Paulo C. Alves    Nuno Ferrand    Klaus Hackländer (Eds.)

Lagomorph Biology
Evolution, Ecology, and Conservation

With 78 Figures, 3 in Color, and 21 Tables

Springer
Preface

The idea to publish this book was born at the 2nd World Lagomorph Conference in Vairão, Portugal, in July 2004. Twenty-five years after the 1st World Lagomorph Conference, a vast amount of literature on this mammalian taxon had been published and it was time to bring together researchers from all over the world to present and discuss the latest knowledge about hares, rabbits, and pikas. After the first announcement for the meeting we received several encouraging e-mails, among them a very special one:

“We want to offer you and your committee congratulations and best wishes on holding the 2nd World Lagomorph Conference in Portugal 25 years after the 1st World Lagomorph Conference in Canada in 1979. The world’s lagomorph workers are a large, widely separated group with broadly different research programs, but, as Guelph showed, form a strongly united group with common interests when they get together like this. A statement on the present position of world lagomorphs, and its publication, are both timely and immensely valuable.

Good luck to you. Yours fraternally,

Ken Myers, Australia, and Charles McInnes, Canada, Convenors, 1st World Lagomorph Conference, Guelph, Canada, 1979”

The approximately 150 participants from over 27 countries and all continents created a great atmosphere in Vairão, and the discussions promoted by the numerous talks, posters, and workshops certainly increased considerably the enthusiasm in working in such a fascinating mammal group. At the end of the conference, nearly all colleagues recognized that there is an urgent need to provide a comprehensive overview on the current fields in Lagomorph research. Therefore, we asked all participants in Vairão to submit manuscripts on their scientific work. As we did not intend to produce a classical conference proceedings, we also encouraged the participants to write reviews on some important issues, and we then made a peer-reviewed selection of the various topics. This book contains 26 contributions covering different topics in Lagomorph biology. All chapters are organized into sections. The first chapter, “Introduction to the Lagomorpha” by Joseph
Chapman and John Flux is an updated version of the introduction done in 1981 (Myers and McInnes 1981, Proceedings of the World Lagomorph Conference held in Guelph, Ontario, August 1979, University of Guelph). Here the reader will be introduced to the main aspects of taxonomy, ecology, behaviour, and conservation in Lagomorphs. In addition, the authors present a historical overview on the research activities in these fields.

Then, four chapters will highlight some reviews and aspects in Palaeontology and Evolution to understand how humans have contributed to the nearly world-wide distribution of rabbits and hares and to demonstrate the state-of-the-art in modern phylogenetics and phylogeography. In the section Population Ecology and Dynamics readers will gain insight into the general role of Lagomorphs in the ecosystems, how environmental conditions affect populations, and how scientists try to uncover the mechanisms of population dynamics. In the section that follows, Physiology and Behaviour, we will get deeper into Lagomorph biology and learn about reproduction and mother–young relationships as well as interspecific competition between Lagomorphs. Another major factor affecting population dynamics is covered in the section Diseases, in which the authors present all the current knowledge on important viral diseases and why these viruses are of interest for conservation and pest control. As some Lagomorph species are highly endangered while others are treated as pest, in the section Conservation and Management a number of chapters will contribute to a better understanding of this apparently antagonistic treatment of Lagomorph species. Here, readers will be updated on the current conservation status of each species and learn why some selected species should be managed and how this should be done.

We close the book by highlighting those aspects of Lagomorph biology that have been improved over the last 25 years, and then follow with some open aspects that should be, in our opinion, developed in the future.

This book evolved with the help of many colleagues who assisted in reviewing the submitted manuscripts. We want to thank Vilmos Altbäcker, David Hik, Karen Hodges, Robyn Hudson, Diana Pöttschacher, Toni Lavazza, John Litvaitis, Jerôme Letty, Pierre Mein, Dennis Murray, Greg Mutze, Benoist Schaal, Ferdy Rühe, Thomas Ruf, Andrew Smith, Becs Smith, Phil Stott, Jean-Denis Vigne, and Dan Williams. In addition, we appreciate the support of the team at Springer Heidelberg, especially Ursula Gramm and Dieter Czeschlik.

Paulo C. Alves, Nuno Ferrand, and Klaus Hackländer
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Introduction

Lagomorphs (pikas, rabbits and hares) are widespread, being native or introduced on all continents except Antarctica. They are all herbivores, occupying an unusual size range between the rodents, “small mammals”, and ungulates, “large mammals”. Pikas weigh 75–290 g, rabbits 1–4 kg, and hares 2–5 kg. Despite the small number of extant species relative to rodents, lagomorphs are very successful, occurring from sea level up to over 5,000 m, from the equator to 80 N, and in diverse habitats including tundra, steppe, swamp, and tropical forest. Some species have extremely narrow habitat tolerance, for example the pygmy rabbit (*Brachylagus idahoensis*) requires dense sagebrush, the riverine rabbit (*Bunolagus monticularis*) is restricted to Karoo floodplain vegetation, and the volcano rabbit (*Romerolagus diazi*) to zacaton grassland. On the other hand, the tapeti (*Sylvilagus brasiliensis*) occurs from alpine grassland at the snowline to dense equatorial forest on the Amazon, and some hares (*Lepus* spp.) occupy vast areas. According to the latest review by Hoffmann and Smith (in press), there are about 91 living species, including 30 pikas, 32 hares and 29 rabbits (see Fig. 1, families and genera of living lagomorphs).

Taxonomy

Lagomorphs were classified as rodents until the Order Lagomorpha was recognized in 1912. Anatomically, they can be separated from rodents by a second set of incisors (peg teeth) located directly behind the upper front incisors. The pikas (Ochotonidae) have 26 teeth (dental formula i. 2/1, c. 0/0, p. 3/2, m. 2/3) and rabbits and hares (Leporidae) have 28 teeth (i. 2/1, c. 0/0, p. 3/2, m. 3/3.). All lagomorphs have an elongated rostrum of the skull, fenestrated to a lattice-work of bone to reduce weight, a feature unique to the order. The soles of the feet are hairy, providing insulation against cold and extreme heat, and a good grip on most surfaces.
Pikas are in the monotypic family Ochotonidae, which includes a single genus, *Ochotona*. They have a long and distinct ancestry separate from the leporids since at least the Eocene (50 million years ago). All are highly adapted to their alpine or steppe environments, both morphologically and behaviorally. Taxonomically, they are a difficult group, partly because of speciation on separate mountain tops or other remote places where recognition is probably by sound rather than sight, and partly because the genus is geologically old, leading to a proliferation of relict species, but only seven recent species have a fossil record (Erbajeva 1997).

The earliest fossil ancestor of hares and rabbits (Leporidae) lived in Mongolia 55 million years ago (Asher et al. 2005). There are 11 genera (ten if the pygmy rabbit (*Brachylagus*) is included in *Sylvilagus*). Most are monotypic: *Brachylagus, Bunolagus* (the riverine rabbit), *Caprolagus* (the hhispid hare), *Oryctolagus* (the European rabbit), *Pentalagus* (the Amami rabbit), *Poelagus* (the Bunyoro rabbit), and *Romerolagus* (the volcano rabbit); but *Nesolagus* has two species, *Pronolagus* three (the red rock rabbits), *Sylvilagus* 17 (the cotton-tail rabbits) and *Lepus* 32 (the true hares and jackrabbits). *Lepus* is another difficult group taxonomically, in this case because the group is recent and has spread on open land following forest clearance by ice ages and man; and specific recognition is probably chiefly by scent, which is not a normal taxonomic character. The world total reached 71 in 1900, but was reduced to 21 in 1960. Since then it has increased again to about 32; even in well-studied Europe, the number rose from two to the current six (Niethammer and Krapp 2003).
These changes in the number of lagomorph species are illustrated in the editions of “Mammal Species of the World”: in 1982 there were 18 pikas, 24 rabbits, and 19 hares (Honacki et al. 1982); in 1993, 25 pikas, 24 rabbits, and 30 hares (Wilson and Reeder 1993); and currently, 30 pikas, 29 rabbits, and 32 hares (Wilson and Reeder 2005). Most of the increase is a result of splitting the existing taxa, but it is remarkable that a completely new species (Annamite rabbit, *Nesolagus timminsi*), which is as distinctive as the Sumatran striped rabbit (*Nesolagus netscheri*), could remain unknown almost into the 21st century (Surridge et al. 1999; Can et al. 2001).

**General Adaptations**

All the lagomorphs have adapted for quick movement in order to escape predators. Pikas and most of the rabbits sprint to thick cover or burrows, but hares are usually long-distance runners that can outlast their pursuers; some reach 80 km/h, and can maintain 50 km/h for hours. Unlike the pikas, which tend to be diurnal, hares have large eyes suited to their crepuscular or nocturnal habits. Young hares are born fully furred and with open eyes; in contrast, rabbits are naked and blind at birth, and have to be cared for by the mother for 2–3 weeks.

The lagomorphs with the greatest natural distributions (holarctic) are the pikas and hares, although more evolutionary diversity is found in rabbits. The New World cottontails, with 17 species, are the most diverse, and include even semi-aquatic forms like the swamp rabbit (*Sylvilagus aquaticus*). The European rabbit (*O. cuniculus*) is now the most widespread, but this is due to repeated liberations and domestication; historically it was restricted to the Iberian Peninsula, although fossils show a southern European distribution prior to the ice ages. Other genera such as *Pentalagus*, *Bunolagus*, *Caprolagus*, *Romerolagus* and *Nesolagus* appear to be “primitive” evolutionary branches now confined to islands or small areas of special habitat; many of these unusual and little-known forms are endangered (Smith 2008, this book).

Economically and scientifically, lagomorphs are one of the most important mammal groups. Domestic rabbits are a major food resource, and they are also key laboratory animals in medical research. Many lagomorphs are also valued game animals, while others are pests of national significance; both aspects have resulted in generous funding for ecological research programs globally.

**Role in Ecosystems**

Lagomorphs make up the base of many predator/prey systems. Their intermediate size and great abundance allows them to support a community of small to medium-sized predators such as weasels, foxes, cats, civets, and a
large number of birds of prey. Thus the conservation status of the European lynx and Spanish imperial eagle depend on the number of rabbits present, and these have declined dramatically following outbreaks of myxomatosis and Rabbit Haemorrhagic Disease (RHD) (Ferrer and Negro 2004).

Most lagomorphs are selected for high rates of reproduction. Their numbers are regulated by extrinsic and intrinsic factors and dispersal of both adults and young. They have evolved survival mechanisms suited to a wide variety of environments and situations, but being herbivores low on the food chain, their habitat must provide forage and adequate escape cover. Even so, annual mortality rates may reach 90% in many species. Such patterns are common to many game species and rabbits and hares are among the top species favored by hunters in Europe and America.

Reproductive patterns vary with latitude. In New World rabbits (*Sylvilagus* and *Romerolagus*), there is a direct correlation between latitude and litter size, with those in the north producing the largest litters in shorter breeding seasons (Conaway et al. 1974). In hares (*Lepus*), the same direct correlation between litter size and latitude and an inverse correlation with breeding season, results in an almost constant annual production of young per female for all species (Flux 1981), a phenomenon which remains to be explained.

Rabbits in northern latitudes also have shorter gestation periods. This allows northern rabbits to produce more litters in the most favorable weather. Conversely, it is an advantage for tropical rabbits to have longer gestations because more fully developed young are better able to avoid predators and fend for themselves (Chapman 1984). Old World hares do not seem to follow this pattern; *Lepus timidus* has a longer gestation than *Lepus europaeus*, but young hares (*L. capensis* and *Lepus crawshayi*) on the equator in Kenya are almost as heavy at birth as young European hares, despite the mothers weighing half as much (Flux 1981). In compensation, the litter size is smaller and the breeding season longer.

**Lagomorph Behavior**

The behavior of the European rabbit has been studied more than any other lagomorph, but it should be remembered that much of this work has been done in Australia and the United Kingdom, where rabbit control is of great importance. These rabbits are now thought to be feral populations derived from escaped domestic stock, which may be atypical in lacking intrinsic population control behavior (Flux 2001). This may explain the tendency for *O. cuniculus* to reach a biomass ten times higher than any other lagomorph and overeat its food supply, causing major agricultural problems. There has been considerable behavioral work on pikas in Japan, the United States, and the Soviet countries, mostly purely scientific with little emphasis on applied
problems, except in China (see Smith et al. 1990). By comparison, there has been little work on cottontails, jackrabbits, and most other genera.

Cottontail males form breeding groups around several dominant females, choosing areas within the habitat that have better food and cover (Marsden and Holler 1964). Linear dominance hierarchies for females are not well defined, but dominance of unreceptive females over males during nest building, parturition or nursing is important in avoiding detrimental male harassment. The closest thing to courtship behavior in cottontails is a dash and jump sequence and related displays. Swamp rabbits (S. aquaticus) are territorial, but Eastern cottontails (Sylvilagus floridanus) appear to defend only the area around a breeding female. Vocalizations are reported for swamp rabbits, brush rabbits, pygmy rabbits, and mating volcano rabbits (Tefft and Chapman 1987).

Pikas have behavior patterns that are remarkably similar throughout their range and are aligned to habitat: pika species that live in rock screes at low, steady densities, are highly territorial and pugnacious, long-lived, with low fecundity; pikas that live in the steppe make burrows in which they live at high density, often in family groups. They are social, short-lived, and have high fecundity (Smith 2008, this book). They are the only lagomorphs with highly developed vocalization and they store food for winter in “hay piles”, which are vigorously defended.

North American jackrabbits and other hares have very similar behavior while mating, which involves fighting between males to establish dominance (boxing) and between an unreceptive female and a male or males (rebuff). Both boxing and rebuff may be followed by vigorous chasing, but copulation follows only if the female, which is almost invariably dominant over the male, is receptive (Lechleitner 1958; Schneider 1978). “Ownership” of a food resource, or of a female, does not confer any advantage in dominance in European hares (Holley 1986). Vocalizations seem restricted to a grunting call by females to their young and loud screams when caught by a predator.

All of the lagomorphs have a digestive system involving coprophagy (the re-ingestion of soft feces to increase the nitrogen content of the diet) and some even eat hard feces if food is scarce (Hirakawa 2001). They also groom extensively; licking the fur, cleaning the feet, and dusting. In heavy rain, water is shaken away and the feet are kicked to dry them.

Lagomorph Conservation and Management

On a world scale, conservation and management of lagomorphs has included: (1) habitat management, (2) stocking programs, (3) harvest, (4) control and (5) protection. Habitat management has been used chiefly to increase stocks of animals for game shooting. Cottontail habitat in North America entails the creation of disturbed, successional, and transitional vegetation for food and cover by planting, clearing or burning; old pasture is one of the best habitats.
In Europe, there is a long tradition of managing estates for game, hares and deer being the most important mammals, but limited shooting seasons and provision of food in winter were the main management tools. Rabbits were highly valued and kept in elaborate warrens from their introduction about 1200 A.D. until the 19th century when increasing numbers and damage to agriculture changed their status to pests, at least in northern Europe.

Stocking programs have virtually been worldwide, beginning over 2,000 years ago, and often with undesirable results. The most notorious was probably the introduction of European rabbits to Australia, New Zealand, and South America, where many farms were ruined; others include the establishment of European hares in Canada, North and South America, Australia, New Zealand, and Russia. Hunters liberated cottontails in Europe to take the place of European rabbits when numbers were reduced by myxomatosis and RHD. Since cottontails can carry myxomatosis but are not adversely affected by it, they would be expected to replace the European rabbit rapidly, but this does not seem to have happened (Spagnesi and De Marinis 2002), perhaps because the cottontails have not adapted to new habitats (Rosin et al. 2008, this book). In North America, stocking cottontails for hunting has a long history with little regard for disease transmission or impact on native species (Chapman and Morgan 1973); the decline of *Sylvilagus transitionalis* in the 1920s led to massive introductions of *S. floridanus* for 30 years (in the 1930s Pennsylvania alone was importing 50,000 a year) and the impact on *S. transitionalis* populations was severe. The mechanism involved seems to be the better ability of *S. floridanus* to exploit small patches of habitat rather than interference competition (Litvaitis et al. 2008, this book). The introduction of *Lepus europaeus* into Italy now threatens the endemic hare, *Lepus corsicanus* (Trocchi and Riga 2001). The decline of European rabbit populations in the Iberian Peninsula is being tackled with restocking programs by hunters and conservationists (Moreno et al. 2004).

The harvest of lagomorphs has a history dating back 120,000 years associated with their value for food and fur. Pikas are generally too small to be a significant food source, but in Russia, as many as 14,000 skins a year were used for high-quality felt until the 1950s (Smith et al. 1990). The market in domestic rabbits (*O. cuniculus*) is enormous and too well known to require comment; wild populations in Europe, South America, Australia, and New Zealand have also been exploited. For example, New Zealand exported an average of 12 million a year to Britain between 1900 and 1945 (Flux 1997). Among hares, the largest harvests are probably of *Lepus americanus, Lepus californicus* and *L. europaeus*; 70 million European hares a year were exported from South America to Europe in the 1980s (Tume 2000).

The control of lagomorphs has usually been a result of conflict with agriculture, and dates back to at least 63 B.C. (Barrett-Hamilton 1912). In North America, problems include snipping or girdling alpine trees by pikas and snowshoe hares, and farm damage by cottontails or, more often, jackrabbits; in some western states, jackrabbits have occasionally become rampant pests requiring widespread control. Four species of pika have been designated as pests in Asia because they damaged crops and valuable trees, and competed
with domestic stock on rangeland (Smith et al. 1990). However, the most serious problems have undoubtedly followed the introduction of European rabbits (Thompson and King 1994).

Protection of lagomorphs also dates back over 2,500 years because of their value as game, and continues in North America and Europe today. Since 1978, when the Lagomorph Group of IUCN was established, more systematic attention has been paid to threatened and endangered species (usually those with very restricted ranges – See Chapman and Flux 1990) but the continuing decline shown in game bags of even widespread species like the European hare in Europe is of increasing concern (review in Smith et al. 2005).

**Trends in Lagomorph Research**

In the 25 years since the first World Lagomorph Conference in 1979, there has been much change in the direction of research. Some of this results from new tools, like DNA analysis, satellite imagery, GPS tracking, night-vision equipment and video filming, and the enormous increase in the computing power available. Some is a result of politics; most countries have adopted research management along business lines, with a whole new jargon of tightly focused outputs, promoting applied research at the expense of basic science. Some problems have risen to prominence such as climate change, loss of biodiversity, and novel diseases like RHD and European Hare Syndrome (EBHS).

In an attempt to measure these changes, I compared the topics covered at the 1979 meeting (Myers and MacInnes 1981) with the present one. There were 93 papers in 1979 and 170 in 2004, but the latter were more specialized, so the number of topics covered increased only from 198 to 272. The biggest decreases since 1979 were in population dynamics (15 to 8%) and general life history (8 to 1%). There were also declines in papers dealing with behavior (13 to 10%), reproduction (9 to 6%), control (8 to 5%) and parasites and predators (8 to 6%). Papers on food habits remained constant at 14%, and those on conservation increased very slightly (from 9 to 10%). However, there was a noticeable increase of interest in diseases (5 to 8%) reflecting work on calicivirus, and in management (2 to 10%), probably a local response to the importance of rabbits in the Mediterranean ecosystem. Finally, there was the obvious expansion of taxonomy (6 to 13%) and population genetics (4 to 10%) associated with modern DNA techniques, giving exciting new results.

On the other hand, many problems remain unsolved. We still have no consensus on what regulates populations; what causes the 10-year cycle in snowshoe hares; how best to control pest lagomorphs, or how to increase the number of desirable ones. In taxonomy, we seem as far from a definitive list of species as ever before, despite the increasingly sophisticated techniques available; even the concept of what constitutes a species remains unclear. Yet this is normal in science, where every question, like a tired hare, raises another to take its place.
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Palaeontology and Evolution
Prehistoric and Historic Artificial Dispersal of Lagomorphs on the Mediterranean Islands

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Introduction

The current Mediterranean fauna is a result of the interactions of diverse factors, primarily the multiple biogeographical origin of the species, Quaternary climatic changes (which produced a repeated turnover of biota) and Late Pleistocene-Holocene human-induced habitat modifications, including hunting and Holocene introductions of a variety of allochthonous continental taxa (Masseti 1998, 2002). Apart from sporadic cases, the complete absence of endemic species from the extant mammalian fauna of the Mediterranean islands is quite surprising. In the majority of the cases, in fact, the existing populations of non-flying terrestrial mammals display undoubtedly a homogeneous composition of elements, predominantly revealing a continental origin (Alcover 1980; Sanders and Reumer 1984; Vigne 1992, 1993; Blondel and Vigne 1993; Masseti 1993, 1998). To assess the range of the original insular distribution of the different species in the Mediterranean region, earlier chronologies prior to the Neolithisation should be considered, after which improved human seafaring skills and the established commercial networks between countries enabled the artificial exportation even of wild animals, together with those already involved in the process of domestication (Masseti 1998; Lorenzini et al. 2002). Recent archaeological investigation indicates that the first transfers of allochthonous faunal elements were carried out subsequent to early Neolithic times, as documented by the discovery of the Pre-Pottery Neolithic site of Shillourokambos on the island of Cyprus (end of the 9th–8th millennium B.C.) (Guilaine et al. 1996, 2000; Cucchi et al. 2002; Vigne et al. 2003). It seems that from these times on, man began to bring with him the animals he needed as economic supplies for the colonisation of new geographical areas. One of the faunal categories much exploited in this sense is represented by the Lagomorph family, originally represented among the Late Quaternary endemic faunal horizons of the Mediterranean islands only by one species, the ochotonid *Prolagus sardus* (Sardinian pika) (Wagner 1829), native and exclusive of the Upper Pleistocene-Holocene of Corsica and Sardinia. In the light of

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archaeozoological evidence, this endemic lagomorph survived on the two islands up to very recent times, probably coinciding with the Iron Age (Delussu 2000; Wilkens and Delussu 2003), or even up to Roman times (cf. Vigne and Valladas 1996; Vigne 1997). According to the Greek historian Polybius (3rd–2nd century B.C.), the island of Corsica of his time was not characterized by the occurrence of any species of hare, but was instead inhabited by this Sardinian pika, locally called the kyniklos. Polybius observed that “… when seen from a distance [it] looks like a small hare, but when captured it differs much from a hare both in appearance and taste. It lives for the most part under the ground” (The Histories, XII: 3.8–4.6 in Paton 1925). However, evidence shows that the extant lagomorphs of the Mediterranean islands exhibit an apparently undifferentiated continental origin. The occurrence of these continental forms on all the islands seems to be linked essentially to the introduction by man during the Holocene.

In the present work, we reviewed the earliest recorded introductions of the Apennine hare, *Lepus corsicanus* (De Winton, 1898), the European hare, *Lepus europaeus* (Pallas, 1778), the Iberian hare, *Lepus granatensis* (Rosenhauer, 1856), the Sardinian hare, *Lepus (“capensis”) mediterraneus* (Wagner, 1841), the Mountain hare *Lepus timidus* (Linnaeus, 1758), the European rabbit, *Oryctolagus cuniculus* (Linnaeus 1758), and the Nearctic Eastern cottontail, *Sylvilagus floridanus* (Allen 1890) onto the Mediterranean islands in the light of recent archaeological investigations. Moreover, we updated their extant insular distribution considering the fact that they have been the object of artificial translocations also carried out in very recent times.

**Materials and Methods**

Data on lagomorph distribution were gathered from: i) literature; ii) field observations (sightings and dead specimens) carried out on the Tuscan Archipelago (Italy), Sardinia, circum-Sicilian and Maltese Archipelagos, Ionian and Aegean Islands, Crete and Cyprus within the last 10 years; iii) museum collections (Natural History Museum, London; Muséum National d’Histoire Naturelle, Paris; Zoological Museum, University of Florence; Natural History Museum, Crete; Natural History Museum, Vienna; Research Institute and Natural History Museum Senckenberg, Frankfurt am Main; Alexander König Zoological Museum, Bonn; Zoological Museum, University of Patras; Zoological Museum, University of Athens and The Bavarian State Collection of Zoology, Munich). The area of each island where lagomorphs are present today has been recorded.

**Islands for Hares**

Apennine hare, *L. corsicanus* De Winton, 1898. Endemic to the south-central Italian Peninsula and Sicily (Palacios 1996; Riga et al. 2003), this taxon was described by De Winton in 1898 on the basis of the examination of some
specimens obtained from Corsica. This fact has given rise to the unproven assumption that this hare was native to Corsica. Hares, however, never figured among the fossil horizons of the large Mediterranean island, where *L. corsicanus* has been possibly introduced shortly before the 16th century A.D. as documented by historical evidence (Vigne 1988a, 1990, 1992, 1999; Fig. 1). The Greek historian Polybius, for example, did not mention the occurrence of any type of hares among the Corsican mammalian fauna of his time (*The Histories*, XII: 3.8–4.6 in Paton 1925). The Apennine hare could have been originally present in the south-central Italian Peninsula and Sicily as an endemic relict population divergent from the hares dispersed in northern Italy, and possibly of a more ancient origin. In fact, these territories harbour several taxa of mammals that differ substantially from their northern counterparts, i.e., the Roman mole, the Apennine chamois, the red fox along with the snow vole, and the Italian roe deer (Frati et al. 1998; Lorenzini et al. 2002). Recent morphometric (Palacios 1996; Lo Valvo et al. 1997; Riga et al. 2001, 2003) and genetic (Pierpaoli et al. 1999, 2003) analyses have confirmed the taxonomic validity of *L. corsicanus*, attesting at the same time its present occurrence in south-central Italy, on Corsica and Sicily (Angelici and Luiselli 2001).

The European hare, *L. europaeus* Pallas, 1778. The European hare is a continental faunistic element characteristic of the Palaearctic Biogeographical Region (cf. Corbet 1978). There is no fully convincing evidence for the importation of this hare on any islands before the Early Bronze Age (Masseti 2003a; Fig. 1). In the light of recent archaeozoological evidence, in fact, the earliest relevant documentation appears to come from the eastern Mediterranean basin from the islands of Crete (Reese 1995; Jarman 1996) and Amorgos (Trantalidou 2000). The existence of the lagomorph in insular environments has been documented by classical authors, such as Homer (*Odyssey*, IX, 116–124) and others. Xenophon (5th century B.C.), in his *Kinegeticon*

![Fig. 1 Earliest recorded introductions of hares, European rabbit, and Eastern cottontail onto the Mediterranean islands](image-url)
(24–26), observed that hares were particularly abundant on islands because predators such as foxes and eagles occur less frequently than on the mainland. The ancient practice of releasing hares on islands, considering the latter as natural enclosures, was maintained up to historical times in the leporaria of the Roman period (Varro, *De re rustica*, III, 12, 1; Bodson 1978) and the Middle Ages (Masseti 2003a). The European hare presently occurs on about 50 islands from the Central Mediterranean basin to Cyprus (cf. Averianov et al. 2003). Most of these islands (93%) are localized in the eastern basin and 71% are larger than 50 km². In the second half of the 20th century, the introduction of the species on Sardinia and Sicily has failed (Lo Valvo et al. 1997). The European hare has become extinct recently on at least five Greek islands: Sifnos (western Aegean Islands), Delos (Cycladic Archipelago), Paximada (Dionysades Islands), Astypalaia (Dodecanese), and Lemnos (north-eastern Aegean Islands). On the other Aegean islands, populations of European hare of ancient and/or modern introductions are today reported from several islands, such as Milos, Naxos, Amorgos, Crete, Karpathos, Rhodes, Ikaria, Samos, and others (Masseti 2003a).

Throughout most of the 19th and 20th centuries, however, there was a widespread practice among scientific explorers to bring home an excessive number of subspecies from their explorations of the Mediterranean islands. These authors often classified many of the insular populations as geographic forms, almost entirely on the basis of arbitrary criteria and the examination of scattered materials. Based on the data given in literature, the various subspecies of the insular hares are distinguished by the coat patterns and by the size of the body and skull. Therefore it is logical that this led to a multiplication of forms which now, however, demand better taxonomic and genetic definition. In this respect, we should therefore consider the extant taxonomic treatment on the part of the international scientific community of the lagomorphs of the Eastern Mediterranean islands, such as *L. e. creticus* Barrett-Hamilton, 1903, from Cephalonia (Miller 1912), Crete (Rate 1906 and 1913), and several small islets off Crete, including Gavdos and the Dionysades Islands (Niethammer 1992), *L. e. ghigii* (De Beaux, 1927), from Astypalaia (De Beaux 1927 and 1929), *L. e. carpathous* (De Beaux, 1929), from Karpathos (De Beaux 1929), *L. e. rhodius* (Festa, 1914), from Rhodes (De Beaux 1929; von Wettstein 1942), and *L. e. cyprius* (Barrett-Hamilton, 1903), from Cyprus (Ellerman and Morrison-Scott 1952).

Iberian hare, *L. granatensis* Rosenhauer, 1856. Endemic to the Iberian Peninsula (Palacios 1983), the Iberian hare is distributed throughout most of the territories of Portugal and Spain and also occurring at present on the Balearic island of Mallorca (Alcover 1988; García-Perea and Gisbert 1999; Alves and Niethammer 2003). It was also formerly dispersed on Ibiza, where it is now extinct (Garcia-Perea and Gisbert 1999). Archaeological evidence documents the appearance of hares on the Balearics not before the Talayot culture (Alcover 1988), which flourished on these islands from 1500 B.C. to 500 B.C. (cf. Pericot Garcia 1972; Fig. 1). The earliest remains of the hare have