The landscape ecology of butterflies in traditionally managed Norwegian farmland

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How to cite:

Fjellstad, Wendy Jane (1998) *The landscape ecology of butterflies in traditionally managed Norwegian farmland*, Durham theses, Durham University. Available at Durham E-Theses Online: http://etheses.dur.ac.uk/4657/

THE LANDSCAPE ECOLOGY OF BUTTERFLIES IN TRADITIONALLY MANAGED NORWEGIAN FARMLAND

A Ph.D. thesis submitted

to

University of Durham

Department of Biological Sciences

by

Wendy Jane Fjellstad

1998

"There is a theory which states that if ever anyone discovers exactly what the Universe is for and why it is here, it will instantly disappear and be replaced by something even more bizarre and inexplicable."

(Douglas Adams; The Hitch Hiker's Guide To The Galaxy)

THE LANDSCAPE ECOLOGY OF BUTTERFLIES IN TRADITIONALLY MANAGED NORWEGIAN FARMLAND

Ph.D. thesis submitted by Wendy Fjellstad, Autumn term 1998.

ABSTRACT

The modernisation of agriculture has lead to changes in Norwegian farming landscapes that have consequences for butterfly distribution and abundance. Particularly important is the abandonment of traditionally managed grasslands and the consequent increase in potential barriers of scrub and trees in the landscape. In this thesis I use a landscape ecological perspective to explore the effects of abandonment on butterfly dispersal.

I demonstrate that landscape elements influence butterfly movement behaviour: tall structures were significant barriers for a range of species and even low features, such as roads, elicited significant behavioural responses which shaped the movement patterns of butterflies. Behavioural differences between species were related to ecological and physiological characteristics.

Movement patterns of Scarce Coppers (*Lyceana virgaureae*) were recorded by mark-release-recapture (MRR) techniques. Of 1711 recorded displacements, over 90 % were under 150 m. Exchange rates between meadows were dependent upon distance and the structure of intervening vegetation. A simple spatial model, parameterised with data from the behavioural experiments, was validated using MRR observations. This confirmed that the behaviour of individuals responding to single landscape elements has consequences at the level of populations and entire landscapes.

The life history and movement behaviour of the endangered Apollo (*Parnassius apollo*), were examined using MRR. The butterfly is well adapted to a mosaic landscape structure; however, inter-meadow movement declined exponentially with increasing distance between meadows. Abandonment of hay meadows on steep slopes, with consequent forest succession, will adversely affect the Apollo by increasing the distances between open habitat. Genetic analyses support the findings of MMR studies and add a wider spatial and temporal perspective. As a conservation management priority, I recommend population mapping to identify key sites in regional networks of populations.

Finally, I consider the links between empirical studies, modelling and the practical application of theory, and discuss the implications of landscape change for the butterflies of Norwegian farmland.

NORWEGIAN ABSTRACT

SOMMERFUGLER I TRADISJONELLE NORSKE JORDBRUKSOMRÅDER: ET LANDSKAPSØKOLOGISK PERSPEKTIV

Ph.D. avhandling av Wendy Jane Fjellstad

REFERAT

Modernisering av driftsmetoder i jordbruket har ført til forandringer i norsk jordbrukslandskap som har konsekvenser for utbredelsen og mangfoldet av sommerfugler. Særlig viktig er nedleggingen av tradisjonelt skjøttede slåtteenger og den påfølgende økningen av mulige barrierer i landskapet i form av busker og trær. I denne avhandlingen undersøker jeg ut fra et landskapsøkologisk perspektiv hvordan opphør av drift påvirker spredning av sommerfugler.

Jeg påviser at landskapselementer virker inn på sommerfuglenes bevegelser: Høye strukturer var signifikante bevegelsesbarrierer for en rekke arter, og selv lave elementer, slik som veier, forårsaket atferd som formet sommerfuglenes bevegelser. Atferdsforskjeller mellom arter forklares i henhold til økologiske og fysiologiske karakterer.

Den østlandske gullvingens (*Lyceana virgaureae*) bevegelsesmønstre ble registrert ved bruk av merke-gjenfangstsmetoder (MRR). Over 90 % av 1711 registrerte forflytninger var på mindre enn 150 m. Utvekslingsraten mellom enger var avhengig av avstanden og vegetasjonsstrukturen mellom engene. En enkel romlig model, med parametre hentet fra atferdstudiene, ble prøvd ut ved hjelp av observasjonene fra merke-gjenfangstforsøket. Denne bekreftet at enkeltindividers reaksjon på de enkelte landskapselementene har konsekvenser på populasjons- og landskapsnivå.

Merke-gjenfangst ble også benyttet for å undersøke livshistorien og bevegelsesatferden til en truet art, apollosommerfuglen (*Parnassius apollo*). Sommerfuglen er godt tilpasset et landskap med mosaikkstruktur; men likevel gikk antall bevegelser mellom enger eksponensielt ned med økende avstand. Nedlegging av slåtteenger i bratte bakker, med påfølgende gjengroing, vil gjennom den økte avstanden mellom åpent habitat komme til å ha en negativ virkning på apollosommerfuglenen. Genetiske analyser støtter resultatene fra merke-gjenfangstforsøkene og bidrar til et bredere geografisk og historisk perspektiv. Ut fra denne innsikten vil jeg foreslå at naturforvaltningen prioriterer identifikasjon av nøkkellokaliteter innenfor et nettverk av sommerfuglbestander.

Til slutt vurderer jeg sammenhengene mellom empiriske studier, modellering og praktisk anvendelse av teori, og diskuterer de følgene landskapsendringer kan få for sommerfugler med tilhold i norsk jordbrukslandskap.

ACKNOWLEDGEMENTS

Firstly, I gratefully acknowledge the Norwegian Institute for Nature Research (NINA) for financing this thesis and providing an office and computer facilities; and the British Council for a Cultural Exchange Scholarship which financed my first year in Norway.

I am indebted to my supervisor at Durham University, Tom Sherratt, for advice, comments and statistical help, and for convincing me that there was light at the end of the tunnel.

And a big thank-you to Gary Fry at NINA for introducing me to landscape ecology and to Norway, for your friendship, and for providing endless opportunities. I can safely say that my life would not have been the same without you! Special thanks for comments on the manuscript (particularly for removing all those nasty weasel-words!).

Kaare Aagaard gave great encouragement throughout the writing of this thesis by sharing his knowledge of butterflies with me and discussing study approaches and methods of analysis. I am also grateful for having been allowed to join in the mnemosyne project, which has given annual doses of motivation.

Wenche Dramstad has been a source of inspiration, particularly regarding the study of landscape change. More importantly, Wenche has been a source of coffee and biscuits and her contagious optimism has been invaluable!

Thanks to Erik Framstad, and colleagues at NINA for help and kind support; to Svein-Erik Sloreid for digitising the map used in Plate 12; and especially to Gerd Aarsand who has given continual encouragement and moral support, in addition to sorting out all manner of practicalities.

Massive thanks to my teams of ace field workers: Jakob Haugen, Norwegian expert in the construction of artificial hedges; Hazel Knight and Marie Schaffer who spent so many hours watching green tarpaulins; Rob McCall and Kate Trumper for walking back and forth along field boundaries, and slogging up the hill at Bandak; Mike and Robert Williams, Simon Barker, Linda Barnett and Craig Emms for watching and enthusiastic catching of Apollos at Hjartdal; Torgrim Fjellstad, Konrad Pütz, Liv Kjersti Finholt, Benoit Baudry and Astrid Eblenkamp for marking all those fiddly little Scarce Coppers.

I thank the farmers and land-owners of my study sites in Telemark, in particular Jon Grøstad, for giving access to their land. Jan Heggenes greatly eased logistics by allowing us to use his summer house in Telemark. Ann Norderhaug introduced me to the Hjartdal cultural landscape and was a big help during the early stages of the field work.

Arne Ivar Sletnes and colleagues at the Norwegian Institute of Land Inventory (NIJOS) provided access to equipment and gave valuable practical help and advice on the analysis of aerial photographs. Geir-Harald Strand contributed helpful discussion on methodology for Chapter 2.

Special thanks to Kjetil Hindar for making the genetics chapter possible, both through technical expertise and for giving me access to hard-won data on Apollos from Oppland and Buskerud. Thank you too for helpful comments on the manuscript. A big thank-you to Torveig Balstad for explaining the procedure of enzyme electrophoresis and for the many hours of analysis that you have contributed. Thank you also to Oddvar Hanssen for your enthusiasm and for practical help during my visit to Trondheim.

I am very grateful to Gugs Lushai at Southampton University for introducing me to molecular genetics. Although I finally decided not to include the PCR work in this thesis, I appreciated the chance to broaden my knowledge concerning methods of biological investigation.

Thanks especially to Anna Fjellstad and Geir Steinheim for your encouragement and understanding; and to Marie Schaffer, my soul-mate from the other side of the world.

Finally, I would like to thank my family: Mark for putting things into perspective; Mum and Dad for being so endlessly patient and supportive and for valuable comments on the manuscript (especially those that made me laugh during the final revision!) and my husband, Jo Inge, for huge assistance in the field, for help with logistics and cars and computers, for putting up with a house carpeted with references, and for comfort through my nightmares.

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CHAPTER 1

GENERAL INTRODUCTION

1.1 THE SCOPE OF THIS THESIS

Across Europe, changes in anthropogenic landscapes are leading to declines in the abundance and diversity of butterflies (Heath, 1981; Thomas, 1984; Kaaber and Nielsen, 1988; van Sway, 1990; Pullin, 1995; van Swaay *et al.*, 1997). This thesis describes a series of studies of butterflies in traditional Norwegian farming landscapes, investigating how the physical structure of the landscape affects butterfly behaviour and distribution. Several methodological approaches are used to explore the links between processes operating at different scales. Hence, the distribution of populations is examined in the light of evidence about the behaviour of individual butterflies and, similarly, inquiry into the functioning of entire landscapes is aided by studies of the role of single landscape elements.

Although this work is not directly applied to a specific conservation goal, it is hoped that the findings will raise awareness of the link between the structure of a landscape and its butterfly fauna, and thus contribute to the general body of knowledge required for effective conservation of butterflies and their habitats. The majority of the field work was carried out in an area considered to be one of the most valuable cultural landscapes in Norway and the conservation angle is given additional weight through study of the endangered Apollo butterfly (*Parnassius apollo*).

In the following background information, I review the status of butterflies throughout Europe and the reasons for their decline. I present an overview of the concepts of landscape ecology and explain their potential practical relevance for butterfly conservation. I then consider the situation in Norway, in particular the conservation of butterflies in a traditional farming landscape, which leads on to the aims of this thesis. Finally, I give a brief outline of the contents of following chapters.

1.2 THE STATUS OF BUTTERFLIES IN EUROPE

1.2.1 Declining butterflies

Butterflies are members of the insect order Lepidoptera, a group comprising some 200,000 known species, about 5000 of which occur in Europe (Vane-Wright and Ackery, 1984; Chinery, 1989). Two of the twenty-two super-families in the order are butterflies, the Hesperioidea (skippers) and the Papilionoidea (true butterflies) (Chinery, 1989; Thomas and Lewington, 1991). The field of butterfly systematics is a problematic one and taxonomic classification continues to be adjusted (see Ackery, 1984 for thorough discussion), however the superfamilies Hesperioidea and Papilionoidea, referred to together as Rhopalocera, are clearly distinct from other European Lepidoptera, and the species of European butterflies are well recognised, even if their generic names are open to discussion. Throughout this work, scientific names will be given on first mention of a species and a list of both English and scientific names is provided in Appendix I.

As relatively large, colourful insects, which fly by day and are associated with flowers and sunshine, it is not surprising that butterflies have attained considerable popularity. They became objects of study at an early stage in the history of zoology, with butterfly collecting a popular hobby in England in the latter part of the seventeenth century (Ford, 1977; Emmet and Heath, 1989). The initial concentration on the collection of different species and geographical variations has, in more recent years, given way to observational studies, both by professional entomologists and keen amateurs, such that much is now known, not just about species distributions and abundances, but about many aspects of butterfly biology and ecology.

Unfortunately, the picture which has emerged from this amassed knowledge is somewhat bleak, showing a butterfly fauna which is on the decline. In 1981, 14 of Europe's 362 butterfly species (4%) were regarded as endangered and a further 50 species classed as vulnerable (Heath, 1981). Ten years later, the number deemed to be endangered had increased to 26 (Thomas, 1991).

On a national scale, Belgium, Denmark, East Germany, Finland and France have all had at least one recent extinction (Thomas, 1984; Thomas, 1991) and as many as fifteen of Holland's seventy-one indigenous butterfly species have become extinct (van Sway, 1990). England has lost two endemic species in recent times (Thomas, 1984; Thomas, 1991) and Luxembourg has lost eight species (Munguira *et al.*, 1993). In all of these countries, national extinctions have been accompanied by high rates of local extinction, such that many species have greatly contracted in range and some are represented in a country by just a few colonies. Hence, there is a high probability of more species losses in the near future unless conservation efforts have considerably more success than hitherto.

In Norway, Lepidoptera is the fourth richest insect order, with some 2100 known species, 94 of which are butterflies. Three Norwegian butterflies are registered as strictly protected in Appendix II of the Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention). They are the Scarce Heath (*Coenonympha hero*); the Clouded Apollo (*Parnassius mnemosyne*); and the Apollo (*P. apollo*). In addition, there are three species listed as vulnerable on Norwegian red lists (Anon., 1994): the Chequered Blue (*Scolitantides orion*), Reverdin's Blue (*Lycaeides/ Plebejus argyrognomon*) and the White-letter Hairstreak (*Strymonidia w-album*). No records of extinctions exist and it is likely that, in this sparsely populated country, butterflies have not been exposed to the same pressures as occur throughout much of Europe. Unfortunately this situation is now changing. There has been relatively little butterfly research in Norway and work is needed if proactive conservation measures are to be taken and the decline witnessed by the rest of Europe avoided.

1.2.2 Causes of decline

Before considering the reasons for butterfly decline, it is important to note that certain species of butterfly are intrinsically more vulnerable to decline than others due to features of their life history or physiology. Particularly important features are the abundance, stability and number of plant species used by larvae, and the mobility of adults (Kudrna, 1986). Butterflies show immense inter-specific variation in phenology, i.e. the timing of their first and last appearances of the year, and in voltinism, i.e. the number of generations occurring each year. Generally, the butterfly species still thriving in modern landscapes tend to be relative r-strategists, having pupal and adult over-wintering, fast larval growth and high mobility (Bink and Siepel, 1986; Bink, 1989).

Small butterflies complete their development faster than larger species so are able to have more generations per year. Development is also affected by temperature, generally being faster in warmer latitudes. Thus the Apollos, living in cold climates and with large body size may take two years to mature (Chinery, 1989) and may take longer to recover from population decline than species with shorter generation times. Butterflies at the northern-most extent of their range might be considered more vulnerable than their southern counterparts; the short summers in Norway, for example, mean that some species (e.g. the Pearl-Bordered Fritillary, *Clossiana euphrosyne*) which have two or three broods per year in mainland Europe rear only one brood in Norway (Chinery, 1989).

1.2.2.1 Climate

There are many factors affecting the range, distribution and abundance of butterflies but climate is a major consideration (Dennis, 1977; Turner *et al.*, 1987). Many large fluctuations in numbers have been attributed to climate changes (Douwes, 1975; Pollard, 1979; Ehrlich *et al.*, 1980; Deschamps-Cottin, 1996). Not only does the weather affect butterflies directly, affecting survival (Puech, 1983), fecundity (Boggs, 1986), development rates (Shreeve, 1986) and influencing the amount of time adults can be active (Douwes, 1976), but it also affects the condition of both larval and adult food plants.

1.2.2.2 Pollution

In addition to the local pollution by increased agrochemical use mentioned below, there are some examples of butterflies suffering from the more indirect atmospheric contamination which results from industrial activity. Heath (1981) highlighted severe declines in a number of species in areas to the north and east of some of western Europe's main industrial regions, where pollutants borne by prevailing south-westerly winds would be high. Janzon (1990) proposes that the decline in Swedish populations of Apollo which occurred during the 1950's may be attributed to pollution by acid rain, the populations which persisted being those in limestone areas where the high pH could act as a buffer against acid precipitation and metal pollution. The evidence though is somewhat circumstantial and it is worth mentioning that one of the few Norwegian populations of Clouded Apollo is found in Sunndal valley, in which one of the largest point sources of pollution in Norway, an aluminium factory, is sited. Even so, during almost a decade of study of this butterfly, no adverse effects have been observed which could be related to pollution (*pers.obs.*). Similarly, Thomas (1991) comments on the case of the Ringlet (*Aphantopus hyperantus*), which disappeared from areas around some of the UK's industrial centres during the industrial revolution. Whilst this may imply a role for pollution, Thomas reports large populations of Ringlet in the heavily polluted regions of eastern Europe and thus suggests that the local extinctions in England were more likely to have been due to changes in land use which were occurring around the same time.

1.2.2.3 Predation

Whilst interest in the role of predation on butterfly population has not been lacking, it has taken many years to gather information on this subject due to the rarity of observing predation attempts and the difficulty of following the fate of individuals in the wild. This has been particularly the case for predation on adults, where indirect methods have been valuable, such as the analysis of beak-marks to determine the frequency of bird predation (e.g. Carpenter, 1941;

Shapiro, 1974), and the analysis of wing coloration in the light of evolutionary theory (camouflage, aposematism, mimicry etc.) (see Bowers *et al.*, 1985, and Brakefield *et al.*, 1992, for an overview).

At all stages of the life cycle, butterflies are vulnerable to attack from predators, with larval and pupal stages appearing to be exposed to the greatest risk (see e.g. Dempster *et al.*, 1976). Both Brown Hairstreak (*Thecla betulae*) larvae (Thomas and Lewington, 1991) and Apollo larvae (Henriksen and Kreutzer, 1982) are reported as being very prone to predation by small mammals. Polish researchers have also observed predation by small mammals on adult Apollos at night (Pawel Adamski, pers. comm.).

Small mammals are polyphagous, as are many of the natural enemies of butterflies, including birds and many arthropods (mites, bugs, beetles, wasps, spiders, harvestmen). By contrast, parasites, for example the Ichneumons, tend to be more species specific. In 1930, Ford and Ford provided evidence of parasitism causing up to 90 - 95 % mortality in a butterfly population. Basic ecological theory would suggest that species-specific predators are unlikely to bring their prey to extinction and polyphagous predators often switch to alternative prey when one prey item occurs in low density, but nevertheless, predation can have dramatic effects and may contribute to the decline of some butterfly populations. See Dempster (1984) and references therein for a thorough discussion of the effects of predators, parasitoids and diseases on butterfly populations.

1.2.2.4 Collecting

Some authors believe that collecting of butterflies, especially on a commercial scale, can cause extinctions (Sheldon, 1925; Ford, 1977; McLeod, 1979). However, there is now a general consensus that collecting does not have such a drastic effect on butterfly numbers as was once thought (Heath, 1981; Thomas, 1984; New, 1991). After a very thorough review of the various categories of private and commercial collecting, New (1991) concluded that only when very rare species are taken is there likely to be a significant influence on species viability. Even in the tropics where butterflies are collected on a huge scale, it is doubtful that this really threatens populations. Results of mark-recapture studies suggest that, without massive sustained effort during an entire flight season, it is physically impossible to capture more than a small fraction of a population, even if the species is a weak flyer and flies often in accessible terrain (Thomas, 1984; Bourn and Thomas, 1993; Munguira *et al.*, 1993).

In Norway, the two endangered *Parnassius* species possibly face some risk from collectors. They are both large, spectacular species and their rarity makes them valuable. Moreover, their life history is such that they cannot recover their numbers as swiftly as many butterfly species (as explained above). However both species inhabit fairly inaccessible terrain and are strong flyers, thus whilst collecting may contribute to their decline it is unlikely to be a major cause.

Guidelines have been established to enable collecting to continue but in a responsible manner, causing the minimum of damage to populations and their environment (Heath, 1981). Whilst the killing of individuals may seem abhorrent to many nowadays, there is no doubt that collecting has greatly contributed to our knowledge of butterflies, and many of today's greatest authorities on butterflies began their careers as enthusiastic collectors. Increasingly though, photography, and even filming using home video cameras, are becoming alternatives to collecting. These pursuits may lead to a new era of discovery of the butterfly world as the focus of attention shifts from wing patterns to patterns of behaviour.

Generally, it seems that habitat alteration has contributed more to butterfly decline than collecting ever could (Pyle *et al.*, 1981). Indeed, of all the reasons for butterfly decline, landscape change has undoubtedly been the greatest (Thomas, 1984; Thomas, 1991; Pollard and Yates, 1993; Warren, 1993).

1.3 LANDSCAPE CHANGE: THE GREATEST CAUSE OF BUTTERFLY DECLINE

1.3.1 Intensification of agriculture

This thesis focuses on the butterfly fauna of agricultural landscapes. Agriculture is one of the major classes of land-use throughout Europe (Agger and Brandt, 1988; Green, 1989; Sugden and Rands, 1990) and as such, its suitability as butterfly habitat will greatly influence the potential range of these insects. Until recently, butterflies flourished in the open, sunny conditions created by man's farming activities. In Britain, 40 species of butterfly (73% of the butterfly fauna) breed entirely or mainly in agricultural landscapes of open grassland and hedgerows (Thomas, 1984). However, the past few decades have seen changes in farming practices which have considerably reduced the quality of these habitats for butterflies.

The alteration of traditionally farmed landscapes through the introduction of mechanisation, agro-chemicals and new breeds of crops and animals has, indeed, had negative impacts on the majority of wildlife (Green, 1986; Norderhaug, 1988; Green, 1989; Smith and McDonald, 1989; Glimskär and Svensson, 1990; Green, 1990; Skånes, 1990; Anon., 1995b), including butterflies (e.g. Kaaber and Nielsen, 1988; van Sway, 1990). The simplification of the environment through modern farming practices, tends to favour a few species whilst eliminating the majority. This is illustrated for butterflies by the Clouded Yellow (*Colias croceus*), which is the only butterfly in the British Isles which is capable of breeding on improved pasture (it uses clover as its food plant), compared with 28 species which breed on the more diverse unimproved pasture (Dennis, 1992, Appendix 2). Similarly, in a sub-alpine region of Central Switzerland, Erhardt (1985-Fig.1b) recorded over 30 butterfly species in unfertilised mown meadows, compared with only five species in heavily fertilised mown meadows.

Mechanisation and subsidies have allowed the drainage and improvement of wet meadows, resulting in the decline of several species, including the Marsh Fritillary (*Eurodryas aurinia*), now one of the most rapidly declining butterflies in Europe (Thomas and Lewington, 1991). Drainage of fen-land and consequent habitat loss also played a major role in the extinction of the Large Copper (*Lycaena dispar*) from England at the end of the nineteenth century (Duffey, 1968).

Mechanisation has also increased the scale of farming, resulting in removal of boundaries and hedges to create larger fields. At the end of the Second World War there were some 800, 000 km of hedgerow in Britain; by 1990 this figure had been almost halved (Chapman and Sheail, 1994), reducing habitat availability for 16 or more butterfly species which breed in hedgerow habitats in at least part of their range. For the more specialised hedgerow species, such as the Brown Hairstreak, hedgerow removal has led to considerable decline. Mechanised cutting of hedges has also been a negative change for these butterflies (Warren, 1992b; Barker *et al.*, 1996). Machines cut deeper into hedges and more uniformly along their length than hand-trimming and, since the eggs are laid on the younger twigs, this leads to considerable egg-loss. Decline in the traditional practice of hedge-laying has further reduced the availability of young shoots for these butterflies.

The direct effects of pesticides on butterflies have not been widely studied, although studies on the Large White (*Pieris brassicae*) and Green-Veined White (*P. napi*) have shown considerable mortality due to spray drift (Davis *et al.*, 1991a; Davis *et al.*, 1991b) and it seems reasonable to assume that other species would be affected in a similar way. Some butterflies are inherently better protected against pesticides than others due to aspects of their behaviour. Thus skipper (Hesperiidae) larvae are unlikely to be affected by direct contact with pesticides due to their habit of spinning food plant leaves into a tube or tent in which they spend most of their larval life. However, it is likely that indirect effects of agro-chemicals play a more important role than direct effects. The modification of floral species composition brought about by use of fertilisers and herbicides, significantly reduces population numbers due to the removal of larval food plants and important nectar sources. Thus many colonies of Dingy Skipper (*Erynnis tages*) have been lost due to herbicides eliminating their food plants, Bird's-foot trefoil (*Lotus corniculatus*) and Horseshoe vetch (*Hippocrepis comosa*). Recently there have been attempts to return some wildlife value to farmland by extending field margins, such that agro-chemicals do not affect the boundary vegetation. This has improved modern agricultural landscapes, providing strips of butterfly habitat around fields, the benefits of which are well documented (Rands and Sotherton, 1986; Dover, 1989; Dover, 1990b; Dover *et al.*, 1990; Dover, 1994; Feber and Smith, 1995).

Norwegian topography is such that mechanised farming is only possible over a relatively small area of the country. Less than four percent of the land is used for intensive agriculture and even here there remain small patches of native vegetation where rocks were deposited by glaciers and the thin soil is impossible to 'improve' for farming. In addition, the Norwegian Ministry of the Environment is now taking steps to increase biological diversity on farmland, being particularly interested in the wildlife potential of field boundary vegetation (Ministry of the Environment, 1991). Thus intensification of agriculture is not such a significant cause of butterfly decline in Norway compared to the rest of Europe. Indeed, as discussed below, lack of farming activity may have more severe conservation implications.

1.3.2 Abandonment of traditional land management

The intensification of agriculture on flat lowlands, including the assimilation and conversion of other habitat types to arable land, has led to such efficiency and high production that many traditionally farmed areas in more difficult terrain have been abandoned (Fry, 1991). Without management to hold the processes of succession in check, grassland becomes invaded by scrub and finally reverts to climax forest vegetation (Losvik, 1981; Losvik, 1988).The arrival of shrubs and trees is accompanied by a decline in grassland butterflies, owing to the disappearance of nectar resources and larval food plants, and the increasingly shady conditions (Erhardt, 1985). However, long before these obvious changes, there are subtle changes in the vegetation composition and structure which affect butterflies. This sensitivity is a result of the very specific requirements of the egg and larval stages of many species.

A dramatic example is that of the Large Blue (*Maculinea arion*), which became extinct in Britain very soon after its dry grassland sites were abandoned by farmers. The reason for the extinction was the reduction in grazing which allowed sward heights to increase to more than 2 cm. This tiny height difference was significant because the butterfly was dependent upon an ant species, *Myrmica sabuleti*, which requires a sward height of less than 2 cm to achieve a sufficiently warm microclimate. The butterfly larvae predate the ant brood and pupate in the ants' nest so when ant numbers declined the butterfly became extinct (Collins and Thomas, 1985; Thomas, 1995). The Adonis Blue (*Lysandra bellargus*) and the Silver-spotted Skipper (*Hesperia comma*) are not dependent on ants, however the larvae themselves require a warm microclimate, so increasing sward heights also affected them unfavourably. These species both declined drastically but their numbers have increased again since farmers resumed grazing regimes (Thomas, 1991).

The Silver-studded Blue (*Plebejus argus*) is yet another species which has suffered from the cessation of agriculture on marginal land. This species lives on heath and, like the grassland species mentioned above, it requires regular disturbance to hold its habitat in suitable condition. Again this is due to the need for the warm microclimate which exists in short vegetation. When the traditional management of rotational cutting and burning ceased, this insect declined. These changes have had greatest effect in cooler, northern parts of Europe. Further south the butterflies are able to survive in longer vegetation.

Changes in management have also occurred in woodland. Whilst coppice rotations once ensured the existence of sunny woodland glades and associated flora, today's silvicultural practices fail to provide clearings with sufficient regularity to ensure that there is always an area of suitable habitat to be colonised. This has particularly affected fritillaries, since their larval food plant, *Viola* sp. require light conditions (Thomas and Lewington, 1991). It should be noted, however, that the White Admiral (*Limenitis camilla*) is rather unusual amongst butterflies in having benefited from the cessation of coppicing, a practice which, for this butterfly of partial shade, allowed too much sunlight to reach the forest floor. Nevertheless, the White Admiral will probably also suffer in the long-term because, whilst 30-40 year old coppice has an open canopy and thus provides ideal light conditions, mature woodland is too shady for this butterfly. Even now the butterfly is beginning to decline again and there are no young coppices to replace the habitat (Pollard, 1979).

Butterflies have also suffered from alterations to wetlands and again it is the lack of traditional land management which is responsible for the change. Peat cutting is now rarely practised and as a result the land surface of fens has risen, the area becomes drier, and carr scrub becomes established. For example, at Wicken Fen, England, an introduced population of the Swallowtail (*Papilio machaon*) was maintained for many years but only with massive artificial support. Probably the only long term solution would be to introduce commercial peat cutting (Dempster *et al.*, 1976; Dempster and Hall, 1980).

The abandonment of traditionally farmed agricultural land has wider conservation implications than simply its consequences for butterfly diversity since it involves a massive reduction in area of entire habitat types, that is, early seral stage communities (Rackham, 1986; Garcia, 1992). Unimproved grassland is now a rare sight in Europe, for example, in the Jura Alps only one percent of meadows are still managed traditionally (Thomas and Furzebrook, 1992). In Scandinavia, where there have been few opportunities to intensify agriculture, small-scale farming still occurs. However, marginal agricultural land, especially in the uplands, is being abandoned at an ever increasing rate. About 80% of the butterflies on Swedish red lists are threatened by scrub encroachment and afforestation of open biotopes in agricultural landscapes (Gustavsson and Ingelög, 1994).

1.4 BUTTERFLIES AND LANDSCAPE ECOLOGY

The changes in land use outlined above and other forms of human intervention in the landscape (e.g. urbanisation, communication networks etc.), have changed not only the quality and quantity of butterfly habitats but also their distribution. They have resulted in a fragmentation of butterfly habitats, that is, areas of suitable habitat that were once connected have been broken up and now exist as patches surrounded by alien habitat. Many butterflies typically move very short distances and are thus unlikely to colonise any but the closest of habitat patches. For example, 85% of the 55 butterfly species resident in the UK, form closed sedentary populations (Thomas, 1984). The spatial arrangement of landscape elements is, therefore, of great importance and attention has recently focused on the relevance of landscape ecology, metapopulation theory and habitat patch dynamics to the conservation of butterflies.

1.4.1 Basic landscape ecology theory

The processes of reduction, fragmentation and isolation of communities are encompassed by the term insularisation. There have been numerous attempts to determine the effects of insularisation on species richness by applying island biogeography theory to habitat fragments (Lovejoy *et al.*, 1986; Wilcove *et al.*, 1986; Simberloff, 1988; Gilpin and Hanski, 1991; Spellerberg, 1991). However, the matrix surrounding a habitat fragment on land is not exactly analogous to the sea around an island and it has been pointed out previously that movement of animals to and from insular habitat patches will be very dependent on the composition of the surrounding matrix (see, for example, Wegner and Merriam, 1979; Janzen, 1983; Harris, 1984). The field of landscape ecology seeks more realistic concepts to apply to the complex patterns of habitat types found in today's landscapes (Forman and Godron, 1986; Ims, 1990; Forman, 1995).

Landscape ecology has been defined as the "study of structure, function and change in a heterogeneous land area composed of interacting ecosystems" (Forman and Godron, 1986). As such, the discipline has broadened the scale of ecological investigation and has lead to a more holistic view of species interactions with one another and their environment. Although landscape ecology developed from the study of landscapes at the human level of perception (Troll, 1968), an important aspect became the issue of spatial scale and the recognition that the 'landscapes' of interest are dependent on the species in question (Wiens, 1989; Wiens and Milne, 1989). The origins, shape, size, spatial arrangement and inter-connection of habitat patches, and the structural and functional roles of landscape components are all important aspects of landscape ecology (Forman and Godron, 1986; Turner, 1989; Forman, 1995).

Alongside landscape ecology, has been the development of metapopulation theory, which focuses on the dynamics of patchily distributed populations. A metapopulation is an assemblage of small, demographically distinct units between which migration occasionally occurs, such that if any of the small populations should become extinct there is the chance of re-colonisation of the habitat patch from one of the other patches. This metapopulation concept requires the chance of extinction to be relatively high for a single small habitat patch, with a correspondingly high level of colonisation allowing the system to persist (Levins, 1969; Gilpin and Hanski, 1991; Hanski and Gilpin, 1997). If the populations persist in each patch over a long time scale they may be better described as local closed populations. If the chance of re-colonisation is lower than extinction rates, then the metapopulation declines and is under threat of regional extinction; this is referred to as a non-equilibrium metapopulation. A special case is the 'mainland-island' type of system, where one particularly large/ permanent population continually supplies migrants to various small populations which frequently suffer extinctions (MacArthur and Wilson, 1967; Boorman and Levitt, 1973).

In this thesis, I view metapopulation theory as a landscape ecological approach, in spite of the separate historical development of the two research areas. Metapopulation theory is more narrowly defined than landscape ecology but has developed to investigate some of the same questions, all be it in a more analytical, model-oriented framework. The fundamental relevance of individual movement to both metapopulation theory and landscape ecology is an important unifying feature (Wiens, 1997).

1.4.2 Butterfly metapopulations

Metapopulation type patterns of butterfly distribution had been observed before the term "metapopulation" became fashionable. See, for example, Shapiro's (1978) discussion of how well the Chequered White (*Pieris protodice*), fitted Ehrlich and Birch's (1967) "mosaic model of population regulation" - Shapiro describes a "dynamic system of local populations coming and going stochastically...". However, most progress in the study of butterfly metapopulations has come in recent years as butterflies have become an increasingly popular study organism for developing metapopulation theories and models (Harrison *et al.*, 1988; Murphy *et al.*, 1990; Thomas and Harrison, 1992; Thomas *et al.*, 1992; Thomas and Jones, 1993; Debinski, 1994; Hanski, 1994; Hanski *et al.*, 1994; Hanski and Thomas, 1994; Hanski and Kuussaari, 1995; Hanski *et al.*, 1995; Hanski *et al.*, 1996; Thomas and Hanski, 1997).

Being relatively easy to catch and mark for studies of movement patterns and with one generation or more per year, butterflies lend themselves well to the analysis of population dynamics. In fact, much of the data used in the development of metapopulation ideas came from butterfly studies which were already published, although data collection at the landscape scale was also initiated to test the resulting models and the new way of thinking spread rapidly through the study of butterfly ecology. The documentation of local extinctions and colonisations, which had been analysed for years to help local conservation efforts, were now seen in a new light, whereby the emphasis shifted to the identification of large-scale trends and processes.

A wide range of metapopulation models have been developed to increase understanding and provide conservationists with predictive tools (see Verboom, 1996 for an overview of model types). The original metapopulation model, proposed by Levins (1969), describes a system of an infinite number of equal patches which are either occupied or unoccupied. Any sub-population has a fixed extinction rate and a colonisation rate which depends only on the number of occupied patches and a colonisation parameter. Whilst the model is obviously a considerable simplification of reality, it illustrates the concept that population dynamics may be stable at a landscape scale in spite of instability on a local scale. It also highlights the importance of dispersal for species living in fragmented habitat, since a species could become extinct even in the presence of suitable habitat if the rate of local extinction exceeds the rate of colonisation.

Hanski (1994) built on Levins work, creating a more realistic model in which patches may differ in size, the number of patches is finite, time is discrete, and colonisation depends on local rather than global conditions. The model makes use of the spatial pattern of occupied and vacant habitat patches at a snapshot in time to derive the parameters governing the processes of extinction and colonisation. For analysing the relationship between occupancy and patch area or isolation, Hanski's model has an advantage over regression models in that it allows numerical iterations of the dynamics of species in any system of habitat patches, increasing the predictive value. When tested on three butterfly species, the Glanville Fritillary (*Melitaea cinxia*), the Silver-spotted Skipper and the Chequered Blue, the model predictions agreed reasonably well with field data regarding the minimum size required for patches to be occupied and the turnover rate (the number of extinctions and colonisations) per year. The model predicts that local populations in patches of around 1ha, supporting around 1000 adults, have a life-span of 20-100 years.

However, the model is still simple and minimalistic, and Hanski warns of the danger of reading too much into its predictions, suggesting that its greatest use will be the qualitative comparison of different landscape change scenarios. Even for this purpose there are some drawbacks; firstly, predictions are unlikely to be accurate for systems with few patches (Hanski suggests that the number of patches should be at least 30, and preferably more than 50). Secondly, the model assumes a state of equilibrium, a condition which will not be filled if there are time lags in the system. For butterflies, for example, a very favourable year may lead to a species colonising unusually many patches and the resulting occupancy pattern would infer lower extinction rates and higher colonisation rates than normal (this may be of particular importance for butterflies since their population numbers fluctuate widely according to weather conditions, as mentioned in section 1.2.2.1). Similarly there may often be a time lag between landscape change and its effect on a population, for example, populations which have become isolated may survive for a number of years and thus cause misleading model results. A third drawback is the difficulty of modelling the "rescue effect" (sensu Brown and Kodric-Brown, 1977), i.e. cases where patch occupancy is maintained by frequent immigration from other patches. This phenomenon will lead to underestimation of extinction rates.

Indeed, for the rare, declining species for which such predictive models are most needed, the model predictions are likely to be most inaccurate. More complex models also have their disadvantages, both in terms of the amount of data collection necessary and the teasing apart of inter-related parameters. However, the development of models has led to some general guidelines and considerable theoretical advance.... perhaps to the extent that empirical studies have been somewhat left behind.

The majority of empirical studies, whether designed with landscape ecology theory in mind, or adapted to those ends at a later date, have been based upon mark-release-recapture techniques (to be discussed in Chapters 4 and 5). Results imply that the high habitat specificity and low mobility of many butterfly species make landscape ecology an appropriate framework.

The Silver-spotted Skipper, in a study by Thomas and Jones (1993), displayed the classical relationships predicted by island biogeography theory: the probability of colonisation increasing with increased patch area and decreasing with isolation from source populations (the maximum observed colonisation distance was 8.65 km). Conversely, the probability of local extinction declined with increasing patch area and decreased with isolation. Regarding metapopulation theory, the authors emphasise that the Silver-spotted Skipper has probably not been at distributional equilibrium in the UK at any time during the past 50-100 years and advise that knowledge of the short-term dynamics of metapopulations may be of more use than predicting their equilibria.

The requirement of the Silver-studded Blue for disturbed land with short vegetation means that its habitat is typically patchy. Thomas and Harrison (1992) mapped nine metapopulations of this species and found that the butterfly was able to colonise all suitable habitat patches within 1km from existing occupied patches but not patches that were more than a few kilometres away. Turnover was found to be high, particularly in small patches. Since the type of heath-land management which produced the cycles of disturbance has now declined, the distance between suitable patches has increased, making survival difficult for this sedentary species. In Norway, the Silver-studded Blue uses hay meadows (*pers. obs.*), again a landscape type in which habitat patches are becoming more isolated from one another due to abandonment of traditional management.

The Silver-spotted Skipper experiences a certain degree of patchiness in the occurrence of ideal habitat, related to the grazing patterns of sheep. However, the scale at which a metapopulation may operate is limited. Thus, even when the quality of sites where Silver-spotted Skippers had become extinct improved, the species was unable to re-colonise due to extremely poor mobility, and, particularly, a dislike of crossing arable crops. According to Thomas and Lewington (1991), it took this species 30 years to colonise a patch just 4 km from an existing population.

Butterflies may also exist as metapopulations within modern arable farmland, where flowers and food plants occur only in patches of native vegetation and around the edges of the crop. Studies by Dover (1989) have shown that the distribution of adult butterflies is closely tied to the distribution of flowers, with very few butterflies flying out into the crop. Hedgerows and flowery strips may link habitat patches by allowing increased migration between them. However, whilst they may act in this way, they are perhaps more important in providing the main butterfly habitat in farmland.

1.4.3 The corridor concept

One central topic of discussion in the field of landscape ecology is the concept of "corridors". It has been proposed that the viability of patchy populations may be considerably increased if strips of habitat, termed corridors, connect habitat patches, thus bridging the alien matrix and allowing increased inter-patch movement (Forman, 1983; Bennett, 1990). Ideally, the term corridor is reserved for a landscape element which is not habitat in itself, but along which movement between habitat patches can take place. In practice, however, the term is often used rather generally for discussing linear landscape elements, even if these areas comprise essential habitat elements for species. For example, Maelfait (1990) discusses the advantages of field boundary 'corridors' for spiders mainly in terms of habitat features, though he does also mention that some rare species may tolerate the sub-optimal conditions in the border zone as viable temporary habitat which can thus serve as a migration route to more suitable habitats. In fact, it would seem fair to state that for many species there is no clear-cut division between movement corridor and linear habitat. Rather, there would appear to be a continuum of linear element quality, at some point along which the precise, species-specific requirements for an optimum transport conduit will be satisfied.

There is now reported to be evidence to support the corridor concept, at least for some species, for example for some birds (MacClintock *et al.*, 1977; van Dorp and Opdam, 1987), small mammals (Getz *et al.*, 1978; Hansson, 1987; Wegner and Merriam, 1990) and spiders (Maelfait and De Keer, 1990). However, it is difficult to demonstrate a true corridor function for natural landscape elements, and debate rages both about whether corridors exist at all and whether they are wise solutions to conservation problems (Simberloff and Cox, 1987; Henein and Merriam, 1990; Simberloff *et al.*, 1992; Andrews, 1993; Bonner, 1994; Dawson, 1994; Mann and Plummer, 1995).

Possible disadvantages of corridors may include the fact that fire, diseases, predators and competitors may spread through a habitat network at least as effectively as the species of conservation interest. In Australia and New Zealand, for example, where one of the over-riding causes of species extinction is the spread of exotic species, the idea of runways through the landscape could seem something of a nightmare. Indeed, in one example from New Zealand, corridors facilitated the spread of exotic feral pigs between forest patches, threatening a genus of tree snail (Simberloff in Saunders *et al.*, 1991).

In Norway, attention has recently been directed to a true island, which was declared a Ramsar site in 1985 due to its colonies of nesting birds such as Eider Duck (*Somateria mollissima*) and Velvet Scoter (*Melanitta fusca*). The island was newly connected to the mainland by a causeway, providing a convenient corridor for predators such as Fox (*Vulpes vulpes*) and Pine Marten (*Martes martes*) which are now decimating the bird populations (Toldnæs, 1997). These examples also illustrate the point that, in any consideration of the corridor question, the exact situation and the species involved must be of deciding importance in choosing a conservation strategy. Of all the factors to consider, the mobility of the species in question must be of particular importance.

1.4.4 Use of corridors by butterflies

There is as yet very little evidence showing that butterflies make use of corridors in the landscape. Dover (1990a) observed that conservation headlands in intensive agricultural land, in addition to providing butterfly habitat requirements such as larval food plants and nectar resources, also seemed to encourage movement, possibly due to the shelter provided by hedgerows.

For forest species, woodland rides may act as corridors between glades (Sutcliffe and Thomas, 1996). Generally, however, the corridor role of linear features for butterflies has not been investigated, although various types of linear element have been demonstrated as providing linear habitat; for example, woodland rides and open areas along access tracks (Carter and Anderson, 1987), road verges (Munguira and Thomas, 1992), stream-sides (Watt *et al.*, 1977), and railway embankments and cuttings (Heal, 1965).

The quality of linear features required to function as corridors for butterflies would not necessarily be as restricted as that needed for habitat. Experiments using grassy corridors, mown to different widths, showed that width was an important factor for small mammal movement (Andreassen *et al.*, 1996) and that corridors which were too wide could slow down movement between patches. Analogous results have been obtained, through simulation studies and empirical data, for snails (Baur and Baur, 1992). A similar effect could be hypothesised for butterflies, whereby movement may be much slower if butterflies frequently stop to feed. Movement may therefore be more efficiently enhanced between patches if corridors are of sub-optimal habitat quality.

1.4.5 Barriers to butterfly movement

Some landscape elements have been shown to act as barriers to animal movement. Roads have received particular attention and have been shown to be barriers to small mammals (Oxley *et al.*, 1974), spiders (Duelli *et al.*, 1990) and carabid beetles (Mader *et al.*, 1990). Vegetation may also reduce movement rates; carabid beetles, for example, move more slowly through grassy banks than through neighbouring arable crops (Frampton *et al.*, 1995). Generally, however, barriers to animal movement have received even less explicit attention from researchers than corridors. There are clues in the literature, though (see below), some dating back considerably in time, which indicate that butterflies are very sensitive to the arrangement of the landscape .

There are, of course, many butterflies which seem to belong to large, effectively panmictic populations, like, for example, the populations of Common Alpine (*Erebia epipsodea*) studied by Brussard and Ehrlich (1970a; 1970c). These butterflies were found to aggregate in areas of suitable habitat but alien habitat did not act as a substantial barrier to movement. Even clearer examples of freely moving butterflies are the great migrants, like the Monarch (*Danaus plexippus*), Painted Lady (*Cynthia cardui*) and Red Admiral (*Vanessa atalanta*).

Many butterflies, however, have been reported to be extremely sedentary. Are these butterflies restricted in their movement by elements in the landscape? Several authors comment briefly on barrier effects of unsuitable habitat in or surrounding their study sites: for example, for Edith's Checkerspot (*Euphydryas editha*) (Ehrlich, 1961; Brussard and Ehrlich, 1970b); the Scarce Copper (*Lycaena virgaureae*) (Douwes, 1975); and the Silver-studded Blue (Ravenscroft and Read, mentioned in Thomas, 1991). However, the picture that emerges is far from clear and further study is needed to determine which features of boundaries affect their permeability to butterfly movement.

Butterfly ecologists had been interested in the influence of landscape pattern on populations long before such concepts as connectivity and barriers to movement emerged within the framework of landscape ecology. Such interests stemmed not least from consideration of evolutionary processes. For example, Dowdeswell *et al.* (1957) were able to explain differences in wing colour pattern between populations of Meadow Brown (*Maniola jurtina*) in the Scilly Islands in terms of the layout of suitable habitat. Morphologically distinct colonies persisted from one year to the next in areas where unsuitable habitat formed a barrier, isolating them from other populations.

Wilcox *et al.*(1986) took a typical island biogeography approach in their study of the butterfly fauna of mountain ranges in the Great Basin, USA. Entire genera were found to be absent from apparently suitable habitat in the upper montane and alpine zones of these ranges, despite the presence of a diverse source of potential colonists in the Rocky Mountains. The authors conclude that the areas of arid lowland which surround the ranges act as barriers to movement, thus preventing butterfly colonisation.

Many butterfly studies have been conducted on a much smaller scale, and detailed behavioural and ecological work has revealed that for many butterfly species, the amount of alien environment required to restrict butterfly movement may be very small. For example, just 100 yards of cattle grazed grass proved a complete barrier to the Meadow Brown (Ford, 1971).

Scott (1975a) recognised the importance of barriers to butterfly dispersal, noting that increased flight would not lead to an increase in the area occupied by a butterfly population or affect the density of butterflies in a habitat, if individuals turn when they come to the boundary of the population.

Perhaps the most important theoretical work in this area is that of Stamps *et al.* (1987) who constructed computer models to examine the relationship between edge permeability and emigration. Edge permeability was defined as "the proportion of potential emigrants which reach a patch boundary and then cross over it"; edges forming barriers to movement were termed "hard" edges and those where a high proportion of individuals crossed were termed "soft" edges. If a habitat originally had a hard edge, even a slight increase in permeability dramatically increased emigration, however, there seemed to be a threshold beyond which further increases in permeability had little effect on emigration. The models also showed that when boundaries act as full or even partial barriers to movement, then permeability has a greater effect on emigration than habitat patch geometry. If these models are realistic then edge permeability plays a very important role in landscape ecology.

1.4.6 Evolutionary consequences of population structure

The arrangement of habitat in a landscape can clearly have evolutionary consequences for species which are dependant upon that habitat. The isolation of gene pools from one another can lead to evolution in different directions, for example due to genetic drift, or because of different selection pressures in different habitat patches. At its most extreme this can lead to speciation, i.e. the separated groups, over time, become reproductively isolated from one another such that even if they were to come into contact again they would not be able to interbreed.

One of the arguments put forward by corridor opponents (e.g. Simberloff quoted in Mann *et al.*, 1991), is that success in linking populations together could have negative consequences on an evolutionary scale, due to the homogenisation of species' gene pools. It is generally accepted that genetic diversity makes a species more robust, since populations with different combinations of genes will respond differently to environmental change (both of biotic and abiotic nature), reducing the chance of all populations going extinct following a single catastrophe.

A fine example of geographic differentiation in butterflies was reported by Dowdeswell *et al.*(1957) in a study of Meadow Brown populations on the Isles of Scilly. The work was based on analysis of the spot pattern on butterfly wings which, although of no apparent selective value in itself, would appear to be associated with some adaptive characteristics, probably physiological. The authors found that the spotting pattern of females varied from one isolated colony to another but were stabilised at a constant value in each. This applied both to colonies on small islands, isolated from others by the sea, and for colonies on larger islands which were isolated from others by ecological barriers of unsuitable vegetation. By analysing detailed habitat characteristics, particularly where these changed during the course of the study, the authors were able to show a correlation between the particular local conditions and the spotting pattern of the butterflies. In areas where colonies were connected with one another, however, the spotting pattern appeared to adjust to the average of the dissimilar ecological conditions.

Thus geographic isolation can be seen to contribute to biodiversity, both at the level of genes and perhaps eventually, through the exaggeration of local adaptations, at the level of species. A third level of biodiversity, community/ ecosystem diversity, results from the chance combinations of relict and immigrant species which occur in any particular patch.

Whilst this may sound very positive, there is one major drawback: in today's landscapes, fragmentation is usually accompanied by habitat loss. Patchy populations cannot be viewed as fractions of a species which, like small experiments, can be allowed to take their chances in the race of natural selection. Increasingly often they are the only examples of the species which remain, at least at the regional level. Isolated populations are often so small that they have too few individuals to hold much genetic diversity, inbreeding may exaggerate the problem by causing deformities and reduced fitness (see, for example, Madsen *et al.*, 1996; Pusey and Wolf, 1996 and references therein) and chance events can wipe out entire populations. For butterflies, populations may fluctuate hugely from one season to the next according to weather conditions and it has been suggested that chance extinction is the most likely fate of any population small enough to suffer genetic decay (Ehrlich, 1983). It is in such systems of small habitat fragments, with small populations, that increased recruitment and recolonisation achieved through landscape ecological planning could play a crucial role in conservation management.

1.5 THE TRADITIONAL NORWEGIAN FARMING LANDSCAPE

This study focuses on an area of traditionally managed farmland in central southern Norway where mountain meadows are cut for hay, and subsequently used for late summer grazing. This management continues today in some areas: the hay is cut by hand, hung to dry on wooden racks placed out in the field and then stored in small barns. It is the removal of nutrients which leads to the unusually rich flora of these areas. It is, therefore, also of conservation importance that artificial fertilisers are not used. This traditional management has survived until today due to the poor accessibility of the mountain meadows and the uneven terrain which inhibits use of machinery. However, younger generations of farmers do not see this labour intensive farming as a desirable or economically viable lifestyle. Thus many mountain meadows are being abandoned.

In recent years, the Norwegian Ministry of the Environment has become interested in the conservation of "cultural landscape", both because of the high biodiversity of such systems and for social reasons. The latter are based on the idea that if people feel a connection to the land they are more likely to want to conserve it and will have more interest in nature in general. The aim is thus to maintain areas where a close bond has existed between human use of the land and natural processes in order to give a sense of cultural identity and historical background, which may make people more considerate both towards their own environment and that which they will leave for future generations (Tishler, 1982; Birks *et al.*, 1988).

Whatever the social arguments, as a biologist it is difficult not to desire the conservation of cultural landscapes, with their associated diversity of flora and fauna. However, their conservation is totally dependent on management (Norderhaug, 1987; Birks *et al.*, 1988; Austad *et al.*, 1991) and, with the expectations of modern society, this management may have to be for conservation rather than as working landscapes for self-sufficiency (Jennersten *et al.*, 1992; Bignal and McCracken, 1996).

Philosophical views on conservation are obviously influenced by personal experiences, preferences and convictions. Some would argue that abandonment of land and its reclamation by natural processes of succession is not something which should be a topic of concern for conservationists. Green (1990) points out, for example, that the most visited national park in the USA, Shenandoah, was orchards and pasture until 1936 but is now attractive second growth forest. It must also be pointed out that Norway is one of the few European countries which still has the opportunity to conserve areas which are little influenced by man. However, I will not take up the debate about the ethical grounds for conservation or the allocation of resources. The fact is that the contribution of traditional cultural landscapes to national biodiversity in Norway is disproportionately high compared with their area. It is for this reason, in combination with social arguments, that these anthropogenic ecosystems have become a major focus of attention and their maintenance a political goal (Ministry of Agriculture, 1995; Ministry of the Environment, 1997).

1.6 AIMS OF THIS STUDY

This study aims to evaluate the role of landscape ecology for butterfly conservation in a traditional farming landscape in Norway. Specifically:

* to investigate whether intensification and abandonment are important processes of landscape change in Norwegian agricultural systems;

* to test whether landscape elements act as barriers to butterfly movement and to identify causative factors responsible for any barrier effect;

* to determine whether the common behavioural responses of individuals to single landscape elements also apply at the scale of populations and entire landscapes;

* to assess how landscape ecology can be of use in the conservation of the Apollo, an endangered species of traditional farming landscapes;

* to explore the genetic implications of a patchy distribution of butterfly habitat.

An important aspect of the work will be an evaluation of three different approaches for studying the landscape ecology of butterflies; observation of the behaviour of individual butterflies, mark-release-recapture studies, and population genetics.

1.6.1 Chapter overview

Chapter 2 draws together national statistics to outline the changes which have occurred in Norwegian farming landscapes. The contrasting trends of intensification and abandonment are illustrated through analysis of aerial photographs from two sample landscapes. The potential consequences for biodiversity are discussed and the relevance of the landscape ecological approach is demonstrated.

Chapter 3 presents the results of experimental trials which examine whether landscape elements can present barriers to the movement of individual butterflies and, if so, which particular characteristics are responsible for the barrier effect.

Chapter 4 uses mark-release-recapture observations of Scarce Copper, together with simple spatial modelling, to examine whether the small scale behavioural phenomena recorded in Chapter 3 can be translated to a larger scale and thus be of significance at the population level.

Chapter 5 focuses on the Apollo, a butterfly of particular conservation interest. Mark-release-recapture methods are used to determine population details and movement patterns, and the conservation implications of meadow abandonment are discussed.

Chapter 6 evaluates a more indirect methodology for determining the influence of spatial distribution, namely population genetics. Enzyme electrophoresis is used to estimate gene flow between the Apollo populations studied in Chapter 5, and to examine the genetic make-up of widely separated populations.

Chapter 7 draws together the findings of the earlier chapters and assesses the overall relevance and importance of landscape ecology for butterfly conservation. The merits and disadvantages of the various methodologies are discussed and experiences from the different studies are used as examples of how, and how not (!) to bridge the gap between theory and application. Finally, I discuss the implications of landscape change for the butterflies of traditional Norwegian farmland.

CHAPTER 2

CHANGES IN NORWEGIAN AGRICULTURAL LANDSCAPES

This chapter sets the scene in Norway and provides the background for why a landscape ecological perspective is of value in studying the wildlife associated with agricultural landscapes. Official statistics are used to examine national trends in the development of the macrostructure of Norwegian agricultural landscapes during the last half century. In addition, aerial photographs from the 1950s and 1990s are analysed to quantify small-scale changes in two contrasting agricultural landscapes; one typical intensively cultivated area and one traditional mountain-farm landscape. The consequences of landscape change for biodiversity on farmland are discussed.

2.1 INTRODUCTION

2.1.1 European trends

The landscape which surrounds us is far from static. The influence of man has been profound and landscapes have been transformed from generation to generation as new practices and technologies became available (Asheim, 1976; Birks *et al.*, 1988; Berglund *et al.*, 1991). Since we invariably change our surroundings to suit our own ends, it is important that we understand all the ramifications that these changes have, for both ourselves and future generations. Whilst the effects of urbanisation are often obvious, changes in agricultural landscapes are not so immediately apparent, and in Norway there has been very little study of the landscape changes which have occurred.

Throughout Europe there have been two opposite trends of agricultural change over the last few decades (Hunziker, 1995; Ihse, 1995; Fry and Sarlöv-Herlin, 1997). Management of relatively flat, fertile land has been progressively intensified, with mechanisation leading to increased field sizes, removal of boundary vegetation, and increased application of agrochemicals. In contrast, traditional farming systems on marginal land, where possibilities for mechanisation are limited due to steep or inaccessible terrain, have been abandoned. These changes have been driven by market forces and agricultural policies which aimed to increase production and efficiency. In general, human labour as a production factor has been increasingly replaced by mechanical and technological advances. It is reasonable to assume that the same trends have also occurred in Norway.

2.1.2 Biodiversity on farmland

The species adapted to agricultural landscapes make a significant contribution to the Norwegian species pool. For example, approximately 3 % of Norwegian plant species and around 10 % of Norwegian birds are considered threatened due to changes in agricultural landscapes (Ministry of the Environment, 1997). Traditionally managed hay meadows are one of the most species rich habitat types to be found in Scandinavia. Records of 50-60 plant species per square metre are not uncommon (Norderhaug, 1987) and this diversity in primary production supports a complex web of species higher up the food chain, including a wealth of insects and birds (Ekstam *et al.*, 1988; Edelstam *et al.*, 1994; Edelstam *et al.*, 1995).

In more intensively cultivated regions, it is the small biotopes of remnant vegetation which provide hospitable habitats for wildlife (Opdam, 1990; Jennersten *et al.*, 1992). Of particular importance in Scandinavian agricultural landscapes are "åkerholmer" (Ihse, 1995); small rocky outcrops, generally glacial deposits, which lie in the midst of arable fields and which cannot be cultivated but are too large to remove. Such rocky outcrops, together with wood-lots, farm ponds etc. act as habitat islands for a wide range of species. Linear elements in the landscape, such as ditches, hedges, field margins, road verges etc. may act as a network linking the habitat patches together. For many species, these linear features may be sufficient as habitats in their own right (Maelfait and De Keer, 1990; Dover, 1991); however, their width, length, history and their degree of connection with other habitat patches will all influence the diversity of wildlife that they can support (Baudry, 1988; Hald *et al.*, 1988; Lagerlöf and Wallin, 1988). The spatial patterns of small biotopes are particularly prone to disruption following changes in agricultural practices.

2.1.3 Patterns of change

In recent years, the landscape ecological perspective of quantifying changes in habitat occurrence has been increasingly recognised (see, for example, Fry, 1991 and references therein). This perspective takes account, not only of the great relative importance of small biotopes on farmland, but also the spatial arrangement of these elements, including their connectivity with one another and with larger patches of habitat. As pointed out by Lipsky [, 1995 #2933, such details about the spatial composition of the landscape cannot be obtained from agricultural statistics. Analysis of aerial photographs, however, has previously been shown to provide a good indication of the microstructure of landscapes and thus their value for wildlife (Ihse and Lewan, 1986; Agger and Brandt, 1988; Ihse, 1988; Robertson *et al.*, 1990; Dunn *et al.*, 1991).

When considering Norwegian agricultural landscapes, it is important to be aware that large regional differences in physical and climatic constraints have resulted in agricultural landscapes which vary considerably in structure between counties. Thus whilst agriculture occupies 20 % of the land area of Østfold county in the south-east, it represents only about 2 % of the land area of mountainous Telemark county. Such large regional differences are likely to have affected the development of agriculture, not least due to a differentiated agricultural policy, designed in part to prevent the abandonment of farmland in marginal areas (Ministry of Agriculture, 1995). All of these factors will play a role in determining the structure and ecological functioning of the resulting agricultural landscapes.

2.2 METHODS

2.2.1 Official agricultural statistics

Norwegian Official Statistics (NOS) were examined to find data on all aspects of farming practice which could have influence on the landscape. Numerous volumes of Agricultural Statistics (Jordbrukstellingene), Population Censuses (Folketellingene) and Regional Statistics (Regionalstatistikk) were used (Statistisk Sentralbyrå, 1939-1997). Much of the information was from decennial censuses of all holdings with at least 0.5 hectares of agricultural land. Generally, comparable statistics were available from the 1939 census onwards (in some cases from 1949).

National statistics were used to examine overall trends in the country, but since regional variation could be large, two counties were chosen for more detailed analysis. The chosen counties were assumed to reflect two extremes of agricultural potential: one flat, fertile county, Østfold; and one mountainous county, Telemark, where extensive farming occurs on marginal land (Figure 2.1).

Even within counties, variation in topography creates a wide range of conditions for farming. Telemark, for example, is a very varied county, with high mountains, steep valleys, flat valley bottoms and coastal landscapes, encompassing a broad spectrum of agricultural possibilities. In order to compare two fairly homogenous landscapes which reflect contrasting trends of agricultural change, it is necessary to compare regions at the level of the 'kommune', i.e. municipality. This is the lowest administrative level for which agricultural statistics are available. Rakkestad municipality, which is the most important agricultural district in the county of Østfold, is representative of the intensive agricultural landscape. In Telemark county, Hjartdal municipality is a typical area where small-scale traditional farming landscapes still remain and is the municipality in which the majority of the butterfly field studies, discussed in later chapters, have taken place.

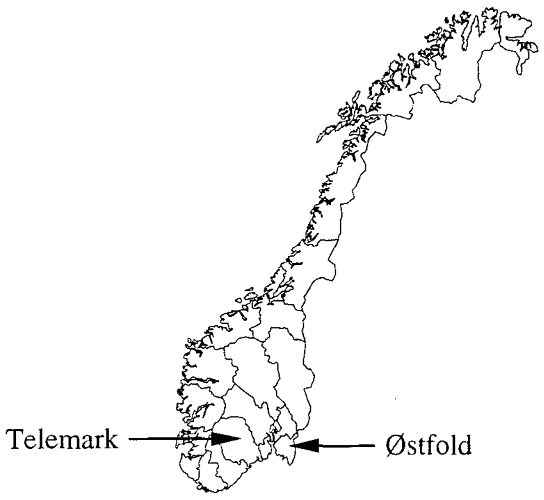

Figure 2.1: Map of Norway showing the location of Østfold and Telemark counties.

2.2.2 Aerial photographs

From each of the two municipalities, a sample landscape of approximately 10 km^2 was selected; each area including a large proportion of agricultural land, bounded by forest (Rakkestad: 59°20' N, 11°20' E; Hjartdal: 59°30' N, 8°40' E). Black and white aerial photographs were obtained for each area; from 1953 and 1992 for the Rakkestad sample landscape (scales 1:18000 and 1:13000 respectively), and from 1955 and 1993 for the Hjartdal landscape (both of scale 1:15000). Stereo pairs of photographs were studied using a P33 Planicomp analytical workstation (Zeiss), and analogue maps of land cover over the entire landscape were produced. Maps produced in 1976 (Norwegian economic series, scale 1:5000, Statens Kartverk) were used as a basis for recording landscape change, being back-dated and updated to represent the 1950s' and 1990s' situation respectively. The following 19 categories of land cover were recorded, grouped according to four classes of landscape element type:

Woodland: Coniferous trees; Deciduous trees; Mixed woodland; Scattered conifers; Scattered deciduous trees; Scattered mixed trees

Open: Intensively cultivated land; Pasture; Grassland[a]

Linear elements: River; Road; Track; Stone wall

Patches: Garden/ farmyard; Building; Rocky outcrop; Mire; Pond; Scree

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[a] The Grassland category included all areas of semi-natural vegetation, such as road verges, rough grassland along fence-lines etc.

Landscape change was quantified from the analogue land cover maps using a traverse method (Forman and Godron, 1986; Kienast, 1993). The method involved recording land use at 25 m intervals along 250 m long transects (i.e. 10 points regularly spaced along a 5 cm map distance). A stratified sample of transects was obtained by using each junction of the map grid reference system as the starting point for a transect. Thus, for each year, 131 transects were recorded from the Hjartdal landscape and 139 from Rakkestad, providing land cover data from, respectively, 1310 and 1390 sample points per year. Randomisation was achieved by drawing a transect of sample points onto a transparent disk and spinning the disk, with a grid reference junction as the central point. When the disk stopped revolving, land cover at each sample point was read directly from the map and recorded. These data were used to compare landscape diversity by means of the Shannon Index (e.g. Magurran, 1988), and to study changes in the frequency of different land cover types between years.

Since sample points were recorded at equal intervals along the transects, landscape ecological context could be quantified in terms of the number of interfaces of different types in each landscape. Thus, four types of interface were registered: woodland/open, open/linear element, open/patch and linear element/patch. For example, a transect record could read: 'open-open-linear element-open-open-open-open-woodland-woodland-woodland'; this transect would be recorded as having three interfaces.

Whilst random samples of points provide good comparative measures of the frequency of landscape elements, both between sites and between years, very uncommon small biotopes may be somewhat under-represented by the transect technique. This was considered to be the case for ponds in the intensively cultivated Rakkestad landscape, yet they are important elements providing very distinct habitat patches. The municipality's biodiversity action plan (Anon., 1995a) suggests a fifty percent decline in the number of ponds since the late 1980s, though empirical data on the subject is lacking. Ponds were therefore counted in Rakkestad and change assessed in terms of actual numbers present at the two snapshots in time. (In Hjartdal, ponds were uncommon in the landscape at both time periods, and therefore this analysis was not performed).

2.3 RESULTS

2.3.1 Official agricultural statistics

2.3.1.1 National trends

In spite of the physical constraints of climate and topography, the modernisation of agriculture which has occurred through Europe is also clearly discernible in Norway. During the past five decades, the replacement of traditional small farms by large, specialised farms has led to a decline of 61 % in the number of agricultural holdings in Norway, accompanied by an almost 70 % decline in labour input (see Figure 2.2).

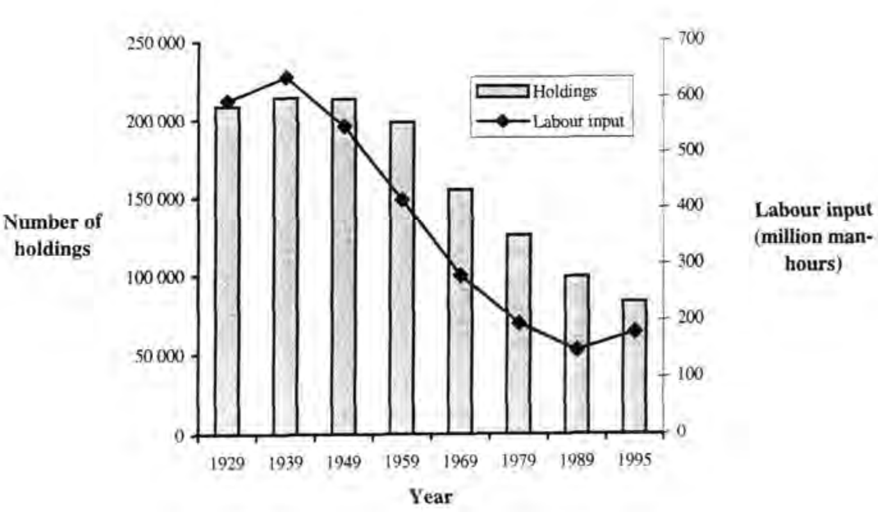


Figure 2.2: The decline in number of agricultural holdings and agricultural labour in Norway. (Data source: NOS Agricultural Statistics).

This process of specialisation has led to dramatic changes in the structure and organisation of agriculture. During the last five decades there has been a shift in the distribution of holdings between size classes, whereby the agricultural landscape became dominated by fewer, larger holdings (Figure 2.3).

In 1949, 90 % of holdings had less than 10 hectare of land, compared with 53 % in 1995. As for large farms, just 2 % of holdings had land of 20 hectares or more in 1949, compared with 16 % in 1995.

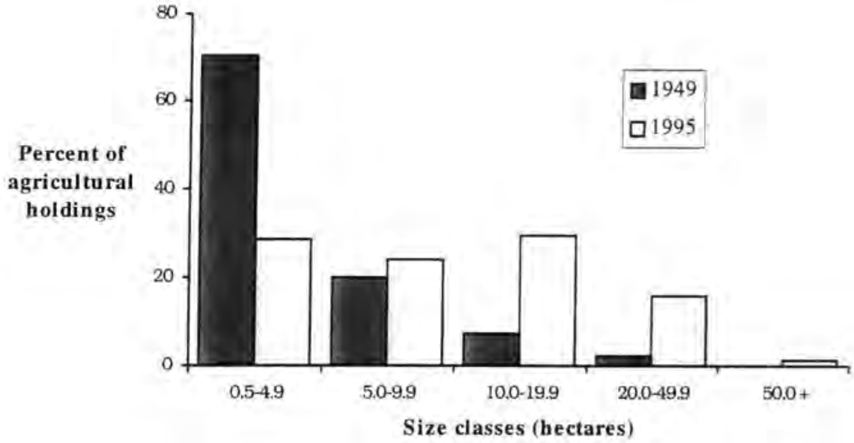


Figure 2.3: The size of agricultural holdings in 1949 and 1995. (Data source: NOS Agricultural Statistics - census of farms which have at least 0.5 hectares of agricultural land).

2.3.1.2 Regional variation

Whilst the trend towards increasing farm sizes has been nation-wide, there have been pronounced differences within the country. During the last five decades, holdings in Østfold have always been much larger than average, whilst those in Telemark have always been smaller, and the regional differences have increased with the years (Figure 2.4).

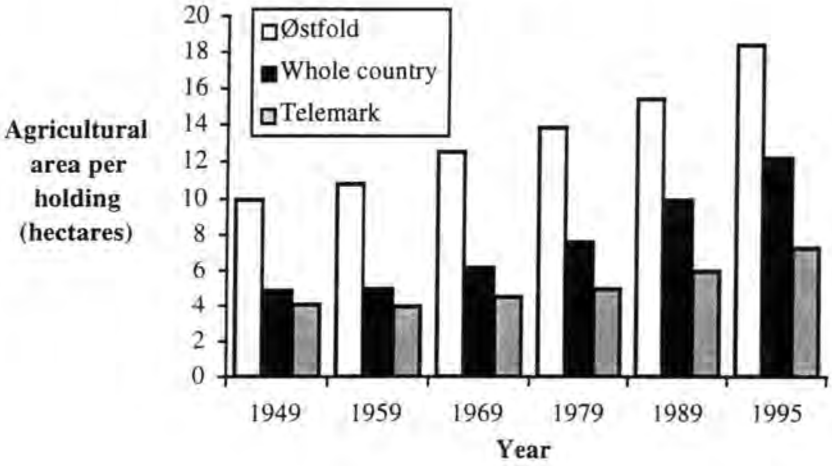


Figure 2.4: Area per agricultural holding in Norway, nationally and for Østfold and Telemark counties. (Data source: NOS Agricultural Statistics).

2.3.1.3 The farming population

The modernisation of farming has clearly affected the human population. Whilst the total area of agricultural land in 1995 was practically equal that in 1949, the percentage of the population required to work that land has declined, and yet yields have nevertheless increased. Again, there are clear regional differences (see Figure 2.5). The proportion of the population in Hjartdal municipality involved in farming is consistently higher than that in Rakkestad.

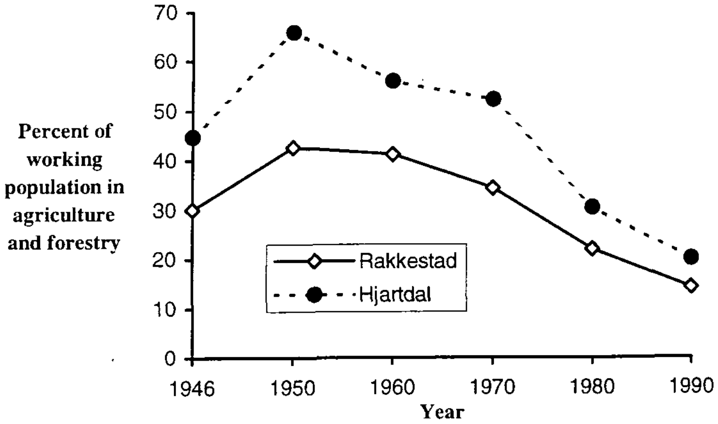


Figure 2.5: Percentage of the working population employed in agriculture and forestry in Rakkestad and Hjartdal municipalities. (Data source: NOS Population Census Statistics).

Differences in the age structure of the communities also indicate the processes of change (see Table 2.1). In Hjartdal, twice the proportion of agricultural workers are over pensionable age compared with Rakkestad, whilst young adults in the age group 25-29 form a much lower percentage of the agricultural population.

Table 2.1: Age structure of the agricultural populations of Rakkestad and Hjartdal municipalities. (Data source: NOS Population Census Statistics).

County	Percent of agricultural population per age class							
	16-19	20-24	25-29	30-39	40-49	50-59	60-66	67+
Rakkestad	4.1	3.3	7.6	18.0	24.6	18.0	16.0	8.4
Hjartdal	7.5	5.0	1.9	16.8	18.6	19.3	14.3	16.8

2.3.2 Agricultural land uses

The total area of agricultural land in Norway has declined by 8 % since 1939, mostly during the first decade of that period. However, the changes in land use are not evenly distributed: Agricultural area has actually increased by 2 % in the intensively cultivated Rakkestad, but declined by 36 % in Hjartdal.

These overall changes are accompanied by shifts in the relative proportions of different types of agricultural land use. In Rakkestad, the area of grain and oil seeds has trebled, whilst the area of permanent grassland and surface cultivated (unploughed) land has declined by 91 % and even cultivated meadow and pasture has declined by over 80 % (Figure 2.6). In Hjartdal, the area of permanent grassland and surface cultivated land has also declined, though to a relatively lesser degree (68 %). The area of cultivated meadow and pasture has remained approximately constant over the years, although representing an increasing relative importance as the total area of agricultural land in Hjartdal declined. Small biotopes such as hedgerows and rocky outcrops are not documented in agricultural censuses.

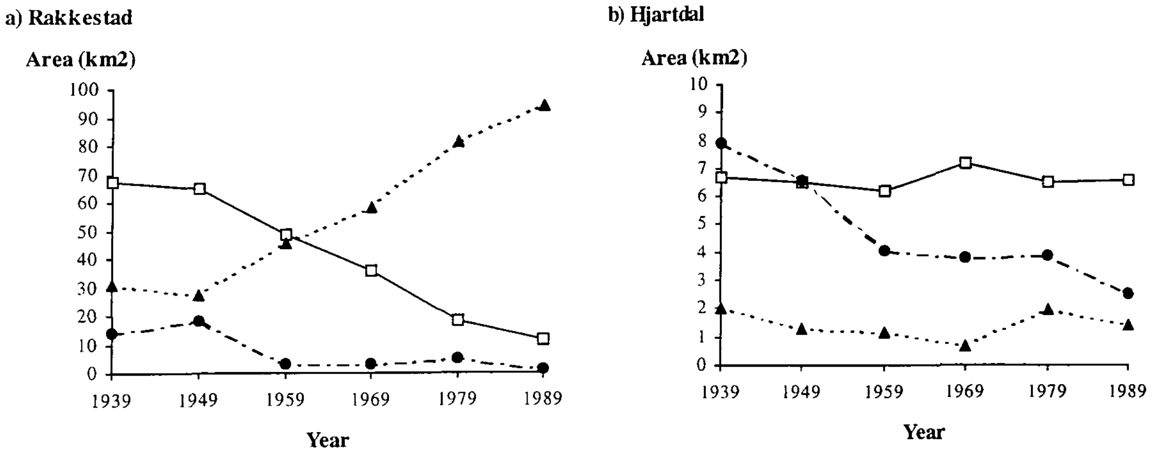


Figure 2.6: Changes in the area of grain and oil seeds (•••▲•••), cultivated meadows and pastures (—□—), and permanent grassland and surface cultivated land (▬•●•▬) in Rakkestad and Hjartdal municipalities between 1939 and 1989. (Data source: NOS Agricultural Statistics).

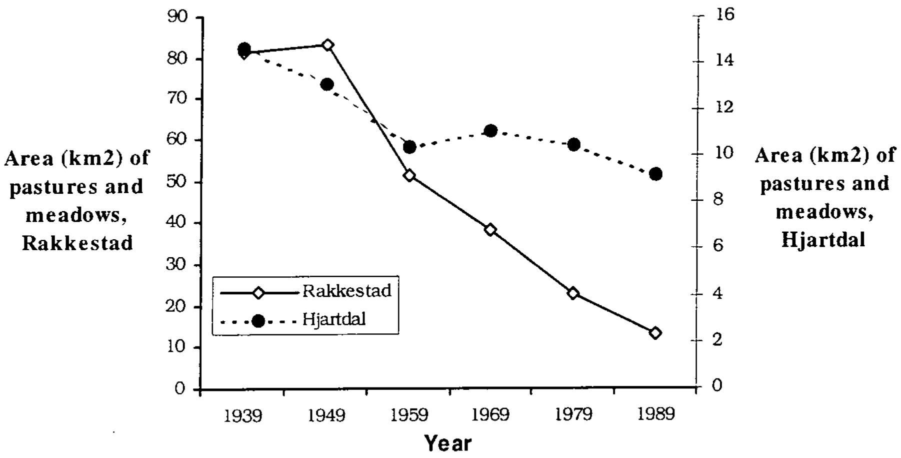


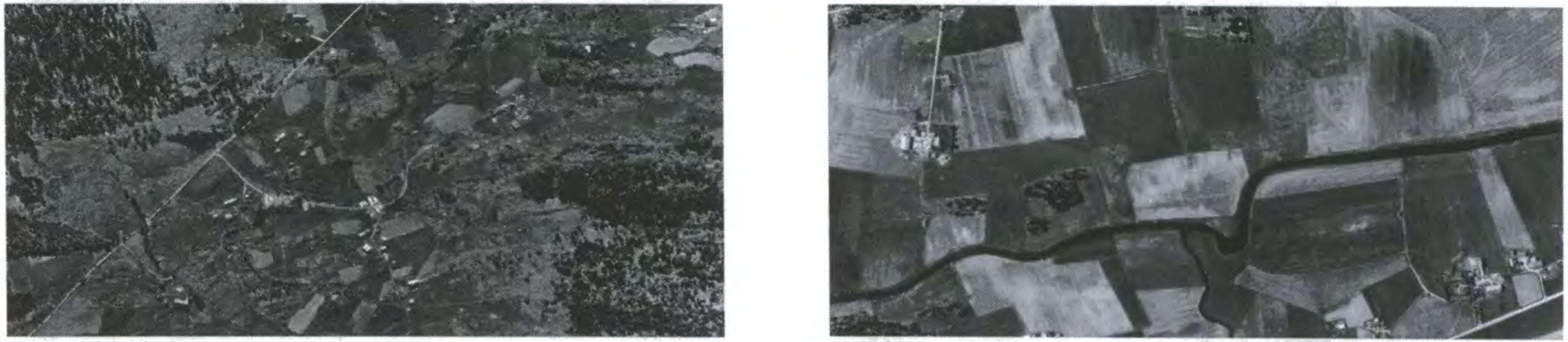
Figure 2.7: The changing area of pastures and mown meadows in Rakkestad and Hjartdal municipalities between 1939 and 1989. (Data source: NOS Agricultural Statistics).

2.3.3 Analysis of aerial photographs

The Rakkestad landscape was dominated by intensively cultivated land and coniferous forest, together comprising 77.2 % of all data points in 1953 and 86.7 % in 1992 (Table 2.2). These two vegetation types were also those which increased the most in terms of total land area, the greatest total increase being of intensively cultivated land (+7.1). In both years, the Hjartdal landscape was more heterogeneous than Rakkestad (Plate 1, p.34), with vegetation types more evenly represented. Four categories must be included to approach a similar percent frequency to the two dominant categories in the intensive system: in the 1950s, coniferous and mixed woodlands, grassland and pasture together comprised 72.8 %. By 1993, deciduous forest had replaced pasture as the fourth most common vegetation type, having undergone the largest area increase (+6.3 %) of any vegetation type in the extensive landscape and paralleling the increase in intensively cultivated land seen in Rakkestad. In contrast with Rakkestad, all categories of open, cultivated land declined in frequency in Hjartdal.

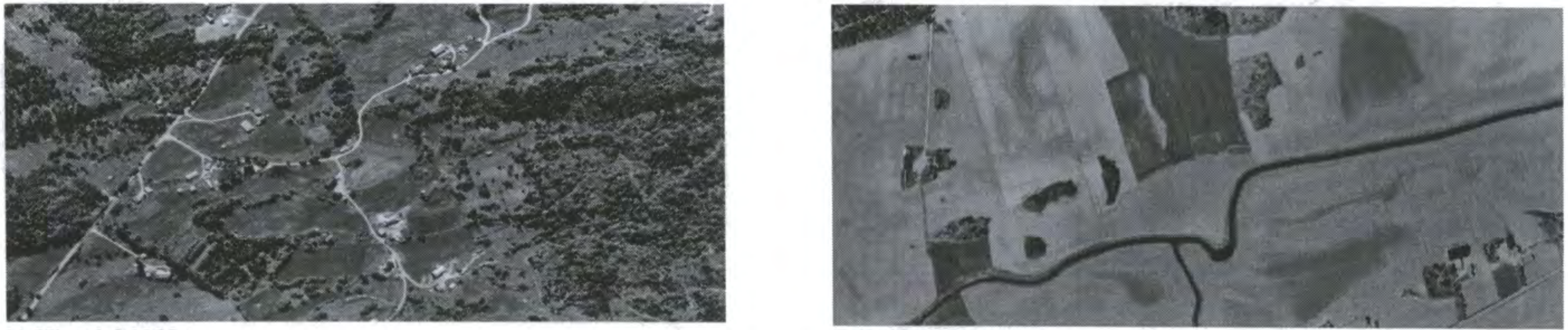
Table 2.2: Percentage distribution of sample points amongst vegetation types in 1950s and 1990s for landscapes in Rakkestad and Hjartdal municipalities. Changes in representation are indicated as percent increase or decline of the 1950s' frequency and as a percent of the total number of points sampled. Changes affecting 2 % or more of the total sample are highlighted in bold.

Vegetation type	**Rakkestad**				**Hjartdal**			
	1953	**1992**	**Percent Change**	**Change as % of total**	**1955**	**1993**	**Percent Change**	**Change as % of total**
Coniferous trees	26.3	28.8	+9.5	**+2.4**	22.5	26.6	+18.2	**+4.1**
Deciduous trees	1.1	0.7	-36.4	-0.4	6.5	12.7	+95.4	**+6.3**
Mixed woodland	1.6	0.1	-93.8	-1.5	14.8	15.5	+4.7	+0.7
Scattered conifers	0.1	1.4	+1300.0	+1.2	1.3	1.6	+23.1	+0.3
Scattered deciduous trees	0.0	0.0	0.0	0.0	3.4	1.6	-52.9	-1.8
Scattered mixed trees	0.0	0.0	0.0	0.0	5.6	2.7	-51.8	**-2.9**
Intensively cultivated land	50.9	57.9	+13.8	**+7.1**	4.4	4.3	-2.3	-0.1
Grassland	5.1	2.2	-56.9	**-2.9**	24.7	19.7	-20.2	**-5.0**
Pasture	6.8	0.8	-88.2	**-6.0**	10.8	8.2	-24.1	**-2.6**
Rivers and streams	1.8	1.4	-22.2	-0.4	0.8	0.8	0.0	0.0
Road	1.7	0.9	-47.1	-0.9	1.1	1.6	+45.5	+0.5
Track	0.4	0.1	-75.0	-0.3	0.4	0.3	-25.0	-0.1
Stone wall	0	0	0.0	0.0	1.2	0.8	-33.3	-0.4
Garden/ farmyard	1.7	3.3	+94.1	+1.6	0.5	2.5	+400.0	**+2.0**
Building	0.5	0.5	0.0	0.0	0.7	0.7	0.0	0.0
Rocky outcrops	1.1	1.9	+72.7	+0.8	0.6	0.0	-100.0	-0.6
Mire	0.7	0.1	-85.7	-0.6	0.0	0.0	0.0	0.0
Pond	0.2	0.1	-50.0	-0.1	0.0	0.0	0.0	0.0
Scree	0.0	0.0	0.0	0.0	0.6	0.2	-66.7	-0.4



a) Hjartdal 1955

c) Rakkestad 1953



b) Hjartdal 1993

d) Rakkestad 1992

Plate 1: Example portions from the aerial photographs of Hjartdal (a & b) and Rakkestad (c & d), from the 1950s and 1990s.

(Thanks to Fjellanger Wideroe for 1950s photographs, and FotoNor for the recent photographs).

As intensive cultivation became more common in Rakkestad, pasture declined to a corresponding degree (-6.0 %), showing the greatest total decrease of any vegetation type in Rakkestad. In Hjartdal, grasslands underwent the greatest total decrease (-5.0 %), although the relative decline in grasslands, i.e. in terms of percentage loss, was actually much greater in Rakkestad (-56.9 % compared with -20.2 % in Hjartdal). Due to the initial low representation of all categories other than coniferous woodland and intensive cultivation, the percent changes in Rakkestad are generally large (Table 2.2).

With the exception of rocky outcrops and scree, which are both uncommon patch elements and therefore somewhat unreliably represented by the sampling technique, the greatest percent declines in Hjartdal were of scattered deciduous and mixed trees. For both categories, the area present in 1955 was more than halved.

The more even spread of data points between the different land cover categories in Hjartdal evinces a greater diversity in the landscape. This was confirmed by the Shannon Index, which rated the Hjartdal landscape as significantly more diverse than Rakkestad at both snap-shots in time ($P < 0.005$ in both cases). There was virtually no change in diversity in Hjartdal from 1955 to 1993 (Shannon Index =2.232 and 2.227 respectively). However, there was a significant reduction in diversity ($P < 0.005$) in Rakkestad from 1953 to 1992 (Shannon Index = 1.510 and 1.229 respectively). The major cause of the reduction in diversity in Rakkestad was the increase in intensively cultivated land.

Counts of farm ponds in Rakkestad revealed dramatic declines, from 44 ponds in 1953 to just 3 ponds in 1992: a 93 % reduction.

As for landscape ecological context (Figure 2.8), the total number of interfaces between different types of landscape element declined in Rakkestad (-14.9 %) but increased in Hjartdal (+8.21 %). However, in Rakkestad there were some increases, the main one being the number of interfaces between woodland and linear elements, with increases also in the numbers of woodland/patch and open/patch interfaces. In Hjartdal, interfaces from woodland to patch elements and linear elements both increased, whilst open/ linear element interfaces declined.

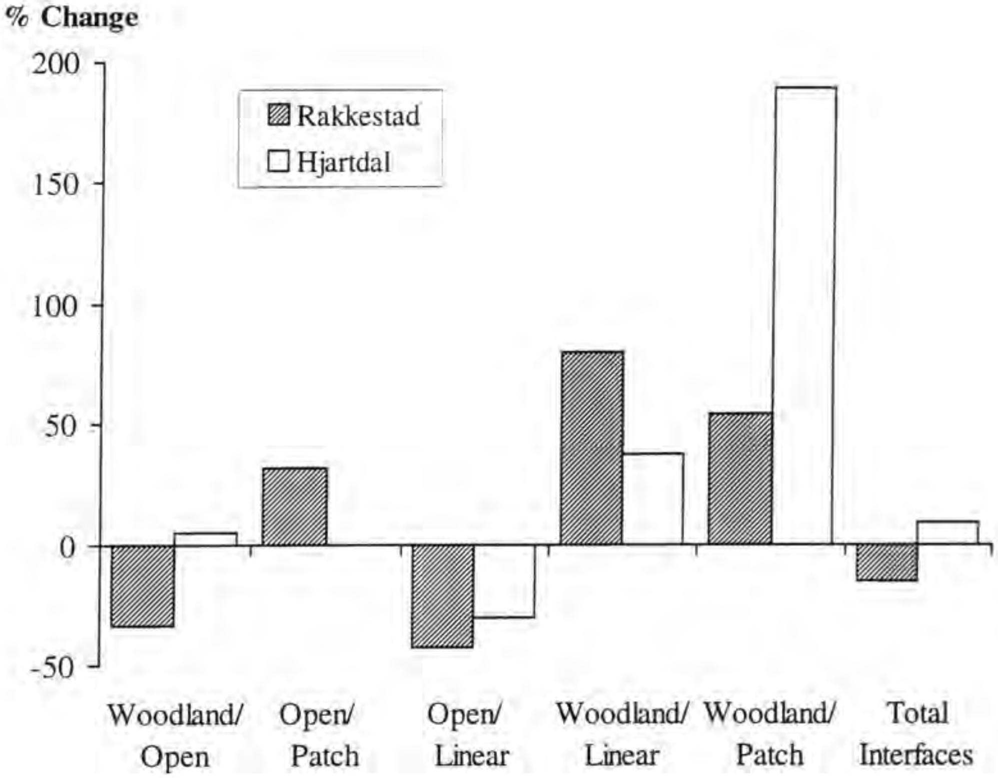


Figure 2.8: Percentage change in number of different types of landscape interface, from 1950s to 1990s, in Rakkestad and Hjartdal landscapes; *Woodland* includes both small and large woodland elements; *Open* includes grazing land and cultivated areas; *Patch elements* include rocky outcrops, ponds, mire, scree, gardens and buildings; *Linear elements* include roads, rivers and stone walls.

2.4 DISCUSSION

2.4.1 Agricultural statistics

At the national level, agricultural statistics reveal that changes in agriculture in Norway show similar trends to those in other European countries. The overall decrease in agricultural land has, though, been slightly less than the average for the European Community for which Green (1989) reports an 8 % decrease between 1965-83. Comparable figures for Norway show a 5 % decrease. This may be due to a desire to maintain as much as possible of the small proportion of Norway which is available for agricultural production; just 3 % compared with, for example, around 80 % in the United Kingdom (Green, 1989) and 65 % in Denmark (Agger and Brandt, 1988).

Legal restrictions on the sale of farmland in Norway, allowing only a small proportion of all farms ever to reach the open market, have been used to hinder loss of agricultural land.

The general trends in farm development have followed the same patterns as in other countries, including increased mechanisation, declines in labour input, reductions in numbers of holdings and increasing size of individual farms (see for example, Brusewitz and Emmelin, 1985; McInerney, 1994; Ihse, 1995). However, although farm sizes have increased, the average farm size in Norway (1996) is still small (12.7 hectares), compared with other countries, such as the UK (69 ha), France (25 ha) or Germany (15 ha) (Green, 1989). The smaller farm sizes are attributable partly to topography, and partly to the strict regulations on sale of agricultural land. In Norway, changes in ownership of agricultural holdings are predominantly through inheritance, and regulations exist to ensure that land-owners do in fact occupy and farm the land that they possess.

Whilst overall statistics are suitable for coarse comparisons between nations, the effects on landscapes are governed by more local-scale changes. At the level of the county and municipality, statistics indicated large regional differences, as has been described from, for example, Sweden (Ihse, 1995), France (Poudevigne and Alard, 1997), Denmark (Agger and Brandt, 1988) and the UK (Fuller *et al.*, 1994). On the plains of Østfold, there have never been many obstacles to mechanisation and the already intensively managed land, dominated to a large degree by cereal crops, became even more intensively cultivated. In the mountainous region of Telemark, agriculture followed the same trend of increased farm sizes but the possibilities for expansion were restricted not only by regulation but also by the topography and soils.

Agricultural statistics give good macro-scale information about the overall area of different types of agricultural land within the sample municipalities, and information about farm sizes gives some indication of the scale of the landscapes. However, agricultural statistics do not record the spatial arrangement of different land uses or their context in relation to one another. Most importantly, they tell nothing about the non-economical elements in the landscape; the rocky outcrops, field boundaries, road verges etc. The analysis of aerial photographs solved this problem, resulting in a clearer overall picture of landscape pattern.

2.4.2 Structural change

Visually, the most striking change in the intensively cultivated Rakkestad landscape was the disappearance of linear elements from open fields (Plate 1, p.34) and this was reflected in the analysis by the reduction of open/ linear element interfaces. This is typical of changes in intensively cultivated landscapes (see, for example, the open plain landscape discussed by Ihse, 1995). In addition to declines in the frequency of roads, tracks and streams, the decline in grassland also indicates reduction of linear features, since grassland elements in this landscape comprised mainly road-side verges, ditch banks and fence-lines. The increase in interfaces between linear elements and woodland in Rakkestad is mainly due to the siting of new roads and power-lines through forest.

The patch elements responsible for the increased frequency of open/patch interfaces in Rakkestad would appear to be rocky outcrops and gardens/ yards. An increased frequency of rocky outcrops appeared anti-intuitive initially, considering the improved technological possibilities for removing remnant vegetation, and compared with southern Sweden, where approximately 50 % of habitat islands in intensive agricultural areas were removed between 1940 and 1970 (Robertson *et al.*, 1990). However, examination of the location of new rocky outcrops revealed two reasons for their increase: firstly, during the conversion of rough pasture to intensively cultivated land, some small rocky areas within pasture in 1953, which were suitable for grazing, could not be cultivated when surrounding land was ploughed and thus remained as rocky outcrops in 1992. Secondly, boundaries would traditionally have been established along natural landmarks such as ditches and ridges which were difficult to cultivate, and stones cleared from the fields were left in piles in the field margins. Some of the present-day rocky outcrops therefore represent the last traces of old field boundaries.

The most striking structural changes in Hjartdal (Plate 1, p.34) were the increase in wooded elements, illustrating a process of abandonment (comparable with the changes in the semi-open, mixed landscape of Ihse's (1995) study). Areas of scattered trees where animals would previously have grazed have now become dense forest and lines of trees have grown up along walls and fences. Although agricultural statistics did record the loss of meadows and pastures in the region, they did not include any details of the processes involved or the spatial dynamics of the transition from meadow to woodland. In this respect, the transect sampling technique provided a finer resolution.

The Shannon Index values confirmed the visual impression of a higher diversity in Hjartdal than Rakkestad for both years. In Rakkestad, the simplification of the landscape over time was due to the increasing dominance of intensively cultivated land. In Hjartdal, on the other hand, the Shannon Index was very similar for 1955 and 1993, the semblance of increased diversity being due to a change in the land cover types contributing to diversity, with trees having a much stronger visual impact than the grassland they replaced.

2.4.3 Heterogeneity

Transect sampling of the two study sites revealed that the Rakkestad landscape was always the most homogeneous of the two, reflecting its early agricultural development. Being so suitable for intensification, the area was altered very quickly following the advent of machinery and by the 1950s, when the first aerial photographs were available, many of the changes had already occurred.

Changes in numbers of interfaces between different landscape element types indicated that, whilst the landscape in Rakkestad became more homogeneous and large-scale over the last four decades, Hjartdal became more heterogeneous and small-scale. This indicates a process of landscape polarisation (sensu McInerney, 1994), resulting in a two state system of large-scale intensively managed, homogenous open landscapes at one extreme, and small-scale, heterogeneous wooded agricultural landscapes at the other. This process is not revealed in national agricultural statistics but becomes more apparent at the county level and is further elucidated in studies at the landscape scale. Landscape polarisation is a consequence of intensification and abandonment, which exaggerate naturally occurring gradients of heterogeneity and scale caused by differences in traditional agricultural practices and environmental factors (topography, soil, climate etc.).

Interestingly, the abandonment of cultivation in the extensive system has been accompanied by an increase in the number of dwellings (reflected in the quadrupling of gardens/yards). In a study of aesthetic assessment of abandoned agricultural land in Switzerland, Hunziker (1995) documented a slight preference for partially reafforested landscapes, due to their high diversity. With the improved road system in the Hjartdal area, it is now possible to live in this aesthetically pleasing landscape whilst working in a nearby town. The irony is that, without management, the landscape will lose its diverse character, becoming more homogeneous as vegetation succession fills in the gaps in the present network of trees. However, many commuter inhabitants are also part-time farmers and the management that they perform may be sufficient to maintain the character, and even some of the species richness, of the traditional landscape.

2.4.4 Driving forces of change

The high proportion of the population involved in farming after the second world war was triggered by the government's wish that Norway should become self-sufficient in food production, following restrictions on food imports during the war. The higher percentage of the population involved in farming in Hjartdal compared with Rakkestad, is due partly to the more labour-demanding nature of Hjartdal's small-scale farming and partly to the higher availability of alternative employment in the more urbanised south-east of the country. In Hjartdal, the high proportion of old people represent the tail end of a generation change, in which younger people have rejected the hard-labour and low economic returns of small-scale farming. Deffontaines et al. (1995) point out that old people will often manage the land, even if there is little financial reward, simply because they "hate derelict land". As reported elsewhere (Poudevigne and Alard, 1997), it is often the older people who still farm in the traditional manner and hence traditional farming practises are, quite literally, dying out.

The changes in Rakkestad from the 1950s to the 1990s, with removal of ponds, ditches and boundary vegetation, are clearly related to agricultural policy. The 1955 Land Act (Jordlova), for example, restricted the sub-division of farms and the 'misuse' of agricultural land. The act mentions that cultivated and tillable land must not be used for purposes which are not directed towards agricultural production. The reduction in aquatic patch habitats can be connected with a law of 1957 (Brønnloven), which made land-owners responsible for safety in connection with ponds and wells. In 1971, subsidies became available for grading the land (bakkeplanering) to enable more effective use of machinery. This involved filling in ditches and levelling ridges which earlier formed natural field boundaries (see Erikstad, 1992 for a full discussion of this topic). The Land Consolidation Act of 21st December 1979 contributed further to the process of boundary removal. Agricultural policy and legislation, supported by economic incentives, are obviously powerful tools in shaping the evolution of landscapes.

2.4.5 Implications for biodiversity

The sample landscapes show patterns of structural change developing in opposite directions, with an overall increase in cultivated land in Rakkestad and a decrease in Hjartdal. More subtle are the qualitative changes, for although the total amount of agricultural land has increased slightly in the intensive landscape, species rich habitats such as pasture and meadows (Edelstam *et al.*, 1994; Edelstam *et al.*, 1995) have been replaced by species poor ones, particularly cereal monocultures (Andreasen *et al.*, 1996). In the extensive system, most concern surrounds the loss of the highly species-rich hay meadows (Norderhaug, 1996). These changes are reflected at the national level, with the area of permanent grassland having been more than halved during the last five decades, posing a significant threat to biodiversity. This trend is all the more worrying since similar changes have been documented throughout Western Europe (Agger and Brandt, 1988; Garcia, 1992). In Sweden, Ingelög (1988) found that of the plant species identified as being threatened or vulnerable, almost 75 % belonged to the agricultural landscape. At the farm level, Brusewitz and Emmelin (1985) describe how 67 out of a total of 321 species of higher plants disappeared following landscape changes caused by intensification.

It is generally very difficult to document changes in biodiversity following landscape changes since historic data for comparison are often lacking. In Norway, the Directorate for Nature Management (DN) points out that even for invertebrates, the largest group in the Norwegian species pool, there are few data available on population trends (Anon., 1992). However, DN identifies agricultural intensification and landscape change as a possible cause behind the significant declines seen in several species (Anon., 1992; Anon., 1994; Ministry of the Environment, 1997). When habitat requirements are seen in the light of documented landscape change, little further evidence is needed to confirm cause and effect relationships in some cases. For example, the smooth newt (*Triturus vulgaris*) and crested newt (*T. cristatus*), both designated the status vulnerable in Norway (Anon., 1992), have been recorded from ten and three ponds respectively in Rakkestad municipality (Anon., 1995a). Clearly the 93 % decrease in number of farm ponds in the Rakkestad study area reflects a pattern of change which must have greatly contributed to the decline of these two species. Similarly, 18 out of a total of 44 species of dragonflies (Odonata), also dependent on aquatic habitat, are now recorded under various red data list categories. In addition to the actual loss of pond habitat, the increased distance between ponds and the loss of areas of scrub and rough grassland in the interstitial land may hinder recruitment to and recolonisation of otherwise suitable habitat (Laan and Verboom, 1990; Vos, 1993; Boothby *et al.*, 1994).

Additional examples of correlations with changes in agricultural landscapes are the reduced abundances of skylark (*Alauda arvensis*) and swallow (*Hirundo rustica*) (Ministry of the Environment, 1997), and the drastic decline of the corncrake (*Crex crex*) (Øyjordet, 1990). Although there has been little research on butterflies in Norwegian agricultural landscapes, those species found in the intensive agricultural areas inhabit the remnant vegetation of field margins and rocky outcrops and the reduction in these areas is generally recognised as having lead to a decline in butterflies (Anon., 1995a).

In addition to the overall losses of habitat, the patches which remain have become increasingly fragmented. In Rakkestad, the network of field boundaries has been much reduced such that some boundaries are now no longer connected with others or with patches of natural vegetation. This reduces the possibilities for plants and animals to colonise (Dunn *et al.*, 1991) and results in small populations which are more likely to suffer chance extinctions (MacArthur and Wilson, 1967). Indeed, the agricultural land may act as a sink, whereby plants and animals attempt to disperse, only to die in the alien environment of the arable fields before reaching another suitable habitat (Jennersten *et al.*, 1992).

In Hjartdal, abandonment of land and the accompanying land cover changes documented here, have resulted in a more fragmented meadow system. In particular the growth of trees along walls and fences has created potential barriers between meadows. Increased landscape resistance between suitable habitat patches can hinder the movement of both plants and animals (Bowers, 1985; Marshall and Hopkins, 1990). Moreover, Norderhaug *et al.*(1996), in a study of meadow plant species in the Hjartdal area, emphasised the negative population consequences of habitat isolation but the study also found that the verges of small roads had very high species richness and may act as corridors for meadow plant species. Verges of the main road were not so species rich and the authors point to the fact that the management (mowing) of verges along small roads was traditionally similar to that in the meadows. Although I recorded a 40 % increase in roads in Hjartdal, small roads (tracks) declined by 20 %, with many of the tracks in 1955 having been converted to roads by 1993. In addition, then, to the increased inter-meadow distances in Hjartdal and the appearance of barriers of trees between meadows, the widening and surfacing of roads may reduce their role as movement corridors through the landscape.

2.4.6 Future prospects

In recognition of the role of small biotopes, there has recently been an increasing focus on the environmental benefits of field boundaries and patches of wild vegetation in intensively cultivated areas. In England, for example, conservation headlands have been shown to have positive effects for flora, invertebrates, birds and small mammals (Game Conservancy, 1993). In addition to conservation value, field boundaries are also widely recognised as having economical benefits, such as increasing populations of crop pest enemies (Wratten, 1988; Thomas *et al.*, 1991; Helenius, 1994). Agricultural policy is therefore now moving towards encouraging maintenance and replacement of field boundaries and habitat patches for wildlife (OECD, 1995). In a study by Kienast (1993), recent photographs showed that the processes of intensification had been reversed, a trend attributed to environmental improvements encouraged by Swiss agricultural policy.

As pointed out by Kienast (1993), there lies a danger in looking only at index values describing, for example, landscape heterogeneity. In their study, heterogeneity had increased in recent times, following a period of very low values. However, the elements contributing to the increase were of lower quality than those originally removed. A similar tendency was documented in a Swedish study by Ihse (1995), where a number of fast structural changes in the landscape, although qualifying for subsidies, had little benefit for biodiversity. It is likely that deterioration of habitat quality has also occurred in the Rakkestad landscape. For example, boundaries are exposed to herbicides, pesticides and high levels of nutrients from spray drift and run-off from fields; ditches may become silted due to erosion from ploughed land; and the isolation of habitat islands from sources of colonisers may, in itself, contribute to declining quality. It is thus clear that agricultural policies designed to improve agricultural landscapes must take account of three factors: total area, spatial distribution and quality.

Few would argue that the landscape changes in Rakkestad have had negative impacts on biodiversity; however, the effects of the changes in Hjartdal are more open to discussion. For the rarer plant species surviving in old hay meadows, traditional management appears to be the key to survival (Norderhaug, 1996). However, in some cases local biodiversity may actually be increased by a slight degree of abandonment. Erhardt (1985), for example, documents higher diversity of butterflies in stages of early abandonment. Other authors point to the advantages for wildlife of shrubs and trees on farmland (Lack, 1988; Burel and Baudry, 1995). There is no doubt that long-term abandonment will lead to severe reductions in biodiversity, particularly at the national level, however discussion is needed to determine the priorities for areas such as Hjartdal. The goal of traditional management over large areas, in a type of 'museum landscape', may be unrealistic (Jennersten *et al.*, 1992; Bignal and McCracken, 1996). However, the encouragement of part-time farming, where some areas are maintained traditionally simply through the interest and enthusiasm of landowners and volunteers, may be a more dynamic, working solution to preserving these species-rich and internationally important agricultural landscapes.

CHAPTER 3

LANDSCAPE ELEMENTS AND THE BEHAVIOUR OF INDIVIDUALS

A deciding factor determining the patterns of butterfly movement through landscapes is the reaction of individual butterflies to the landscape elements with which they are confronted. This applies particularly to the elements at the boundaries of a habitat patch. Even small differences in the resistance of different landscape elements may, by affecting movement patterns, have important implications for butterfly distribution and population dynamics.

This chapter describes a series of experiments that examine the response of individual butterflies to various elements in the landscape. First, a preliminary study, which is reported in my undergraduate thesis (Robson, 1992), is briefly outlined to set the scene. This is followed by a more controlled experiment to quantify the effect of boundary height on butterfly flight patterns. Finally the scope is broadened by looking experimentally at different types of boundary on farmland and their roles in a landscape ecological perspective.

3.1 THE RESPONSE OF INDIVIDUALS TO FIELD BOUNDARIES

3.1.1 Introduction - Preliminary study

A preliminary study in 1991 provided the observational data required for formulation of hypotheses (Robson, 1992). It will be referred to briefly here (with some new analyses) since it represents a starting point for this study.

The study site was an old hay meadow at Sverveli (59°30' N, 8°30' E), on the border between Hjartdal and Seljord municipalities in Telemark county, southern Norway. The site is adjacent to the area used for quantifying landscape change (Chapter 2). The area is mountainous and Sverveli meadow, at about 450m a.s.l., is one of the highest and more inaccessible of the remaining meadows of this valley system. It is well known that abandonment of anthropogenic landscapes tends to progress inwards from areas farthest from roads and farms (Foster, 1992; Deffontaines *et al.*, 1995; Ihse, 1995) and this area was thus a good candidate for studying the effects of agricultural dereliction on butterflies.

Archaeological finds suggest that farming in this area dates from the 6th Century (Blomquist and Puschmann, 1993) and the floral composition of many of the hay meadows reflects a long continuity of management (Norderhaug, 1996). However, since the 1950s abandonment has accelerated (as shown in Chapter 2) and many remnant hay meadows are now held open by grazing of moose, deer, occasional grazing by young cattle and sheep, and sporadic cutting (Blomquist and Puschmann, 1993; Norderhaug, 1996).

The processes of succession were evident in Sverveli meadow, with scrub, particularly Aspen (*Populus tremula*) and Birch (*Betula pubescens*), beginning to invade the meadow edges (Plate 2, p.46). The meadow is 1.5-2 ha in area, divided in half by a wide strip of trees, scrub and rocks. The southern half of the meadow (Plate 3, p.46) is about 4 m lower than the northern half, damper and has a less species rich flora. The meadow is irregular in shape and bounds onto five different types of adjacent habitat: deciduous wood, coniferous wood, clear-felled land, mire and meadow.

3.1.2 Method

3.1.2.1 Recording interactions at field boundaries

To investigate the effects of field boundary structure on butterfly mobility, each boundary was divided into sections five metres long and extending three metres into the meadow from the boundary line. The flight path of butterflies in each recording section was recorded for one minute after an individual had entered the section. The direction of each flight path, in relation to the boundary, was recorded by arrows and the map location recorded to the nearest metre. This process was repeated throughout the day on eighteen suitable days, between late June and early August 1991. Recordings were not made when the mean air temperature was less than 17 °C, during strong wind or during precipitation.

Three categories of flight path were recognised: entering the meadow; leaving the meadow; and 'rebounds'. The latter included cases where a butterfly approached the boundary but turned back into the meadow rather than crossing, or entered the recording section moving parallel to the boundary and then turned into the open meadow.

As a control, butterfly flight behaviour was also recorded, following the same protocol, along a line transect through open meadow.

Plate 2: View of the northern part of Sverveli Meadow ('Upper Main'). Scrub encroachment, particularly by Aspen (*Populus tremula*) and Birch (*Betula pubescens*), was common at meadow edges.

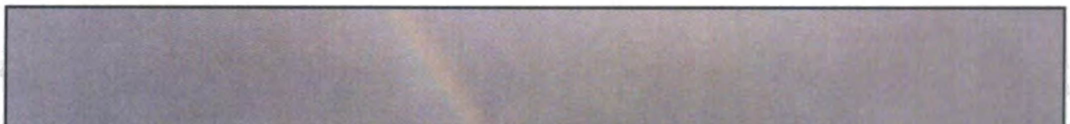


Plate 3: Overview of the southern edge of Sverveli meadow ('Lower Main'). Clear-fell areas can be seen to the South.

3.1.2.2 Butterfly identification

The reliability of species identification of flying butterflies varied considerably according to species. Whilst the sexually dimorphic Scarce Copper could be easily identified as male or female, some of the fritillaries and the various blue lycaenids could not be distinguished to species level whilst in flight. Since the method relied on the observation of undisturbed butterflies, some butterflies were therefore recorded under species groups. In addition, where species did not occur in sufficient abundance to allow for species comparisons, grouping of species allowed at least for comparison of functional groups of species. The following categories were used in the analysis:

Scarce Copper (*Lycaena virgaureae*) (data for males and females were combined)

Blues: Geranium Argus (*Eumedonia eumedon*), Common Blue (*Polyommatus icarus*), Mazarine Blue (*Cyaniris semiargus*), Idas Blue (*Lycaeides idas*) and Silver-Studded Blue (*Plebejus argus*)

Arran Brown (*Erebia ligea*)

Fritillaries: Pearl-Bordered Fritillary (*Clossiana euphrosyne*), Small Pearl-Bordered Fritillary (*Clossiana selene*), Lesser Marbled Fritillary (*Brenthis ino*), High Brown Fritillary (*Fabriciana adippe*), Dark Green Fritillary (*Mesoacidalia aglaja*).

Information about additional species was recorded in the field but numbers of observations were very small and were not included in the analysis. This applied to: Small Heath (*Coenonympha pamphilus*), Small Tortoiseshell (*Aglais urticae*), Orange Tip (*Anthocharis cardamines*), Comma (*Polygonia c-album*), Wood White (*Leptidea sinapis*) and Brimstone (*Gonepteryx rhamni*).

3.1.2.3 Investigating the effects of shade

There was a section of meadow boundary where a five metre wide strip of grassland, 30 m in length, bisected the adjacent forest and linked the main study site to a neighbouring meadow. Numbers of butterflies moving along this strip of land, or approaching it then turning back into the meadow, were recorded, both when the strip was in sun and when it was shaded. All observations were made from the same point, where the grassy strip joined the boundary of the main meadow.

An experiment was conducted using Scarce Copper and Arran Brown butterflies, to look more closely at species differences in response to shade. Butterflies were netted and released at a boundary between sun and shade. The direction of flight paths on release was recorded.

3.1.3 Results

3.1.3.1 Interactions at field boundaries

Butterfly responses to field boundaries were highly dependent on boundary structure (Figure 3.1).

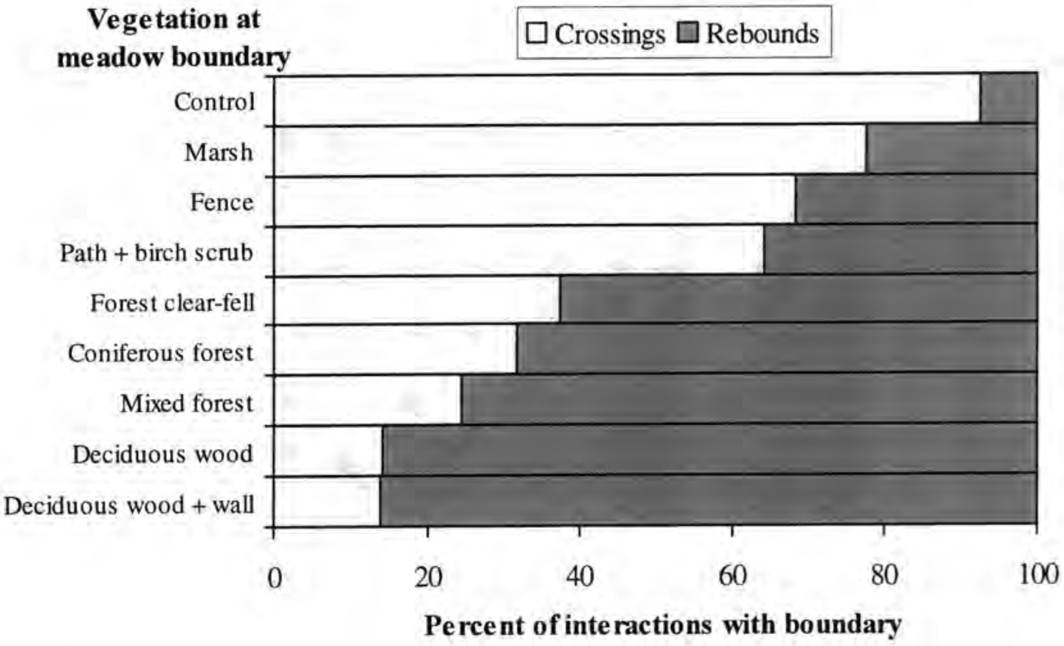


Figure 3.1: The percentage of butterflies crossing the different field margins of the Sverveli meadow system; n = 1445, all species pooled (see text for species details).

Of all crossings observed over natural boundaries, a significantly higher proportion (91%) crossed through gaps than crossed by flying over the boundary vegetation (total sample size, including all species = 1445 butterflies; $P < 0.05$).

The number of butterflies crossing each boundary, as a proportion of the total number of approaches to the boundary, was positively correlated with the percentage of the boundary length where vegetation was less than 1.5 m tall (linear regression; $r^2 = 0.736$; $P < 0.001$). The association was significant for all species groups, i.e. Blues ($r^2 = 0.859$; $P < 0.001$), Fritillaries ($r^2 = 0.841$; $P < 0.001$), Scarce Copper ($r^2 = 0.828$; $P < 0.001$) and Arran Brown ($r^2 = 0.601$, P < 0.02). However, there appeared to be some variation in the sensitivity of the different species groups to vegetation height (Figure 3.2).

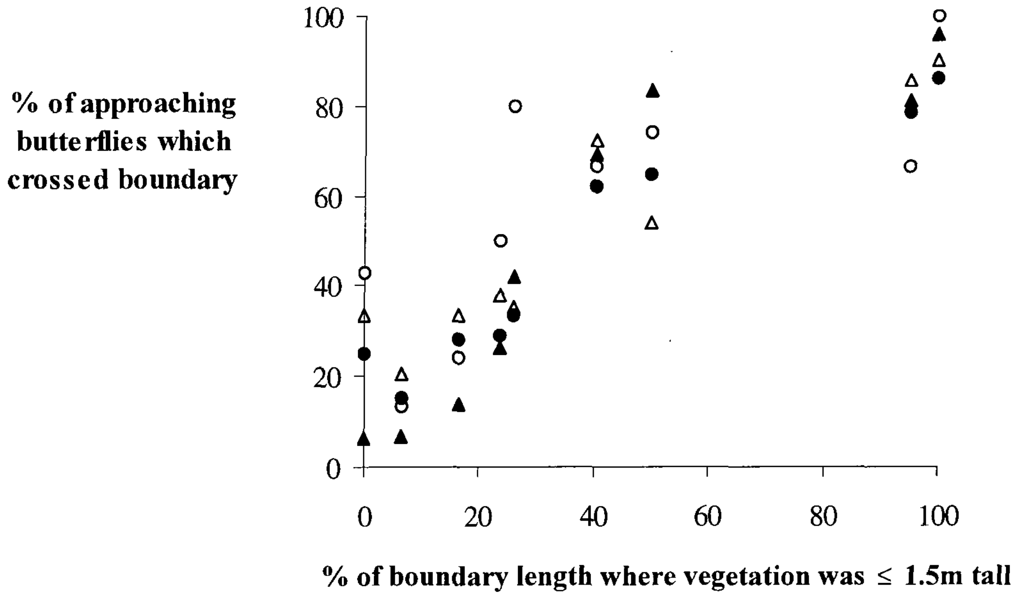


Figure 3.2: The relationship between the percentage of butterflies crossing a meadow boundary and the percentage of boundary length where vegetation was ≤ 1.5 m tall.
▲ Scarce Copper (n =534); ● Blues (n = 489); ○ Arran Brown (n = 156); △ Fritillaries (n = 171).

In order to analyse behavioural differences between species, the data were pooled into two groups: boundaries with less than 30 % of the boundary length comprising low vegetation and boundaries with more than 30 % low vegetation. The results of G-test comparisons between species are shown in Table 3.1. Arran Brown, Fritillaries and Blues showed similar responses to boundaries with less than 30 % low vegetation; around 30 % of individuals which approached the boundary left the meadow. A significantly lower proportion of Scarce Copper left the meadow at these boundaries (Table 3.1). At open boundaries, i.e. with more than 30% low vegetation, proportions leaving were highest for Scarce Copper and Arran Brown (almost 85 %) and significantly lower for Blues (67 %). Fritillaries did not differ significantly from Blues or Arran Brown but crossed open boundaries significantly less frequently than Scarce Copper.

There was no consistent relationship and no significant correlation between the number of butterflies crossing through individual gaps in the boundary vegetation and gap size ($r^2 = 0.005$; $P > 0.10$).

Table 3.1: G-values resulting from pairwise comparisons of the different species categories. Between-species comparisons were made of the numbers of approaching butterflies crossing boundaries with less than and more than 30 % low vegetation (≤ 1.5 m tall). G-values indicating statistically significant differences are shown in bold[a].

	Arran Brown		**Fritillaries**		**Blues**	
% low vegetation:	< 30 %	> 30 %	< 30 %	> 30 %	< 30 %	> 30 %
Scarce Copper	**** 6.660**	0.072	*** 6.218**	*** 5.572**	*** 5.503**	***** 14.572**
Arran Brown			0.003	2.664	0.508	*** 5.140**
Fritillaries					0.414	0.094

[a] Significance for *df* = 1: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

3.1.3.2 The effect of shade

The use of a strip of grassland as a movement corridor between two meadows was dependent on whether the strip was in sunshine or shade ($G = 92.54$; $df = 1$; $P < 0.001$). (Figure 3.3).

Releasing captured butterflies, of two species, on a sun/shade boundary revealed species differences in the strength of the response to shade. Both species avoided shade but the response was stronger for Scarce Copper ($G = 73.66$; $df = 2$; $P < 0.001$) than for Arran Brown ($G = 13.62$; $df = 2$; $P < 0.01$).

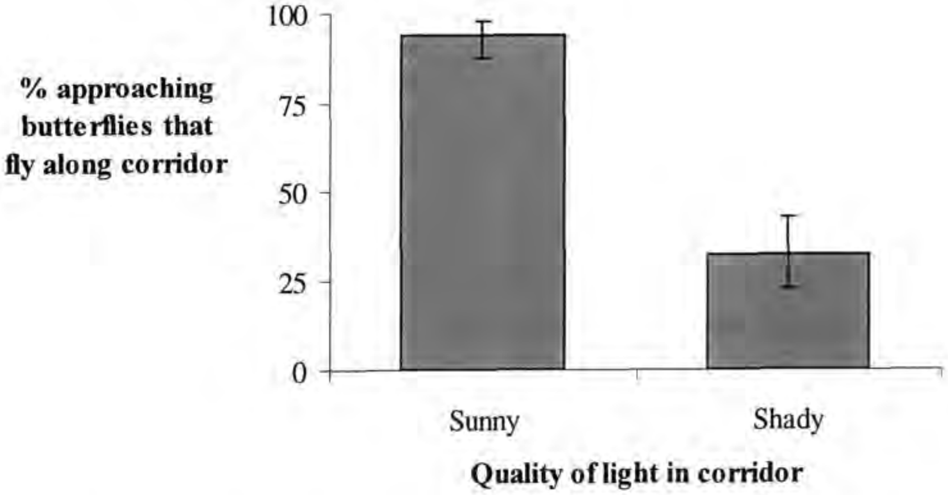


Figure 3.3: Use of a grassland corridor in sunshine (n = 110) and shade (n = 91). Error bars denote 95 % binomial confidence limits.

3.1.4 Discussion of the preliminary study

This preliminary study revealed that vegetation structure at field boundaries influenced butterfly movement. Generally, the more open a boundary, the more permeable it was to butterfly movement. However, there appeared to be a threshold of openness, about 30-40%, beyond which further increases in openness had little effect on movement rates across the boundary (Figure 3.2). This type of threshold, where boundary permeability shows no further increase beyond a certain degree of openness, was proposed theoretically by Stamps *et al.* (1987) who examined edge permeability using computer models. They found that a small increase in permeability of a 'hard' (relatively impermeable) edge, resulted in a dramatic increase in emigration, whilst for moderately permeable edges further increases in permeability had little effect on emigration rates.

Boundary openness appeared to be particularly important for Scarce Copper, possibly reflecting the more restricted meadow habitat requirements of this species compared with Fritillaries and Arran Brown, which are generally associated with open woodland habitat and thus less sensitive to the presence of tall vegetation. Interestingly, the behaviour of Blues more closely resembled that of Fritillaries and Arran Brown than that of the Scarce Copper, although the latter is more similar in size and a member of the 'Blues family', Lycaenidae. However, one of the species in the Blues category, the Common Blue, is a relatively mobile species. In addition, it uses woodland glades (Thomas and Lewington, 1991 and *pers. obs.*) and, although not the most common of the Blues in the open meadow, the method of recording at meadow boundaries would produce results biased towards the behaviour of this species. Behavioural differences between species and their possible causes will be investigated and discussed in more detail later in this chapter.

Another finding of this preliminary study was that even an opening in the boundary vegetation, which was readily used in sunny conditions, may be avoided if shaded by surrounding vegetation. Shade avoidance is almost certainly due to physiological temperature requirements of butterflies. Flight muscles can contract more rapidly and energetically efficiently when warm than when cold (Shreeve, 1992) and few butterflies can fly at all if the ambient temperature is less than 14 °C (Chinery, 1989). In Norway, where ambient temperatures are rarely excessive, flying into a shaded, relatively cool region is seldom likely to be advantageous and butterflies are generally adept in seeking out the warmest of microclimates in their surroundings. The Scarce Copper is a particularly temperature sensitive butterfly, flying only in full sunshine or at very high air temperatures (around 30 °C) (Douwes, 1976).

As a result of the preliminary study, the following hypotheses were proposed:

a) Tall vegetation presents a barrier to butterfly movement, causing butterflies to alter flight direction. Boundaries may therefore function as semi-permeable filters.

b) Butterflies with different ecological/ physiological requirements will react differently to structural features of the landscape.

3.2 BARRIER EXPERIMENT

3.2.1 Introduction

In order to test the hypotheses proposed from the results of the preliminary study, an experimental approach was taken. An artificial hedge was constructed, along which conditions were standardised so that height was the only parameter that varied between treatments. This approach was necessary due to the complexity of natural field boundaries, where replication of even similar conditions is rarely found.

3.2.2 Method

3.2.2.1 Construction of the artificial hedge

Wooden stakes were set into 0.5 m deep holes in the ground and stabilised by filling the holes with rocks and soil. The wooden stakes projected 3 m above the ground and were spaced at 5 m intervals from each other. Guy ropes from the stakes, running 90° to the hedge, provided further stability, in addition to acting as markers of the sides of each recording box. Hooks were screwed into the sides of each stake at 1 m height intervals and green tarpaulins were stretched between the stakes and hung on these hooks, with metal eyelets to protect the fabric against wear and tear. Thus the height of each 5 m long hedge section could be fixed at 1 m, 2 m or 3 m, independently of the height of the rest of the hedge (Figure 3.4). This design meant that the hedge could be quickly dismantled during unsuitable weather conditions and at the end of each day. The hedge was situated in the northern half of the meadow, running in an east-west direction in order to minimise the effects of shadow. The hedge comprised 12 x 5 m long sections, with three replicates of each of the four height treatments; these being: 0 m high, 1 m high, 2 m high, and 3 m high. The experiment used a randomised block design in which the sequence of treatments was changed for each recording of all height replicates (see Figure 3.4).

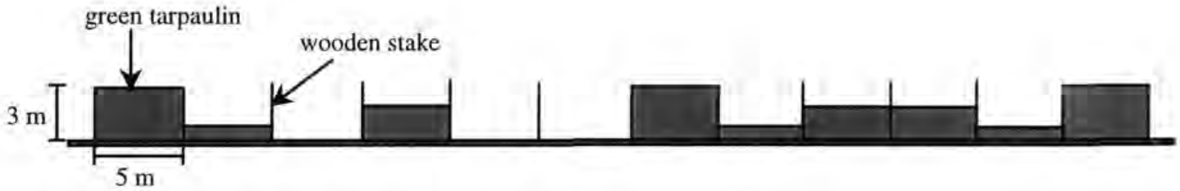


Figure 3.4: Diagram of the artificial hedge. The four height treatments were arranged in a different random sequence for each trial.

3.2.2.2 Recording butterfly flight patterns

Butterfly behaviour at the artificial hedge was recorded on 13 suitable days between 13th July and 9th August, 1993. Butterfly movements were monitored by four observers, each standing 3 m to the south of the hedge and recording butterfly activity over one 5 m section for 30 minutes. This allowed simultaneous recording of each of the height treatments, thus standardising recording for each run.

Butterfly movement patterns were categorised as either crossing, flying northwards ('crossing, north'), crossing, flying southwards ('crossing, south') or 'rebounds' (Figure 3.5). The rebound category included those butterflies that approached to within one metre of the hedge but did not fly over. From 28th July onwards, on the basis of trends seen in the early data, a fourth category was recorded: 'within 3 m', to include those individuals which came within 3 m of the hedge but did not enter the one metre wide strip next to the hedge (and therefore did not qualify as 'rebounds'). This category and the rebound category were only recorded for butterflies approaching from the south (i.e. the side of the hedge where recorders stood). Thus comparisons of proportions of approaches resulting in crossing, use only the 'crossing, north' category.

Once a butterfly left the recording box and had been recorded under one of the above categories, it was ignored. If it entered the box again it was counted as a new record.

Observation of butterfly movements was limited to periods of no precipitation when the air temperature was greater than 15 °C. This temperature threshold was lower than the 17 °C threshold used in the preliminary study since, although there was little activity at the lower temperatures, it was considered important to ensure that butterfly movements were registered under all conditions. At temperatures below 15 °C or during rain there was scarcely any flight activity.

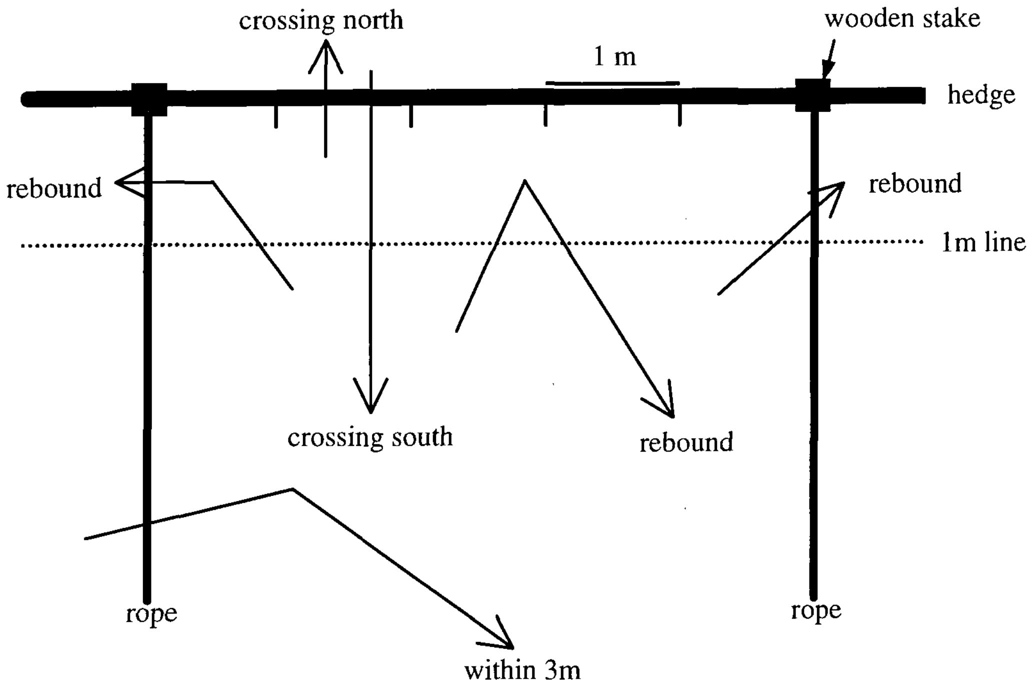


Figure 3.5: Diagram illustrating the main categories of butterfly movement recorded during the barrier experiment.

Species identification was as described in section 3.1.2.2; i.e. species which could not be reliably identified in flight were grouped into categories. With greater experience of the species present in the meadows and larger numbers of observations per treatment, a slightly more refined grouping of species was possible:

Scarce Copper males

Scarce Copper females

Blues: The majority of Blues were Geranium Argus (Plate 4, p.55). Others included Mazarine Blue, Idas Blue, Silver-Studded Blue and Common Blue

Arran Brown

Small fritillaries: Pearl-Bordered Fritillary (Plate 5, p.55), Small Pearl-Bordered Fritillary, Lesser Marbled Fritillary

Large fritillaries: High Brown Fritillary, Dark Green Fritillary

Small Heath

Species observed very infrequently were excluded from the analyses.

Plate 4 (left): One of the most abundant of the blue lycaenids: Geranium Argus (*Eumedonia eumedon*), seen here on Wood Cranesbill (*Geranium sylvaticum*).

Plate 5 (below): Pearl-Bordered Fritillary (*Clossiana euphrosyne*) was recorded in the category 'Small fritillaries'.

3.2.3 Results

3.2.3.1 Comparison of height treatments

The number of butterflies crossing the artificial hedge declined with increasing hedge height (Figure 3.6).

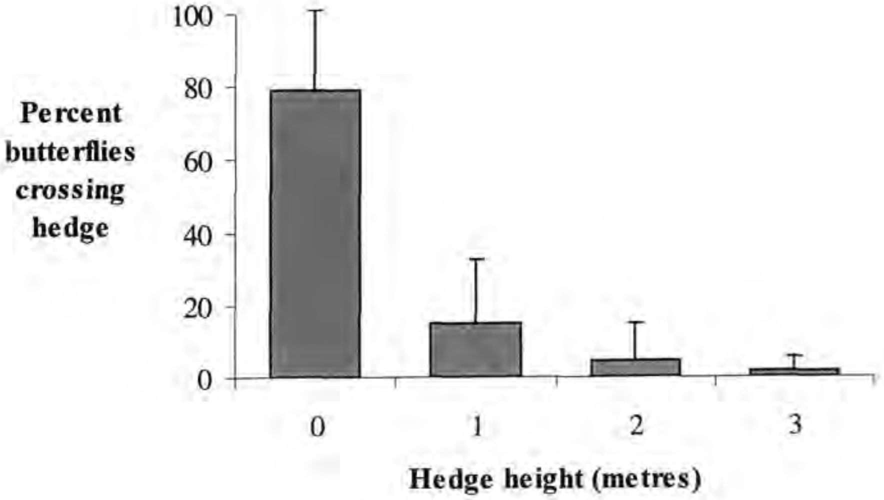


Figure 3.6: Number of butterflies crossing the different experimental height treatments, as percent of total crossings (all species; n=1694). The error bars denote two standard deviations, calculated on the basis of 45 replicates.

Sample sizes per recording session were generally low, particularly for the taller hedge sections. To test for differences between treatments using a method which took replicate variability into account, pairwise replicated G-tests were conducted on the numbers of butterflies crossing both northwards and southwards over the different height treatments (45 replicates of each treatment). Data were grouped when no observations were made in particular classes. The following G-values were obtained:

0 m compared with 1 m: $G = 907.69$ $df = 44$; $P < 0.001$
1 m compared with 2 m: $G = 119.24$ $df = 24$; $P < 0.001$
2 m compared with 3 m: $G = 33.57$ $df = 19$; $P < 0.025$

i.e. there were significant differences between all pairs of height treatments.

3.2.3.2 Species differences

Behavioural differences between species are illustrated in Figure 3.7, which shows the weighted mean percent crossing over the different height treatments for different species. For each height treatment, the means are weighted by the number of butterflies approaching to within 1 m of the hedge, i.e.

$$\frac{\text{Number crossing the height treatment}}{\text{Number crossing } + \text{number 'rebounding'}} \times 100$$

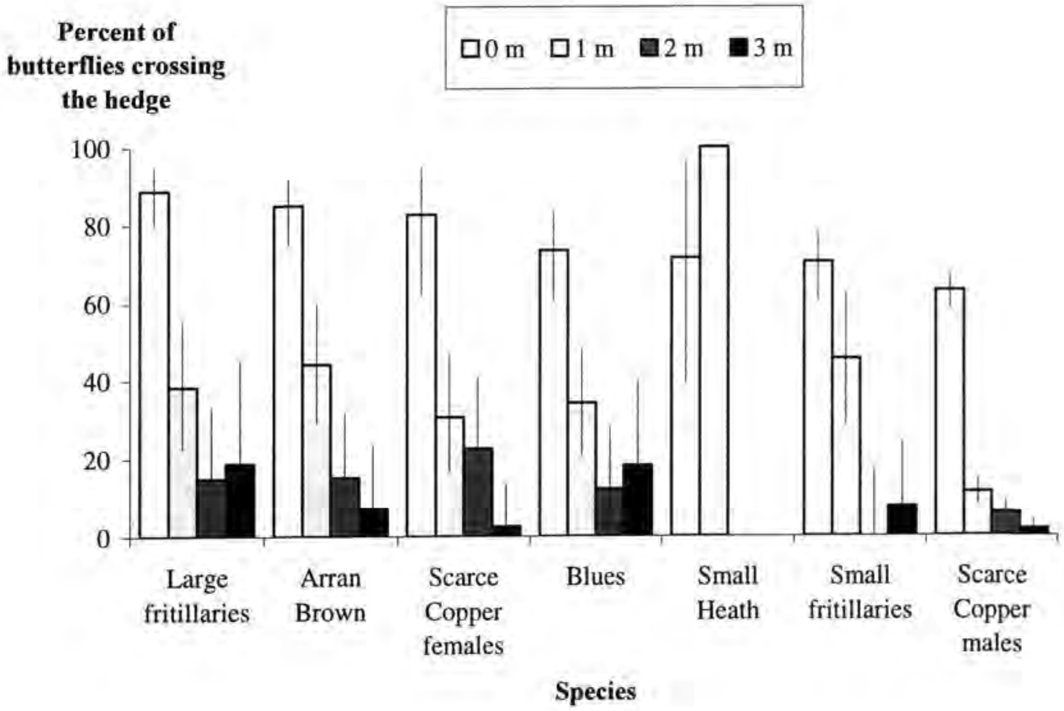


Figure 3.7: Weighted mean number of butterflies crossing the different hedge heights (where means are weighted by the number of butterflies approaching to <u>within 1 m</u> of the height treatment). Error bars denote 95 % binomial confidence limits (for samples greater than 5 individuals). Species are ordered according to crossings over 0 m: Large fritillaries n = 157; Arran Brown n = 177; Scarce Copper females n = 129; Blues n = 160; Small Heath n = 17; Small fritillaries n = 181; Scarce Copper males n = 1588 (See Method for species details).

All species crossed the 0 m treatment far more readily than the 1 m and taller hedges, except for the Small Heath for which the low sample size (n = 17) should be noted. Similarly, for all species the weighted mean percent crossing 1 m high hedge sections was greater than that crossing 2 m. The difference between 2 m and 3 m high sections was less clear-cut, with Blues and all Fritillaries crossing 3 m treatments relatively more than 2 m treatments.

An important feature illustrated by Figure 3.7, is that the proportions of butterflies crossing the 'control' (0 m) treatment differs between species. Crossings of 0 m, as a proportion of approaches to within 1 m, are greatest for Large fritillaries (88.8 %) followed by Arran Brown (84.9 %), Scarce Copper females (82.6 %), Blues (73.4 %) Small Heath (71.4 %) Small fritillaries (70.5 %) and Scarce Copper males (63.1 %).

On discovering that species were reacting differently to the control, the category 'within 3 m' was included in the recording procedure (see Method, section 3.2.2.2) and from the 28th July onwards, approaches to within 3 m of the hedge (rather than approaches to within 1 m) could be calculated, i.e. 'crossings' + 'rebounds' + 'within 3 m'. When mean percent crossings are weighted based on all approaches to within 3 m of the hedge, the ranking of species according to mean percent crossing 0 m changes (Figure 3.8). Small fritillaries (16.2 %), Arran Brown (16.0 %) and Large fritillaries (15.0 %) become more similar to one another; Blues (12.5 %) and Scarce Copper males (10.6 %) continue to have a relatively low proportion crossing 0 m; whilst the greatest change is for Scarce Copper females, which had one of the highest percent crossing 0 m when weighted by approaches to within 1 m, but the lowest percent crossing (7.6 %) when weighted by approaches to within 3 m.

Interestingly, Scarce Copper females and Blues had the highest weighted mean percent crossing of the actual hedges, i.e. the 1 m, 2 m and 3 m treatments combined (9.8 % and 9.6 % respectively), compared with 7.0 % for Arran Brown, 4.4 % for Large fritillaries and just 2.6 % for both Small fritillaries and Scarce Copper males.

A row x column (R x C) test of independence comparing all crossings (both 'crossings north' and 'crossings south', n = 1694) revealed that the numbers of butterflies crossing the different hedge heights were dependent upon species ($G = 50.645$; $df = 15$; $P < 0.001$). Further testing showed that Scarce Copper females were the main cause of the significant relationship (Table 3.2).

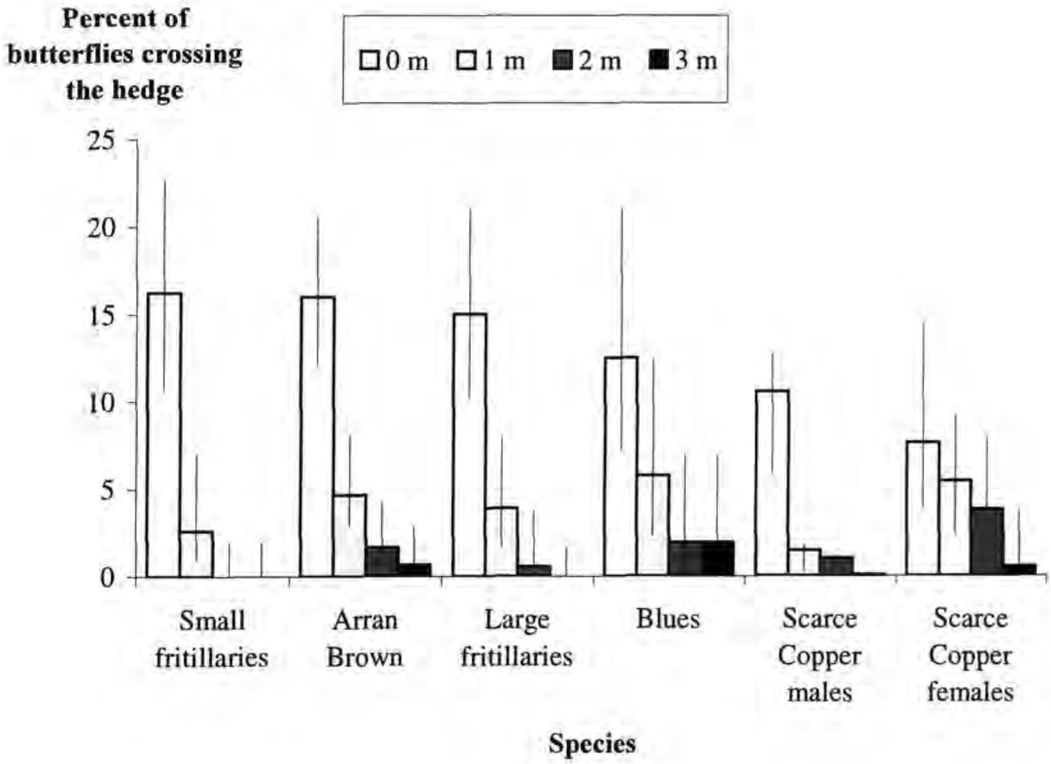


Figure 3.8: Mean percent butterflies crossing the different hedge height treatments, weighted by the numbers of butterflies approaching to <u>within 3 m</u> of the hedge. Error bars denote 95 % binomial confidence limits (for samples greater than 5 individuals). Species are ordered according to crossings over 0 m: Small fritillaries n = 154; Arran Brown n = 300; Large fritillaries n = 180; Blues n = 104; Scarce Copper males n = 1563; Scarce Copper females n = 184 (See Method for species details).

Table 3.2: Results of pairwise G-tests for homogeneity between species [a].

	Scarce Copper males	Blues	Small fritillaries	Large fritillaries	Arran Brown
Scarce Copper females	**** 33.72**	*** 16.68**	**** 28.64**	**** 18.53**	*** 16.32**
Scarce Copper males		8.76	3.11	3.16	7.16
Blues			4.64	1.48	1.22
Small fritillaries				1.82	3.22
Large fritillaries					0.51

[a] Species pairs which are significantly different from one another are shown in bold:

* $P < 0.05$; ** $P < 0.01$ for *k* (number of comparisons) = 15 and *df* = 3.

The reason for the significant differences between Scarce Copper females and all other butterflies is apparent in Figure 3.8. Whilst Scarce Copper females crossed the 2 m height treatment relatively more frequently than all other butterflies, they crossed the control (0 m) treatment relatively less than all other butterflies. The relationship between the 0 m and 2 m treatments was, therefore, a significant cause of the differences between Scarce Copper females and other butterflies (Table 3.3).

Table 3.3: Heterogeneity G-values resulting from comparisons of the numbers of Scarce Copper females crossing the 0 m and 2 m height treatments with the numbers of other butterflies crossing these treatments.

Comparison with:	G_H	Significance [a]
Scarce Copper males	24.38	***
Blues	13.58	**
Small fritillaries	24.73	***
Large fritillaries	15.76	**
Arran Brown	15.00	**

[a] Significance for *df* = 4: ** P < 0.01; *** P < 0.001.

3.2.3.3 Distant reactions to the artificial hedge

The two different methods of weighting the mean number of crossings, explained above, reveal that butterflies reacted differently to the hedge when they were just 1 m away from it than when they were 3 m away. Assuming a null hypothesis that butterflies do not react to the hedge from a distance, we would expect to find equal numbers of butterflies approaching each height treatment. This was not the case for approaches to within 1 m of the hedge, where the overall distribution of approaches between treatments was significantly different from the expected 1:1:1:1 ratio (Pooled G = 161.66; P < 0.001) (Table 3.4). For most species categories, more butterflies approached 0 m and 1 m hedge sections than taller sections, however, the numbers of approaches of female Scarce Coppers and of Small Heath did not differ significantly from the expected equal ratio (G = 11.45 and 12.43 respectively; P > 0.05).

Approaches to within 3 m, on the other hand, did not differ significantly from the null hypothesis when all species are pooled (Pooled G = 7.12; P > 0.05) (Table 3.4). However, there is significant heterogeneity because Scarce Copper females and Small fritillaries do differ significantly from the null hypothesis (G = 11.45 and 12.43 respectively; P < 0.01). Examination of Figure 3.8 shows these two species categories to represent two extremes: female Scarce Coppers cross 0 m sections the least but cross taller sections more than the butterflies of other species categories, whilst Small fritillaries cross 0 m more than all other species but do not cross 2 or 3 m sections at all. Scarce Copper females approach tall treatments more often than low treatments, whilst Small fritillaries approach 0 m and 1 m treatments more than taller treatments. In fact, there was a slight bias towards higher numbers of approaches to 0 m for all the remaining species categories, although not sufficient to be able to reject the null hypothesis of equal approaches.

Table 3.4: Results of replicated G-tests comparing, for each species category and for all species pooled, observed numbers of butterflies approaching the four height treatments with an expected 1:1:1:1 ratio.

Species	**Approaches within 1 m**			**Approaches within 3 m**		
	n	**G**	**Sig.** [a]	**n**	**G**	**Sig.** [a]
Scarce Copper females	129	4.74	n.s.	184	11.45	**
Scarce Copper males	1588	53.46	***	1563	3.92	n.s.
Blues	160	23.18	***	104	5.99	n.s.
Small fritillaries	181	94.78	***	154	12.43	**
Large fritillaries	157	55.25	***	180	4.07	n.s.
Arran Brown	177	25.63	***	300	1.59	n.s.
Small Heath	17	5.23	n.s.	0		
Pooled G	*df*=3	**161.66**	***	*df*=3	**7.12**	**n.s.**
Heterogeneity G	*df*=18	**100.62**	***	*df*=15	**32.33**	**
Total G	*df*=21	**262.29**	***	*df*=18	**39.45**	**

[a] Significance: n.s. not significant; ** $P < 0.01$; *** $P < 0.001$.

As a final test that most species were not influenced by the hedge from 3 m distance, the 0 m hedge crossings and rebounds can be compared with the control from the preliminary study undertaken in 1991 (described in section 3.1). The 1991 control recorded crossings and rebounds at an imaginary line through open meadow, i.e. an uninterrupted ‘0 m line’ which is directly comparable to the artificial hedge 0 m sections except for the lack of neighbouring hedge sections. Pairwise comparisons ($k = 4$) show that the relationship between crossings and rebounds in the 1991 control versus the 1993 control was not significantly different for Fritillaries, Blues and Arran Brown ($G = 1.74$, 3.44 and 5.72 respectively, for $df = 1$, $P > 0.05$) but was significantly different for Scarce Coppers ($G = 67.03$; $df = 1$, $P < 0.001$). There were more Scarce Copper rebounds from the artificial hedge 0 m sections than occurred at the 1991 control.

3.2.3.4 Influence of neighbouring treatments

Since the hedge affected butterfly behaviour from 1 m away, and up to 3 m away for Scarce Copper, it seemed reasonable to expect interactive effects between neighbouring sections of different heights. Comparisons were therefore made of numbers of crossings over different combinations of height sequences. Since the number of replicates of any particular height sequence were low, replicates were grouped into those with low neighbours (0 m and 1 m) and those with high neighbours (2 m and 3 m) (Table 3.5).

Table 3.5: Mean numbers of butterflies crossing hedge sections of different heights when neighbours are low (0 m or 1 m) and high (2 m or 3 m).

Hedge height	Neighbouring sections	Number of replicates	Mean number of butterflies crossing section
0 m	low	10	27.5
	high	8	32.0
1 m	low	10	4.6
	high	9	8.7
2 m	low	10	2.0
	high	6	1.8
3 m	low	14	0.9
	high	5	0.2

Comparisons were made using ANOVA and showed that the heights of neighbouring hedge sections had no statistically significant effect on the number of butterflies crossing 0 m high sections (F = 0.519; *df* = 1, 16; P = 0.482) but did have an effect on numbers crossing 1 m high sections (F = 4.93; *df* = 1, 17; P = 0.040). The numbers of butterflies crossing 2 and 3 m high hedges were too small for meaningful analysis.

3.2.4 Discussion of the barrier experiment

The barrier effect of tall landscape elements, implied by observations at natural field boundaries, was confirmed by the artificial hedge experiment. For every metre increase in height, there was a significant decline in the number of butterflies crossing the hedge. That the 2 m and 3 m hedges were most similar is easily explained by the very small number of butterflies crossing either of these tall treatments.

3.2.4.1 Species differences

Whilst the negative effects of height were apparent for all species groups considered, the strength of the response differed slightly between species, and the movement patterns of Scarce Copper females were significantly different from those of all other species categories. The reaction of the different species to the hedge as a whole was an important part of this variation. When numbers crossing the hedge were plotted as a proportion of approaches to within 3 m of the hedge, there was a clear division between the Blues and Scarce Coppers, for which the proportion crossing 0 m was low, and the larger butterflies (Fritillaries and Arran Brown), for which the proportion crossing 0 m was higher. This division corresponds to a taxonomical division since Blues and Scarce Coppers are members of the family Lycaenidae, whilst Fritillaries are members of Nymphalidae and Arran Brown is a member of Satyridae - sometimes treated as a sub-family of Nymphalidae (Chinery, 1989). The differences between these groups regarding proportions crossing 0 m sections, imply that the small lycaenids are less disposed to crossing through gaps in a barrier than are the larger species. It should be stressed that the Lycaenidae family incorporates butterflies with very different ecological strategies, including species which spend most of their adult lives in the tree-tops. However, the lycaenid species included in this study were all meadow species and of a similar size, and therefore form an ecological grouping.

There are a number of anatomical and ecological differences that could be expected to produce different behavioural responses by the lycaenids in question, compared with the Fritillaries and Arran Brown. One obvious difference between butterfly species is their colouration and the Fritillaries and, in particular, Arran Brown are darker than the Scarce Copper and many of the Blues. It may seem reasonable that butterflies with a high degree of melanisation would absorb more thermal energy from the sun and could therefore maintain more energetic flight. However, this is not always the case since many butterflies, including some lycaenids, use solar reflectance rather than absorbance to regulate their temperature. It must be added, though, that although the wing colouration of Scarce Copper fits the typical pattern of a reflectance basker, as described by Shreeve (1992), the detailed studies of Douwes (1976) suggest that this species is a dorsal absorbance basker, i.e. the same as the Fritillaries and Arran Brown. Thus, in this case at least, dark colour would be an advantage.

More important than colouration may be the larger size of Fritillaries (wing-span 47-63 mm) and Arran Brown (42-53 mm) compared with the lycaenids (less than 35 mm). Once the larger butterflies have reached a sufficiently high body temperature (which may take longer than for the small lycaenids), their larger size increases their thermal stability (Shreeve, 1992). This would allow a greater tolerance of short periods in shade. The larger wing area of Fritillaries is also put to good effect in energy-efficient gliding flight. When butterflies glide, the boundary layer of air around the body is not disturbed and convection cooling is therefore lower than for individuals with rapid wing-beats (Guppy, 1986).

These thermoregulatory advantages suit species that thrive not only in meadows but also in open woodland. The particular lycaenid species in the meadow were, on the other hand, far more restricted to meadow habitat. These ecological differences were illustrated by the stronger avoidance of shade by Scarce Coppers than Arran Brown, described in section 3.1.3.2. In addition, larger size incurs higher energy expenditure and therefore greater energy demand (Wood, 1983); larger insects therefore tend to have larger trivial ranges in which to obtain resources (Southwood, 1978). Considering all these factors together, it would seem that Fritillaries and Arran Brown, which are better adapted to flying through gaps between trees and moving quickly through patches of shade, perceive the 5 m wide gaps in the hedge as a continuation of their habitat. The smaller lycaenids, on the other hand, being generally more restricted to meadow habitat, seem to be more affected by the presence of the rest of the hedge. The comparison with the 1991 control provides further evidence that, for Scarce Coppers at least, the reaction to the 0 m sections in the hedge was different from usual behaviour in open meadow, i.e. the 0 m sections appear to have been perceived as gaps in a boundary rather than as a continuation of the meadow habitat.

Whilst the lycaenids were more reluctant to cross the 0 m sections of the hedge, they crossed the taller hedge sections relatively more frequently than the larger butterflies. At first sight, these trends appear to conflict; however, they may be logically explained by considering the potential importance of motivational state in determining the movement of butterflies. Scott (1975a) distinguished between trivial flights, i.e. flights between flowers or searching for mates etc. within the usual habitat, and migratory movements, i.e. flights away from the usual habitat of the butterfly. It is possible then that the majority of the lycaenid population do not expose themselves to the potential risks and energetic costs of exploring gaps in the hedge during their trivial movements because their requirements for nectar and mates are more likely to be met within the main habitat. Those that do approach the hedge, however, may be butterflies that are in a migratory behavioural state and are thus more motivated to fly over obstacles, even a tall hedge. The effects of motivation are apparent for all species to a certain extent, expressed in the much higher percentages of butterflies crossing the hedge once they have come within one metre of it. Many of the butterflies which come within three metres of the hedge may not have chosen to fly north, regardless of whether the hedge were there or not. Those that have come within 1 m, on the other hand, are on a course of flight that is very likely to force them into a decision to either cross or turn away from the hedge.

3.2.4.2 Sexual differences

The very different behaviours of Scarce Copper females and males is particularly interesting, since it is the females which show the more motivated pattern of movement (i.e. a relatively high percent crossing the taller hedges). The males very seldom cross tall hedges, even on approaching to within 1 m. This may be interpreted as a sign that it is the females who are responsible for larger scale dispersal in this species.

It was unfortunate that any sexual differences in other species could not be detected. However, the patterns observed for Scarce Copper agree well with the results of other studies. It has been noted several times in the literature that within-patch (trivial) movement is often greater in males, sometimes considerably so, such as for Scarce Copper males which have been shown to fly five to ten times as much as females within a habitat patch (Douwes, 1976). This, and the fact that Scarce Coppers are protandrous (the males emerging around two weeks before the females) explains the large difference in number of sightings of males and females in this study. On the other hand, the observation that female Scarce Coppers were much more likely to cross the artificial hedge than males agrees well with previously observed differences in between-patch mobility between the sexes of butterflies. For example, whilst short, within-patch movements of the Glanville fritillary are commonest amongst males, longer, between-patch flights are more common in females (Hanski *et al.*, 1994). Scott (1975a) demonstrated greater female range for eight butterfly species; the same has been shown for Baton Blue (*Pseudophilotes baton*) (Väisänen *et al.* 1994) and Bog Fritillary (*Proclossiana eunomia*) (Baguette and Nève, 1994).

These behavioural data support the suggestion by Brussard and Vawter (in a genetic study of the fritillary *Euphydryas phaeton*) that, at least for some species, it is gravid females which are responsible for maintaining gene flow between populations (Brussard and Vawter, 1975). They reason that male butterflies should be under selective pressure to be sedentary since if they move between patches they risk arriving at a new habitat patch too late to inseminate a female. This risk is particularly high for the many protandrous butterfly species, such as the Scarce Copper. Since males can mate more than once whilst females only mate once, competition for females is intense and migration to a different occupied habitat patch will do little to ease this competition whilst denying the migrant of the possibility to compete for the earliest emerging females. Obviously there is also the risk that migrants will not find a new habitat patch. This risk also exists for females but, whereas males must find an occupied patch and then an unfertilised female, the female need only find food plants on which to lay her eggs. If the patch is unoccupied this may be advantageous, especially in comparison with a crowded original habitat, since her offspring thus have exclusive access to the food resource. In addition, migrating females avoid harassment from males so the energy expended in migrating is at least partly compensated by the reduction in time and energy used avoiding males and the reduced risk of injury due to physical interactions.

3.2.4.3 Approaches to the hedge

Neither the reluctance of Scarce Copper females to cross 0 m sections, nor their ability to cross tall hedges if motivated, can explain why these butterflies are found significantly more often within 3 m of tall hedge sections than low sections. However, it has already been pointed out that Scarce Coppers are very temperature sensitive and that females of the species are generally much less mobile within a habitat patch than males (Douwes, 1976). It is thus possible that Scarce Copper females accumulate by the tall hedge sections to benefit from the warm, sheltered microclimate there. The more mobile males would be less influenced by these very localised microclimate conditions, being distracted into neighbouring sections by skirmishes with other males and in the hunt for unmated females.

The approaches of Small fritillaries also deviated from random, there being significantly more approaches to 0 m sections. This may suggest that these butterflies recognise the presence of a gap from more than 3 m away, though it seems strange that Small fritillaries but not Large fritillaries should be capable of this. A more probable explanation, considering the extremely low percentage of Small fritillaries crossing 1, 2 and 3 m hedges, is that when these butterflies reach a tall boundary, they turn and fly along the hedge until they find a gap, thus being funnelled into the 0 m sections. Considering how successful this apparent 'find-a-gap' strategy was at the artificial hedge, it seems unusual that none of the other species exhibited similar behaviour. Generally, though, a butterfly may have to fly a considerable distance to find a gap in boundary vegetation, with the result that the total energetic expense of flying along a boundary may, on average, be greater than flying over. For the Small fritillaries, however, the balance may be biased in favour of flying along the hedge, since gliding flight is very energy-efficient, whilst gaining height to fly over an obstacle would require flapping the wings, thus expending greater energy.

The Large fritillaries, which also benefit from gliding flight, also show a slight bias towards approaching 0 m sections (n = 54) more often than taller, particularly 3 m (n = 34) sections. However, since the Large fritillaries often fly at a higher level above the ground than the Small fritillaries (*pers. obs.* and Henriksen and Kreutzer, 1982), they have an easier starting point from which to cross the 1 and 2 m high hedges, i.e. a lower energetic cost. The funnelling of Large fritillaries towards gaps is therefore less extreme and is not sufficient to reject the null hypothesis of equal approaches per treatment.

3.2.4.4 Effects of neighbouring hedge sections

Even if butterflies did not fly far along the hedge in search of gaps, as discussed above, it seemed reasonable that more butterflies would cross through a gap between two tall hedge sections than between two low sections, since butterflies deflected by the higher hedge sections would at least be expected to find a neighbouring gap. It is possible that such behaviour accounted for the slightly higher number of approaches to 0 m sections for all species (except Scarce Copper females); so too the slightly higher mean percent crossing of those gaps where neighbouring sections were high (32.0 % versus 27.5 % when neighbours were low). However, the data merely hint at such relationships and do not provide statistically significant evidence.

Neighbours to 1 m high sections, on the other hand, did have significant effects on the numbers of butterflies crossing the hedge, with more crossings when the contrast between sections was great. This gives empirical evidence in favour of the theory that butterflies are deflected from tall sections and find neighbouring gaps. But why should the effect be more obvious over 1 m sections than at 0 m? Consider the 0 m situation again: when neighbours are tall, we assume that butterflies are deflected and cross the 0 m section. However, when neighbours are low, there may also be some extra butterflies funnelled towards the 0 m section because 'low neighbours' include 1 m high hedges, which have been demonstrated to have a significant barrier effect. So in both situations, crossings over 0 m are increased by deflection from neighbours. At 1 m sections, on the other hand, the effect with high neighbours is the same, i.e. an increase in crossings (since 1 m is more permeable than 2 and 3 m) but when neighbours are low, some butterflies may be funnelled away from the 1 m section in favour of 0 m neighbours, i.e. a decrease in the number of butterflies crossing 1 m. The difference between situations with high versus low neighbours is thus greater for 1 m sections.

3.2.4.5 What next?

Some butterflies, even of the more sensitive species, did cross the artificial hedge and in later chapters we will consider the role of these individuals. First, however, I would like to consider behaviour in a little more detail to determine:

a) whether there are more subtle differences in butterfly behaviour at boundaries than were recorded in this experiment, in particular whether butterflies are channelled along boundaries,

and

b) how behaviour differs at different types of man-made boundary in agricultural landscapes.

3.3 BOUNDARIES ON FARMLAND

3.3.1 Introduction

Section 3.1 dealt with the complex situation of the boundaries of an abandoned meadow, where uneven patterns of scrub encroachment and general lack of management had led to rather heterogeneous boundaries. The experiment described in section 3.2, on the other hand, was a simplification of reality, using the strictly standardised conditions of an artificial hedge to tease out the effect of one important factor – height. In this section I aim to combine the advantages of a standardised approach with the study of a realistic situation, to examine the roles of some typical boundary structures occurring on farmland. Homogeneous stretches of boundary will be studied to avoid the complicating effects of gaps, and behaviour will be recorded in a way which permits the analysis of subtle behavioural responses.

3.3.2 Method

Blocks 25 m long and 3 m wide were marked out along five different boundary types: low (approx. 0.5 m) dry-stone wall, high (approx. 1.5 m) dry-stone wall, trees (approx. 4 m), roadside and (for control purposes) open meadow. Care was taken to ensure homogeneity along each stretch of boundary, regarding height of the boundary structure itself, height of vegetation adjacent to the boundary, flower abundance along the boundary, neighbouring land use and general avoidance of atypical features. Each 25 m block was further divided into 5 m long boxes and butterfly movement patterns in each box were recorded in diagrammatic form during 5 minute intervals (see Figure 3.9 for examples). For analysis, each flight path observed was designated one of the following behaviour categories:

Enter: butterfly flies over the boundary, into the recording box

Leave: leaves the recording box by flying over the boundary

Parallel: flies parallel to the boundary for at least 4 m; enters or leaves recording box flying parallel to the boundary.

Short parallel: flies parallel to the boundary for at least 2 m but less than 4 m; enters or leaves recording box flying parallel to the boundary.

Rebound: flies both into and out of the recording box in a direction transverse to the boundary

Other: flight paths which do not match the above definitions (often butterflies nectar-feeding within the recording box).

Some flight paths incorporated two of the above categories, for example Enter + Parallel or Parallel + Leave. The small number of observations of this type did not justify the designation of specific categories for these reaction patterns, so these butterflies contributed two records to the results.

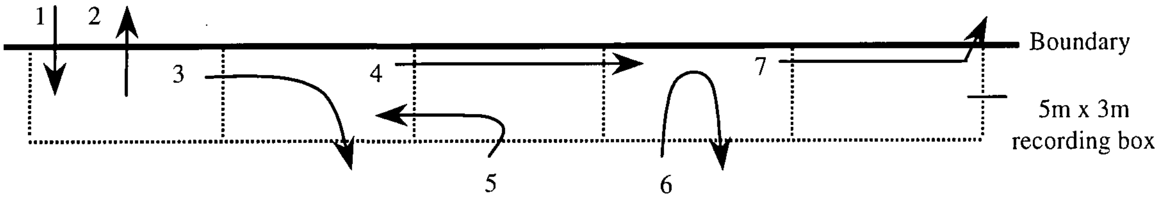


Figure 3.9: Examples of butterfly flight paths. 1= Enter; 2= Leave; 3= Short parallel; 4= Parallel; 5=Short parallel; 6= Rebound; 7= Parallel + Leave.

A computerised record of the flight path drawings was established, using a grid referencing system to describe the metre by metre movement of each butterfly.

A wider range of species was encountered in this study than in the meadow situation described in section 3.2. Again, species were grouped in cases where identification of flying individuals was uncertain, with the following additions to the classification given in section 3.2.2.2: Blues included some individuals of Holly Blue (*Celastrina argiolus*) and Little Blue (*Cupido minimus*), and Large fritillaries included some Silver-washed fritillaries (*Argynnis paphia*). Several additional categories were used in species comparisons:

Small Tortoiseshell (*Aglais urticae*)
Large Wall Brown (*Lasiommata maera*)
Large Skipper (*Ochlodes venatus*)
Whites: Green-veined white (*Pieris napi*), Small white (*P. rapae*) Large white, (*P. brassicae*) and Orange tip (*Anthocharis cardamines*)
Red Admiral (*Vanessa atalanta*)

Since the numbers of observations were very low when divided into each behaviour type for each species category, the analysis first uses pooled data for all species to examine behaviour differences at each boundary type and then focuses on comparisons between species.

3.3.3 Results

3.3.3.1 Differences between boundaries

Finding suitable homogenous boundaries proved more difficult than expected and the aim of three replicates of each boundary type was unfortunately not fulfilled, with only two sites for Road, Low wall and High wall boundary types. In addition, the numbers of butterflies occurring along the boundaries were insufficient to make full use of the replicated block experimental design and numbers have thus been pooled for analysis. Nonetheless, the overall outcome was a clear difference in the patterns of behaviour observed along the different boundary types (Table 3.6)

Table 3.6: Percentage of flight paths in each behaviour category for each of the different boundary types.

Behaviour category	**Transect type**				
	Control	**Road**	**Low wall**	**High wall**	**Trees**
Enter	30.5	17.4	20.5	18.2	9.5
Leave	32.0	20.8	22.2	16.7	8.5
Parallel	17.2	23.6	26.3	46.2	35.8
Short Parallel	5.9	14.6	13.5	12.9	22.4
Rebound	3.6	10.4	6.4	0.8	12.4
Other	10.9	13.2	11.1	5.3	11.4
Sample size	338	144	171	132	201

That there was an association between boundary type and the behaviour of butterflies was confirmed by an R x C test of independence using a G-test, i.e. we can reject the null hypothesis that the frequency of behaviour categories is independent of boundary type ($G = 161.390$; $df = 20$; $P < 0.001$). Pairwise unplanned tests for homogeneity were used to identify which boundary types differed from which (Table 3.7). In fact, all but one pair of boundaries (Low wall and Road) were significantly different from one another, although High wall and Low wall were only significantly different at the $P < 0.05$ level. The greatest differences between boundaries were those between the Control and High wall, and Control and Trees. Interestingly, behaviour at the Trees boundary type was more akin to that at Road than that at High wall.

Table 3.7: Heterogeneity G-values (G_H) resulting from pairwise unplanned comparisons of boundary types.

Pairwise comparison	G_H	Significance[a]
Low wall & Road	2.546	n.s.
High wall & Low wall	20.181	*
Road & Trees	20.772	**
Control & Low wall	21.966	**
Road & High wall	29.390	**
Control & Road	30.064	**
Low wall & Trees	30.123	**
High wall & Trees	37.408	**
Control & High wall	55.243	**
Control & Trees	121.603	**

[a] Significance for $k = 10$ and $df = 5$:

n.s. not significant; * $P < 0.05$; ** $P < 0.01$

3.3.3.2 Determining which aspects of behaviour differ between boundaries

Having demonstrated that the different boundary types elicited significantly different overall patterns of behavioural responses, unplanned pairwise comparisons for sub-sets of behaviour categories (Sokal and Rohlf, 1981) were carried out to identify which aspects of behaviour were responsible for the differences between each pair of boundaries (Table 3.8). In effect, these tests compare the proportions of butterflies in each behaviour category, find the largest possible group of behaviour types which do not differ between the pair of boundaries in question (a 'maximally non-significant set'), and thus isolate the elements of behaviour which differ. For example, the relationship between the number of butterflies Entering and the number Leaving was not significantly different for any pair of boundaries compared (being roughly 50:50 in all cases, as one would expect). However, in the comparison between Control and Trees, any third behaviour category added to the analysis would result in a significant difference between the boundaries. For all other boundary pairs, the behaviour category Other can be added to the analysis without causing significant differences, i.e. the proportions of reactions spread between the Enter, Leave and Other categories are similar.

Table 3.8: Pairwise comparison of boundaries in terms of maximally non-significant sets of behaviour categories. The addition of any behaviour category not listed in a set would make the boundaries significantly differ from one another. The upper part of the table shows maximum homogeneous sets possible using the Enter and Leave categories as starting points. The lower part of the table shows alternative, larger sets in cases where these do not include Enter and Leave.

Pairwise Comparison[a]	**Maximally non-significant sets of behaviour categories (P > 0.05)**	*df*	$G_{(H)}$
Low wall vs. High wall	Enter/Leave/Other/Rebound/Short Parallel	4	7.229
Road vs. High wall	Enter/Leave/Other/Rebound/Short Parallel	4	13.662
Control and Low wall	Enter/Leave/Other/Rebound/Parallel	4	14.105
Control vs. High wall	Enter/Leave/Other/Rebound	3	1.310
Control vs. Road	Enter/Leave/Other/Parallel	3	11.363
High wall vs. Trees	Enter/Leave/Other/Parallel	3	9.948
Road vs. Trees	Enter/Leave/Other/Rebound	3	7.228
Low wall vs. Trees	Enter/Leave/Other	2	6.149
Control vs. Trees	Enter/Leave	1	0.193
Road vs. Trees	Other/Rebound/ Parallel/ Short Parallel	3	2.677
Low wall vs. Trees	Other/ Rebound/ Parallel/Short parallel	3	2.249
Control vs. Trees	Rebound/ Parallel/Short parallel	3	4.290

[a] No. of comparisons of boundary types (*k*) =9

The lack of similarity between Control and Trees is due to the very small proportion of butterflies crossing Trees (18%) compared with Control which, not surprisingly, had the highest proportion crossing of all boundary types (62.5%). If the Enter and Leave categories are removed from consideration, similarity is revealed in the comparative proportions of responses of types Rebound, Parallel and Short parallel. The same is true for comparisons of Road and Low wall with Trees (see last three rows of Table 3.8).

At High wall, boundary crossings were around half that observed at Controls, thus eliminating the extreme effects of the Enter and Leave categories when compared with Trees. The main dissimilarities from Trees were differences in Short parallel and Rebound responses, both being infrequent at High wall and frequent at Trees. The high percentage of Parallel movements along

High wall (46%) was the major cause of the differences between this boundary type and Low wall, Road and Control.

Comparison of the low boundary types reveals variation in Short parallel and Rebound responses as being the main causes of differences. Short parallel responses were twice as frequent at Low wall and Road than over Control. Rebounds were observed least frequently at Control, more so at Low wall and most at Road. In fact, Road was similar to Trees in its relatively high frequency of Rebounds and only the higher frequency of Parallel and Short parallel movements at Trees caused the significant differences between these two boundary types.

3.3.3.3 Proximity to boundary

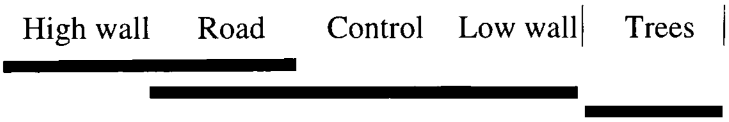
The recording procedure distinguished between butterflies within 1 m from the boundary or greater than 1 m away (Table 3.9). It was therefore possible to test the null hypothesis that the proximity of butterflies to the boundary was the same at all boundary types.

Table 3.9: Observed locations of butterflies within the 3 m wide recording strip, grouped as those within 1 m of the boundary and those more distant than 1 m from the boundary.

Boundary type	% locations within 1 m of boundary	% locations further than 1 m out from boundary	Total observed locations
High wall	52.8	47.2	528
Road	45.2	54.8	485
Control	41.1	58.9	1017
Low wall	40.9	59.1	558
Trees	27.5	72.5	819

An R x C test for independence showed that the proximity of butterflies to the boundary was not independent of boundary type ($G = 97.572$; $df = 4$; $P < 0.001$). A simultaneous test procedure revealed three maximally homogeneous sets (Figure 3.10) and highlighted Trees as significantly different from all other boundary types, with a very low proportion of butterflies approaching to within one metre of the boundary.

Figure 3.10: Illustration of maximally non-significant sets of boundary types regarding proximity of butterflies to boundary. (Chi-square critical value for simultaneous test procedure = 13.277, for *df* = 4, P = 0.01).



3.3.3.4 Species differences

One important factor which could not be standardised when studying real farmland boundaries was the abundance of the different species at each boundary. In fact, this in itself was found to be an important part of the inter-boundary variation.

The abundance and behavioural responses of each species category at the different boundaries is shown in Figure 3.11, for all species groups with more than 30 records. The majority of observations fell into the category Blues (n = 338), of which at least half were Geranium Argus butterflies. The second most common species group was the Small fritillaries (n = 240), followed by Large fritillaries (n = 132). These three species groups were all most abundant at the Control site. Small Tortoiseshell (n = 64) were most common at the High wall, whilst Small Heath (n = 59) and Large Wall Brown (n = 38) were most common at Low wall. Large Skipper (n = 54) were most abundant at Trees. The small number of sightings of Whites (n = 18) and Red Admiral (n = 18) were rather evenly distributed amongst the sites.

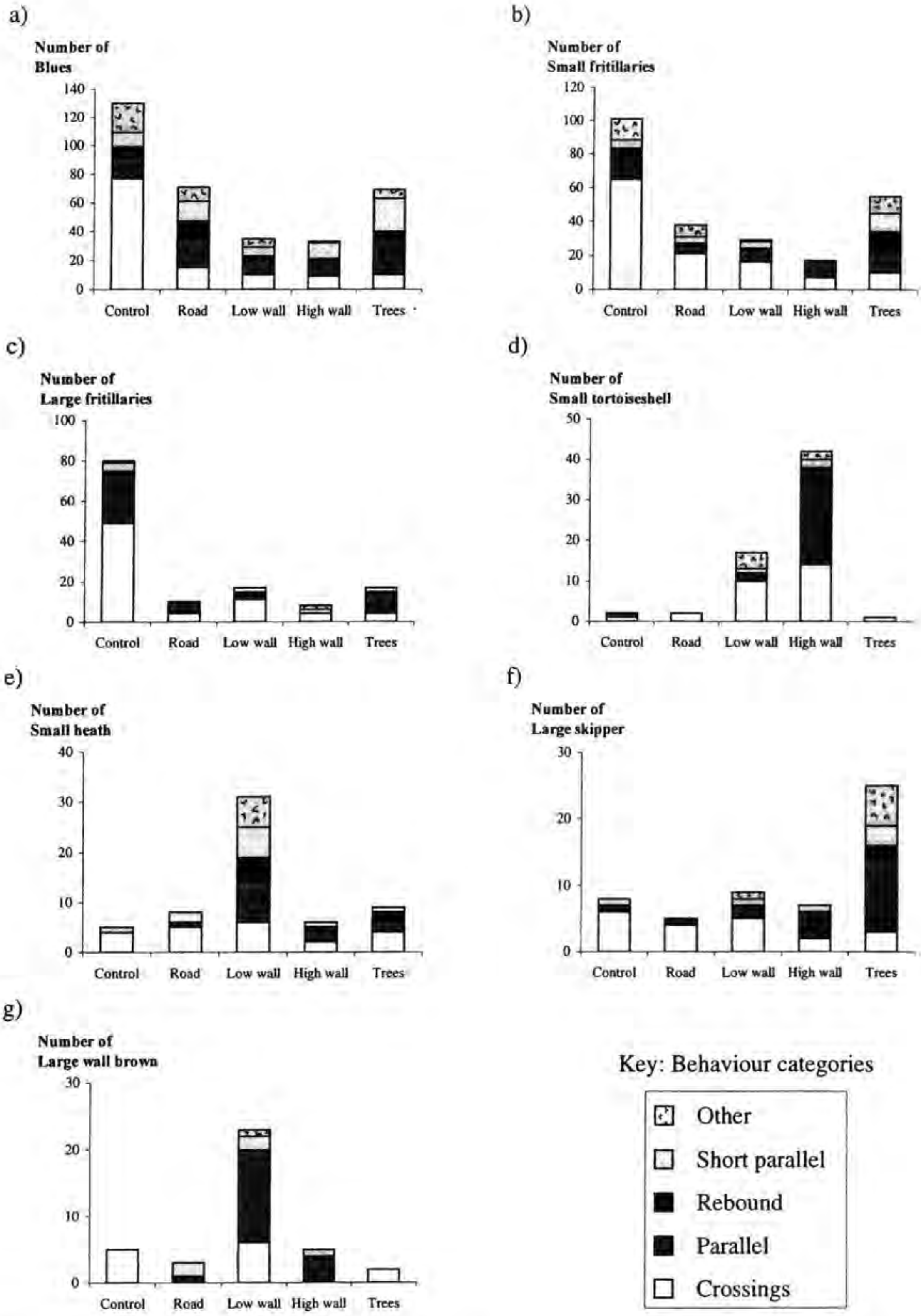


Figure 3.11: Numbers of butterflies in each behaviour category at each of the different boundary types, for a) Blues, b) Small fritillaries, c) Large fritillaries, d) Small Tortoiseshell, e) Small Heath, f) Large Skipper, g) Large Wall Brown (see text for details of species groups). Note the different scales on the x-axes.

Clearly, some of the differences in behaviour at the different boundaries may be due to differences in the relative abundance of species with different behaviour patterns. To take an extreme example, Small Tortoiseshell contribute 33.1 % of the observations recorded at High wall (Table 3.10) compared with only 0.6 % at Control, so if Small Tortoiseshell have atypical behaviour patterns this will affect results from High wall but not results from Control.

Table 3.10: Percentage of observations per species category for each boundary type

Species	**Boundary type**				
	Control	Road	Low wall	High wall	Trees
Blues	38.9	50.7	20.6	26.0	36.3
Small fritillaries	30.2	27.1	17.1	13.4	28.9
Large fritillaries	24.0	7.1	10.0	6.3	8.9
Small Tortoiseshell	0.6	1.4	10.0	33.1	0.5
Small Heath	1.5	5.7	18.2	4.7	4.7
Large Skipper	2.4	3.6	5.3	5.5	13.2
Large Wall Brown	1.5	2.1	13.5	3.9	1.1
Red Admiral	0.3	2.1	3.5	3.9	1.6
Whites	0.6	0.0	1.8	3.1	4.7

Ideally, the relationships between behaviour and boundary type which have been analysed using data pooled for all species, would have been analysed separately for each of the species categories. However, sample sizes become impracticably small when observations are separated into the six behaviour categories at five boundary types for nine species categories. For species comparison, further grouping of species is unreasonable, due to important differences in ecology (see Discussion), so in order to gain at least a crude measure of species differences in reaction to the different boundaries, behaviour categories were grouped into just two classes: 'Crossing' (Enter and Leave) versus 'Not crossing' (Parallel, Rebound, Short parallel and Other).

No significant differences were found between species at Control, High wall or Trees ($G = 5.95$, 8.23 and 12.40 respectively; $df = 8$; $P > 0.05$). However, behaviour was not independent of species at Road ($G = 19.08$; $df = 7$; $P < 0.05$) or Low wall boundaries ($G = 20.40$; $df = 8$; $P < 0.01$). Examination of the data revealed that Blues crossed Road relatively less than the other species (Large Wall Brown did not cross at all but with a sample size of only six individuals this counts neither one way nor the other). When Blues were removed from the analysis, there were no significant differences between the remaining species ($G = 6.56$; $df = 6$; $P > 0.05$). Similarly at Low wall, crossings by Blues, Large Wall Brown and Small Heath were relatively less frequent than for other species, with around 10 % to 15 % of approaches resulting in crossings. These three species categories formed one homogenous group ($G = 0.69$; $df = 2$; $P > 0.05$) whilst the remaining species formed a second homogeneous group ($G = 2.02$; $df = 5$; $P > 0.05$), in which proportions crossing were around 30 % to 50 %.

3.3.4 Discussion of responses to boundaries on farmland

3.3.4.1 Comparison of boundary types

The analysis of movement over different types of boundary structure on farmland supports the general findings of earlier experiments; that is, that tall boundary structures reduce the proportion of butterflies crossing the boundary. Thus, few butterflies entered and left recording boxes beside Trees and High wall transects compared with the more open boundary types.

It is worth noting, however, that the reactions to Low wall and Road boundaries were significantly different from reactions at Control sites, even though Low walls were only about half a metre high and Roads were actually lower than the vegetation. This supports the theory that the processes controlling butterfly behaviour are subtler than a physiological inability to cross boundaries. In fact, there was some evidence that the wide expanse of the road surface, although flat, was more of a deterrent to butterflies than the much narrower, if somewhat higher, strip of tumble-down stones forming a low wall. It seems likely that butterflies can perceive the continuation of resources at the other side of the wall, but not at the other side of a three metre wide road.

The division of behaviour into more refined categories than simply crossings and rebounds did enable the teasing apart of some rather more subtle differences between boundary types. Unfortunately the category Short parallel is not easily interpreted since it may reflect the start or end of either a rebound or a parallel movement (see, again, Figure 3.9 for examples of the categories). So the differences in proportions of Short parallel movements may simply be a symptom of differences in the Parallel and/ or Rebound categories. Generally, very abrupt turns away from the boundary were not as common as might be implied by the experiment with the artificial hedge, where all reactions that did not involve crossing the boundary were termed 'rebounds'. In fact, it was far more common that butterflies turned to fly parallel to boundaries, as was suggested, in section 3.2.4, in explaining the effects of neighbouring hedge sections.

The two boundaries receiving the greatest proportion of Rebounds were Trees and Road. As mentioned above, the wide expanse of Road appeared to create a significant barrier to butterfly movement, comparable to some extent with that created by Trees. However, the high proportion of butterflies found within one metre of Road suggests that these two boundary types differ in that Road, lying at field level, is not as readily perceived by butterflies. Butterflies therefore come closer to Road before responding whereas Trees are very apparent from a distance and invoke an earlier response. This probably also partly explains the lower number of butterflies approaching Trees, although, as discussed below, this will also be a function of habitat preferences.

For all of the landscape elements examined, the proportion of parallel movements exceeded that at Control sites, being particularly frequent at Trees and High wall. Movements following the direction of a linear landscape element would appear to suggest a corridor function, whereby directional movement is enhanced by the boundary structure. It is particularly interesting that the two boundary types showing this type of function to the greatest degree were those which had the greatest barrier effect. Butterflies would therefore appear to have been deflected from their natural course of movement and channelled along in the direction of the boundary through lack of ability or inclination to cross it.

3.3.4.2 Species differences

The most obvious species differences were the large differences in abundance from one site to another, reflecting habitat preferences. Blues and Fritillaries were most common in the meadow, i.e. Control. Small Tortoiseshell, Small Heath and the appropriately named Large Wall Brown clearly favoured wall-side habitats, which is in line with the known ecology of these species.

Small Heath, although a general grassland species, make use of perching sites in mate-location (Wickman, 1985) and, for this low-flying species, low walls would be very suitable sites. When unmated females want to attract the attention of males, they fly to suitable male perching sites and fly back and forth at about a metre above the ground to make themselves conspicuous. This behaviour explains the higher abundance of Small Heath at Low wall, and the relatively large proportion of approaches to the wall which do not result in crossing. The Small Heath is interested in a resource - a mate - which is associated with the wall and is not necessarily interested in the resources beyond the wall.

Both the Small Heath and the Large Wall Brown are members of the family Satyridae and have rather similar ecology (Henriksen and Kreutzer, 1982; Chinery, 1989). These species were not grouped, however, since the large size and more powerful flight of the Large Wall Brown lead to the expectation that they might differ in their reaction to boundaries. Interestingly this was found not to be the case, at least as far as abundance was concerned, with Large Wall Brown also showing a marked preference for Low walls. This lends further support to the idea that butterfly movement behaviour depends not only upon mere physical flying ability but also upon species specific ecological strategies.

Small Tortoiseshell preferred High wall sites, which may be linked to the frequent occurrence of nettle food-plants near taller walls (although none were located within the transects studied). Walls also aid in mate location for Small Tortoiseshell, which establish temporary territories along such features (Baker, 1971; Bitzer and Shaw, 1979). An additional advantage of wall habitats, for both the satyrids mentioned above and the Small Tortoiseshell, is the possibility for butterflies to gain thermal energy by basking against stones.

The only species differences in movement patterns (proportions crossing versus 'not crossing') occurred at Low wall and Road, the two boundary types which would seem to be more behavioural barriers than physical ones. Again, however, it is difficult to separate the effects of the boundary from habitat effects. The low proportion of satyrids crossing Low wall is obviously linked to the high proportion of other movement patterns along this, their linear habitat. The low proportion of Blues crossing Low wall and Road may be due to the same cause since some Blues, such as the very common Geranium Argus and Mazarine Blue, can thrive in the small strip of flowery vegetation alongside a road or wall.

It was unfortunate that so few Red Admiral movements were observed. This species is particularly interesting since it is a long-distance migrant to Scandinavia from Southern and Central Europe. Clearly, a butterfly which can fly such distances is not to be hindered by a wall or a hedge! However, studying the landscape level movements of this butterfly after it has established itself in Norway each year, may contribute to an understanding of the energetic and motivational stimulation behind butterfly movement behaviour.

3.3.4.3 Linear habitat, corridors or barriers?

The role of boundaries as habitat is obviously an integral part of the ecological functioning of landscapes. For small animals such as butterflies, a strip of grasses and flowers can provide all the resources needed for completion of the life cycle. The added benefits of a sheltered microclimate (Dover *et al.*, 1997) can make boundaries more favourable habitat than open meadow. The barrier effect of tall vegetation may also increase the habitat value along a boundary by increasing the probability of males and females coming into contact with one another. It is clear that there must be a particularly strong selective advantage in using the warm, sheltered microclimate of a wall if stray individuals of the opposite sex are likely to be channelled into the same area. It is thus extremely difficult to disentangle the habitat, corridor and barrier functions of boundaries.

Trees would appear to be the only boundary type for which a linear habitat role seems improbable for the butterflies in question. The results of the analysis of proximity to the boundary illustrate that exceptionally few butterflies closely approached the Trees boundary type and it is thus tempting to interpret the high proportion of parallel movements as the result of an inhibition to cross this tall, dark boundary type. Is this a corridor then? Certainly, by hindering flight over the boundary, movement is channelled in the direction of the landscape feature, yet there seem to be few positive features of the trees themselves as far as the butterflies are concerned. On the whole, the term barrier seems more appropriate, but it is clear that the roles of barrier and corridor can be almost synonymous. Similarly, the very fact that a feature can act as a corridor, directing the movements of con-specifics, may be sufficient to make it an important habitat feature for mate location.

The convenient labels that we may wish to give to landscape elements are obviously not clear cut in nature. Rather than trying to categorise landscape features into either the one or the other type, a more realistic view is to accept the multiple functions of landscape structures and reserve these terms simply for the specific function we wish to discuss. This approach is all the more logical when we consider species specific differences in behaviour.

3.4 GENERAL DISCUSSION

In this chapter we have seen that individual butterflies often avoid crossing boundaries. The hypothesis proposed at the end of the preliminary study that boundary height contributes to a barrier effect was strongly supported by later experiments. In addition, there was evidence from roads that boundary width is also important in determining the proportion of butterflies that cross. The second hypothesis, that species with different ecological / physiological requirements differ in their responses to boundaries, was also supported. However, although the strength of behavioural responses varied, the same basic trends were observed in all species studied. Whether the causes of the barrier effect are physiological or behavioural, the consequences will be the same; landscape features will shape the patterns of movement of butterflies in the landscape.

In a meadow, butterflies are free to fly throughout quite a large area where nectar sources and mates are fairly evenly spread resources. If all butterflies follow the same basic rules of flight they will all tend to stay within the same areas such that mate location is efficient and the risks of flying into unsuitable areas are reduced. This theory is supported by work by Keller *et al.* (1966) who demonstrated that butterflies returned to their specialised environment when artificially displaced from it. The authors suggest that the butterflies responded to cues such as topography, degrees of shadow and abundance of nectar sources. Clearly, large physical features in the landscape, such as walls, roads and hedges, would provide far more obvious cues to aid butterfly orientation.

In a large meadow or a system of small meadows which are linked to one another by strips of meadow vegetation, such flight rules should aid the persistence of butterfly populations by preventing individuals from crossing boundaries and flying off into unsuitable habitat. The problem comes when the patch of good habitat is reduced in size and links with other habitat patches are severed. In this situation, the same flight rules would lead to increased isolation of populations; diminished 'rescue effects' (sensu Brown and Kodric-Brown, 1977), i.e. the chance that populations close to extinction will be revived by the arrival of immigrants; and reduced gene flow between populations. Evidence that this has in fact happened in a butterfly metapopulation comes from work by Descimon and Napolitano (1993) who found genetic isolation in fragmented populations of the Clouded Apollo. Other lines of evidence have come from morphological studies of butterflies. For example, Dempster's (1976) studies of the Swallowtail (*Papillio macheaon*) revealed that isolated populations had reduced musculature in the thorax, associated with reduced mobility. This is assumed to have resulted from strong selection pressure, whereby all mobile individuals died before finding another habitat and only sedentary butterflies that stayed in their native patch produced offspring.

Understanding dispersal patterns will aid the conservation of butterfly species and their habitats. However, traditional metapopulation models do not incorporate such information. They show patterns of distribution of populations but lack information on how these patterns come about. For example, Hanski *et al.* (in press) recently developed a spatially explicit model to predict the rate and pattern of spread of two species of butterfly introduced into networks of vacant patches. This model assumed migration to be independent of both butterfly density and patch area but the authors pointed out that migration was likely to be of importance and more information was needed to understand its role in population survival.

If butterfly movement is so influenced by the structure of vegetation then it should be possible to predict movement patterns from landscape layout. Following individuals in the field is a difficult and time consuming task; if general flight rules exist such that the probability of movement in a particular direction can be calculated then a computer model can be used to simulate the distribution of butterflies. To test whether the presumed flight rules are correct, a computer simulation can be carried out for a known region and the resulting distribution of butterflies in the model be compared with real distribution in the field. If it is possible to predict butterfly distribution accurately, the next step would be to simulate an alteration in the landscape layout such that alternative land management scenarios can be assessed in terms of their benefit or otherwise to butterflies. The incorporation of system dynamics into the model, such that population dynamics and temporal changes in the landscape are included in a spatial setting, would greatly improve on present metapopulation models.

If this type of modelling is to be *realistic* however, we first need to find out more about the behaviour of individuals and its consequences for populations. Some butterflies do cross even the tallest of boundaries and it is clearly these individuals who are responsible for gene flow and the colonisation of new habitat patches. But how large a proportion of the population is involved in emigration from the native patch? If different motivational states make some individuals dispersers and others residents, can we recognise particular qualities which characterise these two groups?

The next chapter considers one meadow species, the Scarce Copper, and aims to link the behaviour of individuals at boundaries, with movement patterns at the landscape level and their consequences for populations.

CHAPTER 4

FROM LANDSCAPE ELEMENTS TO LANDSCAPE: A MARK-RELEASE-RECAPTURE STUDY OF THE SCARCE COPPER

4.1 INTRODUCTION

The previous chapter identified tall vegetation as being a barrier to the movement of meadow butterflies. This chapter will examine whether the behavioural responses of individuals observed on a small scale have consequences for the movement patterns of butterflies at the population level. The spatial scale of the study is thus increased from the consideration of single landscape elements to an examination of an entire landscape with all its components.

The species chosen for study was the Scarce Copper (*Lycaena virgaureae*) (Plate 6, p.85), one of the most common meadow species in the study area and thus the species for which most movement data was available from the experimental work with the artificial hedge. Also the sexes of the Scarce Copper are readily distinguishable and the barrier experiment identified differences in the movement behaviour of males and females. Taking into account aspects of the population biology and ecology of the Scarce Copper, this chapter aims to determine the role of landscape structure in shaping patterns of movement within and between patches of habitat. Models were developed using parameters from the experimental work, i.e. from observation of individual behaviour at the level of single landscape elements. The predictions of the models were then compared with observed movement patterns at the population and landscape level.

Mark-release-recapture (MRR) methods are clearly suitable for obtaining spatially referenced data to try to answer some of the questions of how butterflies use landscapes (Scott, 1975a; Scott, 1975b; Warren, 1987a; Both, 1988). Butterfly research has relied a great deal on the technique of capturing and marking butterflies, then releasing them, allowing time for them to mingle with the rest of the population and calculating population size from the proportion of marked individuals present in subsequent capture sessions (Ehrlich and Davidson, 1960; Warren, 1987a; Harrison *et al.*, 1988; Dover *et al.*, 1992). MRR data has been used to determine population sizes, in order to monitor the increases or, more commonly, reductions of butterflies (Douwes, 1970; Brakefield, 1982b; Gall, 1984b; Warren *et al.*, 1984; Thomas *et al.*, 1986; Aagaard and Hanssen, 1992; Väisänen *et al.*, 1994), to study habitat preferences by comparing numbers in different areas (Douwes, 1975; Brakefield, 1982a), and to assess the success of habitat management (Warren, 1987b).

More recently there has been a number of MRR projects to examine how the spatial arrangement of habitat patches influences butterfly populations (Harrison *et al.*, 1988; Thomas and Harrison, 1992; Thomas and Jones, 1993; Hanski *et al.*, 1994; Hill *et al.*, 1996; Lewis *et al.*, 1997). These studies have been complemented by large-scale recording of the presence or absence of butterflies in habitat patches, which explore metapopulation theories through the use of observed patterns of occupancy, often over several years (Hanski *et al.*, 1995).

4.1.1 The study area

The MRR study was centred around the same meadow which was used for the experimental work in Chapter 3. This area lies on the edge of a large area of traditionally managed farmland. The study system comprised nine meadows, separated by up to 800m of different intervening vegetation types, from clear-fell to forest (see Plates 2 and 3, p.46; and Plates 7 to 9, p.85 and p.86).

The traditional hay meadows encompass a fairly broad range of plant communities. Generally though, they may be said to comprise dry to moist meadow type, characterised by, amongst others, Elder-flowered Orchid (*Dactylorhiza sambucina* L.), Fragrant Orchid (*Gymnadenia conopsea* L.), Spotted Cat's-ear (*Hypochoeris maculata* L.), Common Milkwort (*Polygala vulgaris* L.), Purging Flax (*Linum catharticum* L.), Alpine Bistort (*Polygonum viviparum* L.) and Mat Grass (*Nardus stricta* L.) (Norderhaug, 1996, and *pers. obs.*).

The most abundant nectar plants were Wood Cranesbill (*Geranium sylvaticum*), Clovers (*Trifolium* spp.), St. John's Wort (*Hypericum* spp.), Yarrow (*Achillea millefolium*), Sneezewort (*A. ptarmica*), Birdsfoot trefoil (*Lotus corniculatus*), Buttercups (*Ranunculus* spp.) and various yellow composites (including Goldenrod (*Solidago virgaurea*), Nipplewort (*Lapsana communis*), Hawkbits (*Hieracium* spp.) and Hawkweeds (*Leontodon* spp.)).

The larval food plants (as given by Henriksen and Kreutzer, 1982, and Douwes, 1975) available in the area were Common Sorrel (*Rumex acetosa*), which was generally abundant, and Sheep's Sorrel (*Rumex acetosella*), which occurred in a few dense patches in rocky areas with thin soils. Two meadows, Old and Meadow 'A', had only small numbers of sorrel plants (Common Sorrel), located mainly at the meadow edges. Throughout the remaining meadows, sorrel was rather unevenly distributed, being absent from drier, short turf areas such as the eastern part of Upper Main, and otherwise ranging from scattered individuals to dense patches in moister areas.

Photo: Jo Inge Fjellstad

Plate 6: A male Scarce Copper (*Lycaena virgaureae*).

Plate 7: The southern half of Blika Meadow. The boundary vegetation was relatively open at Blika.

Plate 8: Barn Meadow was surrounded by forest and overgrown clear-felled areas, and had relatively impermeable edges.

Plate 9: Signs of abandonment were particularly obvious in Old Meadow.

4.2 METHODS

4.2.1 Recording butterfly movements

The entire study area was marked out into a grid of 20 m x 20 m squares. A grid reference, consisting of a letter and a number, was written on paper tape tied to a stake in the north eastern corner of each square. In order to complete observations over the entire area during a period of similar weather conditions, five recorders covered roughly equal areas during a two hour period. Two to three recording sessions were carried out in a day, depending on weather conditions. Recorders moved between meadows on a rotational basis, to compensate for any recorder bias and to balance the work load.

During marking sessions, recorders walked at a slow pace, up and down this grid system at 10 m intervals, looking for butterflies for 5 m to either side. Walking pace was adjusted in different vegetation types to account for differing apparency of butterflies. Only butterflies within 5 m in any direction from the recorder were captured, thus ensuring equal capture effort in each marking area.

Scarce Coppers were netted, marked with a letter and number code written with felt-tip pen (Artline 250, 0.4 mm), and released at the capture site (Plates 10 and 11, p.88). The whole procedure was performed as quickly as possible to minimise handling stress. This was facilitated by the use of clear plastic envelopes punctured with holes: an open envelope was held over a netted butterfly such that the individual was forced to crawl into it, the envelope was then closed, thus immobilising the butterfly between the two plastic surfaces. An individual code could then be written on the underside of the wings through the holes in the envelope and the butterfly then released. This method prevented the wing damage which occurs when small butterflies are taken between the fingers, since the plastic surfaces of the envelopes did not stick to the wing scales and the amount of pressure applied to the butterfly was more easily controlled. Marking with numbers was considered preferable to the frequently used '1-2-4-7' dot code system (Ehrlich and Davidson, 1960) and its modifications (Brussard, 1970) because numbers are easier to write and remember, whereas dot codes may be more easily misinterpreted (Gall, 1985).

Plates 10 & 11: Butterflies were marked with individual codes.

For each butterfly the following details were recorded:

- date
- time of capture
- an asterisk if the butterfly was marked for the first time
- individual butterfly letter/number code
- sex
- condition: scale cover and wing wear were recorded separately, using a scale of 1 (fresh) to 3 (worn) for each
- exact capture location (to nearest 5 m)
- activity prior to capture (nectar-feeding, resting, basking, flying, interacting with other individuals etc.).

4.2.2 Calculating population sizes

The development of the statistics involved in calculating butterfly population sizes has received considerable attention in the literature (Jolly, 1965; Cook *et al.*, 1967; Roff, 1973; Brown and Ehrlich, 1980). This is in keeping with the generally conservation-oriented goals of many MRR studies, where management plans based on false estimates may have serious consequences for butterfly populations. In spite of this interest, however, the tradition has been to estimate daily population sizes (Chapter 5) and there are very few methods available to calculate the total number of butterflies present in an area during a season (Arnason *et al.*, 1995). Since this study focuses on Scarce Copper movement, using data accumulated throughout the summer, a relatively simple measure of population size for the entire season was more appropriate than estimates of daily population sizes.

Thus, in order to determine whether population size had any effect on movement patterns, estimates of population size per meadow were calculated following the method employed by Seufert (1990). This method assumes that the proportion of all marked butterflies which are recaptured at least once is equal to the proportion of marked individuals in the entire population, i.e.

$$\frac{Xm}{Xtot} = \frac{Xre}{Xm}$$

where Xm is the number of marked butterflies, Xre the number which are recaptured at least once, and $Xtot$ is the entire population size. It follows that:

$$Xtot = \frac{Xm^2}{Xre}$$

The method assumes that:

1) intensive daily marking effort ensures that a constant proportion of new individuals receive marks
2) marked and unmarked individuals have the same probability of dying or emigrating
3) all animals are equally likely to be captured (this includes the assumption that marked animals mix thoroughly with the unmarked population)
4) marks are not lost or over-looked

Since there was evidence from previous experiments that male and female Scarce Coppers differ behaviourally, population estimates were carried out separately for males and females to avoid bias caused by unequal catchability. In addition, the data used for calculating population sizes did not include recaptures which occurred within one hour of original marking.

The assumption that marks are not lost, seemed reasonable after my own experience in other MRR projects (Aagaard *et al.*, 1997), using similar marking procedures and the same type of marking pen.

4.2.3 Residence time

The residence time of a butterfly is the period of time which that butterfly is known to be present, i.e. from the first day the butterfly is observed to the last recapture of the individual (Ehrlich, 1961). The term residence incorporates the fact that, when using MRR data, additions to the population by 'birth' (eclosion of adult butterflies, in this case) cannot be separated from additions by immigration. Similarly, death and emigration cannot be distinguished as causes of loss. Average and maximum residence times were determined separately for male and female Scarce Coppers. Butterflies captured for the first time 10 days or less from the end of the experiment were excluded from the analysis.

It is highly improbable that all butterflies were detected on their first day of flight and seen for the last time on the day of their death/ emigration, and the true residence time of butterflies is thus almost certainly under-estimated. To compensate for this, residence times were also calculated excluding individuals which were only caught once, as recommended by Seufert (1990).

Residence times, in the form of recapture-duration plots, were also employed to examine loss rates of males and females. This method, described by Watt *et al.* (1977), involves inspection of semi-logarithmic plots of recapture numbers against the survival period of the recaptures. Thus the first point on the graph is the natural logarithm (ln) of the number of butterflies known to be in residence for at least one day; the second point is the ln number known to be present for 2 days or more, the third point is the ln number in residence for three days or more etc.

4.2.4 Measurements of movement

For the purposes of analysis, the letter/ number map co-ordinate system used in the field was converted to a co-ordinate system based on metres north and east of an origin. This allowed the trigonometric calculation of distances between capture points to be performed automatically in the Microsoft Excel database. Distances were calculated between successive capture points, as a total of all registered movements for each butterfly, and as displacement between first and last capture.

The time elapsed between captures of an individual were calculated in terms of 'active hours', whereby night-time hours, i.e. the hours after roosting and before butterflies begin to fly early in the morning, are excluded from consideration. From 7:00 am to 7:00 pm were counted as 'active hours'. This is a maximum number of active hours since daily weather variations will shorten the length of time in which butterflies are physiologically capable of flight. Obviously, it is highly problematical to give a true picture of potential flight time since this will be dependent not only on the overall daily temperature, frequency of cloudy intervals, rain showers etc. but also a function of conditions during the night and on previous days. For example, a rainy night will cause a cool microclimate in the vegetation even if the morning air temperature is relatively high, and a run of cold weather, preventing nectar feeding, may mean that a butterfly must spend more time warming up when a good day does come, due to lack of energy. However, whilst the calculation of active hours may not be perfect, it gives a more realistic estimation of displacement over time than would be obtained if night-time hours were included.

4.2.5 Physiological characteristics of between-meadow dispersers

The physiological characteristics of the individuals moving between meadows are of great importance in determining the ecological significance of this movement for the population, since dispersers only influence the future of populations if they give rise to viable offspring. Thus, all between meadow movements were analysed to find the sex and age structure (and hence an indication of the fitness and reproductive status) of dispersers. This procedure was somewhat complicated by the protandry of the species, since males, having emerged up to two weeks before the females, had a longer time period in which to make long distance movements. Also, on any particular day, the average age of males would be higher than the average age of females so it was important to correct the number of dispersers of each age class with regard to the distribution of age classes in the male/ female population at any given time.

4.2.6 Movement in relation to direction / topography

In order to identify any directional preferences in the movement patterns of Scarce Copper, the numbers of flight paths in each compass direction were compared. Movements were divided into the four main compass directions, North, East, South and West (each category comprising a 60° segment) and, between these, the four sub-categories North-east, South-east, South-west and North-west (comprising 30° segments). Chi-square tests were used to compare the movement of males and females and to compare observed movement with expected movement based on a random distribution with respect to direction.

Since the terrain in the study area slopes predominantly in a north-south direction, any preference in this directional axis may reflect a preference for moving uphill/ downhill.

4.2.7 Exchange rates between meadows

In order to exclude the hypothesis that movement between meadows was random, Pearson product moment correlation coefficient was calculated to measure the strength of association between the number of butterflies flying from one meadow to another (say A to B) and the number flying in the opposite direction (B to A). If some constant factor of landscape structure influences movement, it may be reasoned that movement would be of the same magnitude in either direction. Provided this condition is fulfilled, movements in either direction between meadows can be pooled for further analysis, increasing sample sizes. Movement patterns between meadows can then be compared by calculating an 'exchange rate' for every combination of meadow pairs. The exchange rate provides a measure of the number of butterflies observed to have moved between meadows in relation to the total number of observations possible, and is calculated by:

$$\frac{X_{A\to B} + X_{B\to A}}{Xre_A + Xre_B} \times 100$$

where for any pair of meadows (A and B), $X_{A\to B}$ is the number of butterflies flying from A to B, $X_{B\to A}$ is the number flying from B to A, Xre_A is the number of butterflies originally marked in A and recaptured at some point (anywhere in the study area) and Xre_B the corresponding number for butterflies marked in B.

4.2.8 Effects of meadow area and butterfly density on exchange rate

Previous butterfly studies have shown an effect of habitat patch size on dispersal (Hill *et al.*, 1996; Sutcliffe *et al.*, 1997). To examine area effects on Scarce Copper movement, a Mantel test (Mantel, 1967) was used to compare the matrix of exchange rates between combinations of meadows against a matrix of meadow size (i.e. the combined size of the donor and recipient meadow, for each combination of meadows). The Mantel test posits the null hypothesis that there is no association between the elements in one matrix and those in the other. In order to test whether the Mantel statistic was significant, a sampled permutation test was performed, in which the elements of one matrix were randomly rearranged 10,000 times (for an 8 x 8 matrix, the possible number of permutations of the data is 40,320). The observed Mantel statistic could then be compared against a population of 10,000 Mantel statistics (see Sokal and Rohlf, 1981; Legendre and Fortin, 1989; Fortin and Gurevitch, 1993).

The same process was carried out to determine whether exchange rates were correlated with the densities of butterflies in the different meadows. Since estimation of female population sizes was made somewhat unreliable due to small sample sizes, the densities used were the density of males multiplied by two, i.e. assuming a 1:1 ratio of males to females.

4.2.9 The role of landscape permeability

The effect of landscape permeability on butterfly movement was explored with the help of GIS software, Idrisi for Windows (Clark Labs, 1995). A 1:13000 infra-red aerial photograph provided information on the spatial configuration of the different vegetation types in the study area. (The area was photographed in the summer of 1993 by FotoNor, and the positive transparency was scanned and delivered in digital form by the same company).

The image was simplified using 'supervised classification' in Idrisi. This involved on-screen digitising of polygons around representative areas of known land cover, providing the program with a spectral signature for each land cover type. Then each pixel in the image was automatically classified as the land cover type to which its signature was most similar. The result was checked with knowledge from the field. Seven land cover categories were used, thus making the original 256 colour image more comprehensible whilst maintaining a much finer scale of resolution than would be possible if land cover were to be digitised manually.

In order to model the movement of butterflies across this landscape, each land cover type was then given a 'friction value', whereby high friction indicates low permeability to butterfly movement. Friction values were assigned according to approximate vegetation height (0, 1, 2 or 3 m) and made use of the results from the experimental hedge (Chapter 3):

Friction Value = 100 - Percent crossing the artificial hedge

The Idrisi 'cost distance' function was run separately for each meadow, symbolising butterflies moving out from the meadow across the landscape according to the different friction values. In the resulting map, each pixel has a value corresponding to the least cost distance from the starting point. This distance is an 'ecological distance', i.e. a combination of the effect of vegetation type and real (Euclidean) distance, whereby butterflies can fly long Euclidean distances through low friction areas but only short Euclidean distances through high friction areas.

The values at each pixel in the map are not meaningful numbers in themselves and the model cannot give exact probabilities of butterflies emigrating from one meadow to another. However, the pixel values provide an expected ranking of meadows based on the theory that movement is a function of Euclidean distance and landscape permeability. When cost distance is high, a low exchange rate of butterflies can be predicted. The model was run nine times, each time with a different meadow as the starting point. The result of each run was thus a ranking of meadows according to the predicted exchange of butterflies between the starting point meadow and each of the others. This expected ranking was then compared with the observed ranking of meadows according to the exchange rates recorded in the MRR study. Spearman's rank order correlation statistical tests were performed to ascertain whether the theoretical and observed rankings were significantly different. To compare the predictive power of ecological distance based on landscape permeability with that of Euclidean distance alone, the ranking of meadows based on Euclidean distance alone was also compared with the observed exchange rates of butterflies.

The ecological distance model was then developed to take into account the fact that the model was parameterised using data from the study of a boundary. Evidence from the behavioural experiments, discussed in Chapter 3, suggested that Scarce Coppers perceived the artificial hedge as the edge of their habitat. Thus, the data on numbers of butterflies crossing the hedge, and hence the friction values used in the ecological distance model, are relevant for the edges of habitat patches. The digitised image of the landscape allowed objective comparison of the perimeter vegetation of each meadow and it was therefore possible to test the relationship between the vegetation at meadow edges and the butterfly movements detected by MRR. Linear regression was used to determine whether there was any relationship between the numbers of butterflies emigrating from each meadow and the percentage 'openness' of the perimeter vegetation (i.e. the percentage of perimeter pixels which were meadow/ grassy vegetation).

Having confirmed an edge effect, a new cost distance model was created in which the friction values from the experimental hedge study were applied only to the perimeter of meadow and grassy patches. This model assumes that butterflies which once pass the perimeter of a meadow, move through subsequent landscape elements more easily. The model assumes though that butterflies will fly down to investigate grassy, open areas, where nectar sources and potential mates may be found. On leaving small patches, butterflies will again be confronted by edges, thus each grassy patch is surrounded by a buffer of friction values (the same figures as used previously, i.e. from the hedge experiment). The edge model therefore emphasises contrasts in the landscape.

4.3 RESULTS

4.3.1 Population sizes and sex ratios

The first Scarce Copper males emerged on 12th July whilst females did not appear until 19th July. Seventy males had been marked before the first female was found. The greatest numbers of butterflies, both males and females, were marked in meadows Scout and Blika (Table 4.1), whilst Barn was the meadow in which fewest butterflies were marked. In all nine meadows, more males were marked than females, and the proportion of marked individuals recaptured was higher for males. There was no evidence to suggest that the distribution of marked butterflies between the meadows was different for males and females ($G = 14.532$; $df = 8$; $P > 0.5$).

For the entire area, the total population size was estimated as 3390. This is lower than the sum of the estimates for the individual meadows (4949 butterflies). Whilst the ratio of marked males to females was 1.9 to 1, estimated numbers of males and females indicated a ratio closer to unity (0.9 to 1).

Recapture success was significantly different for males and females (non-parametric Mann-Whitney rank sum test; $P < 0.0001$). Overall recapture rates were 28% for females and 58% for males, with females being captured an average of 1.4 times, and males an average of 2.6 times. Some male butterflies were captured up to 15 times, whilst the maximum for any female individual was 5 captures.

Table 4.1: Numbers of Scarce Copper females and males marked and recaptured per meadow. Population sizes were estimated separately for males and females using the method of Seufert (1990). Sex ratios are given; both the proportion of males to females marked in the field and the sex ratio of the estimated male and female populations.

Site	Sex	Total marked (Xm)	Total re-captured at least once (Xre)	Seufert Population estimate	Sex ratio marked males:females	Sex ratio estimated males:females
Barn	f	15	0	- [a]	2.3	- [a]
	m	35	16	77		
Blika	f	106	18	624	1.7	0.6
	m	179	79	406		
Lower Main	f	46	9	235	2.3	1.5
	m	107	32	358		
Meadow 'A'	f	56	16	196	2.8	1.5
	m	155	82	293		
Old	f	37	11	124	1.5	1.1
	m	57	24	135		
Scout	f	151	45	507	1.9	1.1
	m	283	138	580		
Steep	f	29	4	210	3.1	1.2
	m	90	32	253		
Teigen	f	69	13	366	2.1	0.9
	m	145	62	339		
Upper Main	f	40	3	- [a]	2.5	- [a]
	m	99	40	245		
Entire area	f	505	143	1783	1.9	0.9
	m	935	544	1607		

[a] Where sample sizes are very small, estimates are not given in cases where finding one more marked butterfly would change the estimate of population size by more than 50.

4.3.2 Residence time

Residence times were significantly shorter for females than males (Mann-Whitney rank sum test; $P < 0.0001$). The mean residence time was 5.5 days for males (standard deviation = 4.7 days) and 3.6 days for females (sd = 3.5 days), with maximum residence times of 22 days and 16 days, respectively.

When individuals caught only once are removed from the calculation (to compensate for under-estimation), the mean residence times are 7.4 days for males (sd = 4.4 days) and 5.9 days for females (sd = 3.5 days). Again, residence times were significantly shorter for females (Mann-Whitney rank sum test; $P = 0.006$).

Linear regression through all data points of recapture-duration decay plots (Figure 4.1) indicates, on the whole, a relatively constant loss rate of both males (slope = -0.284; $r^2 = 0.959$; $P < 0.0001$) and females (slope = -0.321; $r^2 = 0.977$; $P < 0.0001$). Within this overall pattern, variations in loss rate were apparent, with males and females showing the same trends. There were relatively few short residence times (1 to 3 days), followed by a period of approximately constant loss rate and finally, an increased loss rate after 18 days for males and after 15 days for females (Figure 4.1). During the period of constant decay, the loss rate for females was greater than that for males, as indicated by the slopes of the linear regression lines in Figure 4.1 (-0.323 for females versus -0.255 for males).

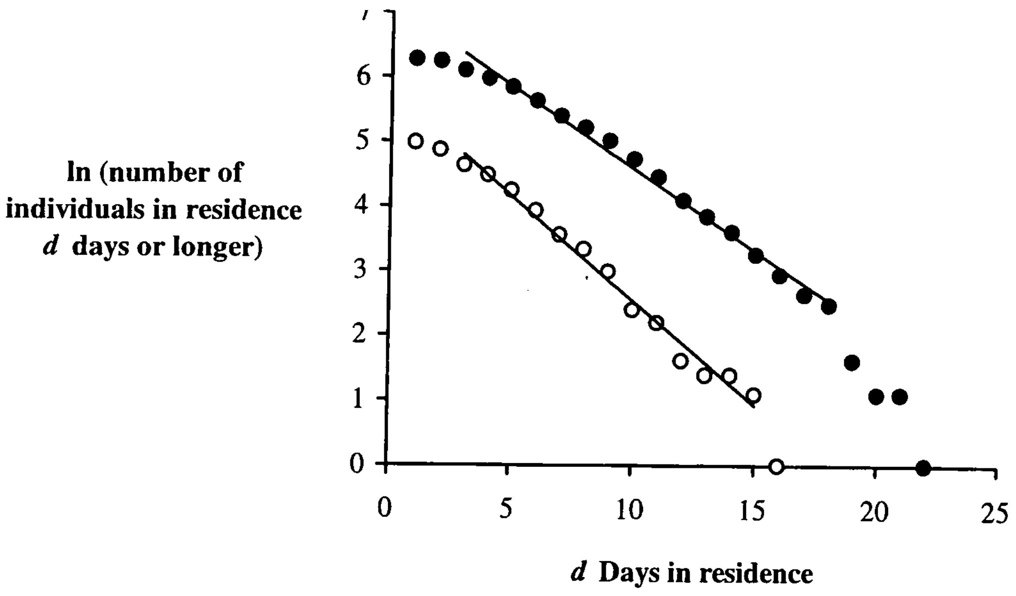


Figure 4.1: Recapture-duration decay plots for Scarce Copper males (closed circles; n = 528) and females (open circles; n = 144). The solid lines indicate linear regression through points which approximate to periods of constant survival: for 3 to 18 days residence for males (slope = -0.255; r^2 = 0.990) and 3 to 15 days for females (slope = -0.323; r^2 = 0.986).

4.3.3 Distances flown

The distances between successive capture locations of male and female Scarce Coppers, including both within and between meadow movements, are shown in Figure 4.2. The lines displaying the cumulative percentage of butterflies at any point show that the vast majority of butterflies moved less than 150 m, and that females moved slightly further than males. Thus, whilst 91.1 % of males moved less than 150 m and 95.2 % were under 250 m, the corresponding figures for females were 86.4 % and 92.0 % respectively. The mean distance between successive captures was lower for males (58.9 m) than for females (79.6 m), and a Mann-Whitney rank sum test identified the difference in distances for the sexes as statistically significant ($P < 0.0001$).

When distances were measured between the first and last capture locations of each butterfly, rather than between all successive captures, the results for females were virtually unchanged. Movement patterns of males, however, more closely matched those of females, and the sexes were not significantly different (Mann-Whitney rank sum test; $P = 0.0713$). Mean distances between first and last capture were 79.8 m for males and 84.6 m for females, with 91.8 % of males and 91.7 % of females moving less than 250 m.

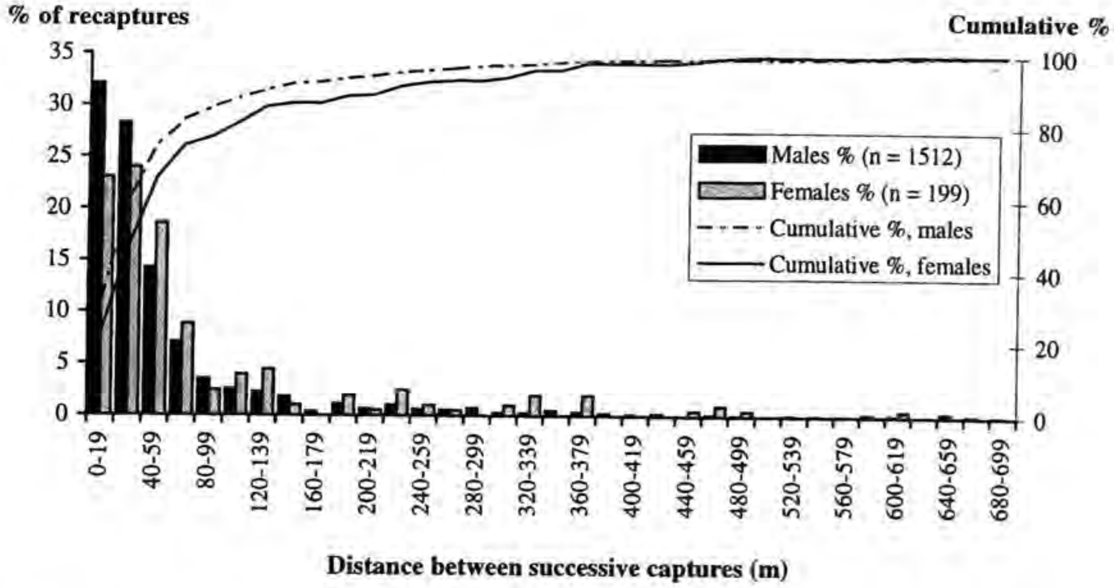


Figure 4.2: Graph showing the distance between successive captures, for males (n = 1512) and females (n = 199). Distances are divided into 20m categories. The lines show the cumulative percent of males and females for each distance.

The greatest total distance registered for any butterfly was for T 15, a male who was captured 6 times over the course of 21 days. The sum of the straight line distances between capture locations for this butterfly was 1424 m. Four other males moved total distances of over 1200 m, after which the greatest distance was 838m. The greatest total straight line distance for a female was 763 m, for A 28 who was captured 4 times over the course of 10 days.

There was no significant difference between the speed of movement of males and females (Mann-Whitney rank sum test; $P = 0.591$). The greatest speed recorded was 771 m per active hour, for a butterfly which was recaptured after 11 minutes, having moved 141 m. Generally, however, butterflies were not recaptured within short time intervals and the most meaningful result was therefore the combination of fastest time for maximum displacement. This was found to be for a butterfly which covered a distance of 657 m, from Blika to Scout, within four hours.

When between-meadow movements are considered alone, the inverse cumulative frequency of butterflies flying any given distance (Figure 4.3) is almost perfectly described by a negative-exponential function ($r^2 = 0.980$; $P < 0.0001$).

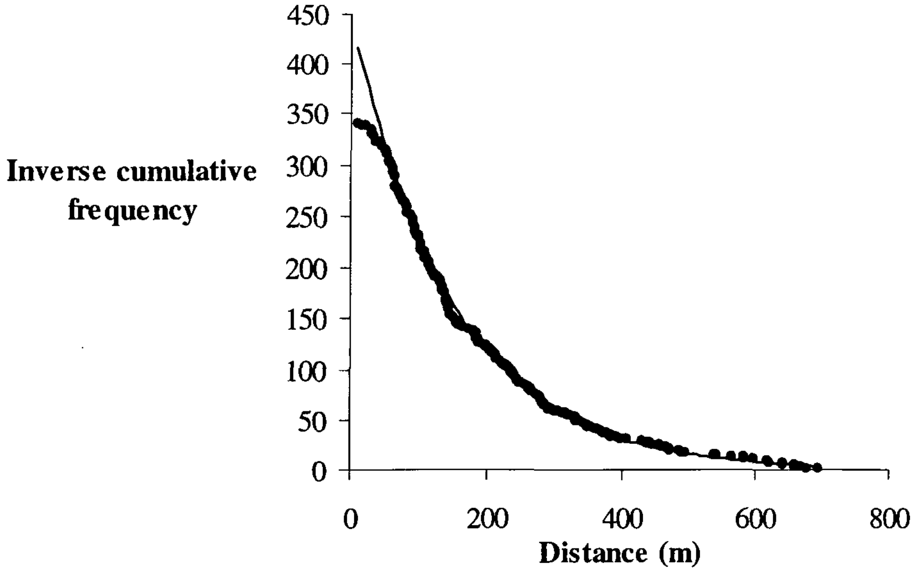


Figure 4.3: For between-meadow movements only: the inverse cumulative frequency of individuals reaching any given distance. The trend-line shows a negative-exponential function ($y = 445.66e^{-0.0066x}$; $r^2 = 0.980$; $P < 0.0001$).

4.3.4 Numbers of emigrants and immigrants

Observed numbers of emigrants and immigrants per meadow are shown in Figure 4.4. Meadows Barn and Old had fewest emigrants and immigrants, followed by Blika and Teigen. The meadows with most emigrants and immigrants, both in actual numbers and as a proportion of marked butterflies, were Upper Main, Lower Main and Steep.

There were no significant relationships between the number of emigrants or immigrants and meadow size, meadow perimeter length, meadow shape (compactness), population size per meadow or butterfly density per meadow (Table 4.2). The most interesting result from the correlation testing was a slight tendency for the number of emigrants to increase as the proportion of males in the population increased (correlation coefficient = 0.657; $P = 0.055$; $n = 9$), however, a larger sample size would be needed to establish confidence in the existence of any such trend. (The explanatory role of distance between meadows is analysed in section 4.3.8).

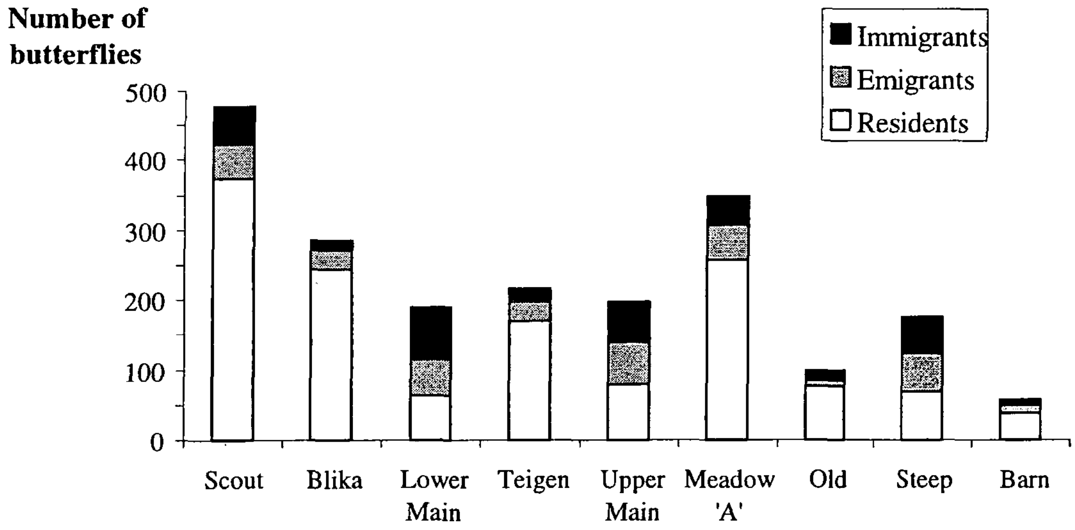


Figure 4.4: Numbers of emigrants and immigrants per meadow. The meadows are arranged along the x-axis in order of size, from largest to smallest.

Table 4.2: Non-significant results of Pearson product moment correlation tests of the relationships between the number of emigrants or immigrants per meadow and various potential explanatory factors (see text).

	Area	Perimeter	Shape	Male population size	Female population size	Sex ratio of marked butterflies	Butterfly density
Sample size	9	9	9	9	8	9	9
Emigrants							
Correlation coefficient	0,251	0,357	-0,047	0,453	0,127	0,657	0,602
P value	0,514	0,345	0,905	0,221	0,765	**0,055**	0,087
Immigrants							
Correlation coefficient	0,370	0,482	-0,075	0,445	-0,043	0,483	0,271
P value	0,328	0,189	0,848	0,230	0,920	0,188	0,481

4.3.5 Exchange rates between meadows

Pearson product moment correlation coefficient revealed that there was a significant association (correlation coefficient = 0.859; $P < 0.0001$; $n = 34$) between the number of butterflies flying from one meadow to another (say A to B) and the number flying in the opposite direction (B to A). It is therefore clear that the pattern of movement between meadows is not random. It also seems justifiable in further analysis to pool movements in both directions between meadows, i.e. to use the concept of 'exchange rate'.

The vast majority of butterflies were recaptured in the meadow where they were originally marked (see Table 4.3).Three meadows stand out: Lower Main, Steep and Upper Main, where the proportions of within-meadow recaptures lay in the region of 55 % compared with figures of around 80% for the other meadows.

These three meadows are also noteworthy when comparing movement between meadows. The three highest exchange rates were between Upper Main and Lower Main, Upper Main and Steep and Lower Main and Steep.

These three meadows are physically closely connected (Plate 12, p.107) and when analysed as a single unit (the so-called 'Central group' in Table 4.3) the exchange rate is 82.59, i.e. very similar to that of the other meadows.

There was no correlation between exchange rates and either the meadow areas (Mantel statistic = 0.0023; $P = 0.991$) or the densities of butterflies in the meadows (Mantel statistic = 0.0640; $P = 0.759$).

Table 4.3: Lattice of exchange rates of Scarce Copper between meadow pairs. The numbers in bold are the number of butterflies recaptured in the meadow in which they were originally marked. (See text for explanation of calculation).

	Barn	Blika	Lower Main	'A'	Old	Scout	Steep	Teigen	Upper Main	Central group[a]	Total butterflies marked & recaptured
Barn	**78.00**	0.31	4.24	0.00	0.00	0.42	1.16	1.20	2.62	(3.26)	50
Blika	0.31	**90.41**	0.78	3.28	0.28	2.02	0.25	0.21	0.49	(0.92)	271
Lower Main	4.24	0.78	**54.78**	3.55	2.49	2.79	10.50	2.55	18.75		115
'A'	0.00	3.28	3.55	**83.44**	2.79	0.55	8.35	0.59	0.89	(8.01)	308
Old	0.00	0.28	2.49	2.79	**89.53**	0.20	0.48	1.05	0.44	(1.51)	86
Scout	0.42	2.02	2.79	0.55	0.20	**88.86**	2.39	4.19	4.97	(6.99)	422
Steep	1.16	0.25	10.50	8.35	0.48	2.39	**56.10**	0.62	10.61		123
Teigen	1.20	0.21	2.55	0.59	1.05	4.19	0.62	**84.92**	0.88	(2.25)	199
Upper Main	2.62	0.49	18.75	0.89	0.44	4.97	10.61	0.88	**56.74**		141
Central group[a]	(3.26)	(0.92)		(8.01)	(1.51)	(6.99)		(2.25)		**(82.59)**	(379)

[a] Central group comprises Steep, Lower Main and Upper Main meadows pooled as a single unit.

4.3.6 Characteristics of between-meadow dispersers

Individuals having scores of 1 or 2 for both scale cover and wing wear, but not those where both scores were 2, were classed as good condition/ young individuals. Butterflies with a score of 2 for both measures of condition, and those having a score of 3 for either scale cover or wing wear were classed as poor condition/ old individuals (see Table 4.4).

Since butterflies appeared to perceive the three central meadows: Steep, Lower Main and Upper Main, as a single unit (as shown above), the division of movements into the categories 'between-meadow' and 'within-meadow' took this into account and all movements between these three meadows were grouped as movements within the central group (i.e. 'within-meadow').

Table 4.4: Condition of male and female Scarce Copper on recapture following a) movement between meadows and b) movement within meadows.

Condition		Males			Females		
Scale cover	**Wing wear**	**Total males**	**% of category (a / b)**	**% of all male recaptures**	**Total females**	**% of category (a / b)**	**% of all female recaptures**
			a) Between-meadow recaptures				
Good							
1	1	71	35.5	4.8	15	45.5	7.7
1	2	11	5.5	0.7	5	15.2	2.6
2	1	34	17.0	2.3	7	21.2	3.6
Total, good condition		***116***	***58.0***	***7.8***	***27***	***81.8***	***13.8***
Poor							
1	3	0	0.0	0.0	0	0.0	0.0
3	1	0	0.0	0.0	1	3.0	0.5
2	2	66	33.0	4.5	4	12.1	2.0
2	3	9	4.5	0.6	0	0.0	0.0
3	2	5	2.5	0.3	0	0.0	0.0
3	3	4	2.0	0.3	1	3.0	0.5
Total, poor condition		***84***	***42.0***	***5.7***	***6***	***18.2***	***3.1***
Grand Total		**200**	**100**	**13.5**	**33**	**100**	**16.8**
			b) Within-meadow recaptures[a]				
Good							
1	1	490	38.2	33.1	96	58.9	49.0
1	2	58	4.5	3.9	19	11.7	9.7
2	1	252	19.7	17.0	20	12.3	10.2
Total, good condition		***800***	***62.4***	***54.0***	***135***	***82.8***	***68.9***
Poor							
1	3	3	0.2	0.2	1	0.6	0.5
3	1	1	0.1	0.1	0	0.0	0.0
2	2	373	29.1	25.2	21	12.9	10.7
2	3	46	3.6	3.1	3	1.8	1.5
3	2	23	1.8	1.6	1	0.6	0.5
3	3	36	2.8	2.4	2	1.2	1.0
Total, poor condition		***482***	***37.6***	***32.5***	***28***	***17.2***	***14.3***
Grand Total		**1282**	**100**	**86.5**	**163**	**100**	**83.2**

[a] The category 'within meadow recaptures' includes movements between Steep, Lower Main and Upper Main, i.e. within the Central group.

The fraction of recaptures involving movement between meadows was very similar for males and females, i.e. dispersal was independent of sex (G = 1.541; *df* = 1; P > 0.1).

The proportions of individuals in each condition category were very similar for butterflies moving between meadows and those moving within meadows, both for males (G = 1.407; *df* = 1; P > 0.1) and females (G = 0.019; *df* = 1; P > 0.5). There was thus no evidence of condition/ age dependent dispersal. The proportions of good condition individuals were consistently higher for females (82.7% of all female recaptures) than for males (61.8% of all male recaptures).

4.3.7 Movement in relation to direction / topography

The distribution of flight paths between the compass directions is shown in Figure 4.5. Totally random movement between the direction categories (see Method, section 4.2.7) would result in 16.7% of captures to each of N, E, S and W, and 8.3% of captures to each of NE, SE, SW and NW. For both males and females there was a majority of movements in the East-West axis.

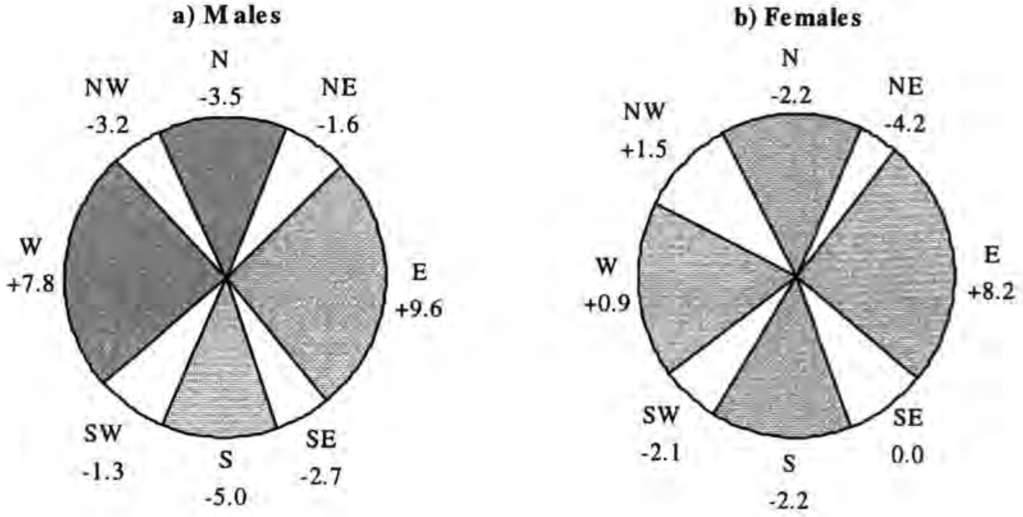


Figure 4.5: The distribution of flight paths between the compass directions for a) male (n = 1395) and b) female (n = 193) Scarce Copper. The numbers refer to the difference between the observed percentage of flights in a given direction and the expected percentage based on a random distribution (16.7 % of captures to each of N, E, S and W, and 8.3 % of captures to each of NE, SE, SW and NW).

There was a slight, statistically significant difference between males and females (Chi-square = 15.5; *df* = 7; P = 0.0302). Females appeared to approach random movement (Chi-square = 7.29; *df* = 7; P = 0.3997), although the power of the statistical test was poor (0.4493) due to small sample size. Male observed flight paths were, however, significantly different from that which would be expected if movement were directionally random (Chi-square = 89.9; *df* = 7; P < 0.0001).

When only those movements which resulted in between-meadow dispersal are taken into consideration, no significant difference could be found between males and females (Chi-square = 10.7; *df* = 8; P = 0.2191) and the total picture, as shown in Figure 4.6, is one of random movement with respect to direction.

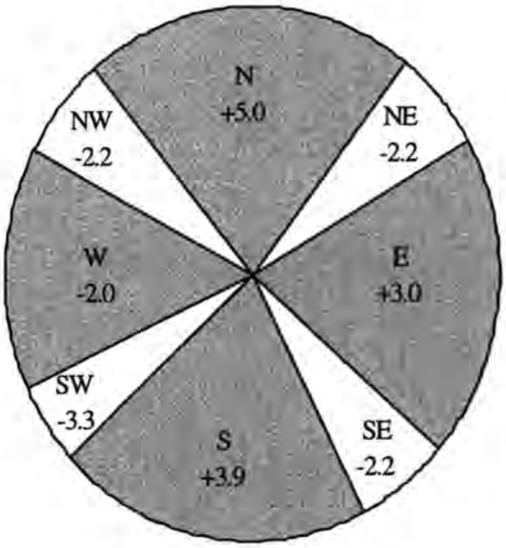
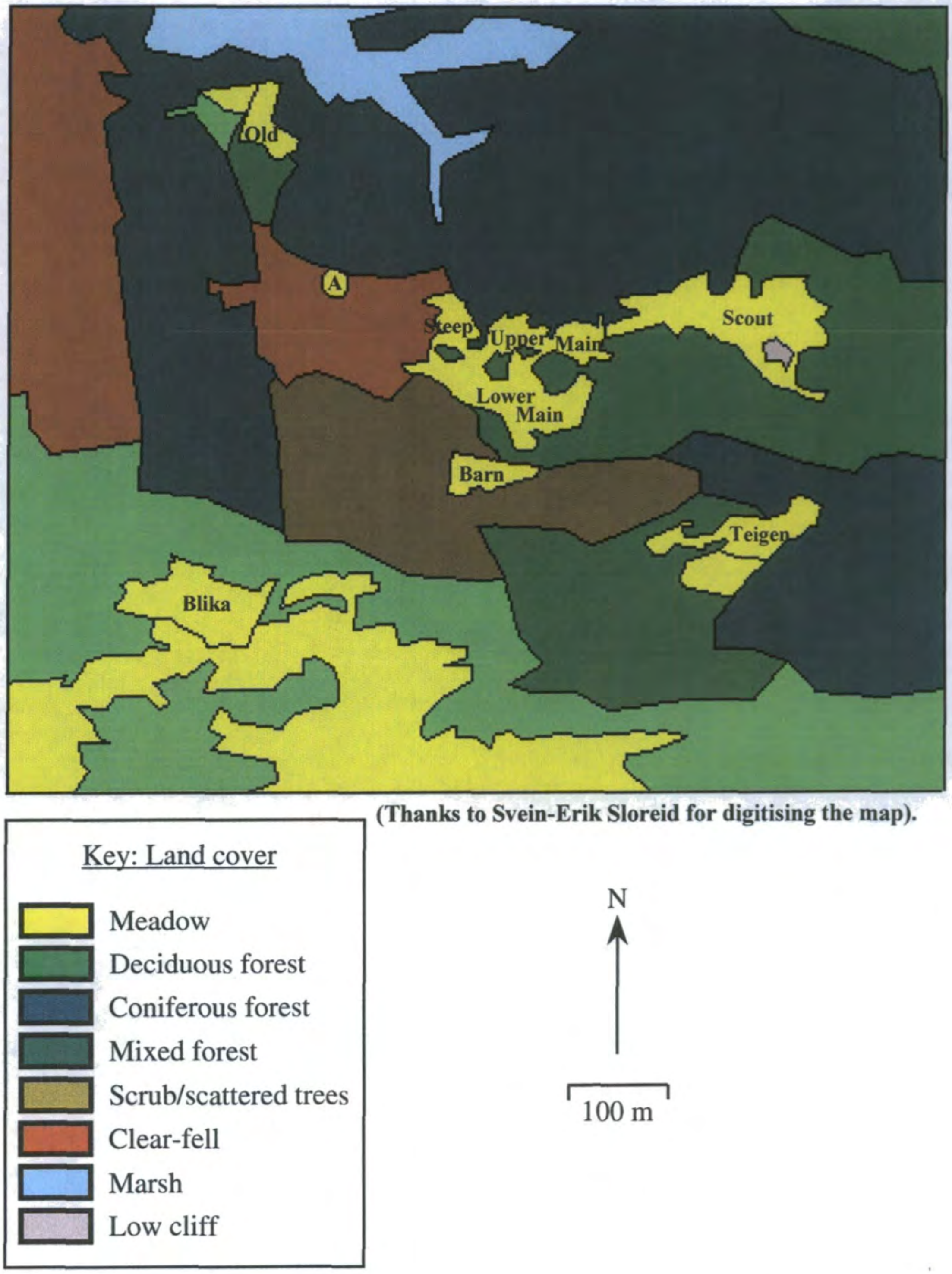


Figure 4.6: Percentage of between-meadow flights in each compass direction (n = 341 recaptures). The numbers refer to the difference between the observed percentage of flights in a given direction and the expected percentage based on a random distribution (16.7 % of captures to each of N, E, S and W, and 8.3 % of captures to each of NE, SE, SW and NW).

The directions of between-meadow movements were evenly spread, with no sign of any strong directional preference. Since the topography of the area was such that the land sloped steeply in a north-south direction, this also indicates that there were no strong preferences for moving uphill / downhill (or that any such preferences were masked by other factors).

4.3.8 The role of landscape permeability

Plate 12 (p.107) shows a hand-digitised land cover map of the study area; Plate 13 (p.108) shows the Idrisi image of the same area following supervised classification of an infra-red aerial photograph. The map in Plate 14 (p.109) is the result of running the cost distance module of Idrisi, using Meadow 'A' as a starting point.



(Thanks to Svein-Erik Sloreid for digitising the map).

Plate 12: Map of the area used for the mark-release-recapture study of the Scarce Copper (*Lycaena virgaureae*). In some analyses, the meadows Steep, Upper Main and Lower Main were treated as a single unit: the 'Central group' (see text for details).

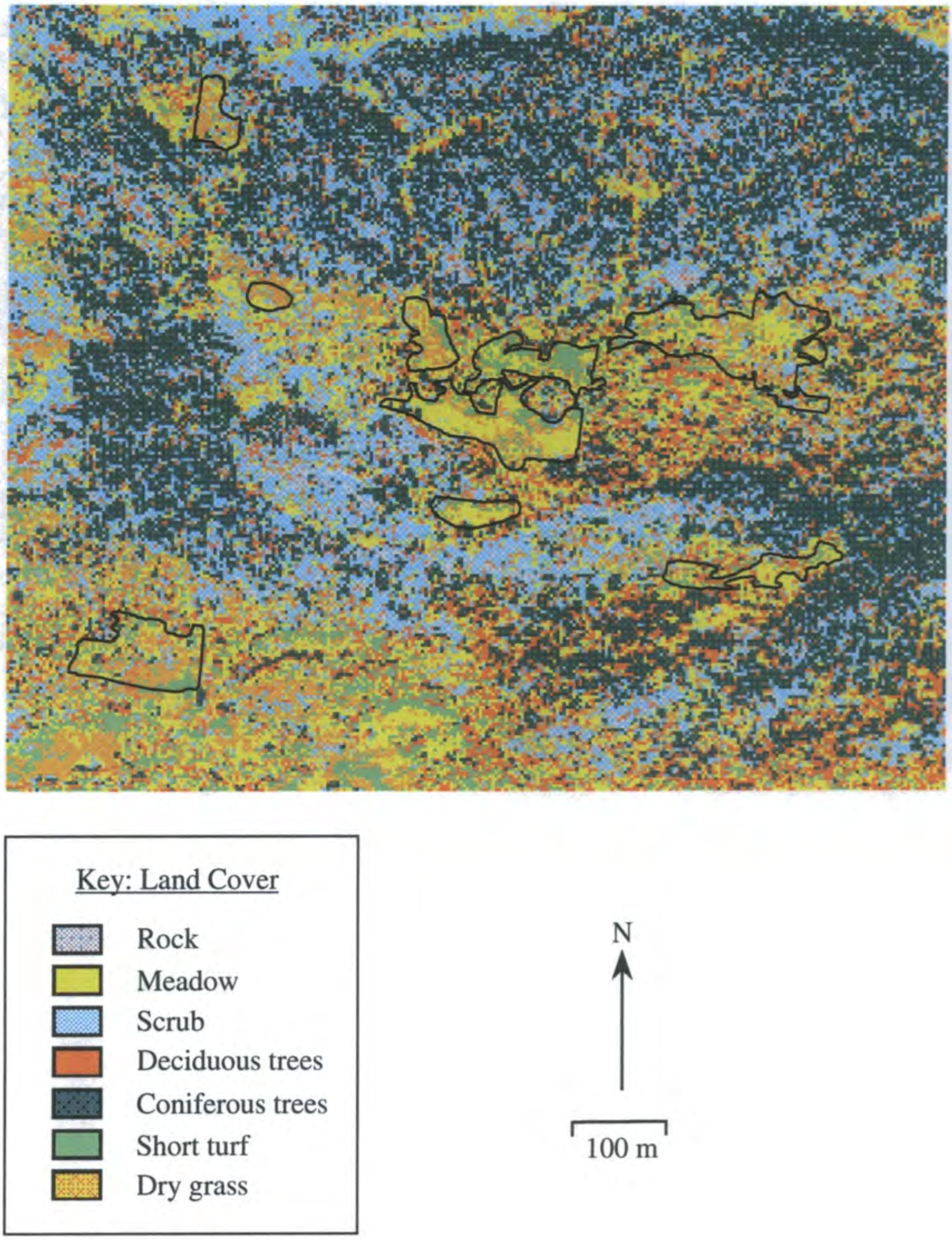


Plate 13: Map of the study area following semi-automatic land cover classification of an infra-red aerial photograph, using Idrisi for Windows. Each pixel in the image was classified as the land cover type to which its spectral signature was most similar. A rough outline of the meadows has been overlaid for illustrative purposes.

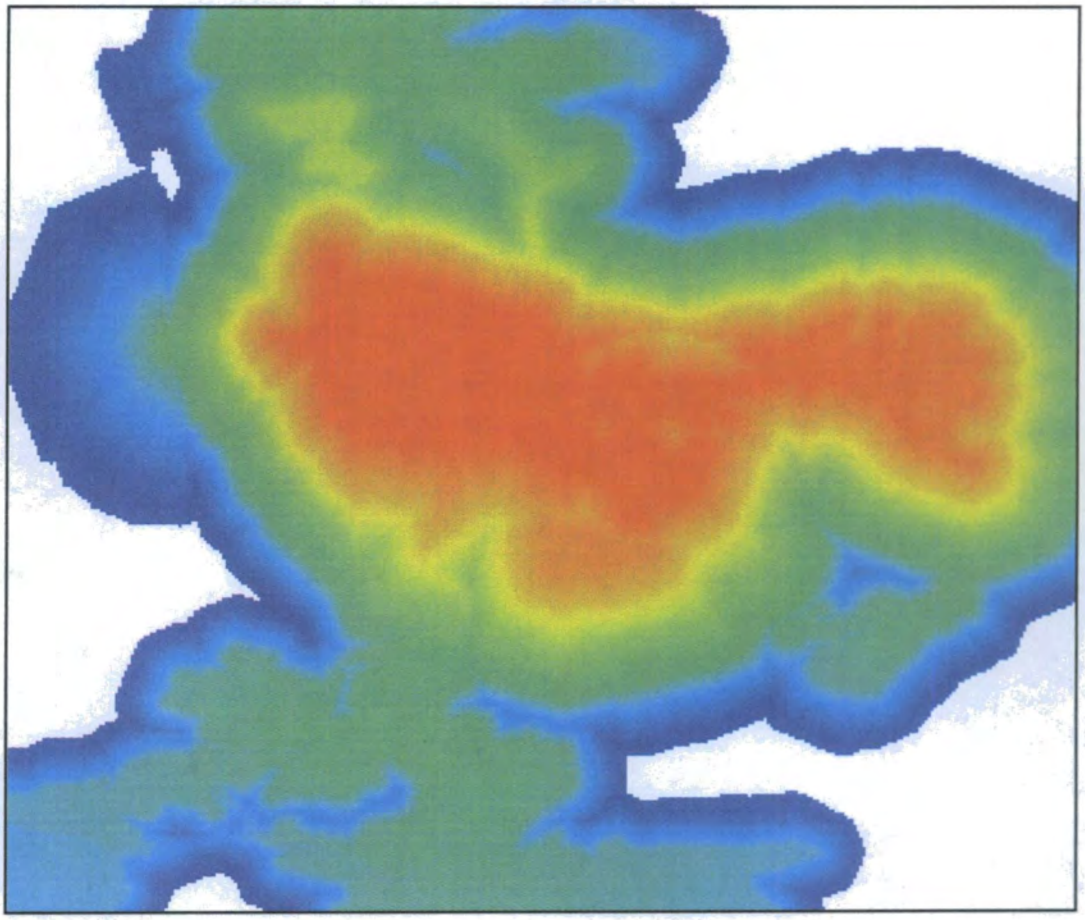


Plate 14: Map of the probability of a butterfly from Meadow 'A' reaching any given point in the landscape, as predicted based on a combination of Euclidean distance and boundary permeability. The probability increases towards the red end of the spectrum and decreases towards the blue end of the spectrum (compare with map on Plate 12).

Euclidean distance alone was a relatively good predictor of butterfly movement patterns. For five of the nine meadows in the study area, the ranking of meadows produced by a pure distance model was significantly similar to the ranking found by MRR, i.e. the meadows which the model predicted as having high probability of receiving emigrant butterflies from a particular starting meadow, were those which had been found to receive most emigrants in the field (see Table 4.5). The meadows from which movement was not similar to that predicted were the more peripheral meadows of the study system.

An ecological distance model, incorporating friction values for different vegetation types, gave marginal improvements in predictive power, and the results for Teigen came very close to the desired 95 % significance level. Although the ecological distance model was only a slight improvement on simple Euclidean distance, the results encouraged further investigation. Of particular interest was any relationship between the vegetation at meadow edges and the butterfly movements detected by MRR.

A plot of numbers of emigrants against the degree of openness at the perimeter of meadows (Figure 4.7) showed a clear pattern of increasing emigration with increasing openness, with one exception - the meadow Blika. When this outlier is excluded, the relationship between movement and perimeter vegetation is highly significant ($r^2 = 0.7993$; $P < 0.003$). Blika is unusual in that it has the most open perimeter of all the meadows (54.6 % of the perimeter comprised grassy vegetation) but relatively few emigrants.

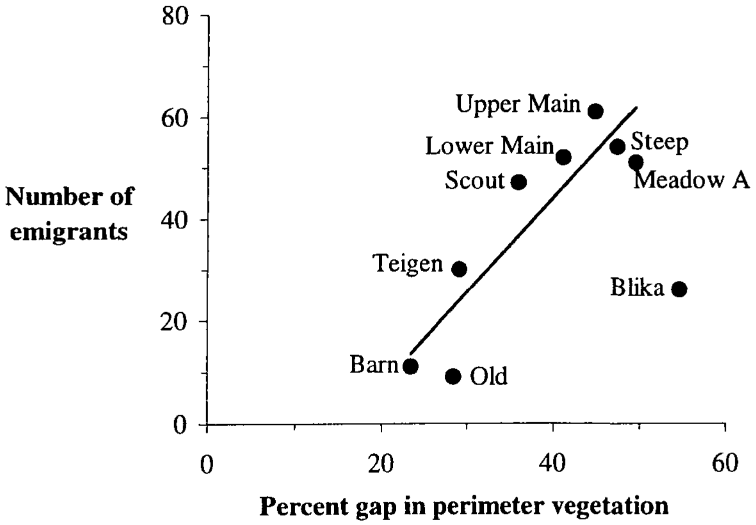


Figure 4.7: The relationship between numbers of emigrants per meadow and the degree of openness in the vegetation at the perimeter of the meadows. The regression line was drawn excluding data from Blika.

The confirmation that butterfly movement was influenced by the vegetation structure in boundaries lead to refinement of the ecological distance model, as described in the Method (section 4.2.9). The resulting edge model was a better predictor of butterfly movement than either Euclidean distance or the original ecological distance model (Table 4.5). Predicted rankings and observed rankings of meadows were significantly similar in seven of the nine cases. Meadows Blika and Old remained unpredictable.

Table 4.5: Results of Spearman's rank correlation tests showing whether or not the ranking of meadows according to observed movements of Scarce Coppers was significantly similar to the ranking predicted by the movement models created using Idrisi.

	Euclidean distance			Ecological distance			Edges model		
Meadow starting point	Correlation coefficient	P-value	Sig.	Correlation coefficient	P-value	Sig.	Correlation coefficient	P-value	Sig.
Barn	-0.870	0.000	***	-0.870	0.000	***	-0.870	0.000	***
Blika	0.190	0.619	ns	-0.190	0.619	ns	-0.190	0.619	ns
Lower Main	-0.980	0.000	***	-1.000	0.000	***	-1.000	0.000	***
Meadow 'A'	-0.524	0.160	ns	-0.524	0.160	ns	-0.691	0.047	*
Old	-0.452	0.233	ns	-0.571	0.120	ns	-0.524	0.160	ns
Scout	-0.762	0.021	*	-0.810	0.010	**	-0.833	0.005	**
Steep	-0.950	0.000	***	-0.930	0.000	***	-0.857	0.002	**
Teigen	-0.548	0.139	ns	-0.667	0.059	ns	-0.762	0.021	*
Upper	-0.980	0.000	***	-0.900	0.000	***	-0.900	0.000	***

4.4 DISCUSSION

4.4.1 Numbers marked and population sizes

The marking of almost twice as many males as females may have been due in part to the earlier emergence of the males. However, the population estimates for the entire period indicate that there were approximately equal numbers of males and females in the study area. It therefore seems that the most important reason for the excess of marked males was the higher catchability of the males. This is explained by the different goals of males and females. Whilst males permanently search for mates throughout their lives, females, once mated, only need to fly to find nectar and egg laying sites. Since interactions between butterflies lead to wing wear and even injury, mated females will benefit by remaining as inconspicuous as possible to avoid the attentions of males. Douwes (1976) found, through studying time budgets of Scarce Coppers, that males fly five to ten times more than females, whilst females spend more time sitting on vegetation. Since such seek and hide strategies of the sexes apply to many butterfly species, capture proportions between the sexes are frequently biased in favour of males in MRR studies (Watt *et al.*, 1977; White and Levin, 1981; Napolitano, 1989; Daily *et al.*, 1991), even for species where laboratory-rearing of butterflies confirms an essentially 1:1 sex ratio (Brussard and Ehrlich, 1970c).

The discrepancy between the direct estimate of the total population size for the study area and the sum of the estimates for each meadow can be explained partly by the smaller sample sizes for the individual meadows, leading to less reliable estimates. This was particularly the case for females, due to the lower numbers captured. In addition, butterflies moving between the meadows will adversely affect the population estimate. Emigration in itself should not affect the estimate, since it is assumed that the loss of marked individuals reflects the loss of unmarked butterflies. However, if the emigrant is then caught in other meadows, the method of estimation does not enable this to be distinguished from the emergence of newly hatched individuals, i.e. increases to the entire population. If the butterfly should then return to the meadow where it was first captured and be recaptured, the estimate for that site will be the same as if the butterfly had been on site continuously. Thus butterflies which move between meadows will lead to overestimation of the total number of butterflies in the area. Clearly then, the direct estimate of total population size will be more accurate, since marked butterflies are only counted once.

4.4.2 Residence time

The recapture-duration decay plots indicate a Type II pattern of survival (Deevey, 1947), that is, a constant loss rate. The slight under-representation of short residence times is a result of the fact that, due to bad weather, there were short gaps in the sampling period (Watt *et al.*, 1977).

The timing of the sampling period also had consequences for the maximum residence time documented for females. Since females emerged a week later than males, and recording was unfortunately ended before the complete end of the flight season, it is likely that female residence times are under-estimated. It should be added though, that there were 22 days between the first emergence of females and the end of sampling, so the maximum residence time of 16 days was not the maximum possible.

Whilst the final high loss rate of females may be an artefact of the sampling period, this is not the case for males. The recapture-duration decay plot shows an abrupt increase in loss rate of older males, over 18 days old, which probably reflects the onset of senescence, i.e. when the butterflies die in greater numbers due to old age. These results, both for males and females, agree well with an overview of residence times provided by Warren (1992a), in which maximum residence times given for six different British lycaenids range from 13 to 25 days. Warren (1992a) also reports that captive butterflies rarely live for longer than this and suggests that these figures represent the maximum age possible for these species. For four of these lycaenids, results were provided separately for males and females, and in all cases the females had the lower maximum residence time. This trend also appears to be common in other families of butterflies (Warren, 1992a).

Although the lower maximum residence time of females is probably linked to the sampling period, this does not explain the higher loss rate of females during the period of constant loss rate. It is unlikely that marking would cause higher female mortality than male mortality, since the sexes were treated equally. If there were any cause for higher mortality, it would probably be a result of the pen markings making butterflies more conspicuous and thus more vulnerable to predators that locate their prey by sight. However, female Scarce Coppers are naturally marked with black markings and the pen marks were thus more conspicuous on males than females. It should be added that an experiment by Morton (1982) on the Marbled White (*Melanargia galathea*) failed to find any effect of the size or colour of marks on butterfly recapture rates. Although this must depend on the type and intensity of predation to which a species is exposed, the results of that experiment are nevertheless encouraging.

Watt *et al.*(1977) suggest that higher loss rates for female *Colias alexandra* compared with males, may be due to increased female mortality caused by the exposure of ovipositing females to ground-dwelling predators, such as crab spiders. This scenario may also be likely for Scarce Copper. As mentioned above, the uneven ratio of males to females captured, attests not only to the earlier emergence of the males, but also to their greater mobility. The more worn wings of the males are probably also a symptom of this higher mobility. But whilst the less mobile females may keep their wings in good condition by remaining hidden in the grass, they may be more vulnerable to predation, for example by crab spiders, which were abundant at the field site.

4.4.3 Distances flown

The higher catchability of males also influences the results regarding flight distances. The shorter distances between successive captures for males are a logical consequence of the fact that males are caught more frequently than females. The apparent difference between the sexes disappears when the number of captures is cancelled out by considering only distances between first and last captures per individual.

The fact that the average displacement of Scarce Coppers is within the same order of magnitude both between successive captures and between first and last capture (60 to 85 m), indicates a general tendency to stay within a home range.

The close fit between the distribution of distances moved by butterflies and a negative-exponential function, lends empirical support to the use of such functions in metapopulation models (Hanski, 1994; Hanski and Thomas, 1994). Nevertheless, it should be noted that other authors have found evidence that an inverse-power function provides a better description of long-distance movements (Hill *et al.*, 1996). Since the MRR study reported here covered a relatively small area, the possibility of a longer tail of distant movements cannot be excluded; however, it is also possible that the relationship differs between species.

The lack of any significant difference in the movement patterns of males and females was unexpected considering the findings from the artificial hedge experiment (Chapter 3), where females showed an apparently more motivated movement behaviour. This discrepancy may be related to the different catchability of males and females and the relative proportion of males and females involved in trivial movements. The resident/ trivial life of males is very visible, involving considerable flight activity. That of females, on the other hand is invisible, involving much time hidden in the grass. Since the MRR study covered a large area, in which butterflies were also marked and recorded when found resting in the grass, it is reasonable to assume that a larger proportion of 'non-motivated' females were observed during the MRR study than during the behavioural experiment. Thus, the proportion of marked females moving between meadows may provide a better measure of the true fraction of the female population involved in dispersal compared with the proportion crossing the artificial hedge.

An alternative explanation may be that the barrier experiment recorded a truer, relatively higher level of female dispersal which was not detected in the MRR experiment due to, for example, limited size of the study area. This highlights one of the fundamental problems of using observation studies to investigate dispersal; namely, that the fate of unobserved individuals will always remain a mystery. When radio telemetry becomes practical for monitoring butterfly movements, our knowledge, especially of less apparent species or behavioural groups, will be significantly improved.

4.4.4 Movement in relation to direction / topography

There is no reason to expect butterflies to have directional preferences in a uniform landscape. However, the location of favourable habitat or adverse conditions may be expected to affect their movement patterns. Thus, the east-west bias in movement is entirely reasonable, considering that the shape of the study area was elongated along an east-west axis. Movements to the NE, SE, SW and NW were probably lower than would be expected if movement were random, due to the fact that the meadows which lay in these compass directions were somewhat peripheral to the main concentration of meadow. Whilst there is clearly a danger that multiple effects can mask one another, the results suggest that there were no strong directional or topographical preferences. Mallet (1986) found similar results in a study of *Heliconius erato*, i.e. no directional bias other than that caused by irregularities in the shape of the sample area.

The flight direction results, particularly the clear-cut picture of random directional movement by dispersers, support the theory proposed by Baker (1984) that equal direction ratios will be favoured in non-migratory butterfly species. Baker argues that it will be evolutionarily beneficial for offspring from the same parent to travel in equal numbers in all directions, to ensure that at least some offspring find suitable habitat. Baker (1984) found approximately equal direction ratios for Orange-tip and White-letter hairstreak.

4.4.5 Determinants of emigration

Wing wear ratings, believed to give a good indication of age (Cook *et al.*, 1976; Watt *et al.*, 1977; Gall, 1984b), lent support to the conclusion from analysis of residence times that there was no age-dependent emigration.

Evidence suggesting that emigration increased as the proportion of males in the population increased, fits theories about optimal thresholds of habitat suitability (Parker and Stuart, 1976; Baker, 1984). The protandry of Scarce Coppers is evidence that unmated females are a critical resource for males and, clearly, the higher the proportion of males flying at a site, the lower the chances of gaining access to an unmated female. Natural selection should therefore favour males which emigrate when the risk of not finding a mate becomes greater than the risks involved in dispersal. As for mated females, they would benefit by avoiding the risks of injury due to male harassment, and dispersing when the risks become greater than those associated with dispersal. The fact that there was no relationship between emigration and butterfly density, implies that habitat availability was not limiting in itself and that the costs and benefits of emigration were relative rather than absolute. This may also be the reason why only a very weak relationship was observed between emigration and the proportion of males.

The lack of any effect of patch size, perimeter or shape, was unexpected, considering the wealth of literature which has accumulated over the last couple of decades propounding the importance of these factors in fragmented landscapes (see Capters 1 and 2, and reviews by Collinge, 1996; Dramstad *et al.*, 1996). However, Stamps *et al.*(1987) concluded, from a theoretical study, that patch geometry may only have important effects in soft-edged habitats and not in hard-edged or insular habitats. The authors used computer simulations to investigate two factors affecting emigration: the influence of edge permeability and the importance of edge-to-size ratio or ESR. The models predicted greater emigration when boundaries were permeable and when patches had a high ESR. For patches with soft edges, ESR was the most important factor but for hard-edged patches, edge permeability was more important than ESR. The results presented here, evincing a strong relationship between Scarce Copper movement and edge permeability, provide empirical support for this conclusion.

4.4.6 Predicting butterfly movement

Comparison of observed and predicted patterns of butterfly movement indicate that Euclidean distance alone was a good predictor of Scarce Copper movements amongst neighbouring meadows. However, as inter-meadow distances increased, the distance model was less able to predict patterns of movement.

A simple model using ecological distance based on landscape permeability, gave slightly better results. In addition, by using the GIS capability to quantify land cover in a buffer zone around the meadows, a close correlation was identified between the openness of perimeter vegetation and emigration. This seemed to confirm the results of earlier behavioural experiments (Chapter 3) that landscape structure plays a role in movement. Blika meadow did not fit this pattern, having a high permeability but low number of emigrants; however, this was explained by the proximity of unstudied meadows to the south of Blika. Whilst butterflies from the other eight meadows had no alternative destination outside the study area, those from Blika could move in a southerly direction and therefore be lost from the study.

The demonstration, both by experiments and MRR observations, of the importance of perimeter vegetation in determining movement, lead to further development of the simple ecological distance model. The results obtained from the experimental hedge applied only to butterfly reactions on meeting boundaries of different heights. Once a butterfly has crossed a boundary, however, it may be unreasonable to assume that the next landscape feature poses an equal barrier effect. For example, if a butterfly flies up above a conifer at the edge of a meadow, it is unrealistic to assume that a second conifer behind the first presents an equally significant obstacle, since the butterfly no longer has to gain height to fly over the second conifer. Indeed, if the wind is blowing in the right direction, travel may be much faster at this height than over meadow habitat. Information about the rate of movement of butterflies within or over non-habitat was lacking, and, it may be added, would be extremely difficult to obtain. However, fast movements of a few individuals between, for example, Blika and Meadow 'A', suggested that once a butterfly has left a habitat patch it may move rather quickly through non-habitat until reaching a new patch. The second model therefore attempted to build in this edge effect around grassy patches, whilst allowing butterflies to move fairly easily (the same friction value as meadow) over remaining vegetation.

The edge model, although still simple, predicted butterfly movement very successfully. The information about the landscape, based on a simple classification according to vegetation height at boundaries, was an improvement over Euclidean distance as an explanatory factor. It would thus appear that the barrier effects measured for individuals responding to single landscape elements (Chapter 3) do have consequences for inter-patch movement at the population and landscape level.

These results provide empirical support for the theoretical prediction (Dunning *et al.*, 1992) that both landscape composition (habitat versus non-habitat) and landscape physiognomy (the spatial arrangement of these elements) will influence the distribution of butterflies. In particular, behavioural responses to barriers will be of significance in determining the connectivity of the landscape (Merriam, 1984; Taylor *et al.*, 1993).

The Scarce Copper populations in this study exchange too many individuals to be classified as a classical metapopulation and correspond more closely to the commoner type of system of extinction resistant 'patchy populations' described by Harrison (1991). The distinction between these definitions can be seen to be a consequence of landscape permeability, whereby the connectivity between patches causes divergence from the simplified metapopulation scenario. The landscape changes caused by agricultural dereliction (Chapter 2), particularly the increased occurrence of barriers of tall vegetation, will disrupt this connectivity and lead to progressively isolated sub-populations.

The strong correlation between number of emigrants and the permeability of boundary vegetation was perhaps one of the most striking results of this study and I suggest that for non-migratory butterflies, the degree of resistance presented by the matrix would be a valuable parameter to include in the growing family of increasingly sophisticated spatially explicit population models (Hanski and Gilpin, 1997).

4.4.7 Potential application of the butterfly movement model

The validation of the predictive model by MRR data suggests a range of potential uses for this approach. Although the model does not predict the distance at which areas become inaccessible to butterflies, it would be useful for comparing the relative effects of different landscape change scenarios on exchange rates between habitat patches. In particular, the model could be used in testing conservation management scenarios, for example to identify the most isolated and hence vulnerable sub-populations or to identify the best locations for meadow restoration.

It would also be possible to model the effects of increased or reduced resistance in the landscape at large; for example, the increased resistance in the Hjartdal area caused by the growth of barriers of trees along walls and fences and the change from areas of scattered trees to closed forest (demonstrated in Chapter 2). In this respect, the semi-automatic mapping of the landscape directly from aerial photographs was particularly useful, since it enabled the construction of a map with a scale of resolution relevant for butterflies, and superior to maps based on manual digitising.

A model which relates directly to a real landscape clearly has considerable advantages for landscape planning, especially with the increasingly user-friendly GIS software now available. The status of the Hjartdal area as one of Norway's most valuable cultural landscapes (Blomquist and Puschmann, 1993) has lead to considerable research activity in the region. A spatially referenced database linked to a GIS would seem a logical method to draw this information together. Thus, maps of predicted landscape accessibility for butterflies could be used in conjunction with maps of the most valuable areas of meadow plant species (Norderhaug, 1996), maps showing accessibility of the landscape for people, and the location of cultural monuments etc. Planning solutions could thus be chosen to maximise the benefits for a range of different interests. For example, the minimum ecological distance between meadows for butterflies may be considerably increased as small farm tracks become overgrown with scrub; a simple conservation measure may be to hold the old pathways open, which would also maintain a corridor for meadow plant species (Norderhaug *et al.*, 1996) and increase accessibility for people. Similarly, creating a woodland glade by clearing trees from the site of an overgrown burial mound would increase cultural heritage interest, whilst creating new butterfly habitat. A GIS model would clearly be a useful tool for evaluating alternative management possibilities and setting priorities.

4.4.8 Conclusion

The MRR study supported the results of the behavioural studies (Chapter 3) that the height of vegetation creates semi-permeable filters in the landscape, which influence the movement patterns of butterflies.

The main drawback of the MRR method was the large number of man-hours required to detect the rare dispersal events that were of most interest. However, the information about movements within meadows was essential to set the dispersal data in a population perspective. In this respect, the MRR observations were an important supplement to the behavioural studies at boundaries (Chapter 3), which may be biased towards a more mobile sub-set of the population. Thus, study at the landscape level provided an important control against which to compare the results of the reductionist, experimental approach. Spatial modelling proved to be a useful technique for comparing these data, and also appeared to offer considerable potential for integrating butterfly conservation management into wider landscape planning.

CHAPTER 5

ECOLOGY, STATUS AND LANDSCAPE USE OF AN ENDANGERED BUTTERFLY: MARK-RELEASE-RECAPTURE OF APOLLO

5.1 INTRODUCTION

This chapter presents an in-depth study of a species which is believed to be at risk from landscape change. The Apollo butterfly (*Parnassius apollo*) is closely associated with traditional farming landscapes in southern Norway, and in mountainous areas throughout Europe. This chapter examines how the butterfly uses the landscape, which landscape elements are important, and how changes in land use by man may affect the Apollo.

The methods used were comparable with those used for the Scarce Copper (Chapter 4), that is:

a) recording the behaviour of individuals to measure responses to individual landscape elements, and
b) a mark-release-recapture (MRR) study to provide spatially referenced data on movement / dispersal patterns at the population level.

5.1.1 The Apollo: a flagship for the cultural landscape

The Apollo was the first insect to be protected in Europe (in Germany, 1936) and continues to receive considerable attention from conservationists (see for example, studies from Sweden (Bengtsson *et al.*, 1989), Poland (Dabrowski, 1984; Witkowski and Adamski, 1996), Bulgaria (Ganev, 1985), France (Napolitano *et al.*, 1990), Spain (Gomariz Cerezo, 1993) and Germany (Seufert, 1990)). The species is listed as strictly protected in Appendix II of the Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention), and also appears in Appendix II of the Convention on International Trade in Endangered Species (CITES) which controls importation and exportation of species.

In Norway, the Apollo is provisionally protected. Although once widespread in areas south of Dovre and east of Langfjellene, the last two decades have seen a decline in numbers and the species has disappeared from its former ranges along the south-east coast (Hansen, 1993). Telemark county, where this study was conducted, remains one of the strongholds of the species.

White in ground colour, with striking black markings and red eye-spots, the adult butterfly is spectacular and is also one of the largest of European butterflies, with a wing span of 73-87 mm (Plate 15, p.123). The butterfly is univoltine and overwinters as a fully developed larva inside the egg, hatching in early spring. Eggs are laid singly on dry vegetation or, commonly, on juniper bushes near the food plant which, in Telemark, is *Sedum telephium* (Orpine). The fully grown larva is short-haired and velvety-black, with almost luminous orange spots along its sides and small, bright blue warts along its back. The warning colours are probably backed up by chemical defence, as is the case for the butterfly's near relative, the Small Apollo (*Parnassius phoebus*) which stores a cyanoglucoside obtained from its Sedum food plant (Nishida and Rothschild, 1995). The larvae pupate for 10 to 25 days, in loose cocoons in hollows under stones etc. (Henriksen and Kreutzer, 1982) and the adults emerge in late June. The flight period lasts until around mid-August, being somewhat variable according to weather conditions.

The habitat of the Apollo comprises mountainous terrain, with steep, rocky, south-facing slopes supporting *Sedum* spp. Open flowery areas are important nectar sources for adults and these areas too are preferably on steep, south-facing slopes, hence the close link between Apollo and the traditional farming landscape. The meadows utilised by Apollo are often on land which is too inaccessible and steep to be exploited by modern, mechanised agriculture so the Apollo thrives best in areas where traditional land management continues. This is true not only in Norway but throughout Europe; including the Polish Carpathians (Dabrowski, 1984; Witkowski and Adamski, 1996), mountains in the Burgos region of Spain (Pierron, 1992), the French Jura (Cosson, 1995) and throughout the Alps (Erhardt, 1995). Being both endangered and beautiful, the Apollo is becoming a flagship species for the conservation of traditional Norwegian cultural landscapes. As such, we need a better understanding of how the structure of this landscape influences the butterfly. The rarity of the Apollo accords high priority to research into how the species will respond to landscape changes.

5.1.2 Objectives

The aim of this MRR study was threefold:

1) to gain empirical data on the population sizes and movement behaviour of Norwegian Apollo populations

2) to evaluate whether the behavioural characteristics and habitat use of Apollo allow the use of MRR as a tool in monitoring Apollo populations

3) to determine how the Apollo uses the landscape, and thus assess how the species is likely to be affected by changes in land use.

Two separate populations were studied, each over two years. The two habitat systems chosen for study incorporated a broad range of landscape components.

5.1.3 The study areas

Two main study areas, both in Telemark county, were used to gain information about the Apollo. One area, lying on the border of Hjartdal municipality (59°30' N, 8°30' E), incorporated the meadow systems already described in previous chapters (referred to as the Blika complex, Plate 7, p.85), but also extended to a second meadow system to the east (the Vallufsin/Ballås complex, Plate 16, p.123). In total, the area was 2.5 km long by 0.6 km wide, forming a belt along a steep, south-facing, valley side. Groups of meadows were scattered throughout this area, ranging in altitude from 370 to 600 m a.s.l. Between the meadows the land was mainly forested, with some areas of scree and cliff. Until recent years, most of the meadows in the area had been managed traditionally. However, many are now abandoned and scrub is beginning to invade.

The second main study area was located on the north side of Bandak lake in Tokke municipality (59°20' N, 8°10' E). This area also comprised recently abandoned traditional farmland; the upper and lower Flekstveit meadows at around 650 m a.s.l. (Plate 17, p.124). To the east of Flekstveit, at 75 m a.s.l., surveys were carried out along Lårdal road, with adjacent meadows (Plate 18, p.124). The area between the road and the two Flekstveit meadows comprised approximately 1.5 km of mature forest. Small open areas created by logging activity a few hundred metres to the east of Flekstveit provided additional patches of Apollo habitat.

Sightings of Apollos were made in quite a range of habitats and, since detection of movement patterns was the major objective, the definition of 'habitat' was generalised as open, flowery areas. This could be called 'feeding habitat' and did not necessarily include suitable breeding habitat. However, at both study sites some patches of breeding habitat were included in the surveys. Since no larvae had been observed prior to the MRR experiment, habitat quality for breeding purposes was assessed according to descriptions in the literature (Henriksen and Kreutzer, 1982; Hansen, 1993). This involved the presence of the larval food plant Orpine (*Sedum telephium*) on steep, south facing slopes, with some rocky terrain and with Juniper (*Juniperus communis*) in close proximity to the food plant.

Photo: Jo Inge Fjellstad

Plate 15: A male Apollo (*Parnassius apollo*).

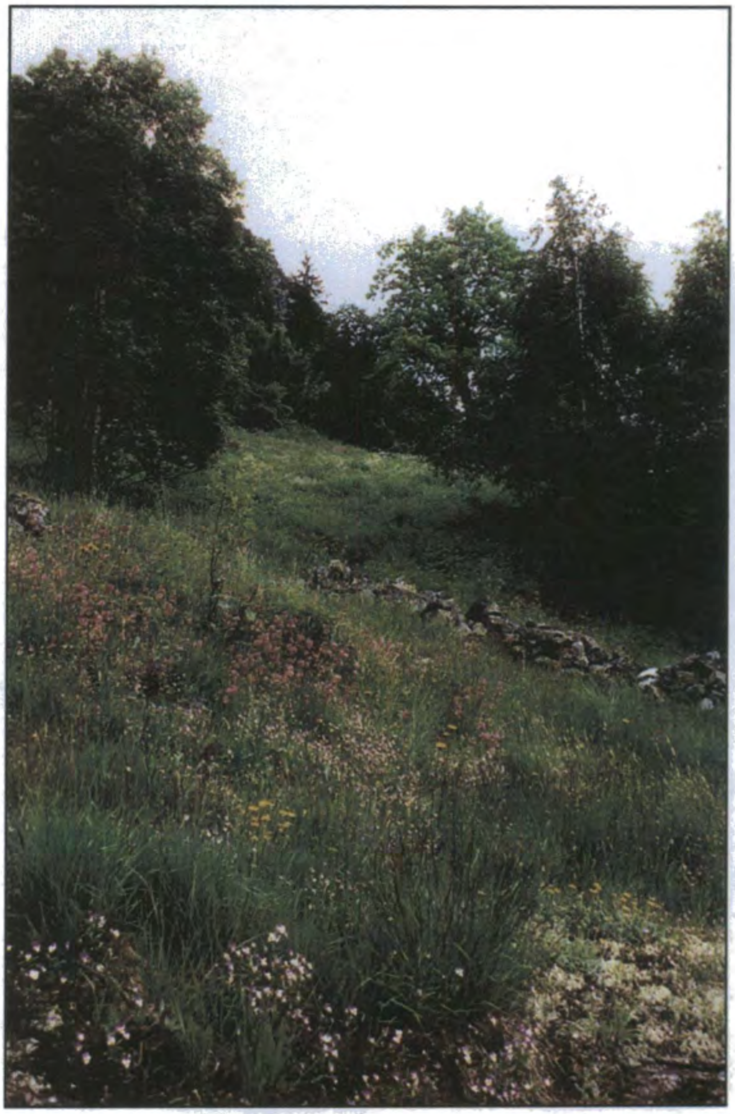


Plate 16: Species-rich slope at Vallufsin, Hjartdal.

Plate 17: Flekstveit Meadow at Bandak.

Plate 18: Important nectar sources along the road verge at Bandak.

Plate 19 (above): Apollos were marked with individual codes.

Plate 20 (left): The sphragis is a hardened secretion from the male that covers the female genital opening and prevents subsequent copulation.

The sphragis of the Apollo is very similar to that seen on this female Clouded Apollo (*Parnassius mnemosyne*).

A third site, referred to as Seljord, was surveyed on the 23rd and 30th July and the 12th August, 1995. The Apollo habitat comprised mainly clear-fell patches and wide forestry tracks on a steep south-facing mountain-side, plus meadows along a road lower down in the valley. The site was discovered in the second year of study and, situated 11 km from Hjartdal and 22 km from Bandak, would have been an interesting additional study area in a larger spatial setting (see Chapter 6). However, logistical limitations prevented more than a preliminary survey at the Seljord site and the results are included here as supportive material to increase the generality of findings from Hjartdal and Bandak.

5.2 METHODS

5.2.1 Field Methods

The methodology used for this experiment was relatively simple, although the scale of the study added some complications. Apollos were captured using a net, from which they were quickly and carefully removed and held by the abdomen. These insects are remarkably strong so care was taken to hold them such that the wings were held down, preventing flapping (see Plate 19, p.125). A letter, designating the site of capture, and a number to identify the individual were written on each fore-wing using a felt-tip pen (Artline 250, 0.4mm). Generally the butterflies were numbered sequentially, although when several field workers were marking in the same area, groups of numbers were allocated to each worker to eliminate the risk of butterflies being marked with identical codes.

For each capture the following information was recorded:

- Date
- Time
- Letter and number code
- Condition. Scale cover and wing wear were recorded separately, on a scale of 1 (fresh) to 3 (worn).
- Sex

- The presence or absence of a sphragis[a] on females (Plate 20, p.125).
- Activity prior to capture; nectar feeding, resting, basking, flying, interacting with other individuals etc. Details of plant species used and flight heights plus any additional notes of interest were recorded.
- Location of capture, as accurately as possible plus a description of movement patterns prior to capture.
- Activity on release.

The scale of the study, rarity of the study organism and difficulty of the habitat terrain precluded a highly systematic procedure for marking individuals. As a general rule, any Apollo seen and no matter which part of the study area it was found in, was captured, marked and the appropriate details recorded. However, to avoid methodologically induced bias in observation of long versus short displacements, care was taken to spread sampling effort evenly throughout the study area. Sightings without captures and failed attempts to capture individuals were also recorded, together with as much information as possible about flight patterns, activity, plant species used etc.

MRR of Apollo took place at the Hjartdal site from 12th to 26th July, 1994; and 14th July to 10th August, 1995. At Bandak, the study periods were 8th to 29th July, 1994; and 23rd July to 13th August, 1995. Sampling effort was more intensive in 1994, since the 1995 Apollo study was run parallel with other field work.

5.2.2 Calculating population size

The aim was to obtain measures of both the total population size, i.e. the entire number of butterflies hatching throughout the summer, and the daily population sizes per site, indicating the development of the population through the season. Total population sizes were calculated using the method employed by Seufert (1990) that was described in the previous chapter (Section 4.2.2).

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[a] A sphragis is a hardened secretion, produced by the male at the end of copulation, which covers the genital opening of the female and prevents subsequent copulation (see Plate 20, p.125). Occasionally males may fail to make a sphragis (for example if matings are very closely spaced in time or if weather conditions are cold and wet over an extensive period), however, the absence of a sphragis is generally a good indication that a female is unmated.

Daily population sizes were calculated using two different methods: the Fisher-Ford and the Jolly-Seber methods. Both methods are suitable for open populations, i.e. allowing for additions to the population (birth / immigration) and losses (death / emigration).

The Fisher-Ford model (Dowdeswell *et al.*, 1940; Fisher and Ford, 1947) is a deterministic model used previously in butterfly studies (Dowdeswell *et al.*, 1949; Brakefield, 1982b; Harrison *et al.*, 1988) and believed to be particularly useful when sample sizes are small (Begon, 1979; Gall, 1985). The model assumes that:

1) there is equal catchability, i.e. all butterflies alive at time *i* have the same probability of being taken in the i^{th} sample. This includes the assumption that marked animals mix thoroughly with the unmarked population, and that emigration is permanent, i.e. butterflies do not leave the study area and subsequently return.
2) marks are permanent, and accurately read and recorded
3) survival / residence rate is constant throughout the study

The method is most easily explained by imagining that each butterfly accumulates day-specific marks; one mark for each day it is captured. Population size is then estimated by:

$$\hat{N}_i = \frac{(n_i + 1)}{(m_i + 1)} . M_i$$

where n_i is the number of individuals captured on day *i*, and m_i is the number of marks captured on day *i* (equivalent to the total number of times that the butterflies captured on day *i* have been captured previously). M_i is the number of marks at risk on day *i* and must be estimated by using the age of marks and a residence rate, ϕ, that is fitted to the empirical data (see Begon, 1979, for details).

The number of losses between days *i* and *i* + 1 is estimated by:

$$\hat{L}_i = (1 - \phi)\hat{N}_i$$

An estimate of total population size can therefore be obtained by adding the total number of butterflies lost during the study to the last estimate of population size. (It might seem more intuitive to add the number of new arrivals ('born') to the first population estimate; however, numbers lost can be calculated even when samples were not collected on all days, whereas calculation of numbers 'born' requires daily sampling).

For the second method for calculating daily population sizes, the population estimation program "Popan - 4" (Arnason *et al.*, 1995) was employed. The "Jolly-Seber full model" was chosen; the model and estimates used being those of Jolly (1965), with some modifications due to Seber (1965). The method has been widely used in studies of butterfly populations (Brussard and Ehrlich, 1970c; Brussard *et al.*, 1974; Watt *et al.*, 1977; Tabashnik, 1980; Brakefield, 1982b; Hanski *et al.*, 1994). The Jolly-Seber model is stochastic, i.e. the model parameters represent probabilities, and the model is therefore more realistic (Brussard and Ehrlich, 1970c; Begon, 1979) than deterministic models such as the Fisher-Ford model.

The Jolly-Seber model shares assumptions 1) and 2) of the Fisher-Ford model (i.e. equal catchability and permanency of marks) but allows residence rate to vary during the study period, assuming merely that all animals have the same probability of survival from time i to time $i+1$.

A total population size was calculated using the Jolly-Seber estimate of the number of individuals 'born' each day and adding this to the first calculated daily population size.

For both the Fisher-Ford and Jolly-Seber methods, the data were first analysed separately for males and females. However, since numbers of observations were very small, and to avoid losing information concerning unsexed individuals, the data presented are based on all butterflies captured (this decision is discussed in section 5.4).

5.2.3 Effects of marking and capturing

Although marked individuals could not be compared with unmarked butterflies, it is possible to test the effects of marking and capturing by comparing butterflies of different capture histories (Begon, 1979). If marking and capturing were detrimental, either by increasing mortality or causing butterflies to emigrate, then butterflies captured several times would be less likely to appear in subsequent samples than butterflies captured only once. Data from each sampling session were therefore arranged into counts of butterflies, of specified capture history, that were subsequently recaptured and those that were not recaptured. Counts in each category were then summed for the entire study period before carrying out statistical analyses. (These analyses were performed only on the more extensive 1994 data sets).

To test the effect of initial marking, the numbers of butterflies captured for the first time and subsequently recaptured versus not recaptured were compared with the number of butterflies that had been captured on one or more previous occasions and were subsequently recaptured versus not recaptured. The null hypothesis that numbers recaptured and not recaptured were independent of previous capture history was tested using a G-test.

Similarly, a G-test of independence was used to test whether the number of times a butterfly had been captured affected future chances of capture. Thus, the subsequent capture history of butterflies captured once previously was compared with that of butterflies captured twice previously, three times previously etc. For high numbers of captures, categories were combined to avoid expected values of zero.

Effects identified by the above tests may be due to either mortality or changes in the behaviour of marked butterflies. However, Leslie (1958, referred to in Begon, 1979) developed a test that concerns only catchability. A group of G individuals are known to be alive on day j and $j + t$, of which g_i are caught on day i (where i lies between j and $j + t$). The mean number of captures per individual is:

$$\mu = \frac{\sum_i g_i}{G}$$

If sampling is random, the expected variance of this will be:

$$\sigma^2 = \mu - \frac{\sum_i g_i^2}{G^2}$$

The observed variance, however, is calculated by:

$$\frac{\sum_x f_x (x - \mu)^2}{G - 1}$$

where f_x individuals from G are caught x times between day j and day $j + t$. If sampling is random, the observed variance will be the same as the expected. As a measure of statistical significance, Leslie demonstrated that:

$$T = \frac{\sum_x f_x (x - \mu)^2}{G - 1}$$

where T provides a satisfactory approximation to χ^2 for (G - 1) degrees of freedom when $G > 20$, and there are at least three samples between days j and $j + t$.

5.2.4 Analysing movement patterns

Movement patterns between meadows were analysed following the method described for Scarce Copper movement analysis (section 4.2.7); i.e. as an exchange rate for every combination of meadow pairs. The exchange rate provides a measure of the number of butterflies observed to have moved between meadows in relation to the total number of observations possible, and is calculated by:

$$\frac{X_{A\rightarrow B}+X_{B\rightarrow A}}{Xre_A+Xre_B}\times 100$$

where for any pair of meadows (A and B), $X_{A\rightarrow B}$ is the number of butterflies flying from A to B, $X_{B\rightarrow A}$ is the number flying from B to A, Xre_A is the number of butterflies originally marked in A and recaptured at some point (anywhere in the study area) and Xre_B the corresponding number for butterflies marked in B.

5.3 RESULTS

5.3.1 Estimates of Population Size

5.3.1.1 Seufert model

Population sizes per site, calculated using the method following Seufert (1990), are given in Table 5.1. At all sites, fewer females were marked than males and recapture rates were lower for females than for males. Lower proportions of marked individuals were recaptured in 1995 than 1994. In all cases, except those where no females were recaptured, the estimated sex ratios more closely approached 1:1 than the observed ratio of marked males to females.

Table 5.1: Numbers of Apollo females and males marked and recaptured per site, with break-down per sub-site at Hjartdal. Population sizes were estimated separately for males and females using Seufert's (1990) method. Sex ratios are given; both the proportion of males to females marked in the field and the sex ratio of the estimated male and female populations.

Site	Sex	Total marked	Percent re-captured at least once	Population estimate	Ratio of marked males:females	Estimated ratio males:females
Total Hjartdal '94	f	46	23.9	192		
	m	71	46.5	153	1.5 : 1	0.8 : 1
Vallufsin/Ballås	f	24	41.7	58		
	m	28	42.9	65	1.2 : 1	1.1 : 1
Blika complex	f	17	0	17[a]		
	m	38	52.6	72	2.2 : 1	4.2 : 1[a]
Total Hjartdal '95	f	26	7.7	338[b]		
	m	84	35.7	235	3.2 : 1	0.7 : 1
Vallufsin/Ballås	f	14	7.1	196[b]		
	m	42	23.8	176	3.0 : 1	0.9 : 1
Blika complex	f	12	8.3	144[b]		
	m	42	47.6	88	3.5 : 1	0.6 : 1
Bandak '94	f	46	32.6	141		
	m	84	48.8	172	1.8 : 1	1.2 : 1
Bandak '95	f	20	15.0	133[b]		
	m	104	28.8	361	5.2 : 1	2.7 : 1
Seljord '95	f	5	0	5[a]		
	m	16	18.8	85[b]	3.2 : 1	17 : 1[a]

[a] indicates cases where none of the marked females were recaptured - the population estimate given is therefore the total number of females marked. The sex ratio is calculated using this minimum estimate.

[b] indicates cases in which the recapture of one more butterfly would change the estimate by more than 10%.

5.3.1.2 Population size estimates: Fisher-Ford method

Fisher-Ford estimates of daily population sizes per site, for 1994, are shown in Figure 5.1. The trend-lines on the graphs are moving averages (calculated by averaging the previous, present and subsequent estimates) and probably give a truer picture of daily population sizes, when variation in sample size is taken into account.

At both sites, but particularly Bandak, the highest population estimate follows a period of poor weather conditions during which few butterflies were observed. The peak value at Bandak, representing a dramatic increase in population size, immediately followed by an equally large decline, was treated as an outlier and excluded from calculation of the moving average.

Estimates of the total number of butterflies alive during the study period are given in Table 5.2. Sex ratios indicate a bias towards males. Males were particularly dominant in 1995, when the numbers of females recaptured were insufficient to enable calculation of female population sizes.

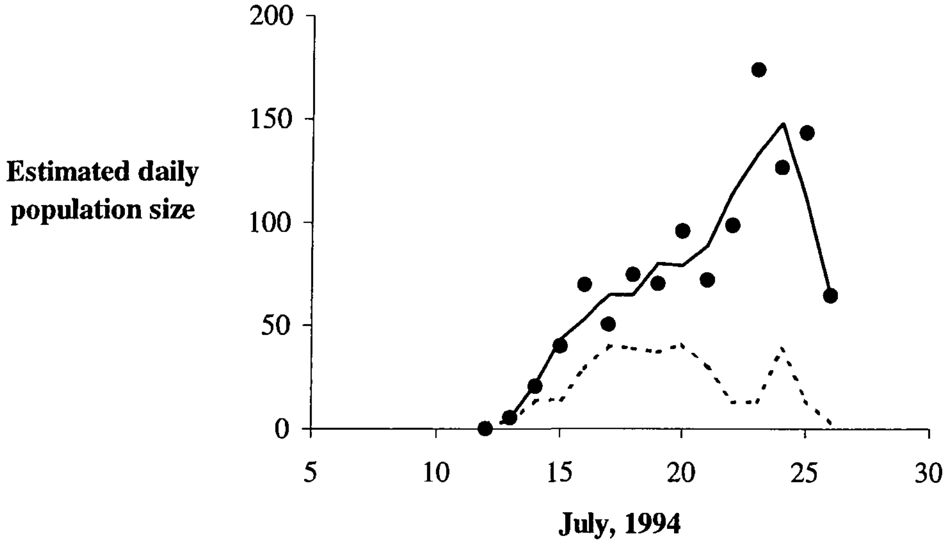
For 1994, the Fisher-Ford model estimated population sizes of approximately 100 butterflies fewer than the Seufert model. However, the separate estimates for males were very similar from the two models. For 1995, both the estimates for males and the total population sizes calculated by the Seufert method were more than double those calculated by the Fisher-Ford method.

Table 5.2: Fisher-Ford estimates of total population sizes and residence rates (in parentheses) at Hjartdal and Bandak. Estimates are calculated separately for males and females, in addition to a total estimate based on all individuals (including those of unknown sex).

Year	Site	Male	Female	Ratio	Total
1994	**Hjartdal**	135 (0.827)	91 (0.964)	1.5 : 1	205 (0.873)
	Bandak	170 (0.883)	73 (0.835)	2.3 : 1	246 (0.869)
1995	**Hjartdal**	134 (0.824)	26 [a]	5.2 : 1	210 (0.823)
	Bandak	112 (0.881)	20 [a]	5.6 : 1	130 (0.868)

[a] Insufficient females were recaptured in 1995 to allow estimation of female population sizes; the numbers given are the total numbers of females marked.

a) Hjartdal



b) Bandak

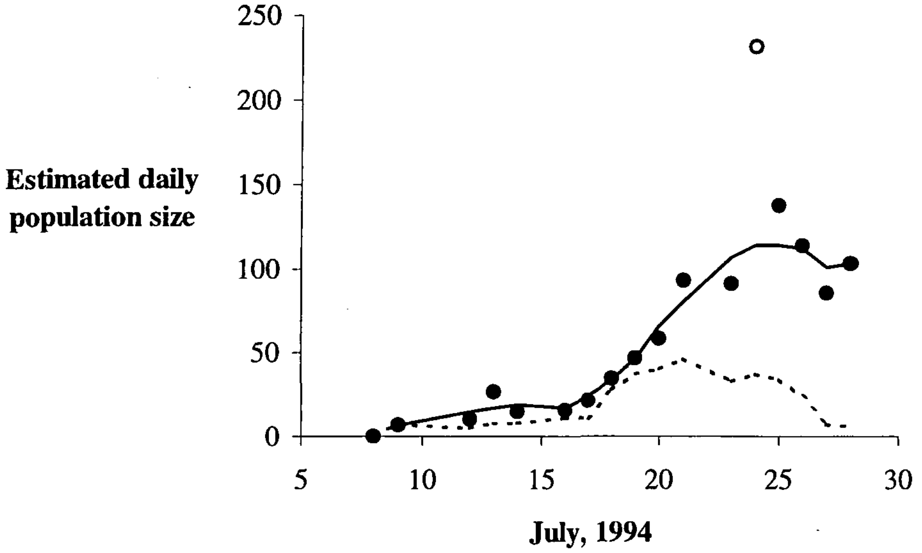
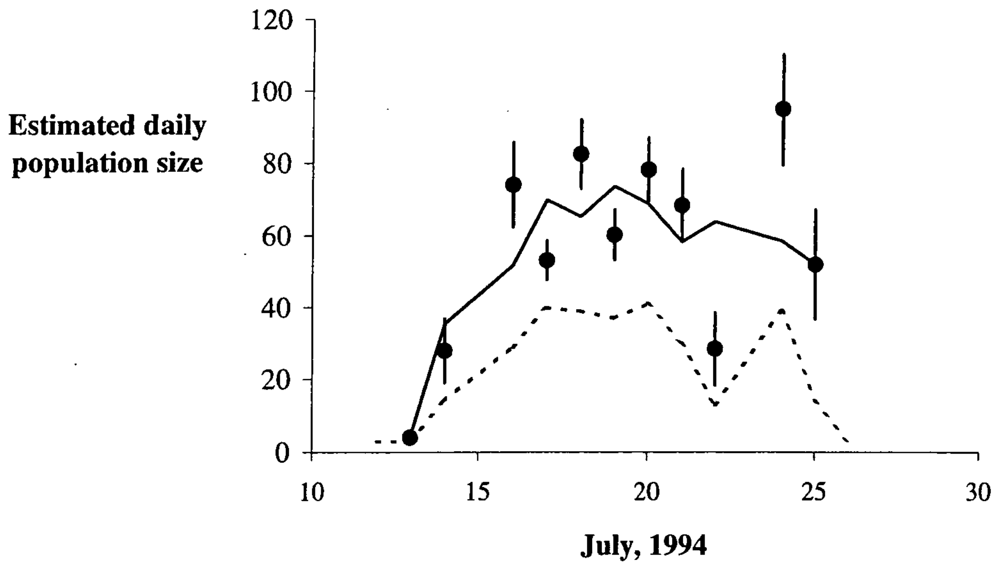


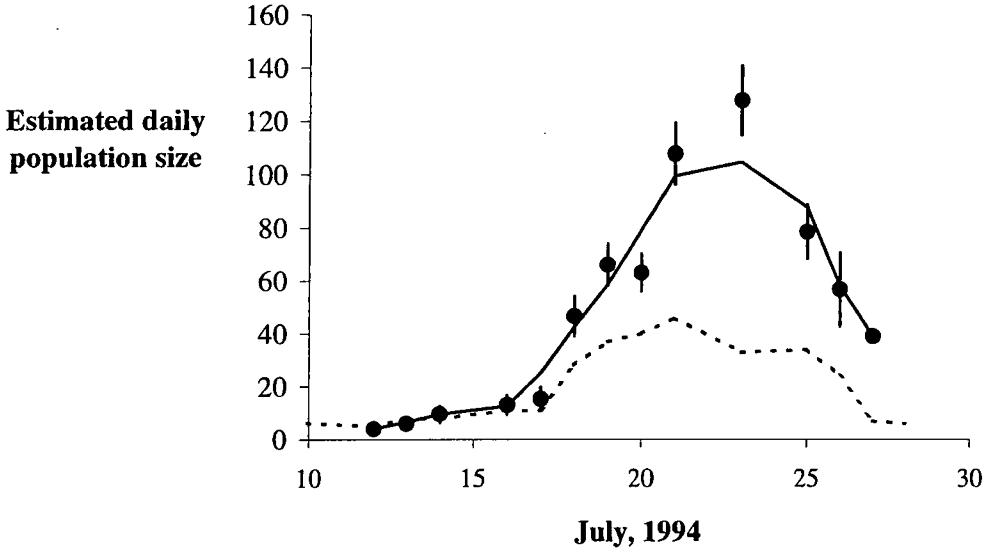
Figure 5.1: Graphs showing the development of Apollo populations at a) Hjartdal and b) Bandak during the summer of 1994. Estimates are based on the Fisher-Ford model. The solid trend-lines indicate moving averages (calculated by averaging the previous, present and subsequent estimates). An outlier at Bandak (open circle) is excluded from calculation of the moving average (see text). The dotted lines show minimum known numbers alive (i.e. observed on or subsequent to each date).

5.3.1.3 Population size estimates: Jolly-Seber model

Estimates of daily population sizes per site, calculated according to the Jolly-Seber model, are shown in Figure 5.2 for 1994. The maximum number of butterflies present on any one day was 95 (standard deviation = 7.7) at Hjartdal on 24th July, and 127 (standard deviation = 6.5) at Bandak on 23rd July. These peaks follow the period of poor weather mentioned above, although they are less extreme than the peak estimates produced by the Fisher-Ford method of calculation. In 1995, peak numbers were 93 butterflies (standard deviation = 7.9) at Hjartdal, on the 25th July, and 105 butterflies (standard deviation = 4.7) at Bandak on 3rd August.



a) Hjartdal



b)Bandak

Figure 5.2: Graphs showing the development of Apollo populations at a) Hjartdal and b) Bandak during the summer of 1994. Estimates are based on the Jolly-Seber model; error bars indicate 2 standard deviations. The solid trend-lines indicate moving averages (calculated by averaging the previous, present and subsequent estimates). The dotted lines show minimum known numbers alive (i.e. observed on or subsequent to each date).

For each site, an approximate estimate of total population size was obtained by adding the estimates of the number of butterflies 'born' (i.e. hatching / immigrating) each day to the first population estimate. Estimates calculated on the basis of all butterflies observed, including individuals of unknown sex, were within the same order of magnitude as the sum of estimates calculated separately for males and females (Table 5.3).

Table 5.3: Total population sizes at Hjartdal and Bandak sites in 1994 and 1995, based on the sum of Jolly-Seber estimates of numbers 'born'. Estimates are calculated separately for males and females, in addition to a total estimate based on all individuals (including those of unknown sex).

Year	Site	Male	Female	Ratio	Total
1994	**Hjartdal**	127	69	1.8 : 1	234
	Bandak	135	74	1.8 : 1	235
1995	**Hjartdal**	230	26 [a]	8.8 : 1	211
	Bandak	131	20 [a]	6.6 : 1	170

[a] Insufficient females were recaptured in 1995 to allow estimation of female population sizes; the numbers given are the total numbers of females marked.

The Jolly-Seber estimates were very similar to those produced by the Fisher-Ford model. The greatest difference in total estimates was a difference of 40 individuals (130 versus 170 butterflies at Bandak, 1995). However, the pattern of population development through the study period appeared a little different with the different models (compare Figures 5.1 and 5.2), with Jolly-Seber estimates forming more bell-shaped curves, i.e. showing more of a decline towards the end of the sampling period.

5.3.2 Differences in catchability between the sexes

The high ratio of marked males to marked females in the field, compared with the more even sex ratios resulting from total population estimates, suggests differences in catchability between the sexes. This was tested statistically using chi square tests in which the total number of individuals recaptured and not recaptured was compared for males and females. Since 2 x 2 contingency tables were used, i.e. with only 1 degree of freedom, Yates correction for continuity was employed, thus increasing the P value and reducing the chance of a false positive conclusion. When data from both the Hjartdal and Bandak sites for both years were combined, catchability was significantly different for males and females ($\chi^2 = 12.7$, 1 d.f., $P = 0.0004$). Breaking down the analysis by site, the catchability of males and females from Hjartdal (both years combined) was significantly different ($\chi^2 = 12.2$, 1 d.f., $P = 0.0005$), however, the nature of the data from the Bandak site resulted in a very low test power of just 0.2662 and it was therefore not possible to determine whether or not there were significant differences in catchability there.

5.3.3 Effects of marking and capturing

There was no evidence to suggest that subsequent capture was any more or less likely for butterflies captured for the first time and marked, than for those that were recaptured and merely examined (Hjartdal: $G = 0.302$; $df = 1$; $P > 0.1$; Bandak: $G = 1.076$; $df = 1$; $P > 0.1$).

Similarly, there was no cause to reject the null hypothesis that subsequent capture history was independent of the number of times a butterfly had been captured (Hjartdal: $G = 5.731$; $df = 2$; $P > 0.05$; Bandak: $G = 4.607$; $df = 4$; $P > 0.1$).

Leslie's (1958) test of random sampling was calculated for both sites, using groups of butterflies known to be alive over 5 samples (i.e. on day j, day $j + 5$, and three intermediate samples). Unfortunately, the numbers of butterflies (G) observed over such time periods were lower than desirable, so the test results must be interpreted with caution:

At Hjartdal, mean numbers of captures per individual did not differ from random for 14 individuals known to be alive on 17th July through to 21st July ($T = 7.854$; $df = 13$; $P > 0.5$) or for 12 individuals alive from 20th to 24th July ($T = 12.00$; $df = 11$; $P > 0.1$).

At Bandak, there were no significant deviations from random sampling for eight individuals known to be alive on 16th through to 20th July ($T = 11.20$; $df = 7$; $P > 0.1$); a different combination of eight individuals on 18th through to 23rd July ($T = 11.13$; $df = 7$; $P > 0.1$), and a third combination of eight on 20th through to 25th July ($T = 7.067$; $df = 7$; $P > 0.1$). Using just two intermediate samples, the test was also carried out on 13 individuals alive on 21st to 25th July ($T = 13.00$; $df = 12$; $P > 0.1$).

Although these tests all fall short of the minimum recommended sample size, they do lend support to the hypothesis that sampling was random.

5.3.4 Residence times

Average residence times were similar between sites, but were shorter for females than males at each site (Table 5.4).

Loss rates, as determined by recapture-decay plots (Figure 5.3), were approximately constant; this being particularly clear from the daily sampling of the 1994 studies (Hjartdal: $r^2 = 0.965$, $P < 0.001$ for both males and females; Bandak: $r^2 = 0.991$, $P < 0.001$ for males, and $r^2 = 0.942$,

$P < 0.001$ for females). Direct observation of the slopes of the regression lines in Figure 5.3 indicates that there were no major differences between loss rates of male and female Apollo.

Table 5.4: Average and maximum residence times for Apollos at Bandak and Hjartdal study sites, in 1994 and 1995. Butterflies that were never recaptured were excluded from the calculations. Standard deviations of the means are given in parentheses.

Site, year	**Females**			**Males**		
	n	Mean (std.dev)	Maximum	n	Mean (std.dev)	Maximum
Bandak, 1994	19	3.0 (2.6)	12	48	4.4 (3.2)	16
Bandak, 1995	4	3.3 (3.2)	8	42	6.0 (4.5)	16
Hjartdal, 1994	15	4.2 (2.4)	9	51	4.5 (3.0)	13
Hjartdal, 1995	4	1.8 (1.0)	3	41	5.3 (4.3)	17

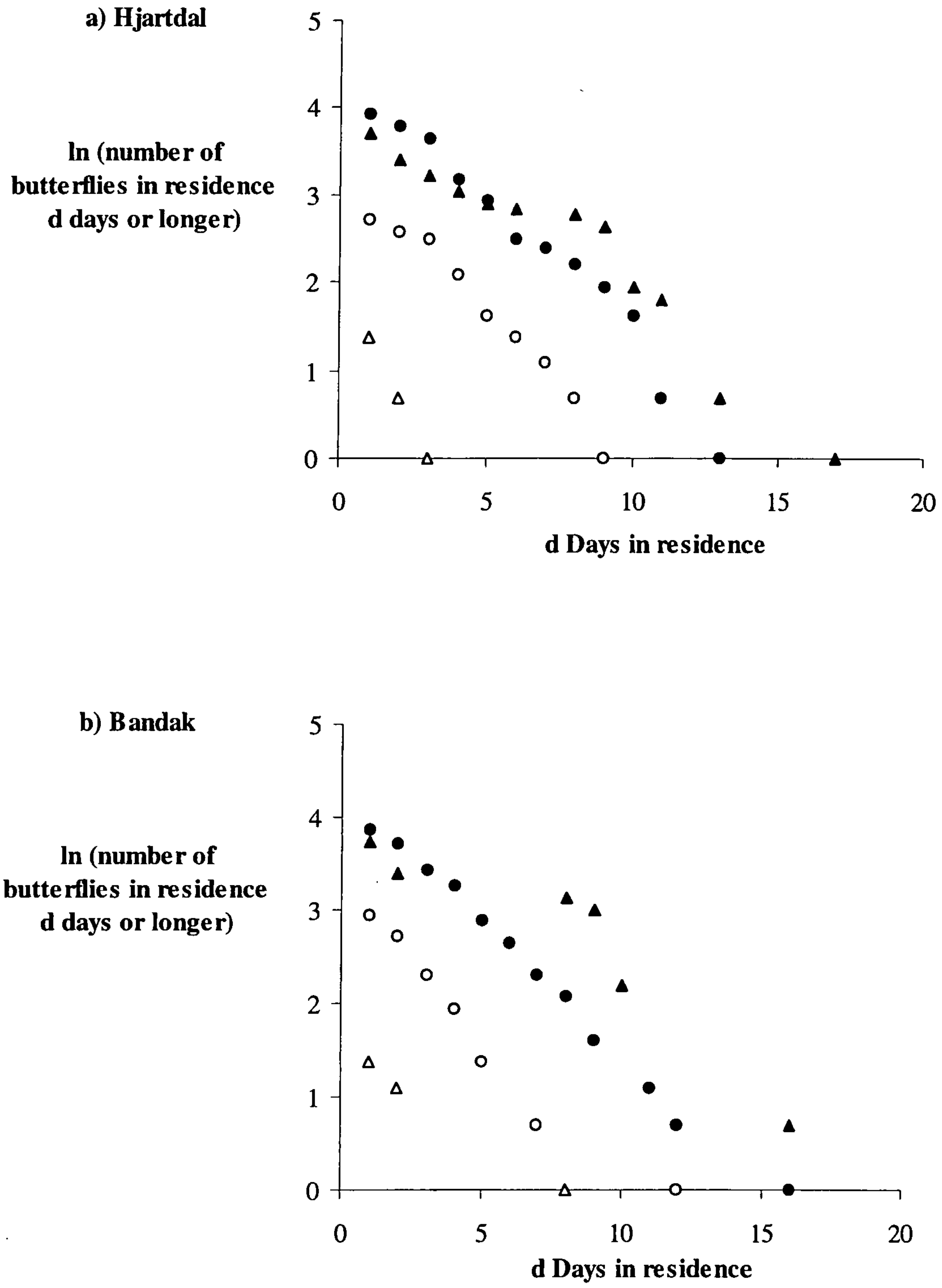


Figure 5.3: Residence times of Apollo in a) Hjartdal and b) Bandak, for 1994 (males = closed circles; females = open circles) and 1995 (males = closed triangles; females = open triangles).

5.3.5 Landscape Use

5.3.5.1 Larval requirements and behaviour

At the Hjartdal site, 11 larvae were found during a survey in mid-May 1995, at 3 sub-sites within the study area (Plates 21 and 22, p.142). Body lengths ranged from 3 to 5 cm. All larvae were found on, or in close vicinity of Orpine plants growing on slopes of 45° or more.

Larvae showed thermoregulatory behaviour. Whilst air temperature varied between 2°C and 14°C, a thermistor held against the black surface of the backs of larvae recorded temperatures from 7°C to 39°C. Larvae were inactive, amongst dry twigs and leaves at the coldest temperatures but responded quickly to sunshine, moving away from shadow to bask on exposed earth or twigs, and climbing up plants to feed. The minimum air temperature at which feeding was observed was 4°C.

5.3.5.2 Adult requirements and behaviour

The Apollo was found to use a range of elements in the heterogeneous farming landscapes studied: meadows, rocky cliffs, roadside verges, and patches of clear-fell still covered by brash and dead branches.

On 6 occasions, females were seen performing egg laying behaviour, always in the vicinity of Orpine on steep, rocky slopes. At Flekstveit meadow (Bandak) a newly eclosed female, incapable of flight, was found in long grass, a few metres away from a slope which had already been designated as a potential egg laying site due to the presence of the larval food plant, Orpine, and nearby juniper bushes. The butterfly remained in the same location for the next 24 hours and was found by a male at 11:30 the day after eclosion. Mating took place in dappled shade, though the pair moved through long grass and up a juniper bush into sunshine (Plate 24, p.143). The butterflies flew away in different directions after mating.

Apollos made use of a wide range of nectar sources, particularly composites with red / purple or yellow flowers. The most frequently visited flower species were the thistle *Carduus crispus*, Brown knapweed (*Centaurea jacea*), Greater knapweed (*Centaurea scabiosa*), Melancholy thistle (*Cirsium helenioides*), Spear thistle (*Cirsium vulgare*), Spotted cat's-ear (*Hypochoeris maculata*), Field scabious (*Knautia arvensis*) and Marjoram (*Origanum vulgare*).

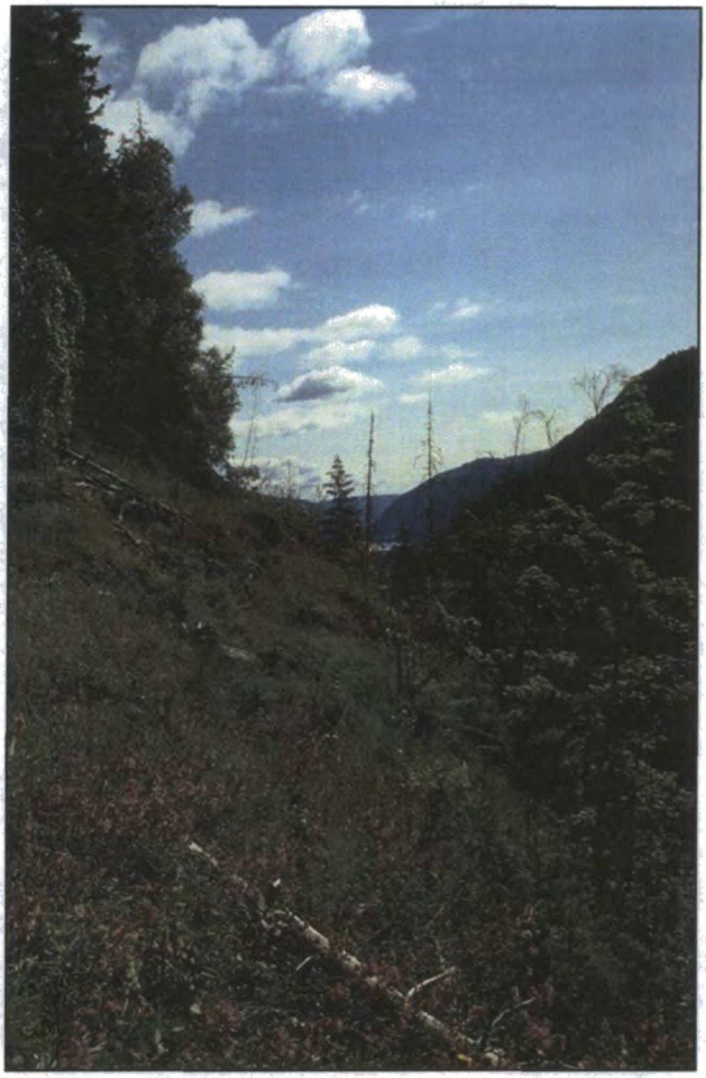


Plate 21 (left): Apollo breeding ground at Ballås, Hjartdal.

Plate 22 (below): Apollo larva basking on exposed ground.

Plate 23: A male, A34, with wings in perfect (1,1) condition

Plate 24: The female, N2, demonstrating that pen marks did not unduly disrupt mating behaviour.

Other commonly visited flowers were various Hawkweed species (Hieracium spp.), Rosebay willowherb (*Epilobium angustifolium*), St John's wort species (Hypericum spp.), Sheep's-bit scabious (*Jasione montana*), Ox-eye daisy (*Leucanthemum vulgare*), Red clover (*Trifolium pratense*) and Yarrow (*Achillea millefolium*).

Additional species for which there was only one observation of an Apollo nectar-feeding were Autumn hawkbit (*Leontodon autumnalis*), Common spotted orchid (*Dactylorhiza fuchsii*), Northern bedstraw (*Galium boreale*), Common toadflax (*Linaria vulgaris*), Sticky catchfly (*Lychnis viscaria*), Tormentil (*Potentilla erecta*) and Burnet rose (*Rosa pimpinellifolia*).

Apollo visited flowers in all open areas, even single flowers, isolated by up to several hundred metres from any other. The butterflies were easily lured to swoop down and investigate a small orange notebook, indicating that they located flowers, at least in part, by sight. The fact that many individuals followed the same route, stopping off at the same isolated flowers, indicates that flight paths are not located at random in the landscape.

5.3.5.3 The physical landscape

The physical structure of the landscape also played a large role in determining the route of Apollo flight paths. The updraft from steep slopes, edges and rocky cliffs was used to enable Apollo to glide without the flapping of wings. Common flight paths over a long south-facing slope would be to zigzag back and forth across the slope, gaining height and finally, at the top of the slope, using the height gained to glide on to new areas. Certain points in the landscape were identified as heavily used flight paths where the probability of catching individuals was much higher than in the surrounding landscape. The same individuals passed by these points several times per day (in spite of their having being caught there previously) and fresh individuals, presumably newly emerged, followed the same routes as the older animals.

The presence of tall trees seemed to be a positive feature of the landscape for Apollo in emergency situations. Startled individuals flew in a swooping flight, 3m or so above the ground, and would often head for the nearest trees. In several cases where only a thin band of trees were present, individuals were seen to resume normal flight after having cleared the trees. (The Clouded Apollo, *Parnassius mnemosyne*, displays similar escape behaviour, also resuming normal flight after flying over tall vegetation).

The microclimate on steep, south-facing slopes appeared to be as important to adults as it had been for larvae. In cool weather, few individuals were seen flying, but a slow walk in favourable areas would reveal Apollos with fully open wings, on bare rock or grasses. In the absence of sunshine, individuals were frequently incapable of flight.

5.3.6 Apollo movement

The greatest straight-line displacement at Hjartdal was flown by a female with sphragis, originally marked at Blika and recaptured 4 km to the west two days later. Distances of ca. 2.2 km were covered by two other mated females, both having flown from the Blika complex to Ballås. Two males made similar movements, one of which being the fastest long-distance movement recorded: 2.2 km in 3 hrs 40 mins. A further two males, originally marked in the Blika complex, were recaptured at Vallufsin and subsequently flew back to Blika. Flights between Blika and Vallufsin/Ballås (across intervening forest, scree and cliffs) comprised 4.3 % of recorded movements. Flights over 1.5 km comprised 2.4 % of movements. Figure 5.4 illustrates the movement of Apollos between groups of meadows at Hjartdal.

At Bandak, the greatest recorded displacement was 4.2 km by a male, recaptured 12 days after original marking. The next longest distance was 3 km, again by a male. These were the only two marked butterflies to cross the 1.5 km of forest between Flekstveit meadows and Lårdal road, representing 1.0 % of recorded movements. Both displacements were in a downhill direction. The numbers of movements over 1.5 km at Hjartdal and Bandak were not significantly different ($G = 1.123$; $df = 1$; $P > 0.10$).

There was no statistically significant difference between distances moved by males and females, either at Hjartdal (Mann-Whitney Rank Sum Test; $P = 0.759$) or Bandak ($P = 0.117$).

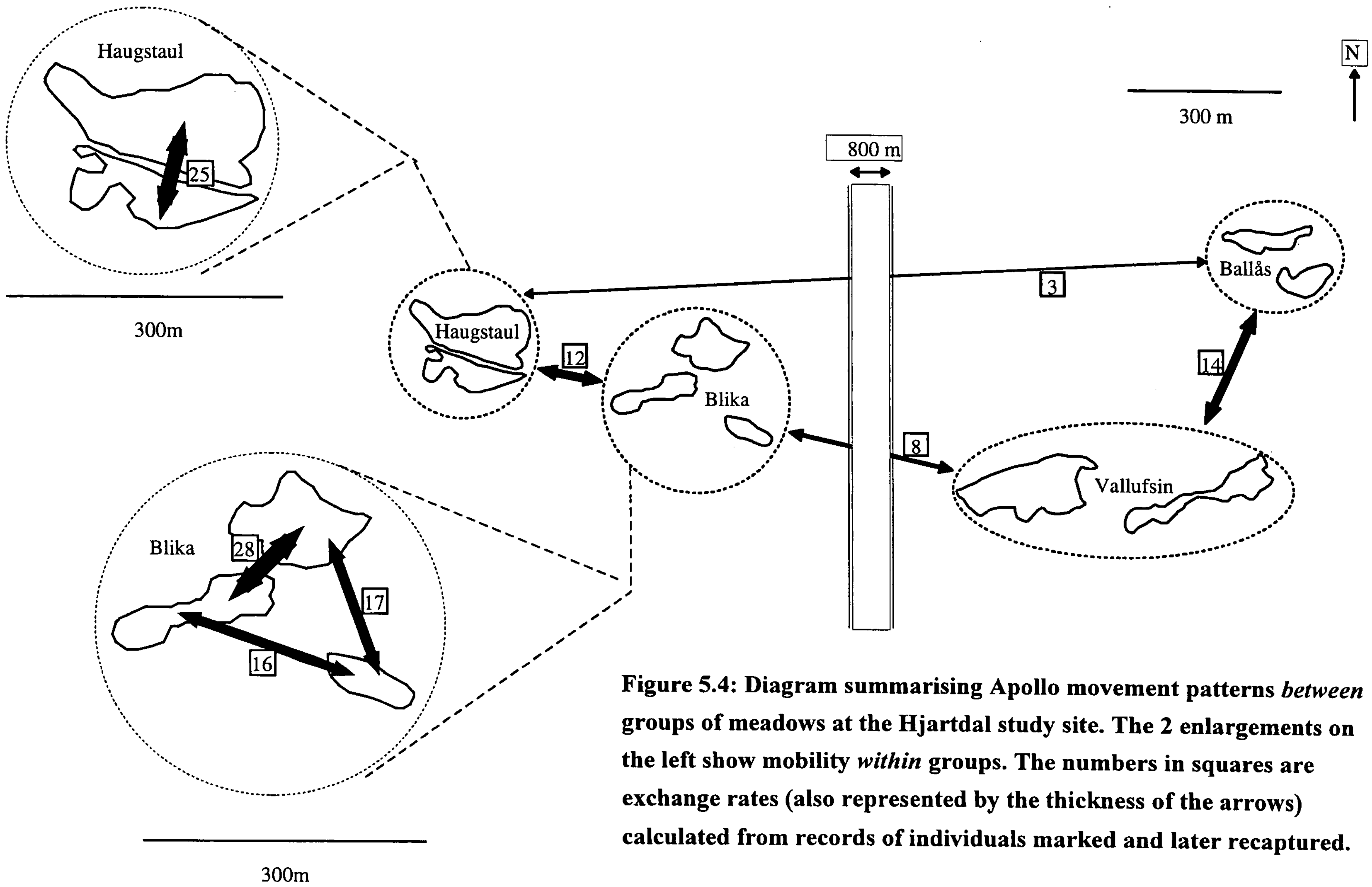


Figure 5.4: Diagram summarising Apollo movement patterns *between* groups of meadows at the Hjartdal study site. The 2 enlargements on the left show mobility *within* groups. The numbers in squares are exchange rates (also represented by the thickness of the arrows) calculated from records of individuals marked and later recaptured.

At Hjartdal, there was a strong exponential decline ($r^2 = 0.914$) in inter-meadow movement with increasing distance between meadows (Figure 5.5). At Bandak, the relationship was weaker but still present ($r^2 = 0.634$).

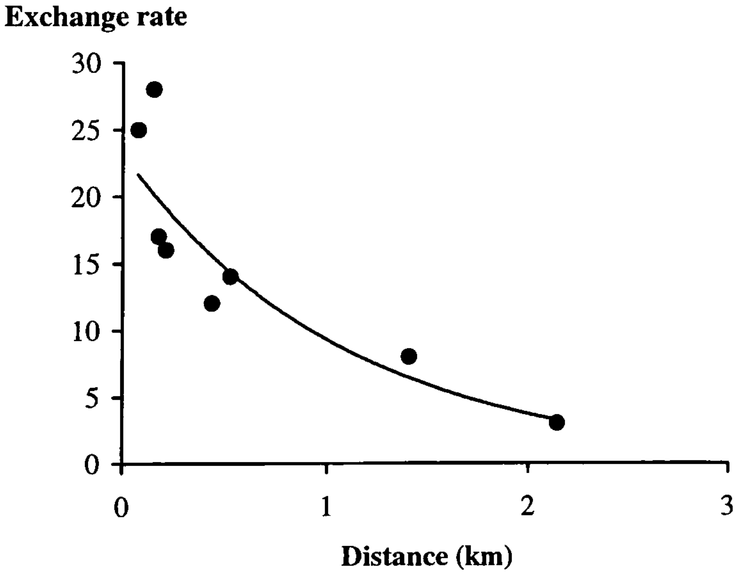


Figure 5.5: Relationship between exchange rate and distance between meadows at Hjartdal, both years combined (n = 208). The trend-line indicates an exponential decline ($y = 23.148e^{-0.9142x}$; $r^2 = 0.9139$).

At Hjartdal, no butterflies were captured more than seven times, whereas at Bandak, 25 butterflies were captured eight times or more (the maximum being 14 times for one butterfly). A consequence of the high number of multiple recaptures was that exchange rates within patches were higher at Bandak than at Hjartdal, i.e. butterflies were more frequently recorded moving within a patch.

5.4 DISCUSSION

5.4.1 Population sizes and effects of marking and capturing

Some doubts have been raised as to the suitability of mark-recapture methods for the study of butterfly population sizes, particularly due to failure of the assumption of equal catchability (Roff, 1973). Individuals may vary in their response to capture; due to age, sex, whether mated or not, location of a home range in relation to the location of netting, and even due to the marking procedure itself.

Morton (1982; 1984) found that the size and colour of marks did not affect probability of recapture, suggesting that conspicuous marks did not necessarily increase predation of marked individuals and that the solvents and pigments in felt-tip marking pens were relatively non-toxic. However, the handling of butterflies did affect recapture rates (Morton, 1982; 1984). Singer and Wedlake (1981) also found that disturbance lowered the chance of recapture of marked individuals. They were able to isolate this effect from that of marking by comparing recapture rates of individuals that were marked without being handled (21 %) against those handled during marking (2 % recapture).

Attempts to approach Apollos undetected generally ended in failure and the paucity of individuals made a control study of non-captured individuals impossible. However, the comparison of individuals of different capture histories suggested that neither the initial capture and marking of Apollos, nor subsequent multiple captures of individuals had negative effects on survival / behaviour. Begon (1979) points out the possible scenario that individuals captured several times may have a reduced probability of survival that is masked by an increased chance of capture. From the observations made, this seems improbable for Apollo, and Leslie's test (although based on few data) lent support to the theory that handling did not affect catchability.

Significant differences in catchability did occur, however, between male and female Apollos, as indicated by the difference in sex ratio of marked animals in the field compared with the more even sex ratios resulting from population estimates (Tabashnik, 1980). When some individuals (males) are consistently more catchable than others (females), population sizes will be under-estimated (Gall, 1984b). However, separate calculations for males and females did not yield very different population sizes than when all butterflies were grouped together. The differences between male and female Apollos are slight, and the early emergence and general dominance of males hinders field workers in gaining experience of sexing individuals. It is probable that any bias in the estimates due to uneven catchability of the sexes was outweighed by the advantage of analysing larger numbers when all observations, regardless of sex, were pooled.

The assumption of non-permanent emigration, required by both the Fisher-Ford and Jolly-Seber model, is important and could be a source of error considering the complex nature of the landscape at the study sites. Although every effort was made to find all possible habitat patches, this was not easy on forested, steep slopes. In addition, the less intensive studies in 1995 inevitably covered a smaller part of the available habitat. However, a substantial degree of non-permanent emigration would produce large over-estimates of population size (Arnason *et al.*, 1995). Based on the total number of butterflies marked and on comparison with Seufert estimates, this does not appear to have occurred. Again, the indication from Leslie's test that the marked population was sampled at random, provides some support for this assumption.

It should be noted that for small samples, variance estimates from the Jolly model and related models may be highly correlated with the parameter estimates they relate to, and there is thus some debate about their usefulness (Robson and Reiger, 1964; Manly, 1971; Roff, 1973). In assessing the accuracy of population estimates, Roff (1973) used computer simulations of sampling ideal populations to determine the accuracy of population estimates and concluded that Jolly's method, carried out over five days, required sampling intensities of 25-30 % to achieve an accuracy of 0.25 (i.e. population size (N) in the range 0.75N to 1.25N). This degree of accuracy is advised for conservation management work (Robson and Reiger, 1964). Such sampling intensities were generally achieved for males but not for females. In addition, the obviously small size of the Apollo populations adds further cause for caution in interpreting estimates (Begon, 1979).

The final conclusion of Roff (1973), following simulation of ideal populations, was that mark-recapture of real populations was probably unacceptably imprecise in all but exceptional circumstances. And as the work of Morton highlighted, striving for mathematical refinement may be pointless if the assumptions behind the estimates are unjustified. However, Begon (1979) considers these viewpoints to be unduly pessimistic and argues that an imprecise estimate is better than no estimate at all. This study has demonstrated that, for the Apollo, a large and relatively robust butterfly, the assumptions that capture and marking do not significantly alter mortality or behaviour appear to be justified, and the use of three models to calculate population sizes did at least give an objective measure of the order of magnitude of the Apollo populations studied.

From the most extensive population monitoring in 1994, the three models for calculating total population sizes resulted in very similar estimates of male numbers, ranging from 127 to 153 at Hjartdal, and from 135 to 172 at Bandak. Assuming that the actual sex ratio of Apollos is 1:1 on hatching, as suggested by captive breeding (P. Adamski, pers. comm.), then the total number of butterflies would be between 250 to 350 individuals. Populations may be a little larger than recorded, since sampling did not continue to the very end of the flight season (as indicated by Figures 5.1 and 5.2, showing the development of the populations through the season). Since the females eclose later than the males, the assumed sex ratio of 1:1 will adjust for this source of error.

There can be little doubt that without the objective estimates resulting from MRR, the highly mobile Apollos would give an impression of much larger population sizes, particularly at the Bandak site where the same individuals were caught up to 14 times.

Interestingly, Apollo populations in the French Jura were found to be much larger than the populations studied here (Cosson, 1995), with population estimates of up to 3000 butterflies. Cosson also noted a relationship between population size and the amount of scrub and trees present at a site; population size declined as scrub cover exceeded 5%. Considering the use by Norwegian Apollos of small meadow patches separated by trees, of road verges, forestry tracks and clear-felled forest, one may assume that the habitat quality of the Norwegian sites was far from ideal by French standards. The areas studied were, however, considered to be representative of potential habitat in Telemark, in an area where Apollo are considered to be relatively common (Hansen, 1993).

The small size of the Norwegian Apollo populations is quite unusual for a butterfly species and adds an element of vulnerability which justifies the conservation concern surrounding this species in Norway. There is a long background of theoretical development concerning the risks associated with small population size, which concludes that small populations are particularly susceptible to all of the fundamental causes of extinction: environmental stochasticity, demographic stochasticity, genetic factors and catastrophic events (see for example Schonewald-Cox *et al.*, 1983; Soulé, 1986; Gilpin, 1987; Burgman *et al.*, 1993).

Further MRR studies at a range of other sites would clearly be valuable to test the theory that small population sizes are typical for Norwegian Apollos. In particular, comparison of high mountain populations with those in cultural landscapes would be of use in investigating the links between population size and habitat structure.

5.4.2 Use of MRR as a tool for monitoring populations

The close agreement between the different estimates of male numbers in 1994 suggests that, when daily sampling effort is intense, MRR may be a useful tool for monitoring Apollo populations. In 1995, however, gaps in the sampling period lead to rather imprecise estimates and precluded meaningful comparisons between years.

It is possible that less intensive studies also fail to meet the assumption of random sampling, since the need to obtain as much data as possible in a short time inevitably compromises the goal of even coverage of the habitat area. (Ironically, the assumptions are also more difficult to test when sampling occurs on fewer days). Random sampling may be difficult to achieve when studying the Apollo, due to the complex nature of the landscapes in which the species flies.

By comparison, MRR monitoring of the Clouded Apollo has given consistent information about populations over a period of eight years (Aagaard *et al.*, 1997). This monitoring program has benefited not only from consistently intensive sampling, but also from the more discrete nature of the Clouded Apollo habitat compared with that of Apollo. The remaining populations of the Clouded Apollo occupy very sharply defined habitat patches (avalanche slopes), separated by dense forest or distances of around 10 kilometres. The patchiness in Apollo landscapes, on the other hand, occurs at a finer scale, with many small patches supporting a single population (see below). Apollos therefore fly over a larger area than Clouded Apollo, resulting in generally lower recapture rates for Apollo and therefore less accurate estimates.

Since there are still a relatively large number of Apollo populations, and considering the high level of resources required to obtain precise estimates of population sizes, it is likely that surveying the presence and absence of the species over a large area will be a more effective approach than MRR for monitoring the conservation status of this butterfly.

5.4.3 Residence times and condition

Since some butterflies were still in good physical condition up to two weeks after marking, it seems probable that the calculated average residence times were unrealistically low. This is due to the fact that recording did not span the entire flight season (Watt *et al.*, 1977).

In comparison with the Scarce Coppers discussed in the previous chapter, Apollos are very strong, robust butterflies. However, their wings are exposed to damage by their more energetic flight in proximity of trees and the greater distances that they cover. Apparent beak marks were also common, suggesting attack by birds.

On several occasions the classification of wing condition indicates an improvement in condition between captures. Some of these cases are almost certainly due to differences between recorders in assessing condition. If a recorder has had a run of very fresh individuals, a less perfect butterfly may be given a much lower grading than a recorder who has had a run of old or damaged butterflies. Such subjective scales are difficult to standardise. A recorder unable to decide whether to class a butterfly as 1 or 2 is easily tempted to write 1.5, whilst a fellow worker may, some hours earlier, have made the decision to grade it 2. In other situations, a tear in the wing may be easily overlooked unless the wing happens to press against something such that the two parts are moved apart. Thus there are some discrepancies in the data. However, on a few occasions, conscious decisions have been made to record an improvement in wing condition. For example, on 20th July, JIF observed that the crumpled hind-wing of A14 gradually straightened out between 3 successive captures, within a four hour period. The following day at 11.15, RM observed the same butterfly, again with a crumpled hind-wing. When caught a second time, at 12.40, the wing had straightened out. To the best of my knowledge, this phenomenon has not previously been reported in the literature. A possible explanation may be that wings sometimes become wet, either from rain or dew. Whilst butterfly wings are normally quite resistant to occasional wetting, it may be that wing edges which have been weakened by damage are more susceptible to crumpling but can support the wing again when thoroughly dry.

5.4.4 Behaviour

The attraction of Apollo to purple flowers of the family Asteraceae is characteristic of many butterfly species (Faegri and Van der Pijl, 1971; Jennersten, 1984; Loertscher *et al.*, 1995). Since thistles and knapweed, for example, commonly grow along road-sides and on disturbed land, the conservation of Apollo cannot be said to be dependent upon traditional management of species-diverse hay meadows. Supplying nectar sources for Apollo should not present any major conservation problem, although the location of flowers near breeding grounds and suitable microclimatic conditions, clearly plays an important role. I believe, therefore, that it is the coincidence of flowers and steep slopes which has lead to the association of Apollo with traditional farming landscapes, rather than a requirement for any particular management regime *per se*.

When isolated flowers are regularly visited by the same individual it may be said that the Apollo displays a degree of trap-lining behaviour. This has been observed for other butterfly species (Ehrlich and Gilbert, 1973; Gilbert, 1975). Trap-lining between flowers may be an important factor determining Apollo movement. However, the fact that Apollos repeatedly locate isolated flowers is not necessarily indicative of spatial memory. The same behaviour could result if Apollos follow, for example, topographical features and thus coincidentally perceive the same flowers *en route*. The fact that numerous Apollos were caught several times a day at the same location suggests that capture did not lead to any association between landscape and negative effects. The alternatives of spatial memory versus short-term flight rules could be explored systematically by placing potted plants in the landscape and noting how quickly plants in different locations are discovered by Apollos, visitation rates at different sites and, in particular, whether Apollos return to flower locations after the plants have been removed.

In general, the flight behaviour of Apollos was interpreted as aerodynamically efficient. Zigzag flights across a steep slope are not only a suitable method for finding mates and flowers, but also a technique for gaining height from the updraft caused when the air-flow is forced over a hill. The dry brown branches covering the clear-fell slopes at Bandak also created a very warm microclimate and thus a source of thermal lift for Apollos. As noted in Chapter 3, gliding flight is energetically efficient, both due to reduced muscle activity and reduced convection cooling (Guppy, 1986).

The escape behaviour of Apollo was clearly related to temperature. In warm weather, zigzag, swooping escape flight was performed, usually until trees were encountered, after which the butterflies often resumed normal flight. The stereotype behavioural pattern, presumably adapted to outmanoeuvre birds, suggests that predation is a significant factor for Apollo adults. In cool weather, when such energy-demanding flight was not possible, the butterflies would stridulate and flash the red eye spots on their hind-wings. Hasselbach (1988) suggests that the noise produced by stridulation mimics the hiss of a snake which, combined with the startling eye flashes, should frighten most butterfly predators. It is worth noting that Adder (*Vipera berus*) were very common at all the Apollo sites, enjoying the same hot, sunny microclimate of the south-facing slopes. Thus, any mimicry system could well be backed up by encounters of butterfly predators with true snakes.

Although reactions to attempted capture and actual handling often evoked escape responses; the physiological state of individuals appeared to play a role. Some individuals, notably also butterflies which had never been caught previously, remained nectar feeding on thistles and made no move to escape until actually taken between the fingers of a recorder. When placed onto the same flower following marking, butterflies were observed to resume feeding, suggesting that energy levels were so low as to preclude other activities.

5.4.5 Dispersal

At both Hjartdal and Bandak, the majority of butterfly movement was within groups of neighbouring patches, and only a small percentage of displacements crossed the longer expanses of non-habitat. At Bandak, only one percent of movements crossed the 1.5 km of forest between Flekstveit and Lårdal road. At Hjartdal, there was a higher proportion of movements from one side of the study area to the other, which may be attributed to the shorter distance from Blika to Vallufsin and possibly also to the more open nature of the intervening landscape. The relatively infrequent occurrence of longer displacements suggests that Apollo flights may be categorised as trivial movements (Scott, 1975a) and dispersal movements (as discussed for a range of species in Chapters 3 and 4).

Although long distance movements were infrequent, the fact that several individuals flew almost the entire length of the study areas indicates that the longest distances recorded by this MRR study are not maximum displacement distances for Apollo. The relationship between the number of individuals marked and the population estimates discussed above, suggests that marked butterflies represent around half of the population. Thus when one marked individual covers a long distance, we can assume that an unmarked butterfly does the same. The short time interval taken for an individual to move over 2 km further adds to the impression of mobility over distances of several kilometres.

Subsequent to this study, reference was found to a study of Apollos in France (Cosson and Descimon, 1996), where movements of 7 km were recorded for two males (three populations were studied of estimated size 1500 to 3000 each). MRR studies have a tendency to underestimate dispersal (Dempster, 1991) because it is practically impossible to mark all butterflies; to be in all the places that a chance migrant could occur; to be there at the right time and to actually see the individual marked butterfly. Thus it is possible that there may be a low level of interaction between some of the populations in Telemark, separated by, say, around 10 to 15 km.

It should be noted that, during nine years of intensive MRR of Clouded Apollo, no dispersal has ever been recorded between sites separated by 9 km or 12 km (Aagaard *et al.*, 1997). Since the Clouded Apollo occupies sites along the south-facing slopes of a very steep valley, topped by rocky, inhospitable mountains, the distribution of habitat for this species is effectively linear. The conditions for successful dispersal would therefore be more favourable for this species than for Apollo, since migrants would be channelled in the direction of suitable habitat. The very similar biology and behaviour of the two *Parnassius* species would suggest an upper limit of around 10 km for dispersal of Apollo.

At a national level, distances of several tens of kilometres separate many of the known Apollo populations in Norway (Hansen, 1993) and it seems highly unlikely that Apollos ever move between these sites. For a butterfly with such a specialised breeding habitat as the Apollo, the risks involved with dispersal compared with staying in the native habitat patch must be immense. In addition, dispersal flight would be more energetically demanding than the gliding flight that is possible along the steep, south-facing slopes within a habitat. Thus, it seems doubtful that the small Apollo populations could produce sufficient migrants to compensate for losses during dispersal, including losses resulting from individuals failing to find suitable habitat.

To obtain a clear picture of the possible connections between Norwegian Apollo populations, a thorough survey of potential habitat and mapping of populations is required. Hansen (1993) has made a good start on this task by collating reported observations, records from museums, private collections, and results of recent surveying. However, further surveying is needed in the areas between known sites to establish the distances between populations, identify potential dispersal routes and provide the base-line data required for monitoring the conservation status of the species in Norway.

5.4.6 Implications of landscape change for Apollo

Different habitat patches, of slightly different character, have been shown to fulfil a range of different functions for Apollo: egg-laying, larval development, mate location, nectar feeding, thermoregulation, and predator avoidance. This is known as habitat complementation (Dunning *et al.*, 1992), a concept of particular relevance in mosaic landscapes, such as those of traditionally managed farmland, where the necessary components for survival may be separated from one another in the mosaic. In addition, the use of multiple small patches indicated a degree of habitat supplementation (Dunning *et al.*, 1992); even if the patches had contained all of the necessary components, many of them were too small to act as habitat in their own right, and movement between them was essential to obtain sufficient resources.

Landscape changes, such as succession, which cause the different components of the habitat to become more isolated are likely to have negative consequences on the Apollo populations. The low degree of movement between the Road and Flekstveit meadow at Bandak, and between Blika and Vallufsin at Hjartdal suggest that distances of 1 km between essential landscape elements required on a daily basis, will be too great. Maximum distances between essential resources are difficult to state however, since the results obtained here are dependent upon the configuration of habitat patches in these specific areas. Habitat quality is also important, with consequences from an optimal foraging perspective. For example, the scattered distribution of flowers in the clear-fell patches at Bandak may be compensated by the energetically favourable flight conditions, allowing Apollos to cover a relatively large area for few resources. Such habitat-specific details must be taken into account when evaluating the consequences of change in an area (Fahrig and Merriam, 1994).

Considering then, that each system of habitat patches is supporting a single population, or at most two sub-populations, we can also ask what the consequences of landscape change will be at a larger spatial scale. In this case, land abandonment and resultant succession may both increase the distances between habitat, and decrease the probability of dispersers locating that habitat.

Obviously, an open landscape, which provides energy sources for a dispersing individual, will present a higher survival probability than a forested landscape. On an evolutionary scale, mortality of dispersing individuals could result in the types of consequences observed in another Papillionid, the Swallowtail, in which (as discussed in Chapter 1) selection favoured morphological forms with restricted dispersal ability (Dempster *et al.*, 1976).

5.4.7 Conclusions

The Apollo is dependent on the presence of its larval food plant, availability of nectar sources for adults, and favourable microclimatic conditions, both for larvae and adults. However, the species appears to be more flexible in its requirements than might be expected of a species listed on an international protection list. Mobility was recorded at a much greater scale than for the majority of non-migratory butterflies, and individuals were able to make use of nectar resources not only in meadows of varying character, but also along road sides and in patches of clear-fell. Regular capture of Apollo at isolated flowers also suggested the possibility of spatial memory (although see discussion above) which may increase foraging efficiency in patchy environments.

These qualities of the Apollo butterfly suggest that landscape management for this species, at the level of single populations, should be relatively straightforward. The butterfly appears to be well adapted to a mosaic landscape structure and the key issue must therefore be to ensure that habitat patches remain close enough together to continue to complement and supplement one another; for example, to secure patches of nectar resources within flight distance of suitable oviposition sites. Conservation of the species, however, requires planning at a larger spatial scale. Specifically, there are three aspects which make the conservation of Apollo populations a priority in Norway:

a) the inherently small sizes of Apollo populations

b) the geographically restricted nature of potential breeding habitat (steep, south-facing slopes)

c) the fact that the steep terrain which is favourable for the species is also the land which is first abandoned by farmers

Metapopulation theory is therefore of relevance to Apollo conservation, where the loss of one population may involve the loss of a link in a population chain or network. Population mapping to identify particularly important links should thus be a priority in the conservation of Norwegian Apollo.

CHAPTER 6

USING GENETICS TO EXAMINE DISPERSAL BETWEEN POPULATIONS:

ENZYME ELECTROPHORETIC ANALYSIS OF THE APOLLO

6.1 Introduction

There are numerous field techniques for studying dispersal between patchy populations, several of which have been discussed in previous chapters. However, these techniques all have their drawbacks, predominantly due to the difficulties of detecting rare events at a landscape scale.

Behavioural studies can be difficult to translate into population scale processes and require observation of large numbers of butterflies, many of which may be involved in trivial movements of no significance to population dynamics (see discussion in Chapters 3 and 4).

Similarly, mark-release-recapture experiments are extremely laborious; the detection of a few important dispersers requires the marking of a substantial proportion of the population. The movement pathways of individuals between captures cannot be deduced (Both, 1988) and the fate of unmarked individuals and those which are never recaptured is unknown. It becomes impracticable to monitor for marked butterflies beyond a certain size of study area, with the result that maximum dispersal distances are likely to be under-estimated (Slatkin, 1985).

Results from any one study may give a false picture if the degree of dispersal varies from year to year, for example due to weather conditions or deteriorating habitat quality. In addition, there may be methodological complications such as alterations to the normal behaviour of the study organisms caused by handling (Morton, 1982; Gall, 1984a; Morton, 1984). Even when dispersers are detected, their significance for population-scale processes cannot be ascertained; immigrants may fail to find mates or suitable breeding sites, and those that fail to produce viable offspring are of no lasting consequence (Mallet, 1986; Slatkin, 1987; Roderick, 1996).

Patch-occupancy studies, which relate the presence or absence of a population in any particular patch to the pattern of habitat patches in a landscape, circumvent problems at the level of individual butterflies (Hanski *et al.*, 1996). However, these studies have their own set of challenges: for example, achieving adequate precision in defining suitable habitat patches; locating all possible habitat patches in the field; and establishing presence or absence with certainty (this can be particularly difficult for butterflies, which may vary in phenology from year to year, and are generally difficult to find in poor weather conditions).

One way of avoiding these problems is to look at the end product of movement patterns: the genetic make-up of populations (Roderick, 1996). If dispersing individuals maintain high levels of gene flow between populations, those populations will be genetically similar. Genetic differentiation, on the other hand, is a sign of limited gene flow between populations.

One traditional method of studying genetic variation is through the use of enzyme electrophoresis. This method makes use of the fact that proteins differ in size, structure and electric charge. When proteins are isolated from organic tissues and allowed to migrate across a gel in an electric current, small differences in these characteristics can result in differential rates of migration. So different versions of an enzyme, coded for by different alleles, can be separated from one another. It is thus possible to record the frequencies of alleles in a population.

The technique of enzyme electrophoresis has been of considerable value in revealing genetic differentiation between populations (see Avise (1994) and Merrell (1981) for examples). In an extreme case, Selander (1970) demonstrated differentiation between populations of house mice (*Mus musculus*) in different barns on a farm, apparently due to a combination of tribal family structure and genetic drift in the small populations.

At the Norwegian Institute for Nature Research, a butterfly research group led by Kaare Aagaard and a genetics group, led by Kjetil Hindar, have been working together for some years on questions of butterfly population genetics. The majority of the work has focused on populations of Clouded Apollo (*Parnassius mnemosyne*), a close relative of the Apollo and similar in its biology. The Clouded Apollo is, like the Apollo, registered as strictly protected in Appendix II of the Bern Convention and is indeed, even more restricted in range and abundance in Norway than its relative. The Norwegian Directorate for Nature Management has therefore financed research on Clouded Apollo since 1988, providing a long time series of demographic data. The collection each year of a limited number of specimens for genetic analysis has led to the accumulation of genetic data for 130 individuals. Results indicate relatively high genetic differentiation of Clouded Apollo populations, even within a single valley (Aagaard *et al.*, 1997).

Although the Apollo is less vulnerable than the Clouded Apollo in Norway, the Apollo is considered to be under greater threat internationally. Thus, in addition to the work on Clouded Apollo, Aagaard, Hindar and colleagues have collected specimens of Apollo from several locations in Norway. The genetic details of these butterflies will here be compared with specimens collected from Telemark by the author. The geographical scale of this study is therefore extended beyond consideration of the populations discussed in Chapter 5, since interpretation of genetic data is easier when variation within the species as a whole is known.

Specimens collected by Aagaard and Hindar's research team included individuals of the darker, smaller mountain form of Apollo from Gjende in the mountains of Jotunheimen, over 200 km north of Telemark. This mountain form has been described as a separate sub-species of Apollo: *Parnassius apollo jotunensis* (Opheim, 1945). In addition to morphological differences, the Apollo in this area use a different larval food plant (*Sedum rosea*) than the lowland Apollo (which use *S. telephium and S. album*) (Lund, 1971). Comparison of Apollos from Telemark with those from Gjende may therefore be expected to encompass the extremes of genetic variation within Norwegian Apollos.

6.2 Method

Apollos were caught by net and killed immediately in the field by freezing in a canister cooled to -70°C by liquid nitrogen. In order to minimise the impact of sampling on the population, the individuals collected were preferably old males, taken at the end of the breeding season. License to kill was obtained from the Directorate for Nature Management.

In Telemark county, Apollos were taken from the sites used for the mark-release-recapture studies. A total of 20 specimens were taken from Hjartdal (59°30' N, 8°30' E); five from the Blika meadow complex and 15 from the Vallufsin/Ballås side of the study site (see Figure 5.5). Of the 21 specimens from Bandak (59°20' N, 8°10' E), four were collected at Lårdal road and 17 from Flekstveit. In addition, 10 individuals were taken from Flå (60°20' N, 9°20' E) in Buskerud county; and 20 specimens came from Vinstra (61°30' N, 9°40' E) and 24 from Gjende (61°20' N, 8°30' E) in Oppland county.

Wings were removed from the dead butterflies and stored in plastic folders (1994 and earlier samples) or paper envelopes (1995 samples) for later studies (morphological analyses and molecular DNA techniques). The bodies were divided each into four samples: the head, thorax and two halves of the abdomen (dissected longitudinally). Samples were stored in a freezer at -20°C before use.

Electrophoresis was carried out using standard techniques, as described in Aebersold *et al.* (1987). Resulting electrophoretic gels were sliced horizontally to create several thin gel layers, each of which was then analysed for a different enzyme. A total of 24 enzyme-coding genes were analysed. Chemical colour staining using dyes which react with specific enzymes allowed visualisation of the allozymes.

The standard nomenclature is used for referring to enzyme-coding genes whereby the gene is referred to by the abbreviation of the enzyme it codes for; the gene which codes for phosphoglucose isomerase, for example, is referred to as PGI. In cases where several loci code for the same enzyme, the loci are numbered sequentially in order of the migration of their enzymes towards the anode in an electric field, with the enzyme closest to the anode designated number 1, for example ACON-1. The allele occurring most commonly at a locus is referred to as the 100-allele and other alleles are then designated according to their migration distance relative to the 100-allele. For example, an allele migrating half the distance of the 100 allele would be called the 50-allele.

For each gene, a row x column test of independence was performed, using a G-test, to determine whether allele frequencies were significantly different at the different localities ($df = 8$ for genes with three alleles; $df = 4$ for genes with two alleles).

Measures of heterozygosity / genetic distance within and between populations were calculated following Nei (1987). Expected heterozygosity for each polymorphic gene in each sub-population was calculated by:

$$h = 1 - \sum p_i^2$$

where p_i is the frequency of allele i. The heterozygosity of each sub-population (H_S) was calculated as the average of the heterozygosity of every gene analysed (including monomorphic genes).

To enable comparisons with mark-release-recapture data (Chapter 5), genetic differentiation was calculated between sub-populations in Telemark. Thus, the genetic differentiation between Hjartdal and Bandak was calculated as:

$$G_{ST} = 1 - (\overline{H}_S / H_T)$$

where $\overline{H}_S$ is the average heterozygosity of the sub-populations, and H_T is the heterozygosity in the total Telemark population (i.e. from the pooled allele frequencies of all Telemark specimens). At a smaller spatial scale, Blika and Vallufsin were analysed as sub-populations in a total Hjartdal population; and Lårdal and Flekstveit were treated as sub-populations in a total Bandak population.

According to Wright's island model (Wright, 1951), genetic differentiation can be used to estimate the degree of exchange of individuals between sub-populations, on the basis of the relationship:

$$G_{ST} = \frac{1}{1 + 4Nm}$$

where N is the effective population size and m is the migration rate; the product of these (Nm) is therefore the total number of migrants per generation. This model assumes that populations are of equal size, have equal migration rates, and that the alleles in question are selectively neutral. The model does not incorporate geographic structure, thus migrants can come from any population.

To examine genetic variation at the national scale, Nei's genetic identity, I, and genetic distance, D, (Nei, 1972) were calculated between the Telemark population (Hjartdal and Bandak combined) and the population of sub-species *jotunensis* at Gjende. I provides a measure of the proportion of electrophoretically identical proteins in the two populations, whilst D is an estimate of the average number of codon substitutions per 100 loci which have occurred between the Telemark (X) and Gjende (Y) populations. For each locus (K):

$$I_K = \frac{\sum x_i y_i}{\sqrt{\sum x_i^2 \sum y_i^2}}$$

where, x_i and y_i are the frequencies of the i^{th} alleles in populations X and Y respectively. Over all loci (including monomorphic), I is defined as:

$$I = \frac{J_{XY}}{\sqrt{J_X J_Y}}$$

where J_{XY}, J_X and J_Y are the arithmetic means across loci of $\sum x_i y_i$, $\sum x_i^2$ and $\sum y_i^2$ respectively. Genetic distance is then calculated as $D = -\ln I$. The assumptions are that the rate of base substitutions per locus is the same for all loci; that substitutions within a locus occur independently of one another; and that the number of substitutions per locus fits a Poisson distribution.

6.3 Results

Of the 24 enzyme-coding genes analysed, 10 were monomorphic, whilst the following 14 (58.3 %) were found to display genetic variation: phosphoglucose isomerase (PGI), phosphomannose isomerase (PMI), phosphoglucomutase (PGM), hexokinase (HK), isocitrate dehydrogenase (IDH), glucose 6-phosphate dehydrogenase (G6PDH-2), aconitase (ACON-1), peptidase leucyl tyrosine (PEP-LT), aspartate amino transferase (AAT-1), alpha glycero phosphatase (AGP), butyrate dehydrogenase (BDH), fructose biphosphate aldolase (FB-ALD), phosphogluconate dehydrogenase (PGDH) and adenylate kinase (AK-1).

Nine of the polymorphic loci had two alleles and five had three alleles. Pooling data for all sites, the most variable genes were PGI, HK, PEP-LT, BDH and PGDH. In most cases the frequency of the 100-allele was close to 1, i.e. alternative alleles were rare (Table 6.1).

The number of genes displaying polymorphism differed between sites: 7 (29.2 %) loci were polymorphic at Gjende, 7 at Flå, 8 at Vinstra, 9 at Hjartdal and 11 (45.8 %) at Bandak. These differences were not statistically significant (R x C test of independence: $G = 2.026$; $df = 4$; $P > 0.10$). Most polymorphic genes were variable in more than one population; however, the ACON-1 and the FB-ALD loci were only polymorphic at Gjende, where 9.8 % of individuals were heterozygous for the former and 3.7 % heterozygous for the latter. Similarly, the IDH gene was only polymorphic at Bandak, where 9.5 % of individuals were heterozygous at this locus.

Between-site differences in allele frequencies were statistically significant for six genes (Table 6.1).

Table 6.1: Frequencies of the 100-allele in polymorphic genes of Apollo from Hjartdal, Bandak, Flå, Vinstra and Gjende. Calculations of heterozygosity are based on analysis of 24 genes. Full names of the enzyme-coding genes are given in the text.

	Hjartdal		Bandak		Flå	Vinstra	Gjende	Between sites signif.[a]
	Blika	Vallufsin	Lårdal	Flekstveit				
N° butterflies:	5	15	4	17	10	20	24	
PGI	1	0.83	0.88	0.85	0.90	1	1	*
PMI	1	0.96	1	1	0.86	1	0.98	n.s.
PGM	1	0.97	1	0.94	1	0.97	0.88	n.s.
HK	0.9	0.90	1	0.80	0.90	0.85	0.76	n.s.
IDH	1	1	1	0.94	1	1	1	n.s.
G6PDH-2	1	0.93	0.88	0.97	1[b]	0.96	1	n.s.
ACON-1	1	1	1	1	1	1	0.83	***
PEP-LT	0.9	0.93	0.88	1	1[b]	0.64	1	***
AAT-1	1[b]	1[b]	1	0.80	1	0.91	1	n.s.
AGP	0.9	0.97	1	0.97	0.94	0.95	1	n.s.
BDH	0.6	0.83	0.88	0.76	0.38	0.53	0.75	**
FB-ALD	1	1	1	1	1[b]	1	0.94	n.s.
PGDH	0.75	0.95	0.88	0.83	0.94	0.96	1	*
AK-1	1	1	1	0.94	0.95	1	0.86	*
Heterozygosity	0.058	0.054	0.046	0.083	0.058	0.070	0.070	

[a] Row x column test of independence using G-test:
n.s. not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

[b] Only two or three individuals analysed

The different populations and sub-populations of Apollo differ in their degree of heterozygosity (Table 6.1). The lowest and highest heterozygosities were in the two Bandak sub-populations; the lowest (4.5 %) in the Lårdal sub-population and the highest (8.3 %) in the Flekstveit sub-population. However, the Lårdal estimate is based on analysis of just 8 alleles (4 butterflies) and the degree of variation is thus likely to be an anomaly due to small sample size. When Lårdal and Flekstveit data are pooled, the heterozygosity for Bandak is 7.4 %, still higher than that in the other populations.

When all Hjartdal individuals are treated together the heterozygosity is 5.8 % which, together with the Flå population, was the lowest within-site heterozygosity. The overall average heterozygosity, (calculated on the basis of all individuals, irrespective of site) was 6.9 % ($H_T = 0.069 \pm 0.021$).

The number of migrants per generation (*Nm*) between the two Hjartdal sub-sites (Blika and Vallufsin/Ballås) was calculated to be 9.6; the number between the sub-sites at Bandak (Lårdal road and Flekstveit) was 1.6. Pooling the data for sub-sites at each locality indicated an exchange equivalent to 6.8 migrants per generation between the Bandak and Hjartdal populations.

Nei's genetic identity between Telemark and Gjende was $I = 0.9945$, and hence genetic distance was $D = 0.0024$.

The allele frequencies of the PGI and PGM loci (see discussion) were compared for Telemark and Gjende using G-tests of homogeneity. The PGI allele frequencies at Telemark were significantly different from those at Gjende (G = 10.722; *df* = 2; $P < 0.01$).The PGM allele frequencies were not significantly different (G = 5.978; *df* = 2; $P > 0.05$), although the observed G-value was very close to the critical value for P = 0.05 (critical G-value = 5.991).

When the PGI and PGM loci were excluded from the calculation, Nei's genetic identity between Telemark and Gjende was $I = 0.9952$.

6.4 Discussion

6.4.1 Degree of genetic variation

The overall average heterozygosity of the Apollo is towards the lower end of the range reported from electrophoretic studies of invertebrates (see Ward *et al.* (1992) who reviewed studies of 370 invertebrate species). The overall heterozygosity of Apollo was also lower (0.069 compared with 0.111) than that in Norwegian populations of Clouded Apollo (Aagaard *et al.*, 1997).

Although not all authors report overall heterozygosity, i.e. based on all populations, the maximum within-population heterozygosities from numerous other butterfly species are higher than those for Apollo: for example, 0.18 for French populations of Clouded Apollo (Napolitano and Descimon, 1994); 0.21 for populations of the Spotted Fritillary (*Melitaea didyma*) (Johannesen *et al.*, 1996); and between 0.12 and 0.19 for five European taxa in the *Pieris napi* complex (Porter and Geiger, 1995). However, extensive electrophoretic study of populations of Edith's Checkerspot (Britten *et al.*, 1995) reveal within-population heterozygosities of as low as

0.03, calculated on the basis of 13 polymorphic loci in 60 individuals. Since monomorphic loci were not included in this estimate, the actual heterozygosity of these butterflies must be even lower. Similarly, Britten *et al.* (1994) report very low heterozygosity estimates (0.01 to 0.04) for the Western Seep Fritillary (*Speyeria nokomis apacheana).*

The relatively low heterozygosity estimates for Apollo, therefore, are by no means extreme compared with other butterfly species. However, Norwegian Apollos were less genetically variable than populations of Apollo from the South of France, being comparable with the least variable, geographically isolated populations identified by Napolitano *et al.* (1990) and considerably less variable than the most heterozygous French populations (where $H = 0.23$). Similarly, the heterozygosity of populations studied by Racheli *et al.* (1983) were higher than for Norwegian Apollos (0.10 to 0.19).

One aspect contributing to low overall heterozygosity is the occurrence of one highly dominant allele at the majority of polymorphic loci, with alternative alleles occurring only at low frequency (and McKechnie *et al.*, 1975; also apparent in the studies of Britten *et al.*, 1995). Often in genetics a locus is referred to as monomorphic if the dominant allele is present at a frequency of 90% or more, in which case many of the genes here referred to as polymorphic would be designated monomorphic. However, this threshold is designed to allow for the presence of low frequency mutations in a population, i.e. mutations which are at so low a level as to be of little consequence for a population. In this study, few individuals were taken from any one site so low frequency alleles are most likely to represent true versions of a gene in the population rather than the chance finding of a rare mutation.

Gregorius (1980), assuming a homogenous mix of alleles in a population, calculated the sample sizes needed to ensure that all alleles occurring at a locus with particular frequency are detected. He found that a sample size of 21 (diploid) individuals was sufficient to give a 95% chance of detecting all alleles occurring with 0.2 frequency in the population. Or, put another way, if there were 5 alleles in the population, there would be a 95% chance of detecting them all. When the sub-populations at Hjartdal and those at Bandak are considered together, the sample sizes from the different Apollo populations are adequate, except for those from Flå. Further, Gregorius calculated that a sample size of 11 individuals would give a 95% chance of detecting all alleles occurring with 0.3 frequency in the population, such that even the sample size from Flå should have been sufficient to detect a greater degree of genetic variation than was found in the population, had it been present. The dominance of one allele at most loci can therefore be reliably accepted as the common state for Norwegian Apollo.

6.4.2 Dispersal within and between Telemark populations

The estimate of 9.6 migrants per generation flying between the two Hjartdal sub-populations, as inferred from genetic differentiation, was in the same order of magnitude as the number of migrants indicated from mark-release-recapture data. In 1994, the year of the most intensive MRR studies, 7 marked butterflies flew between Blika and Vallufsin/Ballås and since estimates of population size suggested that approximately half of the Apollo population were marked, this probably represents around 14 migrants in total.

At Bandak, a total of 4 migrants can be inferred from the two butterflies observed to have moved between the Lårdal and Flekstveit sub-sites, compared with an estimate of 1.6 migrants based on genetic differentiation. As proposed in Chapter 5, the lower number of dispersers between sub-sites at Bandak compared with Hjartdal is probably due to the greater distance of mature forest separating meadows at Bandak.

In spite of the small number of specimens available for electrophoretic analysis from Blika (5 butterflies) and Lårdal (4 butterflies), the degree of correspondence between genetic and MRR results is encouraging.

At a larger spatial scale, the comparison of the Hjartdal population (20 specimens) with the Bandak population (21specimens) was based on a relatively good data-set, not only in terms of numbers of specimens but also regarding the equality of sample sizes. Comparison with MRR data suggests that the estimate of 6.8 migrants per generation between these populations is due to step-wise gene flow rather than individual butterflies flying the minimum straight-line distance of 25 km between Hjartdal and Bandak. One intermediate Apollo population was discovered (the Seljord site mentioned in Chapter 5) and numerous sites with potential habitat occur between Hjartdal and Bandak. A chain or network of populations which exchange individuals therefore seems probable.

6.4.3 The sub-species status of Apollo from Gjende

At the nation-wide scale, it would appear that the heterozygosity which does exist in Apollo is found within populations, rather than between them. Nei's genetic identity between Telemark and Gjende, populations located over 200 km from one another, suggests that virtually all loci (99.45 %) remain identical. This was surprising in the light of the morphological and ecological differences between lowland Apollos and the mountain form from Gjende.

In cases where the specific or sub-specific status of populations has been in doubt, electrophoresis has often been a powerful tool in discriminating populations (Lewontin, 1991). For Norwegian Apollos, the butterflies from Gjende, previously defined as sub-species *jotunensis*, could not be distinguished on the basis of electrophoretic results. The degree of genetic similarity was more characteristic of the differentiation between local populations of insects rather than between sub-species (see overview by Brussard *et al.*, 1985).

Enzyme electrophoresis has been used previously in cases where variability of morphological characters within similar taxa has created taxonomic confusion (Geiger, 1980; Brussard *et al.*, 1985; Geiger, 1988). Examples of butterfly sub-species with genetic similarities of over 99 % have also been found in these studies, amongst the Green-Veined Whites (Geiger, 1980) and the Checkerspots (Brussard *et al.*, 1985). However, these butterflies are probably divided into too many different taxonomic groups even at the generic level (Ehrlich and Murphy, 1982; Brussard *et al.*, 1985) and are hardly ideal examples of butterfly nomenclature. The Apollo sub-species *P. apollo hispanicus*, with a genetic identity of 86.07 % (Racheli *et al.*, 1983), provides a more appropriate example of the level of differentiation which may be usefully separated taxonomically.

On the basis of the electrophoretic evidence alone, it seems more appropriate to refer to the mountain form of Norwegian Apollo as an ecotype. It would, however, be unwise to reject the sub-species classification without additional lines of evidence. Alternative biochemical techniques reveal that the zymograms (band profiles) obtained from electrophoresis do not show all of the genetic variation at a locus (Avise, 1994). Some apparently identical bands may comprise products of numerous different alleles with identical mobilities. In fact, only about 25 % of random code changes resulting in substitution of an amino acid lead to changes in protein charge that can be identified by electrophoresis (Lewontin, 1991). The estimate of variation is, therefore, a minimum estimate. In addition, there is no guarantee that the rank-order of differentiation between populations based on a small sample of enzyme-coding genes would be representative of genome-wide variation (Mitton and Pierce, 1980; Chakraborty, 1981; Collins, 1991).

There are some 650 named forms of Apollo in Europe (New, 1991). Little is known about the basis of their morphological and ecological differences but several studies suggest a genetic component. Napolitano *et al.* (1990) suggested that a part of the genome of homozygous but morphologically variable French Apollos was more responsive to environmental pressures than revealed by electrophoresis. Similarly, Nardelli *et al.* (1989) proposed (but without presenting any evidence) that the morphological characteristics of *P. apollo pumilus* were genetically determined. Racheli *et al.* (1983) found that more morphologically variable alpine Apollo populations were also the most heterozygous.

The evidence for genetically determined morphological differences is not strong however, and in view of the lack of genetic differentiation between populations at Gjende and Telemark, the possibility of ecologically determined morphology cannot be excluded. Experiments involving transfer of eggs and larvae between Norwegian highland and lowland sites, and comparison of larvae reared on alternative food plants and under controlled temperature regimes in the laboratory, would clearly contribute immensely to understanding the mechanisms behind the differences between Norwegian Apollos, and hence the suitability of the sub-species classification.

6.4.4 The assumption of selective neutrality

One important assumption of electrophoretic analyses is that the genetic variability observed is selectively neutral; controversy over this topic has divided the field of evolutionary biology since before enzyme electrophoresis was common practice and continues today (Merrell, 1981). The neutralist viewpoint is that protein polymorphisms are functionally equivalent, i.e. alternative alleles confer no selective advantage (Kimura, 1968; Shaw, 1970; Wallace *et al.*, 1971). In this case, genetic variation is maintained in populations by a balance between mutation, which increases variation, and genetic drift which reduces variation. Selection is believed to be mainly 'purifying', occurring through the removal of deleterious alleles.

The selectionist, or 'balance' viewpoint, on the other hand, is that polymorphism is maintained through balancing mechanisms such as fitness advantages in different environments, heterozygote advantage and frequency-dependent selection (Johnson, 1972; Johnson, 1973; Ayala *et al.*, 1974; Ayala and Campbell, 1974; Johnson, 1974). In spite of the continued wide use of neutralist assumptions in calculating gene flow between populations, there are now numerous studies of enzyme polymorphism in butterflies which have been shown to have significance for individual fitness.

The most thoroughly examined example in butterflies is the relationship between the PGI locus and flight ability. It has been demonstrated that the kinetic and thermal stability of different PGI variants in *Colias* butterflies have direct effects on flight ability, with the commonest heterozygotes being capable of flight over a wider range of temperatures than homozygotes (1977; Watt, 1983; 1983). Similarly, in the Monarch Butterfly, Carter *et al.* (1989) found that samples of active individuals collected early in the day contained a higher proportion of heterozygotes at both the PGI and PGM loci than samples collected later, again suggesting that heterozygotes may have lower temperature thresholds for flight than homozygotes. Goulson's (1993) study of the Meadow Brown demonstrated that individuals homozygous for the 100-allele of PGM could maintain flight for longer than other genotypes at 29°C, but that there was an increase in rare alleles with increasing altitude. Goulson took this to be a sign of heterozygote advantage at cooler temperatures also in this species.

Since adult butterflies are totally dependent upon flight for the location of nectar sources, mates and egg laying sites, it is clear that any extension of flight time will give a competitive edge and increase relative fitness. For *Colias* butterflies, differential survival of certain genotypes has been demonstrated (Watt *et al.*, 1983). In addition, Watt (1992) found fecundity differences between PGI polymorphs, whereby significantly more heterozygotes laid eggs than homozygotes.

In view of the evidence, for several species, supporting heterozygote advantage at the PGI locus in cooler environments, it is noteworthy that all Apollo individuals from Gjende - the mountain population situated at 1000 to 1400 m a.s.l.- were homozygous for the PGI gene. This can be compared with a heterozygosity of 0.24 for specimens from Telemark (altitude: 75 to 650 m a.s.l.), where three different alleles occurred at the PGI locus. Data for the PGM locus were more in agreement with previous studies; the highest heterozygosity was at Gjende (0.22 compared with 0.07 for Telemark populations). However, the overall differences between localities were not statistically significant and, again, there were three alleles in the Telemark population, compared with just two at Gjende.

The effects of a genotype are, of course, dependent on precisely which alleles are present, the biochemical properties of their products and the exact selective forces operating in the habitat. The conditions faced during different stages of the life cycle must also be taken into account; for example, Apollo larvae frequently feed at temperatures close to zero centigrade, surviving sub-zero night-time temperatures and snow (*pers. obs.*). It is possible then, that the inevitable exposure of Apollos to cooler temperatures has lead to the predominance in all populations of a PGI allele adapted to these conditions (it must be borne in mind that the 100-allele of a gene is not necessarily the same in different studies). Clearly, investigation of the selective value of alternative alleles is only possible through linking behavioural, ecological and environmental data with detailed biochemical studies of the properties of the enzymes produced by different genotypes of Apollo at the different sites. The high degree of polymorphism generally found at the PGI locus in butterflies (McKechnie *et al.*, 1975; Watt, 1977; Ehrlich and White, 1980) makes the monomorphic state of the mountain form of Apollo a particularly intriguing aspect for further study.

Other butterfly studies have concluded through more indirect evidence that selection is operating on alleles. For example, contradictory selective pressures have been proposed when different loci are not affected to the same extent by the process of differentiation (Eanes and Koehn, 1978; Napolitano and Descimon, 1994; Bossart and Scriber, 1995). There was no such indication of selection in the results presented here, however, since loci were quite similarly differentiated.

Evidence has also come from the comparison of genetic results with measures of mobility obtained from mark-release-recapture experiments. For example, in the very thoroughly studied Checkerspot butterflies (Ehrlich *et al.*, 1975), knowledge about dispersal can be used to identify populations separated by 'insurmountable barriers to gene flow'. The close similarities in allele frequencies between these populations are thus seen as being due to similar selection pressures operating in similar habitats (McKechnie *et al.*, 1975; Ehrlich and White, 1980). Although allele frequencies were similar for the widely separated Apollo populations studied here, the lowland and mountain habitats are rather different, both in terms of climate and the available larval food plant. The small size of mountain butterflies and their dark colouration can be seen as adaptations to wind-blown slopes and cool temperatures. By contrast, Telemark Apollo tend to be rather large and brightly coloured. The logical explanations of the morphological differences suggest that selection pressures are rather different in the different environments.

6.4.5 Historical factors

The detailed studies of previous authors (Watt, 1977; Watt, 1983; Watt *et al.*, 1983; Carter *et al.*, 1989; Watt, 1992; Goulson, 1993) are convincing examples that allelic variants of some enzyme coding genes, particularly PGI and PGM, can confer selective advantages to their carriers and thereby influence allele frequencies. However, if the PGI and PGM loci are excluded from the analysis, the conclusion still holds that widely separated populations of Norwegian Apollo show very little differentiation.

The amount of dispersal required to maintain an effectively panmictic population is actually very low; it has been suggested that a migration rate of one individual per generation is sufficient to hinder the fixation of neutral alleles by drift (Franklin, 1980; Allendorf, 1983; Chambers, 1983; Frankel, 1983), or even less frequent dispersal if successful migrants are gravid females (Brussard and Vawter, 1975). Nevertheless, considering the degree of mobility detected by mark-release-recapture studies (Chapter 5), and the scattered distribution of Apollo in Norway today (Hansen, 1993), panmixis is highly improbable. In the interpretation of genetic data, however, historical factors often play an important role (Varvio *et al.*, 1986; Avise, 1994).

In an allozyme study of the Green-Veined White species complex, for example, Porter and Geiger (1995) calculated that up to 60 *Pieris napi meridionalis* per year were dispersing between Italy and Corsica. This was judged to be totally unrealistic and the high similarity between populations was explained as being due not to gene flow but to the fact that not enough time had elapsed for genetic drift and mutation to reach equilibrium levels of divergence between the populations. It was further calculated that, taking into account the large size of the population on Corsica, isolation from the mainland as long as 100 000 years ago would still lead to a substantial estimate of apparent gene flow. Similarly, Napolitano *et al.* (1990) explained the lack of genetic differentiation in isolated populations of Apollo as being due to the relatively recent colonisation of these populations.

The high degree of genetic similarity between Apollo populations in Norway today could reflect the more continuous distribution of Apollo in the past, which has been documented by Hansen (1993). This requires the assumption that there is occasional migration between populations within a region, since the small population sizes estimated for single populations (Chapter 5) would otherwise (again assuming no selection) lead to relatively rapid genetic differentiation due to the stronger influence of genetic drift in small populations (Allendorf, 1983). However, the combination of MRR and electrophoretic data support the theory that the small populations in Telemark are part of a larger network of small populations that exchange individuals. With larger effective population sizes and low levels of migration between numerous populations, it may take hundreds of years before within-population heterozygosity and genetic differentiation attain their steady state values (Varvio *et al.*, 1986). Such a population structure throughout the area of the Apollo's historical distribution in Norway, therefore, seems a very probable explanation for the present lack of genetic differentiation.

6.4.6 Future directions for genetic studies

The major drawback of electrophoresis for studying animal genetics, is the necessity for destructive sampling, being referred to as the "find 'em and grind 'em" school of population genetics (Lewontin, 1991). This is particularly important when considering rare species, where sampling of individuals can have adverse effects on the survival of the populations being studied.

However, methods now exist for extracting DNA from tiny amounts of organic tissues and amplifying the DNA using Polymerase Chain Reaction (PCR). A range of molecular markers can then be used to examine genetic variability between populations. These methods open the possibility of non-destructive sampling from individuals. This has been tried on butterflies, where DNA has been successfully extracted from tiny pieces cut from the wings (Rose *et al.*, 1994). The technique has also been tried on Apollo by the author, in a co-operative project between the genetics departments at Southampton University and the Norwegian Institute for Nature Research (Lushai *et al.*, In prep.). Wing tip samples of *ca.* 3 mm^2 were cut from living butterflies (Plate 25, p.173), and isolated into vials using alcohol and heat sterilised forceps. Wing damage that resulted was very similar to that caused by bird attack, and mark-recapture experiments in the field indicated that butterflies sampled by this technique were still flying normally at the end of the flight season. The types of molecular markers which can be used include randomly amplified polymorphic DNA (RAPD), mitochondrial DNA (mtDNA) and microsatellites (Chapco *et al.*, 1992; Hadrys *et al.*, 1992; Mitton, 1994; Weising *et al.*, 1995).

In addition to the obvious advantages of non-destructive sampling, alternatives to enzyme electrophoresis also have immense benefits by allowing comparison of results gained from different methods and considering different aspects of the genetic composition of organisms.

6.4.7 Conclusions

There are at least four alternative explanations for a lack of genetic differentiation between populations:

a) Insufficient sensitivity of electrophoretic techniques

b) Similar selection pressures operating in similar habitats

c) Present-day gene flow between populations

d) Gene flow amongst historically more widespread populations

For Norwegian Apollos, the influence of historical distribution would appear to be of over-riding importance. However, other factors also appear to contribute to the lack of differentiation. In particular, the combination of MRR data (Chapter 5) and genetically based estimates of dispersal support the hypothesis that chains or networks of small Apollo populations exchange occasional migrants, leading to effectively panmictic populations at the regional scale. With larger effective population sizes and hence relatively weak genetic drift, differentiation of historically connected populations would occur only slowly, especially if some similar selective pressures (such as cold spring temperatures) were operating at the different sites.

As other authors have shown (Ehrlich and White, 1980; Lewis *et al.*, 1997; Aagaard *et al.*, 1997) the combination of genetic studies and examination of dispersal using alternative methods (e.g. mark-release-recapture experiments), can strengthen our understanding of the processes operating in patchy populations.

Plate 25: Non-destructive genetic sampling of Apollo in Telemark.

CHAPTER 7

GENERAL DISCUSSION

In this final discussion, I shall draw together the work in previous chapters to reach some conclusions about the links between landscape ecological theory and its application to butterfly conservation issues. I shall evaluate the methods for studying landscape ecological phenomena, suggest some future directions for research and discuss the implications of landscape changes for butterflies in Norwegian agricultural landscapes.

7.1. Study approaches

One aim of this thesis was to compare the suitability of a number of different approaches for studying butterfly movement behaviour in patchy landscapes. As the previous chapter showed, in spite of the problems associated with direct methods of recording dispersal (section 6.1), genetics alone was not the ultimate solution for measuring contact between populations, due to the potential complicating effects of natural selection and demographic history. However, the combination of genetic data and mark-release-recapture observations, facilitated the interpretation of data from both methods of study.

Genetic data add to our knowledge of inter-population relationships at a large spatial and temporal scale, and can highlight situations where gene flow is restricted. When populations are not genetically differentiated, some of the possible causes can be specifically investigated; for example, by experiments to determine the basis of morphological variation and the role of natural selection. Genetic studies will thus remain a valuable tool for determining the relationships between populations and the causes of geographical variation. Newer molecular methods will increase this potential still further, by targeting different components of genetic variation and, not least, through the possibility of non-destructive sampling.

The more direct methods of measuring movement rates, are essential for monitoring dispersal at smaller scales and in rapidly changing landscapes. Clearly, long-term study of the same populations by a combination of techniques increases the possibility of determining the true relationships between populations (Ims and Yoccoz, 1997). In this respect, the work of Ehrlich and colleagues (summarised in Ehrlich *et al.*, 1975; Ehrlich and Murphy, 1987) on Checkerspot butterflies has been exemplary.

One previously neglected area of direct investigation has been 'landscape-conscious' behavioural study (Lima and Zollner, 1996). The behavioural experiments described in Chapter 3 illustrated the potential of this approach for determining the underlying processes behind observed movement patterns, and lead to some surprising findings about the sensitivity of butterflies to the physical features of the landscape. Further research in this field should aim to elucidate the mechanisms behind flight rules, for example the range of perception of flying individuals, and the role of butterfly motivational state. The use of large numbers of laboratory reared butterflies of known sex, reproductive status and even feeding status (fed versus starved) may assist in this endeavour, both through their use in barrier experiments and by artificially adjusting sex ratios, densities and pressure on resources in well defined habitat patches.

In addition to empirical data, modelling will continue to play an essential role in developing our understanding of the processes occurring in patchily distributed populations at the landscape scale. By simplifying reality, models escape the enormous complexity of inter-related factors, which make empirical data so challenging to interpret, and can lead to insights which might otherwise remain hidden. However, it is vital that the models continue to be updated and revised according to an input of empirical data. Individual-based models (for example Metaphor (Verboom, 1996)), which rely heavily on empirical data, bring modelling closer to reality but the species-specific data needed to parameterise such models is often lacking. In addition to information on the scale and frequency of individual movement, MRR studies will play a role in providing the population parameters for such models, while behavioural data will identify the sub-sets of the population which are of importance to dispersal and colonisation events.

By dealing with processes occurring in real landscapes, GIS is another tool that brings theory, empirical data and application closer together. Layers of data that are simplifications of reality, typically formed by classifying physical data into categories, may be linked with precise empirical data, such as numbers of individuals or species. The explanatory power of different factors or combinations of factors can then be explored and specific questions examined, such as the relationship between butterfly movement patterns and vegetation structure demonstrated in Chapter 4. This example also illustrated the power of maps based on digital imagery, which allow mapping of entire landscapes at a scale relevant to the species of interest. By using a combination of aerial photographs with different wavelength information (black and white, true colour, infra-red) this mapping can be made even more precise and could even incorporate the shadow landscape at different times of day. The occurrence of shade could also be simulated in a GIS program, to examine the opening and closing of dispersal routes for shade averse insects during the course of the day. The increasingly advanced capabilities of GIS programs certainly promise an exciting future for both the development and application of landscape ecology.

7.2. Implications of changes in Norwegian agricultural landscapes

In this thesis I have shown that landscape changes occurring in the Norwegian agricultural landscape will have consequences for butterfly distribution and abundance. Of particular importance in the Norwegian situation is the loss of traditionally farmed areas and the increasing occurrence of potential barriers in the landscape. As hay meadows are abandoned, lack of management will allow a general increase in the height of boundary vegetation and enable scrub to invade the open areas and fill in the gaps in the present boundary vegetation, as demonstrated in Chapter 2. The results presented in Chapters 3, 4 and 5 indicate that the occurrence of barriers, the reduced permeability of the landscape and the increased distances between habitat patches will all lead to a reduction in butterfly movement between meadows.

In particular, the behavioural experiments described in Chapter 3 indicate that barriers to many butterflies may be more subtle than commonly assumed. Take, for example, the barrier effect of shade, the avoidance of a hedge in its entirety even though large gaps are present, and the aversion to crossing even very low physical structures and roads. These effects highlight the need for careful thought when evaluating landscapes for butterflies, including the recognition that butterfly landscapes are structured at a finer scale of resolution than can be read from traditional maps. Restrictions to the movement of individuals, whether physiologically or behaviourally based, will reduce recruitment to populations and decrease the possibility of butterflies colonising new habitat patches, or re-colonising habitat following chance extinctions.

On a smaller scale, even the restriction of trivial movements may impinge upon butterfly survival by restricting accessibility of resources. For example, the establishment of isolated Norwegian Spruce trees in an abandoned meadow may cause sub-division of the meadow for butterflies that generally avoid flying through gaps and shade. Due to the subtle, small-scale behavioural responses of individual butterflies in relation to vegetation structure and physical features of the environment, landscape changes due to agricultural abandonment will have detrimental consequences both at local and regional scales.

The emphasis here on the barrier effects of boundaries may act as a counter-balance to the intense focus in the literature on corridor effects. However, the general conclusion that landscape features simultaneously perform multiple functions even for single species cannot be over-emphasised. Chapter 3 indicated that boundaries also play an important role as butterfly habitat, a fact well documented in intensively cultivated landscapes (Feber and Smith, 1995). The loss of boundaries in intensively farmed Norwegian landscapes (Chapter 2) will thus have the same negative consequences for butterflies as identified elsewhere in Europe (Kaaber and Nielsen, 1988; van Sway, 1990; Dover, 1994).

The degree of parallel movement along boundaries also lends empirical support to the idea that boundaries may link larger habitat patches; a corridor role. In many cases, barrier and corridor functions will be practically inseparable, such that any planned directing of movement in one direction may hinder movement in a transverse direction. This may be desirable for single-species conservation plans that aim to save a species from the brink of extinction by efficient channelling of organisms between rare habitat patches. However, such extreme control of movement patterns has far-reaching consequences, not least for the many other species of plants and animals using a landscape.

The paucity of explicit references to barrier effects in the literature may therefore seem surprising, especially since landscape ecology specifically focuses on interactions between different ecosystems. However, much empirical landscape ecological research has taken place in intensively cultivated regions, where the matrix is so deficient in resources for the majority of wildlife that it approximates the sea of original island biogeography discussions. This is rather ironic considering that landscape ecology developed as a more realistic theoretical framework for understanding mosaics of terrestrial ecosystems. To some extent then, intensively cultivated areas represent simplified models for the development of theories. It is important to bear this in mind when transferring these theories to more complex landscapes, such as traditionally cultivated farmland, where the matrix for one species is the habitat for another and connectivity in the one habitat entails fragmentation in the other. Recognition of this fact is likely to lead to a more thorough assessment of the consequences of landscape design for a diversity of animals and plants.

When focusing on the mosaic view of landscape structure (Chapters 4 and 5) it becomes more useful to refer to landscape permeability rather than corridor and barrier functions. This was illustrated for Scarce Coppers by the GIS model, with its pixels of greater and lesser resistance. The species-dependent nature of landscape permeability can be viewed, in the model, in terms of species-specific resistance values. Thus for a butterfly such as the White-Letter Hairstreak, for which habitat patches are Elm trees (*Ulmus* spp.) and food, honeydew, is obtained in the tree tops, the resistance of different vegetation types would be very different from that of the Scarce Copper.

The Apollo illustrated another concept applicable to mosaic landscapes, namely landscape complementation (Dunning *et al.*, 1992). Different parts of the mosaic fulfilled different functions: larval development, nectar feeding, mate location, predator escape, and thermoregulation. In addition, there was also an aspect of landscape supplementation, since many of the small areas, even if they had contained all of these components would not be large enough to support the entire population. The greatest threat from the cessation of mountain farming is therefore the increase in distances between essential components in the mosaic. This increase is of particular relevance due to the patchy distribution of the topographically restricted breeding sites and the relatively small size of Apollos populations.

Examples of the possible genetic consequences of a patchy distribution of populations were discussed in Chapter 6. Unfortunately, however, the nature of the genetic variation in Norwegian Apollo populations was such that conclusions about the degree of gene flow between populations could not be drawn. This may serve as a sobering reminder of the complexity of the issues in hand.

7.3. Linking theory and application

One of the products of landscape ecological theory has been a range of simple guidelines directed towards landscape planners and conservationists (see Dramstad *et al.*, 1996 for an excellent example). Such guidelines highlight a range of ecological processes and functions and have been enormously successful for shifting focus away from single populations to a more holistic, large-scale conservation approach that aims to maintain the ecological functioning of entire landscapes.

However, just as debate raged about the original theories of island biogeography and their implications for conservation (see for example Diamond, 1976; Simberloff and Abele, 1976; Terborgh, 1976; Whitcomb *et al.*, 1976), so too has there been considerable disagreement about the role of certain aspects of landscape ecological theory, particularly the role of corridors (Simberloff and Cox, 1987; Simberloff *et al.*, 1992; Andrews, 1993; Bonner, 1994; Dawson, 1994; Mann and Plummer, 1995). These authors have pointed to the fact that there is a lack of good evidence for the existence of corridors, that corridors have theoretical disadvantages in addition to their possible benefits and that even if movement is enhanced, the implications of this are not always obvious.

The data presented in this thesis also support the conclusion that corridor theory has been over-simplified. As mentioned above, in a small sub-set of conservation situations, the corridor concept may be of specific use. However, for more general conservation efforts, I would suggest that the concept of landscape permeability, with its focus on the multiple functions of landscape structure, may re-introduce the realism and multi-species perspective required for guiding landscape planners.

Another landscape ecological simplification is to treat all patchy populations as metapopulations (Harrison, 1991). Metapopulation theory was, of course, always intended to be a simplification of reality, being developed through the means of mathematically tractable models. It is perhaps partly due to this analytical nature that the metapopulation approach has proved such a fruitful theoretical framework for analysing patchy systems, not least due to the clear formulation of the parameters required from empirical work to test and improve the models. However, in applying metapopulation ideas to practical conservation problems, the distinction between a classical metapopulation versus, for example, a non-equilibrium patchy system may be far more than pure semantics. The different types of patchy populations will require different landscape management strategies according to the relative importance of the individual patches.

Generally, butterfly populations in traditionally farmed mountain areas are most likely to represent non-equilibrium systems that are declining as habitat patches are taken out of production. An important difference between this and the classical metapopulation is that populations die out, not through stochastic processes, but because the patches become unsuitable as habitat, due to succession. Once a patch disappears from the system, it generally does not become suitable again. More recent metapopulation theory takes account of the variation in types of patchy population, and is beginning to incorporate population genetics, rescue effects, processes of migration etc. in real spatial settings (Hanski and Gilpin, 1997). This added realism is likely to help in bridging the gap between theory and its practical application to conservation.

I would like to discuss one other simplification of landscape ecology which is relevant to landscape planners: the commonly held view that populations should be connected by corridors in order to maintain gene flow. The Apollo genetics reported here illustrates, not only the complexity of factors involved in determining levels of genetic variation, but also the fact that the consequences of that variation are largely unknown. Intuitively, it seems obvious that low genetic variability must reduce population viability; in periods of extreme environmental conditions, all individuals will respond in the same manner, with no reserve of unusual genotypes to survive a catastrophe, and over longer periods of more gradual change, lack of a genetic basis on which selection can operate must surely reduce the possibilities for adaptation. However, negative consequences of low heterozygosity are far from unequivocally demonstrated (Avise, 1994). For example, low heterozygosity is generally considered to be the result of population crashes, not the cause of them, and there exist populations which have recovered from population crashes and appear to thrive in spite of low heterozygosity. The Northern Elephant Seal (*Mirounga angustirostris*), for example, recovered from a population of 30 individuals and now numbers tens of thousands (Avise, 1994). The case of the Apollo is less extreme, and the details of its demographic history are not known; however it is worth commenting on the present situation, because, in spite of the overall low heterozygosity of the Apollo in Norway and the apparent lack of differentiation between populations, there can be little doubt that the different races of Apollo represent considerable morphological and ecological adaptation to local environmental conditions.

Another point of relevance to the conservation/ genetic debate, is the fact that not all endangered populations have low heterozygosity. For example, the Greater One-horned Rhinoceros (*Rhinoceros unicornis*), during a population bottleneck of fewer than 80 individuals within a single national park in Nepal, had one of the highest heterozygosities ever reported for a vertebrate (Dinerstein and McCracken, 1990). This emphasises the point that gene flow may be a very minor priority in relation to, for example, habitat availability.

In addition, increasing gene flow may have negative consequences. For example, one of the most clearly documented risks of low heterozygosity is an increased susceptibility to infectious diseases and parasitic outbreaks (O'Brien and Evermann, 1988). How ironic then if the tool for increasing heterozygosity should be corridors, landscape elements which, if they do encourage movement of individuals will also enable the spread of diseases.

There is still debate about the processes involved in speciation; for example, whether this occurs through novel genotypes in small founder populations (genetic revolution), or a more gradual process whereby selection builds on the polymorphism already present within species (see Collins, 1991, for an overview). In either case, gene flow will disrupt the process. Even the process of local adaptation, such as the adaptation of the mountain form of Apollo to a different food plant, may be disrupted by 'too much' gene flow. For general conservation measures aiming to preserve overall biodiversity, some degree of fragmentation may thus have a positive contribution. There is some evidence that heterozygosity may be increased by a population bottleneck or founder effect, such as that occurring when a successful migrant colonises an empty habitat patch (Carson, 1990).

Clearly, one of the first steps in any conservation discussion is to assess the type of present threat in relation to the historical patterns of colonisation and extinction within a population. Simulation models (Fahrig, 1997) and common sense suggest that habitat loss is usually likely to be the greatest cause of population decline. It is also true that fragmentation is frequently caused by habitat loss, and the processes can be difficult to isolate. For example, although many species were very sensitive to landscape structure, Chapters 4 and 5 demonstrated that, even for the strongly flying Apollo, distance was a major limiter of dispersal. Distances will increase between patches as meadows are taken out of production and habitat is lost. The effect may be that of fragmentation – that populations are too far from one another for recruitment and colonisation to occur – but the underlying cause will still be habitat loss.

Chapter 2 illustrated that the changes in Hjartdal, occurring through the growth of barriers between meadows, do involve true fragmentation, i.e. the same amount of habitat becomes divided and isolated by barriers and reduced landscape permeability. However, as noted in Chapter 2, the increased diversity of vegetation types in Hjartdal may even have positive effects for a wider range of wildlife, whereas the national trend of a declining area of lightly cultivated meadows is likely to have a significant negative impact on the general biodiversity of Norwegian agricultural landscapes.

Landscape ecological theory has much to offer applied conservation, but should be seen in conjunction with, rather than a replacement for, traditional concerns regarding habitat area and quality. One can question whether the hard pressure for research and conservation funding occasionally leads to an almost unethical use of 'fashionable' terms such as corridor and metapopulation and their popular recommendation as conservation solutions. As Soulé (1991) points out, 'Guidelines and rules of thumb should stimulate thought, not replace it'.

7.4. Norwegian butterfly conservation at the landscape level

Viable butterfly populations can often be maintained on relatively small areas of habitat and protection in nature reserves might thus seem appropriate for these insects. For example, the White-Letter Hairstreak is a rarity in Norway and listed as vulnerable on Norwegian red lists (Anon., 1994), but it occurs in the Hjartdal study area and will certainly benefit from the Elm/ Lime woodland nature reserve in the valley (although I doubt that the butterfly was considered in the designation of the reserve!). However, as Thomas points out (1984), only a very small proportion of land in most developed countries is protected in nature reserves. In addition, the common tendency of butterflies to breed in habitats at early successional stages means that protection in itself is not sufficient; management is essential to ensure the generation of new habitat. In Norway, nature reserves are areas specifically protected against human intervention and certainly not suitable for the type of management-dependent butterfly conservation that is the focus of this thesis. Landscape protection areas on the other hand, which aim to maintain the landscape in its traditional state would be ideal categories for butterfly conservation areas.

It should be mentioned that conservation in Norway is strongly rooted in resource management and the majority of funding and much public interest are directed at large carnivores, game and fish. The poisoning of entire river systems to eliminate a salmon parasite (*Gyrodactylus salaris*) is, in my personal opinion, an illustration of the low level of priority accorded to invertebrates. Leaving the ethical issues of conservation aside, I merely wish to point out that butterfly conservation as practised in some European countries, such as England, is an unrealistic proposition in Norway; so too is the collection of research and monitoring data by the efforts of volunteer butterfly enthusiasts (Pollard and Yates, 1993). During recent years, however, there has been increasing interest in the conservation of cultural landscapes, inspired predominantly by botanists, and there is even some voluntary management of traditionally farmed areas. There is also political will to maintain and improve biodiversity in both traditional and modern agricultural landscapes. Thus, the surest method of maintaining butterfly diversity in Norwegian agricultural landscapes and to introduce a more widespread public interest in insects, is to highlight the close link between butterfly diversity and general biodiversity of agricultural ecosystems.

There is a wide recognition that butterflies have great potential as biodiversity indicators (Heath, 1981; Gilbert, 1984; Brown, 1991; Eberhardt and Thomas, 1991; Kremen, 1992). Their short life cycles ensure that they respond quickly to changes in habitat quality, and their sensitivity to environmental variables results in a rapid response even to subtle changes in the vegetation, such as changes in sward height (Anon., 1986). In addition to requiring a diversity of nectar plants, each butterfly species demands specific larval food plants, often under particular environmental conditions (degree of shading, for example, can be very important) and many Lycaenid larvae require the presence of particular species of ants. Clear relationships have been proven between the presence of butterflies and the diversity of flowering plants (Settele and Geissler, 1989; Britten and Riley, 1994), suggesting that butterflies would be a suitable indicator group to monitor the state of florally species-rich grasslands.

Butterflies are also pollinators and thus play a role in maintaining biodiversity by cross-fertilising the plants they visit (Levin, 1981; Kevan, 1991). Although there are relatively few plant species with psychophilious flowers (i.e. adapted specifically to butterfly pollination), butterflies may play an important qualitative role in the gene flow of plants since the small amount of pollen they do carry remains attached to the insect for some time and may be carried considerable distances (Courtney *et al.*, 1982). Obviously, the further butterflies are able to travel, the greater will be the potential distance of pollen transfer.

Butterfly monitoring schemes have now been established in many European countries. Butterflies have been shown to respond quickly and clearly to habitat change - both of negative and positive character - and the monitoring schemes have attracted great public support, including that of volunteer work-forces (Pollard and Yates, 1993). Detailed nation-wide mapping of butterfly distributions and monitoring of year to year variations have contributed greatly to research on, for example, the effects of climatic warming on butterflies, and the effectiveness of conservation measures and habitat regeneration (Thomas, 1984; Pollard and Eversham, 1995; Sutcliffe *et al.*, 1996).

In 1981, Heath stressed the absolute necessity of a widespread interest and desire to conserve butterflies before any long-term success could be achieved. He urged the entomological community to strive for a wider acceptance for insect conservation by politicians, legislators, planners and the public, especially the agricultural community. In Norway, this process has scarcely begun but the growing interest in the conservation of the cultural landscape now provides the perfect opportunity to spread enthusiasm and interest in butterflies. Use of butterflies as indicator species in a new project for monitoring of the Norwegian cultural landscape, may play a significant role in this endeavour, not only through encouragement of the management of butterfly habitat but also through increased publicity, and possibly the future establishment of a national monitoring scheme.

There is still a long way to go before insects receive the same recognition and enthusiasm in Norway as in some other European countries, and a Norwegian Butterfly Monitoring Scheme lies some distance into the future. However, it is also the case that the natural wildlife of Norway is in a less critical position than that throughout much of Europe. Butterflies of seral grasslands may still have some naturally occurring habitat, held open by, for example, avalanches, landslides and fires. Indeed, the butterfly habitats in areas like Hjartdal, created by positive landscape management by man for thousands of years, are exceptional. With all the knowledge we do have about the requirements of butterflies, with our GIS programs and our models, and the technology to look at the very molecules of life, it would be ridiculous indeed if we could not manage to achieve with a will that which our ancestors achieved naturally for generations. It is therefore with a cautious optimism that I view the future prospects for butterfly conservation in Norway.

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APPENDIX I:

English and scientific names of the butterflies mentioned in this thesis.

English name	**Scientific name**
Adonis Blue	*Lysandra bellargus*
Apollo	*Parnassius apollo*
Arran Brown	*Erebia ligea*
Baton Blue	*Pseudophilotes baton*
Bog Fritillary	*Proclossiana eunomia*
Brimstone	*Gonepteryx rhamni*
Brown Hairstreak	*Thecla betulae*
Chequered Blue	*Scolitantides orion*
Chequered White	*Pieris protodice*
Clouded Apollo	*Parnassius mnemosyne*
Clouded Yellow	*Colius croceus*
Comma	*Polygonia c-album*
Common Alpine	*Erebia epipsodea*
Common Blue	*Polyommatus icarus*
Dark Green Fritillary	*Mesoacidalia aglaja*
Dingy Skipper	*Erynnis tages*
Edith's Checkerspot	*Euphydryas editha*
Geranium Argus	*Eumedonia eumedon*
Glanville Fritillary	*Melitaea cinxia*
Green-Veined White	*Pieris napi*
High Brown Fritillary	*Fabriciana adippe*
Holly Blue	*Celastrina argiolus*
Idas Blue	*Lycaeides idas*
Large Blue	*Maculinea arion*
Large Copper	*Lycaena dispar*
Large Skipper	*Ochlodes venatus*
Large Wall Brown	*Lasiommata maera*
Large White	*Pieris brassicae*
Lesser Marbled Fritillary	*Brenthis ino*

Little Blue	*Cupido minimus*
Marbled White	*Melanargia galathea*
Marsh Fritillary	*Eurodryas aurinia*
Mazarine Blue	*Cyaniris semiargus*
Meadow Brown	*Maniola jurtina*
Monarch	*Danaus plexippus*
Orange Tip	*Anthocharis cardamines*
Painted Lady	*Cynthia cardui*
Pearl-Bordered Fritillary	*Clossiana / Boloria euphrosyne*
Red Admiral	*Vanessa atalanta*
Reverdin's Blue	*Lycaeides / Plebejus argyrognomon*
Ringlet	*Aphantopus hyperantus*
Scarce Copper	*Lycaena / Heodes virgaureae*
Scarce Heath	*Coenonympha hero*
Silver-Spotted Skipper	*Hesperia comma*
Silver-Studded Blue	*Plebejus argus*
Silver-Washed Fritillary	*Argynnis paphia*
Small Apollo	*Parnassius phoebus*
Small Heath	*Coenonympha pamphilus*
Small Pearl-Bordered Fritillary	*Clossiana selene*
Small Tortoiseshell	*Aglais urticae*
Small White	*Pieris rapae*
Spotted Fritillary	*Melitaea didyma*
Swallowtail	*Papilio machaon*
Western Seep Fritillary	*Speyeria nokomis apacheana*
White Admiral	*Ladoga / Limenitis camilla*
White-Letter Hairstreak	*Strymonidia w-album*
Wood White	*Leptidea sinapis*

APPENDIX II: LIST OF FIGURES

APPENDIX III: LIST OF TABLES