3

The rabbit in continental Europe

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3.1 Palaeontology and history

Lagomorphs have lived on the continents of Europe, Asia, and North America since the late Eocene or early Oligocene. Members of both families of lagomorphs have occupied the Iberian Peninsula during that time. The family Ochotonidae, once represented by some 15 species in 5 genera, became extinct in Europe (with the exception of *Ochotona pusilla* in eastern Russia) at the end of the Pliocene. The Leporidae have been reduced from 7 species in 4 genera to the surviving 3 species in two genera, *Lepus* and *Oryctolagus*.

The late Neogene and Quaternary periods saw many profound ecological changes in Iberia. Late Miocene beds (5–7 million years ago) at Salobreña in the southern Spanish province of Granada have made an important contribution to our understanding of those changes. The deposits reveal a fauna which included many forms of direct African origin—giraffes, antelopes, hyaena, and various murids—lying together with Asiatic forms. The data are too sparse to calculate the rate of faunal change, although it seems certain that the African pre-Pleistocene immigrants must have bridged across Gibraltar or the Alboran sea. One European form, *Prolagus*, must also have made use of that bridge, but in the opposite direction, to colonize North Africa (Table 3.1).

There was a great increase, in both number and kind, of leporids at the end of the Neogene and during the Quaternary, which was probably related to the development of extensive grasslands, the cooling of the climate, and the arrival of Asiatic immigrants.

3.1.1 The origin of *Oryctolagus*

The earliest known specimen of *Oryctolagus* comes from Salobreña. The remains are sparse (one solitary tooth!) and do not permit identification to species (Lopez Martinez 1977*b*). But they show that *Oryctolagus* originated well before the Pleistocene.

There are three plausible hypotheses to explain the ancestry of *Oryctolagus*. The first is that it is derived from the Asiatic *Trischizolagus*, but this is difficult to accept as the two genera co-existed during the Upper Miocene of Salobreña (Granada). The second, which suggests an African origin, and the third, an indigenous origin from *Alilepus*, seem more likely; but the available evidence does not really favour any of the three hypotheses.

In western Europe, *Lepus* co-existed with *Oryctolagus*, although not constantly. *Oryctolagus* can survive in any environment, but only as long as the soil is suitable to dig and hide in. *Lepus* is more widely adaptable, able to live in forest clearings, alpine meadows, or prairie, whatever the soil. Such wide ecological plasticity makes it difficult to deduce much about the habitats available at the time. In Central Europe, *Lepus* co-existed with *Hypolagus* and with *Ochotona*.

3.1.2 Species of *Oryctolagus* in the last 2.5 million years

Lopez Martinez (1977*b*) in an excellent review of Iberian lagomorphs described a new species of *Oryctolagus*. She also reported new data for

Table 3.1 Occurrence of *Prolagus sansaniensis* in western Palearctic deposits

Country	Miocene (lower)	Miocene (middle)	Miocene (upper)	Pleistocene
Spain	X	X	X	X
France	X	X	X	X
Germany	X	X	X	X
Morocco				X
Portugal	X			
Turkey		X	X	
Hungary			X	X
Greece			X	

Source: After Lopez Martinez (1977a).

O. lacosti, already known from France (Lopez Martinez *et al.* 1976) and described the oldest known discovery of *O. cuniculus* on the Iberian peninsula, more than half a million years old.

Oryctolagus lacosti, known from Cataluña (Villaniense and Bihariense), had a large body size (between that of *Lepus* and *O. laynensis*), similar to *O. laynensis* in Italy and France. Cranial and dental characteristics mark it as an *Oryctolagus*, although in body size and in the morphology of the premolars (P3) it had similarities with *Lepus*.

Oryctolagus laynensis appeared in Andalucía, Castilla, and Cataluña in the late Miocene, and is apparently a direct ancestor of present day rabbits. It has also been found in the Pliocene either as a 'descendent' of *Trischizolagus*, also known from the upper Miocene in Murcia, or as an African immigrant. It is the oldest known *Oryctolagus*, with cranial and dental characteristics typical of that genus. Its skeleton appeared to be modified for jumping, but it also had the robust muscular insertions, particularly on the humerus and ulna, common in burrowing animals (Donard 1982).

Oryctolagus cuniculus first appeared in Andalucía, in mid-Pleistocene deposits in Cullar Baza, Granada, co-existing with *Lepus*. It has also been found in the province of Malaga, and in southern France (de Lumley-Woodyear 1969, 1971; Chaline 1976; Lopez-Martinez 1977b; Pages 1980). Dental peculiarities suggest that both *O. cuniculus* and *O. lacosti* are descended from a common ancestor, *O. laynensis*.

A plot of tooth lengths from Quaternary remains in the Iberian peninsula shows that the earliest species of *Oryctolagus*, although smaller than *Lepus*, were larger than the later *O. cuniculus* (*O. lacosti* then *O. laynensis*; Fig. 3.1a). Over the last 15 000 years the sizes of various osteological variables have also tended to decrease in *O. cuniculus* (Fig. 3.1b); which was a smaller rabbit than either of the other species, perhaps because it always coexisted with *Lepus*. The rabbit from Cullar Baza (Granada) was similar to *O. cuniculus* today.

This is consistent with Donard's (1982) research on the recent history of the rabbit in France. From bones in numerous caves she was able to show that from 500 000 years (Mindel glaciation) to 15 000 years ago (Magdalenian epoch) local populations of rabbits showed substantial variation in body size, following changes in climate. Four geological sub-species are thus defined: *O. c. lunellensis*, a rabbit of moderate size and temperate climate, dating from 300 to 200 000 years ago; *O. c. grenalensis*, a large rabbit of very different climates, dating from 150 to 70 000 years ago; and *O. c. huxleyi*, a small rabbit of hot climates some 40 000 years old, still living on the Canary Islands (where it was introduced long ago, or was possibly there before people) and Madeira; and *O. c. cuniculus*.

3.1.3 Geographical variation in contemporary *Oryctolagus cuniculus* in Europe

Not only has *O. cuniculus* become smaller in the course of its evolution over the last 15 millennia; it also exhibits a clear reduction in body size over its
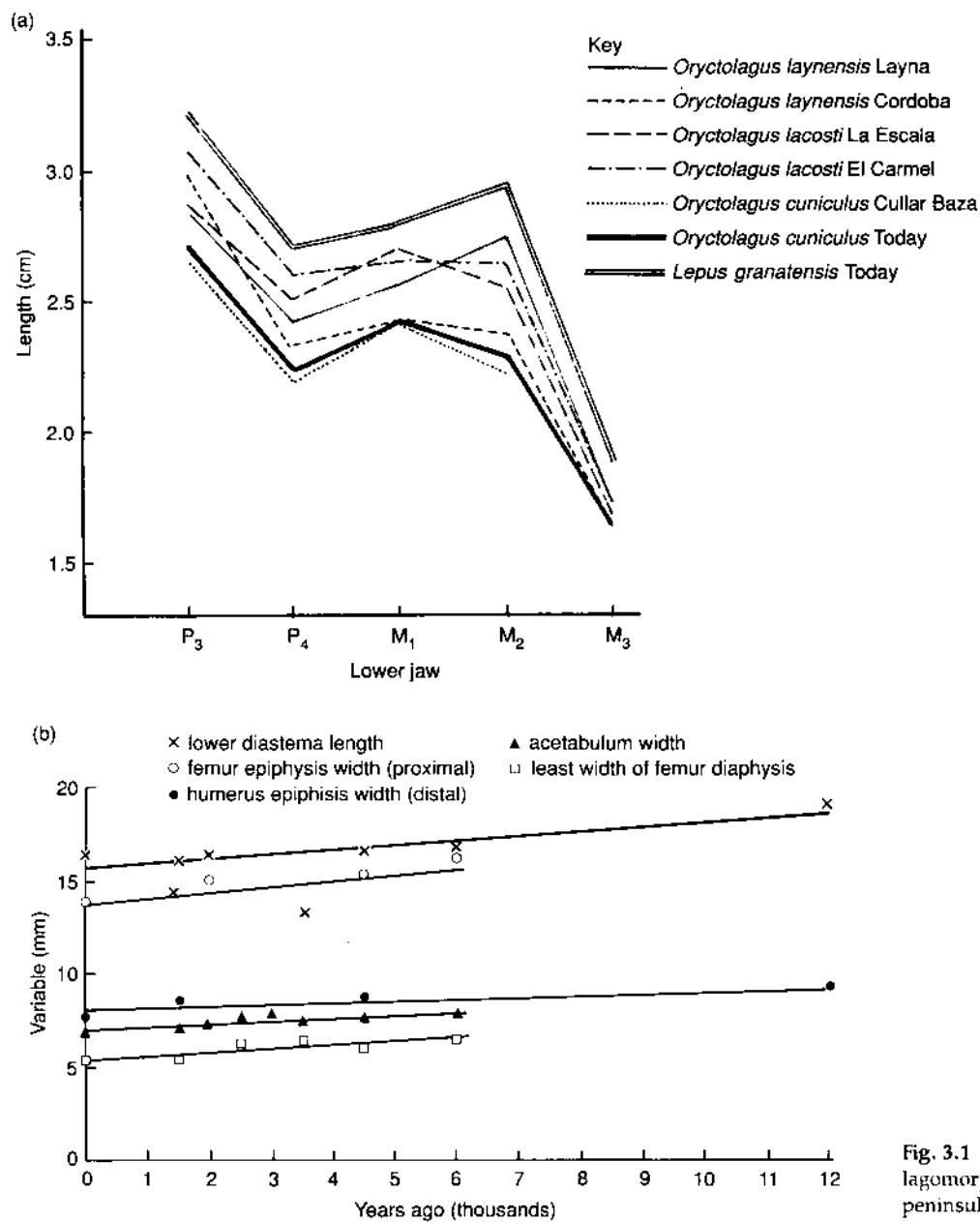
Fig. 3.1 Tooth lengths of lagomorphs on the Iberiar peninsula.

present range, from north to south (Table 3.2). The rabbits of North and Central Europe are much larger than their relatives in Mediterranean Europe and North Africa. Even within France or the Iberian peninsula, there is a clear north–south gradient in body size.

Several hypotheses have been suggested to explain this pattern. One associates selection of body size with various ecological influences (climate, predation etc.). The rabbit apparently conforms to one such hypothesis, Bergmann's law, which predicts larger body size in higher latitudes. Soriguer (1981a, 1983b) has shown that rabbit populations which differ in body size also differ in other respects. The Mediterranean Iberian rabbit grows faster, and as we note later, has smaller litters, breeds younger and dies sooner than its bigger cousins. The final result in terms of the rate of increase 'r' is the same, however, albeit through different strategies. Another explanation suggests the influence of human activities (introductions, 'improvements' etc.) and domestication.

A third possibility is that the northern and southern rabbits represent different evolutionary lines. At the time of the glaciation of Mindel (50 000 BC), *O. cuniculus* had a fairly restricted range. Studies of the systematics of rabbit parasites, principally fleas, suggest that there were then two relict populations of rabbits: one in Spain, where the rabbit was particularly abundant near Gibraltar, and the second in the south of France (Beaucournu 1980a, 1980b). Indeed while *Spilopsyllus cuniculi*, the most common flea on rabbits, is present throughout the rabbits' range, three other fleas, *Xenopsylla cunicularis*, *Caenopsylla lactaevi*, and *Odontopsyllus quirosi*, are present only in France and Spain (including Morocco for *Xenopsylla*). The morphological differences are clearest between French and Spanish individuals of two of these species of flea, suggesting prolonged separation between the two relict rabbit populations (Beaucournu 1980a).

Studies of mitochondrial DNA and different immunoglobulin alleles support this hypothesis (van der Loo *et al.* 1991; Biju-Duval *et al.* 1991). In general there is high polymorphism in southern Spain, decreasing towards the north. Phylogenetic relationships between the rabbit's mtDNA types suggest that the separation of the two relict populations could have begun even before the Mindel glaciation.

Domestic rabbits appear most similar to northern wild rabbits, and least similar to those of Andalucía (Richardson *et al.* 1980; Biju-Duval *et al.* 1991; Van der Loo *et al.* 1991; Van der Loo and Arthur in preparation). This suggests that the foundation stock for domestication came from only one (northern) population. It is interesting to note that the mtDNA of French rabbits is more closely related to that of rabbits in the north of Spain than the south. Almost all the alleles of domestic rabbits are present in the wild genotypes. Rabbit populations could have suffered genetic impoverishment the further they have moved from their ancestral home.

Today's wild rabbits still retain traces of their diverse historical origins. Genetic characters distinguish at least three separate rabbit populations in Europe: one in south, central, and west Spain and Portugal, a central one in northern Spain and southern France, and a northern one which includes rabbits in Belgium, England, Scotland, Wales, and northern France. Rabbits in the last group are genetically similar to those now in Australia and New Zealand (Richardson *et al.* 1980).

3.1.4 History of *Oryctolagus cuniculus* in Europe

Donard's (1982) studies showed no rabbits in all deposits of the Holocene (10 000 years ago) and earlier, north of the Loire. No rabbit bones have been found in all the excavations undertaken in the départements (administrative divisions of France) of Côte d'Or, Eure-et-Loire, the north of Charente, in Seine-et-Marne, Essonne, Yonne, Seine-Maritime and Haute-Savoie, whereas the hare (*Lepus*) is relatively well represented. In contrast, rabbit bones have been found in Charente Maritime, a deposit in the south of Charente, in Gironde, Haute Garonne, Hérault, Bouches-du-Rhône, Ain, Dordogne, Corrèze and Ardèche (Fig. 3.2).

Many deposits in Hérault and Bouches-du-Rhône contain rabbit remains, sometimes in abundance and notably of the geological sub-species *lunellensis*. They confirm that the range of the rabbit has extended progressively northwards from a relict population on the coast of the Mediterranean, and that it was only at the start of the historical epoch (20 000 to 1000 BC) that rabbits invaded other lands to the north of the Loire (Donard 1982).

Table 3.2 North–south variation in contemporary rabbit weights (g)

Country	département (France only)	Sex	Whole weight (mean)	Sample size	Maximum weight	Reference
Sweden		F	1670	521	>2000	Andersson *et al.* (1979)
		M	1670	521	>2000	
Holland		F	1500	–	>1700	Wallage-Drees
		M	1530			(pers. comm.)
France[a] N	Nord	F	1710	45	>2000	Arthur and Guenezan
	(sand dune)	M	1725	25	>2000	(unpublished)
W	Morbihan[bc]	F	1450	47	–	Arthur (unpublished)
	(heathland)	M	1415	56	–	
	Vendée	F	1450	24	1830	Arthur and Aubineau
	(bocage[c])	M	1350	16	1760	(unpublished)
	Deux-Sèvres	F	1355	17	>2000	Arthur and Aubineau
	(bocage)	M	1370	22	1980	(unpublished)
Centre	Loiret[bc]	F	1385	29	–	Arthur and Guenezau
	(bocage)	M	1360	23	–	unpublished
CW	Yvelines	F	1415	67	1830	Arthur and Guenezau
	(farmland)	M	1355	84	1780	(unpublished)
	Yvelines	F	1500	100	1930	Arthur (unpublished)
	(parkland)	M	1510	83	1860	
	Essonne	F	1360	51	1830	Arthur and Angibault
	(woodland)	M	1405	63	1760	(unpublished)
E	Haute-Saône[bc]	F	1350	37	–	Arthur (unpublished)
	(pasture)	M	1360	28	–	
CE	Saône-et-Loire[bc]	F	1375	28	–	Arthur (unpublished)
	(pasture)	M	1345	31	–	
SW	Landes	F	1360	115	1750	Arthur and Avignon
	(fallow/pasture)	M	1430	90	1650	(unpublished)
	Landes	F	1555	15	>2000	Launay (pers. comm.)
	(farmland)	M	1555	8	>2000	
	Haute-Garonne[d]	F	1730	9	>2000	Launay (pers. comm.)
	(farmland)	M	1630	9	>2000	
	Dordogne	F	1345	33	1640	Arthur and Garcia
	(bocage)	M	1310	28	1610	(unpublished)
SE	Hautes-Alpes[c]	F	1290	12	1370	Arthur and Reudet
	(bocage)	M	1295	18	1450	(unpublished)
	Bouches-du-Rhône	F	1245	41	1580	Arthur and Gaudin
	(pasture)	M	1210	28	1510	(unpublished)
	Bouches-du-Rhône	F	1250	22	–	Vandewalle (pers. comm.)
	(fallow)	M	1235	19	–	
	Bouches-du-Rhône[e]	F	1354	101	–	Rogers (1979)
	(salt-marsh)	M	1301	104	–	

Table 3.2 (*cont.*)

Country	département (France only)	Sex	Whole weight (mean)	Sample size	Maximum weight	Reference
France SE						
	Hérault[c]	F	1230	10	1510	Arthur and Taris
	(garrigue/cultiv.)	M	1250	10	1430	(unpublished)
	Corse	F	1255	12	1430	Arthur and Roux
	(maquis)	M	1320	14	1490	(unpublished)
	Vaucluse	F	1300	45	1590	Arthur and Gaudin
	(fallow)	M	1340	65	1540	(unpublished)
Portugal		F	1017	18	–	Lopez Ribeiro (1981)
		M	1023	11	–	
Spain NE		–	1190	4	–	Soriguer (unpublished)
NE		–	1158	71	–	Mañosa and Real (unpublished)
N		–	1224	97	–	Ceballos (unpublished)
N		–	1274	113	–	Ceballos (unpublished)
NW		–	934	6	–	Soriguer (unpublished)
SE		–	1043	28	–	Marquez (unpublished)
S		–	1011	1044	–	Soriguer (unpublished)
S		–	910	16	1050	Soriguer (unpublished)
SW		–	1092	521	–	Soriguer (1980c, 1981a)
SW		–	923	18	–	Soriguer (unpublished)
Morocco		–	1039	–	–	Soriguer (unpublished)

[a] All data except Rogers (1979) are from adult rabbits (>9 months) collected by ferreting in January–February.
[b] Data collected by the Service technique of the Fédération Départementale des Chasseurs.
[c] Data collected during the hunting season (September/October) from adult rabbits (>9 months).
[d] Includes domestic × wild crosses.
[e] Data collected in all seasons by night shooting; January–February mean weights were 1237 g (♀♀, n = 22) and 1282 g (♂♂, n = 28).
[f] A landscape of small fields (pasture or crop) surrounded by hedgerows on mounds.

By Roman times rabbits had become a problem in Spain. In the Balearic Islands they caused so much damage that the colonists asked the Emperor Augustus to send a Roman legion to clear the land of them, or to allocate them land elsewhere (according to Strabo, 58 BC to AD 20). Pliny the Elder, in his *Natural History*, tells of the ramparts of Tarragone being undermined by rabbit warrens, and recommended even then using ferrets against them. The rabbit was already used as the symbol of Spain by the poet Catullus, and imprinted on the reverse of some coins by the Emperor Hadrian. The Romans modified the range of the wild rabbit by introducing it to many countries, including to Italy and Corsica from France (Bodson 1978; Zeuner 1963), and to North Africa from Spain (C. Louzis personal communication).

In France, domestication of rabbits began much later, by monks in the Middle Ages. Their motivation was that newborn rabbits (the famous *laurices*) were considered to be aquatic, so were authorized in the Catholic religion for consumption in Lent. From the second to the fifteenth centuries there are numerous
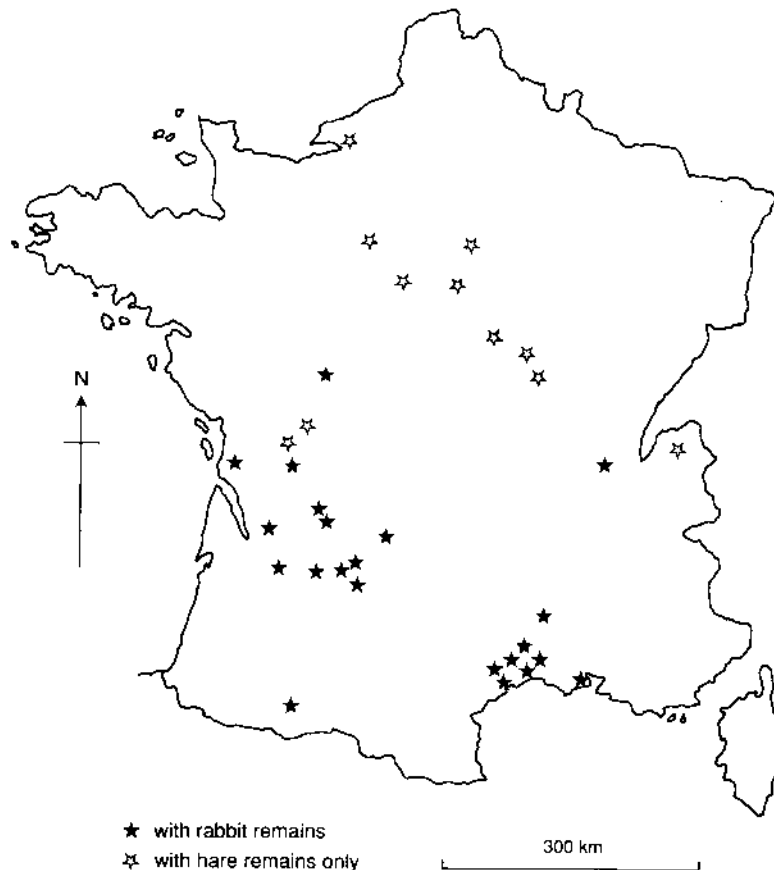
Fig. 3.2 Sites in France with rabbit remains, and with remains of hares but not of rabbits, 300 000 BC to AD 100 (after Donard 1982).

★ with rabbit remains
✪ with hare remains only

300 km

references to rabbits kept by monks and sometimes by peasants, or by the feudal gentry in enclosures of varying extent and degree of security, sometimes made of stone. Rabbits were often sold in markets, as shown in the book *Conejeria de Toledo* (the Rabbitries of Toledo) of the twelfth century. Trade sometimes spread far afield; there are records of the sale of rabbits between the abbeys of Corvey (Germany) and Solignac (France) in 1148, and the despatch of 6000 rabbit pelts from Castile to Devon in 1221 (Delort 1984). However, there is scarcely a mention of rabbits living free in the wild.

Nevertheless the monarchy in France always attempted to restrict 'warren rights', by forbidding the creation of new warrens or the enlargement of old ones, or the re-establishment of old boundaries (there are examples of such rules in the ordonnances of Jean le Bon in 1356 and of Charles VI in 1413). In

the seventeenth century Colbert (prime minister to King Louis XIV) ordered the destruction of rabbits in all the royal forests, and undertook to compensate for rabbit damage where the royal servants were unsuccessful in their task. The French Revolution abrogated Colbert's ordonnance, and annulled the exclusive right of the gentry to control warrens, but the rabbit in France nevertheless remained enclosed and controlled. Not until the Second Empire, in 1862, did Napoleon III declare rabbits to be game, and order that they be allowed to range freely in the forest of Compiegne.

At the end of the nineteenth century, numerous bourgeois hunts were established close to the towns, on agricultural areas which were abandoned after the Industrial Revolution and the phylloxera crisis. The rabbit became their principal quarry. In less than 20 years, from 1845 to 1863, the number of rabbits
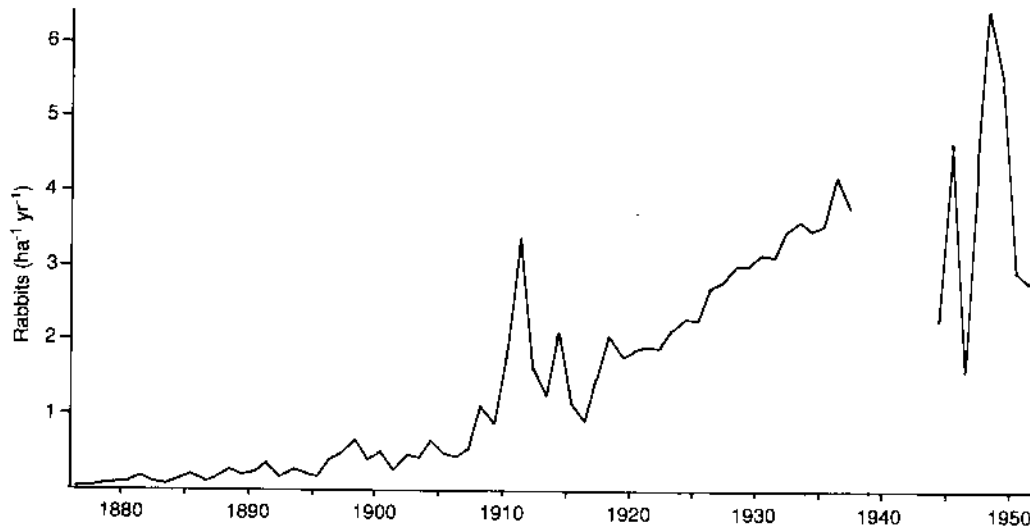
Fig. 3.3 Number of rabbits shot annually per hectare on a private hunt of 720 ha in Loiret, France, 1877–1953 (after Giban 1956).

sold in the markets of Paris rose from 177 000 to nearly 2 million (Gayot 1865). From then on, the extension of the natural range of the rabbit continued progressively. In Sologne, there were so few rabbits in 1880 that it was judged a waste of effort to fence nurseries for reforestation programmes: in 1930, hunters took more than 10 rabbits/hectare in a season from the same area.

At the start of the twentieth century the introduction of winter cereals and the rotation of crops, combined with the massive destruction of all predators (aerial or terrestrial) by gamekeepers, greatly favoured population increases in rabbits. Some gamekeepers even provided food for game (and especially for rabbits) in winter—apples, beetroot, and fodder. Rabbits quickly reached the very high densities recorded from 1920 to 1930 (Fig. 3.3). Bags of over 10 rabbits/hectare were common in northern départements of France from then until 1950–2. In Mediterranean France bags were between 1 and 2 rabbits/hectare (Giban 1956).

Damage to farm crops due to the excessive abundance of rabbits did not generally cause concern in the north of France, but it was nevertheless the reason that, on 14 June 1952, Dr Delille introduced the myxoma virus on Maillebois, his estate in the département of Eure-et-Loire. Because of previous failures to introduce the virus in other countries, and

because he did not know the mechanism of transmission, Dr Delille assumed that any disease would be confined to his 300 ha walled enclosure. But the result of his experiment was a little more spectacular than he expected: by summer 1952 the disease had reached 9 départements. By the end of 1953 the whole of France was affected (Fig. 3.4), and isolated cases of myxomatosis were reported from Spain, Belgium, Holland, Germany, and England (Joubert *et al.* 1972).

For hunters, the rabbit population crash in France was catastrophic. In 1953–4 bags were 15 per cent of those before 1952; in 1954–5, 2 per cent, and in 1955–6 about 7 per cent. Some 90 to 98 per cent of the French rabbit population was killed by myxomatosis between 1953 and 1955. The pressure of public outrage was enormous, and legal proceedings were started against Dr Delille. He was convicted of illegally spreading an animal disease in September 1954, but received only a nominal penalty—a one franc fine. On the other hand, in 1956 the Syndicat National des Forestiers Français presented him with a medal 'in recognition of services rendered to agriculture and sylviculture'. In fact the estimated increase in agricultural and sylvicultural production at that time was in the order of 1000 million francs (using 1992 values for the franc; Siriez 1957).

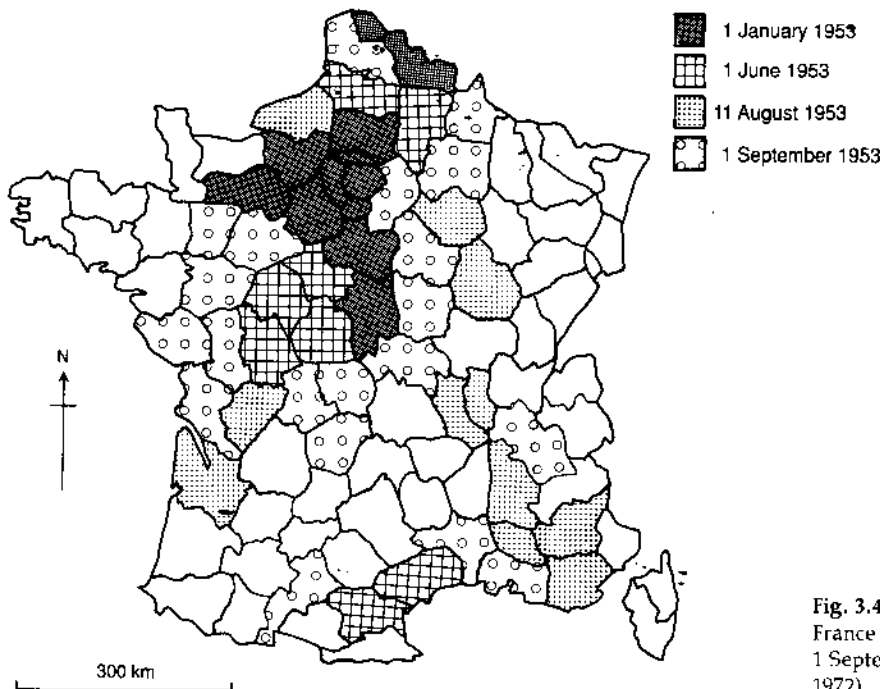French hunters quickly attempted to limit the

Fig. 3.4 Extent of myxomatosis in France from 1 January to 1 September, 1953 (after Joubert *et al.* 1972).

effects of the myxoma virus, trying to establish 'cordons sanitaires' around affected areas, and even,in 1956, importing Australian rabbits reputed to be resistant to the virus. All their efforts failed. Nevertheless, 1956 saw the start of a small increase in bag size. The first attenuated strains of the virus were found in 1955 (Jacotot *et al.* 1956), and they spread gradually until in 1968 more than half the strains isolated from wild rabbits were much attenuated, grade IIIB–IV (Fenner and Ratcliffe 1965). That proportion seems to have been more or less maintained until 1977–8 (Joubert 1979). Over the last four or five years, however, there has been an increase in the more virulent strains.

3.2 Present distribution and regional variations in numbers

The rabbit is now found over most of western Europe, excluding most of Austria, Italy, and Switzerland, and around the coasts of the western Mediterranean Sea (Fig. 2.2). Its eastern range extends as far as the Crimea. It is also found on the Balearic Islands, Corsica, Sardinia, Sicily, and Crete.

Wild rabbits were introduced in southern Ukraine at the end of the nineteenth century. About 80 years later their range was increased extensively by further introductions to shoots in the Ukraine, Maldavia, and the Pre-Caucasus. In 1979 experiments began on establishing rabbits in Uzbekistan, and later in Lithuania. At each site, 2000–3000 animals were released. Irrigation development in Central Asia provided opportunities for wild rabbits to become locally abundant in desert zones (Skulyatvev 1987).

A detailed picture of the distribution and abundance of the rabbit in France was produced by a 1977 survey of all gamekeepers by the Office National de la Chasse (Arthur *et al.* 1980). It showed, with other data (Arthur and Chapuis 1985), that rabbits are found in every département (Fig. 3.5). They are less abundant and more dispersed in mountain areas (Jura, Alpes, Vosges, centre of the Massif Central, Pyrénées) and the north-eastern départements, perhaps discouraged by a high snowline, thin soils, too
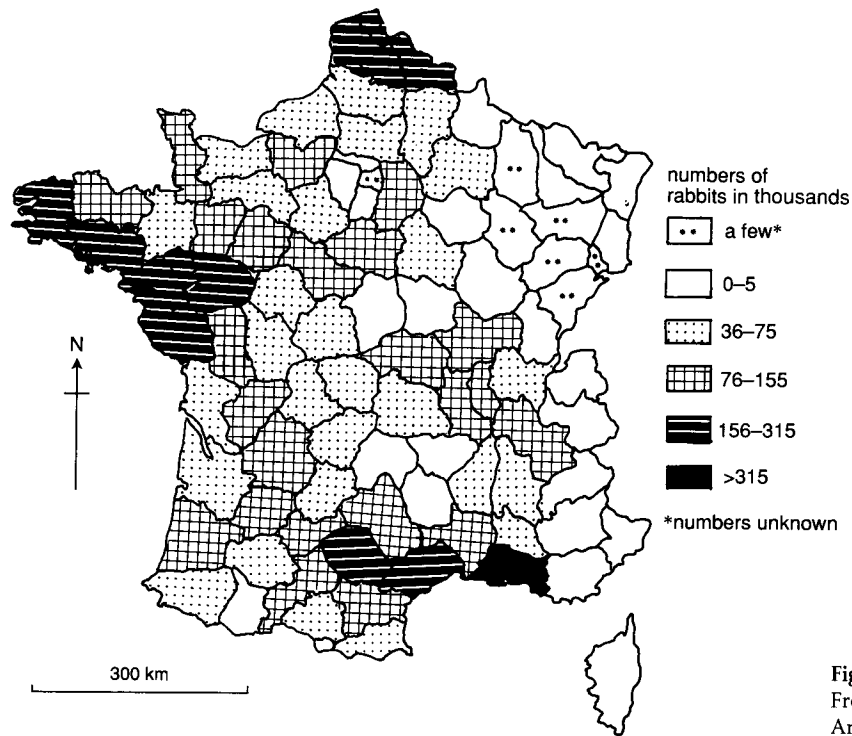
numbers of
rabbits in thousands

☐ •• ☐ a few*

☐ 0–5

▦ 36–75

▦ 76–155

▬ 156–315

■ >315

*numbers unknown

300 km

Fig. 3.5 Numbers of rabbits shot in French départements in 1983 (after Arthur and Guenezan 1986).

Table 3.3 Density and size of rabbit warrens in various French landscapes

Region	Landscape	Area sampled (ha)	Warrens per ha	Entrances per warren	Reference
Camargue	woodland	60	2.6	8.6	Pages (1980)
Camargue	salt-marsh	450	1.4	2.8	Rogers (1979)
Midi	vines	40	1.5*	3.0	Pages (1980)
Midi	garrigue†	25	0.2	1.3	Pages (1980)
Brittany	heath	400	2.0	1.0	Chapuis (1979)
Sologne	wood/cultivated	283	0.7**	3.0	Servan (1972)
Ile-de-France	cultivated	200	0.4**	2.2	Panaget (1983)
	wood/cultivated	85	1.3**	2.1	Arthur and Guenezan (unpublished)
	parkland	250	2.5	24.0	Arthur and Guenezan (unpublished)
Vaucluse	fallow/woodland	38	2.6	15.0	Arthur and Guenezan (unpublished)

† Shrub-covered calcarious land.
* Warrens mostly in the brush beneath the vines.
** Warrens mostly in woods and hedges.

much woodland and, in the north-east of France, harsh winters. In contrast, they have high population densities in Brittany, Vendée, along the Rhône valley, and the Mediterranean coast, where there are smaller fields, more uncultivated land (heathland, garrigue—shrub-covered calcarious land) and many hedgerows. Rabbits are also abundant in Nord-Pas-de-Calais, Sologne, and around the cities of Paris and Lyon, where they are encouraged by many private hunts. The pattern of distribution has remained fairly consistent over the years, although abundance has varied.

As might be expected, landscape also determines the distribution and size of warrens. In most of France the density of warrens is less than 1.5 per hectare, each with a maximum of 3 entrances, but may reach 2.5 or more warrens per hectare, some with over 20 entrances (Table 3.3).

Since the introduction of myxomatosis in France four national surveys have been made to monitor rabbit abundance (Giban 1956; ONC 1976; Arthur et al. 1980; Arthur and Guenezan 1986). Although the survey methods used differed (survey of some private hunts from 1920 to 1956, survey of game-keepers in 1977, sample survey of hunters in 1974 and 1983), the general trend is clear enough.

After the population crash in 1952, hunters' bags remained small until 1956; then they slowly increased, more rapidly after 1970. In 1977, more than 15 million rabbits (about a quarter of the pre-myxomatosis figure) were shot. Thereafter data are limited, but only 6.5 million were shot in 1983—a real reduction in total population since 1977 of around 55 per cent. But counting only the area of grassland, cultivated land, hedgerow and woodland edge, the number shot per 100 hectares per year was 36.4 in 1974 and 37.6 in 1977, dropping to 24.4 in 1983; a real reduction of about 35 per cent. However, the pattern of decline varied in different regions of the country (see below).

Variations in abundance of rabbits have been observed since at least 1880, long before the advent of myxomatosis (Middleton 1934; Giban 1956; Tapper 1985). The explanations offered then were usually coccidiosis or climate; also, natural cycles may be inherent in the population dynamics of rabbits. Part of the reason for the rise and fall in the 1970s and 1980s might be that the years 1970–8 were, in France at least, climatically favourable for the
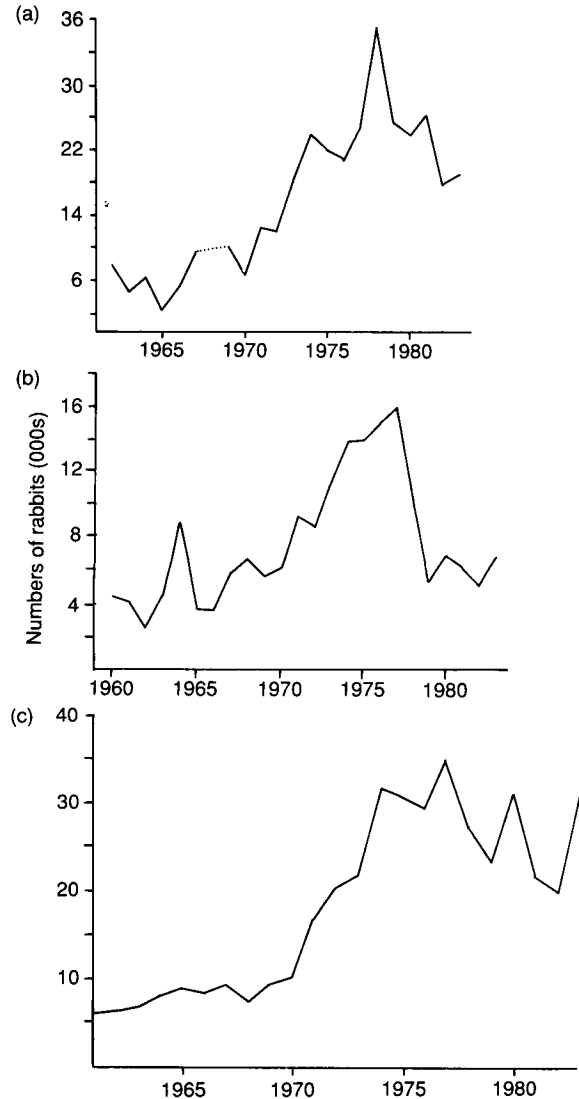

Fig. 3.6 Changes in numbers of rabbits shot in (a) Austria, (b) Germany, and (c) England from 1961 to 1984 (after Tapper 1985 and data from the agricultural ministries of Austria and Germany).

rabbit—high temperatures with low precipitation—while the period 1978–83 often saw high spring rainfalls, which tend to drown nestlings in their burrows (Birkan and Pepin 1984). However, since 1970 it seems more likely that myxomatosis has caused periodic changes in the equilibrium between the virulence of the virus and the resistance of the rabbit (Ross 1982).
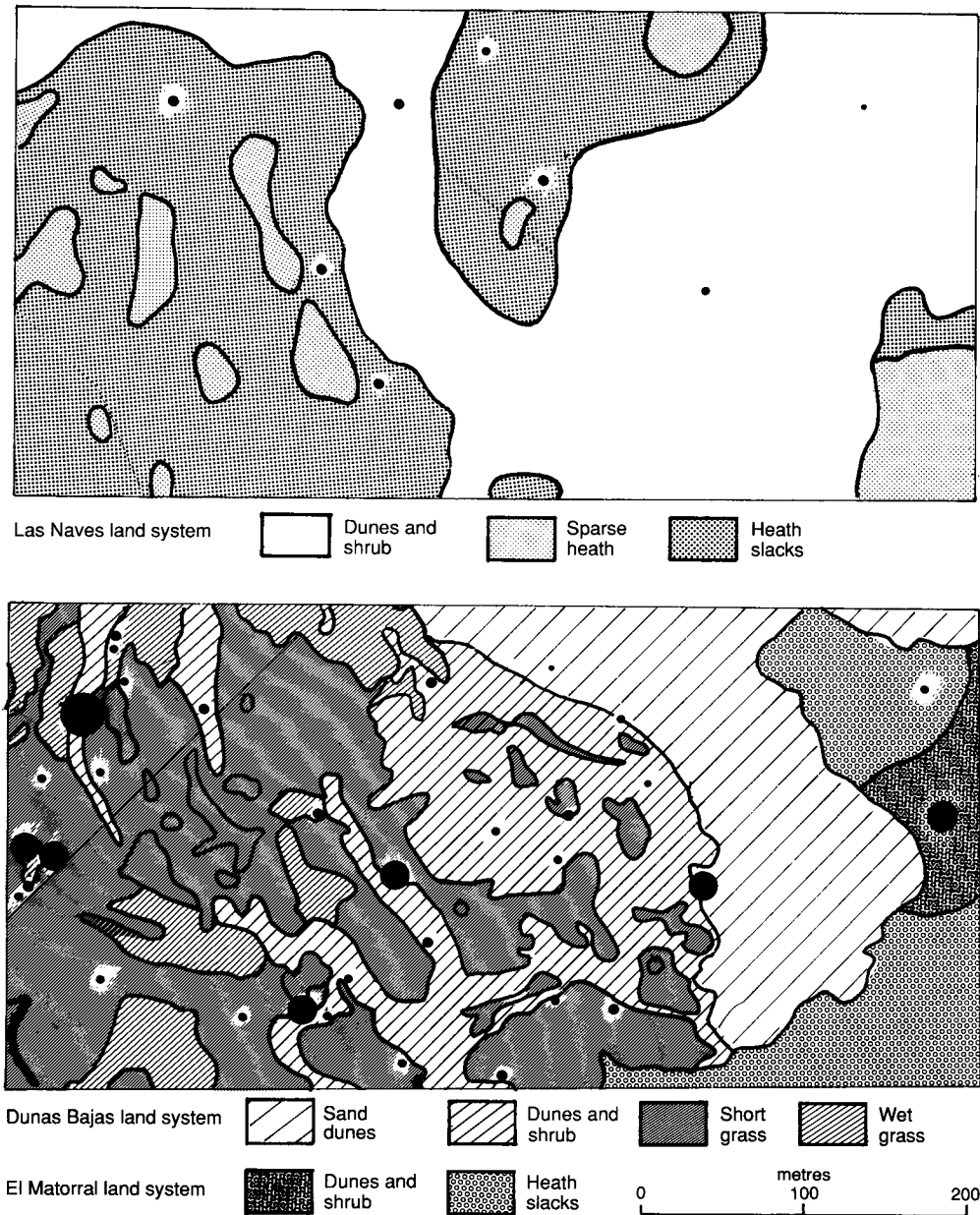
Las Naves land system □ Dunes and shrub ▨ Sparse heath ▨ Heath slacks

Dunas Bajas land system ▨ Sand dunes ▨ Dunes and shrub ▨ Short grass ▨ Wet grass

El Matorral land system ▨ Dunes and shrub ▨ Heath slacks

metres
0   100   200

Fig. 3.7 Distribution of warrens (size of dot is proportional to number of active entrances). Favourable (bottom) and unfavourable sites (top) are in Doñana National Park, southern Spain (after Soriguer and Rogers 1981).

The variation in bag size in other European countries (West Germany, Austria, Britain) mirrors this picture; they also report an increase from 1970, peaking towards 1977 or 1978, then a decrease until 1983, varying somewhat from one country to another (Fig. 3.6).

If the numbers shot per unit area decrease more than the total for the area in question, it implies that there has been a real decrease in abundance associated with a decrease in habitat. Habitat loss has been significant in some areas of France; for example, between 1974 and 1983 many hedges in Brittany were destroyed, while in Normandy grassland increased; in Nord-Pas-de-Calais and Alsace, field size and monoculture of maize or beetroot increased, combined with the destruction of hedges; woodland increased in the Massif Central, Burgundy and Franche-Comté, and so did urbanization in Ile-de-France. In the south-west and north-east there was an increase in garrigue, decrease in the area of vineyards and orchards, and increase in built-up areas which must have decreased the availability of favourable habitat. Those changes were all generally unfavourable to rabbits, and were reflected in bag records.

In northern France and in the Massif Central both bag size and the numbers shot per unit area decreased by 60 per cent from 1974–83. In contrast, in the south-west and north-east the total bag decreased by 42 per cent from 1974–83 but the number shot per 100 ha decreased by only 33 per cent. Our conclusion is that there has been a general decline in the northern populations, less marked in unhunted reserves; the southern populations, though fluctuating annually, have been maintained over a decade.

Data from Spain are less detailed—no comparable surveys have been made. It is clear, however, that rabbits have long since been widespread over almost the whole peninsula. In 1956–8 their range covered all of Spain except the north coastal provinces (Muñoz-Goyanes 1960). We have no data from Portugal for those years. A 1988 survey showed much the same picture, showing in addition that rabbits were distributed throughout Portugal. Limited data from hunters in Cordoba Province indicate a marked increase in abundance from the early 1960s to the early 1980s, rising to a plateau towards the end of the decade. More recently numbers declined markedly, a consequence of the combined effects of myxomatosis and viral haemorrhagic disease (see Sections 3.6 and 3.7 below).

On a smaller scale, the local distribution of rabbits in relation to landscape demonstrates their terrain requirements. Detailed surveys in southern Spain, in areas both favourable and unfavourable for rabbits, showed that they thrive best where sand ridges suitable for warren building interdigitate with or abut moist feeding grounds (Rogers and Myers 1979; Fig. 3.7). Similarly in the Camargue, southern France, warrens are associated with levées and other high ground adjacent to lower, moister areas producing vegetation suitable for feeding. Such a juxtaposition favours a high local population density of rabbits (Rogers 1981).

3.3　Status as a game species and as a pest

Between 6 and 13 million rabbits are shot each year in France by almost two million licensed hunters, and an unknown though probably similar number in Spain by 1.5 million licensed hunters. In stark contrast to Australia and New Zealand, the status of rabbits in much of Europe is that of game rather than vermin. In Spain the rabbit is the most important game species; in France it constitutes 40 per cent of the total bag of small plains species, coming second only to thrushes and blackbirds.

The hunting season in Spain is generally from October to mid-January, varying a little between provinces. Recent legal changes will reduce this period to October and November only. If rabbit numbers are particularly high, however, they may be taken from the first week of July. The season in France also varies, from 15 September to 5 January or from 8 October to 15 January, except in those départements in which the rabbit has been declared a pest, in which case the closing date is either 28 February or 31 March. The taking of rabbits out of season is allowed only when there has been damage to orchards, vineyards, or other crops. Similarly, rabbits, but only bucks, may be taken out of season in Germany.

In France, rabbits are usually hunted with small dogs of the Fauve de Bretagne, beagle, or teckel breeds, or with ferrets. Gas or other poisons, however, are prohibited even where the rabbit has been declared a pest. In Spain, traps and snares are allowed in addition to shooting, but under official control in order to avoid killing predators. Traps are also allowed where rabbits are raised and released for hunting stock. The use of ferrets will be illegal in Andalucía after the 1992 season.

Hunters in France go to considerable effort and expense to ensure that there are adequate numbers of rabbits for shooting. Surveys by the Office National de la Chasse (ONC) show that up to half-a-million rabbits are released each year for hunting, at a cost of 30 to 45 million francs. More than half are captive-bred, of which 40 per cent are sold as pure wild-type and 10 per cent as wild-domestic crosses. In addition, many hunting groups have, in the last decade or so, built artificial warrens with tree stumps, stones, and branches, or have raised areas of earth or sand in which rabbits may build their own warrens protected from predators or flooding.

In Spain the rabbit has never been considered a pest in the way it is in France where, in spite of its status as game, it is still the greatest pest after wild boar. By 1952 damage to agriculture and sylviculture in France had reached the estimated 1000 million francs (1992 values, Siriez 1957), although the level has much reduced since, and 88 of France's 90 départements had declared the rabbit a pest. Only two years later, in 1954, rabbits had been so much reduced by myxomatosis that only 54 considered it a pest throughout the département, and 21 in certain parts of the département: 15 départements considered the rabbit only as game. By 1985 only 45 considered the rabbit a pest throughout the département (Fig. 3.8).

Where the rabbit has been declared a pest translocation of wild rabbits, or raising wild-type rabbits or wild-domestic crosses for restocking, is forbidden. Even so, wild rabbits were restocked in over 70 départements (illegally in 25 of them) and raised for restocking, either as pure wild-types or as crosses, in about 50 départements (again illegally in 5 of them). The law allows rabbits to be raised in départements where they are a pest as long as they are not released in those départements, a condition which is not always fulfilled.
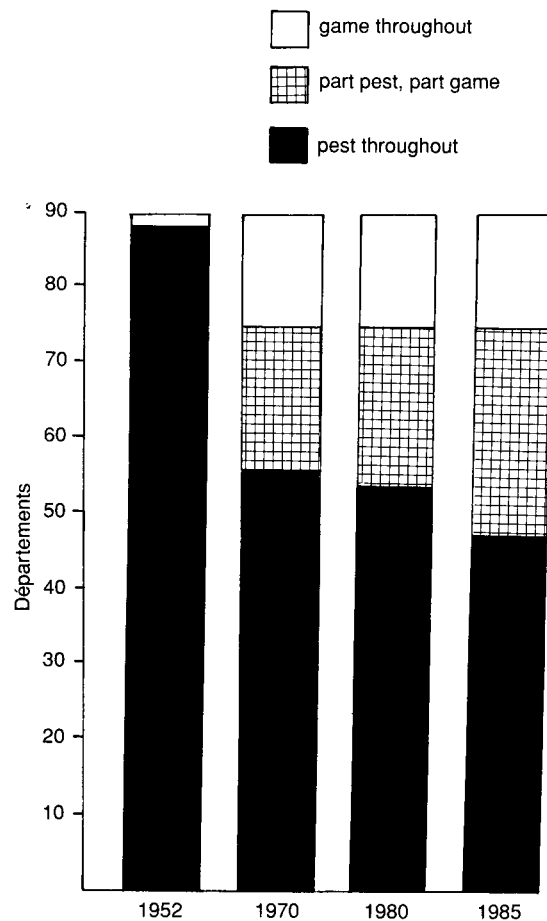

Fig. 3.8 Number of French départements in which the rabbit was declared a pest, 1952–85 (Arthur unpublished).

A 1977 survey by the ONC showed that in those départements having rabbits, they were present, on average, in two out of three communes (the smallest administrative sub-division within a département). Of those with rabbits, only a quarter suffered any damage, mainly in the west of the country, mostly minor, seriously affecting only 7 per cent of cereal crops, and 2 per cent of woodland. Of those communes suffering damage to arable crops, 35 per cent take some form of protective measure, usually repellents; 77 per cent of communes protect plantations, usually with wire netting. The total cost of the damage in 1977 was 30 million francs (1992 values).

To some degree the potential conflict between

farmers and hunters in France (and many farmers are also hunters) is reduced by payment of compensation through insurance policies taken out by the hunting groups. In 1977, 5 per cent of hunting groups made such payments, usually after amicable negotiation between hunter and farmer. Nevertheless each year some cases go before a tribunal which, after expert opinion, defines the extent of damage and rules on the fault of management by the hunters. In 1985 there were 50 such cases, claiming damages totalling 2 to 3 million francs; but in half the cases no payment was awarded, because it was judged that there had been no error of management or unusual damage. It is important to note here that in France it is generally expected that wildlife will feed on agricultural crops to some degree; only when the damage is excessive are there grounds for complaint.

Whatever the cries of despair from farmers, particularly in the north of France, the rabbit is considered the primary game species by hunters of both north and south. The dramatic reduction in populations caused by myxomatosis led to increased hunting pressure on other game, for example hares, partridges, and pheasants, which do not have the ecological plasticity of the rabbit. Their populations too declined rapidly. To compensate, hunters in France, and likewise in Spain, made numerous releases of alternative game species each year; they also attempted to introduce new species, for example *Sylvilagus floridanus* and bobwhite quail, but without success.

Elsewhere in Europe (for example Belgium, Germany, Italy, Spain) hunters reacted similarly to myxomatosis. At least three applications to make legal introductions of *Sylvilagus* in Spain have been denied; the Spanish Ministry of Fisheries and Food (MAPA) prohibited introduction of *Sylvilagus* in 1982. European rabbit populations certainly do recover from epizootics, and with increasing success as time goes on, but in Mediterranean France and Spain the lack of native rabbits has been lamented as much by the hunters (who were sometimes the same farmers who complained of damage!) as by conservationists, albeit for different reasons.

3.4 Rabbit–plant ecology

The diets of rabbits in various parts of Europe have been studied by microscopic analysis of stomach contents or faecal pellets, by chemical analysis both of food eaten and of plants available, by selective exclosures, and by direct observation. The results show considerable differences between sites and, perhaps more significantly, between seasons. There is, nevertheless, a clear general trend showing that rabbits eat mostly grasses and forbs when available, preferring the former, although not always (Table 3.4).

In the Camargue, a deltaic, saline habitat, the diet of rabbits is unlike that documented at other sites studied, except Czechoslovakia and parts of Brittany, in that dicots are the most important items, particularly in summer. Of grasses, only *Bromus* is frequently eaten. The choice of food is also restricted—eight species of plants may account for 86 per cent of the diet throughout the year (Rogers 1979). The staples of winter are *Atriplex, Halimione,* and *Arthrocnemum* spp. In spring the diet is more diverse, reflecting a greater choice available; the winter items are supplemented by *Trifolium, Medicago,* and *Melilotus* spp., which may account for 40 per cent of the diet. *Bromus* is eaten most often towards the end of spring, and *Agropyron pungens* mainly in summer. Rabbits often cut long stems and other parts of plants, apparently without any intention of eating them (Arthur and Rogers, unpublished observations), although Soriguer has observed them doing it to reach flowers and fruits.

In Doñana National Park in Spain, rabbit population densities are highest in the ecotone between shrubland and marshland. There they eat mostly grasses (67 per cent) and forbs (30 per cent) (Soriguer 1988). Other herbivores (red and fallow deer, wild boar, horses, and cattle) are also present in high densities, and with rabbits consume over 70 per cent of the available plant biomass. If they are excluded from the rabbits' feeding places, then the rabbits' diet changes to forbs. It appears that rabbits in Doñana really eat only what is left by the other herbivores, which is mainly grass (Soriguer 1988). In sand-dune systems, where a herbaceous layer is rare, rabbits eat the stems, leaves and fruits of shrubs (Soriguer 1981b; Soriguer and Herrera 1984).

Table 3.4 Analysis of faecal pellets and stomach contents of rabbits in Europe

Country	Sample size[a]	Type[b]	Number of species	Graminae per cent	Dicots per cent	Shrubs per cent	Reference
Holland	–	F	18 (11)	58.0	23.5	18.6	Wallage-Drees (1989)
Czechoslovakia	20	F	43	43.9	41.3	14.8	Homolska (1985)
England	20	F	20 (4)	80.7	19.3	0	Bhadresa (1977)
UK	–	F	20 (<14)	80.0	<15.0	0	Williams *et al.* (1974)
N France I	20	F	–	15.8	74.7	8.1	Chapuis (1979)
N France II	20	F	–	86.2	3.9	6.5	Chapuis (1979)
S France	80	S	33 (9)	15.7	42.8	41.5	Rogers (1979)
S Spain	130	F	14 (5)	66.7	29.6	1.4	Soriguer (1988)

[a] Number of pellets or stomachs.
[b] F = faecal pellet analysis, S = stomach contents analysis.

Rabbits living in scrubland with few forbs and grasses turn to eating woody plants (Table 3.5), selecting different parts of each, often the upper few millimetres. For example, rabbits eat the soft fleshy new stems of *Stauracanthus genistoides*, and 'prune' *Halimium halimifolium* and *Juniperus phoenicea* when eating their seed and fruits. Similar behaviour can be observed in rabbits feeding on *Corema album*, and (in Brittany) on gorse (*Ulex* spp.).

In northern France, variation in diet reflects different landscapes and climates. Those rabbits living on the edge of substantial forests in the Ile-de-France (the region around Paris) eat mainly grasses (including cultivated varieties, for example maize, wheat) from spring to late summer, turning to bramble (*Rubus* spp.) and the bark of trees in winter. There is a greater variety of food plants available in spring, as in southern Europe (Chapuis 1979). In contrast, rabbits living in small wooded plots or hedgerows in cultivated landscapes eat grasses all year round. Again, the cultivated grasses predominate when available: rye, wheat, maize, and particularly barley. As the cereals mature wild grasses replace them in the diet, which are in turn replaced by dicots (bramble, ivy, rape) when grasses are unavailable (Chapuis 1979; Panaget 1983). In the more heathland landscapes of Brittany, rabbits also eat grasses (*Holcus, Festuca*, and *Agrostis* spp.) when available, but turn to gorse (*Ulex europaeus*) and heathers (*Calluna vulgaris* and *Erica* spp.) in winter, and their young buds in spring. Gorse may account for 50 per

cent of the diet of some rabbits at times; bryophytes are also taken (Chapuis 1979).

The quality of food varies considerably over the year, which has important implications for breeding (see below). Different parts of plants also vary in food value, and rabbits are capable of detecting those differences and selecting the best parts. For example, the ratio of protein to fibre is two or three times higher in the diet than in the standing vegetation (Fig. 3.9; Rogers 1979). Seasonal changes in diet accompany, as might be expected, changes in the nutritive value of plants, and of particular parts of plants. Stomach analysis shows the food of Camargue rabbits in spring to be high in protein (19 to 20 per cent) and low in fibre (*c.* 25 per cent). At the end of spring (in May or June, according to the year) the proportion of protein drops quickly to 12–13 per cent, and fibre rises to over 30 per cent, reflecting a change in the quality of food available. It obliges the rabbits to eat more, and coincides with a reduction in the physical condition of adults (Fig. 3.10; Rogers 1979; Vandewalle 1986).

The choice of plants eaten in the Camargue also depends largely on the balance between salt and water in the available standing crops. For example, the reason that rabbits eat apparently unappetizing grasses in summer (dry *Bromus, Agropyron*) may be that *Atriplex* and *Halimione* contain too much salt (Rogers 1979).

The effect of rabbits on vegetation is, at a gross level, predictable—a reduced standing crop. The

Table 3.5 Impact (consumption + pruning etc) of rabbits on woody vegetation in Doñana National Park, southern Spain

Location	Date	Plant density stem ha⁻¹	Plant volume m³ ha⁻¹	Impact			Species	%
				Total[a]	'old[b]	new[c]		
Porquera-Fraile	Oct 1982	11665	8729	25.0	0.0	0.1	*Halimium halimifolium*	0.1
Sabinar-Ojillo	Oct 1992	22835	8539	81.0	3.5	0.4	*Stauracanthus genistoides*	12.5
							Juniperus phoenicea	4.5
Rancho Manuela	Oct 1982	33200	16885	55.5	0.5	0.4	*S. genistoides*	17.5
							G. triacanthos	17.5
							Cistus salvifolius	0.9
							Rosmarinus officinalis	0.4
							H. halimifolium	0.2
							Phillyrea angustifolia	0.4
Sabinar-Cota-32	Jan 1983	46098	11147	41.5	1.7	1.3	*Lavandula stoechas*	17.5
							C. salvifolius	7.6
							H. commutatum	3.5
							C. libanotis	2.4
							J. phoenicea	1.9
							R. officinalis	0.8
Dunas-Cota-32	Jan 1983	4933	2870	19.3	2.4	3.4	*Scrophularia frutescens*	17.5

[a] Total impact of rabbit + others on all parts of plants.
[b] Impact of rabbits on old parts of the plant.
[c] Impact of rabbits on new growth (<1 year old).
Source: Soriguer (1981b).

various exclosure experiments that confirmed this expectation, for example by Bassett 1978; Bassett and Rogers 1979; Soriguer 1981b, 1983a, 1988, must have seemed redundant to many farmers! In early summer in 1976 and 1977 in Doñana National Park rabbits accounted for only 15 to 26 per cent of the total forage offtake (70 per cent) by large herbivores (Soriguer 1983a; Soriguer and Herrera 1984), and slightly more in June 1983. In low Mediterranean mountain areas (western Sierra Morena) rabbits consumed 33 per cent of the standing crop (Soriguer 1981a). In Mediterranean France (Camargue) comparable figures vary from 1 to 27 per cent (Bassett and Rogers 1979). Of four significant herbivores on one Camargue study area, rabbits were second only to horses as consumers of primary production (Table 3.6), ahead of both coypu and grasshoppers (Duncan 1992).

Herbivores may also cause changes in floristic composition. Results from exclosure experiments to determine how much rabbits do so have not been clear cut, largely because it is difficult to assess the effect of herbivore activity on natural succession. In the Camargue the most common winter foods of rabbits (*Halimione, Torilis, Limonium*) increased when rabbits were excluded, but few other changes could be attributed directly to the effects of grazing. Much the same conclusion applies in southern Spain (Soriguer unpublished data).

An important consequence of the feeding behaviour of rabbits, particularly their tendency to select certain parts of plants including whole fruits and seeds, is that they play an important role in seed dispersal. This aspect of the relationship between rabbits and vegetation has been poorly documented (see Staniforth and Cavers 1977), but in Table 3.7 we
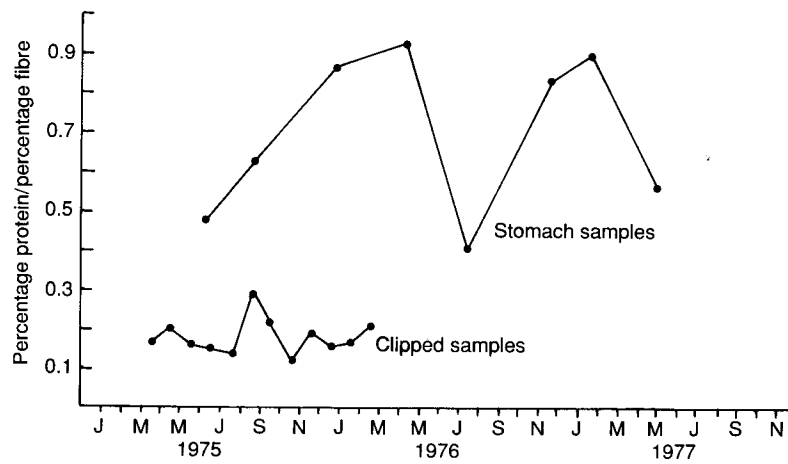
Fig. 3.9 Relationship between season and crude protein/crude fibre ratios in standing vegetation and rabbits' stomach contents (Rogers 1979).
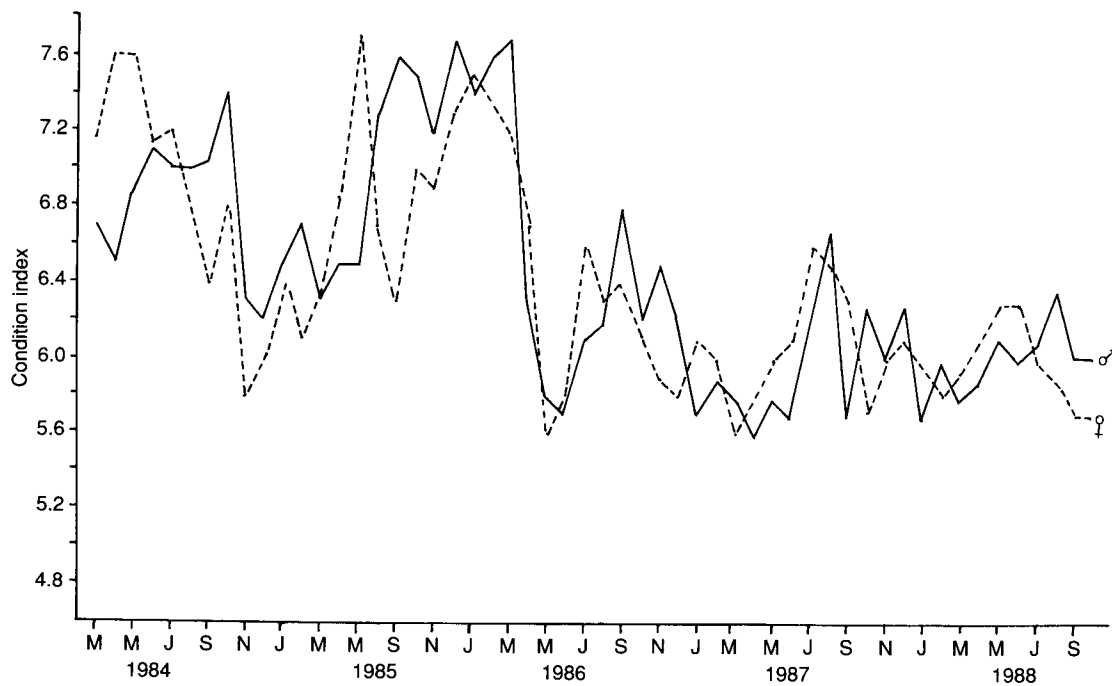

Fig. 3.10 Changes from 1984 to 1988 in indices of physical condition (Bailey 1968) of adult rabbits (>9 months) in the Camargue (Vandewalle unpublished).

Table 3.6 Estimated offtake of herbaceous plants by the main herbivores on a 335 ha Camargue study area (S. France)

Species	Year	Number	Dry matter offtake (t. day^{-1})
Coypu	1977–78	50	0.017
Grasshoppers	1977	–	0.020
Horses	1976	26	0.356
	1977	35	0.466
Rabbits	1976	838	0.087
	1977	670	0.067
	1983	3450	0.352

Data from various sources in Duncan (1992).

Table 3.7 Reproductive parts of plants found in faecal pellets of rabbits in Spain, illustrating their role in seed dispersal

Species	Part of plant
Coremá album	complete fruit
Cistus salvifolius	capsules with seeds
Halimium halimifolium	—ditto—
Lavandula stoechas	flowers and seed
Armeria gaditana	flowers and fruits
Asphodelus aestivus	—ditto—
Juniperus phoenicea	buds, fruit and seed
Rosmarinus officinalis	old flowers and seed
Olea europea	whole ripe fruit
Pistacia lentiscus	ripe fruit
P. terebinthus	—ditto—
Retama sphaerocarpa	seed
Juncus bufonius	—ditto—
Trifolium spp.	—ditto—
Asparagus aphyllus	fruit and seed
Phillyrea augustifolia	—ditto—

Source: Soriguer (1981b).

list the seeds of 16 species found in the faecal pellets of rabbits in Spain. All were checked and found to germinate normally.

3.5 Population ecology

The population ecology of the rabbit is not very well-known in many countries of Europe. We have used European data when they are available, but have otherwise largely relied on data from Spain and France. Those from Spain are from Andalucía, the main study areas being of evergreen-oak forest (highland) and olive forest and scrub (lowland). Much of the French data comes from three areas where many studies have been done: in the north, Ile-de-France, the area around Paris, the landscape is predominantly agricultural, but with extensive woodland, and the climate temperate; in the south the Vaucluse is an upland area with a Mediterranean climate; and southernmost is the Camargue, a flat, saline, deltaic area on the Mediterranean coast.

3.5.1 Reproduction

Just as there is a latitudinal gradient in rabbit weights, so there are clear trends in the length and timing of the reproductive season (Table 3.8). The

larger rabbits of northern France and Sweden start breeding later and continue longer (180 days or more) than the smaller rabbits of the south of France (96 days); in Mediterranean areas the season starts earlier still, but its end is very variable.

Seasonal patterns of reproduction in males are clear throughout Europe, with latitudinal trends. Indices of testicular activity, for example size and position of testes, tend to start rising slightly earlier in the south of Spain (Fig. 3.11) than in the south of France (Fig. 3.12), with variations from year to year, but clearer is a tendency to later decline in testicular indices in the north of France than in the south (April–May) (Fig. 3.13).

Male rabbits can reach sexual maturity at 6 months of age in France, although 8–9 months is the average (Rogers 1979; Arthur 1980); in Sierra Morena (southern Spain), Soriguer (1981a) reports 4–5 months.

In the north, gravid females may be found from early March to mid-August or even mid-September;

Table 3.8 Reproductive season of rabbits for various places in Europe

Locality		First pregnancies		Last pregnancies		Length of season (days)
		Month	Week	Month	Week	
Spain	SW	November	1	May	3	210
"	S1 (dry)	January	1	March	1	90
"	S2 (irrigated)	October	2	June	2	210
Portugal S		September	3	April	4	240
Spain N		December	2	August	1	270
France S	(Camargue)	January	2	May	1	96
"	C (Vaucluse)	January	2	June	1	142
"	N (Paris)	February	1	July	3	192
Holland		March	2	July	3	150
Sweden		March	3	August	2	180

Source: Andersson *et al.* (1979); Arthur (1980); Arthur and Gaudin (unpublished); Lopez Ribeiro (1981); Soriguer (1981*a*); Vandewalle (1989); Wallage-Drees (1983).
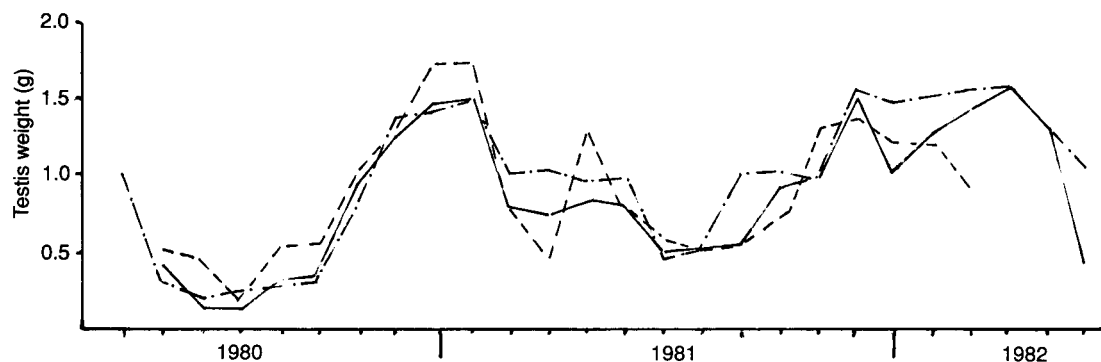
Fig. 3.11 Changes in testis weights of rabbits from 3 plots in southern Spain from 1980 to 1982 (Soriguer unpublished). (– – – –) Plot 1, irrigated throughout all years. (· — · – · –) Plot 2, seasonal rainfall only in 1980, irrigated throughout thereafter. (———) Plot 3, no irrigation, seasonal rain only.

in the south of France, from early January to the end of May; and in southern Spain from December or earlier, to March assuming a dry spring, sometimes later, except on irrigated plots or in exceptional years. The proportion of females that are gravid tends to rise throughout the season, as do other indices of fertility in females (ovary weight, numbers of corpora lutea, *in utero* litter size); 95 per cent of

births in the Camargue were recorded between the 6th and 22nd week of the year (Table 3.9; Rogers 1979; Vandewalle in preparation).

In southern Spain most females become gravid at 3–4 months, whereas in the south of France, where adult weights are 10–15 per cent more, the equivalent age is up to 6 months. In all regions, rabbits are just capable of reproducing in the year of their birth,
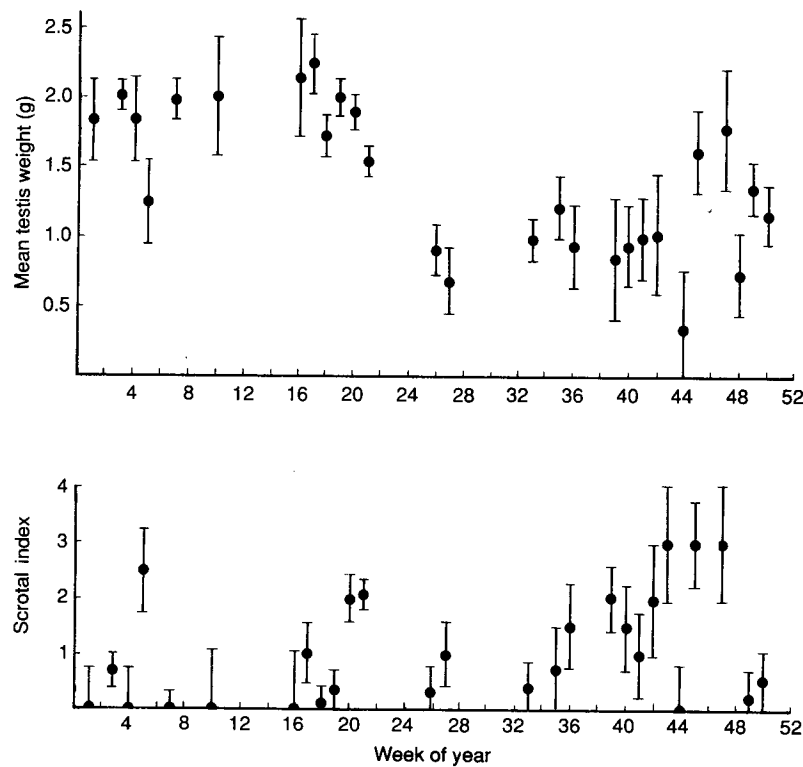
Fig. 3.12 Indices of male fertility in rabbits at La Tour du Valat, southern France, 1975–77 (after Rogers 1979).

though they have more opportunity to do so in the south. However, the contribution made by first-year females to recruitment is questionable, given that they are less fecund than adults, and that they must give birth late in the season when the quality of food is poorer (Rogers 1979).

In general, litter sizes are smaller in the south of Europe than in the north; this may, in turn, be associated with the smaller body size of rabbits in the south (Soriguer 1981a, 1983b). Average litters are around 3 or 4 in the south of Spain. In the south of France, they average about 5 versus 4.5 in the north (Tables 3.10; 3.11), but the season is shorter and the average female produces only 10 to 13 young per year in the south of France versus about 17 in Ile-de-France.

Whilst the reproductive cycles of both males and females appear to be fundamentally linked to photoperiod, geographical patterns of reproduction suggest that changes in temperature and rainfall can modify both the beginning and the end of the reproductive season. For example, at the beginning of the

reproductive season, low temperatures affect both male fertility (Figs. 3.11–3.13) and the weight of the uterus (Fig. 3.14). Conversely, ambient summer temperatures in the Mediterranean are close to the upper limits for spermatogenesis in other lagomorphs (Terroine and Trautmann 1937; Hart et al. 1965). In the Camargue, reproduction may start late if the previous winter was unusually wet and cold (Vandewalle personal communication), and stop early in a dry summer. In Ile-de-France, drought reduces pregnancy and lactation rates, whereas in the south of France, early autumn rain stimulates new vegetative growth and a second reproductive season. The difference in reproductive seasons on irrigated and unirrigated plots near Cadiz (southern Spain), shown in Table 3.8, is consistent with the effect of rainfall elsewhere.

Soriguer and Myers (1986) planned a field experiment to test the effects of climate and food on reproduction in rabbits in southern Spain, their presumed ancestral home. They showed that both male and female reproductive cycles can be pre-
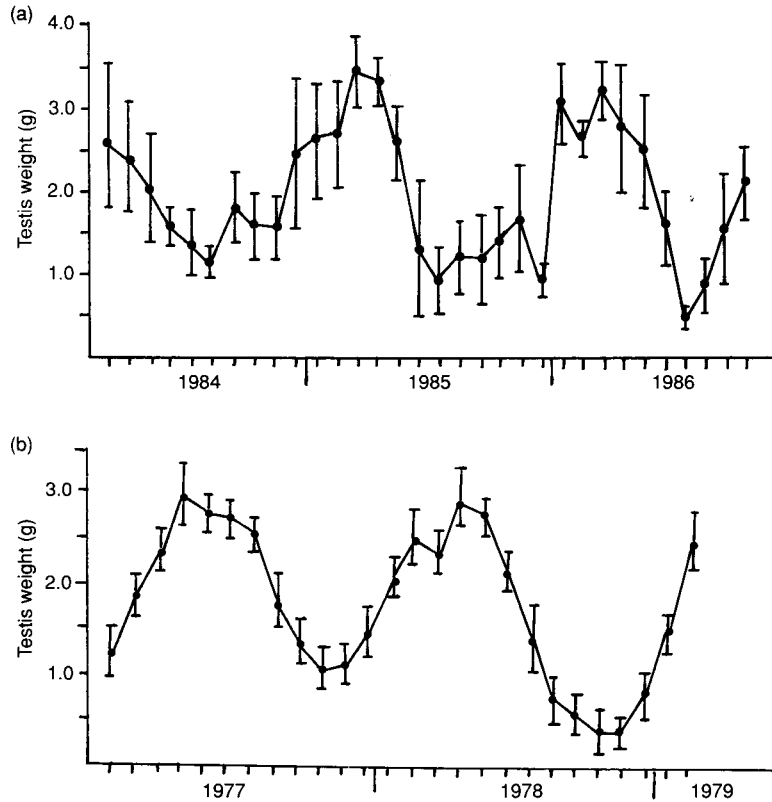
Fig. 3.13 Changes in rabbit testis weights (mean ± standard deviation) in (a) the Camargue and, (b) near Paris (after Arthur 1980 and Vandewalle 1989).

dicted from a combination of climate, food availability, and food quality, although the effect of each may vary between sexes (Table 3.12). Male reproduction is influenced mainly by climatic factors, particularly radiation and temperature, which accounted for 65 to 79 per cent of the variance. Mineral elements in food accounted for only some 5–10 per cent of the variation in males, and the organic components were not relevant. For females, climate was also important, but less so than the quality (organic and inorganic fractions) of food.

In summary, therefore, the rabbit's reproductive activity in Europe is governed by climate within a framework of photoperiod, particularly winter conditions in the north, and summer conditions in the south. Food quantity and quality, also influenced by climate, have a lesser role, albeit an important one, influencing mainly the length of the breeding season. The rabbit's reproductive cycle fits the broad seasonal pattern of the Mediterranean climate. But Mediterranean weather is unpredictable; our experi-

ence is that exceptional years seem to be normal! The rabbit is well placed to take advantage of them as they arise.

3.5.2 Survival and mortality

Survival and mortality again show distinct regional differences. The survival rate of the young rabbits in southern Spain is much lower than in France. Conversely, amongst adults the average survival rates are much higher in Spain. At the three sites within France survival rates are similar (Table 3.13).

In Ile-de-France there are two important periods of adult mortality, May–July (15–20 per cent per month) and September–October (20 per cent). From January to April, adult mortality is almost nil (Fig. 3.15). For all ages combined, monthly mortality in the Ile-de-France samples ranged from a high of 34 per cent from May to July, dropping to an average of 20 per cent until December, and then less than 10 per cent from January to April (Arthur unpublished). In

Table 3.9 Proportion of female rabbits pregnant each month across Europe

Month	Spain				Portugal	France		Holland	Sweden
	SW	S1	S2[a]	N	S	S	N	NW	S
January	0.36	0.60	0.29	0.20	0.11	·0.0	0.0	0.0	0.0
February	0.55	0.33	0.67	0.78	0.22	0.05	0.28	0.0	0.0
March	0.69	0.33	0.22	1.00	0.75	0.65	0.77	0.12	0.20
April	0.65	0.0	0.0	0.86	0.67	0.68	0.57	0.12	0.71
May	0.38	0.0	0.0	0.67	0.0	0.61	0.80	0.36	0.59
June	0.0	0.0	0.10	0.25	0.0	0.21	0.65	0.07	0.68
July	0.0	0.0	0.0	0.67	0.0	0.0	0.65	0.01	0.56
August	0.0	0.0	0.0	0.27	0.0	0.0	0.44	0.0	0.13
September	0.0	0.0	0.0	0.0	0.11	0.0	0.32	0.0	0.0
October	0.0	0.0	0.14	0.0	0.31	0.0	0.07	0.0	0.0
November	0.30	0.0	0.29	0.0	0.20	0.0	0.0	0.0	0.0
December	0.36	0.0	0.05	0.05	0.67	0.0	0.01	0.0	0.0
Mean	0.28	0.10	0.15	0.40	0.25	0.18	0.38	0.06	0.24

[a] Irrigated plot.
Sources:
France S—Camargue: Rogers (1979). Vandewalle (in preparation).
France N—Ile-de-France: Arthur (1980 and unpublished data).
Holland: Wallage-Drees (1983). Data are frequency of births.
Portugal: Lopez Ribeiro (1981).
Spain (north): Ceballos (unpublished).
    (south): Soriguer (1981a, 1983b); Soriguer and Myers (1986).
Sweden: Andersson et al. (1979).

Table 3.10 Some mean annual reproductive parameters of wild rabbits in France and Spain

	Camargue	Vaucluse	Paris region	Andalucía
% pregnant	64 ± 6	58 ± 18	64 ± 9	–
Length of reproductive season (days)	94 ± 30	142 ± 31	174 ± 10	90–150
Date of first conception (week number)	2 (1–7)	2 (1–6)	5 (1–8)	–
No. of pregnancies per female	2.0	2.7	3.4	
No. of embryos per female	4.9 ± 0.4	5.0	4.4–0.3	3.7
No. of live births per female per year	9.8 ± 3.0	13.1 ± 4.2	17.4 ± 2.7	–

Sources: C. P. Arthur (Paris—unpublished); C. P. Arthur and Gaudin (Vaucluse—unpublished); P. M. Rogers (Camargue litters—1979); R. C. Soriguer (Andalucía—unpublished); P. Vandewalle (Camargue other—unpublished).

Table 3.11 Litter sizes of rabbits in Europe and the Mediterranean

Location	Mean litter size	Source
Spain		
NW Andalucía	3.21	Soriguer (1981a)
SW Andalucía	3.88	Delibes and Calderon (1979)
Navarra (N. Spain)	4.11	Ceballos (in prep.)
France		
Camargue	5.20	Rogers (1979)
	4.89	Vandewalle (in press)
Vaucluse	5.00	Arthur and Gaudin (unpublished)
Ile-de-France	4.40	Arthur (unpublished)
Holland	5.00	Wallage-Drees (1989)
Sweden (S)	4.70	Andersson *et al.* (1979)
Great Britain		
Wales	4.36	Stephens (1952)
Caernarvonshire (1941)	4.89	Brambell (1944)
Caernarvonshire (1942)	5.64	Brambell (1944)
Morocco	3.7	Soriguer (unpublished)
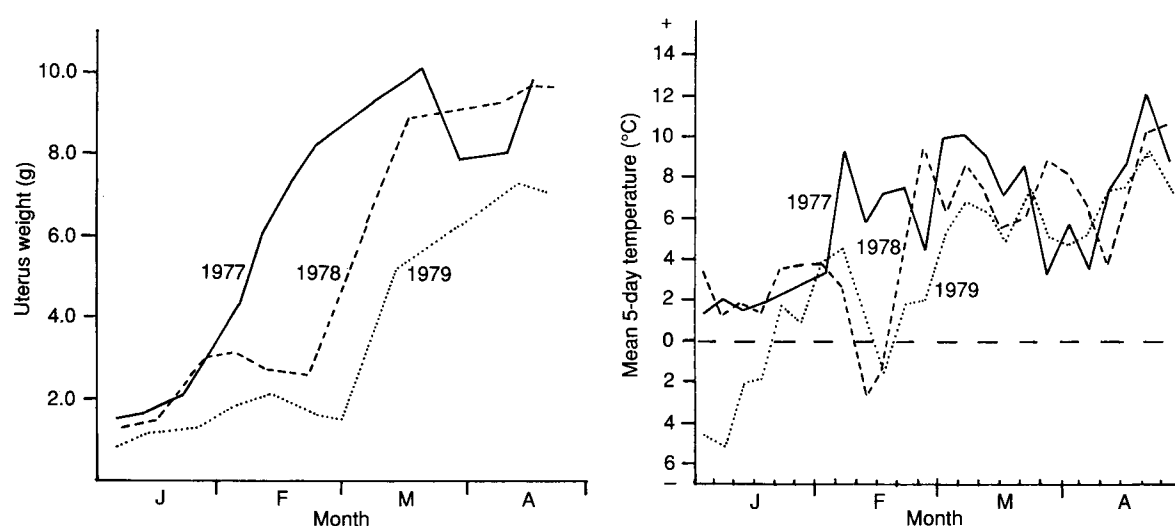
Fig. 3.14 Relationship between uterus weight and ambient temperature in rabbits near Paris, 1977–79. Source: Arthur (unpublished).

Table 3.12 Canonical correlation coefficient (CCR) and probability (in parentheses) for reproductive correlates of rabbits in southern Spain

Canonical variables	CCR—males	CCR—females
A Climate + food availability	0.87 ($<10^{-4}$)	0.84 ($<10^{-4}$)
B Organic fraction	0.65 (0.06)	0.75 (0.03)
C Inorganic fraction	0.71 (0.002)	0.82 (0.001)
A + B + C	0.98 (0.003)	0.99 ($<10^{-4}$)

Source: Soriguer and Myers (1986).

Table 3.13 Survival rates (%) of wild rabbits in France and Spain

Age (months)	Spain	France		
	South	Camargue	Vaucluse	Paris region
0–3[a]	16	32	34	25
4[b]–8	63	58	52	26/49[c]
adult	85	58	42	52/58[c]

[a] 3.7 months for the Spanish data.
[b] 3.8 months for the Spanish data.
[c] 26 and 52 in years with hunting, 49 and 58 in years without hunting.
Source: Arthur (1980), Soriguer (1981, 1983a) and unpublished data from C. P. Arthur, J. C. Gaudin, and P. Vandewalle.

the Camargue, monthly mortality (all ages) also peaks in April and July. During periods of reproduction it reaches 20–30 per cent; in autumn and winter it falls to 5–10 per cent (Rogers 1979). We have few data available on causes of mortality in Europe. Possibilities include hunting, predation, myxomatosis, other diseases, flooding, and injuries, for example from farm machinery.

Survival rates of rabbits over 4-months-old in the three French populations were fairly similar (averaging 42–58 per cent) when they were not hunted—that is, in the Camargue and the Vaucluse all the time, and in the Ile-de-France in some years. But in the years with hunting in Ile-de-France, the mortality of 4–8-month-old rabbits was markedly higher, although the adults were little affected.

Arthur collected dead rabbits whenever he found them throughout a four-year study in Ile-de-France.

Excluding over 1000 rabbits that were shot, for the other 419 rabbits collected, the most frequent causes of death were predators or myxomatosis (Table 3.14), followed by injuries and various diseases (pasteurella, staphylococcus, coccidia, pseudotuberculosis). Agricultural operations (especially mowing and harvesting) were an important hazard for younger rabbits. The importance of predation and myxomatosis was confirmed by radio-tagging rabbits from the same population in non-hunting years (Table 3.15).

In the north, the most important predators of young rabbits are mustelids, and of older rabbits, foxes. However, foxes take many young as well: they may be responsible for 30–50 per cent of nestling mortality in spring (Arthur 1980; Mulder and Wallage-Drees 1979), when young rabbits may comprise 70–80 per cent of the diet of foxes (Fig. 3.16; Julliot
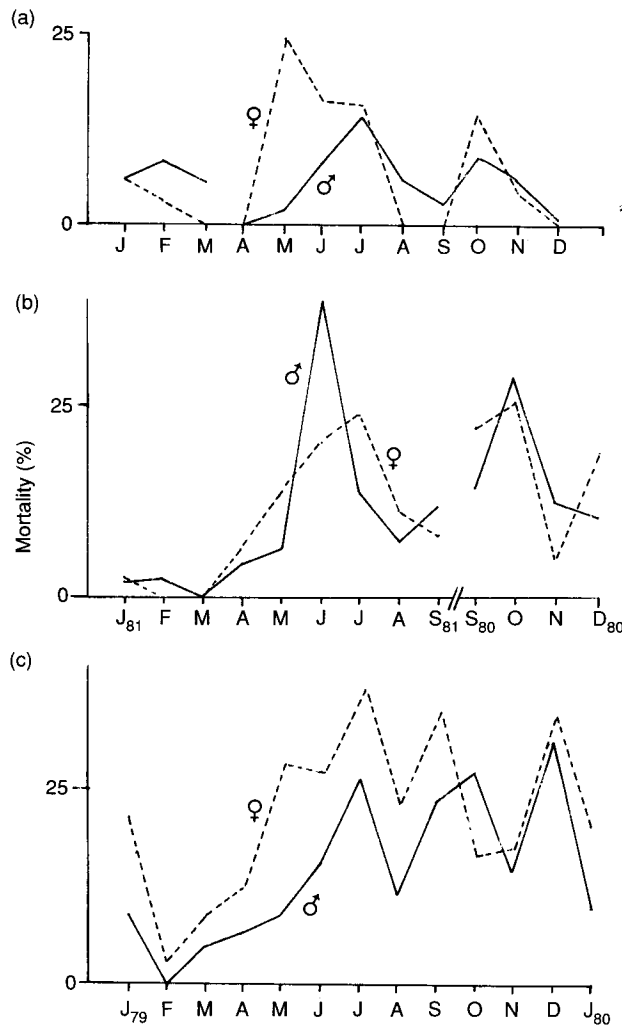
Fig. 3.15 Monthly mortality rates near Paris (a) of rabbits (>4 months) with radio tags, using Trent and Rongstat's (1974) method, 1984–86 years pooled (Arthur unpublished), (b) of marked adult (>9 months) rabbits, 1980–81 (Arthur unpublished), (c) of rabbits known to be alive (all ages >1 month), 1979–80 (Arthur unpublished).

1987). Mortality from myxomatosis may be 10–50 per cent, according to year and season, and evidently influences more immediate causes of death.

In the Camargue, most mortality is due to a combination of predation and myxomatosis (Rogers 1979). Myxomatosis facilitates predation, since the proportion of rabbits in the diet of foxes rises to 70 per cent during myxomatosis epizootics, or during flooding (Reynolds 1979). As rabbits can recover from severe myxomatosis that must affect their susceptibility to predation, the two must to some degree be additive. Over three years myxomatosis was responsible for 13–25 per cent of total mortality

annually (Vandewalle 1986; Arthur 1988), while in the Vaucluse it varied from 10 to 50 per cent over three years (Arthur and Gaudin in press).

In the west Mediterranean in general, and in southern Spain in particular, the number of species of predator is exceptionally high (Table 3.16). Furthermore rabbits are an important item of most predators' diet, especially in southern Spain, where, with the exception of wolf, all predators of medium and large size (3 kg for mammals, 1.5 kg for birds) rely to a large extent on rabbits for food (Delibes and Hiraldo 1981; Jaksić and Soriguer 1981; Soriguer 1981a, 1981b, 1983b; Soriguer and Rogers 1981).

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Table 3.14 Causes of death of rabbits found dead in Ile-de-France, in four body-weight classes

	<300 g		300–1000 g		Immature/ sub-adult		Adult (>9 months)	
	n	%	n	%	n	%	n	%
Predation	33	34.3	19	22.1	31	29.8	55	41.7
Myxomatosis	0	–	26	30.2	48	46.2	38	28.8
Road kill	19	19.8	11	12.8	7	6.7	7	5.3
Injuries/disease	0	–	15	17.4	11	10.6	20	15.1
Agricultural machinery	8	8.33	7	8.1	5	4.8	2	1.5
Unknown	27	28	8	9.3	2	1.9	10	7.6
Total	87		86		104		132	

Source: Arthur (1980).

Table 3.15 Causes of death of radio-tagged rabbits in the Paris region during a three-year study

	Myxomatosis	Other disease	Predation	Road kill	Miscellaneous	Number tagged
Juveniles (<1000 g)	5	5	6	4	3	45
Adults and sub-adults (>1000 g)	12	5	9	2	4	92

Source: C. P. Arthur—unpublished data.
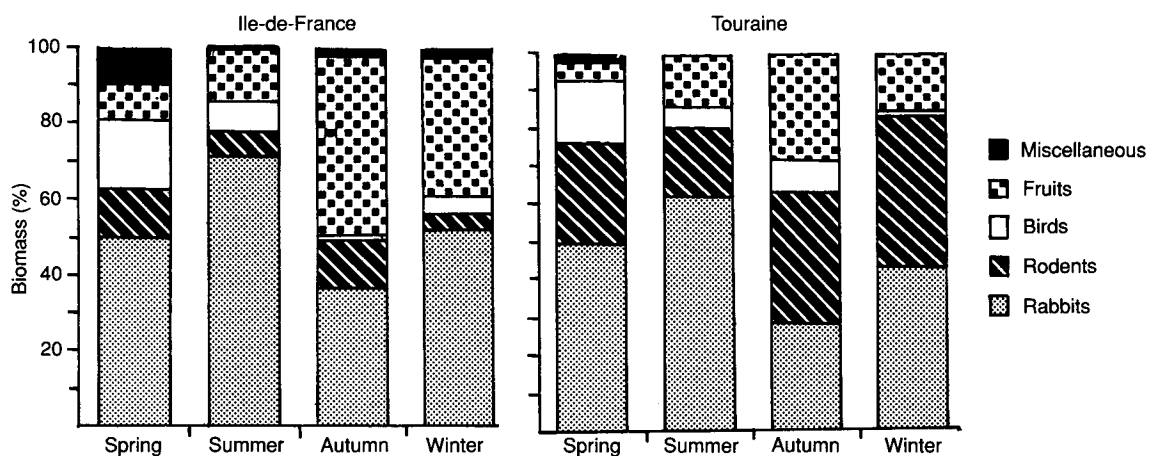
Fig. 3.16 Diets of foxes in two areas of France (Fragner *et al.* 1990). Touraine is 200 km SW of Paris.

Table 3.16 Number of predator species in various parts of the rabbit's range worldwide

Class	Australia	New Zealand	UK	France	Spain
Mammals	3	3	10	10	17
Birds	14	1	7*	13	19
Reptiles	6	0	0	7	4
Totals	23	4	17	30	40

Source: Soriguer (1981*a*), Soriguer and Rogers (1981) except Australia (Myers *et al.*, Chapter 5) and UK (Thompson, Chapter 4).

3.6 Myxomatosis (see also Chapter 7)

3.6.1 Incidence

The rapid spread of myxomatosis throughout Europe, starting from Dr Delille's estate near Paris in June 1952, has been well-documented, but substantial study of the disease in wild rabbits in continental Europe did not begin until 20 or so years later. Up to the 1970s we have data only from domestic rabbits. In France, the number of domestic rabbits with the disease climbed to a peak in 1955, and in 1960 stabilized at around 100 000 cases a year (Fig. 3.17). A clear seasonal pattern became established, in which incidence ranged from a maximum in August–September to virtually zero from December to May–June (winter to early summer), although spring epizootic were not unknown (Fig. 3.18; Joubert *et al.* 1972).

Data on myxomatosis in wild rabbits are now available from different parts of France (Table 3.17), including the Camargue, the Vaucluse, and the Ile-de-France. In the Camargue, epizootics recur regularly every summer, and in the Vaucluse, every autumn. In Ile-de-France, however, myxomatosis may break out at any time. In the Isère, near Lyon, the timing of epizootics is also variable, although it is usually in late spring or early summer (Fig. 3.19; Gilot and Joubert 1980). In the north, epizootics last about 3 months, often longer than in the Camargue and significantly longer than in the Vaucluse (2 months).

In southern Spain, July to September/October used to be the usual period for epizootics, but since 1977 they have been most frequent in winter–spring, lasting 6 months in 1976 and 10 months in 1977,

although some years are without the disease altogether (Soriguer 1980*a*, 1981*a*). More recently the highest mortality has been from July to October (Soriguer 1981*a*; Soriguer and Rogers 1981). The mean interval between successive epizootics is the same (9–10 months) in the three regions for which we have data, but is most variable in the north, where it may be anything from 4 to 24 months.

Estimated mortality, calculated from the ratio of acute to total cases including recoveries, varies from 39 to 61 per cent with little difference between years. The highest mortality is in summer epizootics (43 per cent over 6 months), lower in autumn (13 per cent over 2.3 months), and lowest in winter epizootics (6 per cent in 4.5 months). There is, nevertheless, great variability in mortality rates between areas, and again the most variable region is Ile-de-France. In both the Camargue and the Vaucluse, total losses per epizootic are similar, 32 and 36 per cent respectively. The short autumn epizootics in the Vaucluse seem to be especially intense, affecting some 83 per cent of the juveniles and sub-adults but total losses are few. Many young rabbits there exhibit high levels of resistance to myxoma virus in the laboratory (no deaths out of 11 young rabbits tested in the Vaucluse compared with 5 deaths out of 7 young rabbits tested in Ile-de-France; Arthur, Gaudin and Guénezan, unpublished data).

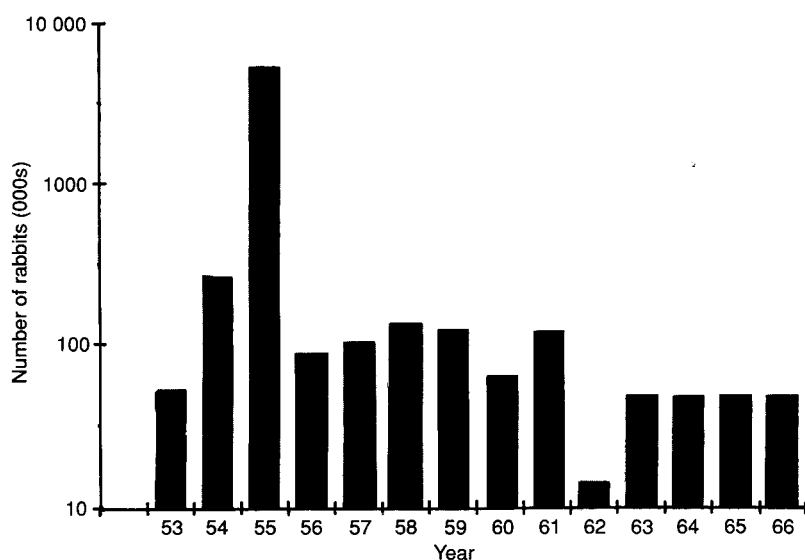The proportion of rabbits affected varies with age–class, region and year (Table 3.18). In southern Spain

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Fig. 3.17 Numbers of domestic rabbits with myxomatosis in France, 1953–56 (after Joubert *et al*. 1972).
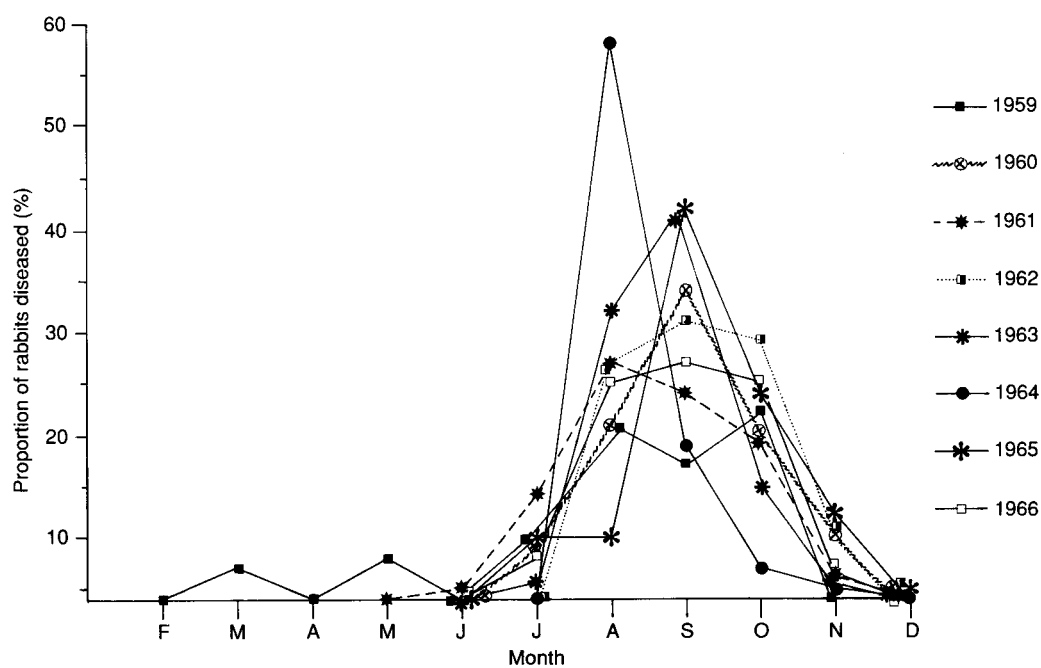

Fig. 3.18 Annual changes in myxomatosis rates in wild and domestic rabbits in France, 1959–66 (after Joubert *et al*. 1972).

Table 3.17 Characteristics of myxomatosis epizootics in three sites in France

	Vaucluse n = 3	Camargue n = 5	Paris region n = 9
1. Duration (months)	2.2 ± 0.6	3 ± 1	3.1 ± 1.9
2. Interval between two epizootics (months)	9.8 ± 0.4	9.7 ± 0.6	9.4 ± 6.5
3. Proportion of animals affected (% cumulative)	83 ± 29[a]	59.9 ± 27[a]	41 ± 31
4. Estimated mortality (%)	39 ± 10	61 ± 10	54 ± 13
5. Population losses (%)	32 ± 8[b]	36 ± 11[b]	22 ± 20
6. No. of epizootics in			
spring	0	0	3
summer	0	5	4
autumn	3	0	
winter	0	0	2

[a] Only juveniles, immatures and sub-adults were affected.
[b] Losses were from the young of the year only.
3. = proportion of infected animals, summed monthly.
4. = proportion of animals with acute and severe clinical sign.
n = number of epizootics observed.
Source: Paris—Arthur (1988); Camargue—Rogers (1979), Vandewalle (1986); Vaucluse—Arthur and Gaudin (in press).

the proportion of juvenile rabbits found with clinical signs is low because, we suspect, they succumb to the disease quickly, often before showing any external sign; the proportion of juveniles with antibodies (13 per cent) is about half of that in adults (Soriguer and Lopez, in press). In the Camargue and the Vaucluse few juveniles are diseased, whereas in Ile-de-France juveniles represent 19 per cent of affected animals. In the north, 33 per cent of adults captured showed clinical symptoms, whereas in the Camargue and the Vaucluse almost no adults are affected.

3.6.2 Epidemiology

Many of the different regional characteristics of the disease reflect variation in transmission routes and in the immunological status of the populations. The relationship between rabbits and myxomatosis has also changed over the years.

In France and Spain, as elsewhere, there are two known vectors, fleas and mosquitoes. Their relative importance and specific roles vary from one region to another. Rabbits in Spain support at least 22 genera of ectoparasites, versus 8 in Australia, all but one of which are also recorded from Spain (Table 3.19).

In the Camargue at least 12 species of mosquito bite rabbits from late March to end-October; they are especially active in May and October, when they may inflict 1200 bites per rabbit per day. Although mosquitoes are relatively uncommon in July–August, when epizootics of myxomatosis are usually at their height, each rabbit is still bitten 60 to 300 times a day during the months that mosquitoes carry the virus. Some 20 to 30 per cent of mosquitoes are carriers, and 50 per cent in *Aedes detritus* and *A. caspius*, the two species most attracted to rabbits (Legrand 1986). The proportion of mosquitoes which are carriers reduces gradually through the season, to nil in October. In contrast, in the Isère some 10 species of mosquito bite rabbits from the beginning of May to the beginning of October, averaging only 40 bites/rabbit/day. In Ile-de-France only 5 species
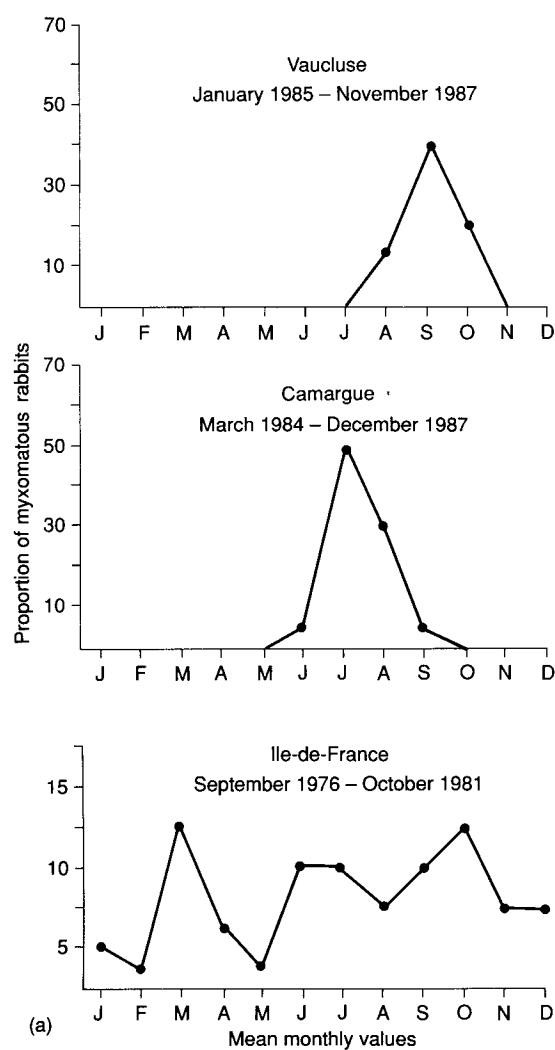
Fig. 3.19 Monthly changes in mean myxomatosis rates in France (a) in wild rabbits in three regions (after Arthur 1988), (b) domestic rabbits in Courtenay, Isère (Gilot and Joubert 1980).
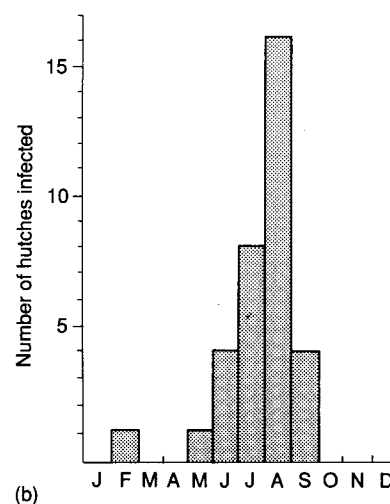
Table 3.18 Percentage of rabbits captured (numbers in parentheses) having clinical sign of myxomatosis during epizootics in France (years pooled) and Spain

	Vaucluse	Camargue	Ile-de-France	Spain	
				1976	1977
Juveniles (<500 g)	1.8 (648)	1.9 (321)	19.1 (833)	0.0 (130)	9.6 (52)
Immatures and sub-adults	47.7 (235)	62.8 (137)	35.4 (768)	8.2 (49)	38.9 (36)
Adults	0.0 (83)	6.0 (73)	32.8 (481)	4.0 (228)	17.6 (131)

Source: Arthur (1988); Soriguer (1980a).

Table 3.19 Genera of ectoparasites found on rabbits in Spain and Australia

Spain	Australia
Amblyoma	*Bdellonypsus*
Boophilus	*Cheyletiella*
Caenopsylla	*Echidnophaga*
Cheyletiella	*Haemadipsus*
Chorioptes	*Haemaphysalis*
Ctenocephalides	*Listrophorus*
Dermacentor	*Spilopsyllus*
Desmodex	*Xenopsylla*
Haemadipsus	
Haemaphysalis	
Hyaloma	
Ixodes	
Linguatula	
Listrophorus	
Notoedes	
Odontopsyllus	
Pulex	
Psoroptes	
Rhipicephalus	
Sarcoptes	
Spilopsyllus	
Xenopsylla	

Source: Soriguer (1980*b*).

Fig. 3.20 Monthly numbers of fleas on rabbits in France. (a) Camargue (Vandewalle unpublished), (b) Vaucluse (Arthur and Gaudin unpublished), (c) Paris (Launay and Arthur unpublished).

bite rabbits, from May until September, and the maximum number of bites per rabbit per day is 12 in July (Vandewalle 1981).

The abundance of fleas, at least on French rabbits, varies inversely with that of mosquitoes. In both the Camargue and Vaucluse the average number of fleas per rabbit (adults and sub-adults) is greatest from March to April (Camargue, 20–30 fleas per rabbit; Vaucluse, 40–60 fleas per rabbit), and is virtually zero during the season of epizootics. In Ile-de-France rabbits carry the most fleas, 60 to 120 per rabbit, from February to May. In summer the number is still 10 to 20 (Launay 1980; Fig. 3.20).

The virus is present on the mouth-parts of fleas throughout the year in all three areas studied in France. That is, while fleas are proven carriers
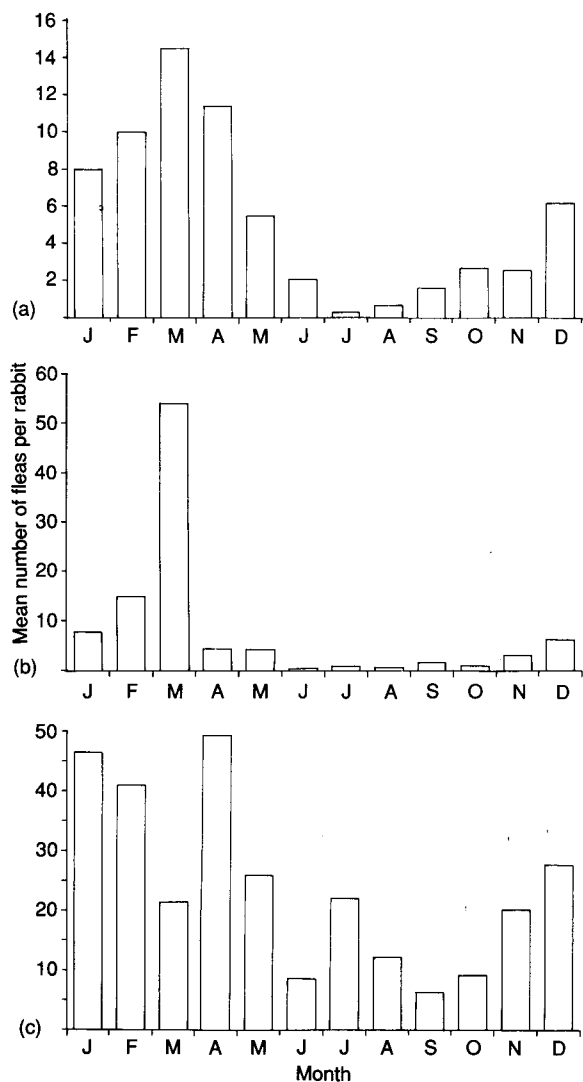
during epizootics, they also carry the virus even when no disease is evident among the rabbits, also in May even in the absence of any sign of the disease (Gourreau *et al.* in preparation). The presence of the virus on known vectors apparently in the absence of
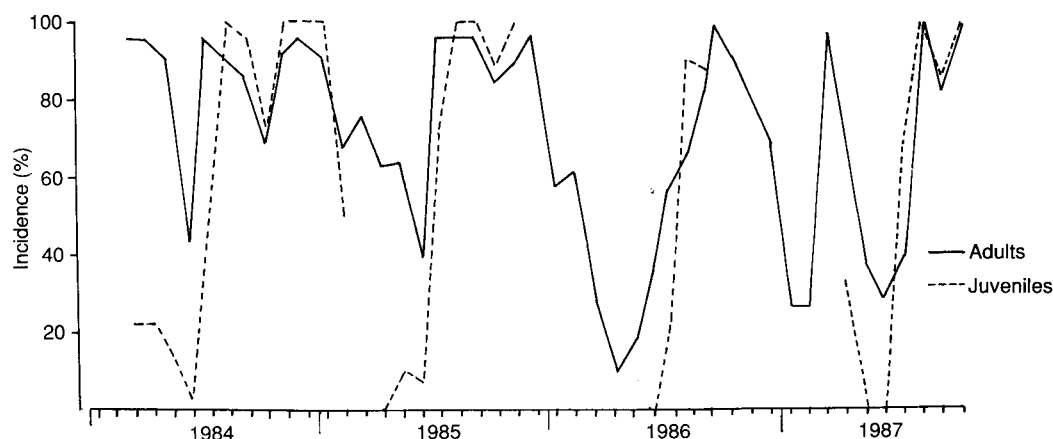
Fig. 3.21 Proportion of juvenile and adult rabbits with myxoma antibodies, Camargue, southern France, 1984–7 (after Vandewalle, unpublished).

any clinical sign of disease is puzzling, and raises important questions about, among other things, the immunological status of the rabbit population.

In the Camargue there is a clear seasonal cycle in the proportion of rabbits with antibodies (Vande-walle 1986). All adult rabbits have antibodies after an epizootic (usually in late August or early September) (see also Chapter 7). They all continue to carry antibodies until January–February, when the proportion gradually decreases to 20–30 per cent in April–May, just before the start of the next epizootic. A variable proportion (0 to 25 per cent) of juveniles carry antibodies until the age of 2 months, but during an epizootic the proportion of juveniles climbs quickly to reach 100 per cent by the end of August (Fig. 3.21). Thereafter they follow the adult pattern.

In the Vaucluse all adults have antibodies from October to June, after which the proportion decreases to about 50 per cent in August. From September, stimulated by the appearance of a new epizootic, the proportion climbs back to towards 100 per cent. Again, some 10 to 50 per cent of young rabbits carry antibodies until the age of 2 months. By June–July usually less than 10 per cent of young still have them, but the proportion rises to 50–60 per cent by the end of October, and 90–100 per cent in January (Fig. 3.22; Arthur and Gaudin, in press).

Results from Spain confirm this pattern. After an outbreak over 90 per cent of rabbits carry antibodies,

declining to 50 per cent five months later. Mortality particularly affects juveniles and sub-adults, because 40 per cent of young rabbits (up to 800 g) do not carry antibodies (Soriguer 1980*a*, 1981*a*).

In the Ile-de-France, there are two different cyclical patterns. When there is no autumn or winter epizootic, the 50 to 60 per cent of adults which have detectable antibodies in May declines to 10–20 per cent by January–February. During the summer, 15–20 per cent of young (up to 2 months) have maternal antibodies, but in August–September they lose their antibodies, and from October–November, when the young of the previous season make up three-quarters of the total population, the proportion with detectable antibodies stays at zero until the onset of the next epizootic. After a new epizootic, the proportion of surviving rabbits carrying antibodies increases rapidly the following spring, according to the intensity of the outbreak, to stabilize by August at 60–70 per cent. About 30–40 per cent of the young of the year have antibodies.

The second type of cycle starts after an autumn or winter outbreak, and its effect is to stimulate a higher level of resistance in winter and spring. After an autumn epizootic, 70–90 per cent of adults and young are carriers by November; or 30–40 per cent by February–March after a winter epizootic, the majority of them being young of the previous season (Arthur, unpublished data).
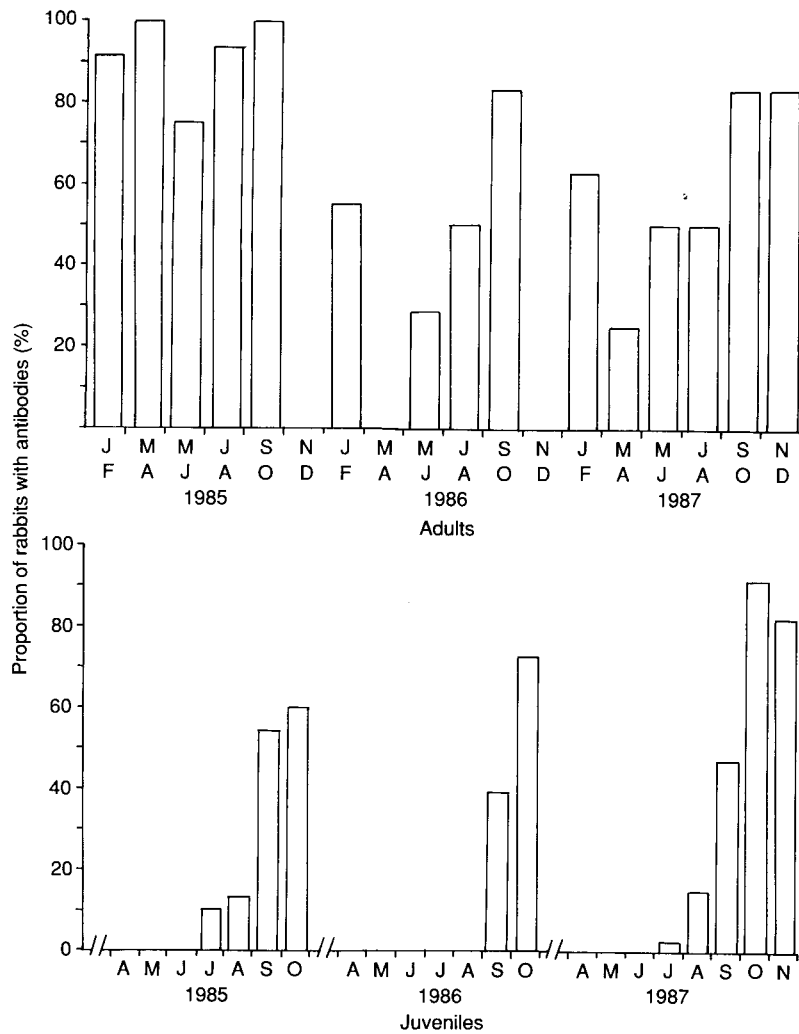
Fig. 3.22 Changes in the proportion of juvenile and adult rabbits with myxoma antibodies, Vaucluse, south-central France, 1985–7 (after Arthur and Gaudin in press).

3.7 Viral haemorrhagic disease

Viral haemorrhagic disease (VHD) was first described in domestic rabbits in China. The cause was a small (28–33 nm diameter) round icosahedral virus, without envelope. The nucleic acid is single-strand RNA (Liu *et al.* 1984). The virus could agglutinate erythrocytes in the blood of sheep, poultry and humans (type 'O'). The incubation period for the disease was 48–72 hours, with death from several hours to one or two days later. The typical symptoms was epistaxis, although often no clinical sign was observed. Characteristic pathological changes included punctate haemorrhage in the respiratory and digestive systems, the spleen, cardiac muscles, and occasionally the kidneys. A rabbit tissue vaccine of virus inactivated with 0.4 per cent formaldehyde was developed with satisfactory results; later modifications improved its efficiency (Arguello 1989; Pages 1988).

A few years after Liu described it in China, the same disease appeared in Europe, under several

aliases: virus 'x', hepatosis, rabbit haemorrhagic disease, haemorrhagic septicemia syndrome,viral haemorrhagic disease. It caused high mortality in domestic and wild rabbits, and also hares, in Italy (Cancelloti et al. 1988), France (Morisse 1988), Spain (Arguello etal. 1988), Germany (Loliger et al. 1989), Austria (Nowotny et al. 1990). VHD is similar to another disease of hares, European brown hare syndrome, which produces VHD-like lesions. VHD can be transmitted to hares, experimentally at least, and in Czechoslovakia hares have been found with VHD antibodies (Morisse et al. 1991).

VHD was first detected in Spain in the spring of 1988, in both domestic and wild rabbits from two widely separated areas, Asturias in northern Spain and Almeria in the south-east (Arguello 1989). A little more than a year after these first two foci were detected, only the south-west parts of the country were VHD-free. The disease was recorded in the adjacent region of Murcia, at Sucina in December 1988, and at Lorca in April 1989 (León Vizcaino, unpublished); one year later the first rabbit with VHD was found in Doñana National Park. In only two years the virus had spread throughout the whole of Spain.

In France, the first outbreak of VHD was recorded in the summer of 1988, in several small rabbitries in the north-east (Haute-Saône, Vosges, Côte d'Or). The deaths were so unusual and unexpected that they were at first attributed to radiation from Chernobyl or some other environmental pollution. Their infectious origin was not discovered until the end of the year (Morisse 1989). Of over 100 dead rabbits

taken from all over France in 1989, about half had died from VHD (ONC 1990). By the end of 1991 VHD was established in 56 out of the 95 départements of France.

In parts of France (in the Camargue, Vaucluse, Hérault) several VHD epizootics break out each year. Their effect on wild rabbit populations, although largely unquantified, has often been dramatic. Soriguer and Cooke (unpublished) observed one of the initial outbreaks of VHD in wild rabbits at El Alquian (Almeria, Spain) in June–July 1988. Because the disease progresses so rapidly, some rabbits died while trying to escape them, yet without showing any external symptom. There were many more dead rabbits on the ground than the predators and scavengers could remove (León Vizcaino, Cooke and Soriguer, personal observations). In Doñana National Park, where systematic observations had been made for some years, VHD was associated with an additional mortality of 60 to 70 per cent or more (Villafuerte and Moreno personal communication). On a reserve in the Vaucluse, the reduction in population was estimated at 70–80 per cent (Gaudin, personal communication).

From an ecological point of view in the predator-rich community of the Mediterranean, VHD represents a catastrophic event. Studies now in progress show that rabbits have begun to develop some genetic resistance to the disease, although annual outbreaks are normal. It is still too soon to make any predictions, but we expect that some equilibrium between the VHD virus and the rabbit will develop eventually, as with the myxoma virus.

3.8   Conclusion

The picture of the rabbit in Europe which emerges from this review is that of a biological opportunist bound by ecological constraints. Like any mammal, the rabbit needs high quality food for reproduction and growth. Its reproductive strategy is flexible enough to allow exploitation of favourable periods of plant growth—indeed it has evolved physiological links with photoperiods to enable it to predict them. Its habitat requirements are not too specific, somewhere to dig a hole and food nearby. Given its requirements the rabbit's productivity is proverbial

(see, for example, Thompson and Worden 1956; or Sheail 1971).

There must, however, be constraints to hold such potential in check. In southern Spain, which is perhaps the nearest contemporary equivalent of the rabbit's ancestral home and where we have relatively undisturbed study sites, there seem to be three groups of constraints: terrain, climate, and predation. The same three reappear in the south of France as part of the recurring theme of latitudinal trends. Terrain determines the security of the burrows.

While it is not uncommon for some rabbits to live above ground, whole populations thrive only where the soil is suitable for building burrows, or where some substitute is available (some thriving populations in Spain use gaps between rocks, where it is impossible to burrow). Climate limits the reproductive season of the rabbit, via its effects on vegetation, quantity in winter, and quality in summer. But even so the rabbit might be able to outstrip its resources but for the third and final constraint, predation. In many places today this may be imposed by shooting, but an impressive variety of natural predators depends on rabbits, especially in the south. Many translocation/reintroduction efforts fail in Spain because predators kill the rabbits before they can establish stable burrows in their new home. The rabbit has also managed to come to terms with catastrophic events such as the arrival of myxomatosis and VHD. Such ecological adaptability allows a stability in southern rabbit populations that is not to be found further north.

Historical changes in land use allowed the rabbit to extend its range northwards. It was a serious pest of agriculture in the north of France by the sixteenth century. But the damage it did was outweighed by its value as a game species, and from the end of the nineteenth century active management by game-keepers encouraged the rabbit to attain very high population densities between 1920 and 1940. The introduction of myxomatosis was a spectacular set-back, but recovery began quickly and continued throughout Europe until 1970. Since 1980, further changes in land use and the appearance of new epizootics have reduced the numbers of rabbits available for shooting. The efforts of hunters in the south to augment game populations have been copied in the north. Conservationists also work to maintain rabbit populations, in order to protect the many Mediterranean predators that depend largely on rabbits—some exclusively, such as Bonelli's eagle *Hieraetus fasciatus* during its nesting season (Iborra *et al.* 1990). The same is true for the Spanish lynx *Lynx pardina* and the imperial eagle *Aquila adalberti* (*A. heliaca*), two of the most endangered species in Europe.

The biology and ecology of the rabbit in Europe, from Sweden where it is an introduced species to its ancestral home in the south of Spain, show a tremendous range which spans the differences measured in other parts of the world. In its ancestral home the rabbit is an essential part of a complex natural environment. Only when it is removed from the demands and constraints of that environment does the ecological opportunism, which allows it to survive at home, turn it into a pest elsewhere.

3.9 Summary

Oryctolagus, first known from the Miocene in southern Spain (5–7 million years ago) is of uncertain ancestry. Of its three known species (*layensis*, *lacosti*, and *cuniculus*) only one is extant, *O. cuniculus*. It was first found in southern Spain in the mid-Pleistocene and co-existing with the other extant lagomorph, *Lepus*. Over the last 15 000 years *O. cuniculus* has become smaller. Today it also exhibits a latitudinal gradient in body size, rabbits in the north of Europe being some 50 per cent larger than the south.

Genetics and ectoparasites indicate 3 groups of rabbits. In southern Spain, their presumed ancestral home, they have been separate from those of southern France (and of northern Spain) for over 50 000 years. Northern European rabbits represent a third distinct group to which domestic rabbits and those introduced elsewhere are most closely related.

Rabbits spread through Europe in the last 10 000 to 20 000 years from the Mediterranean. Their domestication by monks in France in the Middle Ages, where rabbits have long been managed for food or as game, is well documented. Population numbers gradually increased until the 1920s, much higher in the north than the south, staying high until the introduction of myxomatosis in 1952 near Paris. The disease spread throughout most of Europe in little more than a year, decimating populations. After 4 or 5 years, numbers gradually increased until the early 1970s, and more rapidly thereafter.

Inherent population cycles, disease, and climate may all influence changes in population numbers.

Terrain characteristics and changes in land use are also important. The rabbit has the status of game throughout most of Europe, and open seasons and hunting methods are strictly controlled. In France and elsewhere, rabbits (wild-type and crosses) are bred for restocking wild populations. Releases of alien species, notably *Sylvilagus* spp. have occurred, but with little success, and are illegal. Conflict between farmer and hunter is reduced by compensation systems, but not in Spain, where rabbits are not officially regarded as a pest.

Extensive studies show that rabbit diets in Europe reflect landscape and climate. Grasses and forbs are preferred, and a small number of plant species may make up a large proportion of the diet. Exclosure experiments have emphasized the role of rabbits as primary consumers, and in changing floristic composition. Rabbits may have an important, so far unmeasured, role in seed dispersal especially in the south of Spain.

The length and timing of most reproductive parameters also show strong latitudinal trends. Northern rabbits starting breeding older, later, and for longer than their counterparts in the south and produce more young per year. In Mediterranean areas breeding is extremely variable. In southern Spain male reproductive cycles can be predicted mainly from the climate, particularly radiation and temperature; climate is also important for females, but less so than food quality. These characteristics reflect the opportunist strategy of rabbits, a response to the variability of Mediterranean weather patterns.

Survival rates of young rabbits in southern Spain are much lower than in France. Conversely, survival rates of adults are much higher in Spain. Causes of mortality include hunting, predation, often in combination with disease, and injuries from farm machinery. In the west Mediterranean the number of predator species is high. Rabbits are important in most predators' diets, especially in southern Spain, where all medium and large predators except wolf rely largely on rabbits, and some exclusively during breeding.

Both myxomatosis and viral haemorrhagic disease are endemic in Europe. Genetic resistance to myxomatosis is well-established, and resistance appears to be developing to the latter. Both have an extensive influence on population numbers.

In its ancestral home the rabbit is an essential part of a complex natural environment, valued by hunters and conservationists alike. The demands and constraints of that environment have prevented it becoming the pest that it is elsewhere.

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