



# FAUNA *of* AUSTRALIA

## 45. LEPORIDAE

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Rabbit–*Oryctolagus cuniculus* [CSIRO Wildlife & Ecology]

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## DEFINITION AND GENERAL DESCRIPTION

Grouped for many years because of the presence of gnawing teeth, the Lagomorpha and Rodentia are now recognised to have completely separate evolutionary origins. Lagomorphs are distinguished from rodents by the presence of a small second upper incisor. They are divided into two distinct families, the Ochotonidae and Leporidae. The Ochotonidae (pikas) are small rat-sized mammals living at the snow line in rocky habitats of the Northern Hemisphere and possess fore- and hind limbs of almost equal length.

Leporids (rabbits and hares) are larger animals with forelimbs shorter than the hind limbs and a very short tail. There are numerous osteological differences between the Ochotonidae and the Leporidae (McKenna 1982). The dental formula of the Leporidae is I 2/1 C 0/0 PM 3/2 M 3/3. The cheek teeth and incisors are rootless and grow continuously. The rhinarium is naked around the nostrils and covered by flaps of skin which can be retracted. The large caecum has spiral septa.

Of the two species introduced into Australia, the Rabbit (*Oryctolagus cuniculus* Linnaeus 1758) differs from the Brown Hare (*Lepus capensis* Linnaeus 1758), in that its bony palate is longer in relation to the posterior nares and the interparietal bone persists throughout life. The Brown Hare has black-tipped ears and longer legs.

Although one of the oldest of mammalian groups and one of the least specialised, leporids are one of the most successful. They are herbivores of intermediate size and fill a key role in the food chains of the Holarctic. As such, they sustain a community of small mammalian predators (canids, felids, mustelids, viverrids) and numerous birds of prey that are important components of many natural systems.

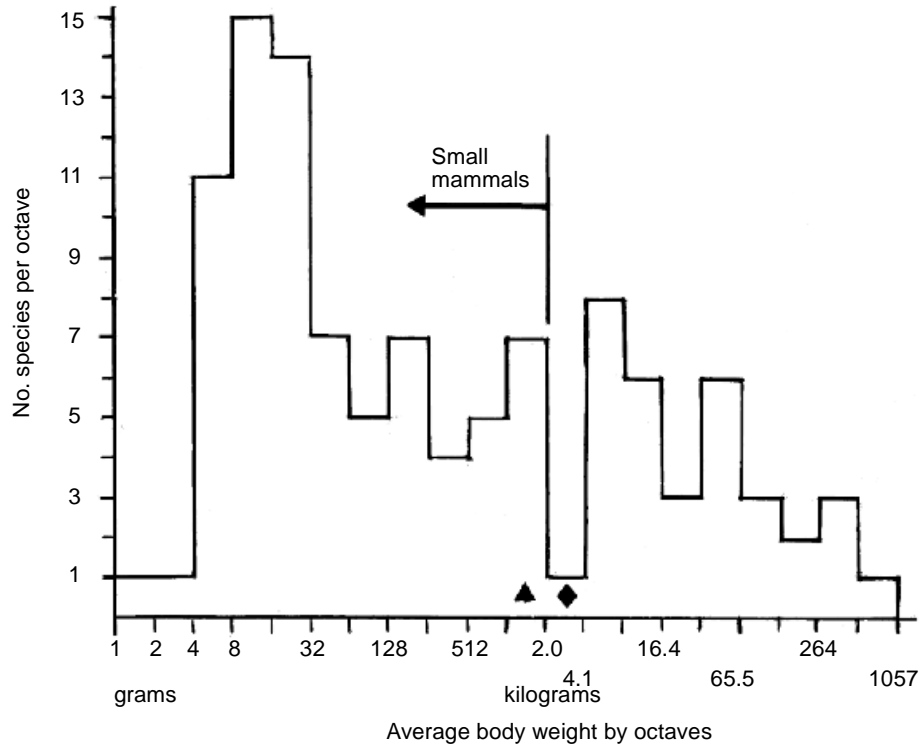
The nature of their importance is expressed in a graph of the weights of coevolved European mammals (Fig. 45.1) (Chew 1978) which shows that only one genus, *Lepus*, spans the 2–4 kg range. Below this size, *Oryctolagus* shares, with several other species, the upper limit of what Chew (1978) defined as small mammals – a large group of species that shows little parental care and has high metabolic rates, short generation times, high rates of increase and is more likely to fall victim to predators. This group is severely affected by environmental change and burrowing and hiding is common among its members. Mammals heavier and with lower metabolic rates than Hares are less affected by environmental events and have life histories based on outrunning predators or hiding; burrowing is uncommon.

Hares are small ‘large mammals’, as can be seen from body size (a shift to the right in Fig. 45.1), and have developed behaviours pertinent to large-bodied mammals, whereas Rabbits remained large ‘small mammals’. The ecological and physiological consequences of this evolutionary divergence are exhibited in many aspects of their respective life histories.

## HISTORY OF DISCOVERY

Hares and Rabbits have been associated with humans for millennia. Fossil hares occur with humanoid deposits 10 million years old in Olduvai, East Africa. Rabbit and hare remains were recently recovered in caves used by prehistoric man in southern France 6000 ybp.

Hares were hunted intensively from antiquity. Murals and decorative paintings on pottery illustrate hunting of hares in Greece, Egypt, Persia and China from about 4000 BC. Xenophon described in great detail the hunters as well as the



**Figure 45.1** Frequency distribution of average weights of European mammal species (triangle = rabbit, diamond = hare). (After Chew 1978)

dogs and nets used in Greece. So popular were hares in Greece that by the end of the 5th Century BC certain hunting districts, including Attica, were declared 'depopulated of hares'.

The Greeks did not know of rabbits that at the time were limited to the Iberian Peninsula and, probably, north-western Morocco. Archaeological evidence shows that rabbits were transported to different parts of the western Mediterranean region as early as 1500 BC. They entered history through the visits of Phoenician traders to Spain. The small burrowing mammal they saw was mistakenly identified as *Procavia capensis* Pallas 1766 (Common Rock Hyrax) that is endemic in the eastern Mediterranean, and the land was called 'i-shephan-im' in its honour. The Romans later translated the name into 'Hispania'. During the following millennium, traders transported rabbits around the Mediterranean on their ships as a source of fresh meat (Bodson 1978).

The first known mention of rabbits in the literature was by Polybius in the 2nd Century BC, who wrote of their presence in Corsica. In the following century the world's first recorded rabbit plague occurred in the Balearic Islands. The citizens implored Emperor Augustus to send the Roman army to save them from the ravages of rabbits that had overrun their islands. The Greeks had already experienced similar happenings with hares, which they had released on islands throughout the Aegean Sea. Xenophon critically examined the differences between the ability of hares to increase on islands where foxes and eagles were absent, and on the mainland where predators were present. There is little doubt that the large enclosures, or leporaria, constructed for keeping hares by the Egyptians, and later the Romans, were also intended to protect them from predators. In the 1st Century BC, Varro suggested that such enclosures might well be used to contain all animals of the hunt, including rabbits. Unlike hares, rabbits propagated very well in leporaria from which they could be caught readily by the use of muzzled ferrets and nets, as was the practice in Spain. For the Romans they quickly became what hares had been for the Greeks.

From this time, the history of spread of Brown Hares and Rabbits became inextricably bound to the cultural development of Europeans. The widespread clearing of forest cover and the development of agriculture and grasslands continually increased the amount of suitable habitat for both species.

The Brown Hare was never domesticated. It did not breed in leporaria and could not be tamed. This hare did however, become an adept 'culture follower', and one of the most abundant and popular game animals on earth. It has been introduced into Ireland and several North Sea islands, Scandinavia, Chile, Argentina and the Falklands, parts of North America, south-eastern Siberia, Asia, Australia and New Zealand. On the southern continents, it proliferated rapidly and became an agricultural and pastoral pest. In Europe and Siberia its populations remained under control and to this day live Brown Hares for the hunt are shipped regularly from countries with good populations (Scotland, Poland, Hungary) to others that are depauperate (Germany, France, Italy).

Domestication of the Rabbit, the deliberate breeding of selected strains for domestic purposes, was achieved between the 5th and 10th Centuries in France and neighbouring countries by monks who kept rabbits in their monasteries, long before forest clearance and agriculture altered the environment sufficiently to permit large numbers of rabbits to exist in the wild. Semi-domestication of the wild strain also continued apace in 'rabbit-gardens' and 'rabbit-islands' in medieval Europe and, later, in 'warrens' in England. These were large enclosed areas of land in the Roman tradition with specially constructed earthworks on suitable soils for breeding rabbits (Sheail 1971). Perhaps as a result of such semi-domestication, the wild form of Britain and France became about 50% heavier than the wild form in Spain. The Australian wild form is the same size as the British. Up to 30 000 per year were harvested from a 3000 acre warren in Lincolnshire from 1850 to 1860. Like the citizens of the Balearic Islands almost 2000 years earlier, the warreners also came to realise that rabbits caused serious damage to plants and soil, often leading to sand-storms in light soils.

For more than 2000 years the Rabbit has been a staple item of food. There can be little wonder at their transport throughout the world by European sailors in the 18th and 19th Centuries, especially during the opening up and settlement of lands in the Southern Hemisphere.

The exact present distribution of Rabbits is not known. The species has been liberated on innumerable islands on the trade routes of the world including the sub-antarctic islands (Macquarie and Kerguelen), tropical Pacific islands in the Hawaiian group (Phoenix and Laysan), numerous Atlantic islands and every mainland explored by Europeans. Because of the lack of predators and competitors they thrived on islands, and in some instances almost completely transformed or destroyed the vegetative cover (Armstrong 1982). A single introduction about 1900 in Chile led to a rapid colonisation of the coastal belt from the extreme south to north of Santiago and into the Andean valleys. Part of the reason for its success in South America was that the native predators did not, and still do not, recognise rabbits as suitable prey (Jaksic & Soriguer 1981). Introductions into Australia and New Zealand were also spectacularly successful.

The early importations into Australia were domestic breeds unfit for feral existence. Wild-type individuals were introduced into Australia in the mid- to late 1800s at places as widely distributed as Canning River (Western Australia), Kapunda (South Australia), Geelong (Victoria), Shoalhaven River (New South Wales) and Woody Island (Queensland). By 1875, the animal was well established in the western districts of Victoria, in South Australia at the southern end of the Flinders Ranges and around Sydney. The South Australian and Victorian infestations had merged by 1879 to cover one large area from Spencer

Gulf to north-eastern Victoria. In 1881 farmers began abandoning their properties in the Mallee and the Wimmera, and by 1890 the rabbit population in south-eastern Australia was out of control.

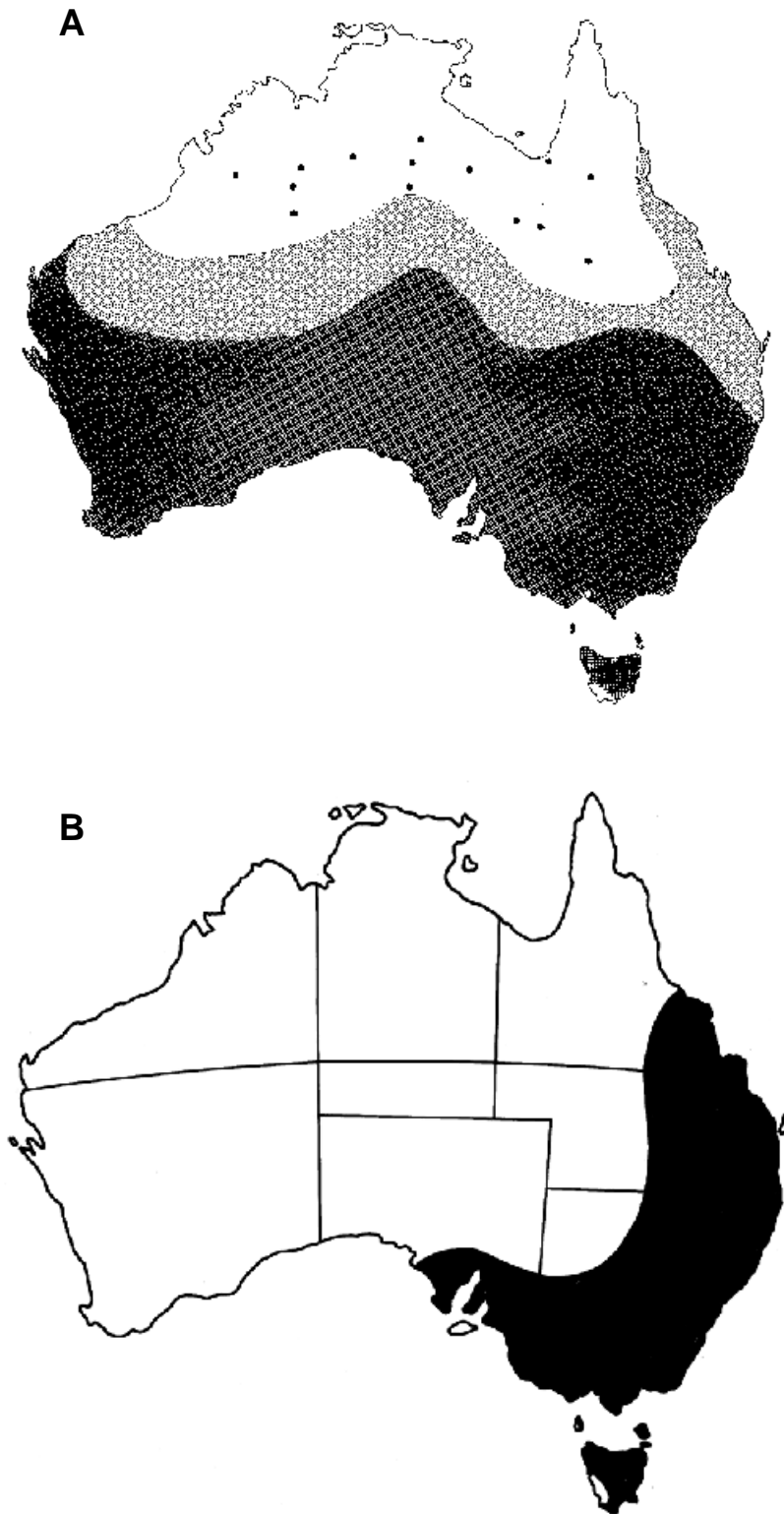
Despite massive attempts to control them by building many thousands of kilometres of rabbit-proof barrier fences, they continued to spread. Making use of the Darling River system and moving at a rate of approximately 125 km/yr, they reached the Queensland border by 1886 and moved up the Diamantina and Georgina River systems onto the Barkly Tableland and to the Gulf of Carpentaria by 1910. Eastwards, their progress slowed to some 15 km/yr. They reached the coastal ranges in 1905, Augathella in 1910 and the Winton District in 1922 (E. Stodart personal communication). In South Australia, they reached Lake Eyre about 1886 and moved up the Finke and other rivers to invade the Musgrave, MacDonnell and other ranges and salt lake systems in central Australia, surging northwards along drainage channels in the Simpson Desert at a rate, according to known records, of up to 300 km/yr (Strong 1983). The Western Australian border was crossed in 1894 and the coast was reached near Geraldton in 1906 and Port Hedland in 1912. The rabbit continues to spread slowly, filling suitable environments along the coast and in the highlands, and progressing along the northern highlands behind Cairns, Queensland, where they have been recently reported at Atherton.

The spread of Rabbits was fastest across the dry, southern savannas and shrub-steppes, and along the arid watercourses, slower in coastal woodlands and forest, and slowest in the tropical north. Today, the species inhabits an area of some 4.5 million km<sup>2</sup>. It is common south of latitude 25° on suitable soils, but it is rare to the north of latitude 20° (Fig. 45.2). Northern Australia has predominantly a summer rainfall and the northern distribution is limited by the unavailability of high quality food in spring, which is the main rabbit breeding season. Within southern Australia, the patchy distribution is strongly influenced by the occurrence of soils in which deep warrens can be dug (Parer & Libke 1985). The greater proportion of their range was covered in 50 years. In the light of modern knowledge, there is difficulty conceiving this explosive emigration as resulting only from the biological capabilities of the species. Nevertheless, despite the confirmed fact that they were carried by people as a food source, no modern biologist believes that the main wave of colonisation and establishment was other than a very real ecological phenomenon.

In southern Tasmania, released domestic forms of the species were common by the 1820s, long before the wild-type had been successfully introduced into mainland Australia. They did not become a significant pest until 1870 (Rolls 1969), possibly as the result of an introduction of a genetically distinct wild strain at about that time (Richardson, Rogers & Hewitt 1980).

The spread of hares in Australia was less dramatic. Introduced at the same time as the rabbit, the Brown Hare became established on the shores of Westernport Bay, Victoria in 1862 and was also common enough to be hunted at a place called The Reedbeds near Adelaide. A colony was set up in 1863 on Phillip Island by the Acclimatisation Society of Victoria where they thrived and became a source for distribution to many parts of the mainland, Tasmania and New Zealand.

By 1870, their range extended throughout south-eastern Australia. They crossed the Murray River in 1875 and moved northwards along the western slopes and tablelands in a series of short eruptive waves to reach the Queensland border about 1900. The rate of spread was about 60 km/year (Jarman & Johnson 1977). Unlike rabbits, the Brown Hare populations of Australia went through only an initial irruption rather than recurrent plagues. In Europe, where agricultural developments and forest clearance have been rapid, hares have been estimated to have spread eastwards at 60–80 km/year during the last 50 years and in South



**Figure 45.2** The present distribution of: A, the rabbit (bold stipple—widespread and common; light stipple—scattered populations; dots—isolated populations); B, the hare in Australia.

America, where it now occupies 4 million km<sup>2</sup>, the rate of spread has been estimated at 18.6 km/year (Amaya 1981). In Australia, the Brown Hare is limited to temperate south-eastern Australia (Fig. 45.2), reflecting its origin in the cool European steppes.

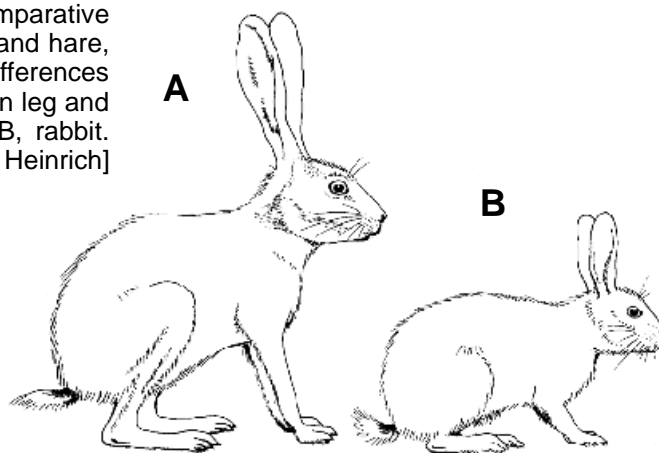
## MORPHOLOGY AND PHYSIOLOGY

### External Characteristics

Leporids are medium-sized mammals ranging in weight from 0.4–7 kg, with an adult head-body length of 250–750 mm. The fur colour varies from brown to grey or white and is thick and usually soft. The pinnae are short in the pikas, but in the leporids are always longer than their width. The pinnae are smaller in rabbits than in hares, where they may be almost half the head-body length of the animal. A Y-shaped groove on the upper lip extends up to and around the nose, more marked in hares, from whence is derived the phrase ‘hare-lip’. The tail, though present in the leporids, is very reduced. The scrotum is anterior to the penis, unlike the situation in most other placental mammals, but similar to the pattern in marsupials. There is no baculum. There are three to five pairs of mammae in females.

The soles of the feet are furred and five clawed digits are present on each foot, though the first digit is small. The forelimbs are shorter than the hind limbs and the elbow and knee joints cannot rotate. The tibia and fibula are fused and the fibula articulates with the calcaneum. Leporids have developed a distinct bounding gait and most of the changes to the limb structure from the ancestral condition are adaptations to this habit (Dawson 1958). These adaptations are seen in their most extreme form in the larger, surface-dwelling hares where speed for escape is essential. Though the same patterns are found in rabbits, they are modified by the habit of retreating to burrows, rather than running to escape (Fig. 45.3). Running rabbits, unlike hares, flash the white underside of their tails, possibly as a warning signal to other rabbits. Because of their short forelimbs and long hind limbs, all leporids are more efficient at running uphill rather than downhill.

**Figure 45.3** Comparative outlines of the rabbit and hare, note especially the differences between the species in leg and ear length: A, hare; B, rabbit. (© ABRS) [H. Heinrich]

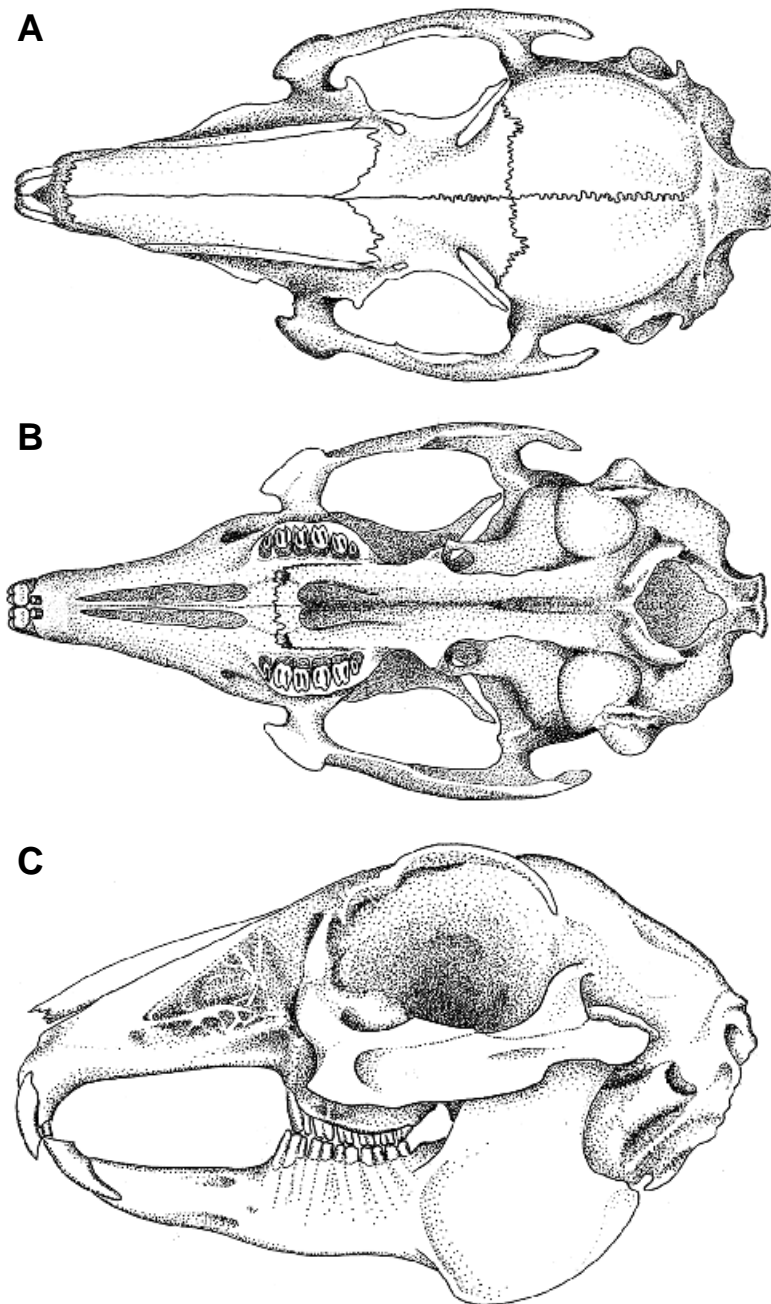


### Skeletal System

A long diastema is present and distinctive fenestrations are found on the side of the maxilla. The orbitosphenoid is large and the supraorbital process is well developed. The glenoid process is not elongated. The auditory bullae are small (Fig. 45.4).

The jaw and dental anatomy of lagomorphs are superficially similar to that of the rodents. Detailed studies, however, have highlighted the convergent nature of these apparent similarities (Gidley, 1912). As in rodents, the functionally





**Figure 45.4** **A**, dorsal; **B**, ventral (cranium only) and; **C**, lateral views of the skull of the rabbit. Note especially the diagnostic fenestrations in the side of the maxilla. (© ABRS) [H. Heinrich]

important gnawing teeth are a single pair of evergrowing incisors. In adult lagomorphs, a second peg-like pair of upper incisors occurs immediately behind the first pair, whereas in juveniles, both second and third incisors are found. The enamel on the first incisors extends around the posterior surface. Cheek pouches are present in both rodents and lagomorphs. Canines are absent. Three upper premolars and two lower premolars occur on each side. Three upper and three lower molars are normally present on each side; the Amami Rabbit (*Pentalagus furnessi*) has only two upper molars on each side. Lagomorphs have more cheek teeth, which are high crowned and rootless, than any rodent. There are usually two transverse ridges on the molars and premolars, and these teeth seem to be adapted for cutting rather than grinding.

The upper tooth rows are further apart than the lower ones. Though the masseter muscles are powerful, they do not extend into the infra-orbital canal. The temporalis muscle is reduced. The two dentaries cannot be moved independently.

### Feeding and Digestive System

Microbial fermentation in the caecum converts some of the cellulose in the diet of leporids to volatile fatty acids which can be absorbed in the large intestine. Vitamins and bacterial protein synthesised in the caecum become available only after the caecal contents are evacuated in the form of soft faeces (caecotrophes) and are ingested directly from the anus (caecotrophy). Rodents, unlike lagomorphs, do not produce special soft faeces, but they do eat a proportion of their normal faeces (coprophagy). The Rabbit excretes its soft faeces in the form of mucus-covered pellets, unlike the Brown Hare. About one-third of the faecal dry matter is in the form of caecotrophes and when reingested provides 5–18% of the dry matter intake and up to 30% of the daily nitrogen intake (Hornicke 1981). Soft pellets are produced and eaten during the daylight hours when the Rabbit is in its warren and, therefore, the ingestion of soft faeces does not reduce the amount of pasture which can be eaten at night. Due to different motor, secretory and absorption processes in the ileocaecal region and the proximal colon, the composition of hard and soft faeces is very different (Table 45.1).

**Table 45.1** Composition of hard and soft faecal pellets in the rabbit. (After Hornicke 1981); \*Concentration in mM kg<sup>-1</sup> dry matter; VFA = volatile fatty acid.

	CRUDE FIBRE (%)	TRUE PROTEIN (%)	Na*	K*	PO <sub>4</sub> *	VFA
Hard faeces	29	7	43	85	4	48
Soft faeces	18	19	102	255	96	180

Unlike ruminants, which reduce intake as pasture quality declines, rabbits and hares can increase intake by shunting a higher proportion of the larger particles to hard faeces production and retaining only the smaller, more digestible particles in the caecum. The passage of food is rapid in rabbits; marker particles can appear in the faeces only 2 hours after ingestion and after 4 hours only 12–20% of the marker particles are in the stomach or small intestine. The mean retention time of marker particles is 13 hours. Because of this short retention, crude fibre digestion is less than 50% of the value for sheep.

Mineral and vitamin requirements are assumed to be similar to those of other mammal species. The Rabbit has a very efficient system for the absorption of calcium. The serum calcium level is not homeostatically regulated within a narrow range as in other mammals, but rises in proportion to the dietary calcium intake. The excess calcium is excreted in the urine, often giving it a milky appearance (Cheeke 1981).

### Circulatory System

The circulatory systems of the two species found in Australia differ significantly, presumably related to their different patterns of activity. In Brown Hares, the heart is large (1–1.8% of total body weight), but in rabbits constitutes only 0.3% of the total body weight. The lungs are relatively heavier in hares. Haematocrit values are 35–40% for rabbits and 55% for hares. The voluntary muscles of the Brown Hare are adapted to high endurance requirements, with more capillaries per square mm, more myoglobin and more oxidative voluntary

muscle fibres allowing higher oxidative capacity. Rabbits, however, have a greater anaerobic capacity in the muscles which is used during short dashes (Schnurr & Thomas 1984).

Temperature is controlled by panting and through heat radiation from the ears (Kluger 1975). The level of blood circulation through the ears is under the control of the central nervous system and up to 40% of heat loss can be via the ears. Leporids do not sweat. Rabbits, unlike Brown Hares, can avoid extremes of climate by using burrows. The Rabbit needs food with more than 55% water and 10–12% protein; thus during droughts, as food with the required water and protein content is not available most of the individuals in an area die.

### **Sense Organs and Nervous System**

As is to be expected from an animal subject to predation by terrestrial and aerial predators, the eyes of the Rabbit are well developed, to give a nearly hemispherical zone of vision with binocular overlap in front, behind and above. The retina of the Brown Hare consists entirely of rods. In the Rabbit 10% of the cones in the retina are sensitive in the blue (425 nm) and green (523 nm) region. Rabbits lack a fovea and are near-sighted frontally and far-sighted laterally. Their hearing range is from 0.3 kHz–32.0 kHz and they are most sensitive to frequencies between 8 kHz and 16 kHz.

### **Endocrine and Exocrine Systems**

Mammals usually have two types of odour-producing glands: sebaceous holocrine and sudoriferous apocrine. Apocrine and sebaceous glands may occur separately as in the chin and anal glands of rabbits and hares, or they may occur in combination as in the inguinal glands. Other odour-producing glands of possible behavioural significance to leporids are the lachrymal and Harderian glands in the eye orbit, and glands in the region of the nipple which produce a pheromone that helps kittens to locate the nipples (Schley 1981).

The size and secretory activity of the chin, anal, inguinal and Harderian glands of rabbits vary in relation to age, sex, social and reproductive status. At puberty, these glands become larger and more active in the male and in both sexes their weight and secretory activity is highest during the breeding season. They are largest in individuals of high social status and these individuals scent-mark most frequently (Mykytowycz & Goodrich 1974). Removal of the olfactory bulb causes atrophy of the genital tract in female rabbits.

Even though the Brown Hare is much larger than the Rabbit, the anal, chin and Harderian glands are much smaller in hares and show no clear sexual dimorphism. The inguinal glands of the latter are larger and the sexual dimorphism is reversed with the females having larger inguinal glands.

Rabbits do not normally defaecate within the burrows, but randomly deposits faecal pellets on the surface throughout their home ranges. As well, special dung hill sites are used mainly by males and the faecal pellets deposited there are more odoriferous (to humans) than pellets deposited elsewhere (Mykytowycz 1968). Faecal pellets deposited on the top of the small dirt mounds made during bouts of paw-scraping also appear to have special behavioural significance. The secretions of the chin gland may be applied to almost any object within the home range, but warren entrances, areas of paw-scraped soil, and other individuals, are the focal points for this behaviour. The secretions of the Harderian and lachrymal glands may be spread over the body surface during episodes of face washing and body grooming. These secretions may pass down the naso-lachrymal duct where the odours would be sampled by conspecifics during the nose to nose greeting ceremony of leporids. Inguinal gland secretions

are not deposited actively throughout the home range and, unlike the odours from the anal and chin glands, only have behavioural significance to conspecifics when the source of the odour is the body of an individual.

Rabbits show a variety of responses to the secretions of a scent gland, unlike insects, where one chemical elicits a specific behavioural response. The chemical composition of the secretions is very complex and, in the case of the inguinal gland, bacterial decomposition of the secretion may be necessary before the odour is fully functional. The behavioural significance of a particular odour may be context and site specific.

The secretions of all scent glands contribute to the general odour of a colony. Young that lack the odour of a particular group are subjected to aggressive chases by the adult females of that group. Information on the identity of an individual and sexual identity is conveyed mainly by the inguinal gland secretions. The territorial function of odours from the anal and chin glands has been shown in laboratory studies in which these odours enhanced the confidence of an individual in the presence of its own odour, and reduced its confidence in the presence of odours from another individual. As rabbits are territorial and hares are not, the anal and chin glands of rabbits are, not surprisingly, much larger.

Rabbits squirt urine onto other rabbits in the course of fighting as well as during mating behaviour. Inanimate objects also may be marked. Urine may convey information about sex, age, social status and individual identity (Bell 1980a). Females are attracted by the urine of dominant males, but it has aversive qualities for other males. Between the nostrils there is a pair of naked S-shaped ridges which have been called 'sensory pads' or 'tactile organs', but their true function is unknown. The urine of adult females (0.05 ml) applied daily to the nasal grooves of young males retarded the onset of sexual maturity, whereas the urine of adult males had no such effect (Bell & Mitchell 1984).

The endocrine system of the Lagomorpha follows the general pattern found in other eutherian mammals. Though they retain many biological attributes which are simple enough to be termed primitive, they are clearly of adaptive value, associated mainly with issues relating to body-size/environment interactions in reproduction and temperature regulation (Austin & Short 1972).

## Reproduction

Unlike the larger mammals, lagomorphs are induced ovulators. The final luteinising hormone (LH) surge, which ruptures the follicles and frees the ova, is caused by nervous stimulation of the hypothalamus during the act of mating. The female does not normally solicit the male to copulate unless she is feeding on actively growing grass or forbs, which are high in the protein needed for newly weaned young.

In many mammals, the placenta can support pregnancy in the absence of the pituitary or functional corpora lutea on the ovaries. In the Lagomorpha, anything that affects the secretion of the luteotrophic complex from the pituitary or stops ovarian oestrogen secretion terminates pregnancy.

The close relationship between the pituitary and the corpus luteum means that adverse environmental change can act quickly to suppress pregnancies doomed to produce young which will not survive. Suppression of pregnancy occurs through resorption of the embryos by the mother. Such a relationship has other effects. If the egg does not implant and the hypothalamus receives no adverse stimuli, the corpus luteum may continue to secrete progesterone, thereby blocking oestrogen production and suppressing further ovulations. The animal then enters a state of pseudo-pregnancy which lasts for approximately 15 days, or half the length of the gestation period of rabbits.



A more interesting aspect of this relationship is shown by Brown Hares in a process known as superfoetation. The underlying cycle in follicular development continues during pregnancy in both rabbits and hares, and occasionally oestrogen production is high enough to affect behaviour and copulation occurs. If this occurs in late pregnancy in Brown Hares, ovulations may occur as the old corpora lutea begin to degenerate, and the newly fertilised ova move down the ducts to find a benign environment and implant readily, effectively reducing the ensuing gestation period by the length of one follicular cycle (7 days). Further evidence of the simplicity of the lagomorph endocrine system is shown during lactation where prolactin alone can support milk secretion.

Unlike those in most mammals, the adrenal glands in lagomorphs are heavier in the male than in the female, despite the fact that the glands enlarge during pregnancy. In males, adrenal glands exhibit seasonal rhythms in size strongly correlated with temperature, photoperiod and testicular size. This is especially marked in hares where photoperiod clearly exerts a strong effect on endocrine responses. In females, no constant pattern is present.

Differences in survival between the sexes in natural populations may be explained partly by observed differences in patterns in hormone secretion. The adrenal gland of unstressed rabbits secretes corticosterone as the normal glucocorticoid. As ACTH (to which the female is more sensitive than the male) increases in the blood, the adrenal shifts from the secretion of corticosterone to the more active cortisol (Myers, Bults & Gilbert 1981). In gestation, the action of high levels of progesterone leads to the loss of salt and causes an increase in secretion of aldosterone, hypertrophy of the adrenal cortex and competition within the gland for hormone precursors. Under extreme conditions, adrenal suppression may occur and death or illness ensues.

Early development of the gonads in lagomorphs is similar to that of other mammals. After puberty in the female, the egg resumes meiosis and is shed in the metaphase of the second meiotic division at a precise time after the LH surge. The majority of oocytes and follicles degenerate by atresia. This process, under the control of gonadotrophins, is continuous throughout adult life.

Evidence exists for intrinsic cyclic patterns in the development of mature follicles in the ovary of rabbits. Hamilton (1951) reported cyclic changes of 4–6 days in vaginal smears from unmated does and Poole (unpublished data) showed a 7 day follicular cycle in a large sample of wild rabbits. Other workers, however, have not found a regular cycle. In rabbits and hares, non-pregnant does showed a 7 day behavioural reproductive cycle (Caillol & Martinet 1981; Myers & Poole 1962).

Sperm are produced continuously throughout adult life with no period of arrested development and no upper limit to gonocyte production. After puberty, the stem cells in any given segment of the seminiferous tubules initiate a series of meiotic divisions at extremely regular intervals of 11 days and the development of spermatozoa then follows in strict progression. The seminiferous epithelium is composed of concentric layers of germ cells progressively more advanced from the periphery to the centre of the tubule. A wave of development travels along the length of the tubule lasting 44 days in rabbits and is comprised of four sperm cycles at any one time. Some adult males are always in breeding condition and can respond to changes in female reproductive condition immediately. About 2 months would be required to re-establish fertility if there were a quiescent phase in the annual cycle of the male (Monesi 1972).

Rabbit spermatozoa possess no special features setting them apart from those of other mammals. Spermatozoa pass passively in the testicular fluids into the epididymis and the wider vas deferens and become functional as they do so. The

sperm transport time of rabbits is unusually long at 3–4 hours, in contrast to that of 5 minutes in other mammals. Sperm have the relatively short life span in the female reproductive tract of approximately 24 hours. Capacitation takes 5 hours from coitus. With sperm entry into the egg, embryonic development proceeds with the resumption of the metaphase stage of the second meiotic division. The entry of further sperm is blocked and the pronuclei move towards each other and fuse 12 hours after fertilisation.

### Embryology and Development

The egg is shed approximately 10 hours after mating and fertilised 10 minutes later in the wide part of the oviduct or ampulla, where it finds the waiting sperm. On occasion, the egg may fail to leave the follicle and become fertilised to form an ectopic ovarian pregnancy or attach to the wall of the oviduct as a tubal pregnancy. The calcified remains of failed intra-abdominal pregnancies also have been observed in wild rabbits.

The fluids of the reproductive tract are dynamic in their response to the changing hormonal environment. The early post-oestrus uterus is an unfavourable environment for eggs while the uterine lining is being primed by oestrogen for implantation. The egg takes 2–4 days in its journey from the ampulla to the uterus, propelled by ciliary action and muscular peristalsis, by which time the uterine lining is ready. A further delay of 3 days occurs in the uterus. In the rabbit, which is a polytocous species, muscles in the uterine endometrium spread the embryos along the tube as the endometrium, now under the influence of progesterone from the corpus luteum, prepares for implantation. The uterine deciduoma reaction is necessary as a defence mechanism to restrict the strong invasive powers of the blastocyst which will develop in any tissue in an animal. The placenta when formed is of a haemochorial type in which the chorionic villi of the embryo become bathed in maternal blood. In rabbits, the synchronous timing of embryonic and uterine development is vital. Faulty synchronisation causes embryonic mortality.

Crosses between hares and rabbits do not develop beyond the blastocyst stage. The chromosome number (2n) is 44 in rabbits and 48 in all members of the genus *Lepus*. Mean heterozygosity in protein coding genes in the lagomorphs varies from 1% in pikas, through 3–5% in *Sylvilagus*, 6% for *Oryctolagus*, 13% for *Lepus* to 15% for *Pronolagus* (Tolliver *et al.* 1985). British and mainland Australian rabbits are genetically similar as measured using protein variation and immunogenetics, but differ from populations from southern France and southern Tasmania (Richardson *et al.* 1980; van der Loo 1986).

## NATURAL HISTORY

### Life History

Leporids are heavily preyed upon by carnivorous mammals, birds and reptiles. Their evolutionary success has been largely due to the development of high and adaptable reproductive rates, acute senses of hearing and smell and an array of other ecological and behavioural traits.

During the day, the Rabbit rests in warrens and hares in forms which are shallow depressions in long grass or under fallen branches. Towards dawn, the Brown Hare doubles back on its tracks and lays a confused trail before entering its form, often by taking a large leap sideways to break its scent trail (Flux 1981). Sometimes the Rabbit may be found during the day in squats which are similar to forms. If a hare in its form or a rabbit in its squat is approached, it will not

move until the intruder is a metre or two away and then breaks cover and flees at high speed. After being disturbed, neither species will use that particular resting place for some time (Flux 1981).

Both species use well-worn runs to and from feeding areas. These runs also are used as high speed runways to escape predators. Both species become active in the late afternoon and remain so throughout the night. After emerging from their warrens, rabbits usually remain near an entrance for some time. During this period there are alternating periods of grooming, grazing, resting and social activities. After moving away from the warren, they graze for long periods. Their home range is 1–5 ha; for hares, it is 5–50 ha.

Warrens vary in size from a simple single entrance burrow to extremely complex structures with over 150 entrances. The Rabbit prefers to dig warrens in deep, well-drained soils. Nests containing kittens often are dug out by foxes from warrens in shallow soils (Wood 1980). Kittens in warrens in poorly drained soils may be drowned or, if the nest becomes wet and loses its insulating properties, the kittens may die from hypothermia. Rabbit kittens have a very limited capacity for thermoregulation until they are 10 days old.

After a gestation period of 30 days (Myers & Poole 1962), rabbit kittens are born blind, deaf and naked into an especially prepared nest lined with grass and belly fur and sealed off with soil from the rest of the warren. Sometimes a doe will dig a nesting burrow, or stop, away from the warren. Young hares, or leverets, are born fully furred, in a rudimentary nest within a form, after a gestation period of 42 days. Several days later the leverets will be lying up separately away from the birth area, but for a period of 30 days they return to the birth place at sunset to be nursed. Both kittens and leverets are fed only once daily for 3–5 minutes. During this brief period a rabbit kitten may drink 20% of its body weight in milk. The composition of hare and rabbit milk is very similar: 12–15% fat, 10–12% protein and 1.5–2.0% lactose (Broekhuizen & Maaskamp 1976). The daily energy output in milk at peak lactation is 555 kcal (45 g kg<sup>-0.75</sup>) for hares and 240 kcal (89 g kg<sup>-0.75</sup>) for rabbits. Leverets and kittens eat solid food at 8–14 and 18–21 days of age and are weaned at 30 and 21 days, respectively.

The Brown Hare is a more or less solitary animal although it may come together in small groups for feeding, which has been interpreted as a response to predation, as those grazing gregariously show fewer interruptions than solitary individuals. The Rabbit is a gregarious species and the size of social groups may range from one male and one female to three males and seven females. One social group may occupy up to five small warrens or a single large warren may be subdivided between several groups. Each group has a dominant male and a dominant female. These animals are responsible mainly for the defence of the group territory. As dominant females are generally older, they tend to have litters earlier in the breeding season than do subordinate females and their young have higher survival rates.

Neither species is very vocal, but both may give a high pitched scream when in danger. In response to a leveret's cries, an adult female hare may attempt to distract the attention of the source of danger. Nestling rabbits emit high pitched squeaks, particularly around feeding time. A hare grunts when boxing and a rabbit doe in oestrus may grunt softly. Both species thump the ground with their hind feet as a warning signal. Leverets drum the ground with their front feet to attract the attention of their mother and adult hares use the same signal during agonistic behaviour.

There have been many reports of a negative correlation between rabbit and hare density. This could be the result of the internal rabbit parasites adversely affecting hares or it could be the result of rabbits dominating hares during

agonistic encounters (Broekhuizen & Kemmers 1976; Flux 1981). Also, adult female rabbits would probably kill any leverets that they found (Evans & Thompson 1972; Mykutowycz 1981).

The physiological life of the Rabbit is about 7 years and that of the Brown Hare, 14 years, but rabbits older than 6 years, or hares older than 10 years are rarely found in natural populations.

### Ecology

Lagomorph populations in different geographical regions show significant differences in almost every aspect of their biology. This can be seen, for example, in autopsy data of rabbits from eastern Australia (Table 45.2) (Myers 1971). These data show differences in body weights, body proportions and variables pertaining to reproduction and physiology. They all may be related to the differences between the environments in which the animals live.

**Table 45.2** Differences in adult male rabbits in different regions of eastern Australia (adjusted for age by regression).

	SUB-TROPICAL	SUB-ALPINE	ARID	MEDITERRANEAN
Paunched weight (g)	1367	1329	1261	1328
Ear length (mm)	82	77	81	78
Foot length (mm)	91	89	91	89
Tibia length (mm)	97	95	94	94
Pituitary (mg)	35	39	32	39
Adrenals (mg)	345	367	228	263
Spleen (mg)	332	420	273	410
Liver (g)	39	39	32	36
Kidneys (g)	10.6	9.0	11.5	9.8
Packed cell volume	35	33	26	37
Serum protein (g/100 ml)	6.0	6.4	5.7	6.2
Sample size	485	429	655	311

Rabbit specimens in the Australian Alps are large, fast growing animals with short ears and legs. The black band in the agouti pattern is longer than in other populations in Australia, making the pelage darker. Except when snow covers the ground, they enjoy a high protein diet. Because of the dampness of the environment, the free-living stages of internal parasites face fewer environmental limits, so breeding females carry heavy burdens of intestinal worms resulting in the young running a risk of death through heavy coccidial infection. In addition to this, the lush grasses of spring are extremely low in sodium, a reflection of the heavy leaching of soils by snow. An examination of the large adrenal glands and blood disclose high levels of production of aldosterone, the hormone promoting salt retention. The alpine Rabbit is avid for sodium and will travel long distances to get it. Salt deficiency in breeding females probably limits the production of young.

In the arid zone, the Rabbit is a slow growing, small-bodied animal with longer ears and legs than those in the Alps. The black band in the agouti pattern is shorter than in other populations, resulting in a pale pelage. Because of the aridity of their environment, internal parasites rarely worry arid zone rabbits, but they



frequently starve or die of thirst. Except after rains, they live on a low protein and high fibre diet. The presence of very small adrenal glands, low levels of circulating aldosterone and large kidneys with the power of concentrating urine all illustrate the nature of their main environmental challenge.

Large differences in reproductive ability of rabbits occur in different Australian environments (Table 45.3), mainly due to differences in rates of maturation of the gonads. The testes of arid zone individuals require 11 months to reach full maturity at a weight of 2 g. In temperate Mediterranean environments, full maturity is reached in 7 months. Females become mature a little later than males (9 months in Mediterranean and 12 months in arid environments). The ability to conceive precedes the attainment of adult size by many months, but high rates of pregnancy in females younger than 6 months of age (47%) occur only in Mediterranean environments.

**Table 45.3** Reproduction in female rabbits older than 3 months from populations in six diverse climatic regions in eastern Australia. (Myers & Parer unpublished); \*Young per female per year.

	SUB-TROPICAL QLD	SUB-ALPINE NSW	SEMI-ARID NSW	TEMPERATE MEDITERRANEAN NSW	COASTAL NSW	SOUTHERN TABLELANDS NSW
Pregnant (%)	32	24	25	43	27	34
Lactating only (%)	19	12	8	6	-	16
Litter size	4.8	4.5	4.5	5.7	5.2	5.0
Litters per year	3.5	3.0	3.8	5.0	2.9	3.6
Mortality to 3 month age (%)	75	28	62	80	21	62
Generation length (months)	23	17	23	16	14	17
Per capita three monthly rate of increase ( $r_c$ )	0.064	0.02	0.046	0.10	0.02	0.06
Actual reproductive rate*	16.9	14.1	16.9	28.0	15.1	17.7
Potential reproductive rate*	35.8	25.8	25.2	37.2	25.4	31.9
Sample size	548	636	937	412	301	889

The number of eggs shed and fertilised usually increases with age, but there are significant differences between populations in this respect. In Mediterranean environments, the mean population litter size continues to increase beyond the second year of life, but in populations from arid zones, no increase occurs beyond the first year (Table 45.4). Although females aged 2 years or older have the highest litter size in the Mediterranean environments, they contribute little to

the annual crop of young as they constitute only 5% of the population (Table 45.4). In the arid zone, females aged 2 years or older constitute a much higher proportion (19%) of the population.

**Table 45.4** Age specific fecundity in female rabbits older than 3 months in Mediterranean and arid environments in eastern Australia (n = 412 and 937, respectively).

Age (months)	MEDITERRANEAN ENVIRONMENT			ARID ENVIRONMENT		
	% of females in age group	Litter size	No. young per female per year	% of females in age group	Litter size	No. young per female per year
3-6	17.7	4.4	12.3	14.0	3.8	2.1
6-12	35.9	5.6	29.1	26.5	4.7	8.1
12-18	30.3	5.9	37.3	21.7	4.6	17.3
18-24	10.7	5.9	31.9	19.2	4.3	19.3
>24	5.3	6.2	40.5	18.7	4.5	18.6

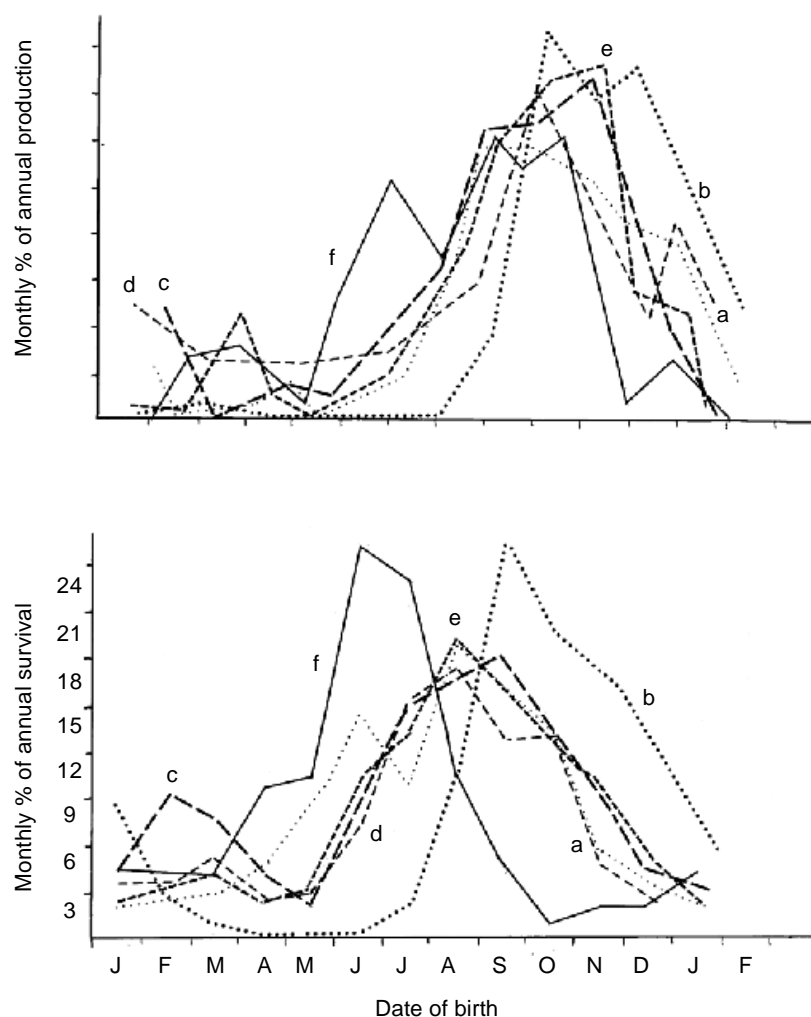
In all populations, testicular weight rises and falls in an annual pattern, commencing growth in winter to reach a maximum in early to late spring. In the arid zone, testicular regression commences in October and by November the testes are small. In subalpine populations testicular regression commences in mid summer, 3 months later than in the arid zone rabbit, and in Mediterranean areas, testis weights peak in September-October and regress in November.

Pregnancies in females follow a similar pattern. There is a clearly defined seasonal rhythm with a trough in autumn-early winter and a peak in the spring-early summer. Pregnancies may occur in all populations in summer but at much lower and more variable rates than in spring.

Since the mean gestation period of the rabbit is known, it is relatively easy to estimate the mean number of young produced per female per month from the observed pregnancy rates, less losses due to the resorption of embryos. There is a surprisingly constant pattern of seasonal production of young in different environments (Fig. 45.5). Without exception, more than 75% of the young are born in the second half of the year, with peaks of production between August and November. Production is skewed towards the summer in the subalpine and towards winter in the arid zone populations.

Most populations approach their theoretical maximum reproductive rate in the spring, with lower rates recorded in summer and autumn. In females of at least 3 months of age, populations in Mediterranean environments have an annual reproductive rate 75% of the theoretical maximum and the highest recorded capacity for production of 28 young per year. In Queensland, although rabbits breed throughout the year and thus have a high potential production of 36 young per year, only 17 young per year are produced in reality (Table 45.3).

Reproduction in all lagomorphs is significantly related to climatic variables affecting physiology and food. This is evident especially in species of the genus *Lepus* that have been studied across a latitudinal gradient. Near the equator the Brown Hare produces eight litters of one to two young each and breeds throughout the year. At mid-latitudes, the breeding season is about 6 months with three to four litters, and in the extreme north only one litter per year of six to seven young is born. The total number of young per female per year thus tends to be fairly constant (Flux, 1981). Similar findings have been shown for Snowshoe Hares (*Lepus americanus*). Thus, in *Lepus* the number of litters in a year is correlated negatively with litter size, whereas in *Oryctolagus* the number of litters



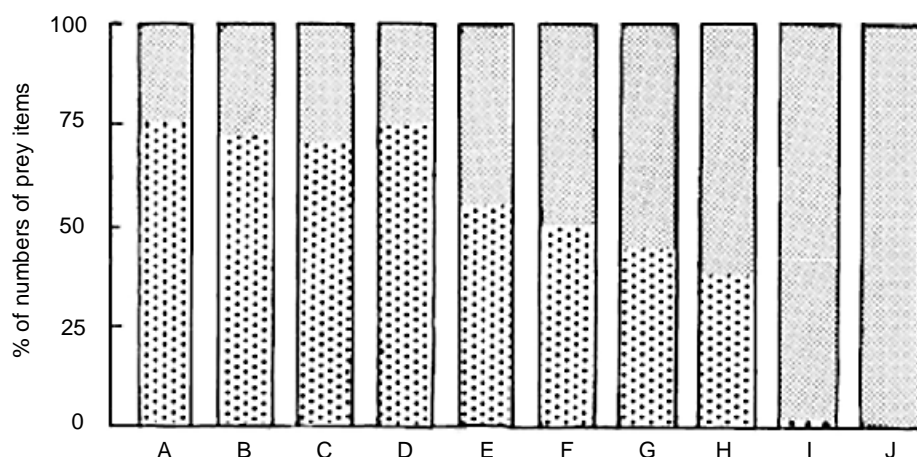
**Figure 45.5** Monthly rates of production and survival of young rabbits in various environments (a = southern tablelands NSW, b = Mediterranean NSW, c = subtropical Qld, d = subalpine NSW, e = coastal NSW, f = arid NSW).

is correlated positively with litter size. Essentially nothing is known of reproduction in Brown Hares in Australia apart from the limited study of Hesterman & Kogan (1963) who showed that in the southern tablelands of New South Wales they bred from August to February and had a mean litter size of 2.3.

The ability of lagomorph populations to increase essentially resides in the rates of survival of the young (Parer 1977). Plotting survival rates of young rabbits against dates of birth shows that there are significant differences between seasonal patterns of survival in different environments (Fig. 45.5). In the subalpine climate, favourable conditions for survival are short, and in the arid zone, they are confined to the cooler months of the year. Modern live studies throw light onto this difficult research problem (Gibb, Ward & Ward 1978; Parer 1977; Richardson & Wood 1982; Wheeler & King 1985).

The survival rate of the Rabbit increases with age. From 6 months onwards, it is fairly similar in all environments (approximately 0.50 per year, for example, Gilbert & Myers 1981; Parer 1977). Young have a very high mortality rate; 80% die before 3 months of age. Mortality factors vary from one environment to another. In pastoral areas, rabbits are the basic food of cats, foxes, dingoes and almost all the raptors. In arid, sandy environments foxes can burrow into warrens and eat as many as 75% of the nestling young (Wood 1980). Predation

by eagles and hawks also can reach significant proportions (Parer 1977; Richardson & Wood 1982), rabbits supplying up to 75% of the food of raptors in south-eastern Australia (Fig. 45.6). Young are also a prey item for goannas and for several snake species. Other important causes of mortality in young are myxomatosis, parasitic infections, especially coccidiosis (Dunsmore 1971) and changes in the quantity or quality of food. The litters born late in a breeding season usually die, either because the doe does not produce enough milk or the weaned young cannot find enough high quality food. There is a general swing in survival against males as sub-adulthood approaches (900–1200 g), probably associated with changes in behaviour as reproductive activities commence.



**Figure 45.6** Percent of rabbit (stippled) amongst prey items (rabbits or other prey) in the spring diet of raptors: **A**, Wedgetailed Eagle; **B**, Little Eagle; **C**, Whistling Kite; **D**, Black Kite; **E**, Brown Goshawk; **F**, Spotted Harrier; **G**, Brown Falcon; **H**, Black Falcon; **I**, Peregrine; **J**, Australian Kestrel: stippled = rabbit, blank = other prey. (After Baker-Gabb 1984)

Adult Brown Hares have few predators, though the annual mortality rate of 40–60% is similar to that found for rabbits. Foxes and wedgetail eagles are the major predators on adult hares and foxes and feral cats on leverets.

Neither the rabbit nor the hare brought its full complement of endoparasites or ectoparasites with it from England. The anoplocephalid cestodes (*Cittotaenia pectinata*, *C. denticulata*, *C. ctenoides*, *Andrya cunculi*) have not been observed in rabbits in Australia. Also lacking is the nematode lungworm (*Protostrongylus rufescens cuniculorum*), a spirochaete (*Treponema cuniculi*) and the two most pathogenic forms of intestinal coccidia (*Eimeria intestinalis*, *E. flavescens*). Three species of nematodes (*Trichostrongylus retortaeformis*, *Graphidium strigosum*, *Passalurus ambiguus*) are commonly found in rabbits in Australia and these three plus *T. colubriformis* also infect hares. Rabbits are host to seven species of coccidia (*Eimeria* species) and six different species are found in hares (Hesterman & Kogan 1963; Dunsmore 1981). Coccidiosis is a significant mortality factor affecting young rabbits, in high rainfall areas and *T. retortaeformis* and *G. strigosum* have deleterious effects on adult rabbits, especially breeding females (Dunsmore 1971, 1981). Both rabbits and hares are accidental hosts to the liver fluke (*Fasciola hepatica*) and to two species of dog tapeworms (*Taenia pisiformis*, *T. serialis*).

The principal ectoparasites of the rabbit in Australia are two mites (*Listrophorus gibbus*, *Cheyletiella parasitivorax*), three fleas (*Echidnophaga myrmecobii*, *E. perilis*, *Spilopsyllus cuniculi*) and one louse (*Haemadipsus ventricosus*).



*Echidnophaga perilis* and *E. myrmecobii* are native species that are commonly found on a variety of marsupials; the louse and the mites came with the rabbit and *S. cuniculi* was introduced in 1968 as a vector of myxomatosis.

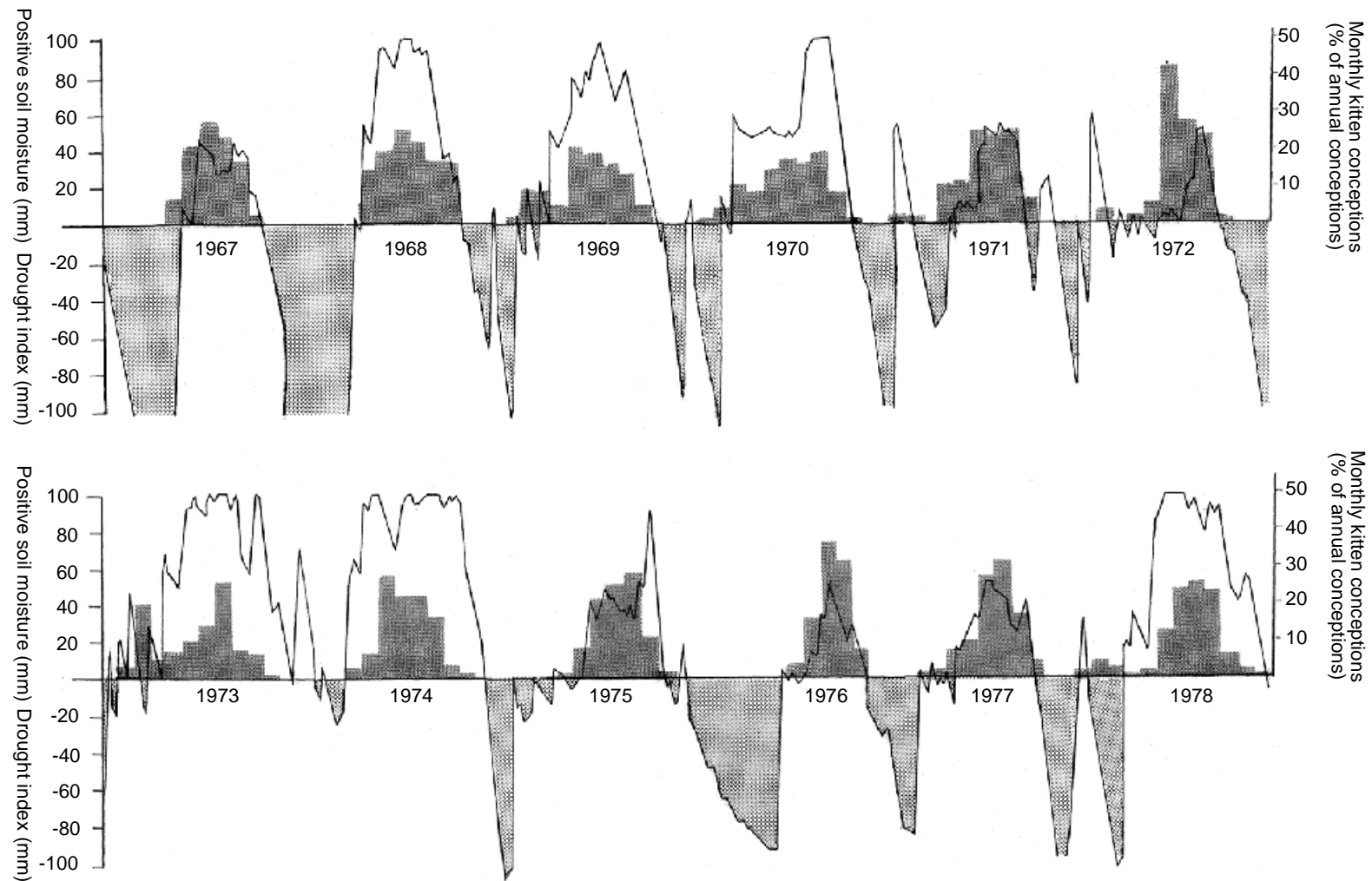
Food quality exerts an important effect on all aspects of lagomorph biology. Green pasture is necessary to stimulate the onset of reproduction in rabbits (Poole 1960). After a dry period the first conceptions usually follow within a week of drought breaking rains (Fig. 45.7; see also Wood 1980). High quality green food is necessary for the continued production of litters and the higher the protein level, the larger the litter size and the lower the mortality to weaning (Omole 1982; Stodart & Myers 1966). As soil moisture declines so does conception rate. The last conceptions usually occur in the month when available soil moisture declines to zero. In a Mediterranean environment (Fig. 45.7), almost two-thirds (63%) of the annual crop of kittens that survive to be trapped are conceived in the months of July, August and September.

In contrast to the opportunistic nature of breeding in rabbits, the breeding season of the Brown Hare is more regular. Because of its mobility, the hare can search out green food in summer while the Rabbit is restricted to eating the pasture in the vicinity of its warrens.

The interplay between variable rates of reproduction and survival leads to significant differences in age structure between populations and to different capacities for increase (Table 45.4). Such data can be analysed to show the levels of mortality of young rabbits that a population can withstand annually and still remain extant. Populations in Mediterranean environments possess the highest rates of increase and can withstand an annual mortality of almost 90% of their young. Rabbit populations in other environments such as the subalpine populations at Snowy Plains, New South Wales, have a low capacity for increase and cannot withstand substantial mortality of young without going into decline.

The operation of the various factors mentioned above results in population fluctuations which are typical of the environment in which the animals live. Arid zone lagomorphs tend to erupt in years of good rainfall and crash or emigrate in large numbers during years of drought. Rabbits that survive live mainly alongside drainage channels. In Mediterranean environments, populations rise and fall in a relatively regular annual pattern in parallel with the regular annual breeding season. The most striking of all patterns in lagomorphs is the cyclic fluctuations of the Snowshoe Hares of the boreal forest of North America that have a periodicity of 9–11 years. The ‘10-year cycle’ is broadly synchronised across the top of the continent and the amplitude of change from trough to peak may be more than 100-fold. The cycle is generated intrinsically by an animal-vegetation interaction which initiates the decline of peak populations and a subsequent hare-predator interaction which extends it (Keith 1981). Winter food shortages develop as Snowshoe Hare populations approach and attain peak densities, leading to lower reproduction and reduced overwinter survival of juveniles from starvation and predation. Predation removes large numbers of these hares during the decline, affecting the amplitude of the fluctuations. These hares of the boreal forest, when in peak numbers, face a critical problem in selection of woody food since they are forced to feed on low preference browse species carrying high concentrations of resins and phenols. The energetics of detoxification of plant toxins (such as these resins and phenols) is developing into an extensive field of work for it is clear that the animal-plant interaction is the key to the whole process of population fluctuation.

Despite the different kinds of population fluctuations in lagomorphs and the different explanations offered for regulation of numbers, the ecological mechanisms involved are obviously similar. Nutrition has a prime place in reproduction and health and predation in mortality.



**Figure 45.7** Monthly percentage of total annual rabbit conceptions (histogram) and soil water balance as defined by soil moisture/drought index (graph; calculated by the method of Slayter 1960 and Newsome 1966) over 12 years at Urana, N.S.W., a Mediterranean environment.

### Economic Significance

The Rabbit and the Brown Hare are regarded highly as game animals in Europe, but in Australia, both are regarded as pests. Hare meat is red with a strong gamey flavour which most Australians find unacceptable. Rabbit meat is white and does not have a gamey taste if the anal glands are removed. It is regarded, however, as a poor person's food as many people were forced to eat it as their staple diet during the Great Depression.

Prior to myxomatosis, there was an active export trade in rabbit skins and carcasses. The main market for carcasses was the United Kingdom and the United States was the main buyer of skins. In the late 1940s up to 6.3 million kg in skins worth \$15 million per year were exported. This trade fell to less than 1 million kg per year by 1970 and during 1983, 1984 and 1985, respectively, registered 37 564 kg, 39 132 kg and 63 855 kg. The skin and carcase trade now earns no more than \$300 to \$400 000 per year (1983 to 1985). Much of the fur was used to make hats, but after peaking during the First World War this market collapsed due to changes in fashion.

As early as 1880 these useful attributes of the Rabbit were disregarded when governments and landholders became aware of the threat posed to agriculture and thousands of miles of rabbit-proof fences were hastily constructed to try and halt their spread. By 1890, the rabbit population in the southern half of south-eastern Australia was out of control. Journals and papers of the time are full of accounts of the desperate measures landholders took to try to safeguard crops and stock. The countryside was subjected to mass campaigns of poisoning with strychnine and phosphorous in pollard baits. Dams were poisoned to kill them when they came to drink. Large concerted drives were held and were directed by wing nets into yards where thousands would be slaughtered with sticks.

Compound 1080 (sodium monofluoroacetate) is the main poison used to control rabbits in Australia today. As 1080 is also very toxic to the main predators, cats and foxes, rabbit populations tend to build up rapidly after initial poisoning. Poisoning should be regarded as a technique to reduce population numbers in the short term whilst other techniques such as deep ripping of warrens and destruction of harbours are carried out. No form of control is economic to use in low rainfall areas where rabbit populations have a substantial, but presently unquantified, economic impact on the pastoral industry.

During 1887, in an effort to control rabbits, the Government of New South Wales offered a prize of £25 000 to anyone who could rid the colony of the pest. Louis Pasteur sent his nephew M. Lois to Australia to investigate the possibility of using chicken cholera and other microorganisms as agents of biological control of the rabbit. The attempt failed, but suggestions for biological control were to come from another quarter. Professor Guiseppe Sanarelli, director of the Institute of Hygiene of the University of Siena, was invited in 1895 to set up a Hygiene Institute in Montevideo. In 1896, a devastating disease occurred in the domestic rabbits Sanarelli was using for the production of immune serum. Sanarelli described the virus and named it infectious myxomatosis of rabbits. After elucidating the natural history of the disease in Brazil, Dr. H. Aragão of Instituto Sierra Cruz, São Paulo, Brazil, brought it to the attention of the Australian Government in 1919. Political pressures vested in the fresh and frozen rabbit carcase and fur trade managed to block the importation of the virus until 1926 when Dr. H.R. Seddon, Director of Veterinary Research in the Department of Agriculture, New South Wales, received living virus from Aragão, which was however, not tested outside the laboratory.

Releases of myxoma virus were made in field populations of rabbits in the arid zone of South Australia in 1942-43, but the disease did not spread beyond the release points. In 1950, inoculations of rabbits in the Murray Valley initiated an epizootic which by the autumn of 1951 had spread along the river systems to

cover large areas of New South Wales and Queensland. Initially, case mortalities due to myxomatosis were in the order of 99%. Mosquitoes, *Culex annulirostris* and *Anopheles annulipes*, were the major vectors. By 1954, the distribution of myxomatosis was coextensive with the distribution of the Rabbit. After laboratory inoculation with myxoma virus, a few Brown Hares have shown symptoms of the disease, but populations have not been affected.

Up to 1958, there was a rapid decline in the virulence of field strains of the virus and also a rapid increase in the genetic resistance of rabbits to myxomatosis (Fenner & Ratcliffe 1965). Since 1958, the rate of change has been slow and the virulence of the virus and the genetic resistance of the Rabbit appear to be approaching an equilibrium. This equilibrium point may be different in different areas. The higher the resistance of animals in an area, the higher the virulence of strains recovered from that area.

Rabbits from various areas in Australia react differently to the strain of the virus isolated from different geographical areas (Table 45.5; Sobey 1983). Those from Yathong near Cobar, New South Wales had a similar survival rate to challenge with the three virus strains used, but those from Urana, New South Wales and Cape Naturaliste, Western Australia had very different survival rates, depending on the test virus.

**Table 45.5** Percentage of rabbits surviving following challenge with one of three strains of myxoma virus. (After Sobey 1983)

AREA OF ORIGIN OF RABBITS	AREA OF ORIGIN OF VIRUS STRAIN		
	Urana (NSW)	Yathong (NSW)	France
Urana (NSW)	79	35	0
Yathong (NSW)	42	57	47
Cape Naturaliste (WA)	47	0	0

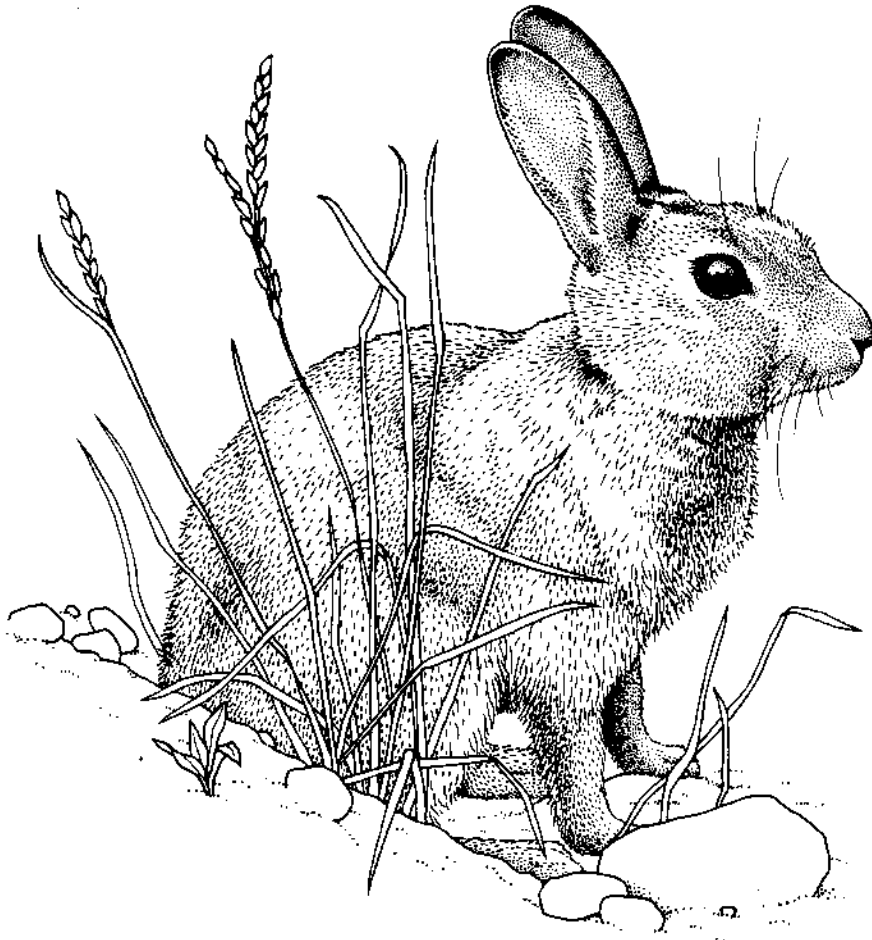
Since the advent of myxomatosis, rabbits have disappeared from many marginal habitats and exist at very reduced densities in the more favoured habitats. At present the number in agricultural areas of Australia may be 1–5% of the numbers present prior to 1950 and, although there are many reasons for these low numbers, myxomatosis is the most important factor. In a recent experiment, the numbers in populations that were immunised against the effects of myxomatosis increased by a factor of 10 in 2 years (Parer, Conolly & Sobey 1985). Although there are numerous examples of the biological control of insect and plant pests, the control of rabbits by myxomatosis is the only example of the biological control of a vertebrate pest.

In the arid zone, even low rabbit densities (0.5–1/ha) prevent the regeneration of many species of trees and shrubs (Lange & Graham 1983). In the higher rainfall areas, expensive netting is required to protect planted trees from rabbits and hares.

## BIOGEOGRAPHY AND PHYLOGENY

Two families containing 11 to 12 extant genera and 62 to 65 extant species comprise the order Lagomorpha (Myers & MacInnes 1981; Nowak & Paradiso 1983b). The family Ochotonidae contains 18 to 19 species called Pikas, Mouse Hares or Conies; all are included in the genus *Ochotona* Linnaeus, 1758. Two species are found in western North America and all other species are found in Asia. They have not been introduced into Australia.





**Figure 45.8.** Under the Endangered species Protection Act of 1992, the Commonwealth promotes the recovery and conservation of native species and ecological communities. Threat abatement plans and recovery plans are key mechanisms in this process. The former plan (Environment Australia 1999a) may be viewed at [http://www.biodiversity.environment.gov.au/plants/threaten/plans/threat\\_abatement\\_plans/land\\_degradation\\_by\\_feral\\_rabbits/index.htm](http://www.biodiversity.environment.gov.au/plants/threaten/plans/threat_abatement_plans/land_degradation_by_feral_rabbits/index.htm). The development and use of Rabbit Calicivirus as a control agent in the 1990s is described by Brian Cooke (1998) at <http://www.science.org.au/nova/001/cooke.htm>. Its use poses a range of possible impacts on native animals, which have been discussed in detail by Newsome *et al.* (1997). (© Environment Australia) [K. McInnes]

The second family, the Leporidae, contains the hares and rabbits. This group had a natural range from northern South America, through North America, Europe and Africa to Asia. One extant species, *Nesolagus netscheri* (Schlegel 1880), is found as far south as Sumatra and occurred in Java during the Pleistocene. The geographic range of the family, however, has been extended greatly by man to include Australia, New Zealand and southern South America by introductions of the Rabbit and Brown Hare. The history and present range of these species in Australia are given in the historical section of this Chapter.

The origins of the lagomorphs are uncertain. The present view is that their closest relations were the Paleocene anagalids (Van Valen 1964) and, perhaps, eurymilids (Szalay & McKenna 1971). Both these groups are Asian and an Asian origin for the lagomorphs in the Paleocene, or probably earlier, may be reasonably assumed (McKenna 1982).

The oldest presently known lagomorphs are found in the Late Eocene in Asia and North America and usually are placed in the family Leporidae (Li 1965). Evolution in the leporids followed a conservative course with increasing hypsodonty of the molars and premolars (presumably related to the herbivorous diet) and changes in the skull and skeleton related to the bounding type of locomotion found in all extant members of the family (Dawson 1958). The next stages of this process seem to have taken place during the Oligocene and Early Miocene with the development of the Palaeolaginae and then the Archaeolaginae. In the Pliocene, archaeolagines are found in Europe. Modern leporids (subfamily Leporinae) make their appearance with *Alilepus* in the Late Miocene of Asia and Europe and occur in the palaeontological record through to the present.

The modern species can be divided into two groups: the hares of the genus *Lepus* and the rabbits, including all other extant genera. The monospecific genus *Oryctolagus* is related very closely to *Sylvilagus* and if *Oryctolagus* had occurred in North America rather than Europe, only a single genus may have been recognised. Presumably due to the process of domestication, the forms of *Oryctolagus* found in northern Europe are larger and genetically distinct from those of southern France and, especially, those from the original undomesticated form found in Spain (Richardson *et al.* 1980; van der Loo 1986).

The two lagomorph species found in Australia are derived from European stocks, though the native range of Brown Hares includes most of Africa and Asia as well as Europe. The Brown Hare may well be a part of a species complex. If the European population is treated as a separate species from the populations in Africa and Asia, the Australian species would be called *Lepus europaeus* (Schneider & Leopoldt 1983).

## COLLECTION AND PRESERVATION

Leporids offer unique advantages for field study. They are active for several hours before nightfall and are large enough to be studied from hides in the manner of large mammals, but small enough to be conveniently captured in relatively inexpensive and portable traps. They are easy to handle.

Rabbits are normally trapped by setting treadle operated box traps, baited with oaten grain and sited on the surface of warrens near burrow entrances. The number of individuals on a warren can be estimated from the number of entrances in active use and the traps can be distributed about the warrens accordingly. There is no need to set traps in a grid fashion as the warrens are the centre of the life of the social groups. Both Rabbits and Hares may be caught with snares set in runways. Animals can be taken from the traps into cloth bags, weighed and examined with ease. Juveniles can be ear tagged with chicken wing tags and adults with sheep ear tags. By colour coding the tags, animals can be identified from hides when they come above ground at dusk. Observations from hides allow estimates to be made of the proportion of the population tagged and the presence and identity of rarely trapped individuals to be detected. Behavioural interactions can be observed directly.

Because of the large numbers of rabbits present in Australia, unless a longitudinal study is planned, collection of animals by spotlighting and shooting is often most convenient. They can also be caught using a long handled net during spotlighting. Unless there is a reason for completely emptying a warren, ferreting has little place in a research program. Gintraps should never be used.

Because of its different behaviour, the Brown Hare is difficult to trap, and grid trapping would be needed. It can be spotlighted and shot in a similar fashion to rabbits.

### Maintenance in Captivity

Wild rabbits may be kept in animal houses in the cages used for domestic rabbits (Parer, Menzis & Sobey 1987a; Parer, Sobey & Conolly 1987b). Standard rabbit pellets tend to be too low in fibre (10%) for wild individuals which need food with more than 15% fibre to help prevent outbreaks of mucoid enteritis. When breeding wild rabbits the doe needs a wire cage with an attached wooden nesting box divided into two compartments: one straw-lined compartment for the litter; and one for the doe to retire into when disturbed. Unlike domestic rabbits, the wild form will not mate immediately after being paired. The buck should be left in the cage of the doe for 3–5 nights and the doe should remain in the same cage until the young are weaned. Coccidiosis may cause high mortalities in young and a coccidiostat should be added to the drinking water. Rabbits also may be bred in small outdoor enclosures (5 x 5 m) if provided with an artificial warren. Lucerne hay is the most convenient food in this situation. In Europe, the Brown Hare has been bred in boxes (2 x 1.5 m) divided into sections with a wire mesh bottom. Mucoid enteritis and coccidiosis may cause high mortalities.

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