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REPRODUCTIVE BIOLOGY OF RABBITS, *ORYCTOLAGUS CUNICULUS* (L.), IN CENTRAL OTAGO, NEW ZEALAND

Summary: Autopsies on over 3000 rabbits collected between October 1980 and January 1983 provided information on the reproduction of rabbits in Central Otago. In contrast to year-round breeding elsewhere in New Zealand, reproduction was restricted to the period September-February. Distinct seasonal cycles occurred in both male and female fertility. Both sexes reached peak fertility when 12-17 months old. Female fertility is also related to carcass weight and condition. Most females (80%) experienced some pre-natal mortality, which accounted for about 30% of ovulations. Pre-natal mortality varied seasonally and was greatest in young « 6 months) and older (>18 months) females. Despite a larger mean litter size (6.04), the annual productivity of 23.1 young per female is about half that of other areas in New Zealand, an effect of the restricted breeding season. Comparisons for most reproductive parameters highlight the effects of seasonally severe but predictable environmental conditions in Central Otago. Poisoning success will be greatest between March and August, when there are fewer territorial and social constraints on a rabbit's ability to encounter baits.

Keywords: Oryctolagus cuniculus, rabbits, Central Otago, reproduction, breeding season, fertility, pre-natal mortality, productivity.

Introduction

Since their introduction and spread last century, rabbits *(Oryctolagus cuniculus* (L.)) rapidly became a serious agricultural pest in many parts of New Zealand, especially in the South Island. Although rabbit numbers have dramatically decreased over much of New Zealand, they remain a serious problem for pastoral agriculture and soil conservation in several areas, particularly the semi-arid region of Central Otago. High rabbit densities on land with an inherently low productive capacity means that the cost-effectiveness of control is often questionable (Kerr *et al.,* 1983).

Rabbit control using compound 1080 (sodium monofluoroacetate) poison in Central Otago often leaves about 30% of the population alive, and numbers may return to their previous levels in only 1 year. The main cause of poisoning failures is the neophobic behaviour of the rabbits (Fraser, 1985b), but other factors such as productivity and survival may contribute to the problem.

Maximising the efficiency of control requires an understanding of the species' reproduction and natural regulation, which makes it possible to integrate control with natural mortality. In addition, control is more effective outside the breeding season (Poole, 1963; Rowley, 1968), when territorial effects do not interfere with an individual's ability to encounter baits.

The reproductive biology of rabbits in Central Otago is of special interest not only because of the serious rabbit problem, but also because of the marked environmental differences between this and other regions of New Zealand. Inter- and intraspecific variation in reproductive patterns are common in lagomorphs (see Myers, 1971; Swihart, 1984), and environmental factors can be important causes of the latter. This paper examines the breeding season, fertility, pre-natal mortality, and productivity. It confirms major differences between rabbit populations in Central Otago and elsewhere in New Zealand and is relevant to the efficiency of control.

Study Area

The Central Otago region (45°8 169°E) consists of several broad basins 300-600 m a.s.1. lying between wide and gently-graded ranges of hills and mountains rising to over 1800 m. All autopsy material was obtained from within the Alexandra Pest Destruction Board district, an area of approximately 1750 km^2 centred on Alexandra. Much of the hill country is craggy, with numerous shallow gullies, low ridges, and outcrops of schist. The predominantly brown-grey earth soils are shallow and stony (McCraw, 1965).

The climate is continental. Temperatures above 25°C are common in summer and below 0°C in winter, with a wide diurnal range in all seasons. Annual rainfall at Alexandra is less than 350 mm, although the surrounding ranges may receive 3-4 times this amount. Most rain falls in summer when temperatures, insolation, and evaporation are high, contributing to the dryness of the area (Maunder, 1965). Ground and air frosts are extremely common, and occasional ground frosts occur in summer.

Much of the area is dominated by two natural vegetation types. Tussock grasslands *(Festuca* spp. and *Poa* spp.) cover most hill country between 500 and 800 m (Mark, 1965). The driest areas are dominated by dense cushions of scabweed *(Raoulia australis),* interspersed with bare soil or small native and exotic grasses and weeds. Pastoral farming has altered the vegetation, and introduced grasses now predominate on the foothills and valley floors.

Since the 1850's the tussock-covered hills have been subject to frequent cycles of burning then heavy grazing by sheep. This facilitated the rapid spread of rabbits by creating ideal habitat, and by the late 1870's they were a serious problem. Overgrazing by sheep and rabbits depleted the tussock cover and caused severe erosion. Since the late 1940's changes in land management have alleviated overgrazing by sheep, but despite frequent control, rabbit numbers remain high over much of the area.

Methods

Monthly samples of approximately 100 rabbits shot or poisoned by the Alexandra Pest Destruction Board during normal control operations were collected between October 1980 and January 1983. Most local habitats were sampled.

Rabbits were autopsied within 24 hours of death. Each rabbit was sexed and its length and weight were recorded. 'Carcass weight' was recorded after the stomach, intestines, kidneys and associated fat, and reproductive organs were removed. From July 1981 onwards ovaries and testes were stored in 10% formalin. Stored material was weighed 2-3 weeks after collection. Testes were weighed to the nearest 0.01 g and ovaries to 0.001 g. Changes in weight of ovaries and testes after this interval in formalin are minor and correction factors were not required (Fraser, 1985a). All weights given for testes and ovaries are for paired data (i.e. total gonad weight).

Condition was assessed from the amount of abdominal fat. The fat around the kidneys was scored on a 4-point scale (Riney, 1955): 0= no fat; 1 = limited fat around the kidneys; 2= moderate fat around the kidneys and extending several cm along the abdominal wall; 3 = large amounts of fat almost obscuring the kidneys and extending in thick bands onto the stomach and small intestine.

Male reproductive status was determined from testes position (abdominal or scrotal) and weight, which are indicators of spermatogenetic activity. In general, males with scrotal testes or with testes weights of 3-4 g are fertile (Myers & Poole, 1962; Andersson, Dahlback & Meurling, 1979). Males with a testis in each position were assigned to the scrotal category.

Female reproductive status was determined by evidence of pregnancy or lactation. Pregnancy is not detectable until the 5th day of gestation when macroscopic swellings are visible in the uterus (Brambell, 1942). Therefore, based on an average gestation period of 30 days (Ward, 1971), actual pregnancy rates were calculated using a correction factor of 1.2 (30/25). The number of embryos and resorption sites were counted, and embryo age was calculated from an age-length curve (J .M. Williams, unpubl.). Uterine swellings containing resorbing embryos are spindle-shaped, slightly wrinkled, and usually highly vascularised. In contrast, uterine swellings containing healthy embryos are spherical, tumid, and clear. Each ovary was longitudinally sectioned at 1 mm intervals, and the number of corpora lutea were counted macroscopically. As rabbits are induced ovulators (Asdell, 1966), corpora lutea indicate pregnancy, not the ability to become pregnant. Corpora lutea persist through pregnancy but regress rapidly after parturition (Brambell, 1944; Watson, 1957) and therefore provide an accurate estimate of potential litter size.

Age was determined from the dried weight of the eye lens (Myers & Gilbert, 1968) according to the formula:

$$\text{age (days)} = -57 + 181.4 / \log_e \left[\frac{34}{\text{lens wt (mg)}} \right]$$

This method is accurate for rabbits up to 24 months old. For some analyses rabbits were classified simply as young < 9 months) or adult (≥ 9 months) to be compatible with earlier studies in New Zealand (e.g. Watson, 1957; McIlwaine, 1962).

Analysis of variance and Student's t-test (Sokal & Rohlf, 1973) were used to test significance. Unweighted least squares linear regression was used to examine the relationship between female carcass weight and the number of corpora lutea, and the relationship between initial litter size and pre-natal mortality. Yates' corrected chi-square was used to test the differences in the number of litters showing pre-natal mortality and the proportion of ova lost at different stages of gestation.

Results

Breeding season

The pattern of pregnancies in Central Otago is seasonal, with almost all breeding between September and February (Fig. 1). Less than 1 % (8/1120) of all pregnancies occurred outside this period. Only females >6 months old were used in the analysis of breeding as most younger females were immature (see p. 82).

As lactation begins only a few days before parturition (Brambell, 1942), the high proportion of females lactating in October 1980 indicated that the 1980/81 breeding season began before the first sample was collected. Similarly, the proportion of females lactating in September 1981 was higher than expected. The normal pattern of pregnancies and lactation at the start of the breeding season is illustrated by the September 1982 sample.

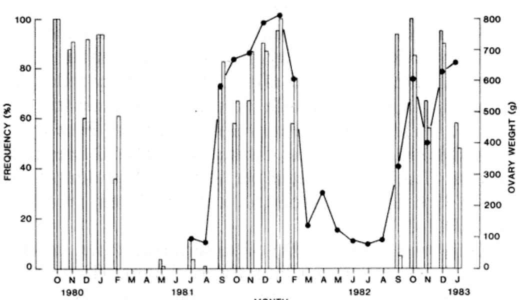

Figure 1: *Frequency of pregnancy (solid bars) and lactation (open bars) for females ≥6 months old, and ovary weight (●) for adult (≥9 months) females.*

The maximum pregnancy rate of 100% occurred only twice (October 1980 and October 1982). Whereas the pregnancy rate was 72% during the 1981/82 breeding season, the almost total absence of breeding outside the September-February period reduced the annual rate to 30% (June 1981 to May 1982). Although data for the 1980/81 and 1982/83 breeding seasons were incomplete, pregnancy rates appeared similar to the 1981/82 breeding season.

The seasonal reproductive pattern was reflected in the ovary weights of adults (9 months old). Ovary weight increased rapidly at the start of the breeding season, remained high (600-800 mg) throughout, and declined in early autumn to significantly lower winter levels (ca. 100 mg; F= 154.2, p<0.001). Females between 6 and 9 months old were still growing and had significantly lighter ovaries (t= 13.4, p<0.001).

Male fertility

A total of 1568 male rabbits were examined, including 880 from July 1981 onwards whose testes were weighed. Although fertile males were present in all age classes (Table 1), only 16% of males < 6 months old had scrotal testes. The youngest fertile males were 4 months old and only three males were fertile at carcass weights of less than 1000 g.

Table 1: *Position and weight of testes according to age and carcass weight. n1 = rabbits weighed October 1980-January* 1983; *n2 = testes weighed July* 1981 - *January* 1983.

Age (months)	nl	Mean carcass wt. (g) ± 95% C.L.	% scrotal	n2	Mean teste wt. (g)
<6	327	1010 ±16	16	158	1.40
6-11	634	1313±7	39	358	3.42
12-17	363	1509±9	52	220	4.24
18-23	143	1538 ±16	44	73	4.50
24	101	1520 ±18	41	71	3.91

The frequency of scrotal testes and testes weight both increased markedly after 6 months of age (Table 1). The highest proportion of males with scrotal testes was in the 12-17 months age class, although the heaviest testes (and carcass weights) were recorded for males 18-23 months old. Slightly fewer of the older males had scrotal testes. Rabbits 18-23 months old had significantly heavier testes than did rabbits;> 24 months old (t = 2.28, p< 0.05).

Although rabbits with scrotal testes were found in all months, there was a distinct seasonal cycle for testes position. Testes weight also varied seasonally (F= 18.2, p<0.001) and followed a pattern similar to that for testes position (Fig. 2). Only adults were used to examine the seasonal pattern for testes weight to avoid bias from younger males whose testes were still growing. The seasonal pattern varied between years, but in general males were most fertile in September-February. In 1981 fertility was lowest between March and May, whereas in 1982 the period of low fertility extended to August when only 16% of males 6 months old had scrotal testes.

Changes in the appearance of the testes accompanied changes in weight and position. heavy testes were usually scrotal, firm in texture, and light-coloured. Regressing testes were more commonly abdominal, considerably lighter in weight, flaccid, and reddish-brown. However, changes in testes position generally occurred more rapidly than changes in testes weight. When breeding ceased in February the proportion of males with scrotal testes declined immediately, but the accompanying decrease in testes weight took several months.

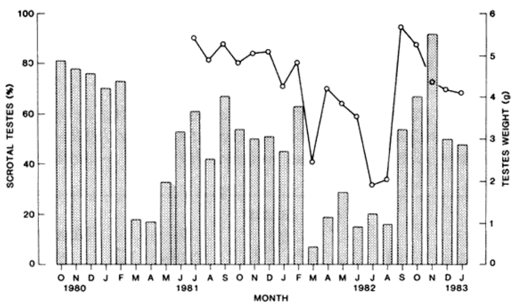

Figure 2: *Frequency of scrotal testes (solid bars) for males ≥6 months old, and testes weight* (**o**) *for adult* (≥9 *months) males.*

Female fertility

A total of 1472 female rabbits were examined, including 1033 from July 1981 onwards whose corpora lutea were recorded. Fertile females were present in all age classes (Table 2), although most females < 6 months old were immature, with only 15% pregnant and 10% lactating. The youngest pregnant rabbit was 4 months old. Only six females were pregnant with a carcass weight of less than 1100 g, the lightest being 1000 g.

Table 2: *Female fertility as indicated by pregnancy, lactation, and number of corpora lutea, according to age and carcass weight. - Sample size in brackets; corpora lutea (d.) counts were restricted to rabbits collected from July 1981 onwards.*

Age (months)	n	Mean carcass wt. (g) ± 95% C.I.	% pregnant	% 1actating	Mean no. d.-
<6	367	l006±31	15	10	5.3 (38)
6-11	592	1280±16	24	20	6.5 (121)
12-17	295	1460±22	52	54	7.0 (124)
18-23	138	1472±19	45	34	6.9 (47)
24	80	1477±38	39	45	6.7 (24)

Frequencies of pregnancy and lactation were slightly greater for rabbits 12-17 months old than for older females (Table 2). Rabbits < 12 months old were in their first breeding season and still growing, as the increase in carcass weight illustrates. The number of corpora lutea ranged from 1 to 12 and averaged 6.6. Corpora lutea counts showed a similar pattern to pregnancy and lactation frequencies; fertility increased with age (F=6.20, p<0.001) and carcass weight to a maximum in females 12-17 months old.

Although carcass weight was related to age, it was an important determinant of fertility among similar-aged rabbits. Among adults, for example, heavy females were significantly more fertile than light females (F= 8.53, p<0.001). Seasonal variation in carcass weight and fertility tended to obscure this trend but within individual months the pattern is clear (Fig. 3). Similarly, the relationship between condition and fertility was concealed by the seasonal variation in fat reserves. However, within individual months abdominal fat and the number of corpora lutea present were positively correlated (e.g. for September 1982, r=0.32, n= 51, p<0.05).

Within the breeding season there was a distinct pattern of female fertility (Fig. 4). The number of corpora lutea increased after the onset of breeding and peaked around the middle of the breeding season before declining in January and February. Fertility was significantly greater during the 1981/82 breeding season (7.0 corpora lutea per female) than during the 1982/83 breeding season (6.2 corpora lutea; t = 4.03, p<0.001).

Only two cases (0.7%) of superfertility (i.e. more embryos than corpora lutea) were found. However, superfertility is difficult to determine and was probably underestimated, as pre-natal mortality reduces the chances of detecting polyovuly or polyembrony.

Pre-natal mortality

Pre-natal mortality occurs through failure of embryos to implant or by their resorption during gestation. Pre-implantation losses were estimated .by comparing the ovulation rate (i.e. number of corpora lutea) with the number of embryos present during the first 10 days of gestation: they accounted for about 14% of ovulations, with 68% of females at this stage of gestation showing some loss (Table 3).

The loss of embryos by resorption was difficult to calculate because some females lost entire litters. However, the proportion of litters with losses and the number of ova lost peaked during the 16-20 day stage of gestation (Table 3). Loss of entire litters caused a marked decrease in the apparent pre-natal mortality rate recorded at subsequent stages of gestation. The reduction in the proportion of ova lost between the

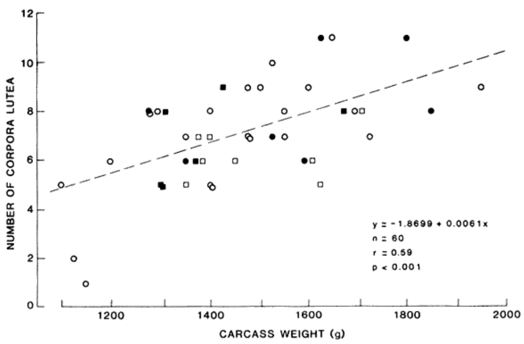

Figure 3: *Correlation between carcas weight and the number of copora lutea according to age class, November 1981; 6-11 months (●), 12-17 months (○), 18-23 months (■), 24 months (□).*

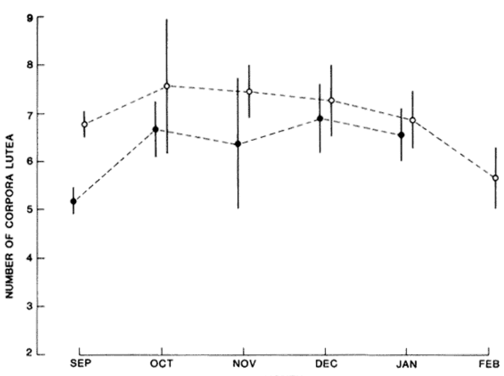

Figure 4: *Mean number of corpora lutea per female with 95% confidence limits for the 1981/82 (○) and 1982/83 (●) breeding seasons.*

16-20 day stage and the 26 day stage of gestation was significant (X^2=6.67, p<0.01). Overall, pre-natal mortality accounted for about 30070 of ovulations and occurred in about 80% of females.

The incidence and magnitude of pre-natal mortality varied according to the age of the female and inversely with fertility (Table 4). Losses were lowest for females 12-17 months old and were more frequent and greater among younger and older females. Overall, pre-natal mortality was positively correlated with the initial size of the litter (r = 0.39, n = 268, p < 0.01): large litters exhibited greater proportional losses than small litters.

Factors such as female age and fertility combined to produce some seasonal fluctuation in pre-natal mortality. The proportion of litters with losses was relatively constant (60-70%) between September and December, but increased (75-80%) in January and February as young females began to breed. Loss of ova increased from about 15% of ovulations in September to about 30% in February.

Table 3: *Pre-natal mortality during the* 1981/82 *breeding season according to the stage of gestation. .*The proportion of litters that survive to full term (p)* is *calculated from the ratio of the proportion of litters without loss at the 11-15 day stage to the proportion of litters without loss at the* 21 *day stage (Watson, 1957*); *for the 1981/82 breeding season, p = (2/7)/(19/58)* = 88% *and, therefore, the proportion of litters lost entirely (1-p)* = 12%.

Stage of gestation (days)	No. of litters	No. with loss*	%	Total no. ova	No. ova lost	%
<6	25	17	68	178	25	14
11-15	7	5	71	51	10	20
12-17	29	23	79	237	58	24
18-23	39	29	74	281	56	20
24	19	10	53	133	14	11

Table 4: *Pre-natal mortality according to female age. Only females with both corpora lutea and embryo counts are included.*

Age (months)	n	% with. loss	Mean no. corpora lutea	Mean no. embryos	Mean no. Ova lost	% loss
<6	25	72	5.9	4.6	1.3	22
11-15	85	65	6.8	5.4	1.3	19
12-17	95	60	7.4	6.3	1.1	15
18-23	39	72	6.9	5.5	1.4	21
24	20	85	7.0	5.3	1.8	25

Productivity

Females less than 6 months old were excluded from estimates of productivity. Because of low pregnancy rates, small litter sizes, and high pre-natal mortality they contributed little to total productivity. Productivity is the product of the frequency of pregnancy and the average litter size. As few embryos were lost during the final stages of gestation, the number of embryos > 20 days old approximated litter size at parturition.

Data for the 1981/82 breeding season (Table 5) were used to calculate annual productivity. The average number of pregnancies per female for this period was 3.82 and the average litter size was 6.04, resulting in an annual productivity of 23.1 young per female. During the breeding season reproductive output was highest in December and decreased markedly to its lowest level by February.

Table 5: *Pregnancy rate and estimated litter size for the 1981/82 breeding season. .*Only females ≥6 months old are included; + Sample size in brackets.*

Month	No of females*	% pregnant	Estimated litter size+	s.e.
June 1981	48	0	-	-
July	53	11	5 (1)	-
August	103	1	-	-
September	57	72	6.05 (22)	0.32
October	15	72	6.67 (6)	0.67
November	80	72	6.33 (21)	0.46
December	32	90	6.67 (6)	0.80
January 1982	14	94	5.38 (8)	0.42
February	20	54	4.25 (4)	1.25
March	39	0	-	-
April	38	0	-	-
May	40	0	-	-
Total	539	31	6.04 (68)	0.22

Discussion

Breeding season

The marked seasonality of breeding in Central Otago differs from elsewhere in New Zealand. In North Canterbury, Wanganui, and Wairarapa the monthly pregnancy rate rarely falls below 20% (Bell, 1977; Gibb *et al.,* 1985; Williams & Robson, 1985). This difference reflects the extreme environmental conditions in Central Otago. From May to August frequent heavy frosts and low temperatures severely limit pasture growth (Radcliffe & Cossens, 1974), an important factor for successful breeding (Myers & Poole, 1962). Elsewhere in New Zealand pasture growth is almost continuous (Coulter, 1975) and reproduction continues year-round. Other environments with strongly seasonal climates, such as subalpine New South Wales and southern Sweden, also show sharply defined breeding seasons (Myers, 1971; Andersson, Dahlback & Meurling, 1979).

The duration of the breeding season in Central Otago appears relatively constant and its onset varied only slightly between years. Such variations have been correlated with weather (Andersson, Borg & Meurling, 1979). Rare out-of-season breeding is also associated with the weather (Fraser, 1985b).

Although a 100% pregnancy rate was recorded in only 2 months, pregnancy rates within the breeding season were similar to those elsewhere in New Zealand (Bell, 1977; Gibb *et al.,* 1985; Williams & Robson, 1985). The high incidence of post-partum pregnancies indicated that between September and February conditions were ideal for breeding and populations were increasing at close to their potential rate.

Recorded fluctuations in pregnancy and lactation rates within the breeding season can be explained by environmental differences between habitats. The higher than expected lactation rate in September 1981 reflected such differences: whereas the August 1981 sample was from unimproved pasture at an altitude of about 600 m, the September sample was from irrigated improved pasture at about 230 m where breeding was more advanced. This obscured the normal pattern expected for the onset of breeding, as observed in September 1982.

Age at sexual maturity

Most rabbits become sexually mature after 6 months of age. Therefore, because of the restricted breeding season in Central Otago, few rabbits bred in their season of birth. Although rabbits in Wairarapa mature at similar ages (Gibb *et al.,* 1985), more females (ca. 50%) 4-6 months old become pregnant than in Central Otago because environmental conditions are less restrictive on the period of breeding. Other studies, especially of high density rabbit populations (e.g. Watson, 1957; Myers & Poole, 1962), have reported greater ages at sexual maturity. Decreasing fecundity and delayed maturity in response to increased population densities are well known among mammals (Christian, 1956).

Male fertility

Male fertility followed a distinct annual cycle, the highest proportions of males with scrotal testes coinciding with the September-February breeding season. Although elsewhere in New Zealand male fertility fluctuates seasonally, the proportion of males with scrotal testes rarely falls below 40% (Bell, 1977; Williams & Robson, 1985).

The marked increase in the frequency of scrotal testes between June and August 1981 indicated that an increase in male fertility can precede the breeding season by several months, as in Hawke's Bay

(Watson, 1957) and North Canterbury (Bell, 1977). This, together with the presence of some fertile males in all months, confirms that the onset of breeding is a product of female fertility (Brambell, 1944; Myers & Poole, 1962). Fluctuations in male fertility between consecutive months and variation in the timing of the annual cycle between breeding seasons reflect the influence of environmental factors such as weather. Several studies in Australia have demonstrated that male fertility is most closely correlated with weather conditions and food availability, although proximate factors such as day length may be important (see King *et al.,* 1983).

Testes position gave a different age for peak fertility than testes weight. Because testes weight declined more slowly than the change in testes position at the end of the breeding season, testes position may be a more accurate indicator of male fertility.

Female fertility

Female rabbits 12-17 months old were the most fertile, which corresponds closely to other populations in Australia and New Zealand (Myers, 1971; Gibb *et al.,* 1985). Although the decline in fertility of older females was not significant, a larger sample of females older than 24 months and a more accurate ageing technique could reveal a real decrease in fertility, as recorded by McIlwaine (1962) and Gibb *et al.* (1985). Female mortality increased in their second breeding season (Fraser, 1985b), suggesting physiological stress associated with reproductive activity. Such stress might also reduce fertility in females in their second or subsequent breeding seasons.

For rabbits of the same age, fertility was positively correlated with carcass weight and abdominal fat reserves. Differences between habitats sampled account for some variation in weight and condition (Fraser, 1985b), and probably influenced female fertility likewise.

Despite a complex set of factors influencing fertility, the seasonal pattern was similar to that found in other studies (Brambell, 1944; Watson, 1957; Andersson, Dahlback & Meurling, 1979). The increase in fertility in the initial months of the breeding season was associated with rises in pregnancy rates and ovary weights. This suggests that conditions for breeding are improving over this period and that the fertility of individual females improves for their second and subsequent pregnancies. The decrease in fertility towards the end of the breeding season is caused mainly by young females < 6 months old) breeding for the first time.

The reason for the differences in female fertility between the 1981/82 and the 1982/83 breeding seasons is unclear. Although rainfall was greater during the 1982/83 season, suggesting better pasture growth and an improved food supply, fertility levels were lower. However, comparisons are difficult because of wide differences in environmental variables, especially habitat quality and population densities, between the areas sampled.

Pre-natal mortality

Female age, fertility, and the stage of the breeding season influenced pre-natal mortality. As ovulation in the rabbit depends on copulation, ova are unlikely to remain unfertilised. Litters may be aborted during the final stages of pregnancy, as in other polytocous mammals, but this is unlikely to be important because of the rabbit's ability to resorb embryos.

The seasonal pattern in pre-natal mortality was produced by a combination of effects including increasing fertility and changing age structure of the breeding population as the season progressed. Besides being most fertile, females aged 12-17 months also had the least pre-natal mortality, confirming that their reproductive potential was greater than that of younger or older females. Younger rabbits are generally subordinate in social status and therefore experience greater stress (Fraser, 1985b), which may account for their higher pre-natal mortality. Although older females are usually dominant, a combination of harsh environmental conditions and high reproductive output at an earlier age could explain the increased pre-natal mortality among females:≥ 18 months old! Gibb *et a1.* (1985) also found greater pre-natal mortality in younger and older females in Wairarapa.

Bearing in mind differences in sampling methods, population densities, and other factors, the overall level of pre-natal mortality in Central Otago appeared lower than elsewhere in .New Zealand (McIlwaine, 1962; Gibb *et a1.,* 1985). If pre-natal mortality is considered as an adaptation to breeding in unpredictable environments (Gibb *et al.,* 1985), this confirms the relative stability of environmental conditions in Central Otago during the breeding season.

Productivity

Compared with other areas in New Zealand, annual productivity in Central Otago was low despite the greater litter size (Table 6), and reflected the shorter breeding season. Although Watson's (1957) and Bell's (1977) original productivity estimates are similar to the

Central Otago figure, they were calculated using litter size and frequency of pregnancy for only that period of the year when the proportion of females pregnant was greater than 50%. As breeding occurs year-round in Hawke's Bay and North Canterbury, this results in a substantial underestimate of productivity. Consequently, estimates for these two areas were recalculated using data for complete 12-month periods. Although the variation in litter size is not great, a consistent increase with latitude is evident similar to that recorded for other lagomorphs (Sadleir, 1969).

Table 6: *Mean litter size and annual productivity for several areas in New Zealand. .*Corrected values, see text for explanation; Watson's estimate for Hawke's Bay is 18.1-25.5 young per female; Bell's estimate for North Canterbury is 29.4 young per female.*

Area	Latitude	Litter size	Annual productivity	Source
Hawke's Bay	40°S	5.03	36-45*.	Watson, 1957
Wanganui	40°S	5.23	47.6	Williams & Robson, 1985
Wairarapa	41°S	5.01-5.30	44.2-45.9	Gibb *et al.*, 1985
North Canterbury	42°S	5.54	42*	Bell, 1977
		5.85	5.85	J.M. Williams unpubl.
Central Otago	45°S	6.04	23.1	present study

The range of variation in annual productivity throughout New Zealand is comparable to that in Australia. For example, Gilbert & Myers (1981) estimated annual productivity of 15 young per female in a subalpine environment (Snowy Plains, NSW) and 38 young per female in a mediterranean environment (Urana, NSW). It appears that the subalpine environment restricts rabbit reproduction to a level similar to that in Central Otago. Productivity in the mediterranean environment is similar to other parts of New Zealand, with reproduction during most months of the year (Myers, 1971).

Implications for control

Since annual productivity is low, the rabbit problem in Central Otago is a result of other factors, most notably large areas of suitable habitat and also relatively high survival of juveniles. Although juvenile mortality is high in relation to adult mortality (Fraser, 1985b), it appears lower than for other parts of New Zealand because of better conditions for juveniles during the breeding season. Short pastures and low rainfall suggest that mortality factors such as coccidial infection and flooding of breeding stops which are important in other areas (Tyndale-Biscoe & Williams, 1955; Bull, 1960) are less significant in Central Otago.

In addition, regular poisoning over the previous 30 years has led to the selection for neophobic behaviour towards baits (Fraser, 1985b). Notwithstanding the effects of neophobia, control has the best chance of success between March and August, when lack of breeding reduces territorial and social hierarchy impediments to encountering baits (Poole, 1963; Rowley, 1968; Fraser, 1985b).

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