Relationships Between Vegetation and the Population Dynamics of Skomer's Rabbits

Denis Bellamy

Department of Zoology
National Museum of Wales

July 1992

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1 Introduction

1.1 This paper is a resume of two decades of intermittent study of rabbits and vegetation on Skomer. It is intended to set a baseline for the continuing use of Calves Park and South Plateau for research into the population ecology of rabbits and their dynamic equilibrium with their grassland habitat. It is referenced to the University of Wales PhD theses of Diana Bell, the research of Paul Slater and the project reports of students of the department of zoology at Cardiff, who worked on the island in fulfillment of the requirements of their second year courses. The latter were lodged with the Welsh directorate of the NCC.

It has to be stressed that the work could not have been carried out without the commitment and unstinting assistance of Mike Alexander, who was the island's warden at a critical phase in the opening up of the national nature reserve to critical conservation management.

1.2 It is difficult for today's visitors encountering Skomer's rabbit dominated landscape to understand that well over a century ago Skomer would have looked much the same as the tidy farms that lined the road from Haverford West to Martin's Haven, It was then a mainland investment set up as a state-of-the art mixed agricultural enterprise and tenanted by a determined young English farmer fresh out of agricultural college. Even as late as the 1950s the tenant at that time seriously contemplated commanding the local market in early potatoes. They were both defeated by the tides surging through Jack Sound and not the depredations of rabbits. In fact, rabbits were kept at a level that did not compromise arable/cattle/sheep enterprises, bearing in mind that twelve rabbits eat as much as one sheep. Annual culling was necessary and their fur and meat were seen to be important agricultural outputs, as they were on mainland farms of the time.

Gradually, in the face of communications difficulties with the mainland Skomer came to be valued for its wildlife, and eventually rabbits took up a dominant position as the major herbivore of the island in a semi natural ecosystem.

Nevertheless, after it became a national nature reserve, it was realised that rabbits were reaching population densities that had never been seen since the Normans set them loose in the13th century. Fears grew that there were too many rabbits, which were seen as having a detrimental effect on soils and vegetation. This in turn led to talk of setting up a management plan for culling rabbits to a level that optimised the populations of all other species they influenced.

2 History from 1972

2.1 The history of work on Skomer's rabbits was first summarised in a report made in 1978. This covered the major factors involved in the vegetation changes that had occurred since the island became a nature reserve. The question occupying the minds of local NCC officers of the time was whether there was a need for a rabbit management plan. Based on predictions from Gillham's research on Skokholm in the mid 50's, supplemented by Bellamy's smaller scale student projects on Skomer between 1972-75, experiments were proposed to answer this question in bracken-free areas using one large enclosure and several smaller exclosures and open plots. The proposition was based on a viewpoint that 'landscape' and 'species diversity' had changed considerably from the condition valued by those who studied the island in the 1950s because rabbits were no longer being culled for 'pot and fur'.

It was the accepted wisdom of the time that there would be advantages to many of the island's important conservation features if rabbits could be controlled. In this respect, an experimental approach would provide information relevant to evaluating the management options and costs, together with an assessment of the long-term logistics of precisely regulating the rabbit population by culling.

2.2 Enclosures and exclosures were set up in the spring of 1979 with NCC funds for posts and wire, and voluntary labour, in Calves Park (Field 7) and South Plateau.

Sponsorships were obtained to purchase a tractor-towed mower, part of the cost of a new tractor, rabbit traps and snares, an observation tower, and the loan of a herbicide sprayer.

The programme was incorporated into the field work requirement of second year zoology and botany students of University College Cardiff, a PhD studentship on rabbit behaviour, and, in 1982, the work of a research assistantship. The last survey organised from Cardiff was in 1988. Since then, monitoring of the exclosures, and counting rabbits in Calves Park has been carried out as part of the Warden's annual work programme.

In the initial stages the warden scheduled a mowing routine in Field 7 with the aim of destroying bracken. This culminated in the removal of persistent scattered fronds using spot applications of herbicide.

The work initiated and stimulated other, separate, but related, programmes:-

(1) the first general systematic botanical survey of the island by Graham Bray (funded by NCC);

(2) the detailed mapping of archaeological features of the entire island (funded as fieldwork for students of the Cardiff Archaeology Department by John Evans. This was initiated, because there appeared to be opportunities for relating the activities of prehistoric settlers to current vegetation patterns and rabbit distribution;

(3) a general heathland survey by Paul Slater (carried out because rabbits appeared to be limiting the spread of heather seeding from existing stands);

(4) a study of the colonisation of bare ground by Rumex sp., Silene maritima, Tripleurospermum maritimum and Armeria maritima. This led to a successful effort to stabilise the cliff top peaty environment with transplants of Silene from outcrops to plots at Skomer Head. Detailed experimental work was carried out on the mainland of seed germination and longevity of the dominant grassland species with a view to understanding the factors governing colonisation of areas of matted dead grass and bare ground. A particular important additional study area was the bracken-free grassland to the west of Captain Kites. This involved pot experiments into the life histories of the island's dominant plant species, which are ongoing at the Forest Farm Nature Study Centre, Cardiff.

The major results were presented in several reports to the NCC, and two PhD theses of the University of Wales.

This report summarises the overall outcome of the programme, with some pointers to the future, taking into account recent work on a computer population model of rabbits, long term monitoring of South Plateau exclosures, and peat loss experiments at Skomer Head.

3 Work in Calves Park

3.1 Enclosure

A 5-acre enclosure was built in Field 7 (Calves Park; Fig 1) in the spring of 1979. It was used for projects involving observing, counting, and marking rabbits, and carrying out quantitative botanical assessments by quadrats and transects in open plots, closed plots, transplanted areas, and limed areas.

Fig 1 The Calves Park enclosure with a grid of 10m squares

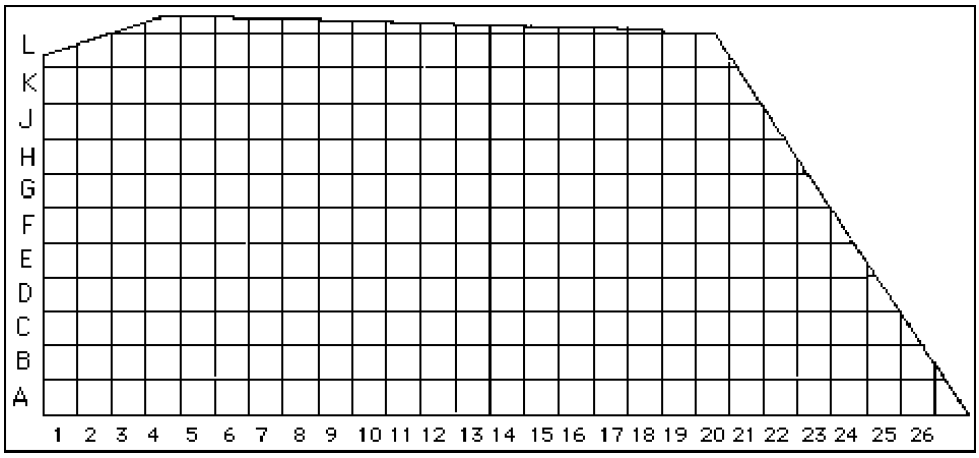
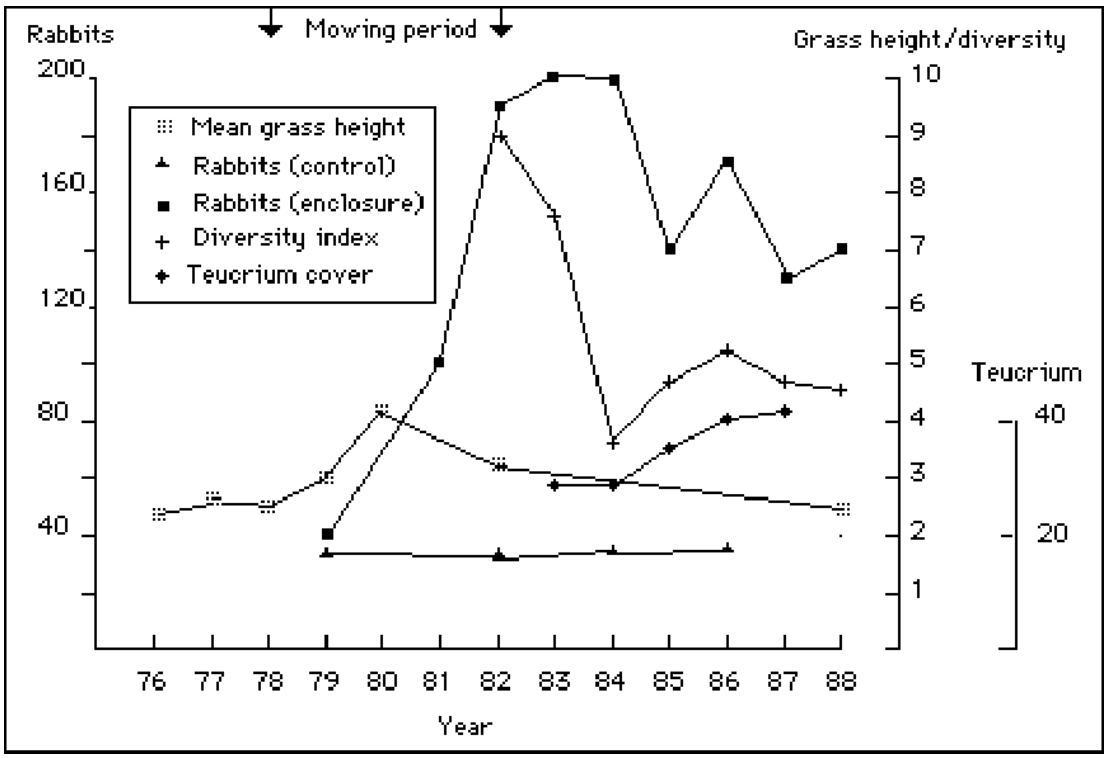


Fig 2 Main findings of work on the enclosure 1976-88

The results refer to the mean grass height (cm); numbers of rabbits at their autumn peak; an index of botanical diversity (average number of species in fixed quadrats); and the ground cover of Teucrium scorodonia (% of total area of fixed quadrats).

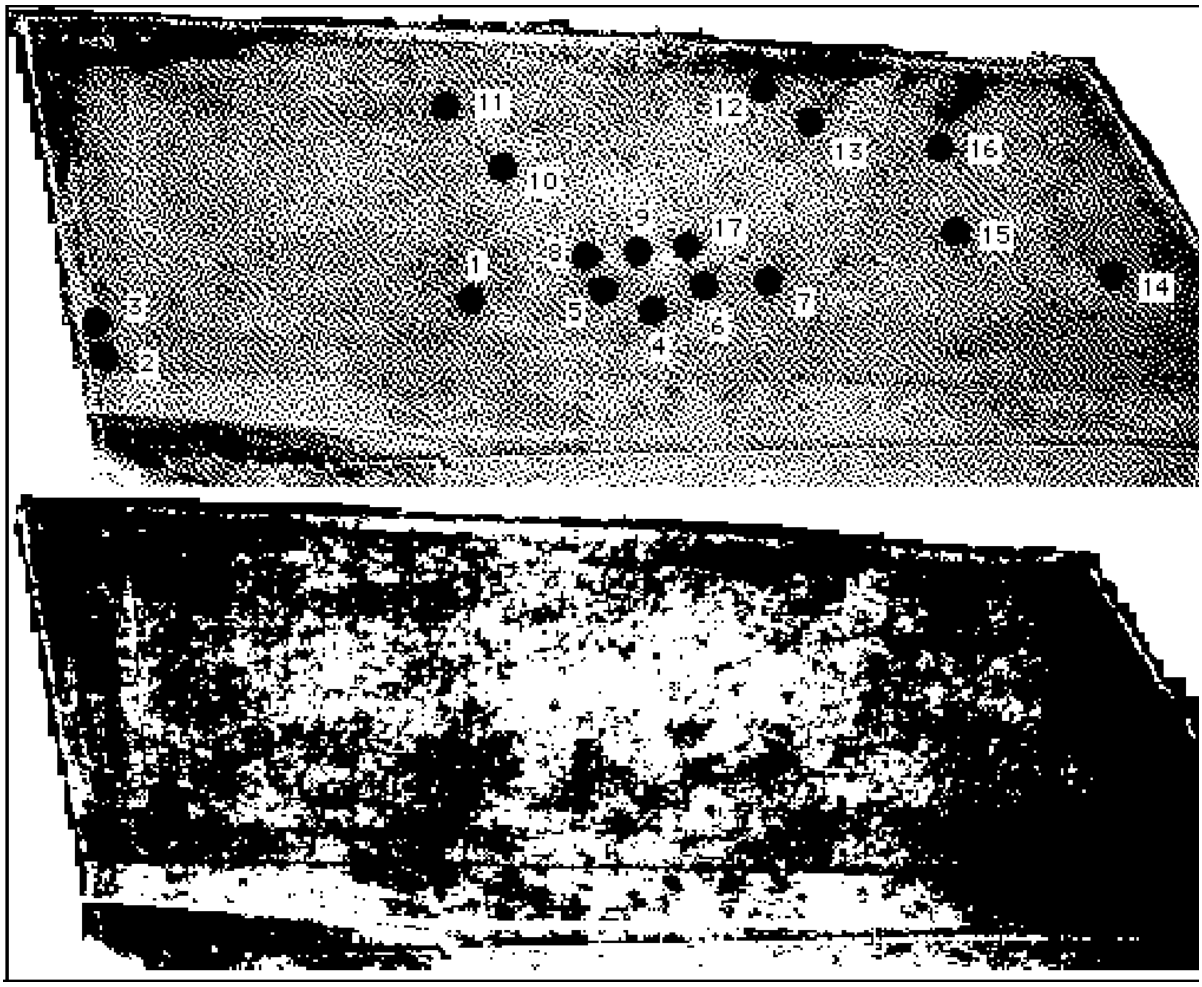


Before the enclosure was established in the spring of 1979, field 7 was grazed mainly by rabbits with burrows at the bases of the surrounding walls. After the enclosure was constructed a much smaller resident population was confined to the centre of the fields. This increased rapidly from about 40 individuals in the autumn of 1979 to a maximum of about 200 in the autumn of 1983-84. The botanical composition of the field changed considerably during this period. Most of the bracken was killed by the programme of late summer mowing, which ended in 1982. The availability of palatable grasses, indicated by mean grass height, increased at first, then dropped as the rabbits reached their maximum population density. The visual impact of 'a green field' was particularly striking, and was welcomed by autumn visitors in 1981-2 as an improvement in the sombre appearance of the island.

There were 17 major warrens in 1982. These were checked on the ground in April 1982, and mapped from photographs taken from a rescue helicopter in October 1982 (Fig 3a) when the field was virtually free of bracken. The warrens were not uniformly distributed throughout the field, and the area of highest warren density was associated with the largest area of closely grazed lawn.

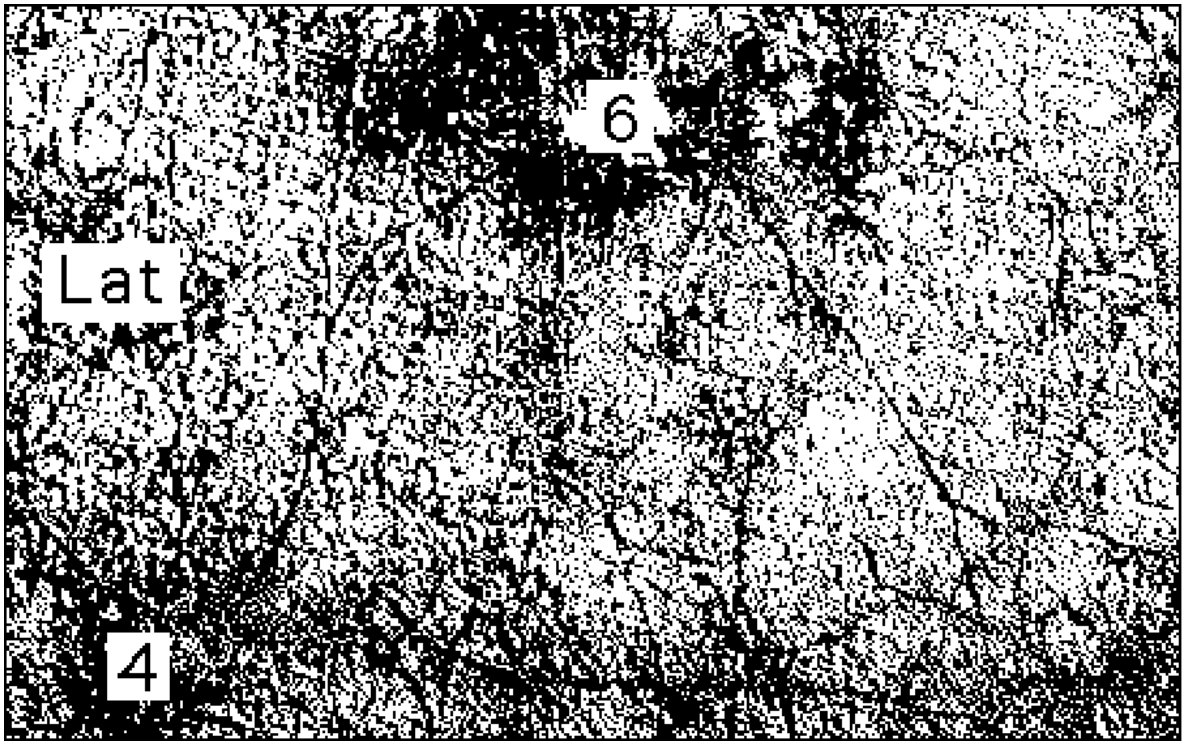
A detailed low altitude aerial survey (Fig 3b) confirmed the findings on the ground that the social interactions between rabbits, on an individual and warren basis, had produced a complex network of paths, grazing areas, and pheromone marking sites (latrines and paw-scrapes).

Fig 3a Distribution of main warrens (black circles; top) and lawns (white areas;bottom) in Calves Park, October 1982



Computer enhancements of photographs taken from a rescue helicopter from RAF, Brawdy

Fig 3b Main routes between warrens (4-6), and cross-paths to latrines (Lat) and pawscrapes, through lawns.



3.2 By 1984 the non-uniformity of grazing in the enclosure from east to west had resulted in a very large increase in vegetation height at the western end, which contained only two warrens. This area, post-enclosure, had been grazed by rabbits burrowing in the base of the western field wall. By 1988 the population in the centre and eastern sections of the field had reached the highest annual peak densities ever recorded for rabbits of about 40 per acre. Its ironic that in the absence of rabbits the field would have supported four to five calves.

There was clearly some adverse situation limiting colonisation in the western part. To test whether this was also responsible for the failure of the western rabbits to increase, the area was fenced off. In subsequent years this sub-compartment became more obviously different and many of the dicots, particularly Lotus, flowered in tall grass. The population of western rabbits did not increase. The reason for this area being different is unknown. This is the only place in Field 7 where the Marsh Thistle is found. It also seems to be a good habitat for Marsh Bird's Foot Trefoil. The distribution of these two species indicates that water drains down the field at this point from a massive southern rock outcrop, and probably makes for damp, unhealthy burrows.

From 1984 the autumn peak in numbers for the centre and eastern areas declined from its maximum, and by the census of 1988 it had fallen from 200 to about 140.

It took some time to find a reliable index of botanical diversity and it was not until 1981 that a suitable method was developed. Applying this index from 1982 onwards revealed an inverse correlation between species diversity and rabbit numbers. A major change in vegetation pattern appeared in 1985 as Teucrium began to spread at the expense of

other species. From 1984 to 1987 there was a 40-50% increase in Teucrium cover making it the dominant botanical species in Field 7. By 1987 it covered 40% of the field. However, at no time did it come to dominate the rabbit lawns.

Altogether, a total of 39 plant species was recorded in the enclosure. Most of these were found in the closely grazed sward of 'rabbit lawns', and rarely flowered. The species diversity of the lawns did not alter very much from year to year, but the relative abundances changed with increasing grazing pressure, most species becoming rarer, and smaller. These lawns were sampled by taking turf plugs 5cm diameter. Each plug usually contained between 4-6 plant species, a few mm high. The biomass of roots was several orders of magnitude greater than that of the stems and leaves.

The control for the enclosure was the open strip of ground between the southern wall of the field and the fence. The rabbit density in this area in 1979 was similar to the maximum density reached in the enclosure in 1983-4. It did not change during the experimental period. In 1988 the control area and the central and eastern parts of the enclosure were very similar in general appearance.

A small population of Barnacle geese used the field for winter grazing from 1981 until the winter of 1985-6. With respect to other birds, throughout the project, rabbits shared the field with nesting shearwaters. There was clearly competition between them but this aspect was not investigated.

4. Exclosures and open plots

4.1 South Plateau and Skomer Head

Annual quantitative assessments of vegetation and depth of soil/ peat were made using set quadrats on fixed transects and 30 X 30 m plots which were sited on South Plateau and Skomer Head.

Four exclosures were established in 1979 on a line from the southwest to northeast facing coastal slopes of South Plateau (Fig 4). The objectives were to examine the pattern of vegetation that would emerge if rabbits were to be eliminated from this area. Apart from 1981, these were monitored every autumn from 1979 to 1988.

Fig 4 Exclosures in relation to path and walls on South Plateau

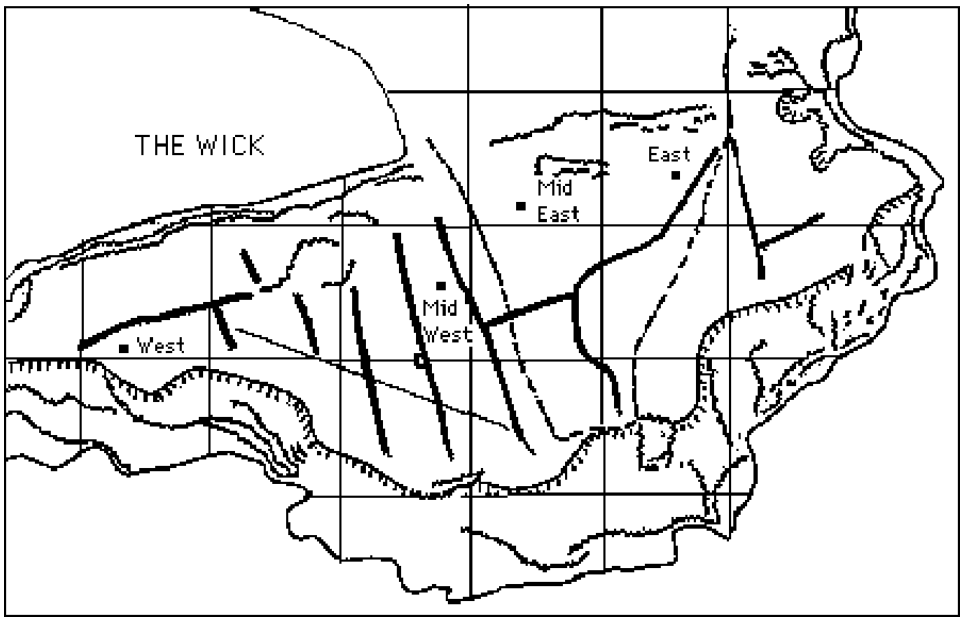


Fig 5 Variation in frequency of three grasses in West control plot

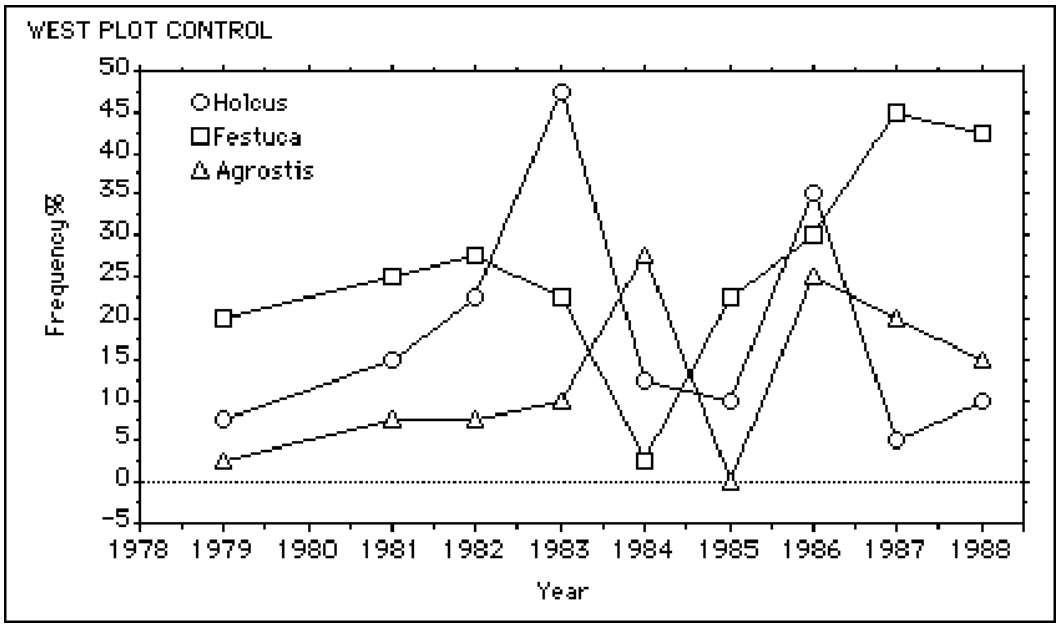


Table 1 % frequencies of species inside and outside exclosures on South Plateau

West

	1979 Outside	1979 Inside	1988 Outside	1988 Inside
Agrostis	2.5	2.5	15	7.5
Armeria	5	7.5	25	5
Silene	7.5	0	7.5	0
Holcus	7.5	5	10	0
Festuca	20	53	42.5	85
Rumex	2.5	2.5	0	2.5
Tripleurospermum	2.5	0	0	0
Dead grass	17.5	10	0	0
Bare earth	35	10	0	0
Moss	0	2.5	0	0
Lichen	0	7.5	0	0

Mid West

	1979 Outside	1979 Inside	1988 Outside	1988 Inside
Agrostis	2.5	2.5	30	35
Holcus	10	10	45	12.5
Festuca	0	0	0	35
Rumex	27.5	73	0	0
Dead grass	2.5	2.5	7.5	2.5
Bare earth	25	7.5	0	0
Pteridium	32.5	5	15	15
Glechoma	0	0	2.5	0

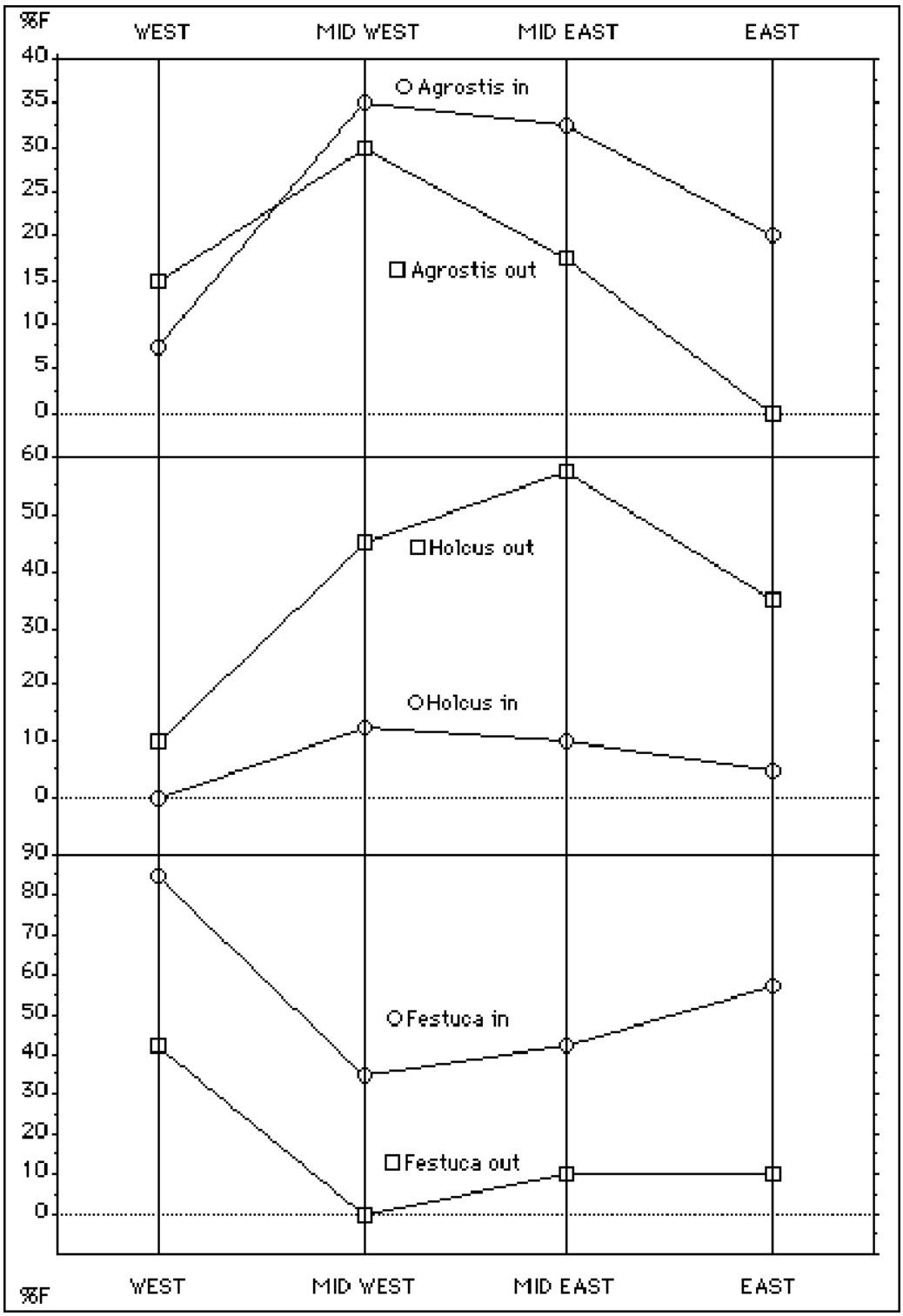
Mid East

	1979 Outside	1979 Inside	1988 Outside	1988 Inside
Agrostis	12.5	13	17.5	32.5
Holcus	37.5	60	57.5	10
Festuca	0	0	10	42.5
Dead grass	2.5	20	0	0
Bare earth	20	2.5	7.5	0
Lichen	0	2.5	0	0
Pteridium	27.5	0	7.5	15
Teucrium	0	2.5	0	0

East

	1979 Outside	1979 Inside	1988 Outside	1988 Inside
Agrostis	0	7.5	0	20
Holcus	50	60	5	5
Festuca	0	5	0	57.5
Dead grass	2.5	0	5	0
Bare earth	22.5	0	2.5	0
Pteridium	25	28	37.5	10
Teucrium	0	0	17.5	7.5
Urtica	0	0	2.5	0

Fig 6 Frequencies (%F) of grass species in four plots on a line, east to west across South Plateau, 1988; in = inside exclosure; out = external control



4.2 Conclusions from the fieldwork

An assessment of the results from 1979 to 1988 is presented in Table 1, and Figs 5 & 6, from which the following main conclusions may be drawn;

-there are long-term trends for the species composition of the exclosures to depart from their surroundings;

-there has been a very large increase in the biomass within the exclosures, with a build up of peat on the western ones and an increase in soil humus in the eastern ones;

-there are significant long-term oscillations and trends in species diversity in both the exclosures and their grazed surroundings;

-there is a cline of species diversity, increasing from west to east, over the relatively small distances which separate one plot from another, which is probably due mainly to the exposure gradient from west to east, with lesser contributions from past land use and differences in soil depth and mineral composition.

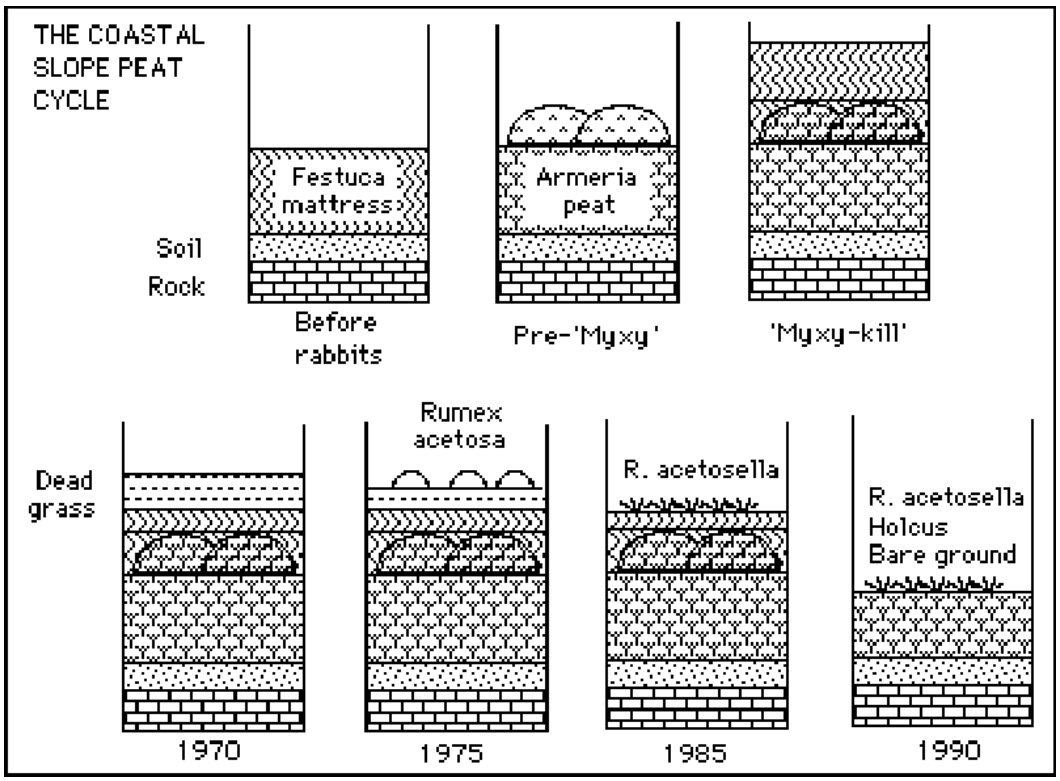
4.3 Peat depth on upper coastal slope

Metal pegs 50cm long were used for marking out large permanent open quadrats on the western side of South Plateau in 1974. They were hammered into a spongy humus soil, with a sparse cover of rabbit-grazed vegetation. In 1980 some of them were found lying on the surface of the soil. At first it was thought they had been dug up by rabbits, but careful examination revealed that the level of the surface of the plots had decreased relative to the underlying rock and that this was the reason for the loss of the plot markers. In some areas, peaty soil equivalent to the entire length of a peg had been lost in 6 years. Examination of other areas along the western coast showed that this was a general phenomenon, being particularly acute on Skomer Head. Here, in the early 1980s, there was very little living vegetation, and the peaty substrate was composed mainly of dead clumps of Armeria and Festuca rubra mattress. A very large set of burrows, which in the early 1970's housed a colony of around 50 pairs of shearwaters, had completely disappeared.

In 1987, 25 rods each 62cm long were inserted into the remaining soil at various points at Skomer Head. When examined in 1989, six showed no change, one showed an increase and the rest all indicated a fall in ground level. The soil depth ranged from 13 to 57 cm and the losses varied from 1 to 12 cm (average depth 27.7; average decrease 1.7cm; or 5%).

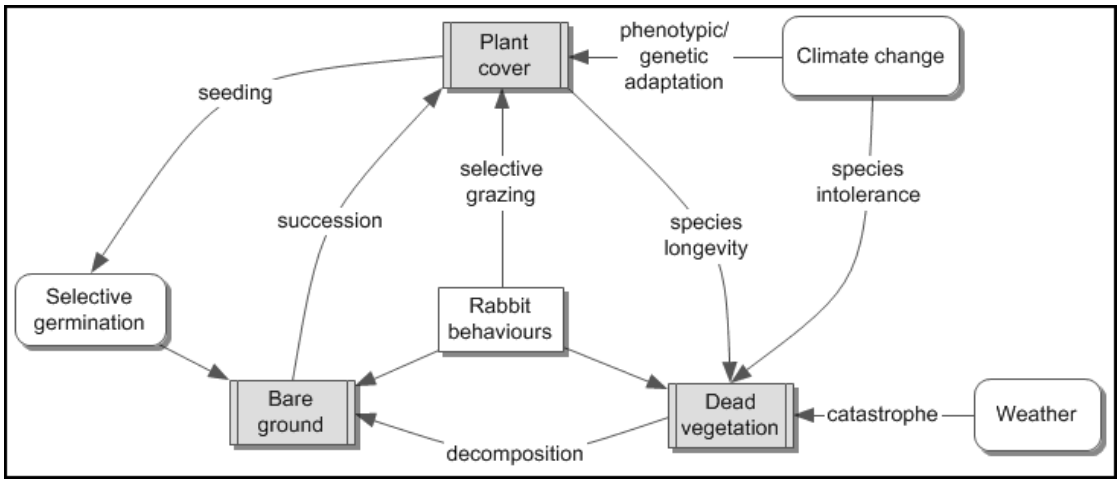
These results, together with associated vegetation surveys since the early 70's, have been assembled as the model of accumulation and loss of peat from the two dominant peat-forming plants on the coastal slopes. This progression is expressed diagrammatically in Fig 7. It was also a feature of the rest of the island with with 'good Holcus' years being followed by a 'dead Holcus' phase etc. There have also been 'good' and 'bad' Teucrium years.

Fig 7 Diagram representing the changes in plant succession and peat formation on the western coastal slopes.



There were also good and bad periods for Tripleurospermum maritimum at Skomer Head and also for Silene maritima at the Wick Saddle, but these were not charted or quantified. Before this work was undertaken, the bad years for cliff top and coastal plateau vegetation were thought to be due to one-off catastrophes, particularly the blanketing of the island by salt spray from violent westerly storms. The situation is much more complex than this (Fig 8).

Fig 8 Concept mindmap of the relationship between rabbits and vegetation



5 Computer modelling

5.1 It was obviously important to take long-term changes in rabbit numbers into account if there was to be a plan for managing grassland. In this respect a simple computer model using STELLA software was constructed in order to predict the effects of culling rabbits on vegetation in Calves Park, and the time-scale involved to make an impact on its biodiversity and grass cover (Fig 9). The cyclic changes in the main vegetation components in relation to rabbit numbers computed from the grazing model are presented in Fig 10. The predicted effects of culling are presented in Table 2.

Fig 9 Computer model linking rabbit population dynamics with botanical diversity

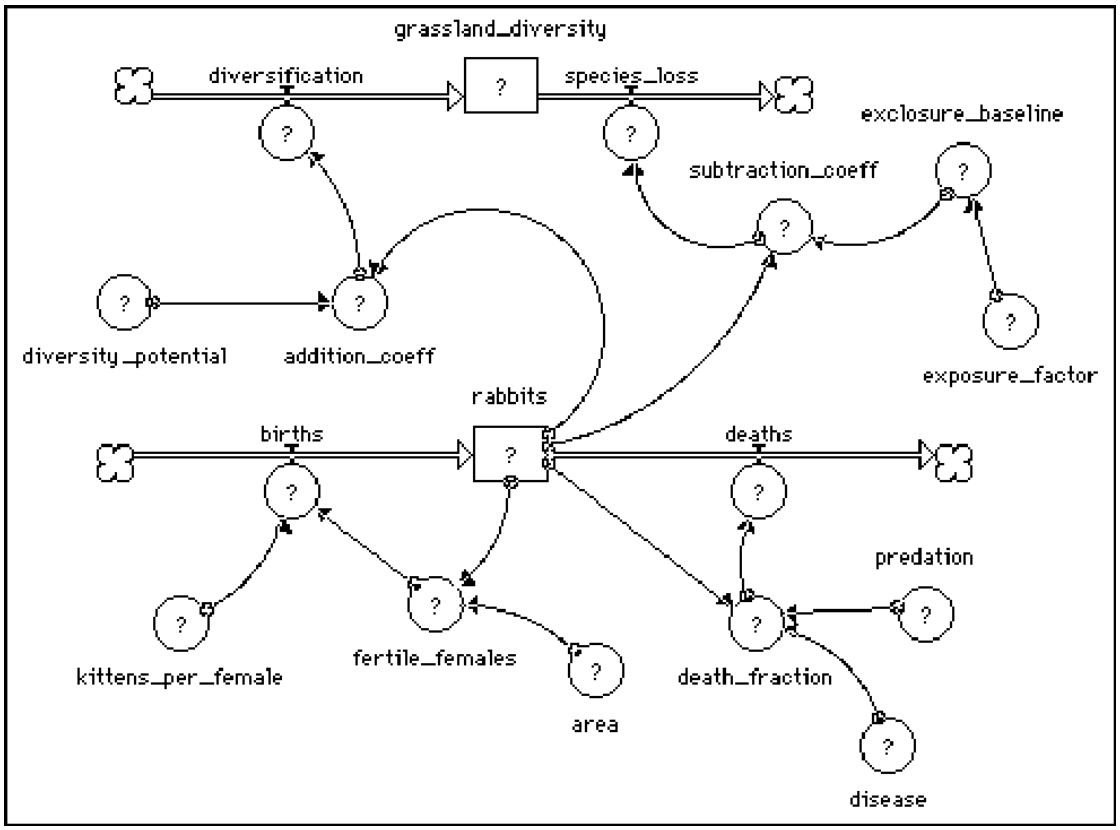
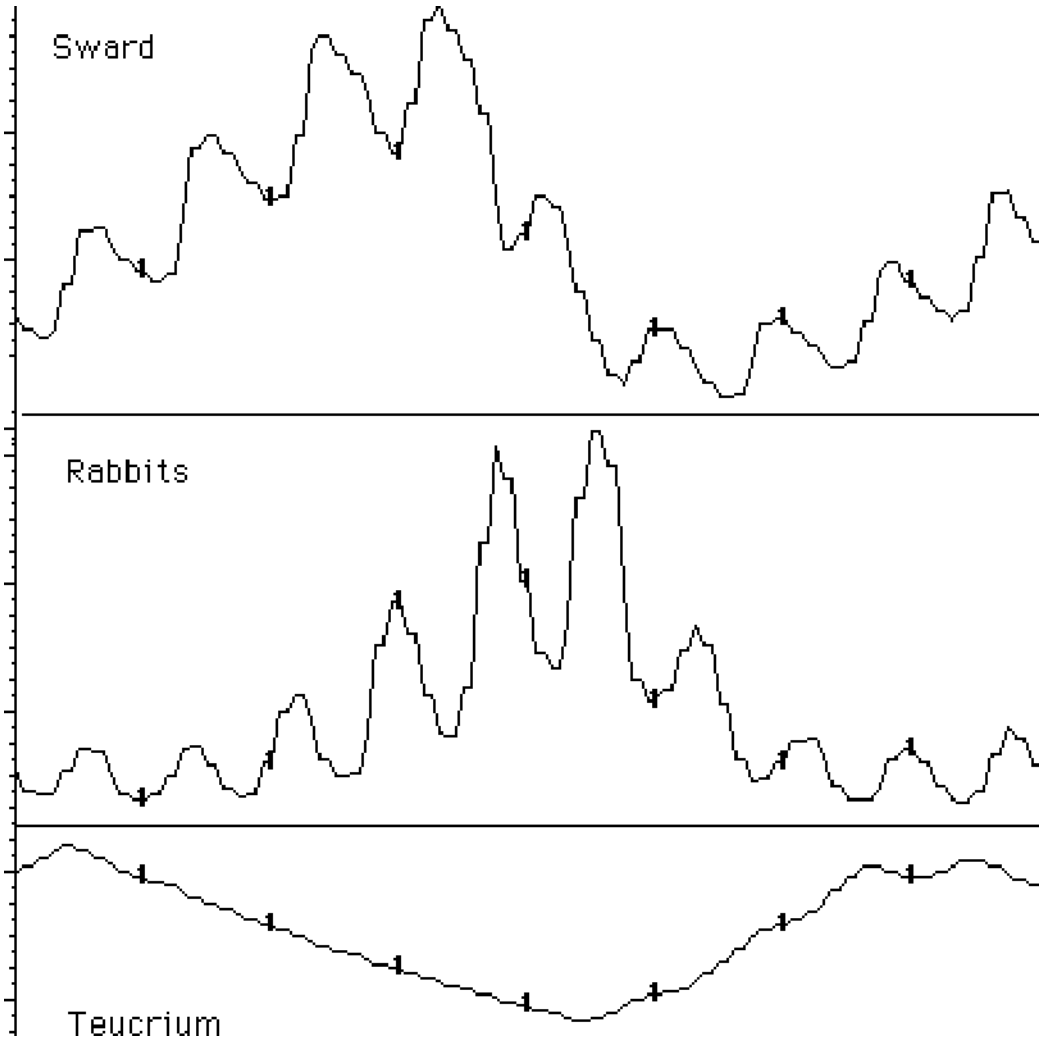


Table 2 Effects of computer culling on the condition of grassland

Cull (% population removed each year)	Nil	15	20	25	30	50
Diversity indices						
Tussocks	0.62	0.77	0.77	0.64	0.65	0.31
Lawns	4.11	3.78	3.57	3.32	3.05	2.27
% increase in grass		14	17	23	32	109

Fig 10 Calves Park computer model comparing annual production cycles of sward height, rabbit numbers and Teucrium cover over an 8 year period.



This model is in agreement with what was discovered on the ground. Others, who have also modelled rabbits reproducing within enclosures have found that the ideal living conditions for rabbits are ten rabbits per acre. Under these conditions rabbits live for an average of seven years. Living conditions for rabbits are crowded when there are more than ten rabbits per acre. When crowding begins to occur, the average lifetime begins to decrease. There is not enough food per rabbit to keep each rabbit healthy. Some die of starvation, while others are more susceptible to disease. From the close living conditions, disease is spread more easily. Many baby rabbits are stillborn, and others are born sick and don't live long enough to reproduce. The limited area does not actually directly affect the average lifetime of the rabbits, it is the density of rabbits per area, that causes the change. Above ten rabbits per acre, the higher the density, the lower the average lifetime. This raises the question of what is the minimum size of an enclosure that will allow a population to be sustainable? Clearly, Calves Park is large enough to be accepted as an experimental model for the island as a whole.

6 The case study in perspective

6.1 Ecology begins with the consideration of broad "natural regions", but these have no precise boundaries in reality. Limitations of national methods of classification emerge when smaller areas are examined in detail through case studies. These are realities because change in ecosystems occurs in precise locations with highly individual outcomes and it is unlikely that local ecological interactions will be repeated exactly in any other area. In this context, the number of "case studies" of small semi-natural environments, such as Calves Park, may be multiplied indefinitely. They reveal that generalisations concerning the ways in which climates, soils, and vegetation affect one another are often wide of the mark. This leads to fears of over-simplification, and the criticism of rigid classifications and maps of types of climate, soil, or vegetation, that may emerge and applied nationally. Also, in the past few years, research on global climate change has expanded and grown. If the idea is confirmed as a long term trend, it adds another feature to be factored into the evaluation of one-off ecological studies.

Skomer is a microcosm of primary interrelationships of climates, soils, plants and animals, and illustrates the complexity of any existing natural order. Because of the island's highly variable sub-maritime situation, quite small differences in climate and soil can be of very great importance to plant life and its dependent animal communities. In this situation, every topographical and edaphic imprint of the early settlers and Victorian farmers can add further variety to a micro-ecological niche. To this diversity can be added considerable variability within species related to spatial spreading.

But just because the ecological features are so intricately inter-dependent, a great deal can still be gained from case studies, which of necessity view the relationships in a fairly simple way. In fact, the Skomer casework has delineated several important principles concerning the feedback between rabbits and vegetation with respect to their behavioural and spatial dependencies. These have been the subjects of two successful University of Wales post-graduate programmes.

6.2 There are many messages from Calves Park and South Plateau for conservation management. The most obvious is that to return the condition of the central grassland to the pre-myxamatosis lightly grazed flower-rich turf of the 1950's would require a great, and sustained, rabbit cull year-on-year. To bring back areas of coastal slope to a peaty condition suitable for shearwater nesting would also require drastic culling of local rabbits, but with uncertain results regarding the top-up rate from rabbits in the vastly greater unculled area. Then there is always the possibility that peat formation would suddenly develop of its own accord.

The island situation ensures that immigration of rabbits from elsewhere is not an option, and the computer modelling of Calves Park indicates that even a population confined to five acres is cushioned from local catastrophe by changes in fecundity or mortality within the population, which compensate for the effects of catastrophe.

In other words, the message for those who desire to manage Skomer’s grassland is, leave the rabbits alone; they are not destructive aliens.

6.3 Skomer is now a remarkable example of species and substrate in a dynamic equilibrium: their ups and downs operate within periods of decades. Long term sustainability arises because death-rates and birth-rates of rabbits and vegetation are not subject to random changes otherwise it would only be a matter of time before either rabbits, and/or forage, became extinct. On theoretical grounds alone, populations, which have a high flux of individual members, and which are stable with respect to long-running population averages, must be cushioned from the random occurrence of high mortality by the action of feedback processes. Here, there are important underlying, unanswered ecological questions of principle concerning the inherent longevity of plants, their ability to colonise the dead grass mat/bare soil complex and compete amongst themselves. We are a long way from understanding the timetables of these arrivals and departures, which take place in a highly variable windswept salty atmosphere. This understanding will involve the study of fecundity schedules and life tables of individual plant species in field and lab alongside measurements of microclimates.

6.4 A mystery to be resolved at a landscape level of the bracken-covered slopes is the remarkable constancy of bluebells in scenic counterpoint with dramatic fluxes of red campion. The major players in bracken-free areas are the two grasses, Holcus and Agrostis which have a visible interaction with the two sorrels and mayweed. The latter three components are the weedy species that colonise the spaces left when the grasses die. The death of sorrel and mayweed initiates another phase of colonisation by grasses. In pot experiments, all five species have surprisingly short lifespans of between 2-4 years and this dynamic underlies the synchrony of rabbits with vegetation. On a smaller scale, there are parts of the island that appear to have a life of their own. For example, nettles are found scattered in small enclosures thought to date to the late Bronze Age, indicating phosphate deposits have persisted from when they were used for livestock and/or crop production. A large patch of bracken, which spread rapidly in the early 1970s at Saunder's Fist, suddenly, over a few years, disappeared!. These are instances of the ecological mysteries that unexpectedly spring up and many would say point to the futility of drawing firm conclusions from one-off studies.

6.5 Finally, these questions have a bearing on the post-Rio emphasis on 'biodiversity' as a bank of genetic resources for future needs. In this context, Calves Park provides a second-to-none 'laboratory' for studying genetic strategies of isolated gene pools in relation to a range of unstable micro-ecological factors. An example of needs that can suddenly emerge is the current interest of the Institute of Grassland and Environmental Research (IGER) in Calves Park. In this respect, the enclosure is seen as a potential source of genotypes for producing commercial strains of grasses and legumes suitable for establishing semi-natural, self-sustaining mainland pastures. Who knows what future values will be attached to this tiny offshore grassland microcosm?

The penultimate sentence of the book describing the first field survey of Skomer reads:

'… we hope that it may be used as a basis on which our successors will build, and from which they will make explorations more thorough and more detailed than our own' .

This is a message for modern managers to maintain relentless surveillance until there is a full understanding of why Skomer appears vaguely different to the annual visitor comparing year-on-year.