

Progress in the conservation of butterflies

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Introduction

The better conservation of butterflies in Europe depends on a complex combination of factors, of which scientific research is only one, though a very important one. In particular, we stress the point that, however good the research is, only its acceptance by an informed and aware body of public opinion and conservation decision-makers can ensure, through implementation of its findings, that it is properly used. In recent years there have been encouraging signs that research has begun to be applied to conservation problems in the field more readily than has previously been the case.

One aspect of the complex nature of the factors affecting the conservation of Lepidoptera populations is the different perceptions that are current about what is important for practical conservation. Despite strong evidence that the primary cause of most declines in butterfly populations is habitat destruction, or what amounts to the same thing, habitat change, much attention continues to be focused on other issues. These may either be themselves relatively unimportant, or may place a wrong emphasis on a particular matter, or may fail to take it far enough. Thus, legislation often tends to be negative, concentrating on the prevention of "over-collecting" or disturbance rather than habitat protection, management and re-creation.

Use of insecticides has assumed an importance in the decline of butterfly populations which is not merited by a critical examination of the evidence available. The acquisition of nature reserves has been given its right prominence, but in some cases without sufficient attention being given to their management.

It is not our intention in this paper to dwell on past failures but to point out some of the successful ways in which the scientific problems associated with the conservation of Lepidoptera have been solved. Many of the suggestions made by THOMAS (1984b) have already been put into effect or started. The importance of survey and monitoring continues to be recognised in many European countries and the results are being used in practical conservation. The proposed emphasis on research, reserves and re-introductions (MORRIS 1981c) is still valid. However, a comprehensive review of progress during the last 9 years is not appropriate or possible, largely because of the great activity which there has been in this field. In this paper we therefore

concentrate almost exclusively on the problems posed by the conservation of butterflies which inhabit grassland, referring only briefly to the species of other biotopes. We draw heavily on experience in the United Kingdom, though many of the problems and their solutions are equally valid elsewhere in Europe.

The historical background

In most parts of Europe, grasslands are communities of plants and animals which have been created by man for the nourishment and breeding of the domestic animals on which he has depended for much of his food, power, transport and clothing. These communities were established by the clearance of the climax forest vegetation (the wildwood) which developed after the end of the last ice age. Grasslands were created by the interaction of available plant species with grazing animals, often sheep and cattle. The agricultural technology in use up to the beginning of the 20th century could be complex, but was not highly developed, and as a consequence utilisation of potential photosynthetic production was inefficient in terms of energy transfer. This allowed for considerable diversity of both plants and animals in the community, although such diversity was produced unintentionally and unconsciously. There was also diversity in the types of grassland created. Partly this was mediated through soil type, but water régime was also an important influence. So also was the use made of the grassland vegetation, whether directly by grazing animals (pasture) or indirectly by growing a crop of hay (meadows). In many cases, of course, direct and indirect use on any one site were combined in seasonal or sequential use. Whatever the exact use, grasslands were established as plagioclimax communities in which succession of the vegetation was opposed by its removal to feed sheep and cattle.

There were few obvious competitors for grassland production in Britain until the rise of the rabbit (SHEAIL 1971). From being an introduced and valued domestic animal kept in managed warrens, rabbits became a feral species and a major agricultural pest. Despite competing with sheep, in particular, rabbits contributed to the maintenance of grasslands by grazing and scratching the sward.

About 1950, two major changes started to become apparent on British lowland grasslands. One was relatively gradual and only dramatic in its most intensive, recent phase; this was the decline of pastoral farming and the rapid conversion of most level or gently-sloping land to arable for the production of cereals by the heavy use of nitrogenous fertilisers. The other change, sudden and very obvious, was the great reduction of rabbit populations by the *Myxoma* virus in the years following 1954.

Current grassland problems

Species-rich lowland grasslands in Britain have been greatly reduced in extent. It is estimated that only c. 4000 ha of semi-natural chalk grassland, for instance,

remain in Britain. Those areas which are left have been either under-managed or managed with difficulty. Nature conservation bodies are not often equipped to keep sheep or cattle just for management of nature reserves. Consequently, even reserves especially established to conserve species and communities dependent on grazing have been neglected. In many cases, other methods of management, such as mowing, have been tried, often without a complete monitoring of the effects on plants, animals and communities.

The association of a wide range of diurnal Lepidoptera with different types of grassland in subalpine Switzerland has recently been demonstrated (ERHARDT 1985). Species-richness was high under traditional, non-intensive management and in the early stages of abandonment after intensive use. But few species persisted under intensive agricultural management, nor in areas where trees and shrubs began to be established.

Even where it has been possible to re-impose grazing management, there has often been a lack of appreciation of the complexities and subtleties of the interaction between the vegetation, the grazing animals and the invertebrate fauna. Possibly because of over-reaction to the need to re-introduce grazing, it has tended to be too intensive or too continuous in some cases. The distinction between reclamation management, imposed to bring a real grassland character back to a neglected site, and maintenance management, designed to keep that character, has not always been recognised.

There has also been little appreciation of the differences in objectives between agricultural and conservation management. The desire to maximise, or increase, agricultural production has been the reason for many of the changes which have destroyed large numbers of sites once rich in grassland Lepidoptera. A realisation that wildlife conservation was an unconscious production of agricultural management is long overdue. The corollary is that conservation management has the potential to be far more responsive to the needs of particular species of plants and animals and the communities of which they are part.

A major problem arising from the destruction of so many sites is that those which are left have become extremely isolated. In these areas, Lepidoptera which become extinct, often through lack of management, do not have the ability, as they once did, to re-colonise from nearby sites. The management of these species requires in many cases the re-establishment of populations by artificial means (MORRIS 1981c, THOMAS 1984b). We discuss some examples below.

Grassland Lepidoptera — some case histories

Several studies of individual species have recently been undertaken in Britain which demonstrate some of the problems which confront butterfly conservationists. These studies also suggest ways in which populations of each species may be enhanced and managed on protected sites, particularly nature reserves.

The species concerned are not great rarities, nor are they especially endangered in Europe as a whole. There is some evidence to suggest that the problems encountered by species on the edge of their range where the climatic environment is generally colder and wetter than elsewhere in Europe may not be widespread. For example, at least 3 of the species described below as needing short or sparse turf to survive in Britain can occupy taller or denser swards further south in Europe where the microclimate is warmer at ground level. Nevertheless, the detailed investigations of the ecology of these species are of interest to most lepidopterists.

C. D. THOMAS (1985a, b) studied the lycaenid butterfly *Plebejus argus* at a number of sites in Britain. This species apparently inhabits a broad range of biotopes in England and Wales, where it is widely distributed (HEATH *et al.* 1984), but local. It is locally common on limestone grassland in North Wales, but has disappeared from many grassland, and other sites elsewhere. THOMAS (1985b) showed that, despite the wide range of biotopes inhabited and foodplants utilised, *P. argus* is actually very restricted in its occurrence. The eggs are laid where short vegetation and bare ground meet, and only where the microclimate is warm. The larvae feed only on the youngest and most succulent terminal shoots of the foodplants. And the adult butterfly is sedentary, so that the rate of colonisation of new ground is also slow. It is this combination of characteristics which has restricted the butterfly's habitat and ensured that many former sites for it have become unsuitable through growth of coarse grasses following myxomatosis and the decline in sheep farming.

Rather similar habitat conditions were required by another lycaenid in Britain, *Maculinea arion*. Historically, this species was much more restricted in the British Isles (SPOONER 1963), and colonies were lost throughout the 19th and 20th centuries, though most rapidly in the period from about 1950 to 1979, when the last-known colony became extinct (THOMAS 1980). The early stages of *M. arion* are dependent on short grassland vegetation, but in this case because the preferred ant host, *Myrmica sabuleti*, occurs abundantly only on very short turf (THOMAS 1984b). On former sites for the butterfly, surveys have shown that although the foodplant of the first 3 instars (*Thymus drucei*) may remain abundant, growth of coarse vegetation has nearly always brought about extinction of *M. sabuleti*. The grassland management necessary to retain populations of *M. arion* is particularly intensive. Now that this is understood, a protected site where it is hoped to re-establish the butterfly is being grazed at an appropriate intensity.

Another lycaenid butterfly of high conservation importance in Britain is *Lysandra bellargus*. Its ecology has several features of interest (THOMAS 1983a). The butterfly is restricted to the south of England and adults are relatively sedentary. The larvae feed on the leguminous herb *Hippocrepis comosa*, which in Britain grows only on calcareous soils. Ovipositing female butterflies lay almost exclusively on plants growing in turf only 1-4 cm high. The daily temperature in spring and summer is much higher here than it

is in taller vegetation. Larvae of *L. bellargus* are almost invariably attended by ants, which are attracted to the honeydew secreted from pores distributed over the body and also from a Newcomer's gland. At night and during moults, ants bury or wall-up larvae in cells constructed of soil particles. Pupae are also attractive to ants and have been found in ants' nests. Several species of ant attend *L. bellargus* larvae; those recorded at the sites where THOMAS worked were *Myrmica sabuleti*, which occurs only in very short turf, and *Lasius alienus*, which is generally a species of dry, warm soils.

Between the years c. 1950 and 1983, numbers of colonies of *L. bellargus* halved every 12 years as a result of lack of grazing making many sites unsuitable for the early stages of the butterfly. Since 1983, grazing has increased on many sites and colonies are being lost at a slower rate. However, because of the butterfly's poor powers of dispersal and the increasing isolation of sites, artificial re-establishment must be used in the conservation of the species; this is discussed later in this paper.

The "skipper" butterfly *Hesperia comma* also inhabits chalk grassland hills in Britain and has a similar range to *L. bellargus*. Before 1940, it occurred in other parts of England (HEATH *et al.* 1984). Only about 49 populations still survive (THOMAS *et al.* 1986). The larval foodplant is the grass *Festuca ovina*, which is widely distributed in Britain and is not confined to the chalk hills of the south. The key feature of the ecology and behaviour of the species is the extreme fussiness of the ovipositing female in choosing egg-laying sites. The small *F. ovina* plants must be largely surrounded by bare ground or chalk scree and they must be growing in sheltered sun-spots. It is clear that myxomatosis has caused a drastic decline in the butterfly; reduced numbers of rabbits have allowed the vegetation on many former sites to grow up and swamp the open habitat of the larvae of the butterflies. There is some evidence that recently-increased grazing by sheep and rabbits has begun to reverse this trend. However, like *L. bellargus*, *H. comma* is a poor colonist and improved sites are mostly only potential, rather than actual, habitats for the butterfly.

The 4 examples so far given — *Plebejus argus*, *Maculinea arion*, *Lysandra bellargus* and *Hesperia comma* — are all dependent on short grassland and hot microclimatic conditions near the ground. However, not all species of butterfly respond to grassland which is intensively managed so as to produce a short sward. *Thymelicus acteon* (Hesperiidae) is a common European species which is very restricted in its distribution in Britain, being confined to only a small part of the coast of southern Britain, particularly the county of Dorset (HEATH *et al.* 1984). The butterfly is thus on the edge of its range in Britain, where its larval foodplant is the coarse grass *Brachypodium pinnatum* (THOMAS 1983b). This is a tall-growing species which has flourished in the absence of grazing by domestic stock and rabbits, and has spread in the unimproved calcareous pastures typical of this part of England. As a consequence, populations of *T. acteon* are now very numerous. In 1978, 83 colonies were found in the county of Dorset, only 36 (43%) of which had been recorded previously. Several of these colonies were very large: one was

Table 1. The habitat requirements of 5 intensively-studied British grassland butterflies

Species	Sensitive stages	Veg. height	Bare ground requirement	Food and quality	Foodplant specificity	Relationship with ants	Colonising ability adults
<i>Plebejus argus</i>	Oviposition Larval feeding Larval adoption by ants	Medium-short	Yes	Young shoots	No	Faculative	Poor
<i>Maculinea arion</i>	Oviposition Larval feeding	Very short	Less important Yes	Buds ; ant eggs, grubs, prepupae Foliage	Yes	Obligate & specific Faculative	Poor
<i>Lysandra bellargus</i>	Oviposition Larval feeding	Short	Yes	Foliage	Yes	Faculative	Poor
<i>Hesperia comma</i>	Oviposition Larval feeding	Quite short	Yes	Foliage	Yes	None	Poor
<i>Thymelicus acteon</i>	Oviposition Larval feeding	Tall	No	Foliage	Yes	None	Poor

estimated to have over 100,000 individuals on the peak day of emergence and 4 had over 10,000 (THOMAS 1983b). It is thought that *T. acteon* is now more abundant in its English haunts than it has ever been since it was discovered in Britain in 1832.

In summary, 4 of the 5 species which have been studied intensively require short turf, hot microclimatic conditions, and, in most cases, bare ground adjacent to the foodplants chosen for oviposition. These conditions are most usually produced by intensive management. But one species requires a minimum of grassland management and flourishes in the absence of grazing. The main habitat features necessary for the survival of each species are summarised in Table 1.

Other grassland insects

The effects of grassland management, or cessation of management, on a variety of other insects have been studied in Britain. Because most of these species do not have the conservation importance of butterflies, many of the studies have examined the effects of management on the species-richness and diversity of the fauna. Investigation of intensive grazing has emphasised the importance of vertical structure of both individual plant species and the vegetation for the diversity of a range of insects, particularly Auchenorrhyncha (Hemiptera) (MORRIS 1967, 1971a, b). Under cutting management as well as grazing, some species are characteristic of short turf, although more species are associated with tall vegetation (MORRIS 1981a, b). Burning, as a method of grassland management, has similar effects (MORRIS 1975), while human trampling of grassland produces very severe reductions in the insects present, for instance Coleoptera (DUFFEY 1975). Various species of Coleoptera are characteristic of short and tall vegetation (MORRIS & RISPIN 1987) and cutting reduces species-abundance and diversity while changing the proportions of phytophagous as against fungivorous, saprophagous and detritivorous species (MORRIS & RISPIN 1988). The rejuvenating effect of reimposing management on a neglected or uncut grassland is important (MORRIS & PLANT 1983). The problem of maintaining short and tall vegetation simultaneously, for the conservation of butterflies like *L. bellargus* and *H. comma*, on the one hand, and *T. acteon*, on the other, together with numerous counterparts in other insect groups, can be solved by rotational management. For most sites, particularly where the aims of management specify the maintenance and enhancement of diversity, rotational management, especially grazing, is to be preferred to uniform intensive treatment.

Colonisation and re-establishment

Some very successful research has been done in both Europe and North America on the population dynamics of butterflies. However, a major problem often exists in studying the adult population, because immigration and emigration cannot be quantified in studies of particular populations. Species

of butterfly vary very considerably in their normal mobility and "strategy" of habitat utilisation. Many species exist as closed colonies, or may be assumed to do so. This can be tested by successive estimates of abundance using the frequency of capture method on marked individuals (CRAIG 1953, EBERHARDT 1967). If population estimates stabilise over time, and provided mortality and emergences are small, then the population may be considered to be a closed one (POLLARD 1977, THOMAS 1983a). However, open populations still present a problem, as it is important that immigration rates be known. A recent approach has been to examine the possibility that "natural markers" can be used to identify the origins of individuals in the populations. DEMPSTER *et al.* (1986) studied differences in the elemental composition of individuals of the common pierid butterfly *Gonepteryx rhamni*. This is a very mobile species and adults are believed to migrate between hibernating and breeding sites (POLLARD & HALL 1980). The chemical composition of individual butterflies was examined by wavelength dispersive X-ray fluorescence spectrometry. Considerable differences were found between the sexes of *G. rhamni*, and between individuals taken on different sites and in different years and seasons. The elements which mostly discriminate between individual butterflies were potassium, calcium, phosphorus, zinc, chlorine and sulphur. Variation in these and other elements studied appears to result from differences in the composition of the soil at the breeding sites and the plants on which the larvae fed. However, despite the promise of this technique, its use seems to be limited because the specific "locality imprint" is soon destroyed as the butterflies feed and age.

More recently, a similar approach has been made to studying movements of individuals and their significance for populations in another mobile pierid, *Anthocaris cardamines*. The larvae of this species feed on a variety of Cruciferae, but mainly in southern England on *Cardamine pratensis*, a plant of wet meadows and woodland rides, and *Alliaria petiolata*, a hedgerow species of mostly drier soils. Analysis of mustard oils present in individual butterflies may help to determine their origin, as these chemicals are highly distinctive of the different larval foodplants (DEMPSTER *pers. comm.*).

The mobility of individual butterflies and the ability of species to found new colonies is an important aspect of their conservation. The examples of *Lysandra bellargus* and *Hesperia comma* emphasise that, under present-day conditions, natural re-colonisation of "vacant" sites is an increasingly infrequent and unlikely event. Even when previously unmanaged areas of grassland are brought back to a suitable condition for butterfly species which required a short turf, the sites are often isolated and surrounded by crops or other biotopes across which the insects do not fly. In these circumstances the conservationist must take on the rôle played by nature in earlier times. Opposition to the artificial re-establishment of species is becoming increasingly muted as the case for controlled and responsible re-establishments becomes more urgent and obvious (MORRIS & THOMAS 1989). A code of practice has recently been produced which sets out the desirable steps which should

be taken before, during and after an attempt at re-establishment is made (Joint Committee for the Conservation of British Insects 1986).

Numerous successful re-establishments of different species have been made in the past, though few have been adequately recorded. One exception is a re-establishment of *Lysandra bellargus* made on Old Winchester Hill, a chalk grassland National Nature Reserve in southern England. The butterfly became extinct on the site before 1960, as a result of cessation of grazing. Management re-started after a period of years, and in particular a rotational grazing system was imposed on the south-facing slope of the reserve in 1980. The site is almost completely surrounded by arable land, and it was calculated that the nearest colony of *L. bellargus* was 25 miles (40 km) distant. The re-establishment, which was made in 1981, was an instant success and the new colony is flourishing, though, like all populations of this species, it has fluctuated considerably in numbers.

This example illustrates a number of important aspects of the re-establishment of butterfly populations. As well as some very successful attempts at re-establishments there have been a few failures. Many of these have occurred because the correct ecological conditions, though well understood, could not be reproduced. A well-documented example is the attempt to re-introduce the English Swallowtail *Papilio machaon britannicus* to Wicken Fen, where it became extinct in 1952. A well-planned release of imagines was made, but the fen is too dry to support an adequate population of the larval foodplant (DEMPSTER & HALL 1980).

Butterflies of other biotopes

In this paper we have concentrated on grassland butterflies, emphasising the importance of biotope management and the changes which are produced when it ceases. These are phenomena of more general application. British woodlands, in particular, are very far from being similar to the primeval "wildwood". It is becoming increasingly evident that management, especially to produce small timber products by the practice of coppicing, has been essential to the maintenance and survival of woodland butterflies. Widespread neglect of coppice woodlands, mostly because of economic forces, together with considerable replacement of deciduous mixed woodlands by single-species plantations of exotic conifers, has resulted in many local extinctions of several species. Some of these are insects which were regarded as common only a few decades ago. Work on the ecology and conservation of these species is continuing. One recent example of such work, and the prescriptions which have been formulated for management and conservation, is the detailed study of the butterfly which was thought to be most at risk of extinction in Britain after *Maculinea arion*, the small nymphalid *Mellicta athalia* (WARREN 1985). This is another species which is rare and local in Britain though abundant and widespread in continental Europe. Its habitats need to be carefully and intensively managed if it is to survive in the British Isles.

A group of species which are rare, declining in numbers of colonies, and thus threatened in continental Europe, is the 4 or 5 species of *Maculinea*. Work on the ecology and habitat requirements of these butterflies was begun by THOMAS (1984a) and is continuing. The 2 species *M. teleius* and *M. nausithous* often inhabit the same small, mesotrophic bogs and have the same larval foodplant (*Sanguisorba officinalis*). Eggs of both species are frequently laid on the same *Sanguisorba* plants, but the larvae of *M. nausithous* survive only in the nests of the ant *Myrmica rubra*, which lives in scrubby, submarginal areas, whereas *M. teleius* parasitises *Myrmica scabrinodis*, which lives in the more open, central region of the bog. The larvae of *Maculinea rebeli* (which, ecologically at least, appears to be specifically distinct from *M. alcon*) survive in the nests of another species of *Myrmica*, *M. schencki*, whilst *Maculinea alcon* uses *Myrmica ruginodis*. With *Maculinea arion* associated particularly with *Myrmica sabuleti*, it is becoming clear that each species of *Maculinea* butterfly characteristically parasitises a different species of *Myrmica* ant.

The conservation of tropical species

The problems of conserving tropical butterflies are often very different from those which beset conservationists in Europe, although in both cases the destruction of habitats is the main threat to populations, and ultimately to species. Western attitudes towards conservation are often highly inappropriate in the Third World, where increasing living standards and the quality of life, particularly for the rural poor, are important and laudable goals. Consequently, development is an overriding objective in most Third World countries and conservation has to be implemented within that context. This is the reason for the emphasis on "Conservation for Development" in the World Conservation Strategy. One aspect of this approach is to consider wildlife, including butterflies and other insects, as a resource to be utilised. The farming of butterflies for the decorative-, and more especially the specialist trades, is already successfully in progress in Papua New Guinea (National Research Council 1983), appears to be spreading to other parts of the tropics. With the rise in popularity of "butterfly houses" in Europe, especially in the United Kingdom and North America, the live trade, too, is well situated to help the Third World utilise its butterfly resource.

Even in Europe it is often difficult to obtain precise information on the status of a particular species, especially for the whole of its range. Accurate data on status may often not be adequate to determine causes of decline, and research will usually be necessary to elucidate these problems. However, documentation is also important. Thus, the report produced by HEATH (1981) has been invaluable in determining priorities for the conservation of Europe's butterflies and in indicating where gaps in our knowledge lie. HEATH's report was built on the various national conservation efforts, particularly the Red Data Books. International RDBs for more popular groups such as mammals and birds have been in existence for some time. A selection of the threatened invertebrates of the world was made by WELLS *et al.* (1983), but the first

comprehensive Red Data Book for an insect group is COLLINS & MORRIS (1985) for the Papilionidae of the world. Naturally, this is only a means to an end: the information published in the RDB needs to be corrected, updated and elaborated. The book can be used to designate an action plan for papilionid conservation, but this in turn will be ineffectual unless practical action can be taken. European lepidopterists and conservationists can contribute to this programme. Closer to home, *Papilio hospiton* is categorised as an Endangered species, yet information on the species and its conservation has been difficult to obtain.

Epilogue

Conservationists often appear to be fighting a lost cause, or at least to be losing in a rearguard action to preserve species, populations and habitats. While it remains true that many of our Lepidoptera species continue to be under threat, we are also beginning to understand the ecology of some of them much better and to see where the priorities for conservation action lie. Economy of effort and means is an important consideration in the promotion of effective action. Future emphasis must be to focus on actual problems and real solutions. Conservation has added a new and important aspect to the study of Lepidoptera, and this may be expected to continue to grow and develop.

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References

- COLLINS, N. M. & MORRIS, M. G., 1985. *Threatened Swallowtail Butterflies of the World*, IUCN, Gland and Cambridge.
- CRAIG, C. C., 1953. On the utilisation of marked specimens in estimating populations of flying insects. *Biometrika* 40 : 170-176.
- DEMPSTER, J. P. & HALL, M. L., 1980. An attempt at re-establishing the swallowtail butterfly at Wicken Fen. *Ecological Entomology* 5 : 327-334.
- DEMPSTER, J. P., LAKHANI, K. H. & COWARD, P. A., 1986. The use of chemical composition as a population marker in insects: a study of the Brimstone butterfly. *Ecological Entomology* 11 : 51-65.
- DUFFEY, E., 1975. The effects of human trampling on the fauna of grassland litter. *Biological Conservation* 7 : 255-274.
- EBERHARDT, L. L., 1967. Population estimates from recapture frequencies. *Journal of Wildlife Management* 33 : 28-39.
- ERHARDT, A., 1985. Diurnal Lepidoptera: sensitive indicators of cultivated and abandoned grassland. *Journal of Applied Ecology* 22 : 849-861.

- HEATH, J., 1981. *Treatened Rhopalocera (Butterflies) in Europe*. Council of Europe (Nature and Environment Series No. 23), Strasbourg.
- HEATH, J., POLLARD, E. & THOMAS, J. A., 1984. *Atlas of Butterflies in Britain and Ireland*, Viking, Harmondsworth.
- Joint Committee for the Conservation of British Insects, 1986. Insect re-establishment — a code of conservation practice. *Antenna* 10 (1) : 13-18.
- MORRIS, M. G., 1967. Differences between the invertebrate faunas of grazed and ungrazed chalk grassland. I. Responses of some phytophagous insects to cessation of grazing. *Journal of Applied Ecology* 4 : 459-474.
- MORRIS, M. G., 1971a. Differences between the invertebrate faunas of grazed and ungrazed chalk grassland. IV. Abundance and diversity of Homoptera-Auchenorrhyncha. *Journal of Applied Ecology* 8 : 37-52.
- MORRIS, M. G., 1971b. The management of grassland for the conservation of invertebrate animals. In : *The Scientific Management of Animal and Plant Communities for Conservation* (Ed. E. Duffey & A. S. Watt), pp. 527-552. 11th Symposium of the British Ecological Society.
- MORRIS, M. G., 1975. Preliminary observations on the effects of burning on the Hemiptera (Heteroptera and Auchenorrhyncha) of limestone grassland. *Biological Conservation* 7 : 312-319.
- MORRIS, M. G., 1981a. Responses of grassland invertebrates to management by cutting. III. Adverse effects on Auchenorrhyncha. *Journal of Applied Ecology* 18 : 107-123.
- MORRIS, M. G., 1981b. Responses of grassland invertebrates to management by cutting. IV. Positive responses of Auchenorrhyncha. *Journal of Applied Ecology* 18 : 763-771.
- MORRIS, M. G., 1981c. Conservation of butterflies in the United Kingdom. *Beiheft Veroffentlichung Naturschutz Landschaftspflege Baden-Wurttemberg* 21 : 35-47.
- MORRIS, M. G. & PLANT, R., 1983. Responses of grassland invertebrates to management by cutting. V. Changes in Hemiptera following cessation of management. *Journal of Applied Ecology* 20 : 157-177.
- MORRIS, M. G. & RISPIN, W. E., 1987. Abundance and diversity of the coleopterous fauna of a calcareous grassland under different cutting régimes. *Journal of Applied Ecology* 24 : 451-465.
- MORRIS, M. G. & RISPIN, W. E., 1988. A beetle fauna of oolithic limestone grassland, and the responses of species to conservation management by different cutting régimes. *Biological Conservation* 43 : 87-105.
- MORRIS, M. G. & THOMAS, J. A., 1989. Re-establishment of insect populations, with special reference to butterflies (chapter 2, *Moths and Butterflies of Great Britain and Ireland*, 7 (1), ed. by J. Heath & A. M. Emmet), 22-36.
- National Research Academy Council, 1983. *Butterfly Farming in Papua New Guinea* 30 pp., National Academy Press (Managing Tropical Animal Resources Series), Washington, D.C.
- POLLARD, E., 1977. A method of assessing changes in the abundance of butterflies. *Biological Conservation* 12 : 114-134.
- POLLARD, E. & HALL, M. L., 1980. Possible movement of *Gonepteryx rhamni* (Lepidoptera : Pieridae) between hibernating and breeding areas. *Entomologist's Gazette* 31 : 217-220.
- SHEAIL, J., 1971. *Rabbits and Their History*, David & Charles, Newton Abbot.
- SPOONER, G. M., 1963. On causes of the decline of *Maculinea arion* L. (Lep., Lycaenidae) in Britain. *Entomologist* 96 : 199-210.
- THOMAS, C. D., 1985a. The status and conservation of the butterfly *Plebejus argus*

- L. (Lepidoptera : Lycaenidae) in north-west Britain. *Biological Conservation* 33 : 29-51.
- THOMAS, C. D., 1985b. Specialisations and polyphagy of *Plebejus argus* (Lepidoptera : Lycaenidae) in North Wales. *Ecological Entomology* 10 : 325-340.
- THOMAS, J. A., 1980. Why did the Large Blue become extinct in Britain ? *Oryx* 15 : 243-247.
- THOMAS, J. A., 1983a. The ecology and conservation of *Lysandra bellargus* (Lepidoptera : Lycaenidae) in Britain. *Journal of Applied Ecology* 20 : 59-83.
- THOMAS, J. A., 1983b. The ecology and status of *Thymelicus acteon* (Lepidoptera : Hesperidae) in Britain. *Ecological Entomology* 8 : 427-435.
- THOMAS, J. A., 1984a. The behaviour and habitat requirements of *Maculinea nausithous* (the Dusky Large Blue Butterfly) and *M. teleius* (the Scarce Large Blue) in France. *Biological Conservation* 28 : 325-347.
- THOMAS, J. A., 1984b. The conservation of butterflies in temperate countries : past efforts and lessons for the future. In : *The Biology of Butterflies* (Ed. R. I. Vane-Wright & P. R. Ackery), pp. 333-353. 11th Symposium of the Royal Entomological Society of London.
- THOMAS, J. A., THOMAS, C. D., SIMCOX, D. J. & CLARKE, R. T., 1986. Ecology and declining status of the Silver-spotted Skipper butterfly (*Hesperia comma*) in Britain. *Journal of Applied Ecology* 23 : 365-380.
- WARREN, M. S., 1985. The ecology and conservation of the Heath Fritillary butterfly, *Mellicta athalia*. Confidential report to Nature Conservancy Council and Institute of Terrestrial Ecology.
- WELLS, S. M., PYLE, R. M. & COLLINS, N. M., 1983. *The IUCN Invertebrate Red Data Book*. IUCN, Cambridge and Gland.

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