Chapter (non-refereed)

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ownership and society's declared wish to control intensification in the uplands; the disadvantage is the high cost.

In the final analysis, the tension between agricultural and forestry development, on the one hand, and the conservation of wildlife is neither ecological nor economic; it is political. The agricultural values are largely contrived by grant-aid or fiscal legislation, and the wildlife values are non-market ones. This situation leaves agricultural development vulnerable to simple withdrawal of the fiscal or subsidy support so that the politician is able to operate not on a basis of economic analysis or ecological principle, but *ad hoc*. The relative merits of farm production and wildlife conservation must remain a value judgement by the politician, with principles not in evidence.

Summary

For a study of the impact of agricultural land use on wildlife and semi-natural habitats, it is essential to take account of the commitment of capital to the managed ecosystem. Ecological principles are less relevant than economic analysis.

The co-existence of wildlife and semi-natural habitats with agriculture, a form of joint production or multiple use, decreases as management pressure and capital investment increase. The objections by conservationists to further agricultural development in the uplands may be resolved by compensation for farmers, as allowed by the Wildlife and Countryside Act, by planning control, or by resource purchase leading to public proprietorship. In practice, the tension is neither ecological nor economic, but political. The politician can influence resource allocation decisively by fiscal regulation, as agriculture is heavily dependent on subsidies or price support, and probably must do so in view of the lack of ecological data and of non-market values of wildlife and conservation, which ecological or economic analysis would require.

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Some ecological principles underlying hill sheep management

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1 Introduction

The relationship between free-ranging hill sheep and their food resource is complex, as the sheep are polyphagous and the food is multi-species. When one includes the spatial aspects such as the presence of stable assemblages of plants occupying specific edaphic niches and the social interactions of the sheep moving between these assemblages, it is clear that there are many difficulties in producing either descriptive or predictive models. In order to reduce the scope of this review, therefore, I have confined myself in 2 ways.

First, I have considered the inter-relationship from the point of view of the effect of plant species on sheep rather than *vice versa*, although this may be a somewhat artificial distinction because the relationship is 2-way. However, this approach can also be justified on practical grounds. Conditions in Wales are dominated by grass sward (or communities with similar structure) rather than the more complex situation in which non-grass species (such as heather) are an important part of the resource.

Second, I have also been biased towards the processes of selection and utilization of food by sheep, rather than the more strictly practical aspects of upland management; and I am concerned only with sheep grazing unimproved upland areas, despite the increasing importance of combinations of improved and

unimproved pasture in the economic management of the uplands (eg Hill Farming Research Organisation 1979; MacEwen & Sinclair 1983). The whole complex has been set against the background of the Pleistocene origin of sheep, a genus which evolved as grazers of stable grasslands on the fringes of the great glaciers. This evolutionary history is vital to understanding the interactions.

2 The relationship between sheep and plant communities

The observation that sheep were not distributed either uniformly or at random over the different plant communities making up the average sheep walk was first formalized by Boulet (1939), although the fact was undoubtedly known to generations of shepherds. His observation was developed further by Hunter (1962), Hughes *et al.* (1964), and by Rawes and Welch (1964). All these observations can be summarized simply. Sheep numbers are relatively higher on plant communities dominated by genera such as bent, fescue and clover, developed on soils of relatively high nutrient levels and without a well defined organic matter layer (the brown earths). Sheep numbers are relatively lowest, in contrast, on plant communities dominated by such species as mat-grass which occurs on soils with a well developed organic horizon. These differences in relative stocking rates are also related to differences in primary productivity, nutrient content and the amount of dead material, and are not necessarily causative but possibly the effect of differential removal of surplus plant material and the return of mineralized nutrients in dung by the selective sheep (eg Floate 1970; Welch 1982; Perkins 1978). Such preferences are understandable in the context of evolution in the Pleistocene, with its young soils and no peat development, and where the opportunist grasses formed extensive areas which to some extent were maintained by the grazing sheep.

These interactions are well understood in general terms, although more work is needed on some specific pathways in the cycle. The relative influence of volatile nitrogen compounds, for example, both directly and indirectly, and the factors influencing losses by leaching from the various soil types present major problems. However, more general features of the sheep/plant community interaction have also received little attention, and are nonetheless of considerable importance. Hunter and Milner (1963) considered the effects of changing stocking rates on the relative occupancy of the different plant communities. They showed that increased stocking rates mainly affected the less favoured communities, with the implication that social pressures within the sheep population were responsible. This effect has now been investigated in greater detail. Milner (unpublished) showed that the occupancy rate of bent/fescue communities was linearly related to overall sheep numbers (up to a maximum of 13.6 sheep/ha), whereas the occupancy rate of mat-grass dominated communities showed no such simple relationships (see Figure 1).

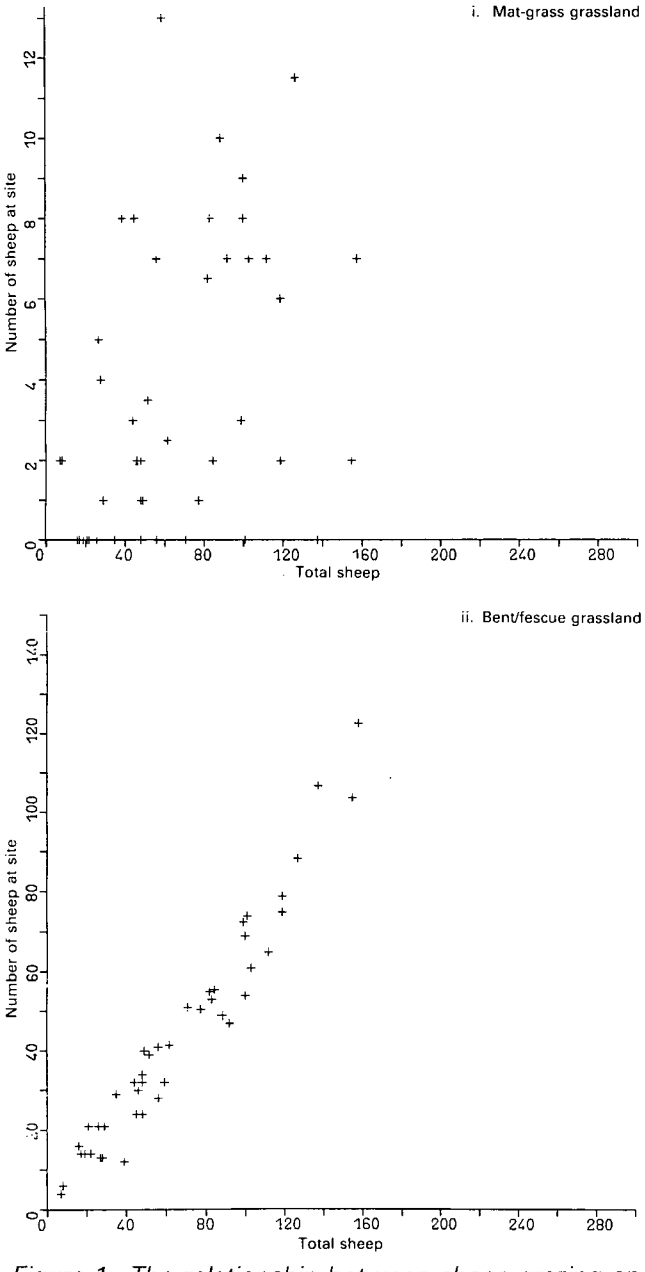

Figure 1. The relationship between sheep grazing on
i. Mat-grass grassland
ii. Bent/fescue grassland
and total sheep numbers on the sheepwalk

The reason for the differential response on different communities requires investigation. Home range behaviour has been observed in hill sheep (Hunter & Milner 1963), but no overt aggressive behaviour such as would result in territories has been observed. Nevertheless, some mechanism is necessary to explain the observed difference in occupancy rate and how individual sheep are 'prevented' from increasing the rate beyond 13.6 sheep/ha. More observation of the process of optimizing (or probably maximizing) the occupancy rates are required, and I have no realistic hypothesis for this apparent self limitation phenom-

enon. Whether scent (possibly via the inter-digital gland), sight, or other secondary mechanisms are involved is not known.

Our classification into simple species aggregations may be entirely inappropriate, if seen from a sheep's view of its environment. Some complex relationship between plant community, edaphic features, shelter, etc, may more appropriately determine the taxonomy of sheep environment than plant community. The interaction between overall stocking rate and occupancy is crucially important in an economic climate favouring increases in sheep numbers on the hills (in north Wales, for example, sheep numbers on hill farms have increased by between 31% and 47% since 1971).

The effects of these increases are already apparent in lower volumes of plant biomass and in increased soil surface movement, expressed as increased erosion and sedimentation in streams draining certain catchments. As yet, there is no observable decrease in the weight of sheep produced per individual (however measured), although comparative data are available.

3 The relationship between sheep and the plant species of the uplands

Animals graze selectively, and a whole range of factors interact to determine the composition of diet on a particular day. This composition may apparently be quite unrelated to the proportions of various species or plant parts present and available to the animal. In upland Britain, the plants selected show remarkable similarities from sheep walk to sheep walk. For example, the preference ratings quoted by Milner and Gwynne (1974) for sheep on the island of Hirta in the St Kilda group of the Hebrides are almost identical to the preferences shown by blackfaced sheep on the Scottish mainland (Martin 1964). Preferences are related to species occurrence in favoured communities, but selection appears to occur within such communities. The preference ratings for species of meadow-grass and Yorkshire-fog are always high, while high in summer for red fescue and bent. What is far from clear is how the preferential selection is affected by the mix of species present. This question is critical, but it is difficult to test experimentally because other factors such as herbage yield, pasture structure and overall digestibility must be constant. The possibility of using multivariate models has not been investigated, but seems plausible.

There have been many vain attempts to relate preference ratings to proximate factors in the plants, but some general agreements emerge. Leaf is preferred to stem, and green material is preferred to dead (Arnold 1964). The material eaten, when compared to the material offered and refused, is higher in nitrogen, phosphate and gross energy, and lower in 'fibre' (eg Cooke *et al.* 1956; Wallace *et al.* 1972). The relationship between selection and other factors (such as soluble sugars, for example) is much less clear. Unfortunately, hill sheep cannot recognize, before selection, such things as nitrogen, 'crude fibre', energy, etc. Where correlations are found between any of these proximate analyses, they must relate to some other specific compounds with a particular taste or smell, or to some physical property of the plant. Even if these specific compounds can be isolated (and some attempts have been made, eg Ashton & Jones 1959), it is important to recognize that a positive or negative correlation is not proof of the unique importance or unimportance of the compound. Because of the multidimensional nature of the selection process, such simple correlations are dangerous and unlikely to have any predictive value.

It is also important to recognize that the actual form of the chemical compound, ie as grazed, is the important parameter influencing choice. The enzymes in saliva, the amount of chewing, and the volatility or otherwise of the determining compound must be considered. At least the availability of gas chromatographs now enables us to examine more quickly these ultimate determinants of species selection.

Although the problems are considerable, there is a need for such work on upland species. There is, indeed, some evidence that grazing, and saliva itself, stimulates the growth response of grasses directly, rather than by reallocating resources within the plant (Owen 1980). Whilst this effect has been disputed, it remains an intriguing and completely logical phenomenon which has important evolutionary and practical consequences.

Consideration of the ultimate factors affecting selection may seem academic. However, if we consider the interaction between a considerable increase in stocking rate and plant community occupancy, the subject becomes much more important. As available forage drops to the level from which free selection is unlikely to be possible (if sheep intake is to be maintained), then knowledge of the mechanisms of selection become important in predicting the effect on plant communities and on the sheep themselves. Whether sheep take species and parts of species in proportion to their presence or availability, or select in particular ways, will dramatically change the relative competitive ability within the plant communities grazed. There is some evidence (Peters 1980) that, even with normal stocking rates (however defined), sheep show little selectivity and only take species and plant parts in proportion to their presence in the sward. Over a short (1-2 week) timescale, the apparent differences in selectivity are expressions of the different population dynamics of tillers within the sward. This observation, if correct, has important implications for assessing the effect on upland grass swards of given stocking levels, and detailed work is required to identify individual tillers, their death rates, and the rate of production of

new tillers. Peters (1980) discusses the possibility of using the tiller or part of the tiller as the unit in a production model.

4 Conclusions

The upland sheep/grass ecosystem is both a moderately productive agricultural system and the background to many other uses of the uplands such as recreation and conservation. Some of the agricultural economic problems have reputedly been solved, but much fundamental research is still required. There is some doubt whether even the economic problems of small upland farms have been solved. MacEwen and Sinclair (1983), for example, maintain that smaller farmers have suffered under the capital intensive improvement mentality induced by grants of various sorts. It is not the purpose of this review to discuss the economics, but to point out that we need to understand the production system in broad terms, if we are to predict the effect of increased (or conceivably decreased) stocking rates. In particular, we need more precise and accurate knowledge of the plant/animal system. If this information can be assembled into models of various kinds, so much the better.

Perhaps the most important feature of upland agriculture in Wales is the overall increase in stocking rate of some 30-40%. We urgently need to know how this increase affects the different plant communities, and whether the effects are irreversible. If the increase in sheep is responsible for the apparent increase in erosion, it may be an irreversible effect which needs urgent attention. Research on the sheep/vegetation/soil interaction is still needed.

5 Summary

The way in which upland plant communities interact with sheep is of major importance in managing the upland resource. However, understanding this interaction and making predictions is not a trivial task, and requires detailed investigation. Topics to be investigated include:

i. the preferences of sheep for different plant species;
ii. the frequency dependent and plant density dependent changes in selection;
iii. the effect of differential selection on competitive ability;
iv. the social interactions between sheep influencing their spatial distribution.

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