European Hare *Lepus europaeus* Pallas, 1778

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Common Names

English	European hare, brown hare, European brown hare, and common hare
German	Feldhase
French	Lièvre d'Europe, Lièvre européen, Lièvre commun, Lièvre brun, hase
Spanish	Liebre europea, Liebre común
Italian	Lepre commune, Lepre europea
Russian	За́яц-руса́к

Taxonomy and Systematics

As it is the case with many *Lepus* species (see Introduction to this volume), taxonomy and systematics are a matter of an ongoing debate also for *L. europaeus* (Fig. 1). The species has no type locality, but according to Trouessart (1910), Pallas had his specimen from S Poland and Pannonia. The true distribution range and the taxonomic status remain still unclear due to smooth transitions between potential species, hybridization within the genus *Lepus,* and vast ecological plasticity. In the past, *L. europaeus* was included in *L. capensis* (see species chapter in this volume). Today, there are contradictory results from genetic studies (e.g., Ben Slimen et al. 2008; Ferreira et al. 2021; Lado et al. 2019). Mitochondrial DNA (mtDNA) data suggest that *L. europaeus* is closer than expected to *L. capensis* from Near East and East Africa regions, despite demonstrating divergence at nuclear level, which might indicate ancestral admixture and mtDNA introgression (Lado et al. 2019). A recent phylogenomic study confirms that the European hare is closer to African hare species, but shows levels of genomic differentiation similar to the ones observed among other pairs of hare species (Ferreira et al. 2021). As long as these uncertainties are dominating the scientific debate, *L. europaeus* remains a distinct species.

Out of the sixteen recognized subspecies of *L. europaeus,* twelve have been described for Europe. However, these are all based on differences in size and coat color and thus are doubtful in the light of the ongoing debate on the species status itself:

L. e. europaeus Pallas, 1778, in W Europe; *L. e. caspicus* Hemprich and Ehrenberg, 1832, in Lower Volga and Kalmykia (Russia); *L. e. creticus* Barrett-Hamilton, 1903, in Crete (Greece); *L. e. cypricus* Barrett-Hamilton, 1903, in Cyprus; *L. e. hybridus* Desmarest, 1822, in the Baltic states, Belarus, Ukraine, Finland, and W Russia; *L. e. karpathorum* Hilzheimer, 1906, in the Carpathian mountains; *L. e. medius* Nilsson, 1820, in Denmark; *L. e. occidentalis* de Winton, 1898, in Great Britain; *L. e. parnassius* Miller, 1903, in C Greece; *L. e. ponticus* Ognev, 1929, at the Black sea coast; *L. e. rhodius* Festa, 1914, in Rhodes (Greece); *L. e. transsylvanicus* Matschie, 1901, in E and SE Europe.

Fig. 1 Two adult European hares. © Rolf Giger with kind permission

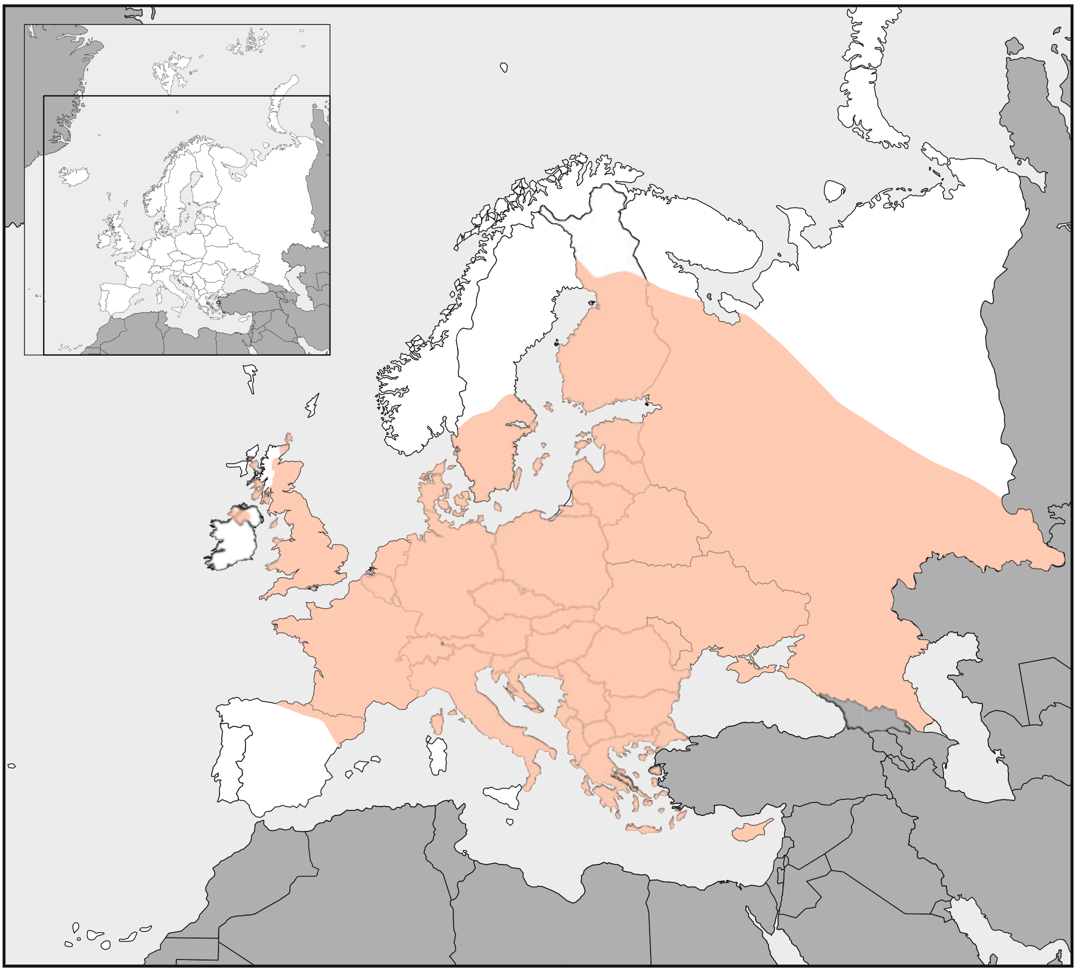
Paleontology

The place of origin of *L. europaeus* is most likely the Middle East. The oldest reliable fossil remains of *L. europaeus* (*euxinicus*) within Europe are from the Late Pleistocene and were found in Crimea and Moldova (Averianov et al. 2003) as well as in C Italy (Angelone et al. 2020). From there on, *L. europaeus* was quite common in S Europe, with fossils reported in more than 60 occurrences from Spain, France, Italy, former Yugoslavia, Bulgaria, Hungary, Moldova, the Ukraine, Crimea, the European Russia, Kazakhstan, and the Caucasus region (Averianov et al. 2003). The Holocene fossil findings of *L. europaeus* come from more than 120 locations in Switzerland, Austria, Poland, former Yugoslavia, Hungary, Israel, Moldova, Ukraine, and Crimea, as well as the Caucasus and the Urals regions. Both the Pleistocene and the Holocene fossil records of *L. europaeus* lie within the current distribution range of the species. The most reliable morphological characters for identifying *L. europaeus* fossil material are dental features. The size of skulls or other bones play only a minor role in the determination of fossil *L. europaeus* as some European Pleistocene populations of *L. timidus* show a similar size (Averianov et al. 2003). In most cases, the determination of fossil remains of *L. europaeus* cannot be verified by descriptions and illustrations of the underlying material; they often only appear in fauna lists. All of these determinations should be taken with great care and classified as indetermined Leporidae (Angelone et al. 2020). Pleistocene hare remains from Spain and Italy, which were ascribed to either *L. europaeus* or *L. capensis*, may also belong to *L. granatensis*, *L. castroviejoi,* or *L. corsicanus* (Kotsakis et al. 2003).

Current Distribution

Originally, *L. europaeus* was distributed over steppes, steppe forests, and open areas in woodlands in SE and C Europe, the Middle East, the Caucasus, the Russian lowlands, and W Kazakhstan. After colonization of continental Europe following human agriculture (Lado et al. 2018), hares increased locally their densities but were still uncommon in the late medieval time (Huber 1973). The rise of European hare population started in the eighteenth and nineteenth century with increasing agricultural efficiency, e.g., through drainage of swamps and field melioration (Huber 1973). Currently, the European hare can be found throughout Europe except the very SW (C and S Iberian Peninsula, south of Cantabria, and the river Ebro) as well as far N (C and N Fennoscandia, N Russia as well as the islands in the Arctic Sea) (Fig. 2). European hares have been introduced to many European islands including several British isles and numerous ones in the Mediterranean Sea (e.g., Crete, Rhodes, Cyprus, and Corsica) (Masseti and De Marinis 2008).

The distribution range in Europe is expanding. Already Ognev (1940 in Angermann 1972) described a shift to N and E in Russia and Kazakhstan beginning 200 years ago. Whereas land use change, namely deforestation and increase of arable land, was the main driver since the beginning of the twentieth century (Angermann 1972), global warming is an additional factor fostering the range expansion of the European hare, as the example in Fennoscandia shows (Jansson and Pehrson 2007; Thulin 2003). In line with that, European hare range expansion toward higher altitude has been reported for the Alps (Schai-Braun et al. 2021a).



Map template: © Getty Images/iStockphoto

Fig. 2 Current distribution of *Lepus europaeus* following Schai-Braun and Hackländer (2016). (Map template: © Copyright Getty Images/iStockphoto)

Description

Size and Morphology

The European hare is a typical leporid with longer hind limbs than forelimbs. It is the largest hare in W Europe, however with huge variation across the distribution range: head-body length 530–760 mm, tail length 70–140 mm, hind-foot length 120–185 mm, ear length 90–150 mm, and body weight 2.5–8 kg (Angermann 1972; Grimmberger et al. 2009; Schai-Braun and Hackländer 2016; Zörner 1981). An increase in size following Bergmann's rule from SW to NE can be observed. Moreover, Pielowski (1969) described an increase in body weight from W to E, i.e., with increasing continentality. In sum, morphological variation within the species can be explained mainly by geographical variation, differences in habitat and climate. However, some morphological features might be forged due to the strong anthropogenic intermixing of hare populations in the last centuries, since hares have been translocated across Europe, and even back from S America (e.g., Uruguay and Argentina, Suchentrunk et al. 2006) where they were previously introduced, mainly for hunting purposes.

There is no pronounced sexual dimorphism, and a distinction between the sexes in the field is quite impossible from the distance, if single hares are observed. However, females are slightly larger (Bujalska 1964) and heavier than males (Caboń-Raczyńska 1974; Flux 1967a; Kröning 1963). Sexing according to the primary sexual characteristics can lead to errors, because the penis and the clitoris look similar at first glance. The penis is pointed, tubular, and curved slightly backward. The clitoris, on the other hand, has a groove with a similar shape like the penis. In addition, during times of sexual inactivity or in younger individuals, males do not have their testicles in the scrotum, i.e., not visible from outside.

The eyes of European hares are large with rounded pupils. The iris color is highly variable ranging from dark brown to bright yellow. Hares can close their nostrils with two skin folds. The upper lip is split in the middle ("harelip"). A hare's forefeet have 5 and the hind feet 4 clawed toes. The sole is densely haired and no pads are visible. Hares have three pairs of teats (but see Massányi et al. 1997) and thus follow Aristotle's "one-half rule" (Diamond 1987), saying that the number of teats in a mammal is twice as high as the average litter size (see "Reproduction").

The skull of European hares is relatively large and elongated, with a broad, dorsally distended nasal part (Fig. 3). The anterior and posterior wings of the supraorbital processes are well developed and mostly free. The maxillaria have a sieve-like appearance. The fossa mesopterygoidea is broad, the bony palate short (ca. 8% of the Cbl), and the choans wide (ca. 130% of the Cbl; Corbet 1983).

Characteristic for all leporids is the relatively large caecum, which exceeds the total body length of a hare. As in other hindgut fermenter, this part of the digestive tract is used to increase the digestibility of fibers with the help of microbial activity (see "Diet"). According to data provided by Caboń-Raczyńska (1964a) and Slamečka et al. (1997), the heart is large, weighing more than 1% of the body weight, which exceeds the general pattern for mammals (0.55%, Lindstedt and Schaeffer 2002). This can be interpreted as an adaption to persistent and high-speed running (see "Locomotion").

Pelage

The pelage is soft and smooth. Hair lengths range between 4 and 10 mm (Borowski 1964). The fur is dominated by dense down hair, which are about 12 μm thick and roughened on the surface (Kayser s.a. in Koenen 1956). Awn hairs are sparse, and only a few guard hairs can be found mainly on the lateral parts of the body. Awn hair are about 84–90 μm thick. According to Toldt (1935), ventral hairs are thinner than dorsal ones. Hairs in the auricles are short, otherwise alternating between about 5 and 10 mm in length on the body.

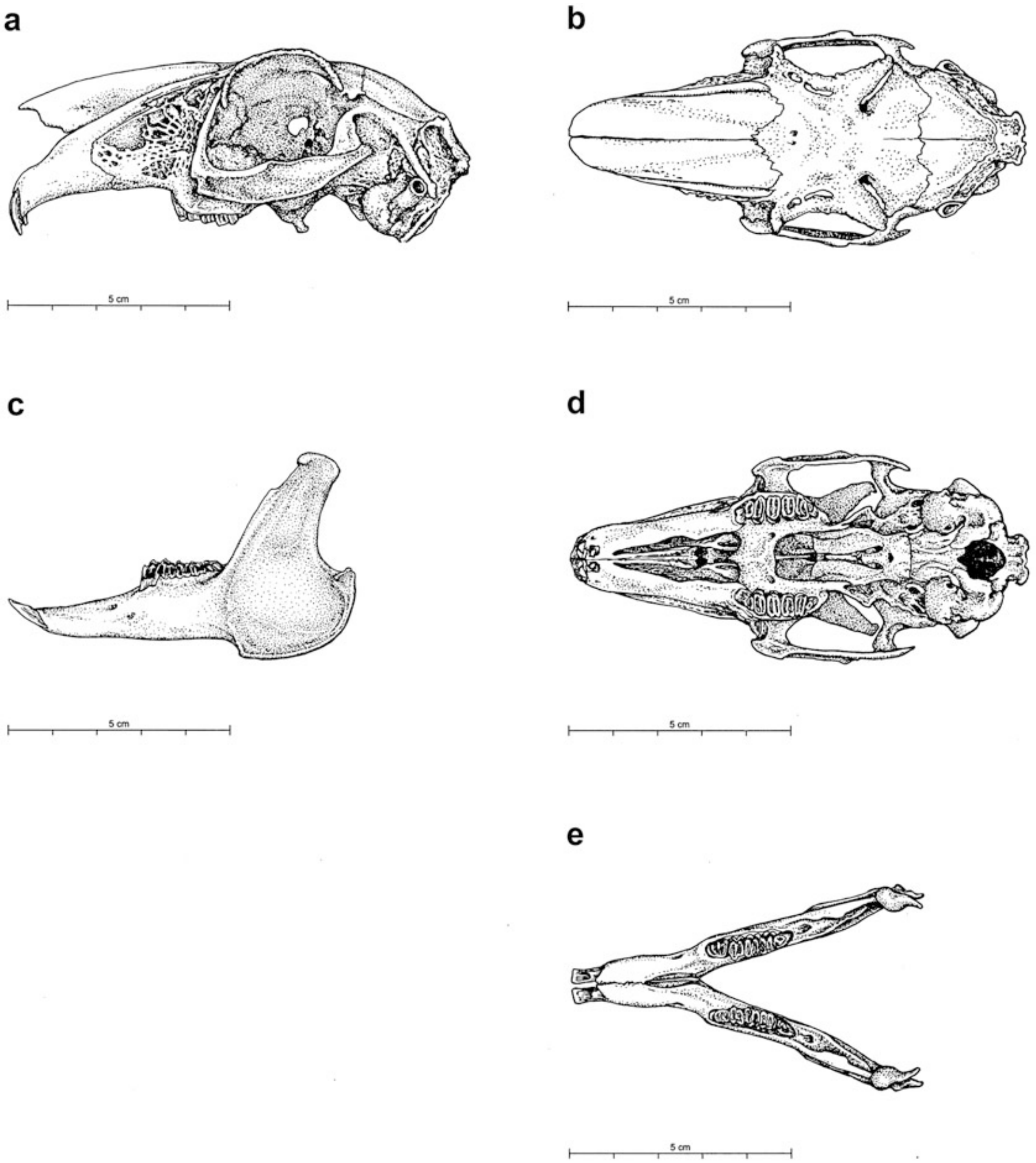


Fig. 3 Skull of *Lepus europaeus*. (**a, b, d**) lateral, dorsal, and ventral view of skull, (**c**) lateral view of left mandible (view from outside), and (**e**) dorsal view of mandible (© Franz Müller with kind permission)

Particularly long hair was found in the anal region, 72 mm in winter coat. Fur density is up to 175 hairs/mm^2 (Waldeyer-Petri s.a. in Koenen 1956). Whisker hairs on the lids and lips are up to 110 mm long, the longer ones are predominantly white.

Hair molt of *L. europaeus* was described in all months with the exception of December and January, but especially in the months of March to June and September. This is interpreted as changing hair twice a year (autumn and spring). Molt is triggered by changing photoperiod and might be accelerated by temperature (Sokolov et al. 2009). According to Borowski (1964), the course of the molt both in spring and autumn begins on the back, then moves to the chest, and later includes the head, ears and neck, and finally the ventral parts. In contrast, according to Hewson (1963), the molting process in autumn is the opposite of that in spring.

In general, the fur is tawny or rusty with a whitish ventral part. The color of the summer fur varies considerably between individuals, from ocher-gray or brownish-yellow or brown to yellowish-gray with a distinct blackish tinge on the back, which is caused by the black or black-brown tips of the awn and down hairs. The latter is silver gray or white with black or brownish black tips. The back of the ears is white or grayish-white with a black or black-brown spot on the tip. The tips of the ears have a large triangular patch on the back that contrasts with the paler gray of the rest of the ear color. The cheeks are ocher-brown or ocher-gray. The chest and flanks are tan or rust-colored. The outer sides of the limbs are ocher-brown, and their inner surfaces and the belly side are white. The tail has a black spot on top but is pure white below. For more information on coat color and inter-individual variation, see Rieck (1953), Koenen (1956), and Borowski (1964).

The winter fur is thicker and woollier. All three hair types are also longer in winter, and the hair density is higher. The winter coat is lighter and grayer compared to the summer coat. All winter coat characteristics (hair length, hair density, and coat color change) get more pronounced along a gradient from S to NE (Rieck 1953). In the S, the winter coat is colored almost like in summer (Sokolov et al. 2009), but in winter there is some white on the sides of the head and at the base of the ears, some gray on the thighs. In individuals from the N (from Belarus eastward), the winter fur is mostly white except for the front back, head, and ears that are darker (Sokolov et al. 2009). Note that the white hairs of *L. europaeus* are blackish at their base in contrast to pure white hairs in *L. timidus* winter coat (Grimmberger et al. 2009).

Dentition

As all European leporids, *L. europaeus* has 28 teeth with I^1, I^2, P^1, P^2, and P^3 and M^1, M^2, and M^3 as well as I_1, P_1, and P_2 and M_1, M_2, and M_3. The incisivi are surrounded by enamel all around. The I^1 have a mesially located longitudinal furrow that, in rare cases, may contain some cement. Typical of the species' I^1 compared to *L. timidus* is the rectangular, nonsquare cross-section (Hauser 1921) with a width-to-thickness ratio of around 1.6. Despite the premolar milk teeth, all teeth are rootless and grow continuously. Problems might arise when a tooth breaks in asymmetric skulls. In this case, the teeth have no counterparts and grow spiraled (Müller-Using 1974).

Age Determination

Due to the size variation within the species, age determination by skull size, body length, or weight is hazardous, both in adults (Suchentrunk et al. 1991) and in leverets (Bray et al. 2002).

In the field, age class (subadult vs. adult) can be assessed by Stroh's sign (Stroh 1931), an epiphyseal protrusion that can be palpated as a lateral ulnar knob close to the carpal joint. In European hares, this protrusion can no longer be palpated at an age of approximately 6–8 months. However, Suchentrunk et al. (1991) reported that some young of the year lost Stroh's sign already at an age of 4 months, and some individuals might still have this sign at an age older than 12 months. However, on average young hares born very early in the year are no longer recognized as subadults during autumn using Stroh's sign. Therefore, the reliability of this age determination method decreases rapidly toward the end of the year (Rieck 1966; Zörner 1977). Thus, the precision of age structure analysis using Stroh's sign in autumnal hunting bag depends on the hunting date: The percentage of undetected young hares ranges between 10 and 20% for hunting dates in November; in December it can be up to 50% (Rieck 1967). Bujalska et al. (1965) mentioned an error rate of up to 70%. Despite these restrictions, Stroh's sign is still the most applicable age determination method in the field if season is considered. This age determination method may be valid in other hare species, too.

A more appropriate age determination is done by determining the dried eye-lens weight (DLW) as described by Andersen and Jensen (1972) and further elaborated by Broekhuizen and Maaskamp (1979) as well as Suchentrunk et al. (1991). This method allows distinguishing between young of the year and adults (hares from the previous year) as well as estimation of date of birth within young of the year to cluster them into birth cohorts. In populations with reproductive pause (see "Reproduction"), young of the year and adults can easily be distinguished when frequencies of DLW are plotted as the distribution has two peaks then. In areas where hares reproduce all year round, the DLW method is less useful, since such frequency peaks might not appear.

Physiology

In optimal conditions, body weight of adults seems to be stable throughout the year (Caboń-Raczyńska 1964a), while body composition varies. For example, body fat reserves fluctuate seasonally. Fat depots are built up during autumn until winter, with males having higher body fat indices (approximately 2.7% of body weight) than females (approximately 2%, Zörner 1981). The body fat reserves are depleted gradually from winter onward (Flux 1967a; Packer 1989; Rieck 1953; Schneider 1978) until no retroperitoneal fat is left in summer. Hence, in terms of reproduction, female hares rely on body fat resources early in the year (capital breeder) and on energy sources from their diet in summer (income breeder) (Valencak et al. 2010). Peak sustained energy assimilation rates in lactating females are highest in autumn when food intake increases to cover the energetic costs of milk production for the precocial young (Valencak et al. 2010).

At rest (in the thermoneutral zone), body temperature is slightly above 38 °C (Paci et al. 2006), heart rate between 95 (Paci et al. 2006) and 140 beats min^{-1} (Noszczyk-Nowak et al. 2009), and oxygen consumption about 0.54 ml g^{-1} h^{-1} (Kronfeld and Shkolnik 1996). The upper critical ambient temperature is about 32 °C (Kronfeld and Shkolnik 1996). In winter, for every 1 °C decrease, adult hares increase food intake by 3.6 kcal kg^{-1} day^{-1} (Myrcha 1968), whereas leverets respond by 7.4 kcal kg^{-1} day^{-1} (Pilarska 1969). All these values have to be considered in the light of allometric effects, but body weights of examined hares were not always given in the studies mentioned above.

The precocial leverets are able to maintain normothermy from day 1 of life when exposed to temperatures down to −8 °C (Hackländer et al. 2002a). Resting metabolic rates in leverets are comparably low during cold, and heat loss might be reduced by peripheral vasoconstriction. This is believed to be an adaption to precociality and low maternal care (see "Behavior"). Heat loss is reduced in the first weeks of life with increasing body weight and decreasing thermal conductance. The slopes of regression of resting metabolic rates (RMR, i.e., in the thermoneutral zone) versus ambient temperatures for each week of life decreased from 0.54 W kg^{-1} C^{-1} in week 1 to 0.21 W kg^{-1} C^{-1} in weeks 3–5 of life (Hackländer et al. 2002a).

Muscles are dark and long-fibered. Polyunsaturated fatty acids (PUFAs) are enriched in muscle phospholipids compared to white adipose tissue lipids and liver phospholipids (Valencak et al. 2003). Especially, the content of n-6 PUFAs in muscles from *L. europaeus* is high, characterizing the hare as a typical persistent runner (Ruf et al. 2006).

In areas with reproductive pause, the reproductive cycle of hares is triggered by photoperiod (Martinet 1976). Reproductive hormones are following this seasonal cycle (Massányi et al. 2000; Slamečka et al. 2001; Stavy et al. 1978). Studies on female sexual hormones concentrated mainly on the phenomenon of superfetation (see "Reproduction"). Progesterone levels dropped after day 35 of gestation indicating the onset of an estrus during pregnancy (Caillol and Martinet 1976). Prolactin increased before that drop prepartum and then increased stronger after the first suckling stimulus (Caillol et al. 1990). Luteinizing hormone (LH) and follicle-stimulating hormone (FSH) are also increasing after day 34 of gestation, indicating estrus and readiness for the induced ovulation while pregnant (Caillol and Martinet 1983; Caillol et al. 1991a).

Genetics

Chromosomes: 2n = 48, NP = 88 (Gustavsson 1971). Genetics studies using mtDNA markers have revealed the existence of two major phylogeographic lineages, the European and the Anatolian (e.g., Ashrafzadeh et al. 2018; Djan et al. 2017; Minoudi et al. 2018). Due to the postglacial spread of *L. europaeus* across the continent and translocations, the species has a low genetic differentiation in Europe, suggesting a high gene flow among populations (Fickel et al. 2005; Hartl et al. 1990, 1993; Mamuris et al. 2001, 2002; Suchentrunk et al. 2000). Nevertheless, rare alleles can be found in the glacial refugal areas (Amoutzias et al. 2016; Suchentrunk et al. 2003).

Hybridization within the genus *Lepus* has been described, especially between *L. europaeus* and *L. timidus* (Conrado zu Baldenstein 1863; Gustavsson 1971; Notini 1941; Thulin et al. 2006). Hybrids are fertile (Schröder et al. 1987) and, in natural populations, are predominantly the result of a unidirectional mating between male *L. europaeus* and female *L. timidus* (Levänen et al. 2018a; Thulin and Tegelström 2002). Moreover, limited genetic admixture was found in the contact zone between *L. granatensis* and *L. europaeus* in N Spain, despite existing evidences of hybridization being found (Melo-Ferreira et al. 2014). It should be highlighted, however, that the great majority of European hare populations in Spain have massive *L. timidus* mitochondrial introgression (Alves et al. 2003; Melo-Ferreira et al. 2009, 2014). In fact, ancient and recent introgression between hare species has been detected in many populations, and in several cases it involves the European hare (Alves et al. 2008; Ferreira et al. 2021; Lado et al. 2019; Levänen et al. 2018b; Melo-Ferreira et al. 2012; Suchentrunk et al. 1999; Thulin et al. 2006; Zachos et al. 2010). The report on *L. timidus* transcriptome allows to identify 4.672 putative diagnostic sites between *L. europaeus*, and a subset of 85 random independent single nucleotid polymorphisms (SNPs) which can be valuable to assess population status and monitor hybridization between these two species (Marques et al. 2017). Nevertheless, microsatellites have been shown to be a useful molecular tool for assessing hybridization between *L. europaeus* and *L. timidus* in the Alps (Rehnus and Bollmann 2016; Schenker et al. 2020).

Life History

Reproduction

It remains unclear whether *L. europaeus* has an estrous cycle (Caillol and Martinet 1983; Caillol et al. 1991b). As in other leporids, ovulation is triggered by copulation and is thus induced and not spontaneous (Martinet 1980). Gestation length is usually 42 days but might last up to 45 days (Sokolov et al. 2009). However, interbirth intervals might be shorter due to superfetation. This phenomenon (see Roellig et al. 2011 for a review) was already described by the Greek philosopher Aristotle in the fourth century BCE (Jennings 2017) and allows females to get fertilized again while pregnant, beginning with day 34 of pregnancy (Caillol and Martinet 1983; Caillol et al. 1991a), and thus to bear two litters of different age in the uterus at the same time. Consequently, interbirth intervals are shorter than gestation length itself. Interbirth intervals can even be as short as 24 (Slamečka and Šebová 1991) or 25 days (Sackmann 1977). The two litters of superfetation were never observed sharing the same of the two uterine horns (Roellig et al. 2011). Although superfetation enables females to produce more young per time (Roellig et al. 2010b), this phenomenon seems to be rather rare in the wild (Broekhuizen and Maaskamp 1981; Flux 1967a; Horáček and Uher 1965; Lloyd 1968; Möller 1971; Raczyński 1964).

Higher probability of superfetation in captivity might be due to improved body condition of female hares, permanent presence of a male during pregnancy, and unlimited availability of high-quality food (Hediger 1948; Martinet et al. 1970). While discussing superfetation, it is worth notifying that males produce a substance that reduces the sperm motility, thus enabling them to survive for a longer time (at least 36 days according to Martinet and Raynaud 1972).

Reproductive pattern of *L. europaeus* is quite variable across the distribution range, whereas reproduction is restricted to spring and summer months in C, E, and N Europe (e.g., Lincoln 1974; Möller 1971; Stieve 1952; Raczyński 1964). Irrespective of this general pattern, sporadic winter reproduction has been found all over the distribution range, e.g., E Austria (Schai-Braun et al. 2020), but is more likely in oceanic climates (e.g., Hackländer et al. 2011 for Belgium; Hewson and Taylor 1975 for Scotland) and in the Mediterranean range (Antoniou et al. 2008 for Greece). In line with this, the pattern of annual testicular activity in males varies between study sites (e.g., Blottner et al. 2000; Eskens et al. 1999; Štrbenc et al. 2003).

Where leverets can be found in all months, number of litters is larger but mean litter size is smaller. In areas without reproduction in autumn/winter, mean litter size is larger but number of litters small (Flux 1981a; Sokolov et al. 2009). Therefore, number of litters per female and year varies from 2 (Kolosov and Bakeev 1947 in Sokolov et al. 2009) to 5 in C Europe (Möller 1976; Petrusewicz 1970; Pielowski 1976a; Rieck 1956a) in the wild, and up to 6 in captivity with unnatural photoperiod (Martinet 1976) or with superfetation (Slamečka and Šebová 1991). The number of litters per female in S or NW Europe, where reproductive pause is less pronounced or even absent (see above), remains unclear, however might be larger than 5.

In areas with reproductive pause (and thus climatic differences between seasons), litter size at the beginning and at the end of the breeding period is smaller than in the middle (Lincoln 1974; Raczyński 1964). Litter size has been described between 1 and 6 individuals in the wild (Pielowski 1976a). However, although reproductive pattern varies across the distribution range, yearly reproductive output per female is similar across the distribution range with 10 leverets per female and year (Flux 1981a). Despite that, the average reproductive output of adult females in a population might reach 13 leverets per year (Schai-Braun et al. 2020; Velek and Semizorova 1976 in Pépin 1989). Maximum number of placental scars per female and year is 22 (Bray 1998; Schai-Braun et al. 2020). The vast amount of studies on litter size and number of litters per year have to be interpreted in the light of female age and body condition as well as reproductive pattern. As a general characteristic, Schai-Braun et al. (2021b) showed that: i) Heavier females have heavier litters at birth, ii) in summer and spring, total litter mass is larger than in winter, and iii) at the end of lactation, the litters of multiparous females are heavier than those of primiparous females.

One has to bear in mind that differences between results on reproductive performance in *L. europaeus* might be due to methodological differences as nearly all studies are based on counting corpora lutea, placental scars or embryos/fetuses in hares that were killed or found dead (but see Göritz et al. 2001 for ultrasound analysis in hares caught in the wild). Differences between litter size at birth and prepartum might be due to prenatal or early postnatal mortality. In fact, a litter size larger than the maximum of 6 (Pielowski 1976a) has been reported, but only prepartum (up to 10 in Broekhuizen and Maaskamp 1981 and even 13 young in von Thüngen 1878 in Zörner 1981).

Prenatal mortality might reach up to 90% depending on climate, season, and female age or body condition (Lincoln 1974; Raczyński 1964). Prenatal mortality includes failed implantation of fertilized eggs, resorption of embryos, and death of fetuses. This late stage of prenatal mortality leads to stillbirths of some or all leverets of a litter. In rare cases, mummified leverets can be found in a female body cavity, i.e., outside the uterus (Zörner 1981).

The proportion of reproducing females in a population depends on age, body condition, and health status of females (Broekhuizen and Maaskamp 1981; Ciberej 1993; Schai-Braun et al. 2021b). In adult females, proportion of reproducing individuals is increasing from winter to summer (Broekhuizen and Maaskamp 1981; Möller 1976). Within 1 year, between 85 and 100% of adult females reproduce (Schai-Braun et al. 2019). Reproductive senescence is reached between 4 and 6.3 years (Schai-Braun et al. 2021b) and is accompanied by pathological alterations in the uterus (Bensinger et al. 2000; Hackländer et al. 2001; Šebová 1991).

Subadults are usually fertile with an age of 4–6 months, with some variation due to time of birth (Caillol et al. 1992; Lincoln and MacKinnon 1976; Möller 1976; Pépin 1977; Slamečka and Šebová 1991): Hares born later in the year and dwelling in areas with reproductive pause in autumn have a delayed puberty for several months, and those females reach sexual maturity at an age of 9–15 months (Sokolov et al. 2009). In moderate to warm climates, hares might take part in reproduction already in the year of birth, although with lower leveret survival (Schai-Braun et al. 2021b). The youngest female to become pregnant was 67 days old, however in captivity (Schai-Braun et al. 2021b). Bray (1998) reported that 14% of the reproducing females in S France were less than 12 months. Toward the N and NE ranges, the proportion of reproductive young of the year diminishes (Averianov et al. 2003). Belova (1987 in Sokolov et al. 2009) did not find any female younger than 12 months reproducing in the Baltic region.

Growth

Prenatal growth is sigmoidal with a maximum growth rate between week 3 and 4 prepartum (Hackländer et al. 2003; Roellig et al. 2010a). Hares produce precocial young, i.e., leverets are relatively mature at birth, with open eyes and ears and fur (for camouflage). Note that hares give birth in forms above ground. Birth weight of European hare leverets depends on litter size and ranges between 40 (Martinet et al. 1970) and 192 g (Zörner 1981), with larger individuals in smaller litters. Crown-rump lengths of newborn European hares range between 90 and 140 mm, averaging 115 mm (Broekhuizen and Martinet 1979; Štěrba 1981). Young are suckled for a period of 11 (Notini 1941) to 60 days (Sokolov et al. 2009), depending on litter size, season (ambient temperature, food availability), and gestational status of the mother. There is an obvious trend that lactation length is longer in harsher environments as highest values are reported from the N and E of Europe.

Females provide a milk rich in fat (at least 20%, Broekhuizen and Maaskamp 1980; Hackländer et al. 2002b; Kučera 1991), with a comparably high content of long-chain monounsaturated fatty acids (Demarne et al. 1978; Lhuillery et al. 1984). Fatty acid composition depends on time of breeding (Valencak et al. 2009). Fat content might be lower (down to about 15%) in suboptimal habitats (Hackländer et al. 2002b) or when fed a low-fat diet in captivity (Lhuillery et al. 1984; Martinet and Demarne 1984). Milk intake has three phases with an increase until day 12, a plateau until day 22, and a decrease until day 30 (Lhuillery et al. 1984). The change of milk teeth starts in week 2 of life (Arkhipchuk 1983 in Sokolov et al. 2009) and is terminated in the fourth week of life. Between an age of 7 and 15 days, solid food is consumed by leverets (Broekhuizen and Maaskamp 1976; Cooper 1970; Hackländer et al. 2002a; Lhuillery et al. 1984; Sackmann 1977). Daily weight gain postpartum is highest between day 20 and 80 and ranges between 22.5 and 32.5 g d^{-1}. Leverets increase their body weight 8.5-fold within 35 days (Hackländer et al. 2002a) in a sigmoidal growth curve (Pielowski 1971a; Pilarska 1969). Usually, leverets are no longer provided with milk when body weight approaches 1000 g (Flux 1967a).

European hares reach adult body size at about 8 months, with some variability due to environmental factors mentioned above. Body weights still increase until the age of 4 years (Pielowski 1971a). The skull increases in some parameters throughout life, at least in hunted populations (Caboń-Raczyńska 1964b) where maximum life span is shorter than in nonhunted or captive populations.

Sex ratio at birth is close to 1:1 and independent of female body mass at mating, season of birth, female age, diet quality or a female's individual reproductive history (Schai-Braun et al. 2021b). The balanced sex ratio remains in the adult population (Frylestam 1979; Jezierski 1965; Misiorowska et al. 2014; Rieck 1953; Semizorová 1982; Zörner 1981), i.e., mortality rate is only slightly affected by sex (Hušek et al. 2015; Marboutin and Hansen 1998; Marboutin and Péroux 1995). Deviations from a sex ratio of 1:1 in adults are discussed in the light of potential effects of sampling (hunting) method and seasonal effects (Möller 1975; Pielowski and Raczyński 1976; Szederei 1959; Zörner 1981).

Survival

In adults, survival rate is depending on study site and year and averages to about 50% (Broekhuizen 1979; Kovács 1983; Pépin 1987; Petrusewicz 1970; Pielowski 1971b). Adult survival is slightly higher in males than in females (Marboutin and Hansen 1998; Marboutin and Péroux 1995), but independent of age (Broekhuizen 1979; Kovács 1983; Petrusewicz 1970). Maximum age reported is 12.5 years in the wild (Pielowski 1971b).

Most leverets die within the early stage of life (Karp and Gehr 2020) leading to very low survival rates of young of the year ranging between 5% (Schai-Braun et al. 2020) and 56% (Abildgård et al. 1972). Averianov et al. (2003) reviewed that juvenile survival rate of 25% is the average. In line with this, the proportion of subadults in the autumnal hunting bag varies predominantly according to juvenile survival. In long-term examinations of game bags, the average proportion of hares with Stroh's sign (Stroh 1931) ranges between 10 and 70% (e.g., Ahrens et al. 1993; Eskens et al. 1999).

Reasons for low survival rates in leverets are predominantly adverse weather, predation, and agricultural activities. Unfavorable weather conditions, especially low temperatures and high precipitation in late spring and early summer (Beuković et al. 2013; Hackländer et al. 2001; Karp and Gehr 2020), are hard on leverets as they rely on their own thermoregulatory capacities (Hackländer et al. 2002a) and are not protected by their mother when there is rain, cold wind, or wet snow (see "Parental Care"). Apart from that, leveret survival will decrease in years with summer droughts (Bresiński and Chlewski 1976), as females might be unable to provide enough milk through food processing. In line with that, adverse weather is associated with lower hare abundances and hunting bags (Eiberle and Matter 1982; Rödel and Dekker 2012; Siivonen 1956). Unfavorable weather decreases also adult body condition (Caboń-Raczyńska 1974) and might lead to reduced reproductive performance, too.

Leveret survival might be negatively affected in areas of high predator abundance and/or a lack of protecting vegetation (Knauer et al. 2010; Reynolds and Tapper 1995; Schmidt et al. 2004). Predators range from small mustelids, like the least weasel (*Mustela nivalis*), to wolf (*Canis lupus*), and from small birds of prey and Corvidae to eagle owls (*Bubo bubo*) (Hell and Soviš 1997; Pielowski 1993). Smaller predators prey on leverets while larger ones can kill adults. Survival rate in adult hares is less affected by predation, except for individuals in bad condition (Severtsov et al. 2017).

Mortality causes include also agricultural activities like mowing of meadows, use of weeder in cereal crop fields, etc. (e.g., Durdík 1981; Kałuziński and Pielowski 1976; Kittler 1979), and road kills (e.g., Haerer et al. 2001; Heigl et al. 2016; Reichholf 1981; Roedenbeck and Voser 2008). Pépin (1986) demonstrated that losses by agricultural activities might have more negative impact on leveret survival than adverse weather conditions. Last, but not least, in all age classes, diseases can significantly contribute to mortality rates (see "Parasites and Diseases").

Habitat and Diet

Habitat

The European hare lives above ground year-round. Originally dwelling in steppe habitats, forest steppes, and open areas in the forest zone, *L. europaeus* followed humans on their range expansion during the Neolithic revolution from SE Europe north- and westward, where the settlers opened the landscape for agriculture (Huber 1973; Lado et al. 2018). European hares can now be found predominantly in arable and pastural landscapes, but also in open woodland, moorland, heathland, or salt marshes. Apart from that, they inhabit also parks and airfields. *L. europaeus* live from sea level up to 2800 m above sea (Huber 1973). Deep and loose snow cover (Sokolov et al. 2009), pastures with livestock (Lundström-Gilliéron and Schlaepfer 2003; Lush et al. 2014), and the proximity of roads (Roedenbeck and Voser 2008) are avoided. However, hares tolerate anthropogenic structures and can be found in cities, too (e.g., Köhler 2008; Mayer and Sunde 2020b).

Hares prefer areas rich in structure providing food and shelter all year round (Pavliska et al. 2018). The distribution of food and cover is of particular importance. At night, open land with low and growing vegetation is preferred for food intake; during the day, protected areas are necessary as resting places (Neumann et al. 2011; Schai-Braun and Hackländer 2014). The day rest areas can be integrated in the nocturnal grazing area but can also be outside the latter.

Arable land is preferred over pastures (McLaren et al. 1997; Vaughan et al. 2003). However, if cereal fields are very compact making it nearly impossible for hares to penetrate, Hewson (1977) and Rühe (1999) showed that hares use only the field edges. Most important for hares is good visibility, at least for the active period during the night (Bresiński 1976, 1983). In line with this, the expanding maize cultivation in Europe leads to an increasing proportion of arable land unsuitable for hares (Mayer and Sunde 2020a; Sliwinski et al. 2019). The same is true for other biomass energy crops like *Miscanthus* (Petrovan et al. 2017) or other tall vegetation (Schrama et al. 2015). Dense thickets of trees and shrubs are avoided at night but are important features of a hare's home range during the day, especially in arable land in winter (Bresiński and Chlewski 1976; Matuszewski 1981; Pielowski 1966). In line with that, in arable land nonfarmed features such as hedges (Cardarelli et al. 2011; Pépin and Angibault 2007; Tapper and Barnes 1986) and fallow land (Cardarelli et al. 2011; Schai-Braun et al. 2013; Smith et al. 2004) are positively selected for shelter during the day. Moreover, field edges are preferred, especially during the inactive phase (day), both for leverets (Voigt and Siebert 2019) and adults (Lewandowski and Nowakowski 1993; Schai-Braun and Hackländer 2014). In the absence of higher vegetation, hares prefer ploughed fields in winter for the resting period (Pépin 1986).

As in other leporids, home range size has a positive allometry with body size (Swihart 1986). Besides that, home range size is affected by habitat heterogeneity, average field size, hare density, season, sex, and, of course, the used method for its estimation (e.g., VHF vs. GPS telemetry, MCP vs. Kernel, length of the observation period, and sample size; for discussion, see Marboutin 1997; Schai-Braun and Hackländer 2014). Usually, males have larger home ranges than females (Belova 1987 in Sokolov et al. 2009; Homolka 1985; Reitz and Leonard 1994; Schneider 1977; Zörner 1981), and males are more active during the night (Zaccaroni et al. 2013). These differences can be explained by reproductive strategies and reproductive behavior: During lactation, females stay near their litter and thus have smaller home ranges. Males, on the other hand, can maximize their lifetime reproductive success by mating with as many as possible females resulting in a higher activity and home range.

Occasionally, the daytime resting place and the nocturnal feeding grounds can be several hundred meters away, e.g., when feeding sites are not providing shelter and a nearby forest is used as a retreat during the day, leading to large home ranges (Homolka 1985). Home range sizes thus depend on the distances between shelter (during the day) and food patches (during the night). Hares travel up to 15 km while feeding in one night (Flux 1967b). In areas with large fields and low variety of crops, annual home range sizes can exceed 330 ha (Pielowski 1972). As hares are nocturnal, the daytime home ranges are much smaller than those at night (Schai-Braun and Hackländer 2014). In contrast, if heterogeneity of habitat is high, home ranges do not differ much between day and night and are rather small (Kunst et al. 2001;

Lewandowski and Nowakowski 1993; Schai-Braun and Hackländer 2014).

The home range of an individual is neither a rigid spatial unit nor a defended territory. As hares do not use self-dug burrow systems like rabbits, their space use is quite flexible and is affected by habitat quality (availability of food, cover, mating partners, and predation pressure). Consequently, home range sizes are larger when observing hares for a longer period and when habitats are changing over the year (as they do especially in arable land). Hares move the center of their home range rapidly during cereal harvest periods (Marboutin and Aebischer 1996; Ullmann et al. 2020; but see Reitz and Leonard 1994), but only in landscapes of low heterogeneity (Schai-Braun et al. 2014). Cereal harvest seems to not affect the stress level of hares if landscape heterogeneity is high (Cybulska et al. 2020). Fields might be used after harvesting as they might provide food and short vegetation (Ullmann et al. 2020). The hare's plasticity in space use leads to comparably low adult mortality rates associated to harvest (Reitz and Leonard 1993).

Some studies showed a high site fidelity of hares (e.g., Bray et al. 2007; Broekhuizen and Maaskamp 1982; Hewson and Taylor 1968), but this can be found only in optimal habitats with high heterogeneity and low levels of disturbance (Avril et al. 2012). Interestingly, *L. europaeus* has an impressive "home instinct," i.e., translocated hares might come back to their original home range, occasionally even up to distances of 464 km (Jezierski 1967).

Disturbances through agricultural activities (Ullmann et al. 2020), hunting (Avril et al. 2014), natural events like floodings (Schrama et al. 2015), or harsh winter conditions might lead to migrations (Sokolov et al. 2009). Food shortages in winter might even lead to mass migrations of several thousand individuals (Fortunatow s.a. and Neschenzew s.a. in Angermann 1972).

While some studies suggested that hares are generally philopatric (Broekhuizen and Maaskamp 1982; Pielowski 1972) and show limited dispersal behavior, Bray et al. (2007) reported a dispersal rate of 43% and a median dispersal distance of 209 m for philopatric individuals and 1615 m for dispersers (maximum 17.35 km). Natal dispersal starts with sexual maturity (between 4–6 months), and males disperse more frequently than females (Bray et al. 2007). In sum, juvenile dispersion is more pronounced in habitats with low quality and low hare density.

Diet

L. europaeus is an herbivore using cultivated crops, weeds, and grasses (predominantly Poaceae). Among weeds in particular species of Fabaceae, Asteraceae, Brassicaceae, and Plantaginaceae are consumed (Brüll 1976; Chapuis 1990; Homolka 1982, 1987; Jennings et al. 2006; Reichlin et al. 2006). In winter, European hares feed also on seeds, buds, twigs, bark, and other woody parts of plants (Frylestam 1986; Rödel et al. 2004; Sokolov et al. 2009), especially when the ground vegetation is covered by snow. Much has been published on plant species used by hares. Information on plant use and preference of plants is of course depending on availability, which is depending on study site. Hence, it is not surprising that the numerous studies differ in their results. Sampling size is quite important, too, as there is a huge inter-individual variation within study sites (Katona and Altbäcker 2002). However, while the food spectrum can include several 100 plant species in one area, the preferred plants are very few. Hence, the European hare has been described as a picky herbivore (Schai-Braun et al. 2015): Of the 349 plant taxa identified in a study site in E Austria, hares used 47 taxa and only 10 were positively selected. Food selection is partly driven by energy content, i.e., crude fat and crude protein, whereas crude fiber is avoided (Schai-Braun et al. 2015; Smith et al. 2005b). While the average crude fat content of food plants for herbivorous mammals is approximately 3.5%, a hare's gut can contain more than 30% fat (Popescu et al. 2011). Dietary fat is important for hares in two ways: first, because reproductive performance is higher in females with access to food rich in fat (Hackländer et al. 2002b) as leverets will have access to a fattier milk. Second, fat serves as source of water when this nutrient is metabolized. Therefore, a positive selection for fatty plant parts is to be expected for a mammal deriving from steppe habitats (Kronfeld and Shkolnik 1996). In line with that, water requirements are usually covered by food metabolization (Kummer 1970), but direct water uptake by hares or feeding of snow is possible (Sokolov et al. 2009) and has been often described for hares living in captivity and fed with dry food (e.g., Landois 1885).

As all lagomorphs, *L. europaeus* uses feces to increase nutrient uptake (Hirakawa 2001), both hard pellets (coprophagy) in times of food shortage (Flux 1981b) and – more importantly – soft pellets (cecotrophy). The cecum is designed as a large fermentation chamber in which bacterial digestive processes of nondigestible fiber and an enrichment of the intestinal contents with proteins and vitamins take place. Leporids incapable of consuming cecotrophs show a protein deficiency (Hirakawa 2001).

Behavior

Activity Pattern

The European hare is mostly active at night (Rühe and Hohmann 2004; Tapper and Barnes 1986). However, in spring and summer hares are more active during the day due to mating activities and shorter nights, respectively (Holley 2001; Homolka 1986; Schai-Braun et al. 2012; Sokolov et al. 2009). In general, the activity pattern is affected by habitat quality, hare density, and disturbances, e.g., by agricultural activities or predation (Pépin and Cargnelutti 1994; Schneider 1978). When active, hares spend most of the time for foraging, between 11 (Flux 1981b) and 14 hours (Homolka 1986), usually in an open area with proper visibility and a vegetation height between 1 and 25 cm (Mayer et al. 2018; Naldi et al. 2020).

During the resting phase, hares use forms, i.e., self-scratched, flat hollows in the ground or simply depressions in higher vegetation (Schneider 1978). The dimensions of these forms are 35–50 cm length and 13–27 cm width (De Vos and Dean 1967; Sokolov et al. 2009) and thus resemble the size of a resting hare. They are deeper (up to 29 cm) in open areas with stronger winds (Sokolov et al. 2009). Usually, hares have their face directed to the open area (Sokolov et al. 2009) or against the main wind direction (De Vos and Dean 1967). In times of heavy snow fall, hares might even dig holes or burrows into the snow (De Vos and Dean 1967; Sokolov et al. 2009) or allow snow to cover them (De Vos and Dean 1967). Formozov (1929 in Angermann 1972) reported that hares dig burrows into sandy soil. However, digging burrows remains an exception.

Forms are reused occasionally (De Vos and Dean 1967). Hares enter these forms usually by approaching them using “backtracking,” i.e., at dawn they move to their daylight range, sit and groom for some minutes at a spot, and then use the same track back to enter the form (Flux 1981b; Koenen 1956). This behavior is interpreted to confuse terrestrial predators. In their forms, they mostly stay immobile relying on their camouflage. The eyes are fully closed when sleeping. Even in deep rest hares are alert and flush full speed out of their forms when in danger. Flight distance is shorter, when protection is given (e.g., in high vegetation); temperatures are higher (danger of overheating while running) and when the soil is muddy (Jerzierski 1973) as mud will stick to the furred paws and thus impede full speed running. While at rest in their forms, *L. europaeus* takes up cecotrophs, starting around 2–3 hours before noon (Kummer 1970; Schneider 1978; Watson and Taylor 1955) directly from the anus (this behavior looks like grooming the anogenital region). Hence, a hare killed before noon will contain a large proportion of fine food particles (less than 0.25 mm length, Naumova et al. 2015) in the stomach.

Locomotion

European hares have different locomotor patterns. The “hobbling” is the calm, normal, and typical gait. The “escape” is a hopping accelerated to a gallop with jumps creating a floating phase without contact to the ground. When a predator comes close, hares speed up by 15.84 km h^{-1} (Taylor

2017). Maximum speed has been reported by Rieck (1953) to be up to 80 km h^{-1}. Hares can jump distances up to 2.7 m long, and 3 m high (Kummer 1970; Rieck 1953). Hence, *L. europaeus* can jump over fences of considerable height or even climb over them. In addition, they can do their typical zigzag escape trick (Kuznetsov et al. 2017). Several other locomotor patterns have been described for *L. europaeus*: When "slipping," individual steps are only carried out with the front legs until the body is more or less stretched out. The hind legs are then jerked forward. "Tip-toeing" is a hopping or walking around, where hare straightens up on all four legs and with largely stretched hind legs. This is probably an impressing position when meeting conspecifics or predators. The European hare can swim distances of more than 1 km (Schneider 1978).

Communication and Signals

Numerous ways of intra- and interspecific communication have been described (Schneider 1981). Among all senses, hearing and smell are most important for hares. As eyes are positioned laterally, hares cannot see clearly but are enabled to detect moving objects around them.

Various fragrances produced in special scent glands are used for individual recognition, for individual orientation in its home range, and as a sign of presence for conspecifics. Apart from that, scents play an important role in mating behavior. Scent glands are in the chin (submandibular gland), the cheek, close to the eyes (Harderian gland), inguinal area (on both sides of the genital opening), and anal region. There are no glands on the paws. Age and hormonal status influence the size of all scent glands (Zörner 1981).

By rubbing against branches, poles, or stones, hares bring out the secretions of the chin gland. The secretions of all head glands are spread over the body with the feet when cleaning the fur. The secretion of the inguinal glands accumulates in hairless skin pockets that are located in the groins. It can also spread over the wider genital area with yellowish crust formation. Inguinal glands are larger in female hares than in males (Mykytowycz 1966).

Schneider (1978) interprets a special type of urination (when the back of the body is lifted and the tail is folded up) as marking behavior. In addition, urine spraying aimed at conspecifics is also observed in the field hare.

Acoustic communication plays a subordinate role in the European hare. A "plaintive" is expressed when hares are in a desperate situation, e.g., when caught by a predator. This call, similar to a bloodcurdling human baby cry, might serve as a warning signal or call for help to conspecific. A "grumble" has been described in various situations, such as fighting or copulating. "Grinding teeth" is interpreted as a threatening or fearful sound, often produced by leverets when disturbed (Hediger 1948). Schneider (1978) also describes a gentle contact sound of leverets before suckling and a warning knocking with the hind legs.

Social Behavior

The European hare lives predominantly solitary, especially at low densities, otherwise in pairs (during mating or mate guarding), or in groups. Grouping is common in spring (Flux 2009), when peak mating starts. At food shortage, hares might gather at food patches, where unusual hierarchies might arise (Lindlöf 1978; Monaghan and Metcalfe 1985; Sokolov et al. 2009). In addition, hares are observed in loose groups at high densities, especially at night during feeding (Broekhuizen and Maaskamp 1982; Marboutin and Péroux 1999). In general, hares are not territorial, and thus there is a high degree of tolerance toward conspecifics, even from the same sex, when food is not limited (Broekhuizen and Maaskamp 1982). When two hares meet, they sniff each other's body and nose. Real fights are rare, even during the breeding season (Schneider 1977), but might get severe and even lethal in captivity where the opponents cannot separate from each other (Landois 1885). The "boxing" behavior, when two individuals stand upright on their hind legs and beat the conspecific's head and fore feet, is usually a fight between a female and a male interpreted as a test of mating partners or preventing males from mating (Holley and Greenwood 1984; Schneider 1978). However, male-male boxing has been reported, too (Flux 2009; Schneider 1977).

Mating Behavior

In spring, hares show a lively mating behavior in groups, even during the day ("March madness," Lincoln 1974). These games include chasing, impressing positions, immediate stoppings, sniffing, urinating, and boxing. Fragrances that convey sexual attraction and individual identity play a major role in this, but also visual stimuli through the ears and tail, both rich in contrast, are important (Schneider 1976). During fights, tufts of hair might fly through the air (Landois 1885). Especially younger females in intensive chases might suffer from severe injuries on their back from male scratches. Copulations take place in segregating couples only after extensive chases and fights. Females ready for copulations sit on their fore legs with erased back (called "lordosis" posture). Belova (1987 in Sokolov et al. 2009) described that lordosis lasts for 6 seconds, mounting by the male 2 seconds and the actual copulation between 5 and 30 seconds. The female terminates the copulation by lifting its hind feet and throwing away the male (Schneider 1977). Usually several matings follow in continued mating runs or in the same place (Schneider 1977; Sokolov et al. 2009). Males show mate guarding and accompany a female after copulation for some days (Flux 1981b; Schneider 1976). Therefore, one can observe a female in her form and a male sitting next to her in alert mode. Competitors are expelled when approaching the couple closer than 3–4 m (Bock 2020).

Parental Care

Leverets are born in the morning (Belova 1987 in Sokolov et al. 2009). The birth takes place in a form, often in a protected and dry place. Usually females do not provide any special preparation of the site, but at cold weather females cover their young with hay (Sokolov et al. 2009). Young-borns have open eyes upon birth and can move immediately after birth, although just in a crawling mode (Hediger 1948). Soon after birth, or after 3–5 days at the latest, leverets separate from each other and hide near the suckling area (Broekhuizen and Maaskamp 1976, 1980; Pielowski 1976a; Zörner 1981). Usually females visit the young only once a day, shortly after sunset, for two to six minutes for suckling (Broekhuizen and Maaskamp 1976, 1980; Landois 1885; Martinet and Demarne 1984). The female and the suckled young are sitting opposite each other, with the female being vigilant (Broekhuizen and Maaskamp 1976; Kummer 1970). Leverets accept several feeding events per day, if provided (Cooper 1970). According to Broekhuizen and Maaskamp (1976), the young get active before the female arrives and gather at the suckling spot which is the birth place. The female approaches the suckling spot always from the same direction, and leverets come toward approaching females with increasing age. Thus, the suckling spot therefore moves from the birthplace toward the direction from which the female reaches the suckling spot every night (Broekhuizen and Maaskamp 1976). Young hares do not recognize their mother by olfactory cues (Broekhuizen and Maaskamp 1980; Martinet and Demarne 1984; Stavy et al. 1985), explaining that they might suckle on other lactating females by chance (Landois 1885; Sokolov et al. 2009). After suckling, a female licks up the leveret urine and finishes the nursing by jumping away (Broekhuizen and Maaskamp 1980). Thereafter, leverets separate themselves again waiting to be suckled 24 h later.

Antipredator Behavior

To avoid being killed by predators, juvenile hares mainly remain on their camouflage and press themselves to the ground staying immobile until the danger has gone (Voigt and Siebert 2019). When disturbed, leverets might grumble or grind their teeth, sometimes even attack the opponent with their teeth (Hediger 1948) or their claws of the forefeet. The adult hare relies both on its camouflage as well as on its locomotor capacities. Hares remain motionless when resting in their forms.

When flushed, they use full speed (with ears pressed to the neck), zig-zag running, jumping, swimming through rivers, or even running through a herd of grazing cattle to escape predation (Sokolov et al. 2009). This flight mode is shown when chased by terrestrial as well as aerial predators. In severe danger, hares might use burrows from other species (Angermann 1972; Sokolov et al. 2009) or holes (even in low trees, Zörner 1981). To confuse terrestrial predators, hares use backtracking (Flux 1981b; Koenen 1956) or large jumps to the side (Sokolov et al. 2009). When flushed, hares often run in loops with variable diameter and come back to their form.

Although red foxes (*Vulpes vulpes*) are the main predator for European hares (see "Population Ecology"), this is not generally true for adults. Red foxes might kill adults only by stalking (when vegetation is high). In habitats with good visibility, hares approached by a red fox will show alertness by standing upright on the hind feet. Note that a hare's nails can be dangerous to predators. Therefore, red foxes do not come as close as 30 m to hares when they are in alert mode (Holley 1992). However, red fox presence affects hare space use. Hares use edge habitat more when red foxes are present (Weterings et al. 2019), tend to feed on patches of lower food quality (Weterings et al. 2018), and are more vigilant and less feeding (Mayer et al. 2020b). Living in groups reduces predation risk in hares, and the frequency of individual vigilant behavior is lower in groups of hares than in individually grazing hares (Broekhuizen and Maaskamp 1982; Marboutin and Aebischer 1996), explaining why hares feed in groups, if possible. Single hares reduce activity in bright moon nights, when red foxes are more active (Viviano et al. 2021). Hence, red foxes might have not only direct effects on hares by predation but also indirect effects by creating a landscape of fear.

Parasites and Diseases

Numerous diseases have been described for European hares (reviewed by, e.g., Boch and Schneidawind 1988; Frölich et al. 2001; Sokolov et al. 2009), many of them with severe effects on population dynamics. Parasite infestations can reach epidemic status and in some years can cause large losses in European hare populations. Among ectoparasites, several species of ticks (Ixodida, most importantly *Ixodes ricinus* and *I. reticulatus*) and fleas (Neoptera, e.g., *Chaetopsylla trichosa*) have been described. The ectoparasite load usually increases from N to S. Among the infectious diseases (often associated with ectoparasites), hares might suffer from pseudotuberculosis (*Yersinia pseudotuberculosis*, e.g., Bartling et al. 2004), pasteurellosis (*Pasteurella multocida*, e.g., Haerer et al. 2001), staphylomycosis (*Staphylococcus* sp., e.g., Tomaso et al. 2018), brucellosis (*Brucella* sp., e.g., Gyuranecz et al. 2011), tularemia (*Pasteurella tularensis*, e.g., Rijks et al. 2013), toxoplasmosis (*Toxoplasma gondii,* e.g., Sedlák et al. 2000), and leishmaniasis (*Leishmania infantum*, e.g., Ruiz-Fons et al. 2013; Tsokana et al. 2016). Note that some of these infectious diseases are serious zoonoses (Tsokana et al. 2020), making hares' sanitary surveillance a key factor in the One Health approach.

Among endoparasites, various nematode (e.g., *Nematodirus aspinosus*), cestode (e.g., *Dicrocoelium dendriticum*), and trematode species have been reported. Endoparasitic diseases include lung strongylosis (*Protostrongylus commutatus*, e.g., Pajerský et al. 1992), stomach strongylosis (*Trichostrongylus retortaeformis,* e.g., Soveri and Valtonern 1983), and sarcosporidiosis; however, coccidiosis (*Eimeria* sp., e.g., Posautz et al. 2015) is the most abundant and important one. Disease prevalence fluctuates between years and differs between study sites, age classes, and sex (Lamarque et al. 1996; Rieck 1956b), partly explained by density and weather effects.

In the recent decades, emerging viral diseases through a calicivirus from the genus *Lagovirus* caused severe declines in hare populations (Salvioli et al. 2017). The first calicivirus infection in *L. europaeus* was described in the early 1980s (Gavier-Widén and Mörner 1991) associated with a disease called European Brown Hare Syndrome (EBHS). This calicivirus (EBHSV) is closely related to the virus causing Rabbit Hemorrhagic Disease (RHD), a fatal hepatitis in European rabbits (*Oryctolagus cuniculus*, Frölich and Lavazza 2008). Hare populations dramatically decline after an EBHS outbreak, especially in low-density populations, where the virus persists longer and the proportion of young individuals (which are less affected) is rather low (Paci et al. 2011). The critical density according to these authors is 8–15 hares 100 ha^{-1}. In the early 2010s, a new calicivirus (RHDV2) spilled over from European rabbits to European hares (Velarde et al. 2017). The rapid mutation of the caliciviruses will be a challenging problem for many hare populations (Le Gall-Reculé et al. 2017), not only in Europe.

Besides this, also the myxoma virus can jump from European rabbits to *L. europaeus* (reviewed in Barlow et al. 2014). Myxomatosis in European hares is usually associated with high prevalence in sympatrically living European rabbit populations (Wibbelt and Frölich 2005).

The European hare is a suitable bioindicator for the local or regional distribution of some agrochemicals and other environmental chemicals (Kleinmann and Wang 2017; Topping et al. 2016). A hare's pesticide uptake has been described through feeding or grooming after pesticide overspray (Mayer et al. 2020a). There are numerous studies on hunted hares regarding residues of heavy metals, pesticides, polychlorinated biphenyls, or microplastics (e.g., Bukovjan et al. 1997; Hornek-Gausterer et al. 2021; Massányi et al. 2003; Nösel and Ahrens 1996; Petrović et al. 2014; Škrivanko et al. 2008; Wajdzik et al. 2017), and even experimental applications in captive individuals (Črep and Švický 1993). However, no clear connections between residue findings and population dynamics have been demonstrated yet (e.g., Edwards et al. 2000; Stubbe and Stubbe 1997), although these contaminants might be detrimental for hares (Linšak et al. 2013; Nováková et al. 1976; Orthwein 1984a, b) and reach values that might be dangerous for humans consuming the affected individuals (Slamečka et al. 2012). Agrochemicals had also no effects on the reproductive performance of a hare population, both for females (Hackländer et al. 2001) or males (Blottner et al. 2001).

Population Ecology

Recruitment and Density

The density of hares in steppe environments is low, approximately 2 hares 100 ha^{-1}. Agricultural activity, especially on fertile, but dry, soil types, lead to higher densities (Sokolov et al. 2009). Population density might reach up to 339 hares 100 ha^{-1} in optimal conditions, as it was observed on a Danish island without agriculture, hunting, and terrestrial predators (Abildgård et al. 1972). Habitat quality influences fecundity, (juvenile) survival, thus yearly recruitment and population density. Across the distribution range, spring densities of 1 (Kilias and Ackermann 2001; Rühe et al. 2000) to 156 hares 100 ha^{-1} (Klansek 1996) are described (reviewed in Averianov et al. 2003). As recruitment might double spring numbers, autumn densities can reach up to 275 hares 100 ha^{-1} (Klansek 1996).

Population growth depends predominantly on juvenile survival rate (see "Survival"), which varies between study sites (habitat quality, predation pressure, and climate) and year (e.g., Frylestam 1979; Haerer et al. 2001). Leveret mortality is high and exceeds nearly 65% within the first month (Voigt and Siebert 2020). Until autumn, the overall postpartum mortality reaches up to 81% (Ciberej and Kačúr 1991) or even 95% (Schai-Braun et al. 2020). Therefore, the proportion of young of the year in relation to older females in the hunting bag varies between 10% and 70% (e.g., Ahrens et al. 1993; Eskens et al. 1999).

In general, a complex interaction of numerous factors is responsible for hare recruitment and abundance, namely landscape heterogeneity, land use (practices), soil type, climate (or weather), diseases, and predation (Petrov 1976; Pielowski 1981; Smith et al. 2005a). Studies trying to figure out the relevance of each mortality factor reached different results. However, in many studies, land use practices were more important than weather and diseases (Eiberle and Matter 1982; Frölich et al. 2003; Lundström-Gilliéron and Schlaepfer 2003; Reynolds and

Tapper 1995; Ristić et al. 2021; Schmidt et al. 2004; Smith et al. 2005a; Weber et al. 2019).

Unfavorable weather associated with high humidity and cold temperatures might increase the proportion of infected hares and thus will allow predators to find more easy prey in hares or make use of carcasses. Impact of predation on yearly recruitment strongly depends on the availability of alternative prey (Goszczyniski et al. 1976; Sokolov et al. 2009). Hence, in the peak of small mammal cycles, young hares are less likely predated (Pegel 1986).

The main predator for European hares in C Europe is the red fox. In Poland, hares formed 12–46% of red fox diet (Goszczyński and Wasilewski 1992; Pielowski 1976b), mainly depending on the yearly variation of alternative prey availability (e.g., voles). Note that impact of red foxes increases after large-scale rabies vaccination (Martini 1983; Nösel and Ahrens 1996; Ponjiger et al. 2019; Spittler 1972). Juveniles are the predominant age class that red foxes prey on. However, up to 50% of adult hare mortality might be attributed to the red fox (Goszczyński and Wasilewski 1992). With respect to this report, it should also be considered that red foxes also use carcasses, e.g., from road kills, and thus (adult) hare mortality and red fox predation are not always linked to each other. According to Goszczyński and Wasilewski (1992), hare biomass in red fox diet was highest in spring (43%), lower in summer (12–15%), and intermediate in winter (28%). This pattern is explained by both leveret availability and vegetation cover. In general, red fox density is negatively correlated with population increase or density of hares (Ahrens 1996; Frölich et al. 2003; Goszczyński and Wasilewski 1992; Pegel 1986; Späth 1989).

Interspecific Competition

Where European hares live in sympatry with other species of the genus *Lepus*, they usually outcompete them (Sokolov et al. 2009). With climate change (less snow, increase of arable land use), European hares tend to expand into the range of mountain hares, where they replace them by direct competition and hybridization (Acevedo et al. 2012; Jansson and Pehrson 2007; Thulin 2003). In addition, introduced *L. europaeus* also outcompete *L. corsicanus* (Angelici and Luiselli 2001); however, they do not interbreed (Mengoni et al. 2015).

Where *L. europaeus* lives in sympatry with rabbits (*O. cuniculus* or *Sylvilagus floridanus*), competition for food and aggressive behavior have been reported (Bertolino et al. 2013; Homolka 1987; Kuijper et al. 2004) but are low when both species are at low densities (Flux 2008; Vidus-Rosin et al. 2012). Rabbits depend on their burrow systems and might be dominant over hares within their territories, but this seems to be a rather local phenomenon.

Conservation Status

The European hare's Red List status has recently been confirmed as "Least Concern" on a global scale (Hackländer and Schai-Braun 2019). It is widespread and abundant across its geographic range. However, especially European populations of *L. europaeus* declined in the twentieth century (Hackländer and Schai-Braun 2018). Note, that despite numerous studies claiming that the decline started in the 1960s (e.g., Bock 2020; Farkas et al. 2020; Smith et al. 2005a), there is evidence from long-term hunting bag statistics (e.g., Schwenk 1985), that the decline started some decades earlier, namely with the beginning of the agricultural industrialization (early twentieth century). The European hare is listed under Appendix III of the Bern Convention in Europe (as "*Lepus capensis* (*europaeus*)," Council of Europe 1979). Although the Red List status in Europe and the European Union is "Least Concern" (Temple and Terry 2007), several European countries (e.g., Austria, Germany, Norway, and Switzerland) have classified *L. europaeus* as "Near Threatened" or "Threatened" in their national Red Lists (Reichlin et al. 2006). Despite that, in most European countries, densities of European hares are above the density known from steppe habitats where *L. europaeus* came from prior to their range expansion (see "Current Distribution"). In line with this, lowered densities might not lead to an extinction of the species. Apart from that, there is increasing concern regarding the status of native local populations of this species (Flux and Angermann 1990; Schai-Braun and Hackländer 2016) as restockings for hunting purposes took and take place in several countries including Denmark, France, Greece, Italy, and Spain (Suchentrunk et al. 2006).

Management

The European hare is the most important small game species across Europe (Flux and Angermann 1990), despite the recent decline (see "Conservation Status"). Usually, hunting is open in autumn (October–December), occasionally extended to January or February in vineyards or orchards to prevent damage (Suchomel et al. 2019). As the European hare is reproductively active already in December in C Europe, already Kutzer et al. (1976) called for a shorter hunting season. In England and Wales, where European hares are allochthonous, a closed season is absent (Jennings 2017) though claimed for animal welfare reasons (Butterworth et al. 2017). At higher densities, hunters harvest hares with shotguns using drive hunts, often with the help of dogs and stalkers. In high-density areas, falconers might hunt European hares with goshawks (*Accipiter gentilis*) or golden eagle (*Aquila chrysaetos*). In addition, single hunt with a small caliber rifle is common. Traditional hunting types in the UK like beagling or hare coursing (hounds tracking hares by sight in arenas) are no longer allowed (Jennings 2017), irrespective of the fact that their impact on hare numbers was low compared to shooting (Stoate and Tapper 1993). However, coursing is still practiced in the Republic of Ireland and beagling in France (Jennings 2017). As hares often run loops when flushed (see "Antipredator Behavior"), hunters with hounds use this behavior by just waiting for the hare at the flushing site while listening to the barking hound chasing the hare on its way back to the form (Hackländer 2011).

Hares are hunted for their meat, which is treated as a delicacy in some areas. The hare meat is low in fat and rich in essential fatty acids (Frunza et al. 2019; Slamečka et al. 1998; Škrivanko et al. 2008; Valencak et al. 2015). Slow stewing or roasting was the most common way of preparing hare meat. A modern trend is toward simple seasoning and grilling (Jennings 2017). In former times, hunted hares were used not only for their meat, but also for their fur to produce felts or fishing flies (Jennings 2017).

A sustainable use is based on monitoring hare abundance or density in spring and autumn (Andrzejewski and Jezierski 1966). Langbein et al. (1999) reviewed appropriate monitoring methods. For counting at night (when hares are active), spotlights (Ahrens et al. 1995; Frylestam 1981; Strauß et al. 2008) or night vision devices (Focardi et al. 2001) are in use. Spring densities and population increase are then used to calculate sustainable harvest rates (Marboutin et al. 2003; Schai-Braun et al. 2019). In areas where night counting is compromised (e.g., high proportion of forest cover), hunting bags have to be checked for age composition before continuing hunting on the same day or later. Evaluating the proportion of young of the year can be done either by Stroh's sign (Stroh 1931) or by determining the dried eye-lens weight (Ciberej et al. 1997; Kovács and Heltay 1981): If proportion of young of the year in the hunting bag is lower than, e.g., 50% (and thus recruitment was weak), hunting should be stopped for the year in that specific area.

The superfactor leading to declining European hare densities is the intensification of agriculture (Lundström-Gilliéron and Schlaepfer 2003; Mayer et al. 2019; Panek 2018; Panek and Kamieniarz 1999; Petrak 1990; Schäfers 1996; Schröpfer and Nyenhuis 1982; Smith et al. 2005a). While the European hare benefitted from extensive agriculture in the past, it is now negatively affected by the intensive use of the cultivated land. One has to distinguish between the reasons for the decline and the measure considered to increase hare populations. To counteract the decline of hare populations in Europe, protected areas (Canova et al. 2020), food supplementation in winter (Matuszewski 1966;

Reichlin et al. 2006), habitat improvements (Genghini and Capizzi 2005; Kamieniarz et al. 2013; Meichtry-Stier et al. 2014; Petrovan et al. 2013; Santilli et al. 2014; Schai-Braun et al. 2020; Sliwinski et al. 2019), and predator control (Panek 2013; Reynolds et al. 2010) have been shown to be beneficial, especially by increasing juvenile survival rate. It is clear that habitat improvement will have long-lasting effects (not only for hares), whereas other measures are just fighting the symptoms, though very effectively. Note that habitat improvements have to be planned in a proper way in order to avoid that they act as ecological traps (Hummel et al. 2017). In addition, organic farming is not a beneficial to population growth per se (Santilli and Galardi 2016).

Hare restocking is still a management measure in several hunting sites across Europe (e.g., Cukor et al. 2018; Ferretti et al. 2010; Fischer and Tagand 2012; Misiorowska 2013; Modesto et al. 2011; Spyrou et al. 2013), although mortality rate of translocated individuals is usually very high in the first month and lies between 40% (Misiorowska and Wasilewski 2012) and 79% (Angelici et al. 2000), mainly due to red fox predation (see also Marboutin et al. 1990). Other adverse effects of hare translocations are disease transmissions and genetic introgression (Pierpaoli et al. 1999; Stamatis et al. 2007; Suchentrunk et al. 2006). Translocated hares derive from captive breeding or have an origin from sites with higher hare densities, sometimes several hundred kilometers away from the release site (i.e., from potentially allochthonous populations). They might even come from areas where they have been introduced, like from Argentina and Uruguay (Suchentrunk et al. 2006). Transport and release are debated also in the light of animal welfare (Paci et al. 2006).

Future Challenges for Research and Management

Clearly, the European hare is the best-studied *Lepus* species in the world with far more than 1000 entries in the modern literature databases. Much of the sources, including leading monographies, are written in former scientific languages like German, French, or Russian. Other milestone publications are conference proceedings (Myers and McInnes 1981; Pielowski and Pucek 1976). All these literature sources are rarely used by modern researchers as most of the relevant sources from the last century have not been digitalized, yet. Consequently, there are plenty of study repetitions during the last century, making it difficult to keep the overview on the literature regarding European hares. Despite the ongoing repetition of knowledge, there are still some major gaps to fill (see Hackländer et al. 2008). We need basic research both in the field as well as in captive European hare populations. In addition, comprehensive meta-analyses on available literature will help to understand the species' evolution and ecology.

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