THE INFLUENCE OF CLIMATE, HABITAT AND NATURAL SELECTION ON THE NUMBERS OF FERAL SHEEP (*Ovis aries* L.) ON CAMPBELL ISLAND (SUBANTARCTIC)

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ABSTRACT

Domestic sheep were introduced to Campbell Island in 1895, and pastoral farming was pursued until 1931. The sheep were then abandoned. From 1916 to 1961 the population had declined at r = -0.05 but between 1961 and 1969 it grew at r = 0.14.

During the farming years the vegetation was burned and overgrazed. It slowly recovered under lighter grazing as the populatin dropped, and in response to a general climatic warming in the southern hemisphere. When they were not longer shorn, the sheep grew double fleeces which may have reduced their ability to copulate. Intensive natural selection has now led to sheep with clean limbs and bellies, and in females the ability to shed fleece each year and breed at one year old. It is postulated that, by the early 1960s, the combined effects of more food and shelter, warmer lambing months, early female fertility and longer reproductive life, resulted in a growth in numbers which has continued to 1983.

INTRODUCTION

This paper is about a population of feral sheep, that is, sheep that have run wild from the domestic state. Unlike the true wild sheep and goats which are of prime interest to this Conference, they are not a valuable game animal nor generally regarded as a rare species to be conserved. Indeed, as aliens on a subantarctic island that has high values for native flora and fauna, they are pests.

Wildlife managers would have exterminated this population long since had there not been two great uncertainties. The first of these was that the population seemed to be declining to natural extinction; and the second was that the sheep may even have been improving the conditions for nesting sea birds (Wilson and Orwin 1964). The resolution of these questions has been a fascinating exercise for New Zealand biologists and wildlife managers for over 20 years.

The circumstances and setting for this study are quite different from those facing North American wildlife managers. Nevertheless, the history of this population does have some useful lessons in emphasising the subtle interplay of environment, habitat, and natural selection in the lives of wild animals and in the business of trying to manage them.

Campbell Island lies some 500 km south of the southern tip of the New Zealand mainland at 52°S 169°E (Figure 1). It is uninhabited except for a meteorological station. It represents the remnant eastern rim of an eroded

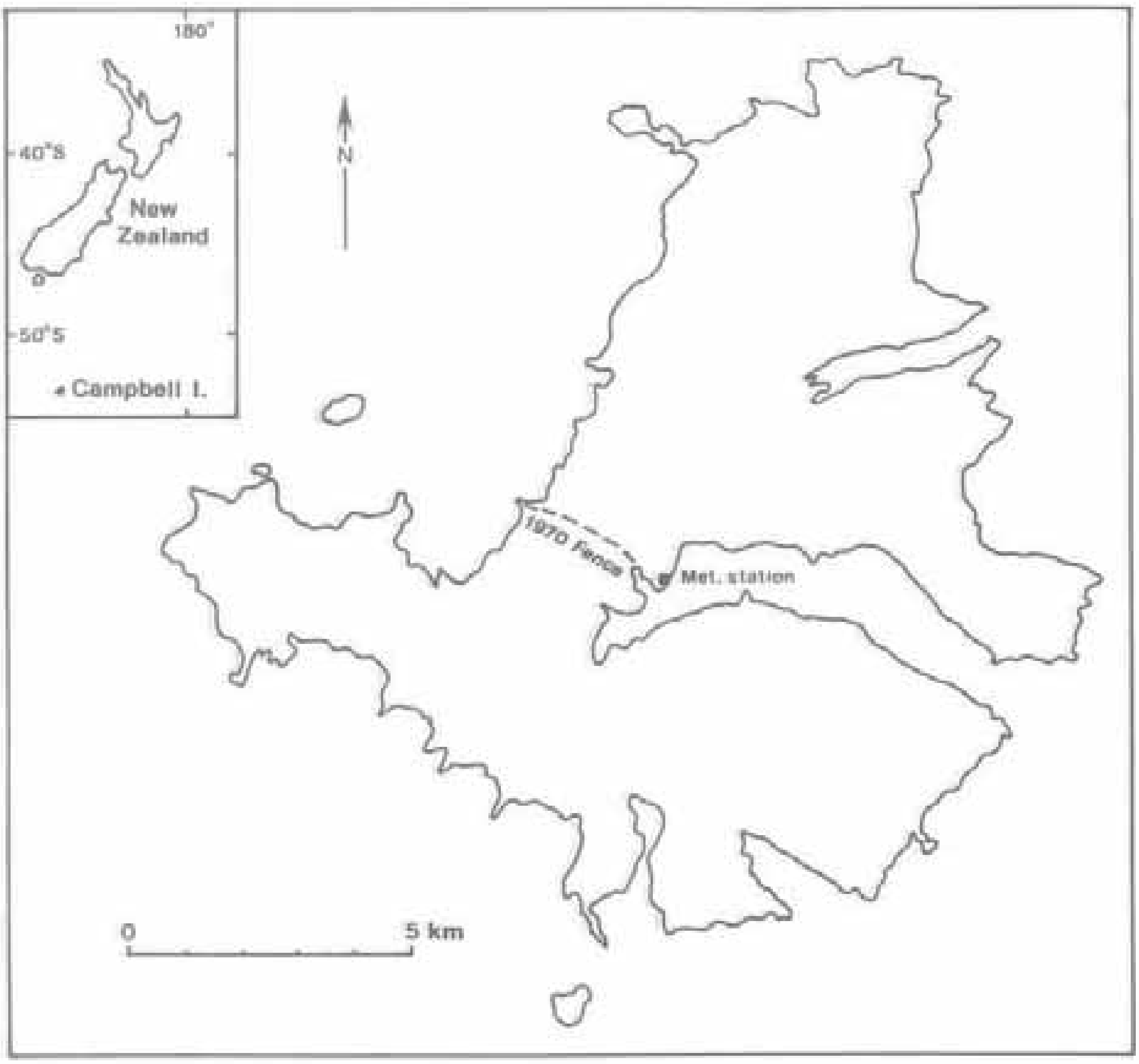

Figure 1. Location of Campbell Island and of place names mentioned in the text.

volcanic cone and has an area of about 109 km^2. The terrain is generally hilly with five peaks over 457 m and it is blanketed with peat. The woody vegetation is a low forest of scrub dominated by Dracophyllum scoparium, D. longifolium and Myrsine divaricata. The original non-woody part of the vegetation was, broadly speaking, a tussock grassland of Chionochloa antarctica with giant endemic herbs. The whole vegetation was burnt and grazed during the farming era, and introduced pasture grasses were sown (Meurk 1975, 1976, 1982). Campbell Island is most noted for being the world's main breeding ground of the Southern Royal Albatross (Diomedeae. epomophora).

Domestic sheep were taken to the island in 1895, and pastoral farming was pursued with varying success until 1931 when it became uneconomic. Over 4000 sheep and about 20 cattle were then left to their own devices. In 1961 there were about 1000 sheep which amounted to a decline of about 5 percent per year since 1916 (Wilson and Orwin 1964). It was suggested that the population might gradually die out naturally.

By 1969 the sheep population had not continued to decline as predicted (Figure 2) but had increased by a factor of about three, an average of 14 percent per year (Taylor et al. 1970). Such a dramatic growth in numbers raised questions about the future of the nesting Royal Albatrosses. The island was thereupon divided into two with a fence, and all sheep on the northern half were killed in 1970 to establish a long-term experiment on albatrosses, sheep and vegetation. Sheep on the southern side were counted until 1984 when all but about 500 were killed.

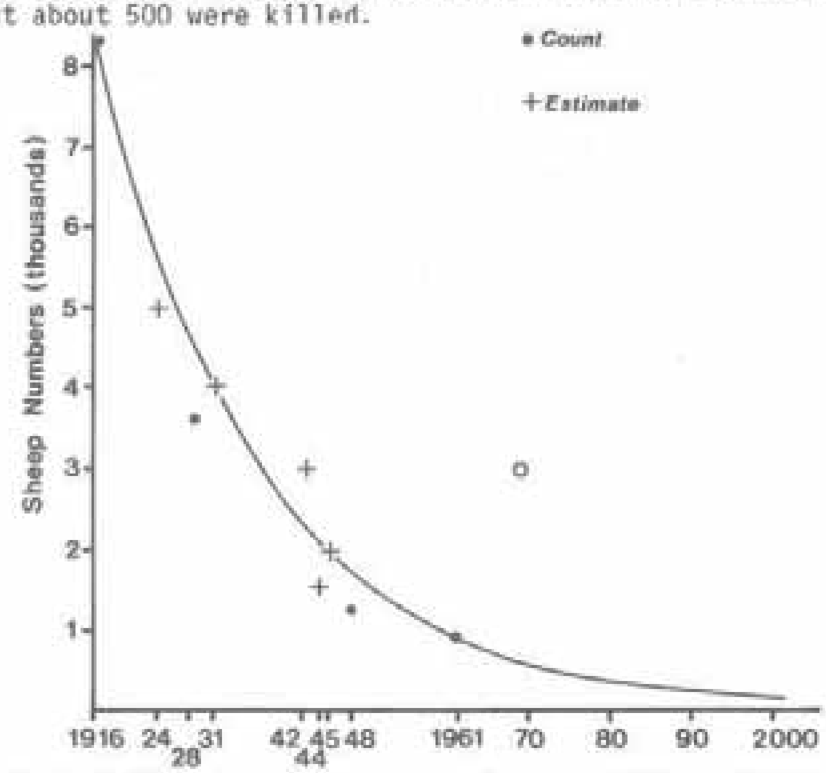

Figure 2. The exponential decline in sheep numbers between 1916 and 1961 extrapolated to 2000 AD. The number actually counted in 1969 (3000) is shown as 0 (modified from Wilson and Orwin 1964).

The age distribution of over 1000 sheep shot in 1970, and changes in the population have now been analysed in some detail (Rudge, in prep.) This present paper summarises some of the changes that have been observed in the environment and carrying capacity of the island, and in the genetic constitution of the sheep.

CHANGES IN THE SHEEP AND THEIR ENVIRONMENT

Conditions on Campbell Island were relatively simple compared with many mainland situations. The population was not influenced by immigration or emigration, there were no mammalian predators, and hunting amounted to providing the occasional roast for the station staff. Although the historical record is blurred, it clearly shows a steady decline in numbers, a dramatic increase, and movement of sheep into untenanted areas. Any explanation for these changing fortunes has to account for both phases of the population performance, and the enhanced carrying capacity of the island that sustained the increasing numbers of sheep.

THE METEOROLOGICAL CONDITIONS

The climate and weather on Campbell Island have two general effects. Firstly, the long-term climatic trends would influence plant productivity, the ratio of woody to herbaceous vegetation, and vegetation zonation. For the sheep these effects determine the amount of food and of shelter. Secondly, there is the severity and frequency of short-term events at crucial times, most particularly at lambing.

The period 1900-1935 (effectively, the farming years) was the coldest in the recorded history of New Zealand. The last shepherds to leave in 1931 saw icebergs floating by and ice stacked up on the shores (Spence 1968). Since 1946 the southern hemisphere has been in a warming phase (Salinger and Gunn 1975, Salinger 1980). Between 1935 and 1975 the mean annual temperature rose by 1°C, and the mid 1950s were particularly warm over the whole New Zealand region. The duration and frequency of strong winds has also fallen so that there is less evaporative cooling, and more actual heat for plant growth. A general integrator of these combined effects is the summation of Growing Degree Days (GDD), = (no. of degrees by which the daily mean temperature is above a base line) X (the number of days). In the period 1942-1955, 8 of the 14 years had GDD values below the long term mean (LTM) for the island, and the other 6 were only slightly above; but from 1956 to 1962 only two years were below the LTM and the rest were above it by about 10 percent (Figure 3). There was another warm period between 1968 and 1971.

The other relevent climatic events are sudden, high-intensity deteriorations in the weather. These are difficult to discern in a general meteorological record and even harder to relate to animal performance and behaviour hour by hour and day by day. The most crucial time is when lambs are born, and if this coincides with prolonged wetting or wind chill then survival is jeopardized. Lambs were born throughout the year, but the resident Meteorologists noted that most appeared between August and December.

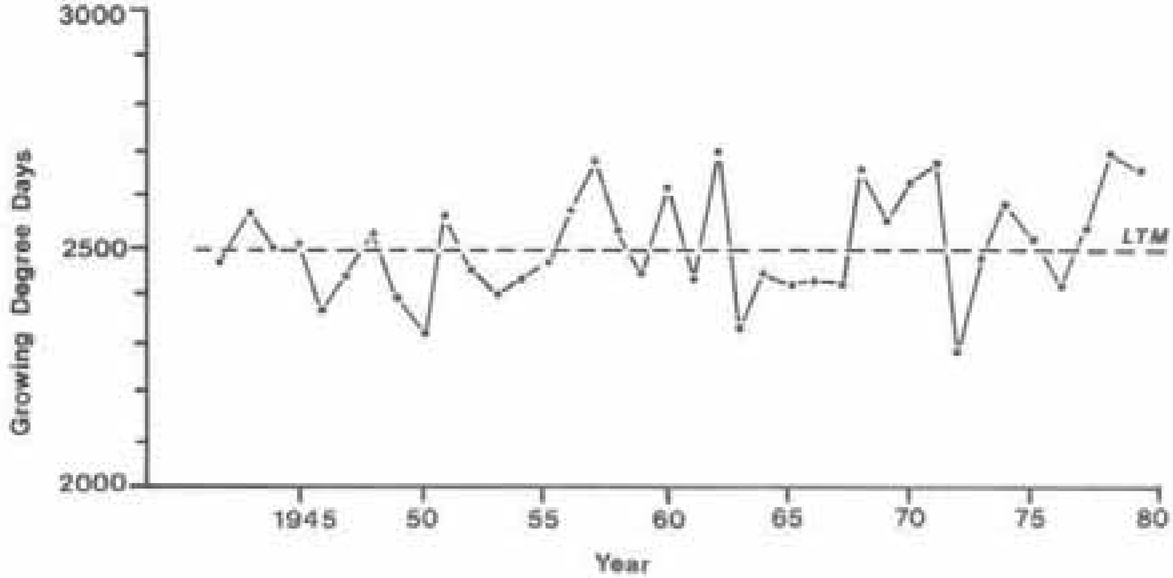

Figure 3. Growing Degree Days on Campbell Island from 1942-1979.

An examination of the island's Meteorological Station record shows that up to 1955 the mean monthly temperatures in four successive lambing months rarely rose above the LTM (Figure 4). From 1955-1962 the pattern was essentially the converse. In the 1965-71 period, August was particularly mild but this did not carry consistently through into the succeeding 3 months. Over the same years the number of raindays (greater than 0.2 mm) remained in the range 70-100 percent.

Hailstorms, which combine a sudden drop in temperature, increased wind velocity, and wetness, showed no consistent trend towards better conditions for lambing. Some individual years such as 1956 and 1965 had relatively few hailstorms, but the period 1959-1964, when the population was apparently beginning its dramatic growth, had some of the highest hailstorm frequencies in the 40 year record. Haildays correlated closely with frequency of winds above Beaufort 8 (gale).

These meteorological records reflect what every summer field worker experiences on the island: brief fine periods broken by sudden, violent squalls of rain and hail.

In summary then, the general climatic conditions were improving slowly and consistently during the years of declining numbers, but lambing was probably still beset by fierce unpredictable storms in most months and years.

THE VEGETATION

During the late 19th century and throughout the farming era when the vegetation was burned, snow tussocks (Chionochloa antarctica), were the chief victims (Meurk 1975, 1976, 1982). At first they re-sprouted vigorously but, after being repeatedly burned and then grazed, they died to be replaced by a pasture consisting mostly of northern hemisphere grasses.

Since 1930, partly in response to steady climatic warming, scrub has spread to higher altitudes and become thicker (Bell and Taylor 1970, Meurk 1976). This spread was assisted by the more open nature of the grazed swards because the scrub seedlings are shade intolerant and are slow to invade tussock grassland (Zotov 1965). The scrub species are unpalatable to sheep but do provide shelter for them.

When farming ended in 1931 there were between 4000 and 5500 sheep (Wilson and Orwin 1964, Spence 1968). They declined to about 1000 by 1960 and this alone, even without an improvement in climate, must have allowed all components of the vegetation to recover in quantity. Some indication of this process was demonstrated on the northern side of the fence in the decade after all sheep were killed there in 1970 (Dilks and Wilson 1979,

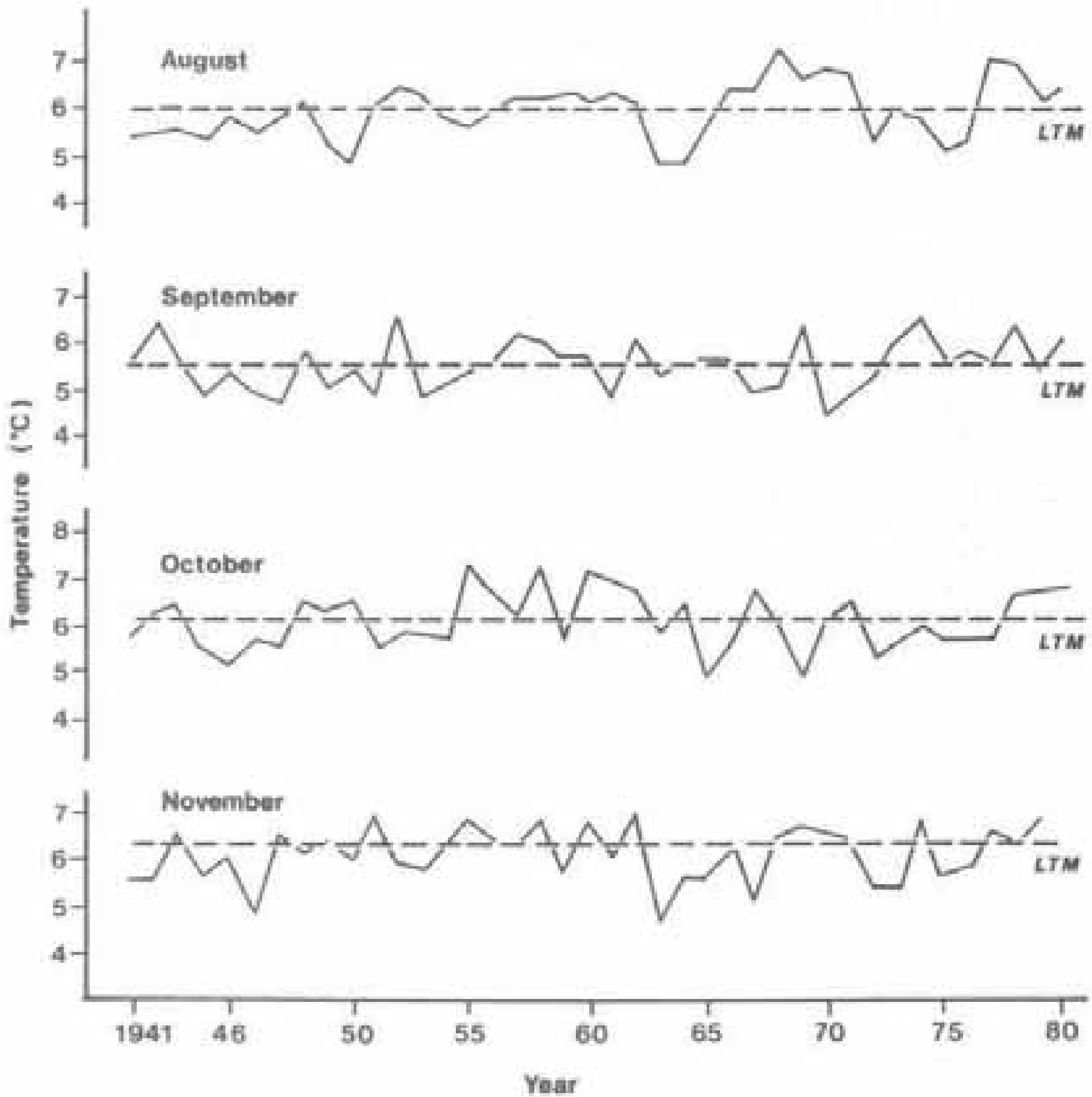

Figure 4. Mean monthly temperature in main lambing months on Campbell Island relative to the long term mean for 1941-1980.

Meurk 1982). Chionochloa tussocks and introduced grasses grew thickly up to 0.5 m tall, and the giant endemic herbs became common. Changes of this sort must have occurred in the lightly populated parts of the island between 1931 and 1960. Indeed, Wilson and Orwin (1964) reported that areas with few sheep in 1961 were covered in rank vegetation. By 1969 many of these same places were carrying hundreds of sheep on closely cropped swards (Taylor et al. 1970).

In particular years there were flushes of plant growth. Meurk (1976) describes the profuse growth and flowering of Chionochloa in 1975 after the unusually warm summer of 1974. Something similar must have happened in the exceptionally warm years of the 1950s.

THE SHEEP

Several lines of evidence suggest that the Campbell Island sheep are genetically rather different today from those that were abandoned. During the farming period some natural selection would have already been operating because management was so poor. By 1931 there were already at least 1000 'wild' sheep which had habitually escape the musters (Spence 1968). The flock was not treated for internal parasites, nor culled for quality. Skuas (Stercorarius skua lonnbergi) "used to get down on quite a few lambs" (Spence 1968). In 1975 even penned adults had to be protected from skuas (Regnault 1976). Hydatid cysts were common in livers, but as soon as sheep dogs left the island the disease would have died out.

Un-mustered animals developed double fleeces that trailed on the ground (Spence 1968), and such multiple fleeces would have been universal once shearing was discontinued. But by the mid 1970s, most of the females were progressively shedding their whole fleece, and most rams were shedding at least their belly fleece (Regnault 1976). In other sheep populations that have been feral for 40-70 years both sexes completely shed their fleeces and this is correlated with an increase in pigmentation (Rudge 1983, Orwin and Whitaker 1984). Adalsteinsson (1984) has shown that pigmented sheep have an enhanced fertility. However, the Campbell Island population remained predominantly white (98.7 percent) during the expansion phase. Even so, productivity virtually doubled from about 34 lambs per 100 ewes in farming days (Wilson and Orwin 1964) to 62 in 1970.

Even though pigmentation did not change, other features of fleece growth may be closely correlated with early fertility and a longer reproductive life in females (Regnault 1976). Thick fleece on the belly of males and round the perineum of females, matted with peat and faeces, could impede copulation. Any females inseminated as yearlings would have the combined stresses of pregnancy and winter to induce fineness and breaks in the fibre. Females thus freed of their fleece could breed in succeeding years, but those which did not breed as yearlings would possibly never do so. In males the selection would be for clean bellies. Observations consistent with Regnault's hypothesis are that: double fleeced females were almost invariably lambless, the untidiest females usually had the biggest, healthiest lambs, legs were long and clean, and most rams had clean bellies (Regnault 1976); and that Campbell Island sheep go into oestrus at 8 months old which is earlier than other breeds under the same management regime (Bigham and Cockrem 1982).

CONCLUSIONS

It seems clear that no single factor precipitated the changed performance of the sheep on Campbell Island, but there remains the problem of why population growth did not seem to begin until about 1960. The mid 1950s were, afer all, exceptionally benign in general climatic character, and possibly also in the particular months of lambing. The vegetation had been lying fallow for some 25 years and must have been well along in its recovery from the burning era. Genetic changes would have been accumulating in the sheep and being manifested during the period of decline rather than waiting to erupt at some particular date.

The behaviour of the animals may well have played a part in delaying their resurgence. The shepherds remarked that when sheep were released from shearing pens they always went back to their own part of the island. Limited observations on family groups (Regnault 1976), and personal observations showed that females and lambs lived in very circumscribed ranges. The genetic balance may well have been changing within localised groups but until population pressure built up in the familiar ranges, animals did not move out and exploit the resurgent growth elsewhere. The descriptions by Wilson and Orwin (1964), of rank vegetation in areas that were to become densely populated within 10 years, support this view. Even then, the colonizers had to pass another threshold of breaking down rank vegetation to promote fresh young growth by their own grazing. Once the colonization phase began the way was open for the sheep to exploit the rich food resources and their new genetic constitution.

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