

Introduction to the Lagomorpha

JOSEPH A. CHAPMAN¹ AND JOHN E.C. FLUX^{2,*}

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.

¹President’s Office, North Dakota State University, Fargo, ND, USA

²Ecological Research Associates NZ, PO Box 48147, Silverstream, Upper Hutt, New Zealand

*E-mail: flux@paradise.net.nz

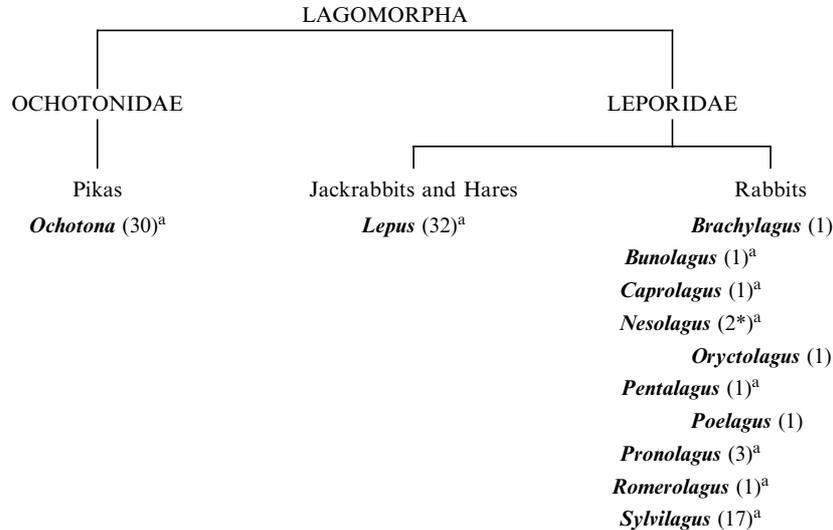


Fig. 1 Families and genera of living lagomorphs. After each genus is indicated the number of species

^aGenera with at least one endangered species

*Includes the recently described species in Vietnam, *N. timminsi*

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 hispid 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 cottontail 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 scree 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 *L. 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.

Acknowledgements: We are very grateful to the organizers of the Second World Lagomorph Conference, especially Paulo Alves and Nuno Ferrand, for all the work entailed in producing such a stimulating, informative and enjoyable meeting. Dr. Renate Angermann kindly supplied taxonomic lists of lagomorph species; Prof Andrew Smith alerted us to the work on Mongolian fossils; and Klaus Hackländer and Paulo Alves provided many useful suggestions.

References

- Asher RJ, Meng J, McKenna MC, White JR, Dashzeveg D, Rougier G, Novacek MJ (2005) Stem Lagomorpha and the antiquity of Glires. *Science* 307:1091–1094
- Barrett-Hamilton GEH (1912) A history of British mammals. Gurney and Jackson, London
- Can D, Abramov A, Tikhonov A, Averianov A (2001) Annamite striped rabbit, *Nesolagus timminsi*, in Vietnam. *Acta Theriol* 46:437–440
- Chapman JA (1984) Latitude and gestation period in New World rabbits (Leporidae: *Sylvilagus* and *Romerolagus*). *Am Nat* 124:442–445
- Chapman JA, Flux JEC (1990) Rabbits, hares and pikas. Status Survey and Conservation Action Plan. IUCN, Gland, Switzerland, p9.
- Chapman JA, Morgan RP (1973) Systematic status of the cottontail complex in western Maryland and nearby West Virginia. *Wildl Monogr* 36:1–54
- Conaway CH, Sadler KC, Hazelwood DH (1974) Geographic variations in litter size and onset of breeding in cottontails. *J Wildl Manage* 38:437–481
- Erbajeva M (1997) The history and systematics of the genus *Ochotona*. *Gib Faun Sauv* 14:505
- Ferrer M, Negro JJ (2004) The near extinction of two large European predators: super specialists pay a price. *Cons Biol* 18:344–349
- Flux JEC (1981) Reproductive strategies in the genus *Lepus*. In: Myers K, MacInnes CD (eds) Proceedings of the world lagomorph conference, University of Guelph, Guelph, pp 155–174
- Flux JEC (1997) Status of rabbits (*Oryctolagus cuniculus*) and hares (*Lepus europaeus*) in New Zealand. *Gib Faun Sauv* 14:267–280
- Flux JEC (2001) Evidence of self-limitation in wild vertebrates. *Oikos* 92:555–557
- Hirakawa H (2001) Coprophagy in leporids and other mammalian herbivores. *Mamm Rev* 31:61–80
- Hoffmann RS, Smith AT (2007) Lagomorphs. In: Wilson DE, Reeder DM (eds) Mammal species of the world, 3rd edn. Smithsonian Institution Press, Washington DC (in press)
- Holley AJF (1986) A hierarchy of hares: dominance status and access to oestrous does. *Mamm Rev* 16:181–186
- Honacki JH, Kinman KE, Koepl JW (1982) Mammal species of the world. A taxonomic and geographic reference. Allen Press and the Association of Systematics Collections, Lawrence
- Lechleitner RR (1958) Certain aspects of behaviour of the black-tailed jackrabbit. *Am Midl Nat* 60:145–155
- Litvaitis JA, Barbour MS, Brown AL, Kovach AI, Oehler JD, Probert BL, Smith DF, Tash JP, Villafuerte R (2008) Testing multiple hypotheses to identify causes of the decline of a lagomorph species: the New England cottontail as a case study. In: Alves PC, Ferrand N, Hackländer K (eds) Lagomorph Biology: Evolution, Ecology and Conservation. Springer, Berlin Heidelberg New York, pp 167–188
- Marsden HM, Holler NR (1964) Social behavior of the New England cottontail and swamp rabbit. *Wildl Monogr* 13:1–39
- Moreno S, Cabezas S, Lombarda L, Villafuerte R (2004) Wild rabbit restocking for predator conservation in Spain. *Biol Conserv* 118:183–193
- Myers K, MacInnes CD (1981) Proceedings of the world lagomorph conference. University of Guelph, Guelph

- Niethammer J, Krapp F (2003) Handbuch der Säugetiere Europas, Band 3/II: Hasentiere Lagomorpha. Aula-Verlag, Wiebelsheim
- Rosin AV, Gilio N, Meriggi A (2008) Introduced lagomorphs as a threat to “native” lagomorphs: The case of the Eastern cottontail (*Sylvilagus floridanus*) in northern Italy. In: Alves PC, Ferrand N, Hackländer K (eds) Lagomorph Biology: Evolution, Ecology and Conservation. Springer, Berlin Heidelberg New York, pp 153–166
- Schneider E (1978) Der Feldhase. BLV Verlag, Munich
- Smith AT, Formozov NA, Hoffman RS, Zheng C, Erbajeva MA (1990) The pikas. In: Chapman JA, Flux JEC (eds) Rabbits, hares and pikas. Status survey and conservation action plan, IUCN, Gland, Switzerland, pp 14–60
- Smith RK, Jennings NV, Harris S (2005) A quantitative analysis of the abundance and demography of European hare *Lepus europaeus* in relation to habitat type, intensity of agriculture and climate. *Mamm Rev* 35:1–24
- Smith AT (2008) The world of pikas. In: Alves PC, Ferrand N, Hackländer K (eds) Lagomorph Biology: Evolution, Ecology and Conservation. Springer, Berlin Heidelberg New York, pp 89–102
- Spagnesi M, De Marinis A (2002) Mammiferi d'Italia. *Quad Cons Nat* 14:1–309
- Surridge AK, Timmins RJ, Hewitt GM, Bell DJ (1999) Striped rabbit in Southeast Asia. *Nature* 400:726
- Tefft BC, Chapman JA (1987) Social behavior of the New England cottontail, *Sylvilagus transitionalis* (Bangs) with a review of social behavior in New World rabbits (Mammalia: Leporidae). *Rev Ecol Terr Vie* 42:235–275
- Thompson HV, King CM (1994) The European rabbit. The history and biology of a successful colonizer. Oxford University Press, Oxford
- Trocchi V, Riga F (2001) Piano d'azione nazionale per la lepre italiana (*Lepus corsicanus*). *Quad Cons Nat* 9:1–102
- Tume L (2000) Farming European hare. A report for the Rural Industries Research and Development Corporation. RIRDC Publ 00/75:1–44
- Wilson DE, Reeder DM (1993) Mammal species of the world, 2nd edn. Smithsonian Institution Press, Washington, DC
- Wilson D, Reeder DA (2005) Mammals of the world, 3rd edn. Johns Hopkins University Press, Baltimore