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POPULATION ECOLOGY OF RABBITS IN THE WAIRARAPA, NEW ZEALAND

Summary: An aged sample of over 17,000 rabbits *(Oryctolagus cuniculus)* from the Wairarapa, in the North Island of New Zealand (area 2535 km^2, 41 °10'S), was autopsied between September 1965 and September 1967. The sample represented about two-thirds of all rabbits shot by the Pest Destruction Board. Information included: date; property; age; sex; body-weight; if male – testes scrotal or not, if female – whether pregnant / lactating, number and size of healthy / resorbing embryos.

About 52% of the rabbits shot were males. Percentages of rabbits in the 1st, 2nd, 3rd and> 3rd year age-classes were: males 52.2, 30.7, 9.6,7.5; females 60.9, 27.9, 6.9, 4.3. Young up to at least 3 months old were under-represented in the sample. The age distribution of the samples differed between years.

About 10% of young conceived May-November survived at least 6 months, compared with about 0.1 % of those conceived in other months. Relative changes in numbers through the year of 1st, 2nd and 3rd year, and of older rabbits, are illustrated. The average annual survival rate beyond age 6 months was 0.4t.

About 33% of males aged 4-6 months had scrotal testes, rising to 62% of those> 12 months old. Some males were found with scrotal testes in every month. Few females < 4 months old were pregnant. Above this age, over 90% were pregnant in September-November, and fewer than 50% in April, May and June.

Pre-natal mortality of embryos may be adaptive in matching litter-size at birth to environmental conditions. In some months pre-natal mortality affected at least 28% of pregnant females; it was more frequent among older than younger females. Mean monthly litter-size at birth ranged from 4.17 in June to 6.55 in October. Females aged 10-12 months were more productive than younger or older females. On average, about 45 young were born annually per adult female.

Both sexes gained in weight until> 3 years old. Adult females weighed more than adult males, the difference depending on the proportion pregnant.

Overseas, dates of breeding vary widely even at similar latitudes and productivity varies with the length of the breeding season. In Spain, where the rabbit evolved, summer rainfall is sparse and the arrival of autumn rain is erratic. Rabbits breed opportunistically in Spain and in parts of Australia, but rarely in New Zealand. Litter-size of *Oryctolagus* seems not to vary latitudinally, unlike that of *Sylvilagus* spp. in America.

The first summer was on average 1.5 ºC warmer than the second. Females were heavier and more of them were pregnant in the first summer, but they had smaller litters; males were lighter and fewer had scrotal testes. Productivity was similar in the two years.

An average annual kill by the Pest Destruction Board of about 15,000 rabbits of mixed ages probably accounted for less than 20% of the adult population. This is unlikely to have reduced the size of the population a year later, though it may have reduced average survival.

Introduction

From his study of the reproduction of rabbits *(Oryctolagus cuniculus* (L)) in Hawke's Bay, New Zealand, Watson (1957) concluded: 'The reproduction of the rabbit also needs investigating . . . where this animal lives without ever building up dense populations, its numbers being naturally controlled at a low level. . . It is very desirable to know what are the causes of this, how far it is due to increased mortality, and how far to reduced productivity.' The present study, based on over 17,000 rabbits shot in the Wairarapa between September 1965 and September 1967, goes some way towards answering this question.

The sample was obtained 5-7 years after rabbits had been reduced, mainly by poisoning, to low levels following peak abundance in the early 1950s (McLean 1966). Conditions were thus very different from those of higher density described by Wodzicki (1950), Tyndale-Biscoe & Williams (1955), Watson (1957), Bull (1958, 1964) and McIlwaine (1962). The density of rabbits in the Wairarapa has not changed much since about 1965. Consequently this account is probably still applicable to extensive areas
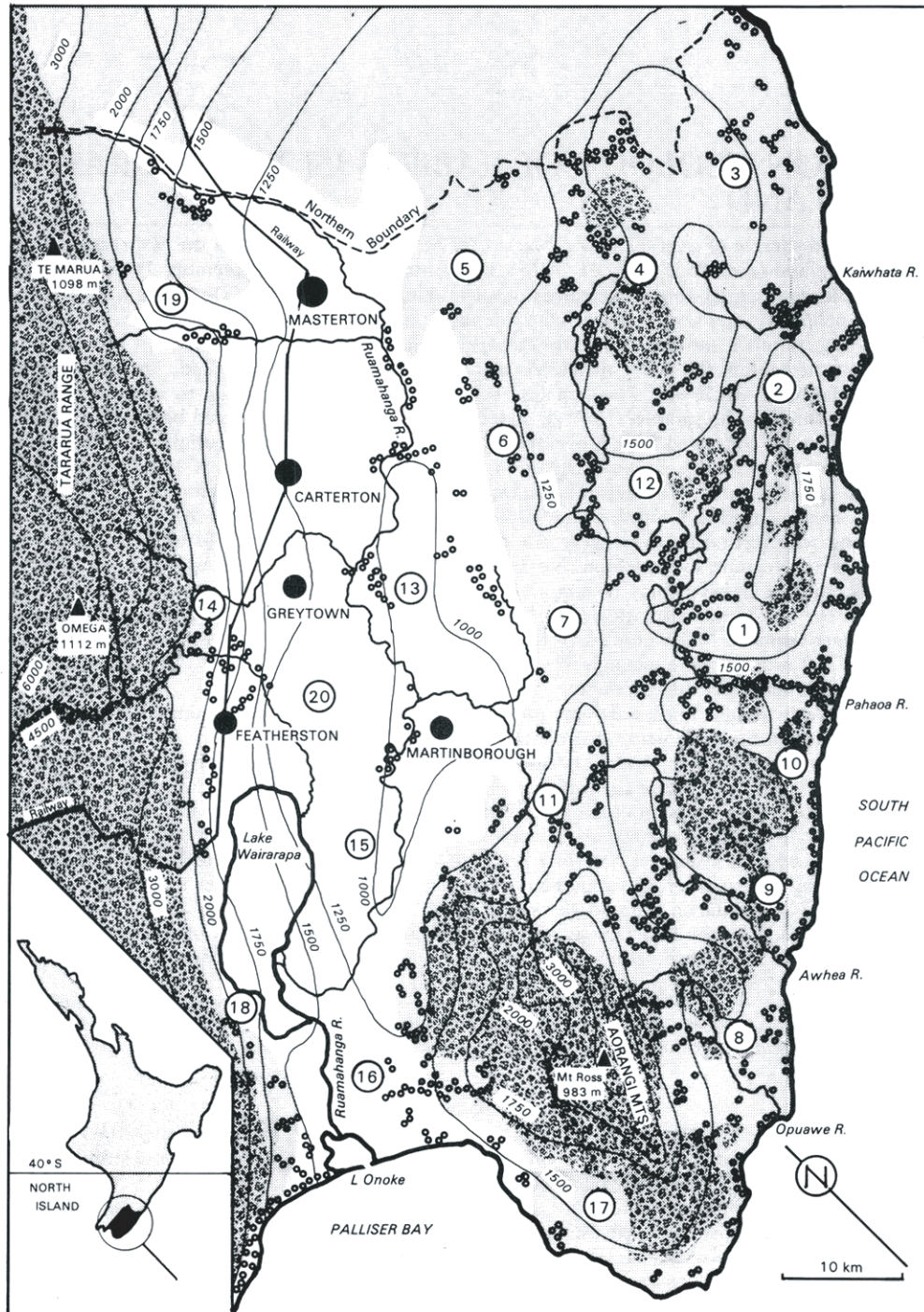
Figure 1: *Map of the Wairarapa showing: forest (densely hatched), cleared hill country (lightly hatched), and the plain (not hatched); isohyets of average annual rainfall in mm; and concentrations of rabbits (W. H. McLean, pers. comm.) (small open circles). Circled numbers 1-20 refer to centres of districts listed in Table 10.*

Table 1: *Mean monthly temperature and rainfall at Ngaumu State Forest (175º 53' E, 41º 02' S) in eastern Wairarapa.*

Month	Mean monthly temp., ºC Mean					Mean monthly rainfall, mm Mean			
	1948-82	1965	1966	1967		1948-82	1965	1966	1967
Jan	16.3	17.3	16.3	15.0		59	56	98	22
Feb	16.4	14.9	18.4	15.5		51	43	40	92
Mar	14.9	14.0	14.4	14.2		86	306	52	72
Apr	12.0	11.0	11.3	12.0		98	57	94	61
May	9.3	8.9	8.4	8.4		135	76	251	67
Jun	6.9	6.3	7.1	5.9		141	149	74	53
Jul	6.3	4.7	6.1	4.4		156	125	216	45
Aug	7.3	6.7	5.9	8.5		137	328	185	196
Sep	9.0	8.6	8.8	7.3		89	53	54	55
Oct	10.9	9.4	9.9	11.1		79	45	30	36
Nov	13.0	12.2	11.5	13.1		61	53	71	103
Dec	14.9	15.0	13.9	14.8		83	50	265	159
Mean	11.4	10.8	11.0	10.8	Totals	1175	1341	1430	961

of the east coast of the North Island, where conditions are similar (Radcliffe 1975).

Methods

Study area

The Wairarapa (Fig. 1) is a sheep and cattle farming district, with extensive cropping and horticulture on the plain from Palliser Bay in the south to north of Masterton. Agricultural land adjoins native forest in the foothills to the west and around the Aorangi Mountains in the south, and there are patches of forest and extensive scrublands in the eastern hills. Most of the plain was cleared of forest for grazing in the late 19th century. Apart from the string of small towns following the railway, the district is sparsely settled. Farm properties, of which more than 500 were rated for rabbit control, are much smaller on the plain than in the hills.

Average rainfall (Fig. 1, Table 1) rises steeply from less than 1000 mm on the plain to over 5000 mm in the ranges, and to about 1500 mm in the eastern hills and 2500 mm in the Aorangi Mountains. It is reasonably well distributed through the year, though summer droughts are frequent. Mean monthly temperatures range from about 5 ºC in mid-winter to 16 ∞C in mid-summer. Frosts are frequent, but except in the main ranges snow seldom lies for more than a few days at a time.

Soil types range from recent soils on the flood plain of the Ruamahanga River, through stony fans and silty soils, to moderately leached, yellow-brown earths in the wetter hill country. Pasture growth peaks in October and falls to a minimum in late summer. Growth normally resumes after autumn rains from about March to May, and falls again in mid-winter (Radcliffe, 1975). The weather and pasture growth vary markedly from year to year.

Rabbits were collected from throughout the Wairarapa Pest Destruction Board's district of about 2535 km^2, which comprises the whole southeastern tip of the North Island (Fig. 1). Sites of minor concentrations are shown in Fig. 1, based on extensive observations by W. H. McLean (pers. comm.) who supervised the Board for 15 years. Rabbits were absent only from the forest and from urban districts. They were more numerous in the eastern hills than on the plain, especially bordering scrubland, along stretches of coast with sand dunes, and on stony ground beside the main rivers, which was their main habitat on the plain. By the mid 1960s rabbits were nowhere really abundant and caused negligible damage to agriculture.

Domestic and feral cats *(Felis catus)* and stoats (M*ustela erminea)* were widely distributed and common, but feral ferrets *(M. putorius),* formerly common wherever rabbits were numerous, were rather scarce. Weasels *(M. nivalis)* had always been rare. Australasian harriers *(Circus approximans)* were common but they take only a few rabbits, usually young of less than 500 g in weight (Gibb *et al.,* 1978). Other than farm dogs, which seldom run wild, there were no other predators on rabbits.

Shooting operations

Regional Pest Destruction (formerly Rabbit) Boards are wholly responsible for controlling rabbits in New Zealand. The shooting of rabbits for sport or the pot

is discouraged on the grounds that it makes the survivors more wary; and it is still illegal to sell rabbit carcases or their products for fear of the rabbits being deliberately 'farmed'.

The Wairarapa Pest Destruction Board estimated that it shot the following numbers of rabbits each year: 1965,13463; 1966, 14167; 1967, 15611; 1968, 17901; 1969, 15809; 1970, 17856. All the 17,326 rabbits autopsied here were shot with 12-gauge guns at night using spotlights from Land-Rovers, between September 1965 September 1967, inclusive; they represented about two-thirds of all the rabbits shot by the Board during the study. Of these, 7572 rabbits were autopsied in 1965-66 and 9754 in 1966-67 (13 months).

About 16 men with eight Land-Rovers worked systematically over the country each year in an operation known as the safari, which was then the Board's main method of controlling rabbits (McLean, 1966). The Land-Rovers covered flat and gently undulating land quite thoroughly, but in the hills they were largely restricted to farm tracks, valleys and ridges, where they probably covered less than half of the ground.

The usual route taken by the safari followed the districts numbered 1-20 in Figure 1. They began on the east coast north of the Pahaoa River in spring and back up the coast to the Board's northern boundary. Then, in summer, the safari turned inland and south from Masterton to the coast east of the Aorangi Mountains. In autumn, they worked first east of Lake Wairarapa and through the coastal districts of Palliser Bay, and then in the foothills west of the lake and north beside the Tararua Range, towards Masterton. The plain between Grey town, Featherston and Martinborough was left until winter. The shooters occasionally returned to the eastern hills in autumn and winter to check places where rabbits had previously been found numerous.

This was the normal route followed each year, not just during this study. Consequently some districts were always visited in spring, and others in summer, autumn, or winter, and rarely at other seasons. Aside from the implications of this on the efficacy of controlling rabbits, it follows that our analyses are based on samples obtained from different districts at different times of year. Nonetheless we have compared samples of rabbits (a) from the plain as opposed to the hills; (b) from areas of high as opposed to low average rainfall; (c) from areas of high as opposed to low population density; and (d)

from each of the twenty districts into which the Board's area was divided for operational purposes (see Fig. 1).

The number of rabbits shot per km' is used as a rough index of the density of rabbits on each property. This index ignores variability of shooting effort and patchiness of the rabbits' distribution, which were not measured. No record was kept of the few properties visited without any rabbits being shot. Properties on which 1-4 rabbits were shot per km' each year are classed as of low density; those with 5-9 rabbits shot, as of medium density; and those with more than nine, as of high density. For convenience, much of the material is grouped either monthly, or quarterly as follows: spring (September-November), summer (December-February), autumn (March-May), and winter (lune-August).

Sampling bias

The shot samples of rabbits mayor may not have been representative of the wild population. Young rabbits less than four months old were certainly under-represented, as others have found (e.g. Cooke, 1981; King & Wheeler, 1981; Parer, 1982), probably because of their small home ranges (Hughes & Rowley, 1966; Daly, 1980; Parer, 1982; Richardson & Wood, 1982) and retiring habits (l.A.G. personal observations). Watson (1957) suspected that the method of collection was responsible for an increasing proportion of males among older rabbits in his samples, obtained by trapping and poisoning, but he found no difference in their sex ratio (cf. Thompson & Worden, 1956). On average, adult males netted by Parer (1982) were 149 m from their home warrens, and adult females 115 m. If distance from the warren influences which animals will be caught (or shot) at night, then males may be more vulnerable than females. Gilbert and Myers (1981) believed that spotlighting produces representative samples of rabbits more than three months old.

Gibb *et al.* (1969) found that two samples of rabbits obtained from one area simultaneously by night-shooting and by poisoning with strychnine had an identical age composition. This reinforces our confidence in night-shooting for obtaining representative samples of older rabbits.

Ageing rabbits

The shot rabbits were aged from the progress of epiphyseal fusion, based on the measurements of

Table 2: *Criteria used for ageing rabbits*.

Est. age (months)	Tibia length (max. mm)	Body-weight (max. g)	Est. age (months)	Epiphyseal fusion complete
1	54	530	6	Tibia, distal
2	70	825	10	Tibia, proximal
3	80	1030	14	7th ant. vertebra
4	83	1180	16	6th ant. vertebra
5	85	1350	18	5th ant. vertebra
			19	4th ant. vertebra
			21	3rd ant. vertebra
			23	2nd ant. vertebra
			25	1st ant. vertebra
			26	7th post. vertebra
			33	6th post. vertebra
			35	5th post. vertebra

Watson & Tyndale-Biscoe (1953) and Taylor (1959), augmented by additional known-aged material in the Ecology Division collections (Table 2). The known-aged skeletons (up to 40 months old) did not include specimens of every month of age up to 36 months; the few gaps were filled by referring to slightly younger or older skeletons.

The ageing criteria in Table 2 were drawn up by R. H. Taylor and CPW at the start of the study. Rabbits up to and including five months of age were aged from the length of the tibia, excluding both epiphyses. The distal epiphyses on the tibia fuse at 5-6 months, and the proximal epiphyses at 9-10 months. Rabbits 10-13 months old have the epiphysis at the head of the tibia fused, but none of the epiphyses on the lumbar vertebrae. Rabbits 14-25 months old were aged from the extent of fusion of the anterior epiphyses of the lumbar vertebrae to the centrum. Posterior epiphyses become progressively fused to the centrum at least until the rabbit is 36 months old. Within the age groups of 6-9, 10-13 and 26-32 months, the rabbits were aged to the nearest month from the degree of epiphyseal fusion to the tibia (at 6-9 months), or to the 6th and 7th lumbar vertebrae.

The difficulty in deciding whether particular epiphyses are or are not fused is a disadvantage of ageing rabbits this way, compared with using the weights of eye-lenses (Lord, 1959; Dudzinski & Mykytowycz, 1961; Myers & Gilbert, 1968; Wheeler & King, 1980). However, variation between rabbits in the rate of epiphyseal fusion

(Rogers, 1982) may be no greater than variation in the growth of eye-lenses. Ageing by epiphyseal fusion is useful with large samples of rabbits provided that the results are calibrated against skeletons of known age. The method does not require fresh material and can be used on rabbits that have been deep-frozen (which splinters eye-lenses; Myers & Gilbert, 1968).

Before the study began, AJW, who aged all the rabbits during the study, re-examined the 80 known-aged skeletons and aged each of them to the nearest month. This trial was repeated five times at intervals of several days, giving a total of 400 determinations spread over the five age-groups: 7-12 months, 13-18 months, 19-24 months, 25-36 months, and > 36 months. The estimated mean age for each group differed from the actual mean age by + 0.9 month for the first group, + 1.7 months for the second, - 0.2 month for the third, and + 0.3 month for the fourth. Some discrepancies may have been due to individual variation between rabbits of the same age-group and others to uncertain interpretation of the criteria. Once the study began, each rabbit was aged from a single examination.

Anyone using this technique over long periods is liable to favour certain ages at the expense of others. Although ages were estimated to the nearest month, they were pooled for analysis in groups of three months or longer. This has not entirely eliminated the effects of such bias. There are still rather too few rabbits in the 10-12 and 13-15 month groups and too many in the 16-18 and 19-21 month groups; too few in the 28-30 month group and too many in the 34-36 month group. This will not seriously

distort comparisons of the performance of rabbits of different age.

Estimates of survival

Survival was estimated in 3 different ways, all of which assume that the population was static over the 2 years of the study. Observations over a longer period suggest that this was the case, but if the population was actually increasing then calculated survival rates will be too low and *vice versa;* any such discrepancies are not likely to be great, however. First, N. E. Gilbert (pers. comm.) used a simulation program applied to similar Australian data (Gilbert & Myers, 1981), to deduce survival rates from the observed reproductive rates and monthly age-distributions, averaged over years and districts. He computed both the survival rates of young rabbits from mid-pregnancy to 6 months of age at different seasons of the year (Fig. 2), and average age-specific rates for older rabbits averaged over seasons. Caughley (1977) pointed out the dangers of doing this, and of the other methods, but

it seems justified here by the exceptionally large samples and enables comparison with the Australian study of Gilbert and Myers (1981). Second, an estimate of survival on an annual basis was made from the ratio of numbers of animals in their second and third years, averaged over all districts. Younger or older rabbits could not be used for annual estimates, since the very young are under-represented in samples and the mean age of those more than 3 years old was unknown. Finally, more detailed age-specific survival rates from age 6 months were obtained from the ratios of numbers shot in successive 3-month age-classes, pooled over all districts and seasons and over both years.

Results

Sex, age and survival

i) Sex ratio

The seasonal sex and age distribution of the rabbits shot is given in Table 3. Of all those shot from spring 1965 to winter 1967, inclusive, 52.1 % were

Table 3: *Number, sex (M, F) and age of rabbits autopsied.*

Age (months)	Spring M	F	Summer M	F	Autumn M	F	Winter M	F	Sep. only M	F
1965–66										
1– 3	189	208	164	230	161	229	15	22		
4– 6	156	122	290	290	375	287	54	54		
7– 9	55	87	85	73	225	218	74	60		
10–12	156	244	42	62	31	30	40	33		
13–18	279	242	158	142	75	86	59	57		
19–24	131	89	169	112	175	160	55	52		
25–30	52	36	43	33	41	33	21	23		
31–36	94	48	42	28	70	40	22	13		
>36	93	47	113	54	129	48	22	25		
Totals	1205	1123	1106	1024	1282	1131	362	339		
1966–67										
1– 3	217	278	115	117	117	141	24	29	44	46
4– 6	176	153	441	329	258	157	93	37	47	22
7– 9	166	199	122	234	329	455	104	135	29	69
10–12	138	198	51	66	64	76	51	42	14	28
13–18	425	358	254	195	99	98	60	52	42	37
19–24	310	245	220	188	158	125	50	33	51	39
25–30	73	56	52	57	75	51	25	19	18	9
31–36	66	46	68	37	49	31	18	5	14	5
>36	95	73	99	49	93	39	14	13	14	8
Totals	1666	1606	1422	1272	1265	1173	439	365	273	273

males. This percentage did not vary significantly between seasons or years of the study, but it did vary with the rabbits' age.

Table 4 shows the highly significant (p<0.00l) discrepancy in the sex ratio of rabbits 4-6 months old with 56.6% males, compared with those 1-3 months old with 44.6% males and 7-9 months old with 43.7% males. This preponderance of males among rabbits 4-6 months old varied slightly at different times of year, but persisted throughout the study. Young males thus appear less vulnerable to shooting than young females for their first 12 months of life, except when 4-6 months old when the reverse is true.

On average, males comprised 48.2% of the first-year rabbits, 54.4% of the second-year rabbits, 60.3% of the third-year rabbits, and 65.4% of those more than three years old. Thus males more than about six months old either survived consistently better than females or were more easily shot. A shift in the sex ratio of first-year rabbits from 45.7% males in spring to 48.2% in summer, and from 49.5% in autumn to 52.4% in winter, is not quite statistically significant (p > 0.05).

ii) Age and survival

Table 5 shows the percentage age composition of rabbits shot at different times of year. Predictably, the autumn samples contained most first-year rabbits and the spring samples the fewest, while spring samples contained the largest proportion of older animals and autumn samples the fewest. The age compositions differed significantly (p < 0.001) between the two years in all four seasons. The differences were quite erratic; for example, the relatively high proportion of rabbits up to six months old in the summer and autumn of 1965-66, compared with 1966-67, was reversed six months later, when there were relatively few rabbits now 7-12 months old in the winter and spring of 1966. Such inconsistency between successive seasons is probably a result of successive samples coming from different districts.

Using Gilbert's method, the computer survival rates of young rabbits from mid-pregnancy to six months of age, at different times of year, are shown in Fig. 2. The data only permit calculation of average rates for young conceived between May and November, hence the plateau in the Figure, but any peak concealed within this period is likely to have

Table 4: *Variation in sex ratio with the rabbits' age*.

Age (months)	Spring 1965	Summer 1965-66	Autumn 1966	Winter 1966	Spring 1966	Summer 1966-67	Autumn 1967	Winter 1967	Spring 1967	All seasons
					Percentage of males					
1- 3	47.61	41.62	41.28	40.54	43.84	49.57	45.35	45.28	48.89	44.59
4- 6	56.12	50.00	56.65	50.00	53.50	57.27	62.17	71.54	68.12	56.57
7- 9	38.73	53.80	50.79	55.22	45.48	34.27	41.96	43.51	29.59	43.73
10-12	39.00	40.38	50.82	54.79	41.07	43.59	45.71	54.84	33.33	42.97
13-24	55.33	56.28	50.40	51.12	54.93	55.31	53.54	56.41	51.96	54.42
25-36	63.48	58.22	60.33	54.43	58.51	56.07	64.19	64.18	69.57	60.31
>36	66.43	67.66	72.88	46.81	56.55	66.89	70.45	51.85	63.64	65.37

For sample sizes, see Table 3.
All the 'All seasons' percentages are highly significantly different from 50%.

Table 5: *Seasonal age composition, sexes pooled*.

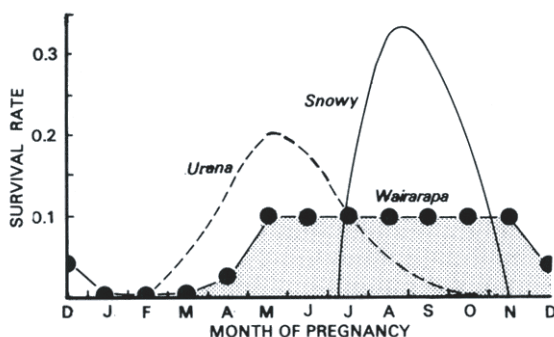| Age (months)	Spring 1965	Spring 1966	Summer 1965-66	Summer 1966-67	Autumn 1966	Autumn 1967	Winter 1966	Winter 1967
				Percentage age composition				
1- 6	29.0	25.2	45.7	37.2	43.6	27.6	20.7	22.8
7-12	23.3	21.4	12.3	17.6	20.9	37.9	29.5	41.3
13-24	31.8	40.9	27.3	31.8	20.6	19.7	31.8	24.3
>24	15.9	12.5	14.7	13.4	15.0	14.8	18.0	11.7

Figure 2: *Survival rate of young rabbits, males and females pooled, from mid-pregnancy to six months of age in the Wairarapa (computed by* N. *Gilbert), compared with Urana and the Snowy Plains in New South Wales (after Gilbert & Myers, 1981).*

fluctuate closely in unison (r = 0.916, p<0.00l). However, for reasons which are not clear the average survival rate is lower than that derived by Gilbert's method, and the individual rates vary widely between seasons. As each quarterly estimate of annual survival overlaps the previous one by nine
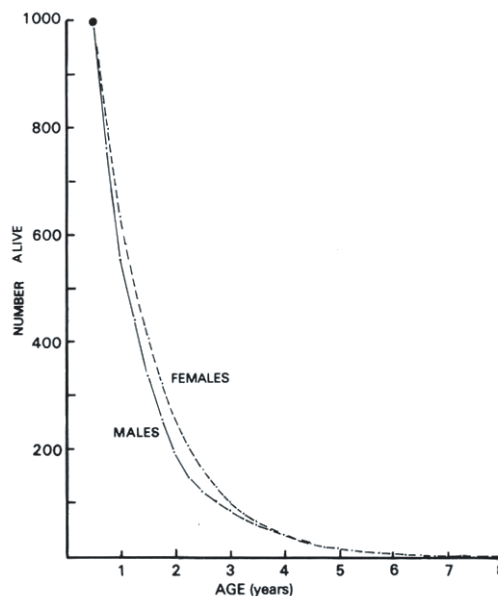
been less pronounced than in Australia, where the spring flush of vegetation is short-lived. On average, slightly more than 10% of the young conceived between May and November survived a further six months, compared with a mere 0.1 % of those conceived between December and March. Average annual survival for rabbits over 6 months old, using the same method, was 0.41.

Table 6 shows numbers of rabbits shot in each year age-class, for each season and year, and the annual survival rates calculated from them as ratios of numbers in the 2nd and 3rd years. The seasonal estimates of the survival of male and female rabbits

Figure 3: *Survivorship curves from initial populations of 1000 rabbits of each sex at age 4-6 months.*

Table 6: *Age composition and annual adult survival estimates.*

| | Number shot, aged. . . months | | | | | | | | Estimated mean annual survival, yr 2-yr 3 | |
| | Males | | | | Females | | | | | |
Season	1-12	13-24	25-36	>36	1-12	13-24	25-36	>36	M	F
Spring 1965	556	410	146	93	661	331	84	47	0.356	0.254
Summer 1965-66	581	327	85	113	655	254	61	54	0.260	0.240
Autumn 1966	792	250	111	129	764	246	73	48	0.444	0.297
Winter 1966	183	114	43	22	169	109	36	25	0.377	0.330
Spring 1966	697	735	139	95	828	603	102	73	0.189	0.169
Summer 1966-67	730	474	120	99	746	383	94	49	0.253	0.245
Autumn 1967	768	257	147	93	829	223	82	39	0.572	0.368
Winter 1967	272	110	43	14	243	85	24	13	0.391	0.282
Total	4579	2677	834	658	4895	2234	556	468		

Table 7: *Age composition of rabbits from areas of different average annual rainfall*

Age	Percentage age composition Rainfall groups (mm)			
(months)	775-1025	1026-1150	1151-1275	1276-1400
1-12	53.11	54.87	56.95	58.51
13-24	29.30	29.68	29.92	28.72
25-36	9.87	9.56	7.62	7.49
>36	7.73	5.90	5.51	5.29
n	2898	2898	6220	4767

months, successive estimates should agree closely. In fact, however, the autumn samples (especially of males) contain unexpectedly many animals 25-36 months old, thereby boosting the estimates of survival based upon them. The difference between the autumn samples and those of the year as a whole is highly significant $(\chi^2 = 37.34$, 1 df, p<0.00l) when both years and both sexes are pooled. Once again, the difference presumably arises because different districts were sampled at different times of

year, and the age composition of the rabbits varied between districts (see Table 10, below).

The survivorship curves in Figure 3 are derived from the ratios of the numbers of rabbits in successive 3-month age-groups, beginning with 1000 six-month-old rabbits of each sex and using average survival rates between the ages of 6-24 months, 25-36 months, and more than 36 months. Males apparently survived less well than females up to an age of 24 months, but thereafter better than the females. Assuming a constant mortality after the age of 36 months, the oldest rabbits from the initial
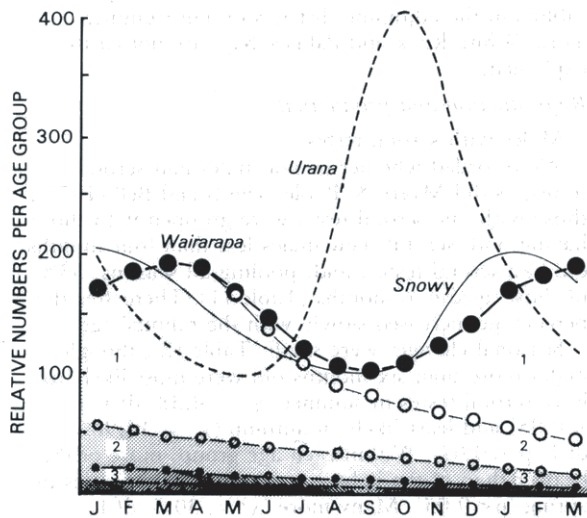

Figure 4: *Changes in the total population (–•–), and in proportions of first-year (1), second-year (2), third-year (3), and older rabbits through the year in the Wairarapa (computed by N. Gilbert), compared with changes in the total population at Urana and the Snowy Plains (after Gilbert & Myers, 1981). Each population is drawn to an arbitrary minimum of 100, and ages relate to breeding seasons (1 = young born in current season, 2 = young born in previous season, etc).*

Table 8: *Age composition of rabbits from areas of different population density (see text for definition).*

Age	Percentage age composition Population density		
(months)	Low	Medium	High
1-12	52.19	59.56	59.57
13-24	30.59	26.89	28.56
25-36	9.38	8.36	7.13
>36	7.84	5.22	4.75
n	6005	5099	5501

Table 9: *Sex ratio of rabbits from areas of different population density (see text for definition).*

Age	Percentage of males Population density		
(months)	Low	Medium	High
1-12	50.56	49.30	47.18
13-24	55.68	54.38	52.40
>24	64.22	58.32	59.54
All ages	54.64	51.81	50.25
n	6160	5440	5652

1000 would have died when about 8-10 years old, and the average age of rabbits more than 36 months old would have been about 48 months. Average annual survival is close to the 0.41 derived by Gilbert's method.

The samples of rabbits came from various habitats with differing population densities. Though actual densities could not be determined, Gilbert (pers. comm.) computed the relative changes in numbers throughout the year, of the whole population and of individual cohorts born in successive breeding seasons (Fig. 4). The annual pattern of change in Figure 4 would be repeated endlessly so long as population trends remained unchanged, with minimum numbers in about September and maximum numbers (about twice the minimum) in March.

iii) Regional differences

The age composition of rabbits shot on the plain was not significantly different (p> 0.05) from that of those shot in the hills. However, rabbits shot in low rainfall districts included significantly fewer first-year animals than did those from wetter districts ($\chi^2 =$ 56.11, df 3, p <0.001) (Table 7), presumably due to the earlier drying-out of the pasture. Overall, slightly more rabbits in total were shot per km^2 in districts of low than of high rainfall (6.90 d. 5.08 per km^2). Abnormally many of the rabbits were over 24 months old on properties where the population density was low ($\chi^2 = 208.24$, df 3, p < 0.001) (Table 8), and these properties included unusually many males of all ages ($\chi^2 = 40.36$, df 2, p < 0.001) (Table 9). Some difference in sex ratio was to be expected as rabbits survived longer at low than at high density, and the percentage of males increased with the rabbits' age (Table 4). The sex ratio did not differ significantly between the plain and the hills, or with the average rainfall.
Given the number and age of rabbits shot in each of the Board's districts (Fig. 1) in each season of the year, the actual age composition of the rabbits shot in each district (usually spread over two or more seasons) was compared with the expected age composition (pooling both sexes and both years). This expected age composition was based on the mean age composition of all rabbits shot each season from all districts, weighted for each district by the number of rabbits actually shot there each season.

However, this over-all, seasonal, mean age composition may not have been representative of the Wairarapa as a whole because most of the rabbits on which it was based will have come from just those few districts shot in that one season. Each seasonal mean age composition (b) was therefore smoothed (a + 2b + c)/ 4 with the all-district mean of the immediately preceding and following seasons (a, c), thereby considerably expanding the spatial and temporal base of the expected age compositions.

Table 10 discloses numerous local differences in the rabbits' age composition. For example, the proportion of first-year rabbits ranged from 9.4% more than expected in the Palliser Bay district to 11.6% fewer than expected in the adjoining district of Pirinoa, though both districts were shot in autumn. Districts with significantly fewer than expected first-year rabbits (Weraiti, Carterton-Featherston-Martinbourgh, Longbush, Otaraia and Pirinoa) all lie more or less in the low rainfall belt (Fig. 1), where late-summer breeding may have been relatively unproductive. However, other significant differences, as in the varying proportions of first-year rabbits in the adjoining districts of Tuturumuri, Tora, White Rock and Palliser Bay, are not easily explained.

Reproduction and productivity
i) Males with scrotal testes

We recorded whether or not males had scrotal testes, as did Myers & Poole (1962) and Bell (1977); those with one scrotal testis were grouped with those having both scrotal. Few males less than four months old had scrotal testes, and, pooling all seasons, 33% of those aged 4-6 months (Table 11). Thereafter the percentage increased slowly with the rabbits' age.

Seasonal changes were small (Table 12), though males more than six months old were most likely to have scrotal testes in summer ($\chi^2 = 4.38$, df 1, p <0.05) and least likely in autumn ($\chi^2 = 13.96$, df 1, p < 0.01). Within each age group, more of the heavier than of the lighter males had scrotal testes in spring (p<0.05). Many more ($\chi^2 = 30.5$, df 1, P<0.00l) of the males over six months old had scrotal testes in 1966-67 than in 1965-66.

ii) Females pregnant and / or lactating
Females with embryos visible as swellings of the uterus were recorded as pregnant. Pregnancy was probably not detected during the first five days of gestation. The data in Tables 13 and 14 have not

Table 10: *Actual compared with expected age composition of rabbits shot in each district. Districts are listed in the order in which they were shot, starting in spring, and are numbered as in Figure* 1 .

	District	Percentage age distribution (months)						Rabbits shot,	Diff. in age shot vs expo
		Shot			Expected				
		1-12	13-36	>36	1-12	13-36	>36	n	P =
1.	Hinakura	54.5	41.5	4.0	53.7	40.7	5.6	1584	<0.05
2.	Te Wharau	58.7	36.0	5.3	55.9	38.4	5.7	2274	<0.05
3.	Homewood	56.9	38.6	4.5	54.6	40.1	5.3	1367	N.S.
4.	Westmere	57.8	37.4	4.8	56.5	38.1	5.4	1919	N.S.
	Brancepeth	46.3	42.8	10.9	56.3	37.5	6.2	339	< 0.001
5.	Werain								
6.	Maungaraki	54.9	41.5	3.6	55.5	38.7	5.8	605	<0.05
7.	Longbush	45.9	49.2	4.9	55.7	38.4	5.9	388	<0.001
8.	White Rock	55.1	34.8	10.1	56.6	37.4	6.0	597	<0.001
9.	Tora	52.8	40.0	7.2	56.8	37.1	6.1	752	N.S.
10.	Tuturumuri	62.2	34.5	3.3	57.1	36.8	6.1	1404	<0.001
11.	Ruakakoputuna	59.4	33.0	7.6	58.5	35.5	6.0	786	N.S.
12.	Admirals Rd	54.7	39.0	6.3	56.8	37.2	6.0	651	N.S.
13.	Ponatahi	60.5	33.0	6.5	59.1	34.9	6.0	697	N.S.
14.	Woodside	57.0	37.6	5.4	59.4	35.0	5.6	500	N.S.
15.	Otaraia	54.4	35.6	10.0	61.0	32.9	6.1	671	<0.001
16.	Pirinoa	49.6	38.9	11.5	61.2	32.9	5.9	724	<0.001
17.	Palliser Bay	70.6	25.5	3.9	61.2	32.7	6.1	330	<0.01
18.	Western Lake	62.7	31.5	5.8	60.8	33.0	6.2	569	N.S.
	Pigeon Bush								
19.	Waingawa	57.0	39.0	4.0	58.2	36.1	5.7	521	N.S.
	Masterton								
	Carterton								
20.	Featherston	48.9	41.9	9.2	56.4	38.2	5.4	523	<0.001
	Martinborough								

Table 11: *Percentage of males with scrotal testes, according to their age; all seasons pooled.*

Age (months)	1965-66		1966-67		Both years
	n	% scrotal	n	% scrotal	% scrotal
<4	528	3.2	473	1.5	2.4
4- 6	875	30.1	968	35.7	33.0
7- 9	439	54.2	721	56.3	55.5
10-12	267	55.4	304	64.2	60.1
13-24	1100	55.8	1574	65.1	61.3
25-36	385	58.4	449	64.4	61.6
>36	357	57.7	301	68.1	62.5

Table 12: *Percentage of males more than six months old with scrotal testes, by seasons.*

Season	1965-66		1966-67	
	n	% scrotal	n	% scrotal
Spring	857	54.49	1273	66.61
Summer	652	60.12	864	64.24
Autumn	706	54.69	890	57.75
Winter	293	55.97	322	62.73
All seasons	2548	56.16	3349	63.27

been corrected for this, but elsewhere observed pregnancy rates have been multiplied by 30/25 (following Gilbert & Myers, 1981; cf. Adams, 1960) to measure the proportion of females actually pregnant

On average over the two years, more than 90% (observed % x 30/25) of the females over three months old were pregnant in September, October and November (Table 13), over 80% in August and December, and over 60% in July and January-
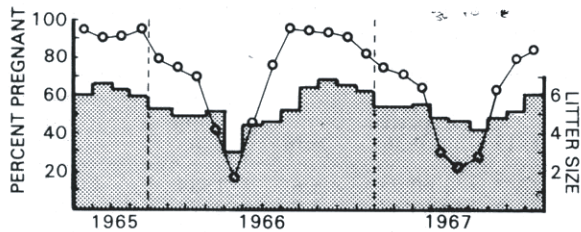
Figure 5: *Monthly percentages of females more than three months old that were pregnant* (-0-), *with their mean litter-size (shaded).*

March. April, May and June were the only months with fewer than 50% of the females pregnant. This seasonal pattern was similar in the two years (Fig. 5).

Pooling all seasons in Table 14, only 3.2% of the females less than four months old were pregnant, all of them in spring or summer. Above this age, the percentage of females pregnant rose steeping to 87.0% at 10-12 months of age, and then gradually

declined to 76.5% for females more than 36 months old. Similar percentages of the females more than six months old were pregnant on the plain as in the hills, and in districts of different average rainfall and population density.

Table 13 also shows that among all age groups the maximum percentage of pregnant and / or lactating females recorded as only pregnant occurred at the start of breeding in winter, with little change from spring through to autumn. The maximum percentage recorded as only lactating occurred at the end of the breeding season in autumn. The maximum percentage of females recorded as both pregnant and lactating occurred, as expected, at the peak of breeding in spring, when successive pregnancies follow quickly one after another; this percentage declined from summer through the autumn to a minimum in winter.

Many females up to six months old were breeding for the first time, so they included relatively few that

Table 13: *Percentage of females more than three months old that were visibly pregnant (P) and/or lactating (L), with the estimated total percentage pregnant (observed* x *30/25).*

Month	n	1965-66 Percentage P only	P+L	L only	Est. tot. %P	n	1966-67 Percentage P only	P+L	L only	Est. tot. %P
Sep	77	22.08	57.14	12.99	95.06	151	34.44	45.03	15.89	95.36
Oct	349	24.07	51.86	14.90	91.12	580	27.07	51.21	13.97	93.94
Nov	486	39.09	37.04	11.52	91.36	592	24.49	*51.52*	14.53	91.21
Dec	197	39.09	40.10	6.09	95.03	266	28.20	39.85	18.42	81.66
Jan	137	33.58	32.85	13.87	79.72	319	36.99	25.39	13.79	74.86
Feb	350	34.57	28.00	20.29	75.08	550	31.82	27.45	18.00	71.12
Mar	582	26.12	32.13	22.16	69.90	379	25.33	28.76	25.07	64.91
Apr	270	17.41	17.04	24.44	41.34	309	16.18	8.74	18.45	29.90
May	47	10.64	2.13	10.64	15.32	341	14.08	4.99	12.90	22.88
Jun	117	35.04	4.27	10.26	47.17	198	22.22	*1.52*	10.10	28.49
Jul	102	52.94	10.78	14.71	76.46	52	44.23	7.69	19.23	62.30
Aug	91	39.56	40.66	17.58	96.26	86	36.05	30.23	I 7.44	79.54
Sep						227	28.19	42.29	19.82	85.58

Table 14: *Percentage of females visibly pregnant (P) and/or lactating (L), with the estimated total percentage pregnant, according to their age; all seasons pooled.*

Age (months)	n	Percentage P only	P+L	L only	Est. tot. %P
<4	1276	2.60	0.08	0.49	3.22
4- 6	1414	29.69	11.06	7.69	48.90
7- 9	1517	27.76	25.76	17.89	64.22
10-12	767	29.29	43.17	15.16	86.95
13-24	2263	28.11	42.72	19.02	85.00
25-36	559	26.97	38.90	22.57	79.04
>36	342	28.14	35.63	21.56	76.52

were lactating (Table 14). There were similar percentages of females in the three categories (pregnant only, lactating only, or both) among those 7-12 months and more than 12 months old. Females over six months old were distributed similarly among the three categories in both years, but many more of those up to six months old were pregnant as well as lactating in the summer and autumn (and perhaps also in the winter) of 1966 than of 1967.

iii) Pre-natal mortality and litter-size
Pregnant female rabbits may lose some or all of the embryos in a litter, usually early rather than late in the gestation period (Brambell 1942, Lloyd 1963). Though corpora lutea were not counted, the numbers of live and dead embryos were recorded separately, together with the average length of live embryos in each litter.

Pre-natal mortality could not be measured precisely for several reasons: (i) corpora lutea were not counted, and (ii) neither pregnancy nor resorption were detected during the first five days of gestation; (iii) females that had recently lost whole litters were not identified; (iv) traces of small resorbing embryos disappear within 2-3 days of their death (Brambell, 1944), whereas traces of older embryos persist longer and so bias the record in their favour; and (v) embryos dying when more than about 20 days old

may be aborted without trace, rather than resorbed. Moreover the finding of dead embryos in the uterus does not mean that others have not died earlier or would not have died later in the gestation period (Lloyd, 1963).

The incidence of pre-natal mortality was extremely variable, but at times considerable; and it was consistently $(\chi^2 = 16.53$, df 1, p<0.001) more prevalent in 1966-67 than in 1965-66 (Table 15).

The percentage of pregnant females with at least one dead embryo visible at autopsy ranged in different months from nil to 28%. Although pre-natal mortality was recorded more commonly in spring and summer than in autumn and winter, there was no agreement in its month-to-month occurrence between the two years of the study (r = - 0.16); the percentage of pregnant females with one or more dead embryos fluctuated erratically from month to month.

Pre-natal mortality was positively associated with the age of the female (r = 0.939, p<0.001), as in domestic rabbits (refs in Adams, 1970). Thus about 15% of pregnant females up to two years old had dead embryos, compared with about 28% of those more than 36 months old (Table 16, Figure 6).

The number of dead embryos per pregnant female ranged from none or one to the whole litter. Losses

Table 15: *Percentage of visibly pregnant females more than three months old having dead embryo(s)*

Year	Spring	Summer	Autumn	Winter	All seasons
		Percentage of females having dead embryo(s)			
1965-66	15.09	16.95	9.59	12.16	13.92
1966-67	18.56	18.36	21.61	14.50	18.74

Table 16: *Percentage of pregnant females with one or more dead embryos visible at autopsy, according to their age all seasons pooled.*

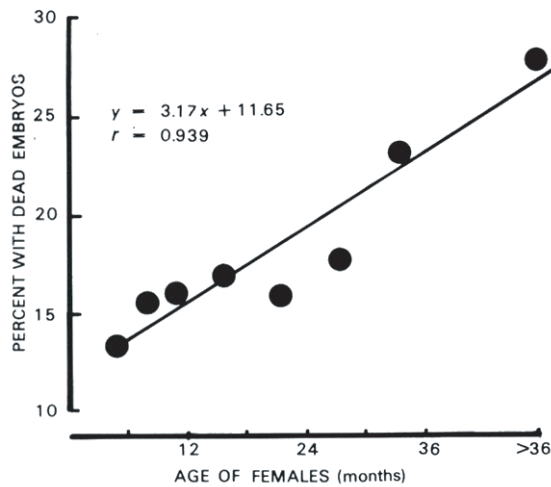| Age (months)	Number 1965-66	Number 1966-67	% with dead embryo(s) 1965-66	% with dead embryo(s) 1966-67	Both years
<7	365	236	11.78	15.68	13.31
7- 9	256	519	9.77	18.50	15.61
10-12	276	259	15.94	16.22	16.08
13-18	364	493	13.74	19.27	16.92
19-24	278	407	12.59	18.18	15.91
25-30	82	116	18.29	17.24	17.68
31-36	90	76	21.11	26.32	23.49
>36	99	114	22.22	33.33	28.17
All ages	1810	2220	13.98	19.01	16.75

Figure 6: *Percentage of females more than five days pregnant having one or more dead embryos, related to the age of the female; all seasons and both years pooled.*

were similar in both years and Table 17 shows that, pooling years, females with pre-natal mortality lost 28.7% of their embryos in spring, 30.7% in summer, 31.9% in autumn, and 36.9% in winter (the difference between spring + summer and autumn + winter is significant: $\chi^2 = 5.379$, df 1, $p < 0.05$). These figures are conservative since they apply only to observed mortality. There were 23 cases of whole-litter mortality, involving only 3.5% of the 667 litters with some mortality (cf. Brambell, 1942; Lloyd, 1963).

Table 18 shows the loss of embryos by females of different ages; as before, only females with at least one dead embryo are included. Considering how closely the frequency of pre-natal mortality varied with the female's age (Fig. 6), its extent was surprisingly similar in females of all ages. Females 7-24 months old lost about 29% of their embryos, compared with 32-33% by younger + older females ($\chi^2 = 5.349$, p<0.05). Litters with at least one dead embryo started significantly larger (by 0.19 embryo; $\chi^2 = 14.80$, df 5, p<0.05) than those with no dead embryos, and, as expected, more of the larger litters

Table 17: *Mean litter-size (a) before and (b) after observed pre-natal mortality; females of all ages pooled. (Data for September 1967 excluded.)*

Season		Litter-size					
1965-67		(a)		(b)		Difference	%
	n	Mean	S.D.	Mean	S.D.	(a-b)	loss
Spring	107	6.24	1.93	4.50	1.91	1.74	27.88
Summer	82	5.56	1.62	3.80	1.49	1.75	31.47
Autumn	42	5.14	1.60	3.69	1.87	1.45	28.24
Winter	22	4.68	1.13	3.09	1.06	1.59	33.97
Spring	190	6.86	1.56	4.83	1.88	2.03	29.59
Summer	130	5.69	1.72	3.99	1.57	1.70	29.88
Autumn	75	5.11	1.43	3.29	1.60	1.82	35.61
Winter	19	4.63	1.07	2.79	1.36	1.84	39.66

Table 18: *Mean litter-size (a) before and (b) after observed pre-natal mortality, by age of female; all seasons pooled. (Data for September 1967 excluded.)*

		Litter-size					
Age		(a)		(b)		Difference	%
(months)	n	Mean	S.D.	Mean	S.D.	(a-b)	loss
<7	82	4.71	1.54	3.18	1.69	1.52	32.38
7- 9	130	5.68	1.69	4.02	1.76	1.65	29.14
10-12	86	6.52	1.79	4.66	2.00	1.86	28.15
13-24	261	6.21	1.67	4.38	1.90	1.83	29.52
>24	146	6.07	1.76	4.07	1.82	2.00	32.96
All ages	705	5.94	1.76	4.14	1.86	1.80	30.31

Table 19: *Mean litter-size (including dead embryos) of pregnant female rabbits with and without dead embryos; all seasons pooled.*

| Litter-size | Number of litters | | Total | Percentage with |
| | without | with | | |
	dead embryos			dead embryos
1- 2	108	16	124	12.90
3- 4	589	122	711	17.16
5- 6	1391	277	1668	16.61
7- 8	914	206	1120	18.39
9-10	136	43	179	24.02
11-12	6	3	9	33.33
Totals	3144	667	3811	
Mean	5.75	5.94	5.79	17.50
S.E.	0.03	0.07	0.03	
P		<0.05		

than of the smaller ones included one or more dead embryos (Table 19). On average (Table 17), females with pre-natal mortality had 1.80 dead embryos, which reduced the size of their litters to 1.58 below the overall mean.

Table 20 shows the percentages of litters with embryos of different length that included at least one dead embryo. This Table must be interpreted cautiously since litters with only dead embryos had to be omitted, and, more importantly, because the rapid resorption of small dead embryos will have favoured the recording of large ones. Additional complications arise from the uneven number of days' gestation spanned by each of the evenly-spaced growth intervals. The effect of this cannot be gauged

Table 20: *Percentage of litters with embryos of different lengths having one or more dead embryos; seasons and females of all ages pooled. Embryos were measured in inches; lengths in mm in Tables* 20 *and* 21 *are the nearest metric equivalents.*

| Approx. length of embryos (mm) | Approx. day of gestation | Total litters measured | Litters with dead embryo(s) | |
			n	%
6-17	10.0	757	51	6.74
18-30	16.0	951	259	27.23
31-42	19.5	589	195	33.11
43-55	22.5	467	102	21.84
56-67	25.5	433	49	11.32
68-80	28.5	516	26	5.04
>80	30.0	239	10	4.18
Totals		3952	692	17.51

exactly, but it might reduce the improbably large difference between the percentage of litters with dead embryos 6-17 mm and 18-30 mm long (6.74% d. 27.23%). Nonetheless, at least some litters with embryos more than 67 mm long (i.e. in the last week of gestation) contained dead embryos; these might have been resorbed or aborted (Brambell & Mills, 1948).

Litters with embryos 6-17 mm long were significantly smaller (p<0.05; Table 21) than those with embryos 18-30 mm long, presumably because some of the smaller embryos were missed from the counts. In addition, some litters with small embryos 6-17 mm long may have been dying sequentially, so might have been smaller than average. Otherwise average litter-size was inversely related to size of embryos (r = -0.957, p<0.00l), decreasing by 4.7% from 5.96 for those with embryos 18-30 mm long to 5.68 for ones with embryos 68-80 mm long (Table 21). This decline was common to females of all ages except those aged 10-12 months; if females of this age lost any embryos, they must have done so when the embryos were less than about 5 mm long. Only 237 litters had embryos more than about 80 mm long (compared with 507 with embryos 68-80 mm long), and they were significantly smaller than those with embryos 68-80 mm long (Table 21). Evidently it was mainly these very small litters that produced such large embryos. Also, significantly fewer (x^2 = 13.430, p<0.001) of the larger litters, than of the smaller ones, had embryos more than 67 mm long.

Table 21: *Recorded litter-size (including dead embryos), (a) at different seasons pooling females of all ages, and (b) of females of different ages pooling all seasons, according to the length of their embryos at autopsy.*

(a) Season, and (b) Age of females (months)		Recorded litter-size Length of embryos (mm)							All lengths
		6-17	18-30	31-42	43-55	56-67	68-80	>80	
(a)									
Spring	Mean	6.45	6.69	6.72	6.56	6.54	6.47	5.89	6.54
	S.E.	0.10	0.09	0.12	0.11	0.11	0.12	0.22	0.04
Summer	Mean	5.56	5.67	5.60	5.51	5.23	5.29	5.23	5.50
	S.E.	0.12	0.10	0.12	0.13	0.16	0.13	0.22	0.05
Autumn	Mean	4.92	4.99	5.09	5.25	5.06	5.14	4.97	5.06
	S.E.	0.14	0.12	0.13	0.16	0.13	0.14	0.16	0.05
Winter	Mean	4.71	5.06	4.74	4.98	4.53	4.50	4.17	4.79
	S.E.	0.20	0.15	0.18	0.20	0.27	0.21	0.58	0.08
(b)									
4- 6	Mean	4.60	4.74	4.43	4.78	4.14	4.69	3.50	4.53
	S.E.	0.15	0.15	0.17	0.20	0.21	0.24	0.30	0.07
7- 9	Mean	5.47	5.66	5.62	5.45	5.67	5.22	4.77	5.49
	S.E.	0.15	0.13	0.16	0.19	0.16	0.15	0.25	0.06
10-12	Mean	6.47	6.34	6.56	6.39	6.40	6.54	6.67	6.46
	S.E.	0.19	0.15	0.18	0.16	0.20	0.18	0.32	0.07
13-24	Mean	6.24	6.37	6.26	6.24	6.04	5.96	5.72	6.18
	S.E.	0.10	0.09	0.12	0.12	0.12	0.12	0.17	0.04
>24	Mean	5.71	6.01	5.90	5.94	5.77	5.48	5.56	5.80
	S.E.	0.17	0.14	0.21	0.16	0.20	0.19	0.32	0.07
Totals	n	742	930	570	461	428	507	237	3875
	Mean	5.79	5.96	5.90	5.87	5.69	5.68	5.37	5.81
	S.E.	0.07	0.06	0.08	0.08	0.08	0.08	0.12	0.03

$$y = 35.399x + 3.397$$
$$r = 0.803$$
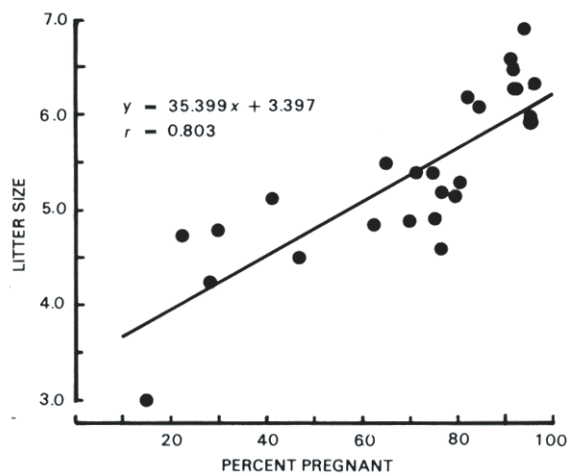
Figure 7: *Mean monthly litter-size related to the percentage of the females that was pregnant.*

If litter-size is taken as the number of healthy embryos of any size counted per pregnant female, then the mean monthly litter-size of females of all ages (pooled for both years) varied from 4.36 in June to 6.72 in October (Table 22). As with the percentage of females pregnant, average litter-size first increased with the female's age from 4.53 for females 4-6 months old to 6.46 for those 10-12 months old; and then declined to 5.80 for females more than 24 months old (Table 21). The seasonal pattern of change was similar in both years (Fig. 5, above). The mean monthly litter-sizes over the two years varied $(r = 0.803,$ p<0.001) with the percentage of the females pregnant at the time (Fig. 7).

iv) Productivity
Mean litter-sizes referred to thus far were obtained from counts of embryos made between about the sixth and last days of gestation. During this period,

Table 22: *Frequency distributions of recorded litter-sizes, females of all ages pooled.*

Litter-size	Number of litters												
	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
1965-66													
1- 2	1	1	14	5	9	18	10	2	1	2	2	1	
3- 4	11	23	36	22	36	57	109	24	3	20	24	17	
5- 6	19	90	121	49	80	101	165	45		19	29	39	
7- 8	21	85	140	49	38	31	30	11		2	2	7	
9-10	3	35	27	7		1	0	1				1	
11-12		1	2				1						
Totals	55	235	340	132	163	208	315	83	4	43	57	65	
Mean	6.01	6.63	6.30	5.97	5.30	4.92	4.89	5.14	-	4.48	4.59	5.19	
S.E.	0.81	0.43	0.34	0.52	0.41	0.34	0.28	0.56	-	0.68	0.61	0.64	
1966-67													
1- 2	1	4	16	3	3	17	3	2	4	3	1	1	5
3- 4	11	14	41	23	45	61	43	25	20	22	8	15	13
5- 6	54	143	129	69	94	161	121	42	34	17	14	33	63
7- 8	45	225	196	70	43	70	40	3	4	1	2	5	58
9-10	6	38	42	11	1	3	2					1	4
11-12	2		3										
Totals	119	425	427	176	186	312	209	72	62	43	25	55	143
Mean	6.34	6.81	6.51	6.22	5.44	5.38	5.45	4.78	4.73	4.24	4.86	5.14	6.10
S.E.	0.58	0.33	0.31	0.47	0.40	0.30	0.38	0.56	0.60	0.65	0.97	0.69	0.51

Table 23: *Productivity*.

Month	% ♀♀ pregnant (observe x 30/25)		Mean litter-size at birth		Young born per female	
	1965-66	1966-67	1965-66	1966-67	1965-66	1966-67
Sep	95.06	95.36	5.81	6.14	5.52	5.86
Oct	91.12	93.84	6.43	6.66	5.86	6.25
Nov	91.36	91.21	6.10	6.31	5.57	5.76
Dec	92.26	82.10	5.77	6.02	5.32	4.94
Jan	80.28	74.86	5.11	5.23	4.10	3.92
Feb	75.08	71.35	4.73	5.18	3.55	3.70
Mar	69.90	64.91	4.71	5.25	3.29	3.41
Apr	41.33	29.90	4.94	4.58	2.04	1.37
May	15.32	22.42	2.80	4.53	0.43	1.02
Jun	47.18	28.49	4.28	4.05	2.02	1.15
Jul	76.48	62.30	4.39	4.65	3.36	2.90
Aug	96.26	79.54	4.99	4.94	4.80	3.93
Mean	72.89	66.36	5.01	5.30	3.82	3.68
S.E.	7.42	7.51	0.28	0.24	0.50	0.54
Total young born per female each year:					45.86	44.21

the mean observed litter-size at first increased with increasing length of the embryos and then decreased (Table 21). On average, litter-size at birth was about 0.2 young less than the mean observed litter-size, and this figure was used to calculate productivity.

The annual production of young per female was estimated by multiplying the percentage of females pregnant .by the mean litter-size at birth, for each

Table 24: *Body-weights of rabbits according to their age, all seasons pooled.*

Age (months)		Males			Females		Difference between males and females	
	n	Mean	S.E.	n	Mean	S.E.	g	%
4- 6	1840	1277	3.33	1427	1304	5.35	27	2.114
7- 9	1160	1481	3.87	1462	1584	4.06	103	6.955
10-12	574	1491	5.27	749	1729	6.45	238	15.962
13-18	1409	1535	3.17	1229	1762	4.69	227	14.788
19-24	1269	1571	3.36	1001	1790	3.99	219	13.940
25-30	383	1602	6.40	308	1821	4.02	219	13.670
31-36	453	1626	5.75	246	1837	3.92	211	12.977
>36	658	1629	5.13	351	1839	4.08	210	12.891
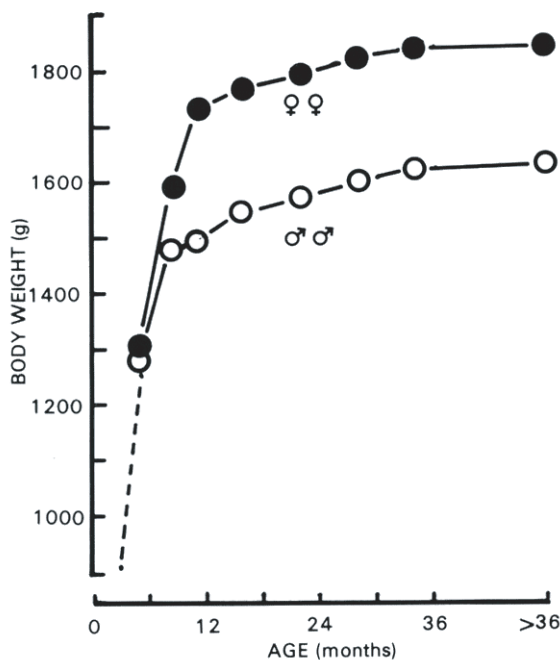
Figure 8: *Mean body-weights of male and female rabbits, pooling all seasons, with the weights of rabbits up to five months old (pecked line) recorded by Tyndale-Biscoe & Williams (1955).*

month, and, since gestation lasts about 30 days, we can allow one litter per female per month (Table 23). More of the females were pregnant in 1965-66 than in 1966-67, but the average litter-size was smaller. These two variables tended to cancel out to produce similar estimates of 45.86 young born per female per

year in 1965-66 and 44.21 young in 1966-67. Monthly production per female peaked in October and was least in May, in both years.

The number of young produced each year by females of different age (pooling all seasons) likewise varied with the mean proportion pregnant and their litter-size at birth, as follows (age of female, number of young): 4-6 months, 26.47; 7-9 months, 42.15; 10-12 months, 67.20; 13-24 months, 61.00; 25-36 months, 53.12; and more than 36 months, 51.42.

v) Body-weight

All the rabbits were weighed before autopsy, on the day after they were shot. Figure 8 shows the growth curve of the rabbits, extending that for younger rabbits from Hawke's Bay (Tyndale-Biscoe & Williams, 1955). Both sexes continued to gain in weight slowly, at least until they were 36 months old (Table 24).

Females were on average only 27 g heavier than males at 4-6 months of age, when fewer than 50% of them were pregnant. By the time they were 10-12 months old and 87% pregnant, the females were on average 238 g heavier than the males - a bigger difference between the sexes than at any other age (Table 24). Female rabbits older than 36 months were 210 g heavier than males of the same age, and pregnant females were then 95 g heavier than those judged not pregnant (or >6 days pregnant). Brambell (1942) and Watson (1957) found no difference in the weights of paunched rabbits of the two sexes. The proportion of females pregnant can be predicted from the difference in body-weight between the sexes ($r = 0.874$, $p < 0.001$; see Fig. 9), which varied seasonally.
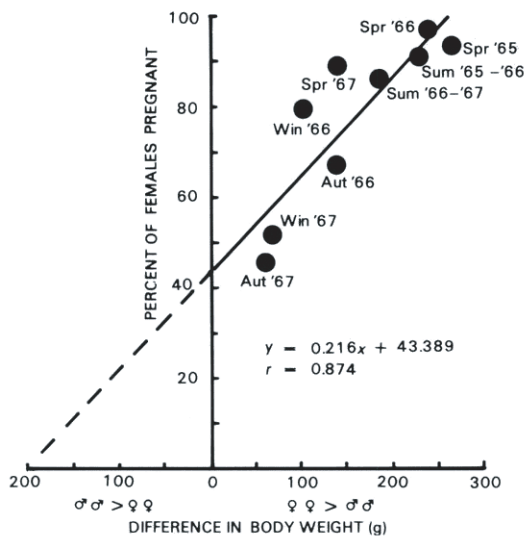
Figure 9: *Percentage of females pregnant related to seasonal differences between the mean body-weights of male and female rabbits more than six months old.*
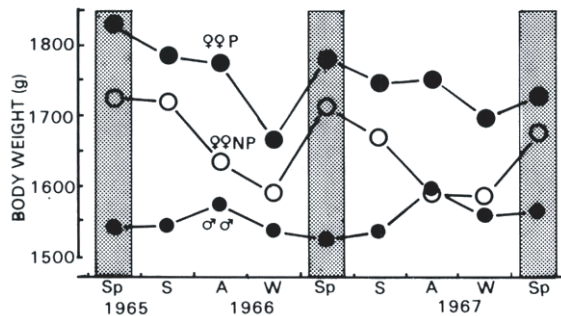

Figure 10: *Seasonal mean body-weights of male and female rabbits more than six months old:* P, *pregnant; NP, not more than five days pregnant*.

More than 45% of the females over three months old were pregnant in every three-month season; on average they were invariably heavier than the males, as was the mix of females judged either not pregnant or not more than six days pregnant. A downward, straight-line extrapolation of the trend in Figure 9 predicts that if males were on average 200 g heavier than females, none of the latter would be pregnant. Correspondingly, in our enclosed population of

rabbits (Gibb *et al.,* 1978), females ranged from being 275 g heavier than the males in spring to 175 g lighter than the males in autumn.

Figure 10 shows that the body-weights of males peaked slightly at the end of the breeding season in autumn, while females were understandably heaviest in spring and lightest in autumn-winter. More of the females were pregnant in the summer-autumn-winter of 1966 than in the same period of 1967; consequently females were heavier (and relatively heavier than males, which were 21 g lighter) in 1965-66 than in 1966-67.

There were no significant differences in the mean body-weights of rabbits, male or female, young or old, from the plain compared with the hills, or from areas of varying average rainfall or population density. Such uniformity in rather different environments may result from the rabbits living generally at very low density with minimal intra-specific competition, more or less removed from any real shortage of resources.

Watson (1957) recorded the weights of paunched rabbits, collected mainly by poisoning and trapping and not precisely aged, so his data are not exactly comparable to ours.

Discussion

Sex, age and survival

In the wild, male and female rabbits are born in about equal numbers (Brambell, 1942; Watson, 1957). Discussion of the sex ratio, and hence of the relative survival rates of the sexes after leaving the nest, is bedevilled by the variety of ways in which rabbits have been sampled and survival expressed. Lloyd (1963), for instance, obtained 58% males in a sample of 194 trapped rabbits (i.e. not different from parity, *P>0.05),* and only 24% (significantly fewer; $\chi^2 = 27.05$, P< 0.001) of 84 rabbits obtained by ferrets; Tyndale-Biscoe & Williams (1955) recorded 51 % males in a sample of ferreted young in New Zealand. Watson (1957) warned that the observed sex ratio may be affected by how the rabbits are collected, though he found no difference between trapped and poisoned rabbits.

Two aspects of the sex ratio of rabbits shot for this study merit attention: the exceptionally high proportion of males among rabbits 4-6 months old; and the increasing proportion of males in the older cohorts (Table 4).

A possible explanation for the apparently high proportion of males (or, more accurately, the scarcity of females) among rabbits 4-6 months old is that females breeding for the first time at this age may be especially retiring. If under other circumstances young females breed for the first time when older than 4-6 months, or over a wider span of ages, then their scarcity in shot samples may be correspondingly delayed or spread over a longer period.

Useful comparison of sex ratios and survival rates must recognise Parer's (1977) observation that rabbits trapped tended to be those furthest from their warrens. As males have larger home ranges than females, and first-year rabbits than older ones (Gibb *et al.,* 1978), males and first-year rabbits may be shot preferentially.

N. E. Gilbert and K. Myers (pers. comm.) kindly supplied figures for the sex ratios of rabbits shot in the same way and by the same people at six sites in Australia (Table 25). On average, 52.5% of the first-year rabbits and 51.1 % of the older ones were males, compared with 48.8% and 56.7%, respectively, for rabbits shot in the Wairarapa. The site at Mitchell, was relatively benign for rabbits and produced a sex ratio very similar to ours. Only in the harsh, semi-arid conditions of Tero Creek were males in the minority in both age groups, and there

were significantly $(\chi^2 = 14.01, P<0.0l)$ fewer of them than in other localities.

When physiologically stressed, female rabbits survive better than males (N. E. Gilbert & K. Myers pers. comm.; Gibb *et al.,* 1978). Combining both age groups at the other Australian sites, the percentages of males ranged only from 50.4% at Canberra to 54.5% at Urana, $(\chi^2 = 4.04,$ df 1, $P<0.05)$. Thus only at Mitchell did males seem to survive better than females, as in the Wairarapa. However, the difference between males and females at Mitchell is barely significant $(\chi^2 = 3.83,$ df 1, $P>0.05)$, whereas that in the Wairarapa (based on larger samples) is highly significant $(\chi^2 = 112.53,$ df 1, $P<0.001)$.

As young rabbits less than four months old were obviously under-represented in samples from the Wairarapa, their survival could not be measured. Southern (1940) thought that only about 10% of weaned young survived the breeding season in Britain, compared with about 30% in a low-density population in New South Wales (Myers & Schneider, 1964).

More detailed estimates (Fig. 11) from when the young first emerge above ground, about three weeks of age, make it clear that survival is extremely variable for at least the first three months then stabilises as adult survival rates are approached. In

Table 25: *Sex ratio of rabbits shot in Australia (N. E. Gilbert & K. Myers pers. comm.) compared with the Wairarapa.*

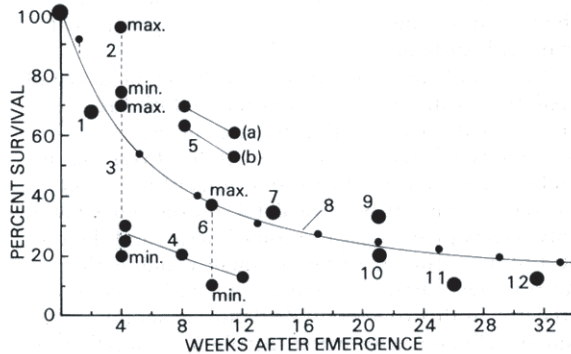| Site | Age (months) | | | |
| | 0–12 | | >12 | |
	n	% Males	n	% Males
Mitchell, Queensland (subtropical)	424	48.93	786	54.66
Snowy Plains, N.S.W. (subalpine)	883	54.82	532	52.94
Tero Creek, N.S.W. (semi-arid)	728	47.01	1076	48.55
Urana, Riverina, N.S.W. (semi-arid)	522	56.64	399	52.40
Mogo, N.S.W. (moist coastal)	519	55.77	172	48.88
Canberra, A.C.T. (dry inland)	1164	51.78	689	49.01
All Australian sites		52.49		51.09
Wairarapa, N.Z.		48.78		56.73

Figure 11: *Percentage survival of young rabbits after emergence (when about three weeks old) in Australia and New Zealand. Key to sites:* 1, *Grassy Creek, A.* C. *T. (Richardson & Wood,* 1982); 2, *Snowy Plains, N.S. W., no foxes or cats (Dunsmore, unpubl. quoted by Richardson & Wood,* 1982); 3,6 & 12, *Urana, Riverine Plain, N.S.* W. *(Parer,* 1977); 4, *Chidlow and Cape Naturaliste, W.A. (King & Wheeler,* 1981); 5, *Grassy Creek, A.C. T., warrens (a) protected and (b) unprotected from bird predation (Richardson & Wood,* 1982); 7, *Hawke's Bay,* N.Z. *(Tyndale-Biscoe & Williams,* 1955); 8, *Darling River, arid N.S.* w. *(after Wood, 1980, adjusted to survival from emergence);* 9, *Snowy Plains, N.S. W., optimum survival (Gilbert & Myers,* 1981); *10, Urana, N.S. W., optimum survival (Gilbert & Myers,* 1981). 11. *Wairarapa, N.Z., optimum survival (this paper). Line fitted by eye to points* 8.

the first four weeks after emergence, recorded survival ranges from 96% in a sparse population recovering from myxomatosis on the Snowy Plains, said to be without cats and foxes, to a low of 20% at Urana (see Fig. 11 for references). We recorded almost as wide a range in survival in different years in our enclosure (Gibb *et al.,* 1978). There, as near Canberra (Richardson & Wood, 1982), predation was the principle agent of mortality, by cats and mustelids in New Zealand and by cats, foxes and birds of prey in Australia.

Southern (1940) believed that young born early in the breeding season in Britain survived less well than those born later, but the reverse is true in Australia and New Zealand (Parer, 1977; Gibb *et al.,* 1978; Richardson & Wood, 1982). During moderate drought at high density in New Zealand, late-born young grew very slowly and survived poorly (Gibb *et al.,* 1978).

At each site in Figure 2, young conceived either

early or late in the breeding season appear to have survived less well than those born mid-season. This differs from other studies (e.g. Mykytowycz, 1961; Myers & Poole, 1963; Dunsmore, 1974; Parer, 1977; Gibb *et al.,* 1978; Wood, 1980; d. Southern, 1940; Tyndale-Biscoe & Williams, 1955), which stress particularly the poor survival of late-born young. The graph for the Wairarapa reflects the long breeding season, the resulting higher productivity being balanced by poorer survival than in Australia.

Seasonal changes in the survival of young are dictated by fluctuations in the food supply, as well as by predation. In one year of low density and abundant green feed, the rabbits in our enclosure (Gibb *et al.,* 1978) had a second breeding season, in autumn, when the population almost doubled in numbers. Young females born in the previous season participated, together with older ones, and the young survived quite well despite the unpropitious time of year. This is evidently a rare example of opportunistic breeding in New Zealand.

The sudden switch from relatively good survival of young conceived before the end of November to much poorer survival of those conceived later (Fig. 2) coincides with the flowering of grasses and other pasture plants and with the drying-off of the pasture (Radcliffe, 1975; see also Fig. 13, below); this is likely to impair lactation. Indeed, it is surprising that 90% of the adult females remained pregnant through to the end of December. We do not know exactly when or why these young rabbits died. Their survival is poorer than in Australia (Gilbert & Myes, 1981), as it must be in a stable population to offset the rabbits' greater productivity in New Zealand.

The limiting effects of food shortage in late summer need not imply that weaned young die of starvation, though some do in both Australia and New Zealand. A ready supply of food enhances prospects of survival whatever the immediate agent of mortality (Gibb, 1981). Predation by feral cats and mustelids is probably important, and may be aggravated by moderate food shortage in dry summers (Gibb *et al.,* 1978).

At the start of the breeding season in Hawke's Bay, nearly 60% of the rabbits present were less than 10 months old, and more than 75% of the breeding stock had been born in the previous 12 months (Watson, 1957). These percentages are rather higher than ever recorded in the Wairarapa, where

rabbits less than four months old were under-represented in the shot samples. Parer (1977) recorded an average annual adult survival of 55% at Urana and Gilbert & Myers (1981) give 46% for rabbits on the Snowy Plains, which compare with the 41 % calculated for the Wairarapa, or the rather lower estimates of 31 % and 25% for males and females respectively, based on the ratios in Table 6.

The survival of young rabbits improves as they get older: Parer (1977) recorded about 50% survival per 40 days when the young were 60-140 days old, compared with 65.5% when they were 141-180 days old. King & Wheeler (1981) thought that the survival of sub adults and adults more than 8-9 months old was unaffected by their age in Western Australia. In our confined population (Gibb *et al.,* 1978) survival continued to improve slightly until the' rabbits were at least three years old. In fact, older cohorts survived a population crash and subsequent long decline so well that eventually they predominated in the breeding population. In confined populations at Canberra, Myers & Poole (1963) noted that survival diminished as population density rose, and in our confined population both reproductive rate and survival rate were inversely density-dependent (Gibb *et al.,* 1978).

Seasonal changes in numbers
Figure 4 showed that in the Wairarapa the maximum population density in March was scarcely twice the minimum in September, despite prolific breeding. This limited seasonal change emphasizes the severity of the mortality that falls most heavily on the very young (see Fig. 2). Much more exaggerated seasonal changes in numbers often occur in enclosures and on small islands, where predation is reduced and dispersal impossible (d. the 'fence effect' of Krebs (1971)). Gilbert & Myers (1981) described comparable population trends for populations of rabbits at Urana (a large enclosure) and on the Snowy Plains (see Fig. 4). Actual densities are not known, but at Urana and probably on the Snowy Plains density was generally higher than in the Wairarapa. Of the eleven Australian sites considered by Gilbert & Myers (1981), Urana had the highest and the Snowy Plains the lowest annual productivity (38 d. 15 young born per adult female). Although rabbits were more productive in the Wairarapa than at Urana, the amplitude of seasonal changes in numbers in the Wairarapa was similar to that on the

Snowy Plains. Clearly the amplitude of seasonal changes in numbers has less to do with productivity than with subsequent survival.

Patterns of survival may vary with the incidence of predation at different stages in the rabbit's life history, and on seasonal differences in the availability of green food. In Australia, foxes dig out rabbits' nests and feral cats and birds of prey take emerged young. In New Zealand, on the other hand, only ferrets gain access to rabbits' nests, and the only bird of prey capable of killing small young is the Australasian harrier, a common but rather ineffectual predator in this role. New Zealand's generally more equable climate, with better distributed rainfall than in Australia, permits a long breeding season which in turn provides a supply of young prey for much of ,the year. This and the presence of alternative prey (Gibb *et al.,* 1978) may prevent depletion of predator populations between breeding seasons of the rabbit. The greater intensity of predation on young may in turn account for the smaller fluctuations in rabbit numbers through the year in the Wairarapa than in Urana, and perhaps also for the difference between Urana and the Snowy Plains (Fig. 4).

Males with scrotal testes
On average about 60% of the males more than six months old had scrotal testes in the Wairarapa, compared with about 70% in North Canterbury (Bell, 1977). More of the males had scrotal testes in spring and summer than in autumn and winter, and more of the older than of the younger ones. Seasonal changes were similar to, but less pronounced, than in North Canterbury. At higher density in Hawke's Bay, Watson (1957) recorded maximum testes weights in September-October, and a minimum in December which was earlier than the minimum with scrotal testes in the Wairarapa. Myers & Poole (1962) slightly misinterpreted Watson (1957) by claiming that in New Zealand rabbits' testes have regressed by the end of October; Watson actually wrote that they begin to regress from October.

Andersson, Dahlback & Meurling (1979) described the breeding season of rabbits near their northern limit at 55º42 'N. in Sweden, and Skira (1978) near their southern limit at 54º 36'S. on Macquarie Island. At these high latitudes testes are heaviest 1-2 months after the spring equinox and lightest 1-2 months after the autumn equinox, i.e. about a month later than in New Zealand. At the low latitude of 24 ºS on the coast of Western

Australia, fecund males occurred throughout the year, as in New Zealand; but testes were heaviest about two months earlier than in New Zealand (King, Wheeler & Schmidt, 1983).

With many male rabbits fecund in every month in the Wairarapa, as elsewhere in New Zealand, the timing of the breeding season must depend on the females, as Watson (1957; cf. Brambell, 1944) also concluded.

Female breeding season
The peak percentage of females pregnant in the Wairarapa coincided with the seasonal peak in pasture production (Radcliffe, 1975), but whereas pasture production peaks sharply in October-November, the rabbits' breeding was sustained from August through to December inclusive (Fig. 12). Over 60% of the females were still pregnant in January, February and March, and their young born
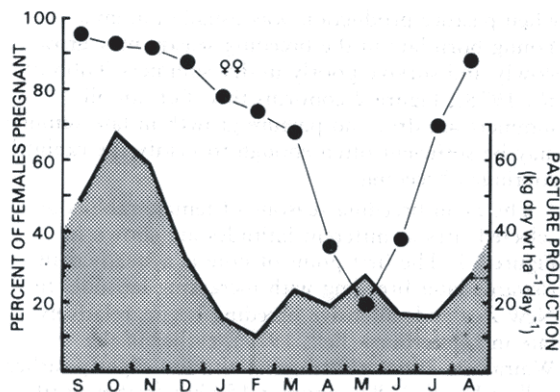
Figure 12: *Percentage of females pregnant (mean of both years, 8_8), and pasture production (mean of 5 years 1968-73, near Masterton, Wairarapa (after Radcliffe, 1975).*
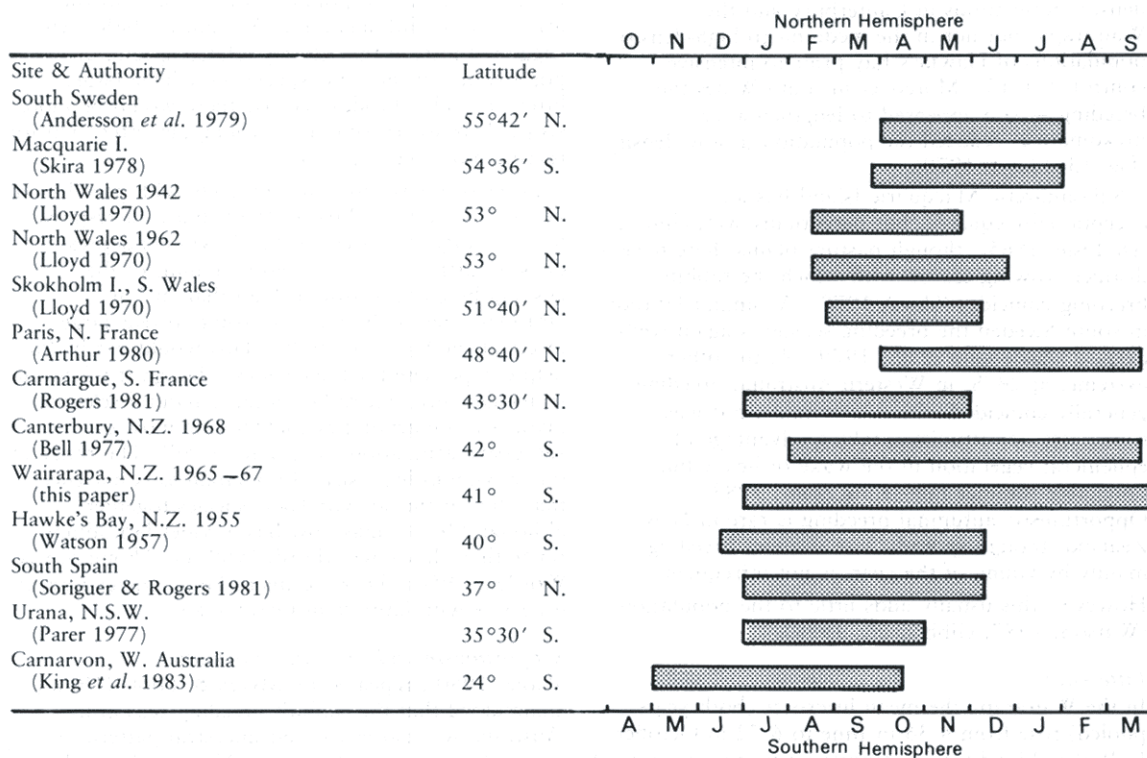
Figure 13: *Main breeding season of female rabbits (> 50% pregnant) at different latitudes.*

when pasture production was usually minimal.
Young born late in the breeding season may grow
slowly and survive poorly in dry summers (Gibb *et
al.,* 1978); Figure 2 confirms this. But not all
summers are dry, and pasture growth in late summer
may be sufficient often enough to justify the rabbits'
continued breeding.

The main breeding seasons of female rabbits at
selected sites at different latitudes are shown in
Figure 13. The first point of note is a steady drift
towards later breeding with increasing latitude. In
New Zealand, intensive breeding begins relatively
late in Canterbury (Bell, 1977), earlier in the
Wairarapa 200 km further north, and slightly earlier
still in Hawke's Bay another 150 km further north
(Watson, 1957). Secondly, the breeding season in
two of the New Zealand populations appears
unusually long. This may be in part a density-related
effect, for summer breeding is prolonged in the low-
density populations in Canterbury and the
Wairarapa, but not in the medium- to high-density
populations of Hawke's Bay prior to intensive
control (Fig. 13). Moreover in south Wales the
breeding season appeared to lengthen after
myxomatosis reduced the population to low density
(Fig. 13; Lloyd, 1970).

Sub-antarctic Macquarie Island has an
exceptionally equable, but perpetually wet, climate
(De Lisle, 1965), though pasture plants there have a
distinct growing season with which the rabbits'
breeding coincides (Skira, 1978). At similar latitude
in south Sweden the breeding season is again well-
defined (Andersson *et al.,* 1979). At the other
extreme, at 24°S. in Western Australia, breeding
generally coincided with winter rains, but was
sometimes opportunistic, taking advantage of
ephemeral vegetation in the wake of heavy but
unreliable summer rain (King *et al.,* 1983).
Opportunistic autumnal breeding is rare in New
Zealand, though sporadic late summer breeding,
mainly by young of the year, is not infrequent.
However, this usually adds little to the population
(Watson, 1957; Gibb *et al.,* 1978).

Litter-size
In the Wairarapa the mean litter-size (both years
pooled) rose from 4.36 in June to 6.72 in October.
In Wales, Lloyd (1963) reported a mean litter-size of
about six in February-June at low density after
myxomatosis, where Brambell (1942) had recorded

5.1 at high density before myxomatosis. Andersson
et al. (1979) recorded a range from 4.0 in March to
5.8 in June in southern Sweden, and Skira (1978) a
maximum of about 6.5 from mid-October to
December on Macquarie Island. The rabbits on
Macquarie are a domestic breed and may retain a
larger litter-size. Litter-sizes are similar in Australia,
rising to a seasonal maximum of about six in
September at Carnarvon in Western Australia (King
et al., 1983), and ranging from 2.5 in November to
about five in August at Urana (Parer, 1977).

Lord (1960) demonstrated a positive correlation of
litter-size with latitude among six *Sylvilagus* spp. in
North America. He attributed this to 'the principle of
inversity as expressed by Errington (1946)', whereby
'the species of the high latitudes experiencing the
high mortality rates will have correspondingly high
reproductive rates to help compensate for their
losses'. Lack (1948) pointed to the fallacy of this
argument; so did Spencer & Steinhoff (1968), who
suggested instead that closely related species or
populations of the same species may have larger
litters at high latitudes because there would be more
scope there for rearing more young per litter than for
rearing more litters per year.

Litter-size may also vary inversely with population
density, not *per se* (Myers, 1964) but as a response
to *per capita* resources. If harsh winters depress
density further below the resource limit of the
ensuing breeding season at high than at low
latitudes, then it should be possible to rear larger
litters at the higher latitudes. This would not be 'to
help compensate for their losses', though it might do
so incidentally; but rather because natural selection
favours those genotypes contributing most to
successive generations (e.g. Lack 1954). The range in
the maximum litter-size of *Oryctolagus* is narrower
than that of the six *Sylvilagus* species together,
although *Oryctolagus* now has a wider latitudinal
range than they cover (Lord, 1960; d. Thompson &
Worden, 1956). There seems to be no correlation of
litter-size with latitude in *Oryctolagus*.

Opportunism and pre-natal mortality
Poole (1960), repeated by Myers & Poole (1962),
maintained that the rabbit's breeding season in
Australia was closer to their ancestral pattern in
Spain than it was in Britain or New Zealand. This
may be so, but the Australian norm is not just a relic
of early rabbit biology, since rabbits quickly adapt to

novel circumstances (Andersson *et al.,* 1979). Poole (1960) also first pointed out that the rabbit evolved in a region with a high risk of drought and erratic rainfall, endowing it with a capacity for opportunistic breeding. This is advantageous in Australia (see also Wood, 1980; King *et al.,* 1983), where opportunism is characteristic of the indigenous fauna of arid regions.

Opportunistic breeding is coupled in the rabbit with a facility for reducing the number of embryos in a litter during gestation (Brambell, 1942; Lloyd, 1963; Andersson *et al.,* 1979, Watson, 1957; Myers & Poole, 1962). Pre-natal mortality may be seen as another adaptation to breeding in an unpredictable environment, whereby the number of young born can be matched to deteriorating conditions almost up until the date of birth, thus maximising the production of viable young. It is thus not surprising that the incidence of pre-natal mortality varies unpredictably in the Wairarapa as elsewhere (Watson, 1957; Lloyd, 1963).

Effects of age on fertility
Female fertility increases then declines with age, the most fertile females being those aged 10-12 months. A higher proportion in this age-group was pregnant, than in younger or older ones (Table 14). They also had the largest litters (Table 21), and their percentage pre-natal mortality was least (Table 18). Moreover, females were invariably heavier than males of the same age, and this difference, indicative of reproductive activity (Table 24), was greatest in females 10-12 months old. As a result, the annual productivity of females 10-12 months old was 23.5% greater than that of those more than three years old. The proportion of males with scrotal testes increased steadily with their age up to and including the oldest animals (Table 11).

Watson (1957) could not age rabbits more than 10 months old, but he doubted if wild rabbits would live long enough to have reduced fertility. Since the survival of both sexes and the fertility of males continue to improve at least until they are over three years old, the declining reproductive performance of females more than one year old, long before they become senescent by any other criterion, is puzzling.

Adams (1970) attributed the declining fertility of female rabbits with age to the 'fallibility of the uterus'. However, the declining fertility of female rabbits more than 10-12 months old may be

adaptive; for if prolific reproduction carries some extra cost for the female, then, with a low survival rate, it may profit a young female to invest more heavily in reproduction in her first year than subsequently (Stearns, 1976).

The density of rabbits in the Wairarapa was greatly reduced, mainly by poisoning, in the late 1950s and early 1960s (McLean, 1966). Since then, the population has stabilized at a much lower level and observations suggest that annual changes in numbers have been slight. This is in spite of the fact that the number of rabbits shot each year by the Pest Destruction Board increased by 33% between 1965 and 1968, and by 22% over the 2 years of this study. Although this suggests an increase in the density it could also be due to an increase in efficiency of the Board's operations.

There is some debate about the degree of continuing control necessary to ensure that rabbit numbers remain low. An annual kill of about 15,000 rabbits of mixed ages amounts to about 5 adult rabbits shot per km' of the Board's area. We do not know the density of rabbits over any large block of country in the Wairarapa, but field work in the eastern hills (e.g. Gibb *et al.,* 1969) suggested typical densities of about 25-50 adult rabbits per km'. With marked density-dependence in reproduction and survival (Gibb *et al.,* 1978) and an annual productivity of 45 young per pair, an annual kill of less than 20% of the adult population is unlikely to reduce the size of the population a year later. Nonetheless average survival rates may be slightly diminished, as found before (Gibb *et al.,* 1969).

Whether density was constant or increased slightly, details of the rabbits' reproductive performance certainly differed between the two years of the study. Each of the months November 1965 to February 1966 was warmer (on average by 1.5°C) than the same months of 1966-67, and there was at least adequate rainfall through both summers (Table 1). Associated with this warmer first summer and the presumably enhanced pasture growth: (i) the females were heavier and relatively heavier than the males; (ii) more of the females were pregnant each month from December 1965 to April 1966, inclusive; and (iii) pre-natal mortality was less prevalent. On the other hand: (i) average litter-size was smaller each month from September 1965 to March 1966; (ii) the

males were on average 21 g lighter; and (iii) fewer of them had scrotal testes. In terms of annual productivity, the higher pregnancy rate of 1965-66 was offset by the smaller litters, with the result that each female produced on average 45.9 young in the first year and 44.2 young in the second.

Although productivity was similar in the two years, the age composition of the samples was not (Table 5). Moreover, the autumn samples and those from properties with a low population density of rabbits contained unusually many animals more than two years old (Tales 6 & 8), while first-year rabbits were less numerous in low-rainfall districts than elsewhere (Table 7). Table 10 identified yet other irregularities in age composition between different districts. It is often necessary, of course, to pool samples collected at different times and in different places so as to emphasize regional trends; yet it is also unrealistic to think in terms of a single, uniform population throughout the Wairarapa. Instead, the population as a whole may be seen as a kaleidoscope of sub-populations, each liable to change independently of the rest.

Compared with the possibilities of geometric increase, annual fluctuations in over-all population density are clearly trifling. They are to be expected and must not be mistaken for long-term trends. However, the population of rabbits in the Wairarapa appears to have stabilized at a very much lower density than existed before about 1950, when Pest Destruction Boards first became effective. Although, at the time of this study, the Wairarapa Board's shooting seemed of little consequence, the mechanism whereby the population of rabbits was confined naturally within such narrow limits remains obscure.

Acknowledgments

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