

# Overview of Lagomorph Research: What we have learned and what we still need to do

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## Palaeontology and Evolution

Lagomorphs can today be found on all continents, however, the present world-wide distribution does not reflect the relatively recent geographical expansion. The vast palaeontological data shows that lagomorphs are indeed an ancient taxonomic group and probably had (and still have) a great ecological importance. Some living genera lack fossil records, but there are a lot that only have been recorded with fossil data (Lopez-Martinez 2008, this book). It shows a large dynamic process in lagomorph evolution and morphological proximity among several lagomorph species. This complexity has resulted in intensive discussions among palaeontologists up to today (e.g. Erbajeva 2005; Lopatin and Averianov 2006). However, there are still some important open questions, such as: when and where does the common ancestral lagomorph appear, in Asia or America? Did the main lagomorph groups of ochotonids and leporids evolve independently? Why are there important time lags between the first arrival and definitive settlement in some areas, e.g. Europe? How can we solve some of the taxonomic uncertainties in the fossil data of some groups, e.g. *Lepus*? What is the closest taxonomic group to lagomorphs; and how can we calibrate the molecular data with paleontological data?

The last two questions are indeed very current, both for genetic and palaeontological studies. Lagomorphs are usually considered as being close to rodents (forming the *Glires* group), but not everyone agrees (see e.g. Douzery and Huchon 2004). In the last two decades, primarily due to the exploding increase in genetic studies, a great number of papers have appeared assembling molecular phylogenies (e.g. Halanych et al. 1999; Niu et al. 2004; Wu et al. 2005; Robinson and Matthee 2005). In some cases, these molecular phylogenies clarify some of the puzzling taxonomic situations, but in others they are not congruent with fossil data, causing even more confusion. We know today that each molecular set of markers tells us one story and only the combination of several

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markers would eventually clarify some situations (Alves et al. 2006; Ferrand 2008; Suchentrunk et al. 2008, both this book).

On the other hand, although these studies constitutes the most comprehensive intergeneric study on leporids, showing the monophyly of 11 genera, there are still several intrageneric questions to be resolved. A good example is found in the genus *Sylvilagus*. Somewhat surprisingly, a comprehensive molecular phylogeny that includes the majority of cottontail species is still lacking. Phylogenetic relationships among pikas are also not well resolved. Yu et al. (2000) reported the phylogeny of the genus *Ochotona* using mtDNA sequences and suggests a division into three subgenera. However, this study only includes 19 *Ochotona* species and a more recent comprehensive study by Niu et al. (2004) thus does not support this view. In addition, as mentioned previously, molecular phylogenies based solely on one mitochondrial characteristic should be avoided, and thus we consider that the evolutionary processes of *Ochotona* are also poorly understood.

Apart from phylogenetic aspects, other fields of genetics should be stressed, too. Several studies have been conducted on lagomorph population genetics. However, most of these studies have been done on the European hare and on the European rabbit. As mentioned in this book (Ferrand 2008, this book), the European rabbit population genetic studies have made achievable preposterous inferences about the population history of this species as well as important assumptions for other molecular and ecological studies. On the other hand, the European hare genetic studies also give important information about ecological features and evolutionary adaptations. In general, the available data shows a remarkable gene flow, even over long-distances, resulting, in a large panmictic population of European hares in Central Europe (see e.g. Suchentrunk et al. 1998; Kasapidis et al. 2005). Also, the recent genetic papers show that hybridisation on hares is not that uncommon. Introgressive hybridisation was initially demonstrated in Sweden between the Mountain hare and the introduced European hare (Thulin et al. 1997). More recently, it has been shown that it also occurred in the past between the Mountain hare and other hare species in the Iberian Peninsula (Alves et al. 2003). This past and ongoing hybridization have been confirmed in several other geographical regions and between different hare species (Thulin et al. 2006; Alves et al. 2003; Melo-Ferreira et al. 2004, 2005). Taken together, there is an urgent need to strengthen the cooperation between groups working on genetics and palaeontology in order to produce holistic views on the evolution in lagomorphs.

## Population Ecology and Dynamics

Basic data on population ecology (e.g. rates for mortality of fecundity) are crucial for the development of sound strategies in the conservation and management of lagomorphs (see Morrison and Hik 2008; Rödel and von Holst 2008, this book). As stressed by various authors in this book, we know

nothing or very little about the biology or ecology of numerous lagomorph species. In some cases, like the recently described Annamite Striped rabbit (*Nesolagus timminsi*) we know only the potential distribution (Can et al. 2001; Smith 2008a, this book). In other species like the Omilteme rabbit (*Sylvilagus insonus*), which has been described long ago, only fragments of its biology and ecology have been uncovered. To date, we do not know if this species even still exists. In contrast, we have comprehensive knowledge about one of the best-studied lagomorph species, the Snowshoe hare (*Lepus americanus*). This leporid has been studied over the last 75 years in order to understand the well-known 10-year population cycle which is mentioned in standard textbooks in ecology (summarized in Krebs et al. 2001). However, due to new methods and insights, new factors affecting the population dynamics are still being revealed, among them climate change (Stenseth et al. 2004) and forest fires (Ferron and St-Laurent 2008, this book). Hence, a lot of work remains to be done in order to fully understand the ecology of this species. In parallel, ecologists should begin to focus on those lagomorphs that are rare or have been only poorly studied (before they get extinct).

As mentioned above, global climate change also affects the 10-year cycle of Snowshoe hares. However, global climate change might also have a strong impact on a number of lagomorphs, especially those with a tiny ecological niche. For example, the Mountain hare (*Lepus timidus*) and its subspecies are affected by the warming phase both in the glacial refuges (e.g. the Alps) as well as in their northern ranges (Scandinavia). In both areas, potential habitat is declining and the European hare (*Lepus europaeus*) replaces its relative, either through competition or genetic introgression (Thulin 2003, see above). This will reduce the distribution range and thus endanger isolated subspecies (e.g. *Lepus timidus varronis*). Hence, there is a need for further studies about the ecological flexibility in lagomorph species, especially regarding adaptability to changing environments.

One adaptation of some lagomorph species to seasonal climate change is the change in fur colour from brown to white in autumn. This strategy camouflages Mountain hares and other Palaearctic lagomorphs when their habitat gets covered with snow, but it could be dangerous for them when there is a delay in snowfall or less snowfall than normal. One species of Mountain hare, the Irish hare *Lepus timidus hibernicus*, does not change fur colour, which seems to be an evolutionary stable strategy as snow in Ireland is rather rare (Dingerkus and Montgomery 2002). However, we hypothesise that climate change should result in a delayed moult or even no change at all in the fur colour in these species. It will be the task of ecological genetics and ecophysiology to discover the mechanisms related to these aspects and their plasticity.

Even more pronounced in their potential vulnerability to climate changes are pikas that live in cold environments and have high body temperatures (see Smith 2008b, this book). In this case, even small changes in the mean annual temperature might not only change the habitat (vegetation, moisture) but also result in heat stress. To sum up, climate change might have various

effects on several lagomorph species and we need basic data on their ecology to understand the potential impact of changes in temperature and precipitation on their population dynamics.

## Physiology and Behaviour

Studies on lagomorph physiology are often conducted in the lab. Here, we get detailed insights into fundamental aspects of lagomorph biology, such as mother-young-relationships (Schaal et al. 2008; Bautista et al. 2008, both this book) or reproductive energetics (Hackländer et al. 2002a, b). In the field, however, many lagomorph studies (like Stott et al. 2008, this book) describe physiological phenomena which call for a closer combination of field and laboratory work. Similar prominent examples for this are caecotrophy and superfetation. Lagomorphs are known to produce two types of faeces: soft and hard. Both are re-ingested; the soft ones obligatory (caecotrophy) and the hard ones facultative (coprophagy). This re-ingestion enables lagomorphs to use the available diet more efficiently and to live in habitats with poor food and nutrient availability. It is believed that this phenomenon, which is quite rare in other mammalian taxa, is the reason for the current success of lagomorphs (Hirakawa 2001). Although we understand the mechanical processes in the gut that are responsible for the separation of food particles and the production of soft and hard faeces, we are not aware of the physiological impact of caecotrophy (Hirakawa 2001). We know that lagomorphs will die if they are prevented from re-ingesting their soft faeces and we also know that these soft faeces contain a high amount of nutrients, but we do not know why. It could be the presence of bacteria in the caecum or just the nutrient concentration process. When we discover the physiological impact of caecotrophy we can start to reach insights into its role for lagomorph ecology.

Another biological phenomenon that can be found at least in the genus *Lepus* is superfetation: female hares can have an ovulation while they are pregnant leading to two litters of different age in one uterus. This is quite unique, but superfetation has been described for hares since the classical philosopher Herodot (Zörner 1990). Several studies showed that it is common in captivity (e.g. Hediger 1948), but rather rare in the field (Flux 1967). Therefore, it has been discussed thoroughly whether superfetation in hares is just pathological (like it is humans) or an important reproductive strategy: Using superfetation hares are able to shorten interbirth interval and to produce more litters per year. To clarify the open questions on superfetation, studies on the mechanisms behind it and its pros and cons are mandatory. With this, we would be able to understand why it is so rare in the field or whether superfetation depends on other extrinsic factors such as population density or costs for gestation and lactation.

This book provided an excellent example of interspecific competition in two prominent lagomorph species (Flux 2008, this book). Often this competition is

followed by translocations of lagomorphs for restocking of introduction (see Masetti and De Marinis 2008, Letty et al. 2008 or Rosin et al. 2008; Williams et al. 2008, all this book). However, translocations of individuals are often accompanied by translocations of diseases and alien genes, both potential threats to rare subspecies or species (e.g. Litvaitis et al. 2008, this book). In addition, autochthonous lagomorph species may be suppressed and expelled by the dominant behaviour of allochthonous ones (see Rosin et al. 2008, this book). Nevertheless, while DNA markers and antibodies are easily and quickly detectable, behavioural strategies of mammals have to be revealed by extensive observational studies. Even in common lagomorph species there is still a lack of information about space use, dispersal, sociality, and other aspects. Improvements in telemetry and mark-recapture-techniques may help to fill this gap and thus to develop sustainable strategies for successful restocking (Letty et al. 2008, this book) or pest control (Mutze et al. 2008, this book).

Interestingly, many of the translocated lagomorphs show a high adaptability to a huge number of various habitats. In general, lagomorphs can be found in almost all environments, from desert to arctic, as well as in different latitudes and longitudes. Although most of the species are well adapted to different regional environmental conditions (like the Swamp rabbit, Snowshoe hare, and other examples), some forms have a remarkable ecological plasticity, occurring in very different kinds of habitat. A good example of this is the European rabbit (*Oryctolagus cuniculus*). Notwithstanding this species is original from the Iberian Peninsula, it can be found in desert regions as well, like in Morocco, and in completely arctic areas, like Macquarie Island. This makes the European rabbit by far the most successful colonizing lagomorph (Long 2003), which is even able to improve its own habitat (Gálvez et al. 2008, this book). Another classical example is the European hare. Although this species is very common in continental climates in central Europe, it can also be found in subdesert (Israel), subtropical (Argentina), and in subarctic (Scandinavia) habitats. Why some species are so adaptable to different habitats and others are restricted to some small regions is an open question that should be explored in future works.

## Diseases

Lagomorphs and their diseases are studied to understand basic backgrounds of important pathogens (Frölich and Lavazza 2008; Lavazza and Capucci 2008, both this book), to improve restocking processes (Letty et al. 2008, this book) and to use pathogens to manage lagomorph pest species (Mutze et al. 2008, this book). It is evident in all three fields of research, that lagomorphs play an important role as vectors of many diseases. There are several cases of described zoonoses, namely tularaemia, leptospirosis, brucellosis (Winkelmayer et al.

2005), toxoplasmosis (Sroka et al. 2003), encephalitozoonosis (Smielewska-Los et al. 2004) and mycosis (Nakamura 2003). Among them, tularaemia might be the predominant zoonosis, as infected humans are more abundant in areas where infected wildlife had been recorded. Apart from that, even considered anecdotal, there are several other reports of zoonoses between lagomorphs and humans. For instance, Scaife et al. (2006) recently described that several visitors of a natural park in Norfolk (UK) became infected with verocytotoxin originating from *Escherichia coli* (VTEC) 0157, which was associated with European rabbit faeces. In addition, lagomorphs can also be responsible for several diseases that affect domestic animals like sheep or dogs.

Interestingly, diseases and parasites have often been neglected in recent reviews for population dynamics in lagomorphs (e.g. Smith et al. 2005). However, several studies provide evidence for important impacts of diseases, e.g. in the Mountain hare (Newey et al. 2005). Knowledge about the causes of population increases or decreases will increase in the future if ecologists and veterinarians would combine their work more intensively.

## Conservation and Management

In the first view, lagomorphs are everywhere, extremely abundant and widespread, and can become a pest, thus not requiring a conservation status. However, this is true only for a few species in very specific cases, for example the European rabbit in Australia (Cooke 2008, this book). Indeed, approximately a quarter of lagomorph species are threatened with extinction, which represents about 18 species (see Alves and Hackländer 2008, this book). As outlined in Smith (2008a, this book), during the last years the number of threatened lagomorphs increased because (1) the knowledge about some species increased, and (2) new species were described (e.g. *N. timminsi* in Vietnam). Since most of these species are locally adapted, representing evolutionary units of a specific region, the main conservation concern is associated with habitat perturbation, either from humans or from natural competitors (Farías et al. 2008; Yamada 2008, both this book). However, another important issue for the conservation status evaluation are monitoring surveys. This is a key point since we need to know population trends. Several improvements have been made in this respect, namely in developing census methods (such as using pellets or genetics methods), but there is a huge lack of information, namely in most of the *Ochotona*, *Lepus* and *Sylvilagus* species, as well as in several other genera like *Caprolagus*, *Nesolagus* and *Bunolagus*.

Interestingly, in the last few years another conservation problem has arisen. While European rabbits and European hares are widely distributed and very abundant in some areas, these species are endangered in some areas. For example, the European rabbit is decreasing in Spain and Portugal, resulting in the fact that European rabbit have been classified as near threatened in the



Portuguese Red Data Book (see also Smith 2008a, this book). As the European rabbit is the main prey of critically endangered predators (e.g. Iberian lynx, Ferrer and Negro 2004) the Spanish and Portuguese governmental institutions spend a large amount of money and effort to reverse the rabbit decline in the Iberian Peninsula. One strategy is to reintroduce rabbits from other areas (Letty et al. 2008, this book). However, there is an urgent need for detailed genetic studies to detect subspecies in order to avoid the loss of endangered subspecies by introduction of allochthonous subspecies. In general, taxonomic problems in lagomorphs are enlarged by the unclear situation of subspecies and their status (see above).

Finally, managing lagomorphs can range from conservation to pest control. Another aspect is hunting. The World Conservation Union, IUCN, recognised in its Policy Statement on Sustainable Use (IUCN 2000) that the use of wild living resources, if sustainable, is an important conservation tool because the social and economic benefits derived from such use provide incentives for people to conserve them. One form of use is hunting, and in fact, many lagomorph species are important game species (see Chapman and Flux 2008, this book). However, only few studies have been conducted to prove the sustainability of harvesting in lagomorphs or to model sustainable harvest rates (e.g. Marboutin et al. 2003). The lack of such models is due to missing data on mortality and fecundity rates of numerous lagomorphs (see above). Hence, the study of these issues is needed for both the general understanding of population dynamics as well as for the development of strategies for a sustainable wildlife management.

## Conclusion

This book calls for an increase in lagomorph research, both on basic and applied aspects. We are convinced that different disciplines of lagomorph research have to intermingle in order to enhance the knowledge about this fascinating mammalian taxon. Hopefully, this book will help to turn the balance.

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