Lagomorpha Life History



Anthony Caravaggi School of Biological Earth and Environmental Sciences, University College Cork, Cork, Ireland School of Biological Sciences, Medical Biology Centre, Queen's University Belfast, Belfast, UK

Synonyms

Growth; Hare; Leporid; Longevity; Pika; Rabbit; Reproduction

Definition

Mammalian life history traits include length of gestation, size and number of offspring, growth patterns, weaning age, timing of sexual maturity, adult body mass, reproductive lifespans, individual longevity, population density, and group composition and size (Jones et al. 2009).

Introduction

The term "lagomorph" describes species of the mammalian order Lagomorpha (lit: "hareform"), which is made up of two families, the hares and rabbits (Leporidae; also known as leporids) and the pikas (Ochotonidae). These two groups are united by shared morphological

traits which are unique among extant mammals, including several aspects of cranial anatomy and a circulatory channel running through the heel bone (Fostowicz-Frelik and Meng 2013). The evolutionary history of lagomorphs is not clear, though ongoing research continues to shed light on the origins of the order. Leporids and pikas diverged in the Eocene, around 40 million years ago (mya), a split which may have been facilitated by abrupt changes in climate. Lagomorphs were certainly more diverse than they are in the present, with over 230 species from over 75 genera represented in the fossil record. Pikas initially diversified much more rapidly than leporids, but, over time, this situation was reversed and there are now fewer species of pika, which occupy a far smaller overall area, than there are of hares and rabbits. In addition to genetic differences, the families are easily distinguished visually by comparative morphology (Fig. 1 and subsections herein).

There are around 91 living species of lagomorph, many of which are classified as threatened (vulnerable, endangered, and critically endangered) by the International Union for Conservation of Nature (2017) and/or are Evolutionary Distinct and Globally Endangered (EDGE) species (Fontanesi et al. 2016). The order has a global distribution, with representative species being found on every continent with the exception of Antarctica, from between the equator and 80°N and between 0 and 5000 m above sea level (Fontanesi et al. 2016). Habitat requirements can vary considerably, with some species being more



Lagomorpha Life History, Fig. 1 Photographic examples of **(a)** hare, Indian hare (*Lepus nigricollis*; photo by N. A. Nazeer); **(b)** rabbit, mountain cottontail (*Sylvilagus nuttallii*; photo by USFWS Mountain-Prairie; **(c)** pika, American pika (*Ochotona princeps*)

specific in their requirements and, hence, having a more limited distribution than others. For example, volcano rabbits (*Romerolagus diazi*) are an endangered species found in four volcanoes in southern Mexico which, even within their limited, fragmented range, have a strong preferences for subalpine habitats, particularly pine forests (Velazquez and Heil 1996). In contrast, the European hare (*Lepus europaeus*) can utilize a wide range of habitats; it has a broad distribution in its natural range and has been successfully introduced to a number of countries and islands, worldwide (Flux and Angermann 1990).

Lagomorphs have considerable ecological, scientific, and economic importance as they are human food sources, agricultural pets, quarry for field sports, model laboratory animals, and

significant components of ecological systems and processes (Chapman and Flux 2008; Fontanesi et al. 2016). These mammals feature prominently in the diets of many predators, with annual mortality rates of up to 80–90% in some species. Fortunately, all lagomorphs have short gestation periods, newborns grow rapidly, and there is little maternal investment in the young after weaning. This means that they are often highly fecund, producing multiple litters of several young, per year (Table 1).

All of the lagomorphs are herbivores; the breadth of the diet varies between species and depends on local environmental conditions and relative availability of food items. With a diet rich in tough cellulose, these mammals have solved the problem of cellulose digestion by

Lagomorpha Life History, Table 1 Selected life history information for 30 of the 90 extant species of lagomorphs. The data describe ranging behavior (home range), breeding ecology (gestation length, litter size, and litters per year), and growth (neonate body mass, adult body mass). Species are sorted alphabetically according to their Latin names (Data were derived from Ernest 2003, IUCN 2017, and Jones et al. 2009)

		Average						
Common	Latin name	Home range (km²)	Gestation length (days)	Litter size	Litters per year	Neonate body mass (g)	Adult bod mass (g)	
Rabbits								
Pygmy rabbit	Brachylagus idahoensis	0.004	39	5.81	2.00	16.40	431	
Riverine rabbit	Bunolagus monticularis	0.140	35	1.22	DD	42.42	1750	
Assam rabbit	Caprolagus hispidus	0.004	40	3.46	2.81	DD	2497	
Swamp rabbit	Sylvilagus aquaticus	0.010	37	3.00	2.94	55.70	2133	
Desert cottontail	Sylvilagus audubonii	0.030	28	3.00	5.00	34.36	881	
Brush rabbit	Sylvilagus bachmani	0.002	27	3.35	4.50	27.25	715	
Eastern cottontail	Sylvilagus floridanus	0.010	27	4.62	4.81	34.15	1207	
Marsh rabbit	Sylvilagus palustris	0.030	33	2.96	6.00	DD	1355	
New England cottontail	Sylvilagus transitionalis	0.004	28	4.41	2.50	30.00	814	
European rabbit	Oryctolagus cuniculus	0.040	30	5.24	4.50	39.11	1591	
Hares				1				
Antelope jackrabbit	Lepus alleni	4.530	42	1.96	3.50	182.00	3930	
Snowshoe hare	Lepus americanus	0.040	37	3.54	2.50	67.84	1568	
Arctic hare	Lepus arcticus	2.260	52	5.62	1.50	105.00	4413	
Black-tailed jackrabbit	Lepus californicus	0.560	42	2.68	4.05	84.93	2422	
Cape hare	Lepus capensis	0.410	42	2.44	3.00	114.09	2047	
European hare	Lepus europaeus	0.310	42	2.14	4.40	123.00	3816	
Indian hare	Lepus nigricollis	0.010	36	1.76	7.15	DD	2294	
Alaskan hare	Lepus othus	DD	46	6.15	1.00	102.46	4837	
Scrub hare	Lepus saxatilis	DD	38	1.52	5.35	98.00	2594	
Mountain hare	Lepus timidus	0.860	50	3.16	3.00	113.49	3105	
White-tailed jackrabbit	Lepus townsendii	DD	41	4.49	3.29	89.99	3372	

(continued)

Lagomorpha	Life History,	Table 1	(continued)
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		Average						
Common name	Latin name	Home range (km²)	Gestation length (days)	Litter	Litters per year	Neonate body mass (g)	Adult body	
Pikas								
Alpine pika	Ochotona alpina	0.009	29	3.07	2.00	8.19	150	
Gansu pika	Ochotona cansus	0.001	24	3.65	2.25	DD	69	
Collared pika	Ochotona collaris	0.001	30	3.35	2.00	DD	129	
Plateau pika	Ochotona curzoniae	0.001	23	4.39	3.50	11.20	159	
Northern pika	Ochotona hyperborea	0.002	28	3.02	DD	9.59	120	
Pallas' pika	Ochotona pallasi	0.002	25	7.45	2.50	7.00	180	
American pika	Ochotona princeps	0.001	30	2.88	2.00	11.00	158	
Steppe pika	Ochotona pusilla	DD	22	8.59	3.50	6.74	143	
Afghan pika	Ochotona rufescens	DD	26	6.05	4.00	11.40	250	

DD data deficient

utilizing hindgut fermentation and reingestion of first-feces (coprophagy), soft black pellets known as caecotrophs. The secondary digestion allows lagomorphs to further digest the plant matter and maximize nutrient extraction.

Here I give an overview of differences in life history traits between the leporids (subdivided into hares, and rabbits) and pikas, illustrating the variation in the order. While this text details a number of species, there are many for which we have few life history data (Jones et al. 2009).

Hares

Hares are the most diverse of all the lagomorphs, comprising 32 species, all of which occur within a single genus, *Lepus* (ITIS 2017). The genus contains several species which are commonly known as jackrabbits, e.g., the Tehuantepec jackrabbit (*L. flavigularis*). They are all, however, true hares. Hares are generally the largest of the

lagomorphs, weighing between 2 and 5 kg and are readily distinguished from rabbits by their long ears and hind legs. Their long legs allow them to run at extremely high speeds to escape predators; both the antelope jackrabbit (*L. alleni*) and the European hare have been recorded at 72 kmh (Garland 2009), and it is likely that other large hares can attain similar speeds. The cost of high-speed flight can be substantial, however, and hares will often remain in their forms until a predator is almost within striking distance before fleeing.

Hares can be found in a variety of habitats, from dry, hot deserts to the Arctic tundra. Across their range, they display an array of physiological and behavioral adaptations which have allowed them to thrive. For example, the ears of the antelope jackrabbit, which is found in arid regions of Arizona and Mexico, are extremely large and have an abundance of blood vessels, helping the animals to dissipate heat while minimizing water loss (Dawson and Schmidt-Nielsen 1966). In contrast,

those of the mountain hare (L. timidus), an arctoalpine species complex with a circumpolar distribution which inhabits uplands and northern latitudes, are much smaller and heavily furred to reduce heat loss. Hares also molt their coats, from a relatively thin summer coat to thicker, insulating winter pelage and vice versa. In some species such as the European hare in which the summer coat is a light brown compared to the reddish-brown winter coat, there are few obvious differences between seasons. Others, such as mountain hares, go from brown in the summer to white in the winter. This seasonal change confers additional protection from predators via camouflage with snowpack, though the trait has limited plasticity, meaning that white animals at the southern edge of the species range will become increasingly vulnerable as snow cover recedes under climate change (Zimova et al. 2014).

The majority of hare species are largely solitary, only coming together during the breeding season. However, some species such as the Arctic hare (L. arcticus) can be highly social, resting and feeding in groups which may number dozens of individuals. The mating behavior of hares is, broadly speaking, very similar across the genus. Males aggregate around receptive females, which they will regularly chase at high speeds, and actively compete to establish a dominance hierarchy. Direct competition occurs in the form of "boxing," the hares rearing up on their hind legs and striking with forepaws, as well as striking with the hind legs while on all fours. Females, which are dominant, also use boxing, as well as grunts and aggressive body language to fend off amorous males (Chapman and Flux 1990).

Most hare species favor an open landscape featuring sufficient cover for rest and offering protection from predators. There are a number of exceptions, including the Manchurian hare (*L. mandshuricus*) which inhabits forests in northeastern China and Russia (Loukashkin 1943), and the snowshoe hare (*L. americanus*), which inhabits successional boreal forests, swamps, and transitional habitats (Flux and Angermann 1990). The snowshoe hare also demonstrates the importance of many lagomorphs to trophic food webs as the abundances of avian and mammalian predators and secondary prey species fluctuate in

accordance with the snowshoe hare's 10-year population cycle (Krebs et al. 2001). Hares are largely nocturnal and/or crepuscular, feeding at night and during hours of twilight and resting during the day. These patterns often show seasonal variation, however, with activity commencing before sunset and ceasing after sunrise (i.e., during hours of daylight) when days are longer (Schai-Braun et al. 2012). Hares have among the largest home ranges of the lagomorphs; home ranges for antelope jackrabbits average 4.5 km², and most hares have ranges in excess of the largest found among rabbits (Table 1).

The length of the breeding season varies according to a number of factors including day length and ambient temperature; some species have breeding seasons which last for over 250 days of the year. Reproductive patterns vary by latitude, with larger litters occurring during the shorter breeding seasons in the north. Hares generally have litters of two to four young (Table 1), although litters as small as one and as large as six have been recorded in some species, and several litters may be produced each season (Rioja et al. 2011). They do not dig burrows or holes in which to give birth, instead creating a depression in the ground, known as a "form," which is sometimes covered with grass or other vegetation. Young hares, or leverets, are born precocial; their eyes are open, they are fully furred, and they are capable of independent movement soon after birth. This is in contrast to rabbits, which are born much earlier in development (see Rabbits). Females place leverets under vegetation such as trees and shrubs (Arctic hare) or grass (Cape hare, L. capensis) to hide them from predators. Leverets are nursed once per day with highly concentrated milk. Early offspring survival (i.e., survives the first 3 weeks) is usually between 40% and 50% (Rioja et al. 2011). The average lifespan of a wild hare is between 4 and 7 years.

Rabbits

The rabbits comprise 29 species across ten genera (Brachylagus, Bunolagus, Capolagus, Nesolagus, Oryctolagus, Pentalagus, Poelagus, Pronolagus, Romerolagus, Sylvilagus). Some

species are referred to as "hares," for example, the Natal red rock hare (*Pronolagus crassicaudatus*), though all of the aforementioned species are true rabbits. The most speciose of these are the New World cottontails (Sylvilagus sp.), with 17 extant species (ITIS 2017). Rabbits are a diverse group, ranging from species of uplands like the Appalachian cottontail (S. obscurus), to dense tropical like the Sumatran striped (N. netscheri), to swamps like the semiaquatic swamp rabbit (S. aquaticus). Their ranges vary considerably, for example, the European rabbit (O. cuniculus), historically restricted to the Iberian Peninsula, has been introduced to a large number of countries and islands and so is one of the most widely distributed mammalian species. In contrast, many other species, including members of more primitive genera such as Caprolagus, Pentalagus, and Nesolagus, many of which are endangered, are restricted to small habitat patches and/or islands (Alves et al. 2008).

Rabbits are generally smaller than hares, weighing 0.5–2 kg (Table 1). Like hares, they also have large eyes and long ears and back legs, though both are shorter in rabbits. Unlike hares which rely on speed and endurance to evade predators, rabbits generally move in swift, darting movements, relying on burrows and/or vegetation for protection. However, most species are far from ponderous; cottontails (Sylvilagus spp.) can attain speeds of 40 kmh, while the European rabbit has been recorded at 56 kmh (Garland 2009). Home range sizes vary between species, from 0.002 km² in the brush rabbit (S. bachmani) to 0.140 km² in the riverine rabbit (Bunolagus monticularis; Table 1). Home range sizes also vary according to sex, habitat quality, and population density. In cottontails, for example, males range further than females – the territory of a single male overlaps those of several females - and home ranges are smaller when population densities are higher as there is increased competition for resources (Chapman and Flux 1990).

Rabbits are generally thought of as being much more gregarious than hares, often occurring in groups and at high densities (e.g., the European rabbit). This is not the rule, however, and population densities can vary considerably showing marked differences within and between species and depending on a wide variety of factors including local climate, habitat, and predator guild composition and relative abundance. The riverine rabbit, one of South Africa's most endangered mammals with a restricted distribution following widespread habitat destruction, is a largely solitary species which produces very few litters, annually (Table 1). Riverine rabbits also occur at low densities of around 11 individuals per square kilometer (Duthie et al. 1989).

Rabbit social behavior is highly variable, with some species like the European rabbit and the swamp rabbit being highly territorial, while others like the eastern cottontail (S. floridanus) are nonterritorial. With the exception of the volcano rabbit which emits high-pitched sounds, they are largely nonvocal, alerting others of potential threats by thumping their feet on the ground. The breeding behavior of rabbits is broadly similar to that of the hares, with males competing for access to receptive females. Both the European rabbit and swamp rabbit display synchronized mating, where matings across the population occur around the same time, resulting in multiple conceptions and an abundance of similarly aged young.

All rabbits give birth to altricial young (kits), which are born naked and with their eyes closed after a gestation period of between 25 and 40 days (e.g., Table 1). However, there is a trade-off between the length of gestation and litter size. Longer gestation results in larger, more developed young which can more ably fend for themselves. However, larger young generally means smaller litters. For example, swamp rabbit kits weigh 56 g when born, after a gestation of 37 days, compared to those of the desert cottontail (S. audubonii) which weigh 34 g after a gestation period lasting 28 days. The average litter size of both species is comparable at three kits per litter, but the desert cottontail has more litters per breeding season (five, compared to three for the swamp rabbit; Table 1). Moreover, as with hares and other nonhibernating mammals, the reproductive patterns of rabbits have been observed to vary according to latitude. For example, new world rabbits have shorter gestation periods and produce larger litters

in the northern parts of their range when compared to individuals of the same species in the south (Conaway et al. 1974). Such adaptations are a response to latitudinal variations in environmental conditions; breeding seasons are shorter in the north than in the south, and the rabbits maximize their reproductive output, while conditions are favorable (Chapman and Flux 2008).

Old World rabbits actively excavate holes and burrows within which they create a nest of grasses and fur; these offer the vulnerable kits protection from predation and the elements. New world rabbits do not dig, instead utilizing burrows dug by other species, but do create nest holes which are depressions similarly lined with soft vegetation and fur and hidden by a covering of vegetation (e.g., Chapman and Willner 1981). The kits of all species require intensive parental care by the mother (doe) for 2-3 weeks after which they are fully weaned. Young rabbits attain sexual maturity at around 3 months. Mortality can be extremely high, with as few as 8% of young surviving past their 1st year, depending on several factors including population densities, predator abundance, and disease.

Pikas

Pikas are a complex of 30 species within a single genus, *Ochotona*, which is itself split into three subgenera: *O.* (*Pika*), which is comprised of 8 species; *O.* (*Ochotona*), which is comprised of 9 species; and *O.* (*Conothoa*), which is comprised of 13 species (ITIS, 2017). Most species of pika occupy cold, remote, mountainous habitats in Asia, Eastern Europe, and North America, though several inhabit open steppe or forest and shrubland. Two species are found in North America, with the remainder found in Asia, particularly China (24 species).

Pikas are smaller than hares and rabbits (70–300 g; Fig. 1; Table 1) and have rounded bodies, rounded ears, and no visible tail. They also differ in skull morphology and dentition (Smith 2008). Adult individuals of the largest species, which include the Chinese red pika (*O. erythrotis*), weigh over 250 g and can reach

30 cm in length. Unlike hares and most rabbits, they are very vocal, communicating via highpitched calls and whistling barks. They move swiftly in response to a potential threat, taking cover among rocks and/or vegetation, though their hind legs are proportionally shorter than those of other leporids and their gait is very different, being more of a bounce than a hop. Most pikas are diurnal, and they do not hibernate. The average home range of most pika species is small at around 200 m (Table 1). Most species of pika collect caches of vegetation, known as "haypiles," during the summer which they use as sustenance throughout the winter (Smith 2008). They defend their haypiles vigorously, attempting to ward off potential thieves.

The pikas are split into two major groups: (1) long-lived, territorial species with low reproductive rates which live in rocks or talus, which includes all North American and half of Asian species and (2) species which generally have short lifespans, high reproductive rates and live in grassland or steppe habitat and are very social (Fontanesi et al. 2016; Smith 2008). There are a few intermediate species which utilize both habitats, adopting the life history traits of the relevant group. Intermediate species include the Afghan pika (O. rufescens) and Pallas's pika (O. pallasi) (Smith 2008). Pikas are cold-temperature specialists, with high body temperatures; they are sensitive to high ambient temperatures (MacArthur and Wang 1974) and changes in climate (Leach et al. 2015), making them superb indicators of localized warming. This sensitivity means that their distribution is directly associated with climate. While recent studies on American pika (O. princeps) have found that they are able to adapt to variations in climate by utilizing favorable microclimates and adjusting their foraging and thermoregulatory behaviors (Beever et al. 2017), pikas are nevertheless generally highly susceptible and likely to experience range contraction to the extent that some species, such as Kozlov's pika (O. koslowi), may be driven to extinction (Leach et al. 2015).

There are several differences between the two pika groups. For example, burrowing species such as the steppe pika (*O. pusilla*) have larger litters (around 9 young) and more litters per year (3.5)

than rock-dwelling species like the collared pika (O. collaris) which gives birth to 2 litters of around 3 young, annually (Table 1). Rockdwelling species utilize a monogamous mating system, largely due to the dispersal of females across the landscape. Burrowing species also employ monogamy but will also use polygynous, polyandrous, or polygynandrous systems. Both groups are similar – as indeed are all lagomorphs – in that the young are cared for by the absentee mothers; females visit and nurse the young infrequently and for short periods of time. Burrowing pikas are capable of breeding during the summer in which they were born, giving them a higher reproductive capacity than rock-dwelling species which breed in the following year (Smith 1988). There are also differences in population dynamics with rock-dwelling pikas that are largely asocial, occurring at low densities that are generally stable, year-on-year. Adults vigorously defend territories, though they may be less aggressive toward potential mating partners than other members of the population (Smith and Ivins 1984). In contrast, burrowing pikas are often highly social, utilizing familial burrows; they can occur at high densities (300/ha in plateau pikas, O. curzoniae) and their populations exhibit temporal fluctuations. Annual mortality is low in most rock-dwelling species which live for an average of 3–4 years when compared to mammals of comparable size, while mortality is high in burrowing pikas, which also have shorter lifespans (around 2 years) and whose populations have a large yearling cohort (Smith 1988, 2008).

Cross-References

- **▶** Conservation
- ▶ Home Range
- ► Lagomorpha Diet
- ► Lagomorpha Navigation
- **▶** Mammalia
- ► Movement/Locomotion
- ► Social Behavior

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