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THE DECLINE AND INCREASE OF FERAL SHEEP (*Ovis aries* L.) ON CAMPBELL ISLAND

Summary: Sheep introduced to Campbell Island in 1895 for farming reached numbers of over 8000 in 1916 then declined to 1000 by 1961 (exponential growth rate r = -0.05 p.a.). Numbers increased to around 3000 from 1961 to 1969 (r = 0.14 p.a.). The island was divided into halves by a fence in 1970, and all sheep north of it were killed. The southern population continued to grow from 1970 to 1984 (r = 0.053 p.a.). The southern half of the island was cleared of sheep in 1984 except for about 800 fenced off on a peninsula.

Censuses in 1961 and 1969, and the sample shot in 1970, showed that population growth rate, lambing rate, sex ratio, and time of breeding varied in different places on the island, and from year to year. The average number of lambs present per 100 females ranged from 30 to 40 in the farming years up to 1931, and from 60 to 80 by 1970. The age structure in 1970 was consistent with a stable age-distribution in an expanding population.

During the farming years the southern hemisphere was in a cold climatic phase. From the mid 1930s there was a general warming, especially during the 1950s. These better conditions, together with falling grazing pressure and absence of burning, allowed an increase in the island's woody and herbaceous vegetation. The sheep developed traits for self shedding of the unshorn fleece and for breeding at one year old. These changes are discussed in relation to the decline and subsequent increase of the population.

Keywords: Feral; sheep; *Ovis aries*; Campbell Island; subantarctic; population history.

Introduction

Campbell Island is a subantarctic island some 500 km south of New Zealand at 52∞S 169'E (Fig. 1). It is the remnant eastern rim of an eroded volcanic cone and has an area of about 10.9 km². The western side, facing the prevailing seas, is fringed by high, sheer cliffs and rocky promontories. The eastern side slopes more gently to sea level and is indented by narrow inlets, the largest of which, Perseverance Harbour, runs 8 km inland and nearly bisects the island.

The terrain is generally hilly with five peaks over 450 m, of which the highest is Mount Honey (569 m). Rock is exposed in places but the slopes are generally covered in deep peat.

The dominant woody plants are *Dracophyllum scoparium, D. longifolium, Coprosma* spp., and *Myrsine divaricata*. These occur as scrub associations up to an altitude of 200 m and as dwarf trees up to 5 m tall at lower levels and where there is shelter. Both the original woody and herbaceous vegetation was greatly altered by burning and grazing. The original tussock grassland *(Chionochloa antarctica)* and large endemic herbs have been replaced as dominants by the less palatable *Bulbinella ross, Poa litorosa* tussock, and other unpalatable native herbs. European pasture grasses were sown which, when grazed, produced extensive open swards (see Meurk, 1975, 1977, 1982). General accounts of the history and natural history of the island have been given by Bailey and Sorenson (1962) and Kerr (1976).
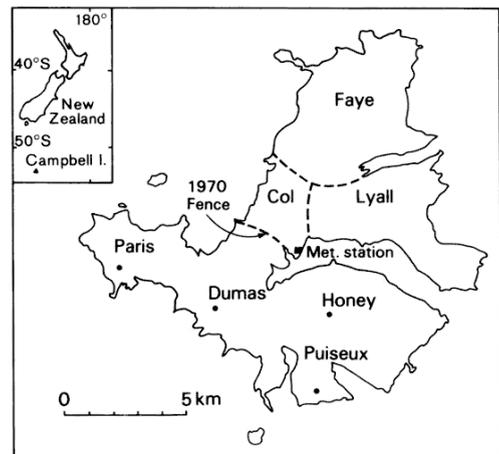

Figure 1: *Location of Campbell Island, and the place names used in the text. Col corresponds to North Col; Faye to Faye + Fizeau; and Lyall to Lyall + Mowbray of Wilson and Orwin* (1964). *All sheep were removed from north of the fence in 1970. A study population was restricted to the area round Mt Paris when animals in the southern half were exterminated in 1984.*

Domestic sheep (*Ovis aries* L.) were introduced in 1895, but pastoral farming met with indifferent success. Stock numbers were highest in 1916 (over 8000), after which there was a steady decline (Wilson

and Orwin, 1964). When farming was discontinued in 1931, over 4000 sheep and about 20 cattle *(Bos tauros* L.) were abandoned. Estimates made by coast watchers during the second world war (1940-45) indicated that sheep numbers continued to decline.

　　Campbell Island is the main breeding ground for the southern royal albatross. When the island became a reserve for the protection of flora and fauna in 1954, a case was made to eradicate the sheep because they were thought to threaten nesting sites, the vegetation pattern, and some plant taxa (Westerskov, 1959, 1963). A census in 1961 showed that the remaining cattle ranged over a small area of limestone country, that the sheep had declined at 5% per year since 1916, and that the number of breeding albatrosses had apparently not changed for decades (Wilson and Orwin, 1964). Wilson and Orwin therefore suggested erecting a fence across the 'waist' of the island, and eradicating the sheep to the north so that vegetation and albatrosses could be studied with and without sheep, and plant taxa could be protected. This proposal was not adopted.
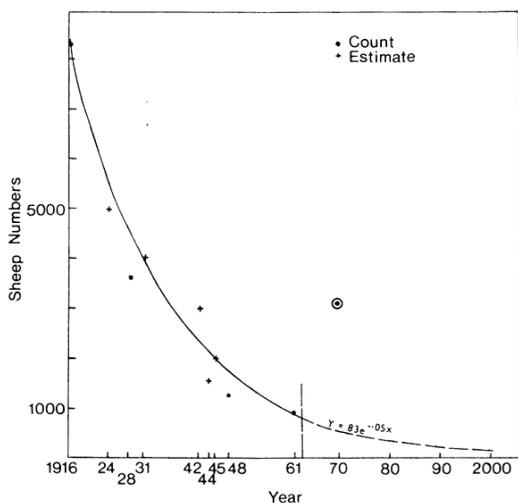

Figure 2: *Exponential decline in sheep numbers on Campbell Island from 1916 to 1961 extrapolated to A.D. 2000. Modified from Wilson and Orwin (1964) with the actual count in 1969 added.*

　　A count in 1969 showed that the sheep population had not continued to decline as predicted (Fig. 2). Instead, numbers had increased by a factor of about three, and the royal albatross numbers had doubled since 1958 (Taylor, Bell and Wilson, 1970). In view of the increase of sheep and their uncertain relationship to albatross numbers, the 1964 proposal to build a fence was adopted.

　　The fence was erected in January-March 1970. Most of the sheep north of it were shot (Bell and Taylor, 1970) and the remnant was shot over the next year. From the sheep shot in 1970 hunters collected jawbones so that an age distribution could be prepared which might indicate the beginning of population growth. Vegetation quadrats and photopoints were established on both sides of the fence.

　　From 1970 to 1984 the remaining sheep have been counted in most years, and in 1984 the first winter study was conducted (Ballance, 1985). Vegetation changes with and without sheep have been compared (Meurk, 1982). In 1975 10 sheep were taken to a research farm for studies of reproduction and physiology (Cockrem, 1976). Thus, since 1970 our knowledge of the sheep themselves and their numbers on the island has greatly increased compared with the flimsy record before 1961. In this paper the 1970 age structure and the characteristics of the sheep and their island environment are described. The synthesis is used to account for both the decline and the increase in numbers.

Methods

Hunters removed and labelled lower jaws, and recorded the locality (as Faye, Color Lyall, see Fig. 1), sex, fleece colour, and occurence of horns. A tally was kept of all sheep shot and not recovered. Jaws were boiled and scraped clean, and a few were lost when Norway rats *(Rattus norvegicus)* dragged them away at night. Of the 1281 sheep shot, 1066 (83%) were eventually represented by a usable lower jaw and field sheet.

　　The sequence of eruption of the permanent dentition was recorded and any abnormalities in the teeth and supporting bone were described. The first permanent incisors were extracted, the root was ground transversely, and growth lines in the cementum were counted.

　　Age classes up to 4 years old were separated using a combination of relative jaw size, replacement of the deciduous dentition, and lines in the cementum of the first permanent incisor. Beyond 4 years (jaws with permanent teeth), relative wear on cheek teeth

augmented the cementum line counts. Cementum lines in 70% of known-age domestic sheep were accurate to within I year (Rudge, 1976). Subsequent studies of feral goat teeth showed that errors in reading lines were not biased in anyone direction, so over a large sample they should cancel out. To minimise errors three assessments of the tooth replacement sequence were made several months apart, and two people read cementum lines in incisor I and then repeated the procedure using the second incisor of the II pair.

Some of the females were dissected for examination of the uterus and ovaries. Ovarian follicles were counted and corpora lutea exposed by slicing each ovary into a 'book' of leaves 2 mm thick.

Results

The results described are from the 1970 shot sample.

Appearance

The majority (98.7%) of the sheep were white, and the remaining 1.3% were equally divided among wholly pigmented animals and those with pigmented patches. Double fleeces were common, but most females were shedding fleece from the neck, belly and flanks.

Horns were visible on 67% of males and 20% of females. An additional 22% of males and 29% females had scurs - small horny growths on the frontal bones. Horned animals could be sexed because age for age, male horns had about twice the basal circumference and length of female horns (Appendix I) and were curled, whereas those of females were erect and curved. As the sex ratio was 43:57, the hornless sheep would be distributed 24:76 in a live population census.

Tooth eruption sequence

The frequencies of various combinations of teeth were scored as a rapid indicator of relative ages, especially over the first 4 years. Eruption did not follow a predictable, linear sequence (Table 1). For example, molar 3, incisor 2 and premolars 2, 3 and 4 tended to erupt almost simultaneously, and chances were about equal as to which appeared first. The sequence resembled that for domestic sheep (Habermehl, 1961), except that the appearance of incisor 2 and the premolars was commonly reversed in the island sample.

Sex ratio

Within the total sample there were 461 males and 605 females (1:1.3) (X^2 for female:male = 24.16, 1 d.f., P < 0.005). In Faye and Col samples the ratio

Table 1: *Number of jaws in which different combinations of permanent teeth occurred in Campbell Island sheep.*
Sequence: $M_1 > (M_2 > I_1) > (M_3, P_{2,3,4})$ _ $I_2, > I_3, > C_1,.$
Habermehl (/962) gives: $M_1 > M_2 > I_1 > M_3, (I_2, PM_{2,3,4}) > I_3 > C_1.$
_ indicates that the sequence may be reversed.

I_1	I_2	I_3	C_1	P_2	P_3	P_4	M_1	M_2	M_3	N
							*			164
							*	*		47
*							*			3
*							C	*		72
*							*	*	*	4
*				*	*	*	*	*		4
*				*	*	*	*	*	*	8
*	*						*	*		2
*	*			*	*	*	*	*		3
*	*.			*	*	*	*	*	*	79
*	*	*		*	*	*	*	*		4
*	*	*		*	*	*	*	*	*	90
*	*.	*	*	*	*	*	*	*	*	333

favoured males. Lyall samples differed in that the sex ratio was equal (Table 2). No great biological significance is given to these differences because animals may have moved around during hunting.

Although the overall sex ratio favoured females, it varied between age-classes (Table 3, and Fig. 3). In age-classes 73-84 months and 97-132 months the bias towards males was significant (p < 0.005).

Table 2: *Distribution of sexes between three localities on the north of Campbell Island. Overall contingency $X^2 = 5.85$, d.f. = 2, p<0.05. The value for Lyall is significantly different at p = 0.05 because the ratio is the reverse of the others.*

	Males	Females	Ratio	X^2
Col	54	63	46:54	0.41
Faye	325	463	41:59	1.29
Lyall	82	79	51:49	4.15

Age structure

The age structure formed a broad-based triangle, consistent with but not necessarily implying a stable age distribution and an expanding population (Fig.3). There were no inflated age classes to indicate augmented cohorts in the 1960s. A sharp waist in 1966 suggested a drop in recuitment or survival of that cohort, but there was continuing strong recruitment in the following three years.

Reproductive condition and lambing

During January-March 1970 no new-born lambs or pregnant females were seen, and none of 15 females

Table 3: *The observed number of animals of each sex in each age class, and their calculated number in cohorts of 1000 in the three localities and in the total sample (1067) of sheep shot on Campbell Island in 1970. The age-class sex ratio differs from the*

Age-class (months)	Col Males Actual no.	Col Males Cohort size	Col Females Actual no.	Col Females Cohort size	Combined cohort size	Faye Males Actual no.	Faye Males Cohort size	Faye Females Actual no.	Faye Females Cohort size	Combined cohort size
0-12	16	1000	13	1000	1000	85	1000	119	1000	1000
-24	6	375	17	1307	793	56	659	78	655	657
-36	11	687	8	615	655	39	459	74	622	554
-48	4	250	7	538	379	21*	247	47*	395	338
-60	3	187	7	538	345	31	365	55	462	421
-72	5	312	4	307	310	27	318	39	328	324
-84	5	312	2	154	241	24	282	17	143	201
-96	3	176	3	230	207	21	247	22	185	211
-108	1	62	2	154	103	8⎫	94	9⎫	76	83
-120	0	0	0	0	0	8⎬*	94	3⎬*	25	54
-132	0	0	0	0	0	5⎭	59	0⎭	0	25
	54		63			325†		463†		

Age-class	Lyall Males Actual no.	Lyall Males Cohort size	Lyall Females Actual no.	Lyall Females Cohort size	Combined cohort size	Total Sample Males Actual no.	Total Sample Males Cohort size	Total Sample Females Actual no.	Total Sample Females Cohort size	Combined cohort size
	19	1000	25	1000	1000	120	1000	157	1000	1000
	14	737	13	520	613	76	633	108	688	664
	11	579	16	640	613	61	508	98	624	574
	8	421	5	200	295	33	275	59	376	335
	8	421	10	400	409	42	350	72	458	411
	9	473	5	200	318	41	342	48	306	321
	6⎫	316	2⎫	80	182	35*	292	21*	134	202
	3⎬	158	2⎬	80	114	27	225	27	172	195
	3⎬*	158	1⎬*	40	91	12⎫	100	12⎫	76	87
	1⎭	53	0⎭	0	23	9⎬+	75	3⎬+	19	43
	0	0	0	0	0	5⎭	42	0⎭	0	18
	82		79			461†		605†		

dissected was visibly pregnant. Ten of the 15 less than 9 months old had ripe ovarian follicles, so were about to ovulate. Five others had corpora lutea. Three of these five were also lactating a little and were presumably nursing. The two not lactating may have been in earliest pregnancy without visible embryos. Because females could breed soon after they were 12 months old, the definition of a 'breeding' female and
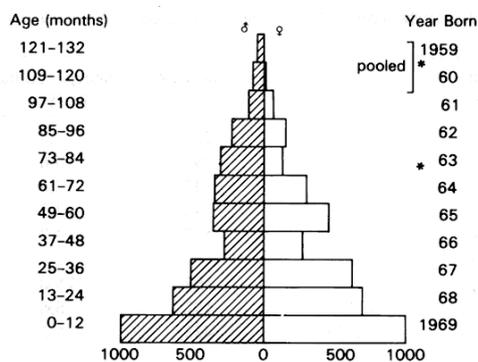
Figure 3: *Distribution of ages in each sex (cohorts of 1000) in the aged sample of sheep on Campbell Island in 1970 (N = 1066 or 83% of animals shot. * sex ratio departs from population expectation of 43:57 at p<0.05).*

of 'lamb' used below is greater or less than 12 months old respectively. This definition allows for the extended breeding period.

The overall proportion of Iambs to adults was 350/0, and did not differ significantly between the three localities. These ratios were similar to those recorded in 1969 by Taylor *et al*.,(1970) except that lambing on Faye was 10% higher in 1970 (Table 4).

The proportion of Iambs younger than 6 months old (Table 5) was significantly greater on Faye $(X^2 = 10.23$, 2 d.f., $p < 0.01$); that is, lambing was later there than on Col and Lyall.

Clearly, reproduction extended over a long period. According to Mr C. Clark (pers. comm.), a meteorological observer who had spent several years on the island, Iambs were born throughout the year but most between August and December.

Table 5: *Number of Iambs alive, and percentage born within 6 months of the sample date (early February 1970) in 3 localities on the northern half of Campbell Island.*

	Col	Faye	Lyall	Total
Total lambs	29	204	44	277
% < 6 months old	76	91	77	87
Sheep present	117	789	161	2067
Area (ha)	604	2580	2112	5296
Density/l00 ha	19.3	30.6	12.1	20.15

Discussion

Censuses and studies of these sheep were generally carried out during brief summer expeditions until Ballance (1985) recently studied them in winter. There have been no year-round studies. The main population has now been exterminated from the south of the island except for a study flock of about 800.

Table 4: *Comparison of lambing percentages expressed as lambs/100 adults (and as lambs/100 ewes) during and after the farming period on various parts of Campbell Island.*

Year	Col	Faye	Lyall	All northern half	All southern half	Whole island	Ref
1909						24 (37)	Wilson & Orwin, 1964
1916						23-	Wilson & Orwin, 1964
1928						20 (31)	Wilson & Orwin, 1964
1960/61						15 (23)	Wilson & Orwin, 1964
1968/69	33	25	37	28	26	26.5	Taylor *et al*. 1970
1970	33 (58)	35 (59)	38 (81)	35 (62)			(this paper)
1971/72					25		Dilks & Wilson, 1979
1975/76					22		Dilks & Wilson, 1979
1976/77					30		Dilks & Wilson, 1979
1977/78					29		Wilson & Elliott, unpublished
1979/80					33		ç
1980/81					24		ç
1982/83					20		Dilks & Grindell, unpublished
1984					20 (35)		Balance, 1985

Table 6: *% increase in the number of sheep in 7 localities on Campbell Island between 1961 and 1969 compared with the density in 1961. r = yearly exponential growth rate between 1961 and 1969.*

Locality	Area (ha)	No. in 1961	No. in 1969	r	% increase	Sheep/100 ha in 1961
Faye	2580	194	634	0.148	227	7.5
Lyall	2112	12	107	0.273	791	0.6
North Col	604	105	154	0.479	47	17.4
South Col	466	57	81	0.439	42	12.2
Paris	1011	48	774⟩		1512	4.7
				0.171		
Dumas	1194	308	626⟩		103	25.8
Honey	2300	153	447	0.134	192	6.6
Puiseux	570	30	160	0.209	433	5.3
		907	2983	0.148		

Variation in time and place of population growth and recruitment

From 1916 to 1961 the population declined at an average exponential rate of r = -0.05 each year (Fig. 2). By 1969 this trend had become an average increase of r = 0.14 but with marked local differences. In the northern half the population increased by a factor of 2.9, and in the southern half by a factor of 3.5 (Taylor *et al.*, 1970). Even between smaller subdivisions of the island, population growth was markedly different (Tables 4, 6). Mount Honey, the area with the lowest population density in 1961, showed the greatest growth by 1969 (Table 5). Movement of animals from areas of locally high recruitment may have precipitated this growth but clearly some areas were, or became, capable of holding many more sheep than they had in 1961. Taylor *et al.*, (1970) found that in 1969 there was a negative correlation between density and lambing rate (r = -0.68, p<0.05). From 1970 to 1984 the population on the southern half of the island continued to grow but at a slower rate (r = 0.053, Table 7).

During the farming period, lambing lasted at least six months (Wilson and Orwin, 1964). Lambing percentages were obtained at the main docking and shearing muster, which could extend from October to May depending on the weather (Timms, 1978). The values thus contain a varying error because of differing opportunities for mortality. Lambing

Table 7: *Number of sheep on the southern half of Campbell Island from 1961 to 1982. From 1960/61 to 1970/71 (10 years) exponential growth rate r = 0.144; from 1970/71 to 1984 (13 years) r = 0.053. For the whole period 1960/61 to 1984 (23 years) r = 0.089.*

Year counted	Total Sheep
1960/61	596
1968/69	2088
1970/71	2521
1975/76	2400
1976/77	2861
1977/78	3175
1979/80	3561
1980/81	3341
1982/83	3540
1984	4700

estimates from later censuses have come mostly from between December and February (Table 4).

Lambing percentage is a useful guide to the performance of the population, but the various figures have been derived in three different ways. In the farming period they came from musters in which the count of ewes and lambs was sound but was spread over 6 months. In live censuses the adult sex ratio was uncertain because hornless animals could not be infallibly sexed; and the 'lamb of the year' designation was suspect because of the extended breeding period. In the 1970 sample both sex ratio and age were

unambiguous. In farming convention, lambing percentage is expressed as a ratio of lambs to females. Wilson and Orwin (1964) derived 37% and 31 % for two years of the farming era, (using an assumed sex ratio of 35% males) and 23% for their 1961 census (Table 4). Their estimate for lambs was obtained by halving the number of immature animals which would have made some allowance for year-round breeding, but would have underestimated lamb production.

Despite the different methods, the estimated productivity in 1970 was so much greater than in earlier years that there must have been a genuine increase. For example, lambing on the northern half of the island as a whole increased from 28% in 1969 to 35%, and on Faye from 25% to 35% (Table 4). Clearly, large variations can occur from year to year, so that no single estimate necessarily reflects the prevailing average performance of the population.

As well as year-to-year variations, local conditions induced local differences in breeding performance and time of lambing. In both 1969 and 1970, there were higher lambing percentages on Lyall than elsewhere in the north. In 1970 there were 81 lambs/100 ewes on Lyall. For an unmanaged population after perinatal mortality had taken its toll this was remarkably high given that the long-term average on New Zealand hill country farms is about 100%. Lambing times too, may have varied around the island as there was some indication of later lambing on Faye in 1970 (Table 5). These differences in lambing percentage and timing do not simply reflect movements of early-lambing ewes from Faye to Lyall, because the sex ratio favoured males on Lyall and total numbers there were low. During the farming years Lyall ("The Peaks") was considered un favourable for sheep and the shepherds never mustered many from it (Wilson and Orwin, 1964). In 1969 it had the lowest density of sheep on the island.

These annual and local differences in reproduction suggest that the growth of the population as a whole was variable in time and place. However, there also seems to have been a consistent increase in lambing % from an average of 20.5 up to 1961 to one of 28.0 thereafter (Table 4).

The population age structure in 1970

Despite precautions and checks, two unavoidable problems remained in producing an accurate age distribution from jaws. They are particularly pertinent to this study, which seeks specific years showing especially good or bad recruitment.

Firstly, Campbell Island has an oceanic climate which minimises seasonal alternations of growth rate (and hence of cementum lines) compared with continental conditions (Klevezal, 1973). Thus there will be some errors in absolute age, even though the relative distribution is probably real. Secondly, lambing was not tightly pulsed although more than 75% were born in a 5-month period of winter and spring. At the time of sampling (midsummer) over 75% of animals aged by cementum lines would have been in the correct age-class even though their actual ages spanned 9 months. The remainder would have been in the next highest class.

Clearly there are constraints on what can be deduced from this age distribution. But there would have to be greater distortions than are accounted for by the known sources of error to materially alter the overall shape of it. In this discussion therefore the age structure in 1970 is taken to be biologically real (Table 3, Fig. 3). Each age-class represents net recruitment, that is, the indistinguishable combination of births and subsequent survival.

By 1970 the population had been growing rapidly for at least part of the preceding decade. Consistent with this, the age distribution showed no greatly expanded age-class that reflected a single pulse of recruitment within the 1960s. Either there was a sudden and sustained change in recruitment or mortality around 1960, or one or both gradually changed throughout the 1960s.

Changes in the sheep and their environment
(a) Meteorological changes

Climate and weather have two general classes of effects. Firstly, long-term climatic trends influence plant productivity and accumulated biomass, the balance of woody to herbaceous species, and altitudinal zonation. For the sheep these combine to determine carrying capacity and shelter. Secondly, the severity and frequency of short term climatic events (the weather) at crucial times can affect survival, particularly of lambs.

Taylor *et al.,* (1970) found no tendency towards better weather from 1957 to 1970, but if a longer period is taken there has been a steady trend to warmer, less windy conditions since the farming days. The period 1900 to 1935, which included the farming years, was the coldest since records began in New Zealand and was termed a mini ice-age (Salinger and Gunn, 1975; Salinger, 1980). The last shepherds saw icebergs, and ice washed up on the beaches (Spence, 1968). Between 1935 and 1975 mean annual temperatures rose by 1 °C over the whole New Zealand region and the mid 1950s were much warmer than average. Simultaneously, the duration and frequency

of strong winds fell so that there was less evaporative cooling (Salinger and Gunn, 1975). For Campbell Island this meant an increase in Growing Degree Days for plants (i.e. no. of degrees by which the daily mean temperature exceeded 0∞C x the number of days). From 1942 to 1955, nine of the 14 years fell below the long-term mean, and the other five were only slightly above, but from 1956 to 1972 eight years were below and nine substantially above the long-term mean. There was an especially warm period between 1968 and 1971 (Fig. 4).
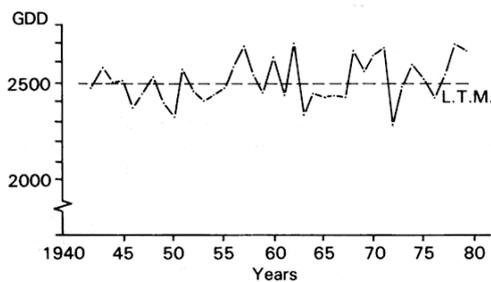
Figure 4: *Growing Degree Days (GDD) per year above base O∞C compared with the long term mean (LTM) on Campbell Island from 1942 to 1969. From 1942 to 1955, 9 years were below the mean and 5 above; from 1956 to 1972, 8 years were below and 9 above.*

Short-term, high-intensity events in the weather are harder to discern in a general meteorological record and to relate to animal performance and behaviour. An analysis of mean monthly temperature, rainfall, and hailstorm frequency in the four main lambing months (August-November) showed no consistent trends. Mean monthly temperatures rarely exceeded the long-term mean from 1941 to 1955. From 1956 to 1962 that patten was reversed, but in succeeding years it was again erratic. From 1960 to 1980, total rainfall rarely showed any consistency from month to month. A series of drier Septembers and Octobers ran from 1955 to 1962 but even so, 70-100"70 of days were rain days (precipitation> 0.2 mm). Hailstorms correlate closely with a sudden drop in temperature and increasing wind speed above Beaufort 8 (gale). Between 1959 and 1960 the lambing months had more hailstorms than in much of the 40-year record.

In summary, general climatic conditions became consistently warmer and calmer from the mid 1930s to present. Some of the main lambing months were warmer and drier than average, but there was no

consistent improvement. Unpredictable storms occurred in these months in most years.

(b) Changes in the vegetation
Meurk (1975, 1976, 1977, 1982) has summarised the modification of the island's vegetation and flora. During the late 19th century and throughout the farming era, much of the vegetation was burnt. At first the tussocks re-sprouted vigorously, but after repeated burning and grazing they died and the shepherds scattered seeds of introduced grasses to create new pasture. The large subantarctic herbs could not withstand any burning or grazing.

There were 4000-5500 sheep when farming ended in 1931, but only about 1000 by 1960 (Wilson and Orwin, 1964; Spence, 1968). Under this reduced grazing pressure, and the improving climate, the sub-antarctic vegetation would be expected to recover, providing more scrub for shelter, and herbs and tussock grasses for food. Since 1930, the scrub line has spread upwards to 200 m and become thicker (Bell and Taylor, 1970; Meurk, 1977). This would have been assisted by the warming climate, and also by the existence of open swards because scrub seedlings are shade intolerant and slow to invade *Chionochloa* (Zotov, 1965). Although the scrub species are largely unpalatable they do provide shelter.

The capacity of the vegetation to respond to reduced grazing was shown after the sheep were removed from the northern half of the island in 1970. By 1980, *Chionochloa,* introduced grasses *(Poa pratensis, P. annua, Festuca rubra* and *Agrostis tenuis)* grew dense with massed seedheads up to 0.5 m tall (Dilks and Wilson, 1979; Meurk, 1982). Palatable endemic herbs, *Pleurophyllum speciosum, P. crini/erum, P. hookeri, Anisotome lati/olia, A. antipoda* and *Stilbocarpa polaris* became common. Such changes could well have occurred in the lightly populated parts of the island between 1931 and 1960. Wilson and Orwin (1964) and P.R. Wilson (pers. comm.) described the areas with few sheep in 1961 as being covered in rank vegetation. By 1969 many of these places carried large numbers of sheep (Taylor *et al.,* 1970) and continued to do so up till 1984. As numbers built up the sheep created lanes through the scrub (Dilks and Wilson, 1979; Meurk, 1982).

In particular years, surges of plant growth occur. Meurk (1976) described the profuse growth and flowering of *Chionochloa* tussocks in the summer of 1975/76 after the unusually warm summer of 1974/75, and again in 1980/81 (C.D. Meurk, pers. comm.). Something similar would have happened in the exceptionally warm years of the 1950s. Such bursts of

growth may have had a flushing effect on both sexes, enhancing ovulation and spermatogenesis through an increase in liveweight.

(c) Changes in the sheep
The shepherds observed that virtually every common breed could be recognised in the population (Spence, 1968; Timms, 1978). Wilson and Orwin (1964) found that Merino, Lincoln, Corriedale and Romney had been among the establishment flocks.

In 1953, three Cheviot rams were landed, the first new blood since 1923 (Wilson and Orwin, 1964). Presumably they were vigorous animals to justify the effort but there is no record that they survived. The Cheviot breed is noted for its clean limbs and willingness to forage into scrub, both of which are features of the present sheep. However, no evidence of Cheviot blood can be diagnosed in the conformation or wool character of the population (W.R. Regnault, pers. comm.). These three rams must therefore be discounted as a trigger for the resurgence of the population.

During the farming period management was minimal. Mustering was so incomplete that in 1929/31 there were, reputedly, 4500 managed sheep and about 1000 'wild' ones (Spence, 1968). Sheep were not culled for quality, and ewes were not assisted with lambing. Apparently, skuas *(Stercorarius skua lonnbergi)* used to attack lambs (Spence, 1968), and in 1975 even penned adults had to be protected from them (Regnault, 1976). The sheep were not treated for internal parasites, and hydatids were so common that a clean, edible liver was a rarity. Animals missed at shearing developed double fleeces that trailed on the ground (Spence, 1968), and rams with long belly wool were trimmed to increase their mobility in the muster (Timms, 1978). When animals were no longer shorn and docked, multiple fleeces would have been commonplace and all would have had long tails.

Most females now progressively shed their whole fleece and rams shed their belly fleece (Regnault, 1976). Self-shedding is genetically linked to pigmentation in other feral sheep populations. On Pitt and Arapawa Islands, most animals now show both characteristics although the populations there were non-shedding white sheep 40-70 years ago (Rudge, 1983; Orwin and Whitaker, 1984). However, the Campbell Island sample shot in 1970 was still 98.7% white, and later censuses up to 1984 have not revealed increasing pigmentation.

Pigmented sheep are generally more fertile than white ones (Adalsteinsson 1984), yet the expanding population on Campbell Island has not shown an increasing proportion of pigmented phenotype. Nevertheless, there has been a marked improvement in lamb production. During the farming years, lambing percentage was only 30-40 (Spence, 1968), whereas it is now about 60-80. Regnault (1975) found that double-fleeced females were almost invariably lamb less and that the untidiest (Le. shedding) females usually had the biggest, healthiest lambs. In captivity the Campbell Island yearling females went into oestrus earlier than Romneys under the same management regime, and though they produced no twins, almost all became pregnant and their lambs had excellent survival rates (Bigham and Cockrem, 1982). Regnault (1976) therefore proposed a relationship between reproduction (increased lambing, early fertility and longer reproductive life of females) and field observations on lambing and fleece growth. Thick fleece on the belly of males and the perineum of females, matted in both sexes with peat and faeces, could impede copulation. If females were inseminated as yearlings when they still had their initial short fleece, the combined stress of pregnancy and winter would augment the normal fineness break in the fibre. Freed of her fleece, the female could continue to breed each year. If she did not breed as a yearling she would possibly never do so as fleece and tail became a greater impediment to copulation. In males the selection would be for clean bellies.

The hypothesis has not been tested experimentally on Campbell Island or in commercial flocks, but farming practice suggests that it has a sound basis. Each year at mating time all sheep farmers shear the bellies of rams and the perineum of ewes (crutching) to remove fleece and dags. In some circumstances males can even develop a suppurating infection of the penis if encasing belly fleece is not removed. Long daggy fleece and tails would have been an impediment rather than a total barrier to copulations. But the indications are that it could have significantly reduced successful mating and productivity until the self shedding trait spread through the population.

In terms of fleece growth and distribution, and early sexual maturation, the Campbell Island sheep have changed since they were abandoned in 1931. By 1961 they had experienced 30 years of natural selection in addition to that operating during the farming era. The rate at which fleece characteristics have changed in other feral populations (Orwin and Whitaker, 1984) confirms that this is long enough for the pelage traits to have emerged. It is curious that on Campbell Island there is no phenotypic evidence of increased pigmentation to accompany the self-shedding and enhanced fertility, but it may yet emerge
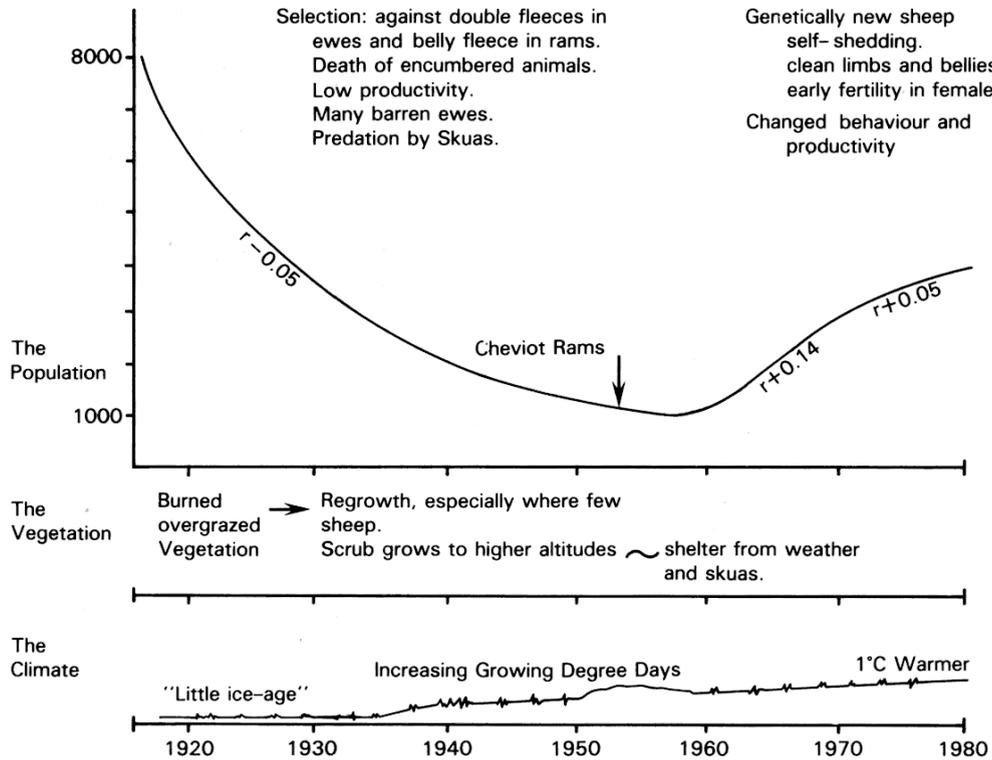
Figure 5: *Diagrammatic synthesis of changes in the sheep population, the vegetation, and the climate (as Growing Degree Days/year) from 1916 to the 1980's on Campbell Island; GDD/year based on atmospheric warming, from Salinger and Gunn (1975).*

in the remnant flock left on the island.

To summarise, this paper has drawn together both historical facts and numerical information to explain the decline and growth of the sheep population and also the timing of events (Fig. 5). The island was probably overstocked in the first place, and the vegetation was soon unable to withstand continuing burning and grazing. Coincidentally, the farming years spanned a phase of climatic cooling. A warming phase from the mid 1930s together with reducing grazing pressure, encouraged recovery of the vegetation. Sheep numbers ceased to decline by the mid 1950s, to produce a stable and expanding population by 1970. Fleecy tails and the matted double fleeces grown when shearing was discontinued, impeded copulation and reduced productivity. The sheep gradually evolved a self-shedding trait in the

fleece, and early sexual maturation which together led to improved productivity.

Home range behaviour may have also played a part in the increase. Shorn sheep always returned to their own part of the island (Spence, 1948), and females and Iambs lived in very circumscribed ranges (pers. obs. Regnault, 1976). Such conservative behaviour could account for the different local population growth rates. Population growth would probably not have begun at the same time in all parts of the island, and until pressure built up in the familiar ranges the animals did not need to move into new areas. When the colonisation phase began there would then have been a lag in population growth to the stage where rank growth was broken down and fresh young growth was induced by grazing.

Acknowledgements

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Appendix I: *Length* (1) *and circumference (c) of horns in cm, and eviscerated carcass weight (w) in kg, of Campbell Island sheep.*

Age (months)		Males			Females		
		n	mean	SE	n	mean	SE
3-6	l	8	28.9	3.64	3	12.6	0.59
	c	8	13.9	0.04	3	8.1	0.44
	w	2	20.5	0.05	7	14.1	1.28
7-12	l	4	29.8	1.8	-	-	-
	c	4	15.4	0.58	-	-	-
	w	4	23.2	2.13	-	-	-
13-24	l	3	52.3	3.53	4	17.32	0.99
	c	3	18.1	0.5	4	9.25	0.32
	w	1	34.0	-	4	24.25	2.34
25-36	l	7	55.7	4.0	2	19.65	1.8
	c	7	19.0	0.7	2	10.0	0.49
	w	3	40.0	3.2	1	29.5	-
37-48	l	6	66.3	4.2	-	-	-
	c	6	19.8	0.64	-	-	-
	w	1	57.0	-	1	27.7	-
49-60	l	4	62.7	2.92	3	21.7	0.95
	c	4	20.5	0.41	3	9.8	0.8
	w	2	49.5	3.5	5	34.6	1.44
60	l	5	69.5	3.07	2	27.65	1.3
	c	5	19.5	0.32	2	12.75	1.2
	w	3	54.6	2.7	-	-	-