Infection occurs mainly by mating, but also via an aborted fetus, infected food, or suckling. Tularemia caused by *Francisella tularensis* is a re-emerging disease worldwide with recent outbreaks in the United States, Asia, and Europe (Maurin et al. 2011). Disease carriers are not only *L. europaeus* but also insects, birds, or rodents. Infection occurs via animal–animal contact, infectious food, or indirectly via bloodsucking insects. Affected animals die within a few days when the course is acute septicemic or if chronic after 2–3 weeks. Symptoms are not obvious; however, the animal is emaciated at death. Pathoanatomical symptoms are

swelling and hyperemia of lymph nodes and spleen. Grayish-white foci with diameters of 0.1–1.0 cm are areas of granulomatous inflammation, frequently necrotic. This pathogen can also lead to symptoms in humans which arise after 2–3 days with fever, headache, sweating, and vomiting. Infection occurs mainly when eating insufficiently cooked meat or if hunters get injured during preparation of *L. europaeus* after hunting (e.g., cut in the hand—Frölich et al. 2001; Gyuranecz et al. 2010). Generally, antibiotic therapy is successful. Staphylococcus (*Staphylococcus aureus*) is a widespread disease affecting also mucous tissue of healthy animals. Infections occur via food uptake or indirectly via insects or wounds on the skin, especially during the breeding season when mating fights occur. In the chronic course of the disease *L. europaeus* loses weight and eventually dies. Pathoanatomical findings are encapsulated, purulent abscesses that can reach remarkable dimensions. In most cases they are located in the skin or subcutaneous tissue but can also appear in organs or joints. Another special form is malignant eczema. Hair follicles on the soles of the foot inflame, leading to parakeratoses and eventually to serious necrosis (Gyuranecz et al. 2010).

Among protozoal infections coccidiosis is caused by several (host-specific) *Eimeria* species (*Eimeria europaea*, *E. hungarica*, *E. leporis*, *E. robertsoni*, *E. semisculpta*, *E. septentrionalis*, *E. stefanskii*, *E. townsendi*, *E. stiedai*—Frölich et al. 2001). It is widespread and infections are favored by food scarcity and bad weather. Leverets are especially prone. Infection occurs via food uptake (of *Eimeria* oocysts), grooming, or during suckling infected teats. *Eimeria* species mostly affect intestinal surfaces and gland epithelium, leading to enteritis combined with diarrhea. Abdominal swelling is caused by fermentation. Symptoms are mostly catarrhal enteritis and yellow-white lentil-sized deposits. Toxoplasmosis caused by *Toxoplasma gondii* leads to cyst formation in liver, spleen, and intestinal lymph nodes. The final host is *Felis silvestris catus* (domestic cat); *L. europaeus* and other animals can be intermediate hosts. When affected, *L. europaeus* shows inactivity, loss of appetite, and lies on the ground. The disease is often acute with subsequent death. Some individuals show catarrhal enteritis and white nodules in the liver (Frölich et al. 2001).

Diseases caused by trematodes, cattle liver fluke (*Fasciola hepatica*), and sheep liver fluke (*Dicrocoelium dendriticum*) depend on the presence of certain snail species as intermediate hosts. Infections occur via food uptake (Frölich et al. 2001). *F. hepatica* symptoms are emaciation, weakness, and edema. However, on the acute course animals generally show a good nutritional status. Pathoanatomically, bile ducts can be expanded vial-like with walls bloated, and the abdominal cavity can be filled with red liquid. *F. hepatica* is rare in *L. europaeus*, whereas *D. dendriticum* affects *L. europaeus* more frequently especially in sheep-grazing areas. Gastrointestinal worms (nematodes) of importance are *Trichostrongylus retortaeformis* affecting the duodenum, *Graphidium strigosum* affecting the stomach, and *Trichuris leporis* affecting the cecum. *G. strigosum* inhibits secretion of gastric juices and leads, when

parasite load is heavy, to anemia, emaciation, and increased sensitivity to stress. *T. retortaeformis* symptoms are similar to those of *G. strigosum*. *T. leporis* produces toxic metabolites, leading to intestinal necrosis and in leverets also to developmental disorder and weight loss. The lungworm, *Protostrongylus commutatus* (synonym *P. pulmonalis*), is widespread and can be found in up to 60% of populations. Symptoms are cough, nose secretion, dyspnea, pleurisy, and pneumonia (Frölich et al. 2001). *P. oryctolagi* has recently been found in 55% of 347 *L. europaeus* in France (Guitton et al. 2016). Additional parasites are fleas (*Ctenocephalides canis*, *C. felis*, and *Spilopsyllus cuniculi*, the rabbit flea); *Haemodipsus lyriocephalus*, sucking hare lice; *Ixodes ricinus*, the castor bean tick; *Ixodes hexagonus*, the so-called hedgehog tick; *Listrophorus gibbus*, the rabbit fur mite; and *Psoroptes communis*, the common scab mite (Frölich et al. 2001).

Recently, *Leishmania infantum* infections could be confirmed in *L. europaeus* in Greece and Spain (Ruiz-Fons et al. 2013; Tsokana et al. 2016). Leishmaniasis is a vector-borne mammalian disease caused by a protozoan flagellate of the genus *Leishmania*, transmitted by phlebotomine sandfly species. Although, *L. infantum* seems not to cause clinical disease in *L. europaeus* is an important pathogen for humans and other mammals, thus should be subject for further examination.

Interspecific interactions.—Predators of *Lepus europaeus* include all carnivorous mammals, for example, the red fox (*Vulpes vulpes*) and domestic cat, mustelids, omnivores, for example, wild boar (*Sus scrofa*), birds of prey from the size of the goshawk (*Accipiter gentiles*), and sparrow hawk (*Accipiter nisus*); also corvids are a danger especially for leverets. In Europe, the red fox is the main predator. There are many speculations that predators do not have the potential to limit population sizes of *L. europaeus*; red fox control in Sweden, England, and France increased leveret survival, but appears to have no effect on *L. europaeus* density in following years (Letty et al. 2016). Predator avoidance strategies include camouflage, cryptic behavior, and frequent surveillance, deep crouching in forms or vegetation, and specialized escape behavior, for example, running at high speed at up to 50–80 km/h with sudden turns to mislead the predator. Also the ability to jump is extraordinary; if in danger *L. europaeus* can jump 2 m high and 2.7 m wide (Zörner 1981). In New Zealand, *L. europaeus* experiences little predation pressure (Flux 1990).

Miscellaneous.—Because of decreasing numbers of *Lepus europaeus* since the 1960s it became important to find a survey method to estimate trends in population density apart from hunting tallies as in past years. Survey techniques investigated included line transects, belt transects, spotlight counts (direct methods) and as an indirect method fecal pellet counts (Langbein et al. 1999). The current method of choice is spotlight counts over 800 ha carried out during periods of good weather in spring before crops are too high and in autumn after crops are harvested. Counting is carried out two to three times during the 1–2 h after sunset using lights reaching to 150 m

with a gap of at least 10 days between the count. The driver keeps to 25 km/h and the counter notes *L. europaeus*. Recently, the ability of drones, carrying thermal imaging cameras, to identify animals as small as mice from 200 m is likely to supersede ground counts (Karp 2016).

For research purposes it is possible to keep *L. europaeus* in captivity but there is not much information available for *L. europaeus* except in France (e.g., Martinet 1970; Verdier 1976) and Italy (Spagnesi and Trocchi 1980). In Germany there are only a few facilities that keep *L. europaeus*, mainly in rabbit cages. Kirchner et al. (2012) compared the solitary cage system to spacious enclosures with unisex groups using the stress indicator fecal glucocorticoid metabolite. There was no significant difference (mean $\pm$ SE) between solitary cage systems (39.38 $\pm$ 16.89 ng/g) and spacious enclosures (38.83 $\pm$ 12.63 ng/g). However, the latter cage system allows normal behavior and locomotor activity. Paci et al. (2006) determined that glucose level was a good indicator of stress level finding 234 $\pm$ 9.4 mg/dl (mean $\pm$ SE) was the mean glucose value of nonstressed *L. europaeus* and 128 $\pm$ 7 mg/dl the mean value of stressed *L. europaeus*.

As *L. europaeus* is also a valuable game animal, hunters can breed and release them to increase the stocking density. However, breeding requires a lot of knowledge and experience to be successful. Rigo et al. (2015) studied behavior, welfare, health performance, and mortality of farmed *L. europaeus* in Italy. Mortality was between 2.5% and 22.9% in newborn and 15.4% and 24.7% in adults. Main causes were respiratory diseases, starvation, and traumas in young and respiratory diseases and ulcerative pododermatitis in adult *L. europaeus*. Thus, farmed *L. europaeus* seem to be affected by diseases resembling those of rabbits reared under intensive conditions. Husbandry has to be improved to reach satisfactory technical standards and to preserve the health of the caged individuals (Rigo et al. 2015). In any case although individual *L. europaeus* may be tamed (e.g., Drane 1895), it is a wild animal and should not be domesticated like a rabbit (Zörner 1981).

Historically, *L. europaeus* has been hunted since the Bronze Age (2,200–800 years BC). Numbers of *L. europaeus* increased in the northern hemisphere slowly after the Ice Age (10,000 BC) but decreased again due to expanding forests (Zörner 1981). It is an important game species throughout its distribution, including those areas where it has been introduced (<http://www.iucnredlist.org>—Flux and Angermann 1990). Hunting methods changed in the course of history. Hunting with hounds, pub hunt (= Falconry, hunting of small game by means of falcons or hawks in natural habitat, dating back to approximately 2,000 BC), and hunting with nets were used for a long time. However, with refining weapon technique hunting for *L. europaeus* changed. Hunting with hounds is not carried out anymore, pub hunt is just carried out to maintain the tradition, and hunting with nets is used if living *L. europaeus* are needed. The most common hunt nowadays is the battle or witch hunt with special rules; others are hide hunt, single hunt with a dog, and rough shooting. However, especially in areas with low densities the number of *L. europaeus* to be shot should be determined by previous census (Zörner 1981).

BEHAVIOR

Grouping behavior.—*Lepus europaeus* has long been supposed to be a solitary animal except during the breeding season (Flux 1990) but actually keeps in contact with neighbors even in areas with low densities, and in pairs or groups of two or three at higher densities (Schneider 1979; Zörner 1981; A. Bock, in litt.). If food is unevenly spaced it benefits from higher group sizes allocating more time to feeding with increased corporate vigilance. However, when food is clumped in small patches dominant *L. europaeus* attempt to monopolize the resource. When breeding, it gathers in groups of up to 13 (Lincoln 1974; Zörner 1981; Monaghan and Metcalfe 1985; Flux 2009; Bock 2013).

Grouping is dynamic and hierarchies do not exist as in herds with leaders. There is a high tolerance among conspecifics and only under harsh conditions does it rebuff other approaching *L. europaeus*. In the breeding season, males fight for females; however, serious fights are rare. Rather, it shows a series of displays; “showing off,” humility gestures, and conciliation gestures. Between mother and litters social contact is restricted to suckling once a day and possibly also support in dangerous situations, when females approach their squealing young (Schneider 1979; Zörner 1981; Krapp 2003).

Reproductive behavior.—The breeding season for *Lepus europaeus* starts around mid-December in the northern hemisphere and in June in the southern hemisphere. Sexual hormone production (e.g., testosterone) increases, leading to increased activity during daylight hours (Flux 1965; I have observed this daylight activity during two field seasons, June 2015 and 2019). *L. europaeus* gathers in mixed-sex groups, some may leave the group, others arrive. Courtship includes several changing sequences. Males seek to win a female by chasing; it makes conciliation sounds, approaching the female, trying cautious contact, chasing away or fighting with other males. Boxing between males establishes rank and the right for a female. Fights can be distinguished as “distance fights” and “breast fights.” In both cases *L. europaeus* stands on hind legs. In distance fights however, they stretch the back and touch only each other’s front paws; in breast fights front paws touch also each other’s face. If males come too close, females show defense either in turning around and sitting in a threatening position or by directly rebuffing the male. Active phases are often interrupted by resting phases with grooming and feeding. Mating games in the group continue until male–female pairs separate from the group. If the female does not respond to the males’ courtship the pair separates; however, if the female does respond chasing is prolonged. Courtship can continue several days, body contacts increase, finally leading to more intensive contacts where the male touches repeatedly the belly of the female thus triggering ovulation. Eventually, the male jumps on the back of the female for mating several times in succession (Krapp 2003). Either the couple separates or the procedure starts anew. Often, there is a so-called satellite-male

nearby that observes the pair over days, approaches, and tries to mate with the female (Schneider 1979; Flux 1981; Krapp 2003). However, I have observed that if a male wins a female he defends her by chasing away other competitors coming closer than 3–4 m.

Communication.—Vocalizations play a minor role in *Lepus europaeus* communication. There is a loud squeal when injured or threatened. It growls while chasing and mating (like rabbits). *L. europaeus* grinds its teeth which is considered to be a threat or fear sound. However, rabbits grind when lying peacefully and relaxed, so this might be the same in *L. europaeus*. Like the European rabbit, *L. europaeus* uses a special way of urinating. First, there is so-called mark urination, where the back and tail is lifted during urination; second, it sprays urine deliberately toward conspecifics (Zörner 1981; Krapp 2003).

Miscellaneous behavior.—*Lepus europaeus* is mainly nocturnal or crepuscular. However, physiology does not indicate nocturnal activity based on its visual anatomy and cornea size. *L. europaeus* is actually classified as cathemeral (Kirk 2006). This adaptation allows them to avoid aerial predators by feeding at night, and run fast to escape predators hunting by day. In areas with no disturbance *L. europaeus* is also active by day. Furthermore, patterns shift with day length and breeding activity (Krapp 2003). *Lepus europaeus* does not hibernate, but in snow it builds hollows for shelter. On days with temperatures over 25°C it seeks shade and postpones activity to nightfall (Zörner 1981; Holley 2001; Schai-Braun et al. 2012). Nevertheless, resting takes most of the time in the 24-h cycle, even active phases are interrupted by spontaneous resting phases. If active, it spends the time foraging, avoiding predators, grooming, and mating. During the breeding season, lactating females may spend 11 h feeding (Flux 1981). Mutual grooming could be observed in captivity, thus can be expected in the wild, too (Zörner 1981).

GENETICS

As in other members of the genus, the karyotype of *Lepus europaeus* is characterized by a diploid number (2n) of 48 chromosomes (Schroder et al. 1978; Arslan 2010; Tez 2012). A study in Turkey (localities İçel and Konya [south]) designated the fundamental number (FN) and the number of autosomal arms (FNa) as 90 and 86, respectively (Arslan 2010). Three autosomal pairs were described as large metacentrics, five pairs as submetacentrics, one pair as a small subtelocentric, and three pairs as small acrocentrics. The X chromosome was the largest submetacentric and the Y chromosome was acrocentric and the smallest in the set (Arslan 2010). Karyotypic analysis of *L. europaeus* in Turkey (localities Kayseri, Çankırı–İlgaz, Nevşehir–Gülşehir [north and central]) determined the fundamental number of chromosomal arms (FN) and the number of autosomal arms (FNa) to be 84 and 80, respectively (Tez et al. 2012). Furthermore, they classified the autosomal pairs as three metacentric, four submetacentric, 10 subtelocentric, and six

acrocentric with the X chromosome as a large submetacentric chromosome, and the Y chromosome a small acrocentric chromosome. This variation in types of chromosomes and arm numbers might be a result of different classification systems, variation in techniques, or possibly geographic variation in *L. europaeus* (Schroder et al. 1978; Arslan 2010; Tez 2012).

Hybridization of *L. europaeus* and *L. timidus* occurs but is very rare. Gustavsson (1971) studied mitotic and meiotic chromosomes of *L. europaeus* and *L. timidus* and hybrids obtained from controlled experiments in captivity. Hybridization of *L. europaeus* males and *L. timidus* females occurred spontaneously; however, artificial insemination was necessary for the reverse cross because *L. timidus* males refused to mate with *L. europaeus* females. In both types of crosses, normal meiosis and the formation of secondary spermatocytes with a normal haploid chromosome complement occurred; both hybrids had normal fertility and showed a diploid chromosome number of 48. The karyotype was identical to both parental species. Thus, the reproductive barrier was obviously not because of sterility factors (Gustavsson 1971).

In a different study on artificially bred hybrids between *L. europaeus* and *L. timidus*, the male hybrid resembled *L. timidus* but had features of *L. europaeus* too, like the black dorsal part of the tail (Schröder et al. 1987). When immunoglobulins of these hybrids were analyzed by immunodiffusion against an anti-serum (e15) that reacts with *L. europaeus* but not with *L. timidus*, immunoglobulins showed a reaction with sera of *L. europaeus* but not with those of *L. timidus*; thus, the paternal allotype is expressed in the hybrids. In the wild, sympatric *L. europaeus* and *L. timidus* in Finland showed no evidence of hybridization when analyzed with the test described above (Schröder et al. 1987). In Sweden (1 out of 199) and Russia (3 out of 71) *L. europaeus* mitochondrial genome and apparent *L. timidus* nuclear genome showed rare evidence of interspecific hybridization (Thulin et al. 2006).

Čížová et al. (1993) investigated genetic variation in *L. europaeus* with serum allozymes. Polymorphisms were found in transferrin alpha 1B glycoprotein, protease inhibitors ATC2, ATC3, and AT1, esterase ES1, and in an unidentified postalbumin PO. There is evidence that the variants observed in these proteins are under genetic control by codominant alleles of autosomal loci.

The evolution of *L. europaeus* and its position in the *Lepus* phylogenetic tree is still unresolved, especially when compared with *L. capensis*. Analysis of microsatellite loci resulted in total of 162 alleles (Slimen et al. 2008). There was a pattern of population variability and differentiation with a relatively high number of unique alleles. However, it appears that regionally differentiated gene pools (neighboring populations) exist and are still connected by gene flow. On the other hand, mtDNA restriction fragment length polymorphism showed a marked divergence between North and South African *L. capensis* and Anatolian and European *L. europaeus* (Slimen et al. 2008) populations.

In an effort to resolve phylogenetic relationships among 11 species of hares, including *L. europaeus*, Melo-Ferreira et al. (2012) used sequence data from two mitochondrial and 14 nuclear DNA fragments. They also evaluated potential mtDNA introgression and confirmed that there is extensive sharing of mtDNA haplotypes between *L. europaeus* and *L. timidus* that could only be explained by introgression. Furthermore, during the last glaciation period when *L. timidus* and *L. europaeus* simultaneously occupied regions of the Iberian Peninsula, hybridization occurred; obviously to the extent that *L. timidus*-like mtDNA is present in *L. europaeus* (Alves et al. 2008). Freitas (2006) could also confirm hybridization between *L. europaeus* and *Lepus granatensis* (Iberian hare) in the Iberian Peninsula based on microsatellite and mtDNA data.

In studies by Hartl et al. (1993) of 469 Austrian specimens and Suchentrunk et al. (2000) of 157 Bulgarian specimens, starch-gel electrophoresis was used to analyze more than 30 enzymes. Low genetic differentiation and rare alleles led to the suggestion of high migration, thus gene flow, within and between *L. europaeus* populations in central Europe. However, subsequent studies determined that some alleles were found only in Austrian populations but not in Bulgarian populations. Suchentrunk et al. (2003) compared the data from Bulgarian populations generated by Suchentrunk et al. (2000) with allozyme variability of 91 *L. europaeus* from seven regions in Greece aiming to find specific alleles, possibly stemming from an isolated late Pleistocene refugial population. Results of protein analysis from 35 loci revealed three alleles (Es-1-162, Pep-2 114, Mpi 88) at low frequencies, which were not found in Bulgarian or any other *L. europaeus* population studied at the time. In contrast, some alleles from the Bulgarian populations and other regions of Europe were absent in the Greek samples (Suchentrunk et al. 2003).

Mamuris et al. (2001, 2002) used the Random amplified polymorphic DNA method to compare specimens from Greek wild populations with specimens from Austria, Poland, Germany, France, and Bulgaria, and specimens of *L. europaeus* that were reared in captivity and released to investigate the impact of the releases on the native populations' genetic structure. The absence of diagnostic bands separating *L. europaeus* populations confirmed the high level of gene flow between *L. europaeus* populations over long geographic distances. The reared individuals clustered with the Austrian, Polish, German, and French populations, whereas the Greek populations did not cluster with the Bulgarian population. Within Greece the distribution of the six wild populations did not follow any geographical trend (Mamuris et al. 2002).

A study using data from five microsatellite loci and the mitochondrial d-loop was used to investigate genetic variability within populations of *L. europaeus* in Germany (Fickel et al. 2005). The study confirmed a high degree of genetic variability, matrilineal structured populations, male-biased gene flow, and a lack of inbreeding.

The genetic variability of *L. europaeus* in its native range, including European and Anatolian regions was investigated by Koutsogiannouli et al. (2014) who studied 80 *L. europaeus* from 16 geographically different populations, classified into four phylogeographic groups. Data were analyzed with regard to genetic polymorphism in the MHC (major histocompatibility complex) particularly DQA and DRB1 loci and functional polymorphism in binding pockets (amino acid substitutions). There is a high and stable genetic polymorphism due to balancing selection and a significant difference between Anatolian and European populations with the Anatolian population exhibiting the highest genetic polymorphism for both loci. Functional polymorphism of the binding pockets also revealed the existence of distinct geographic patterns (Koutsogiannouli et al. 2014).

Genome-scale RNA-sequence data was used to investigate SNPs (single-nucleotide polymorphisms) in European and Anatolian lineages (three samples per pool—Amoutzias et al. 2016). A total of 66,185 polymorphic sites were found in 7,665 genes of which 2,050 (in 1,147 genes) can possibly be used to distinguish both lineages. Among the differences are genes involved in cellular energy production, namely the glycolysis, Krebs cycle, and the oxidative phosphorylation machinery. These differences can be suggested to be the result of lack of gene flow during the Late Glacial Maximum which allowed mitochondrial- and nuclear-encoded genes of isolated populations to co-evolve (Amoutzias et al. 2016).

Data from a broad genetic analysis of *L. europaeus* specimens ($n = 154$) from mainland and island populations in Greece as well as captive-reared individuals ($n = 110$) were compared with existing sequences ($n = 310$, includes the 110 captive-reared individuals) retrieved from GenBank with the aim to create a pan-European analysis (Minoudi et al. 2018). The results confirm the deviation of the phylogenetic tree into two clades, the Anatolian and the European. In the analyzed 264 Greek samples 57 haplotypes could be found in wild and 20 in domesticated individuals; only three were shared between both groups. Comparing all sequences (384) used in this study, it is noteworthy that the number of haplotypes in Greece outnumbered slightly that of Central and West Europe (149 versus 130 haplotypes) despite the fact that sample size is almost one-third of the Central and West European (287 versus 841). Although climatic conditions of the Pleistocene influenced the distribution of *L. europaeus* into the Balkan peninsula, the Greek populations still represent preglacial diversity, thus supporting Mamuris et al. (2001, 2002). Hence, compared to the center-periphery hypothesis, Minoudi et al. 2018 favors the “refugia within refugia” model for Greek populations of *L. europaeus*.

CONSERVATION

Since the 1960s populations of *Lepus europaeus* have been declining in many European countries, a result of multiple factors. A number of publications address possible reasons (e.g., Jennings et al. 2006; Reichlin et al. 2006; Reid and Montgomery

2007; Jensen 2009; Schai-Braun et al. 2013). The primary causes suggested are intensification of agriculture with the loss of crop and landscape diversity (Tapper and Barnes 1986; Smith et al. 2005) and disease. Posautz et al. (2015) found increased sensitivity toward bacterial, protozoic, and worm infections followed by the marked increase in corn cultivation. Herbicides do not seem to play a major role (Edwards et al. 2000).

Lepus europaeus is now listed in the Convention of the Conservation of European Wildlife and Natural Habitats/Bern Convention under Appendix III (Vaughan et al. 2003). In Britain *L. europaeus* is also classed as a priority species of conservation concern by the United Kingdom government, and thus has a Biodiversity Action Plan (BAP—Jennings et al. 2006). In Norway, Germany, Austria, and Switzerland, population declines have resulted in country-specific Red Listing as “Near Threatened” or “Threatened” (Vierhaus 2001; Reichlin et al. 2006). However, the actual extent of vulnerability is controversial. The International Union for Conservation of Nature and Natural Resources (Hackländer and Schai-Braun 2019) still lists *L. europaeus* as a species declining but of “Least Concern.”

Nevertheless, among suggested protective measures are the establishment of shelters such as bushes or hedgerows; increasing food variability by including green zones with herbs, especially in areas with intensive agriculture. A recent study by Schai-Braun et al. (2020) confirmed that the leveret survival rate was higher in study sites with high proportion of set-asides (9% and 13%) than in sites with lower proportion of set-asides (3% and 5%).

Regarding *L. europaeus* as an important game animal, management implications are important to maintain sustainable population sizes. As changes in populations may be sudden, tracking down the dynamics of *L. europaeus* by careful annual monitoring is necessary. By now, this is customarily carried out by hunters in central European countries. Implementation of policies by the government to collect long-term data on the vital rates and densities of important game species like *L. europaeus* is recommendable (Schai-Braun et al. 2019).

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LITERATURE CITED

ABILDGÅRD, F., J. ANDERSEN, AND O. BARNDORFF-NIELSEN. 1972. The hare population (*Lepus europaeus* Pallas) of Illumø island, Denmark.

- A report on the analysis of the data from 1957–1970. Danish Review of Game Biology 6:1–32.
- ALVES, P. C., J. MELO-FERREIRA, H. FREITAS, AND P. BOURSOT. 2008. The ubiquitous mountain hare mitochondria: multiple introgressive hybridization in hares, genus *Lepus*. Philosophical Transactions of the Royal Society of London, B: Biological Sciences 363:2831–2839.
- AMOUTZIAS, G. D., ET AL. 2016. SNP identification through transcriptome analysis of the European brown hare (*Lepus europaeus*): cellular energetics and mother's curse. PLoS ONE 11:e0159939.
- ANDERSEN, J., AND D. JENSEN. 1972. Studies on the European hare XXVIII: the weight of the eye in European hares of known age. Acta Theriologica 17:87–92.
- ANGERBJORN. 2018. *Lepus timidus* Linnaeus, 1758. Mountain hare. Pp. 212–216 in Lagomorphs: pikas, rabbits, and hares of the world (A. T. Smith, C. H. Johnston, P. C. Alves, and K. Hackländer, eds.). Johns Hopkins University Press, Baltimore, Maryland.
- ANGERMANN, R. 1983. The taxonomy of Old World *Lepus*. Acta Zoologica Fennica 174:17–21.
- ANGERMANN, R., J. E. C. FLUX, J. A. CHAPMAN, AND A. T. SMITH. 1990. Lagomorph classification. Pp. 7–13 in Rabbits, hares and pikas: status survey and conservation action plan (J. A. Chapman and J. E. C. Flux, eds.). International Union for Conservation of Nature and Natural Resources, Gland, Switzerland.
- ARSLAN, A. 2010. Cytogenetic studies on European brown hare, *Lepus europaeus* Pallas, 1778 (Lagomorpha: Leporidae) in Turkey. Journal of the Faculty of Veterinary Medicine, University of Kafkas, Kars (Turkey) 16:319–322.
- BACHMAN, J. 1837. Observations on the different species of hares (genus *Lepus*) inhabiting the United States and Canada. Journal of the Academy Natural Sciences of Philadelphia 7:282–361.
- BALOUTCH, M. 1978. Etude d'une collection de lièvres d'Iran et description de quatre forms nouvelles. Mammalia 42:441–452.
- BARRETT-HAMILTON, G. E. H. 1903. The hares of Crete and of Cyprus. The Annals and Magazine of Natural History, Series 7 11:126–127.
- BARYSHNIKOV, G. 2003. *Mammuthus primigenius* from the Crimea and the Caucasus. Deinsea 9:41–56.
- BECHSTEIN, J. M. 1801. Gemeinnützige Naturgeschichte Deutschlands nach allen drey Reichen: ein Handbuch zur deutlichen und vollständigen Selbsterlehrung besonders für Forstmänner, Jugendlehrer und Oekonomen. Bey Siegfried Lebrecht Crusius, Leipzig, Germany.
- BENECKE, N. 1999. Die Tierreste aus dem mesolithischen Abri Span'-Koba im Krimgebirge, Beiträge zur Archäozoologie und Prähistorischen Anthropologie, Band 2. Gesellschaft für Archäozoologie und Prähistorische Anthropologie e. V. (GAPA), Braunschweig, Germany.
- BLANCHARD, M. J. 1957. Le lièvre a oreilles bleues et a dos brun, des Alpes (*Lepus cyanotus* (nov. spec)). Les cahiers de Chasse et de Nature, Paris fasc 30:7–38.
- BLASIUS, J. H. 1842. Amtlicher Bericht über die 19. Versammlung Deutscher Naturforscher und Ärzte in Braunschweig im September 1841. Friedrich Vieweg und Sohn, Braunschweig, Germany.
- BOCK, A. 2013. The effect of environmental factors on activity patterns of the European brown hare (*Lepus europaeus* Pallas, 1778). M.Sc. thesis, University of Hamburg, Hamburg, Germany.
- BOGDANOV, M. N. 1871. Birds and animals of the black earth belt of the Volga region and the valley of the Middle and Lower Volga. Transactions of the Society of Naturalists at the Imperial Kazan University, Tartarstan, Russia.
- BONINO, N., D. COSSIOS, AND J. MENEGHETTI. 2010. Dispersal of the European hare, *Lepus europaeus* in South America. Folia Zoologica 59:9–15.
- BRAY, Y. 1998. Vers une meilleure connaissance des flux démographiques chez le Lièvre d'Europe. Mémoire de DSER. Université de Bourgogne, Dijon, France.
- BRAY, Y., S. DEVILLARD, E. MARBOUTIN, B. MAUVY, AND R. PÉROUX. 2007. Natal dispersal of European Hare in France. Journal of Zoology (London) 273:426–434.
- BROEKHUIZEN, S., AND F. MAASKAMP. 1979. Age determination in the European hare (*Lepus europaeus* Pallas) in the Netherlands. Zeitschrift für Säugetierkunde 44:162–175.
- CAILLOL, M., M. MEUNIER, M. MONDAIN-MONVAL, AND P. SIMON. 1986. Seasonal variations in the pituitary response to LHRH in the brown hare (*Lepus europaeus*). Journal of Reproduction and Fertility 78:479–486.
- CAILLOL, M., M. MONDAIN-MONVAL, M. MEUNIER, AND B. ROSSANO. 1992. Influence of season of birth on onset of gonadotrophic and ovarian functions in young doe hares (*Lepus europaeus*). Journal of Reproduction and Fertility 96:747–753.
- Chapman, J. A., AND J. E. C. FLUX (eds.). 1990. Rabbits, hares and pikas: status survey and conservation action plan. International Union for Conservation of Nature and Natural Resources, Gland, Switzerland.
- ČIZOVÁ, D., F. KRÁL, A. STRATIL, AND V. GLASNÁK. 1993. Intraspecific variation in serum proteins of brown hare (*Lepus europaeus* Pallas, 1778). Comparative Biochemistry and Physiology, B: Comparative Biochemistry 106:977–982.
- DE BEAUX, O. 1927. *Lepus europaeus ghigii*, subsp. nova. (Nota preliminare). Bollettino del Museo di Zoologia e di Anatomia comparata Regia Università di Genova 7:2.
- DE BEAUX, O. 1929. Ricerche faunistiche nelle isole italiane dell'Egeo. Mammiferi. Archivio Zoologico Italiano, 12–13, 1928–1929 VII:135–154.
- DE WINTON, W. E. 1898. On the hares of Western Europe and West Africa. Annals and Magazine of Natural History, Series 7 1:149–157.
- DEMIRBAŞ, Y., AND I. ALBAYRAK. 2014. The taxonomic status and geographic distribution of the European hare (*Lepus europaeus* Pallas, 1778) in Turkey (Mammalia: Lagomorpha). Turkish Journal of Zoology 38:119–130.
- DESMAREST, M. A. G. 1822. Mammalogie ou Description des Espèces de Mammifères. 2nd part. Chez Mme. Veuve Agasse, Imprimeur-Libraire, Paris, France.
- DIETRICH, U. 1985. Populationsökologie des in Argentinien eingebürgerten europäischen Feldhasen (*Lepus europaeus*). Zeitschrift für Jagdwissenschaft 31:92–102.
- DÖHLE, H.-J. 1999. Die nacheiszeitliche Verbreitung einiger Wildsäugetiere (Carnivora, Leporidae) in Mittel- und Norddeutschland. Säugetierkundliche Mitteilungen 44:154–161 (not seen, cited in Fickel et al. 2008).
- DRANE, R. 1895. The hare in captivity. Transactions of the Cardiff Naturalists Society 27:101–109.
- EDWARDS, P. J., M. R. FLETCHER, AND P. BERNY. 2000. Review of the factors affecting the decline of the European brown hare, *Lepus europaeus* (Pallas, 1778) and the use of wildlife incident data to evaluate the significance of paraquat. Agriculture, Ecosystems and Environment 79:95–103.
- ELLERMAN, J. R., AND T. C. S. MORRISON-SCOTT. 1966. Checklist of Palearctic and Indian mammals 1758–1956. Trustees of the British Museum (Natural History), London, United Kingdom.
- EVERSMANN, E. A. 1850. Estestvennaya istoriya Orenburgskogo kraya (The Natural History of the Orenburg Region.). Part 2. Kazan University, Kazan, Republic of Tartarstan, Russia (in Russian).
- FESTA, D. E. 1914. Ecurioni zoologiche del Dr. Enrico Festa nell'Isla di Rodi. XI Mammiferi. Bollettino dei Musei di Zoologia ed Anatomia comparata. Vol. 29. 686:1–21.
- FICKEL, J. 2003. Molekularbiologie und Phylogenie von *Lepus europaeus* Pallas, 1778 – und anderen europäischen *Lepus*-Arten. Pp. 27–34 in Handbuch der Säugetiere Europas, Bd. 3/II, Hasentiere (F. Krapp, ed.). Aula, Wiesbaden, Germany.
- FICKEL, J., H. C. HAUFFE, E. PECCHIOLO, R. SORIGUER, L. VAPA, AND C. PITRA. 2008. Cladogenesis of the European brown hare (*Lepus europaeus* Pallas, 1778). European Journal of Wildlife Research 54:495–510.
- FICKEL, J., ET AL. 2005. Genetic structure of populations of European brown hare: implications for management. Journal of Wildlife Management 69:760–770.
- FISCHER, K., AND W. D. HEINRICH. 1983. Skelettreste von *Lepus europaeus* Pallas, 1778 (Lagomorpha, Mammalia) aus dem fossilen Tierbautensystem von Pisede bei Malchin. Wissenschaftliche Zeitschrift der Humboldt-Universität zu Berlin. Math-natwiss Reihe 32:713–717.

- FITZINGER, L. J. 1867. Versuch einer natürlichen Anordnung der Nagethiere (*Rodentia*). Pp. 57–168 in Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Band 56. Carl Gerhold's Sohn, Wein, Germany.
- FLUX, J. E. C. 1965. Timing of the breeding season in the hare, *Lepus europaeus* Pallas, and rabbit, *Oryctolagus cuniculus* (L.). *Mammalia* 29:557–562.
- FLUX, J. E. C. 1981. Field observations of behaviour in the genus *Lepus*. Pp. 377–394 in Proceedings of the World Lagomorph Conference (K. Myers and C. D. MacInnes, eds.). University of Guelph, Guelph, Ontario, Canada.
- FLUX, J. E. C. 1987. Myths and mad March hares. *Nature* 325:737.
- FLUX, J. E. C. 1990. Brown hare. Pp. 161–172 in The handbook of New Zealand mammals (C. M. King, ed.). Oxford University Press, Auckland, New Zealand.
- FLUX, J. E. C. 2009. Notes on New Zealand mammals 10. Effect of observer position on group size and level of aggression of mating brown hares. *New Zealand Journal of Zoology* 36:81–82.
- FLUX, J. E. C., AND R. ANGERMANN. 1990. The hares and jackrabbits. Pp. 61–94 in Rabbits, hares and pikas: status survey and conservation action plan (J. A. Chapman and J. E. C. Flux, eds.). International Union for Conservation of Nature and Natural Resources, Gland, Switzerland.
- FREITAS, H. 2006. Natural hybridization between the Iberian hare (*Lepus granatensis*) and the brown hare (*L. europaeus*) in northern Iberian Peninsula. M.Sc. thesis, Faculdade de Ciencias do Porto, Porto, Portugal.
- FRÖLICH, K., S. THIEDE, AND J. WISSER. 2001. Infektionskrankheiten des Feldhasen. Wo liegt der Hase im Pfeffer? NUA-Seminarbericht 7:34–36.
- FRYLESTAM, B. 1979. Population ecology of the European hare in Southern Sweden. Ph.D. dissertation, University of Lund, Lund, Sweden.
- FRYLESTAM, B. 1986. Agricultural land use effects on the winter diet of brown hares (*Lepus europaeus* Pallas) in southern Sweden. *Mammal Review* 16:157–161.
- GEHLE, T. 2002. Zur Biologie und Ökologie des Feldhasen. Institut für Waldbau und Forstschutz, Hamburg, Germany.
- GERVAIS, P. 1859. Zoologie et Paléontologie Françaises. Nouvelles Recherches sur les Animaux Vertébrés. Arthus Bertrand, Paris, France.
- GOODWIN, G. G. 1939. Five new Rodents from the eastern Elburz Mountains and a new race of hare from Teheran. *American Museum Novitates* 1050:1–5.
- GRAY, J. E. 1867. Notes on the skulls of hares (Leporidae) and pikas (Lagomyidae) in the British Museum. The Annals and Magazine of Natural History Including Zoology, Botany, and Geology. Series 3 20:219–224.
- GRIGERA, D. E., AND E. H. RAPOPORT. 1983. Status and distribution of the European hare in South America. *Journal of Mammalogy* 64:163–166.
- GUITION, J.-S., ET AL. 2016. Epidemiology of pulmonary protostrongyliasis in the European hare (*Lepus europaeus*) in France. P. 63 in Proceedings of the 5th World Lagomorph Conference (P. Kelly, S. Phillips, A. Smith, and C. Browning, eds.), 11–15 July 2016, Turlock, California.
- GUSTAVSSON, I. 1971. Mitotic and meiotic chromosomes of the variable hare (*Lepus timidus* L.), the common hare (*Lepus europaeus* Pall.) and their hybrids. *Hereditas* 67:27–34.
- GYURANECZ, M., ET AL. 2010. Tularemia of European brown hare (*Lepus europaeus*) a pathological, histopathological, and immunohistochemical study. *Veterinary Pathology* 47:958–963.
- HACKLÄNDER, K., W. ARNOLD, AND T. RUF. 2002a. Postnatal development and thermoregulation in the precocial European hare (*Lepus europaeus*). *Journal of Comparative Physiology B* 172:183–190.
- HACKLÄNDER, K., AND S. SCHAI-BRAUN. 2018. *Lepus europaeus* Pallas, 1778. European hare. Pp. 187–190 in Lagomorphs: pikas, rabbits, and hares of the world (A. T. Smith, C. H. Johnston, P. C. Alves, and K. Hackländer, eds.). Johns Hopkins University Press, Baltimore, Maryland.
- HACKLÄNDER, K., AND SCHAI-BRAUN, S. 2019. *Lepus europaeus*. The IUCN Red List of Threatened Species 2019: e.T41280A45187424. <https://dx.doi.org/10.2305/IUCN.UK.2019-1.RLTS.T41280A45187424.en>. Accessed 13 August 2020.
- HACKLÄNDER, K., F. TATARUCH, AND T. RUF. 2002b. The effect of dietary fat content on lactation energetics in the European hare (*Lepus europaeus*). *Physiological and Biochemical Zoology* 75:19–28.
- HALL, E. R. 1951. A synopsis of the North American Lagomorpha. University of Kansas Publications 5:119–202.
- HANSEN, K. 1992. Reproduction in European hare in a Danish farmland. *Acta Theriologica* 37:27–40 (not seen, cited in Krapp 2003).
- HARTL, G. B., F. SUCHENTRUNK, K. NADLINGER, AND R. WILLING. 1993. An integrative analysis of genetic differentiation in the brown hare *Lepus europaeus* based on morphology, allozymes, and mitochondrial DNA. *Acta Theriologica* 38:33–57.
- HEMPRICH, W. F., AND C. G. EHRENBERG. 1832. Symbolae physicae, icones et descriptiones. Mammalium, part 2. Ex Officina Academica, Berolini (Berlin), Germany.
- HEPTNER, V. G. 1948. K nomenklature nekotorykh mlekopitayushchikh [On nomenclature of several mammals]. *Doklady Akademii Nauk* 60:709–712.
- HILZHEIMER, M. 1906. Die europäischen Hasen. Zoologischen Anzeiger, band 30. Verlag von Wilhelm Engelmann, Leipzig, Germany.
- HIRAKAWA, H. 2001. Coprophagy in leporids and other mammalian herbivores. *Mammal Review* 31:61–80.
- HOFFMANN, R. S., AND A. T. SMITH. 2005. Order Lagomorpha. Pp. 185–211 in Mammals of the world: a taxonomic and geographic reference (D. E. Wilson and D. M. Reeder, eds.). Vol. 1. Johns Hopkins University, Baltimore, Maryland.
- HOLLEY, A. J. F. 2001. The daily activity period of the brown hare (*Lepus europaeus*). *Mammalian Biology* 66:357–364.
- JENNINGS, N., R. K. SMITH, K. HACKLÄNDER, S. HARRIS, AND P. C. WHITE. 2006. Variation in demography, condition and dietary quality of hares *Lepus europaeus* from high-density and low-density populations. *Wildlife biology* 12:179–189.
- JENSEN, T. L. W. 2009. Identifying causes for population decline of the brown hare (*Lepus europaeus*) in agricultural landscapes in Denmark. Ph.D. dissertation, Aarhus Universitet, Danmarks Miljøundersøgelser, Afdeling for Vildtbiologi og Biodiversitet, Aarhus, Denmark.
- KARP, D. 2016. A practical guide to study brown hare leverets (*Lepus europaeus*) in the wild. P. 90 in Proceedings of the 5th World Lagomorph Conference (P. Kelly, S. Phillips, A. Smith, and C. Browning, eds.), 11–15 July 2016, Turlock, California.
- KATONA, K., Z. BIRO, L. SZEMETHY, T. DEMES, AND M. NYESTE. 2010. Spatial, temporal and individual variability in the autumn diet of European hare (*Lepus europaeus*) in Hungary. *Acta Zoologica Academiae Scientiarum Hungaricae* 56:89–101.
- KIRCHNER, M. K., C. MARSCHNER, G. L. STALDER, F. SCHWARZENBERGER, F. KNAUER, AND C. WALZER. 2012. The effect of housing systems on the welfare of the European hare (*Lepus europaeus*). P. 70 in Proceedings of the 4th World Lagomorph Conference (T. Hackländer and C. Thurner, eds.), 23–27 July 2012 in Vienna, Austria.
- KIRK, E. C. 2006. Eye morphology in catemeral lemurids and other mammals. *Folia Primatologica* 77:7–49.
- KLANSEK, E. 1996. Biotoprevitalisierung und neue Überlegungen zur jagdlichen Nutzung des Feldhasen. Zur Besatzentwicklung des Feldhasen in mitteleuropäischen Niederwildrevieren 2:31–36.
- KÖNIG-WARTHAUSEN, R. 1875. Verzeichniss der Wirbelthiere Oberschwabens. Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg, 31:193–335.
- KOUTSOGIANNOULI, E. A., K. A. MOUTOU, C. STAMATIS, L. WALTER, AND Z. MAMURIS. 2014. Genetic variation in the major histocompatibility complex of the European brown hare (*Lepus europaeus*) across distinct phylogeographic areas. *Immunogenetics* 66:379–392.
- KOVACS, G., AND I. HELTAY. 1985. The brown hare. Ecology, management, hunting. Mezogazdasági Kiadó, Budapest, Hungary.
- KRAPP, F. 2003. Handbuch der Säugetiere Europas, Bd. 3/II. Hasentiere. Aula, Wiesbaden, Germany.
- KRONFELD, N., AND A. SHKOLNIK. 1996. Adaptation to life in the desert in the brown hare (*Lepus capensis*). *Journal of Mammalogy* 77:171–178.

- KUZNETSOV, B. A. 1944. Order Rodentia. Pp. 262–362 in *Opredelitel' mlekopitayushchikh SSSR* [Guide to the mammals of the USSR] (N. A. Bobrinskii, B. A. Kuznetsov, and A. P. Kuzyakin, eds.). 2nd ed. Proveshchenie, Moscow, Russia (in Russian).
- LANGBEIN, J., M. R. HUTCHINGS, S. HARRIS, C. STOATE, S. C. TAPPER, AND S. WRAY. 1999. Techniques for assessing the abundance of brown hares *Lepus europaeus*. *Mammal Review* 29:93–116.
- LE GALL-RECULE, G., ET AL. 2017. Large-scale lagovirus disease outbreaks in European brown hares (*Lepus europaeus*) in France caused by RHDV2 strains spatially shared with rabbits (*Oryctolagus cuniculus*). *Veterinary Research* 48:1–16.
- LETTY, J., ET AL. 2016. Effect of an experimental reduction of red fox on brown hare population dynamics. P. 59 in *Proceedings of the 5th World Lagomorph Conference* (P. Kelly, S. Phillips, A. Smith, and C. Browning, eds.), 11–15 July 2016, Turlock, California.
- LINCOLN, G. A. 1974. Reproduction and “March madness” in the brown hare, *Lepus europaeus*. *Journal of Zoology* 174:1–14.
- MAMURIS, Z., A. I. SFOUGARIS, AND C. STAMATIS. 2001. Genetic structure of Greek brown hare (*Lepus europaeus*) populations as revealed by mtDNA RFLP-PCR analysis: implications for conserving genetic diversity. *Biological Conservation* 101:187–196.
- MAMURIS, Z., A. I. SFOUGARIS, C. STAMATIS, AND F. SUCHENTRUNK. 2002. Assessment of genetic structure of Greek brown hare (*Lepus europaeus*) populations based on variation in random amplified polymorphic DNA (RAPD). *Biochemical Genetics* 40:323–338.
- MARTINET, L., J.-J. LEGOUIS, AND B. MORET. 1970. Quelques observations sur la reproduction du lièvre européen (*Lepus europaeus* Pallas) en captivité. *Annales de Biologie Animale, Biochimie, Biophysique* 10:195–202.
- MASSETI, M. 2012. Atlas of terrestrial mammals of the Ionian and Aegean Islands, Italy. Walter de Gruyter GmbH, Berlin, Germany.
- MATSCHIE, P. 1901. Sitzungs-Berichte der Gesellschaft Naturforschender Freunde zu Berlin. R. Friedlander and Sons, Berlin, Germany.
- MAURIN, M., I. PELLOUX, J. P. BRION, J. N. DEL BANÖ, AND A. PICARD. 2011. Human tularemia in France, 2006–2010. *Clinical Infectious Diseases* 53:e133–e141.
- MELO-FERREIRA, J., P. BOURSOT, M. CARNEIRO, P. J. ESTEVES, L. FARELO, AND P. C. ALVES. 2012. Recurrent introgression of mitochondrial DNA among hares (*Lepus* spp.) revealed by species-tree inference and coalescent simulations. *Systematic Biology* 61:367–381.
- MILLER, G. S. 1903. A new hare from Greece. *Proceedings of the Biological Society of Washington* 16:145–146.
- MINOUDI, S., I. PAPAPETRIDIS, N. KARAIKOU, E. CHATZINIKOS, C. TRIANTAPHYLIDIS, AND T. J. ABATZOPOULOS. 2018. Genetic analyses of brown hare (*Lepus europaeus*) support limited migration and translocation of Greek populations. *PLoS ONE* 13:e0206327.
- MONAGHAN, P., AND N. B. METCALFE. 1985. Group foraging in wild brown hares: effects of resource distribution and social status. *Animal Behaviour* 33:993–999.
- MUSIL, R. 1985. Die Fauna der Magdalénien-Siedlung Oelknitz. *Weimarer Monographien zur Ur- und Frühgeschichte* 17:1–43 (cited in Fickel et al. 2008).
- MYERS, K., I. PARER, AND B. J. RICHARDSON. 1989. Leporidae. Fauna of Australia. Vol. 1B. Australian Government Publishing Service, Canberra, Australia.
- NELSON, R. J., BADURA, L. L., AND GOLDMAN, B. D. 1990. Mechanisms of seasonal cycles of behavior. *Annual Review of Psychology* 41:81–108.
- NIETHAMMER, J. 1992. Über einige Hasenschädel (*Lepus europaeus*) von der griechischen Insel Paximada vor Kreta. *Säugetierkundliche Mitteilungen* 34:43–49.
- NILSSON, S. 1820. Skandinavisk Fauna en Handbok för Jagare och Zoologer. Vol. 1. Trycki uti Bolingska Boktryckeriet, Lund, Sweden.
- NOSZCZYK-NOWAK, A., J. NICPOŃ, M. NOWAK, AND P. SLAWUTA. 2009. Preliminary reference values for electrocardiography, echocardiography and myocardial morphometry in the European brown hare (*Lepus europaeus*). *Acta Veterinaria Scandinavica*. 51:6.
- OGNEV, S. I. 1929. Zur Systematik der russischen Hasen. *Zoologisch Anzeiger* 84:69–83.
- OGNEV, S. I. 1940. Zveri SSSR i prilozhashchikh stran: Gryzuny. (Zveri vostochnoi Evropy i severnoi Azii) [Mammals of the USSR and adjacent countries: rodents (mammals of eastern Europe and northern Asia)]. *Akademiya Nauk SSSR* 4:1–615 (in Russian).
- OGNEV, S. I., AND K. A. VOROBYOV. 1923. The fauna of the terrestrial vertebrates of the Government of Woronesh. *Novaya Derevnnya*, Moscow, Russia (in Russian, English translation published by Israel Program for Scientific Translations, Jerusalem, 1966).
- PACI, G., M. BAGLIACCA, AND A. LAVAZZA. 2006. Stress evaluation in hares (*Lepus europaeus* Pallas) captured for translocation. *Italian Journal of Animal Science* 5:175–181.
- PACI, G., A. LAVAZZA, M. FERRETTI, F. SANTILLI, AND M. BAGLIACCA. 2011. Relationship between anti-European brown hare syndrome serological titers and brown hare (*Lepus europaeus* Pallas) densities. *International Journal of Zoology*:436193. doi:10.1155/2011/436193.
- PALLAS, P. S. 1778. *Novae Species Quadrupedum e Glirium Ordine*. SVMTV Wolfgang Waltheri, Erlangae, Germany.
- PETTER, F. 1961. Elements d’une révision des lièvres européens et asiatiques du sous-genre *Lepus*. *Zeitschrift für Säugetierkunde* 26:30–40.
- PFISTER, H., L. KOHLI, P. KASTLI, AND S. BIRRER. 2002. Feldhase. Schlussbericht 1991–2000: Bundesamt für Umwelt, Wald und Landschaft, Bern, und Schweiz. Vogelwarte, Sempach, Switzerland.
- PIKULA, J., M. BEKLOVA, Z. HOLEŠOVSKÁ, AND F. TREML. 2004. Ecology of European brown hare and distribution of natural foci of tularemia in the Czech Republic. *Acta Veterinaria Brno* 73:267–273.
- POSAUTZ, A., ET AL. 2015. Health screening of free-ranging European brown hares (*Lepus europaeus*) on the German North-Sea island Pellworm. *Acta Veterinaria Scandinavica* 57:43.
- QUMSIYEH, M. B. 1996. *Mammals of the Holy Land*. Texas Tech University Press, Lubbock.
- REICHLIN, T., E. KLANSEK, AND K. HACKLÄNDER. 2006. Diet selection by hares (*Lepus europaeus*) in arable land and its implications for habitat management. *European Journal of Wildlife Research* 52:109–118.
- REID, N. 2011. European hare (*Lepus europaeus*) invasion ecology: implication for the conservation of the endemic Irish hare (*Lepus timidus hibernicus*). *Biological Invasions* 13:559–569.
- REID, N., AND W. I. MONTGOMERY. 2007. Is naturalisation of the brown hare in Ireland a threat to the endemic Irish hare? *Biology and Environment: Proceedings of the Royal Irish Academy* 107b:129–138.
- REYNOLDS, J. K., AND R. H. STINSON. 1959. Reproduction in the European hare in southern Ontario. *Canadian Journal of Zoology* 37:627–631.
- RIGO, N., A. TROCINO, L. POPPI, M. GIACOMELLI, G. GRILLI, AND A. PICCIRILLO. 2015. Performance and mortality of farmed hares. *Animal* 9:1025–1031.
- ROBINSON, H. C. 1918. A new race of hare from the Persian frontier of Mesopotamia. *Records of the Indian Museum* 15:49–50.
- ROELLIG, K., F. GOERITZ, AND T. B. HILDEBRANDT. 2010. Ultrasonic characterisation of prenatal development in European brown hares (*Lepus europaeus* PALLAS, 1778): an evolutionary approach. *Reproduction, Fertility and Development* 22:448–458.
- RÜHE, F., AND U. HOHMANN. 2004. Seasonal locomotion and home-range characteristics of European hares (*Lepus europaeus*) in an arable region in central Germany. *European Journal of Wildlife Research* 50:101–111.
- RUIZ-FONS, F., E. FERROGLIO, AND C. GORTÁZAR. 2013. *Leishmania infantum* in free-ranging hares, Spain, 2004–2010. *Eurosurveillance* 18:20541.
- SATUNIN, K. A. 1905. Neue und wenig bekannte Säugetiere aus dem Kaukasus und aus Transkaspien. *Mitteilungen des Kaukasischen Museums* II:45–86 (in Russian).
- SCHAIÉ-BRAUN, S. C., AND K. HACKLÄNDER. 2016. Family Leporidae (hares and rabbits). Pp. 62–149 in *Handbook of the mammals of the world: vol. 6: lagomorphs and rodents I* (D. E. Wilson, T. E. Lacher, Jr., and R. A. Mittermeier, eds.). Lynx Edicions, Barcelona, Spain.
- SCHAIÉ-BRAUN, S. C., C. KOWALCZYK, E. KLANSEK, AND K. HACKLÄNDER. 2019. Estimating sustainable harvest rates for European hare (*Lepus Europaeus*) populations. *Sustainability* 11:2837.
- SCHAIÉ-BRAUN, S. C., H. G. RÖDEL, AND K. HACKLÄNDER. 2012. The influence of daylight regime on diurnal locomotor activity patterns of

- the European hare (*Lepus europaeus*) during summer. *Mammalian Biology-Zeitschrift für Säugetierkunde* 77:434–440.
- SCHAI-BRAUN, S. C., T. RUF, E. KLANSEK, W. ARNOLD, AND K. HACKLÄNDER. 2020. Positive effects of set-asides on European hare (*Lepus europaeus*) populations: leverets benefit from an enhanced survival rate. *Biological Conservation* 244:108518.
- SCHAI-BRAUN, S. C., D. WEBER, AND K. HACKLÄNDER. 2013. Spring and autumn habitat preferences of active European hares (*Lepus europaeus*) in an agricultural area with low hare density. *European Journal of Wildlife Research* 59:387–397.
- SCHNEIDER, E. 1979. Ethologie und Biologie des Feldhasen *Lepus europaeus* (Pallas, 1778): Eine Freilandstudie. Ph.D. dissertation, Mathematisch-Naturwissenschaftliche Fakultät der Georg-August-Universität zu Göttingen.
- SCHRODER, J., J. ANTONI, AND W. VAN DER LOO. 1978. Comparison of the karyotypes in the Jack rabbit (*Lepus californicus deserticola*) and the European hare (*Lepus europaeus*). *Hereditas* 89:134–135.
- SCHRÖDER, J., T. SOVERI, H. A. SUOMALAINEN, L. A. LINDBERG, AND W. V. D. LOO. 1987. Hybrids between *Lepus timidus* and *Lepus europaeus* are rare although fertile. *Hereditas* 107:185–189.
- SLIMEN, H. B., ET AL. 2006. Evolutionary relationships among hares from North Africa (*Lepus* sp. or *Lepus* spp.), cape hares (*L. capensis*) from South Africa, and brown hares (*L. europaeus*), as inferred from mtDNA PCR-RFLP and allozyme data. *Journal of Zoological Systematics and Evolutionary Research* 44:88–99.
- SLIMEN, H. B., F. SUCHENTRUNK, A. MEMMI, AND A. B. A. ELGAAIED. 2005. Biochemical genetic relationships among Tunisian hares (*Lepus* sp.), South African cape hares (*L. capensis*), and European brown hares (*L. europaeus*). *Biochemical Genetics* 43:577–596.
- SLIMEN, H. B., ET AL. 2008. Population genetics of cape and brown hares (*Lepus capensis* and *L. europaeus*): a test of Petter's hypothesis of conspecificity. *Biochemical Systematics and Ecology* 36:22–39.
- SLUDSKI, A. A., AND E. I. STRAUTMANN. 1980. Mammals of Kazakhstan. Vol. 2: Lagomorpha. (Mlekopitayushchie Kazakhstana, T. 2, Zaitseobraznye). Izd. Nauka, Alma Ata, Russia.
- SMITH, R. K., N. VAUGHAN JENNINGS, AND S. HARRIS. 2005. A quantitative analysis of the abundance and demography of European hares *Lepus europaeus* in relation to habitat type, intensity of agriculture and climate. *Mammal Review* 35:1–24.
- SPAGNESI, M., AND V. TROCCHI. 1980. Riproduzione in cattività della lepre europea (*Lepus europaeus* Pallas). *Coniglicoltura* 17:47–52.
- STOTT, P. 2003. Use of space by sympatric European hares (*Lepus europaeus*) and European rabbits (*Oryctolagus cuniculus*) in Australia. *Mammalian Biology-Zeitschrift für Säugetierkunde* 68:317–327.
- ŠTRBENC, M., AND S. V. BAVDEK. 2001. Apoptosis and proliferation in the testes of the brown hare (*Lepus europaeus*) under the influence of photoperiod. *Pflügers Archiv* 442:r161–r162.
- STROH, G. 1931. Zwei sichere Altersmerkmale beim Hasen. *Berlin Tierärztliche Wochenschrift* 12:189–181.
- SUCHENTRUNK, F., Z. MAMURIS, A. I. SFOUGARIS, AND C. STAMATIS. 2003. Biochemical genetic variability in brown hares (*Lepus europaeus*) from Greece. *Biochemical Genetics* 41:127–140.
- SUCHENTRUNK, F., C. MICHAÏLOV, G. MARKOV, AND A. HAIDEN. 2000. Studies on the European hare. 55. Population genetics of Bulgarian brown hares *Lepus europaeus*: allozymic diversity at zoogeographical crossroads. *Acta Theriologica* 45:1–12.
- TAPPER, S. C., AND R. F. W. BARNES. 1986. Influence of farming practice on the ecology of the brown hare (*Lepus europaeus*). *Journal of Applied Ecology* 23:39–52.
- TEZ, C., Y. ÖZKUL, AND O. İBIŞ. 2012. Karyological comparisons of the European hare (*Lepus europaeus* Pallas, 1778) from the Asian part of Turkey, with morphological contributions. *Archives of Biological Sciences* 64:935–942.
- THULIN, C. G., M. FANG, AND O. AVERIANOV, ALEXANDER. 2006. Introgression from *Lepus europaeus* to *L. timidus* in Russia revealed by mitochondrial single nucleotide polymorphisms and nuclear microsatellites. *Hereditas*. 143:68–76.
- ТИХОМИРОВ, А. А., AND А. Н. КОРЧАГИН. 1889. Известия Общества любителей естествознания, антропологии и этнографии, состоящего при Московском университете (Izvestia of the Society of Lovers of Natural Science Anthropology and Ethnography) 4:31 (in Russian).
- TROUESSART, E. L. 1910. Faune des Mammifères D'Europe. R. Friedlander & Sohn, Berlin, Germany.
- TSOKANA, C. N., ET AL. 2016. First evidence of Leishmania infection in European brown hare (*Lepus europaeus*) in Greece: GIS analysis and phylogenetic position within the *Leishmania* spp. *Parasitology Research* 115:313–321.
- VALEČEK, T. G., K. HACKLÄNDER, AND T. RUF. 2010. Peak energy turnover in lactating European hares: a test of the heat dissipation limitation hypothesis. *Journal of Experimental Biology* 213:2832–2839.
- VAUGHAN, N., E. A. LUCAS, S. HARRIS, AND P. C. WHITE. 2003. Habitat associations of European hares *Lepus europaeus* in England and Wales: implications for farmland management. *Journal of Applied Ecology* 40:163–175.
- VERDIER, M. 1976. Performances de reproduction chez le lièvre et viabilité des levrauts. Mémoire de fin d'études, INRA Toulouse, Ecole Nationale Supérieure Agronomique de Toulouse Montpellier, France.
- VIERHAUS, H. 2001. Warum steht der Feldhase auf der Roten Liste? NUA-Seminarbericht 7:63–68.
- WATSON, J. S., AND R. H. TAYLOR. 1955. Reingestion in the hare *Lepus europaeus* Pal. *Science* 121:314.
- WETTSTEIN, O. 1943. Eine neue Hasenrasse vom Peloponnes. *Zoologischer Anzeiger* 143:282–284.
- WHITAKER, J. O., AND W. J. HAMILTON. 1998. Mammals of the Eastern United States. 3rd ed. Cornell University Press, Ithaca, New York.
- WIBBELT, G., AND K. FRÖLICH. 2005. Infectious diseases in European brown hare (*Lepus europaeus*). *Wildlife Biology in Practice* 1:86–93.
- ZÖRNER, H. 1981. "Der Feldhase" Die Neue Brehm-Bücherei. A. Ziemsen Verlag, Wittenberg Lutherstadt, Germany.

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