

# Low-intensity livestock systems - defining ecological attributes

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## Summary

It is well recognised that modern land use, particularly agriculture, is more intensive, more specialised and more mechanised than traditional land-use systems. Modernisation is accompanied by biological impoverishment and many steps have been taken to ameliorate this on intensively managed land. However, many agricultural systems, which have their origins in traditional, low-intensity farming, high in biodiversity do still survive in Europe. Unfortunately these systems have until recently been undervalued both ecologically and economically; they are also relatively little studied by ecologists

Many European livestock systems have a long history and mimic the ecological conditions needed by the plants and animals of Europe's "natural" open habitats previously grazed by large herbivores. However, characterising European livestock systems in terms of their ecological attributes is not straightforward. The complex interactions between "wildlife" and pastoral farming (the ecology of pastoralism) vary regionally as a result of differences in physical characteristics, climate, and the history of pastoral land use. Even within areas different livestock types and breeds can have fundamentally different effects on vegetation. To complicate things further the distribution of some animals is influenced by their own social behaviour as well as by environmental factors. Examples of two species (a bird, the red-billed cough, and a butterfly, the marsh fritillary) are presented which illustrate the ecological complexity within some of these more traditional systems and the importance of maintaining the system's status quo before introducing "conservation management".

The ecological complexity needed by both examples is linked to scale.

The objectives of managing land either for high biodiversity or for modern livestock production are generally regarded as being incompatible. There are certainly costs as well as benefits for nature, but as a rule as the intensification of livestock production increases (and systems become increasingly divorced from their origins in nature) biological diversity decreases. This being the case it should be possible to define relationships between plant and animal communities and livestock systems if suitable data were available.

Previous attempts (by desk studies) to categorise livestock systems in terms of nature conservation value are described together with suggestions for a classification methodology which would give a more objective basis on which to define low intensity systems.

## Introduction

On the more industrialised farmland of southern England, Belgium, Holland, and parts of Germany and France farming practices are now characterised and dominated by the use of chemical fertilisers, pesticides, mechanisation instead of manual labour and the ever increasing output of specialised products. At the same time changes in farming practice have been accompanied by diminishing biological diversity.

Animals, plants and the habitats they comprise, cannot be considered in isolation to the farming systems of which they are, or were, integral parts. Today low-intensity livestock systems survive mainly as extensive areas of large-scale rangelands, supporting extensive pastoralism (this often being associated with mixed farming and cropping).

Bignal *et al.*, (1996) drew attention to a recent report (Beaufoy *et al.*, 1994) which estimated that over 55 million ha of low-intensity farmland existed in the nine European countries studied (see Table 1). In the UK it was estimated that there is still 2 million ha of this low-intensity farmland (of which 65% is outside Environmentally Sensitive Areas (ESAs)). More than 50% of Europe's most highly valued biotopes (in Annex 1 of the EU Habitats and Species Directive) occur on low-intensity farmland; of the 75 biotopes in Annex 1 which occur in the UK, 32 (42%) are farmland (e.g. northern Atlantic wet heaths, blanket bog, lowland hay meadows, Molinia meadows on chalk and clay, species-rich *Nardus* grassland and Machair).

**Table 1. Estimated area of low-intensity farmland in each of nine European countries studied by Beaufoy *et al.* (1994) and reported by Bignal and McCracken (in press)**

	Land surface (ha)	Utilised agricultural area (UAA ha)	Farmland under low-intensity systems (ha)	Low-intensity farmland as percentage of UAA
France	54 702 600	31 016 400	7 754 000	25
Greece	13 194 400	9 183 300	5 600 000	61
Hungary	9 303 000	6 493 500	1 500 000	23
Italy	30 122 500	22 650 000	7 100 000	31
Poland	31 267 700	19 135 800	2 735 000	14
Portugal	9 208 200	4 558 100	2 735 000	60
Republic of Ireland	7 028 300	5 650 750	2 000 000	35
Spain	50 478 200	30 589 800	25 000 000	82
United Kingdom	24 413 900	18 425 500	2 000 000	11
<b>Total</b>	229 709 500	147 703 150	56 424 000	38

The situation in southern Europe is even more striking, with for example, the dehesa and montado wood pastures of Spain and Portugal, the alpine pastures of Spain Italy and France, and the grassland and non-irrigated cereal psuedo-steppes in Spain all included in Annex 1 of the Directive.

## The ecological history of Europe

So why is so much of Europe's low-intensity farmland of high biological diversity? After all, it is not "natural"

There is a widespread assumption that forests are the natural vegetation in western and central Europe and that open spaces, mostly grasslands of various types, were always very rare, being maintained by large herbivores, beavers and natural catastrophes such as fires, landslides, avalanches etc. (Ellenberg, 1986). This stems from the conventional palaeo-ecological view that in post-glacial Europe forest spread northward in the wake of the retreating tundra until it clothed the landscape from the northern Mediterranean to the limits of climatic tolerance.

However, such a large proportion of Europe's wildlife is morphologically or behaviourally adapted to open habitats that this logic is plainly flawed.

In order to persist and evolve, the plants and animals of open habitats (grasslands, plains, wood, pastures etc.) would have demanded more than the rare open spaces envisaged by Ellenberg, (1986). Accordingly, other authors (van Dijk, 1996; Tubbs, 1996) all suggest that the open component of the European landscape was far more important than hitherto supposed, as was the role of large herbivores, some of which are now extinct

Neither bustards nor vultures, both now viewed as "flagship species" in Europe, could persist in a forest environment and moreover require very extensive open landscapes. The same can be said for most of Europe's rich steppeland, upland and mountain plants and animals. Even many woodland species (e.g. lichens) are very demanding of light. Many insects have complicated and bizarre life cycles which could only have evolved in open conditions, e.g. the symbiotic relationships between blue butterflies and some ants. The importance of open ground is further underlined by the high number of species which rely on these habitats. For example, in the former West Germany, Korneck and Sukopp (1988) have listed 588 species of higher plants and ferns in dry grasslands (steppes) and 297 in wet grasslands (marshlands); Holzner *et al.*, (1986) lists 1041 species of insect in Austrian dry grasslands, of which 85% are now Red List species (see van Dijk, 1996).

Logic points to the development of a more diverse, ecologically more chaotic landscape than the neat progression from tundra to forest.

Tubbs (1997) describes the Holocene ecological history of Europe as "*a panorama of continuous change, a succession of more or less traumatic events of varying duration and amplitude, each of which has given the ecosystem a shift in direction.*" He regards this process as "*one in which man is part of the ecosystem, not, as is commonly perceived, set aside as a predatory witness waiting for opportunities to exploit it*".

The precise nature of the open habitats which existed in the early millennia of the post glacial era will remain largely conjectural and always a good topic for debate. A quote from Swengel (1996) in a paper describing the importance of open habitats for butterflies in North America (Anne Swengel 1996) echoes closely my own views. She says "*I get nervous when I hear simple and conclusive assertions about how nature functioned prehistorically - and thus should function through habitat management today. After all only fragments of evidence from centuries and millenia ago exist today. Even though I think I've learned a lot about nature over the years, I continually encounter things that surprise and puzzle me. How can we be more certain about how nature operated back then, when we haven't even seen it, than about how nature operates now, even though we observe it and study it all the time*".

Perhaps a more realistic perception of the past is a mix of woodland, heathland, grassland and wetland, occurring regionally in extensive tracts as well as in more intimate mosaics and strongly influenced by the perturbations of grazing vertebrates. This is a landscape more open and more diverse than typically conjured up by the conventional palaeoecological portrayal.

### *The development of extensive farming*

In an already diverse and mixed landscape man's activities from Neolithic times have resulted in a rich variety of farming ecosystems. These are the croplands, meadows, wood pastures, coppices and other habitats which derive most obviously from continual human intervention, as well as the moorlands, mountain pastures, steppelands, saltmarshes and other "wilderness" lands which derive much of their present character from extensive pastoralism. Many of the agricultural and pastoral ecosystems that were created by man's activities mimicked the natural conditions that they replaced.

Given the relatively short time frame involved I am not suggesting (and neither I think are Tubbs, 1996 or Swengel, 1996) that plants and animals have co-evolved with and adapted to these agricultural practices (although some may have). Instead it appears that they have been able to move out of trouble (Elias, 1994), or perhaps more precisely, persist in those places where they didn't get into trouble. This is true even when the compatible land use was novel, for example in North America where hay making replaced bison grazing in providing the conditions needed by many prairie butterflies. In other words, by happy coincidence, the ecological result of some agricultural activities happened to be compatible (Swengel personal communication).

We are familiar with the idea of intensive livestock systems mimicking the conditions needed by generalists (e.g. weeds) and so perhaps we should also think of low-intensity livestock systems as mimicking the ecological conditions needed by specialists.

Low-intensity farming systems have enriched Europe's open ground fauna and flora by enhancing small scale diversity whilst also creating and maintaining the large tracts of relatively uniform vegetation required by the plants and animals of steppe, moorland, mountain and comparable habitats. Interestingly, in the case of Hampshire, England, Tubbs (1993) suggests that the period of maximum biological diversity occurred around the middle of the 18th century rather than at some earlier period.

### **The inherent difficulties in characterising livestock systems**

The complex interactions between plants and animals and the livestock systems that form their environment makes characterising (as well as evaluating) them using biological attributes difficult, especially at the species level.

The differences in measure of biodiversity that we see on the ground (sometimes quite fundamental) can actually relate to very subtle management differences within systems. Alternatively, there can be little or no difference in management (either spatially or temporally) and very big differences in some elements of biodiversity.

Whilst clearly many factors are involved, there are two important ones to highlight in this context. Firstly, difficulties arise because of the different effects of different grazing animals

on vegetation (and the consequent effects on invertebrates, mammals, and birds) and secondly because the distribution, abundance and productivity of animals is not always directly correlated with the environment. In some cases this is due to behaviour and only recently have the full effects of this been regarded as a significant factor (Moss *et al.*,1994; Bignal *et al.*, 1997).

The effect on the ground is that you can find large areas of apparently "suitable habitat" in which the expected species is not present at certain times. This is, in fact, what we should probably expect if we accept that when natural processes are operating species populations are much more likely to fluctuate than to remain stable. There is increasing interest in the concept of population dynamics (e.g. meta-population dynamics) and the problems which this raises for the management of small isolated habitat remnants in otherwise intensively managed landscapes (Warren, 1994). Part of the reason that management on some of these sites has failed may well be that managing for stability is in fact counter-productive for many species.

The examples below illustrate some of this in more detail

*Example 1. The ecological effects of herbivores*

The most common domestic livestock in Europe are sheep, goats, cattle and horses. The ruminants possess the ability to digest cellulose in the rumen and in general are more efficient converters of mature vegetation swards than non-ruminant grazers such as horses and ponies. Rumen size is critical in determining whether the animal can utilise poor quality forage (pasture of natural vegetation) as indigestible herbage takes longer to break down in the rumen. This slows down the rate at which the grazer can ingest the extra feed that it needs to compensate for the poorer quality diet (Grayson, 1997). Regional (often ancient) livestock breeds generally have large rumens and perform best on diets of moderate to poor nutritional value. In the UK there are more than 50 breeds of sheep and 20 breeds of cattle, each suited to particular environments or production systems and each potentially having different effects on vegetation. For instance in Swaledale, North Yorkshire, UK, recent research (Braithwaite *et al.*, 1997) comparing the effect of grazing by Hebridean and Swaledale sheep, stocked at the same live weight per hectare in replicated plots on moorland produced the results shown in Table 2.

**Table 2. Changes in the cover of purple moor grass and heather when grazed by Swaledale or Hebridean sheep**

	Purple moor-grass ( <i>Molinia</i> )	Heather ( <i>Calluna</i> )
Grazed by Swaledales	+20%	-8%
No grazing	+10%	No change
Grazed by Hebrideans	-10%	+17%

Tubbs (1997) recently reviewed the ecology of pastoralism in the New Forest, England, a unique survival of medieval England with a pastoral economy based on common rights and common land. He concluded that 1 pony is equivalent to 2.5 cows and that they consume a lot of woody growth, leaves from trees, shrubs and crop vegetation close to the ground. In contrast cattle (and deer) consume less food, feed for shorter periods and browse less than ponies but eat more heather (around 20% of the diet compared with less than 10% for ponies). Neither cattle nor ponies eat bell heather (*Erica Cinerea*) or cross-leafed heath (*Erica*

*Tetralix*). During the growing season 75% of the diet of both horses and cattle comprises grasses, the most important being purple moor grass. The pastoral history of the New Forest has diversified the vegetation by suppressing the potentially dominant *Molinia*, heathers and some trees and shrubs, thereby allowing a greater variety of herbs, sedges and grasses to form a diverse array of plant communities. The effect that this intensity of grazing has on the woodlands themselves is not so beneficial and they show impoverished shrub and herb layers without the compensatory gains of new communities adapted to grazing. Nevertheless the total absence of grazing eventually leads to pasture woodland becoming a more simplified habitat (Table 3).

**Table 3. Effects of grazing in woodland on the number of species**

	Grazed woodland	Ungrazed for 30years
Species of epiphytic lichen	64	31
Species of flowering plants	68	31

(Source: Chatters and Sanderson, 1994)

*Example 2. The influence of behaviour on distribution and abundance*

*The red-billed chough *Pyrrhocorax pyrrhocorax**

The chough is a rare bird listed in Annex I of the EC Wild Birds Directive. Its distribution in Europe is fragmented. Over half the minimum estimated European population of 16,000 pairs is concentrated in Spain, Greece and Italy; most populations are small and many are declining (Tucker and Heath, 1994). The chough's bill is a specialised tool for probing in the soil and for pecking immobile or relatively slow-moving food items off the ground. Choughs feed principally on soil-living, surface-active and dung-associated invertebrates, which they obtain from extensive pastures (i.e. managed at low intensity) grazed by sheep, cattle, horses and goats.

*Chough dynasties and kin clusters*

Young male choughs tend to nest close to their natal site, whereas female choughs disperse long distances (Bignal *et al.*, 1989). This means that male choughs nest close to male relatives and that groups or clusters of relatives (or dynasties) develop as territorial males are less aggressive to kin than to non-kin. Recent research on Red Grouse (*Lagopus lagopus*) has shown a similar pattern and led to the hypothesis that changes in the territorial behaviour of cocks might be the cause red grouse population cycles (Watson *et al.*, 1994 and summarised in Moss and Bacon, 1996). The importance of this is that it provides a mechanism through which social behaviour may contribute to changes in the species numbers and distribution. It may also point to limiting external factors, which (through behaviour) exacerbate the decline in population.

For choughs the hypothesis would be that because territorial males are less aggressive to kin neighbours than to non-kin, a group of closely related pairs develops. However, for this to happen, two important conditions must be fulfilled:

- Adult mortality must be high enough to allow new kin to recruit next to each other and low enough to allow family groups to develop
- Juvenile survival to maturity must be high enough to allow recognisable kin to recruit

Since adult birds do not appear to survive without a territory, the breeding population falls if potential recruits are unrelated to existing territorial males. The latter simply hold a bigger territory, reducing the risk of interference from, or the need to share resources with, non-related neighbours, and attempt to rear a big brood. If sub-adult mortality of potential recruits is high, group size will not develop to give a big enough pool of relatives as potential kin recruits. Dispersal is not an easy option for unrelated birds because both sub-adult survival and adult breeding performance are higher in groups than in isolation. In this way changes in the size and distribution of the breeding population may occur which cannot be attributed to "habitat" change caused by management. The physical conditions for though may be no less suitable yet there may be fewer breeding pairs.

#### *The marsh fritillary butterfly Eurodryas Aurinia*

The marsh fritillary butterfly is a species which is facing extinction right across Europe and which has its largest populations in the UK. The butterfly is on the wing for only a short period during May or June when the temperature is high enough and the wind speed low. Adults lay their eggs on the underside of the leaves of the larval food-plant, devil's bit scabious (*Succisa pratense*), where three weeks later they hatch to form colonies of caterpillars. Soon after emergence the caterpillars spin a dense web over the food-plant, beneath which they live and feed, moving to another plant when the first is consumed. During August a more substantial web is constructed, inside which they hibernate, emerging the next spring to bask on sunny days and recommence feeding. They eventually leave the colony having spent about ten months in the larval stage. The caterpillar pupates close to its food-plant and hatches about a fortnight later.

In Britain the marsh fritillary butterfly is native to the heathland and acid grassland pastures of western Wales and western Scotland. A survey in Scotland (O'Keefe, personal communication) found that the height of the vegetation on which caterpillars were found in mid-summer (from larval sites marked in the spring) ranged from 11-35cm, but that the vegetation on 80% of sites were within a narrow range of 11-14 cm. These measurements were significantly different to those taken of a random sample of vegetation in the same areas and suggest that the caterpillars had shown a preference for this height of sward.

The type of vegetation, within which eggs and caterpillars were found, was a mosaic of wet heathland and grassland, maintained by extensive grazing by cattle. All UK colonies show similar attributes with optimum conditions being a summer sward 11-14cm high, abundant *Succisa pratense* and a vegetation structure giving the butterfly and the food-plant shelter without dense shading.

These conditions are found on pastures where the vegetation of grass and heath is maintained through the routine, seasonal, grazing pressure of cattle and sheep managed in an extensive system. Sheep grazing alone, supplemented by periodic burning (a common management

regime today requiring a low labour input) does not provide suitable conditions and instead leads to heather monocultures and short, sheep-grazed grassland.

In areas where the grazing pressure for this species is optimal, the density of grazing animals, primarily cattle, is low enough to ensure that the risk of livestock trampling colonies of caterpillars is kept to a minimum. Yet at the same time grazing pressure is high enough to remove the coarser vegetation growth, favour the food-plant and produce vegetation of the optimum height.

This species typically undergoes large fluctuations in population size and colonies regularly reach low levels (Warren, 1994, Ford and Ford, 1930, Porter, 1983). This may be a result of parasites, changes in habitat suitability, weather conditions or short periods of inappropriate management. However, since the species is relatively mobile (with a colonisation range of 15-20km.) the nature of the land between the core areas of colonisation, may be crucial in determining the success or otherwise of recovery after a population declines. In other words, the long term future of populations may depend as much on "sub-optimal" habitat, which is only occupied in "good" years, as on core areas.

In this respect colonies of the marsh fritillary butterfly are likely to be interconnected and may function as meta-populations (Levins, 1969; Hanski and Gilpin, 1991). A meta-population is defined as a collection of local populations, connected by occasional dispersal, in which there are local cases of extinction and colonisation.

The implication is that the species' long term survival is dependent upon the degree to which large areas of pastureland grazed by cattle at low intensity survive. Also implicit, is that the range of conditions needed by the butterfly and its caterpillar, are likely to be most effectively created through extensive pastoralism rather than by the management of small isolated sites. In many regions (e.g. in Berkshire and Oxfordshire, UK) the butterfly is probably already doomed as colonies have become too small and too isolated to persist for long (Warren, 1994).

### **Correlating livestock systems with areas of high biodiversity**

Despite the problems outlined above, some attempts have been made to develop typologies of livestock systems and to characterise them in terms of biodiversity and nature conservation value. In the report, *The Nature of Farming* (Beaufoy *et al.*, 1994) a typology was produced of groups of low intensity farming "systems". Livestock and mixed farming groups were further subdivided into systems on the basis of location. However, the research pointed to a lack of standardised or quantitative information describing either the farming systems or their biological characteristics, and had to rely heavily on "expert knowledge" from each of the nine countries studied. As a result the information in the report was not standardised between countries, or in some cases even within countries.

However, if biodiversity decreases as intensity of management increases (that is, as the systems become divorced from their origins in nature) it ought to be possible, at least in theory, to characterise low-intensity livestock systems in terms of biodiversity parameters.

To some extent the methodology developed will be determined by the use intended for the end results, e.g. to influence the thinking and decision making of policy makers dealing with the

Common Agricultural Policy's (CAP) ongoing reforms. The European Forum on Nature Conservation and Pastoralism (EFNCP) and the Centre for European Agricultural Studies (CEAS) recently conducted a research project for the European Commission (DG XI) looking into possible options for better integrating environmental concerns into the various support systems for animal production (Goss *et al.*, CEAS / EFNCP report to DGXI, 1997). The project divided Europe into seven "Agri-environmental zones" based on the regions of the EU Habitats and Species Directive and the Less Favoured Areas boundaries. In order to be able to make a more structured appraisal of the ecological attributes or indicators of low-intensity livestock systems, it is first necessary to have a stratification with some ecological meaning, to which production systems can be related. The seven zones of the above report are given below:

Agri-environmental zones:    Atlantic mountain  
   Atlantic lowlands  
   Mediterranean mountains  
   Mediterranean lowlands  
   Alpine

Boreal and Macronesian could be added to these to give more complete pan-European coverage.

In the report it was suggested that further sub-divisions could be developed by Member State, regions within Member State or by habitat. For the purposes of ELPEN further division might be into "agri-environmental zones" based on the occurrence of livestock production systems or combinations of these from the ELPEN typology.

With this in place it would then be much easier to characterise both the systems and the zones in terms of some measures of biodiversity and to make more objective analyses of the differences and of indicators.

In a policy context what would ultimately be useful would be some simple descriptive models of each of the production systems using the agri-environmental zones to give spatial and ecological meaning. This would enable a more regionally targeted policy to be developed and a more objective assessment of relative importance in terms of biodiversity and high nature value. From an ecological perspective it would be far closer to describing the biological context which could be of great significance in developing many of the agri-environmental schemes initiated under the Regulation 2078/92. It would also be structured in a way that could be linked with existing policy zonation in Less favoured Areas (LFAs) and with the Habitats Directive.

### **Conclusion**

From a nature conservation perspective the value of description, evaluation and policy development at the scale of the livestock production system relates to the fact that, in low-intensity systems, ecological processes operate at a scale which is generally larger than the individual farm. The current prescriptions of Regulation 2078/92 prescriptions focus on the farm not the system and many are having limited success because actions at the detailed farm, or field-scale, will only work if the system (the agri-ecological context) also survives. In the CEAS/EFNCP report (Goss *et al.*, 1997) the contradictory pressures of mainstream agricultural and environmental policy were highlighted and that in many cases the system was

collapsing. Of even greater danger is that the detailed prescriptions may themselves tend to change the systems if the implications are not considered at a larger spatial scale (e.g. standardising the cutting dates for fodder, in previously diverse systems). If the ELPEN project could contribute towards a structure which would enable decisions to be directed towards the "system" then it might be more feasible in the longer term to develop a mainstream policy (either agricultural or rural) rather than a peripheral one. This would then be focused more sharply on the ecological setting and with this secure more detailed and refined prescriptions at a smaller scale would be more likely to succeed.

### **Acknowledgements.**

Many of the ideas in this paper evolved from discussions with colleagues in EFNCP particularly the late Colin Tubbs.

## References

- Beaufoy, G., Baldock, D., and Clark, J., 1994. The Nature of Farming: Low Intensity Farming Systems in Nine European Countries. IEEP, London.
- Bignal, E.M., Bignal, S.M. and Curtis, D.J., 1989. Functional unit systems and support ground for choughs - the nature conservation requirements. In Choughs and Land-Use in Europe (eds. E.M. Bignal and D.J. Curtis), pp.102-109. SCSG, Argyll.
- Bignal, E.M. and McCracken, D.I., 1996. Low-intensity farming systems in the conservation of the countryside. *J.App.Ecol.* 33, 413-424.
- Bignal, E.M., Bignal, S.M. and McCracken, D.I., 1997. The social life of the chough. *British Wildlife*, vol 8, no. 6.
- Braithwaite, D., Grooby, L. and Newborn, D. 1997. Hebridean sheep. ENACT, Managing land for wildlife Volume 5, No.4, 8-10.
- Chatters, C. and Sanderson, N. 1994 Grazing Lowland Pasture Woods *British Wildlife* volume 6. No. 2, 78-88.
- Dijk, G. van. 1996. Nature conservation and agriculture in Europe. Proceedings of Seminar on Nature Conservation and Agriculture in Central and Eastern Europe 11-14 May 1996. IEEP London.
- Elias, S.A. 1994. Quaternary insects and their environments. Smithsonian Institution Press, Washington D.C.
- Ellenberg, H., 1986. *Vegetation Mitteleuropas mit den Alpen*. Ulmer, Stuttgart.
- Ford, H.D and Ford, E.B. 1930 Fluctuations in numbers, and its influence on variation in *Melitaea aurinia* Rott. (Lepidoptera). *Trans. Entomol. Soc. London* 78, 345-51.
- Goss, S., Beaufoy, G. and Bignal, E.M., 1997. Policy options for the better integration of environmental concerns into the various systems of support for animal products. CEAS /EFNCP report to DG XI EC.
- Grayson, W., 1997 Does conservation farming work? *Enact* vol 5, no. 4, 19-22.
- Hanski, I. and Gilpin, M., 1991 Metapopulation dynamics: brief history and conceptual domain. *B.J. Linn.Soc.*, 42, 3-16.
- Holzner, W., Horvatic, E., Kollner, E., Koppl, W., Pokorny, M., Scharfetter, E., Schramayr, G. and Strudl, M. 1986. *Österreichischer Trockenrasenkatalog*. Grüne Reihe des desministeriums für Gesundheit und Umweltschutz Band 6.
- Korneck, D. and Sukopp, H. 1998. Rote Liste der in der Bundesrepublik Deutschland ausgestorbenen, verschollenen und gefährdeten Farn-und Blütenpflanzen und ihre Auswertung

für den Arten-und Biotopschutz. Schriftenreihe Vegetationskunde 19.  
Bundesforschungsanstalt für Naturschutz und Landschaftsökologie, Bonn, Bad Godesberg.

Levins, R., 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bull. Entomol. Soc. Amer. 15, 237 - 240.

Moss, R. and Bacon, P.J., 1996. Red grouse population modelling. In Institute of Terrestrial Ecology, Annual Report 1995-96.

Moss, R., Parr, R.A. and Lambin, X., 1994. Effects of testosterone on breeding density, breeding success, and survival of red grouse. Proc. Royal Soc. Lond. B, 255, 91-97.

Porter, K., 1983. Multivoltinism in *Apanteles bignellii* and the influence of the weather on synchronisation with its host *Euphydryas aurinia*. Entomol. exp and appl., 34, 155 - 62.

Swengel, A.B. 1996. Effects of fire and hay management on abundance of prairie butterflies. Biol. Con. 76, 73-85.

Tubbs, C.R., 1993. An introduction to Hampshire. In: Birds of Hampshire: pp.7-30. Hampshire Ornithological Soc.

Tubbs, C. R., 1996. Wilderness or cultural landscapes: conflicting conservation philosophies? British Wildlife vol 7, no.5, 290 - 296.

Tubbs, C.R., 1997. A vision for rural Europe. British Wildlife vol 9, no.2., 79-85

Tucker, G.M. and Heath, M.F., 1994. Birds in Europe: their conservation status. BirdLife Int. Cambridge, UK. pp. 420.

Watson, A., Moss, R., Parr, R., Mountford, M.D. and Rothery, P. 1994 Kin land ownership, differential aggression between kin and non-kin, and population fluctuations in red grouse. Journal of Animal Ecology, 63, 39 -50.

Warren, M.S. 1994 The UK status and metapopulation structure of a threatened European butterfly, the Marsh Fritillary *Eurodryas aurinia*. Biological Conservation, 67, 239-249.