CONSERVATION BIOLOGY OF THE MARSH FRITILLARY BUTTERFLY *EUPHYDRYAS AURINIA*

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The candidate confirms that the work submitted is her own and that appropriate credit has been given where reference has been made to the work of others.

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ABSTRACT

The conservation biology of *Euphydryas aurinia* was investigated, analysing its metapopulation dynamics, interactions with parasitoids and the efficacy of habitat restoration.

Euphydryas aurinia has undergone a widespread national decline in recent years. This decline is quantified at a 10km scale. The distribution in 2020 was predicted for *E. aurinia* from the 1995-99 distribution, assuming that the current causes and pattern of decline continued. The predicted distribution in 2020 represented a 48% loss in 10km grid square records, with only the core regions surviving. The distribution and persistence of the butterfly was quantified at a regional scale in one, intensively studied area (25km by 25km) in Dorset (England, UK). The metapopulation approach was useful in understanding the occupancy pattern and persistence of *E. aurinia* within this landscape. The probability of patch occupancy increased with patch connectivity (isolated patches were less likely to be occupied), vegetation height and resource area (patch area multiplied by host plant cover). Such a pattern was consistent with the interpretation that the butterfly persists as a metapopulation. This supported the use of the Incidence Function Model, as a tool to explore the possible fate of *E. aurinia* in fragmented landscapes in Dorset and in five pairs of independent networks across the species' range in England and Wales. The threshold network area was predicted to be 71ha, to achieve a 95% probability of persistence for 100 years, for a network within a 4km by 4km area. However, this figure may actually be an underestimate of the area required, if extinction debt is a reality.

Parasitoid attack, principally by *Cotesia bignellii*, appears to have an effect on the population dynamics of *E. aurinia* and may help to explain the requirement of *E. aurinia* for large habitat patches. This preliminary work suggests that the parasitoid also has a metapopulation structure and that it is of equal conservation concern. At a local scale the results suggest that the parasitoid and host may have a shifting distribution, with the butterfly 'escaping' parasitism in some areas.

Habitat restoration and re-creation will be necessary in many networks with insufficient habitat area. Experimental investigation into methods of habitat restoration showed that unsuitable but potential habitat may be restored through cutting twice a year in combination with grazing. Habitat re-creation has been shown to be feasible for agriculturally improved sites, but may be more difficult to achieve due to the higher nutrient status and the competitive interaction of other species with the host plant *Succisa pratensis*.

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DECLARATION

This thesis involved collaboration with Richard Fox (RF), Lucia Galvez Bravo (LGB), Alison Holt (AH), Justin Lyons (JL), Otso Ovaskainen (OO), Andy Polkey (AP), Mark Shaw (MS), Martin Warren (MW), David Wheeler (DW) and Robert Wilson (RW).

CHAPTER 2

National distribution data provided by RF.

CHAPTER 3

Field data collected with AH and LGB. Past distribution data provided by MW. RW ran the parameterisation calculations and assisted with modelling. Metapopulation capacity of networks was calculated by OO.

CHAPTER 4

MS identified parasitoid samples.

CHAPTER 5

Cutting of experimental plots undertaken by JL, AP and DW.

... to know which brood of Holly Blue
feeds on ivy, spring or summer,
and what distinguishes the Gatekeeper

from the Meadow Brown, at twenty feet.
To hear you talk of flight patterns
and favourite plants, how Wood Whites drift

like snowflakes in the sun,
and even where the Devil's-bit persists,
the Marsh Fritillary's now rare.

By Heart, Ruth Sharman 1997

1.0 INTRODUCTION

1.1 General introduction

Human induced changes in habitat quantity, quality and structure affect the distributions and persistence of species. This is an increasingly important subject of research for ecologists and conservation biologists. Habitat destruction and fragmentation result in the direct loss of suitable habitat, reduction in size of the remaining habitat, increased isolation of these remnants, an increased proportion of edge habitat and sometimes a reduction in habitat quality (Fahrig 1997). Habitat destruction and fragmentation is reported to be a major cause of species extinction (Groombridge 1992; Pimm *et al.* 1995) and can severely affect the distribution, evolution, long-term persistence and extinction probability of species (Dempster 1991; Saunders *et al.* 1991; Verboom *et al.* 1991; Soulé *et al.* 1992; Fahrig & Merriam 1994; Andrén 1994; Hanski *et al.* 1995a; With & Crist 1995; Andrén 1997; Brooks *et al.* 1997; Thomas C. D. *et al.* 1998a; Harrison & Bruna 1999; Hill *et al.* 1999; Zscchokke *et al.* 2000; Gibbs & Stanton 2001).

Species that inhabit these fragmented and isolated habitat patches are at increased risk of extinction from demographic and environmental stochasticity (Hanski & Gilpin 1991). How species persist in fragmented landscapes and at what level of fragmentation extinction occurs, has become a focus for spatial ecology with direct relevance to conservation biology. One commonly adopted approach (Forman 1995) is through the concept of species persisting within a regional network of suitable habitat, as a metapopulation (Hanski & Gilpin 1997; Hill & Caswell 1999). This approach has demonstrated the importance of the size and spatial distribution of habitat (affecting extinction and colonisation processes), on the persistence of species occupying discrete patches. For many rare and threatened species, remaining habitat may be too small for the long-term persistence. The focus for these species will be to secure existing habitat and increase the area of suitable habitat through restoration and re-creation, in addition to managing the habitat to maximise the potential carrying capacity of the remnants that do survive. Species do not occur in isolation and the complex relationship with other species, such as natural enemies, must also be understood because they may influence the probability of extinction.

This thesis examines a model species, the butterfly *Euphydryas aurinia*, which exemplifies many of these issues. The thesis uses the metapopulation approach as a tool to understand the regional persistence of the species and its network area requirements and to explore its conservation needs. Results of an initial investigation into the relationship between the specialist primary parasitoid and the host butterfly are also presented, which have implications for further research. The results of an experimental investigation into habitat restoration and re-creation methods for suitable *E. aurinia* habitat will be discussed and its role in increasing network size for butterfly metapopulations.

This introduction will discuss the metapopulation concept, critically review the main assumptions and discuss the application of metapopulation models to species conservation. I will then discuss spatial aspects of the interaction between parasitoids and their hosts. Then I will approach the problem of habitat restoration and re-creation in relation to the need to increase habitat network size to ensure long-term metapopulation persistence.

1.2 Metapopulation approach

1.2.1 History and definition

The metapopulation concept has taken some time to develop, but was first formalised by Levins (1969, 1970) as a 'population of populations' occupying discrete habitat patches with extinction-colonisation dynamics. Prior to this Andrewartha & Birch (1954) gave evidence to support their view that local population extinction was a common occurrence. MacArthur & Wilson (1963) published their dynamic theory of island biogeography, concerned with explaining the equilibrium number of species on islands. (See Hanski 1999a; Hanski & Simberloff 1997 and Hanski & Gilpin 1991 for a full historical review).

A metapopulation may be defined as a network of local populations occupying discrete habitat patches, where all local populations have a substantial probability of extinction. When extinction occurs, patches may be re-colonised by individuals dispersing from other occupied patches. The long-term persistence of the species may only occur at the metapopulation level, through a balance between local extinction and colonisation (Gilpin & Hanski 1991; Hanski & Gilpin 1997; Hanski 1998; Hanski 1999a).

Many butterflies have declined over the last century and this has been documented in Europe (van Swaay & Warren 1999) and in Britain (Heath *et al.* 1984; Asher *et al.* 2001). The ecological requirements of Lepidoptera are relatively well understood compared to most insect groups, but despite this, declines have occurred in nature reserves (Thomas J. A. 1984, 1991, 1995a; Warren 1992, 1993a). This has initiated research into the ecology and conservation of butterflies (New *et al.* 1995; Pullin *et al.* 1995). There has been a move from the more traditional approach of single-site habitat management protection, towards the goal of long-term maintenance of groups of populations through a metapopulation approach (Thomas C. D. 1995; Thomas & Hanski 1997). Butterflies are particularly useful taxa for testing metapopulation theory. Most species (apart from 'open' or migratory species, Warren 1992) tend to occur in well-defined areas where resources such as nectar and host plants are concentrated; once the ecological requirements of the species are known, these areas can be relatively easily delimited. A sea of unsuitable habitat, which has been further enhanced by habitat destruction and fragmentation, usually surrounds these good quality 'patches'. Such a structure is consistent with the metapopulation approach. Butterflies are relatively large and easily observed, so the occupancy of patches can be determined, including evidence of breeding (such as larval groups of the fritillaries). Generation times are short, so patch turnover can be observed over a number of generations. Empirical studies of butterflies have thus helped to test and develop metapopulation theory (Hanski *et al.* 1995a; Thomas & Hanski 1997; Kuussaari 1998). However, for metapopulation models to become a useful tool for conservation biology, these theories must continue to be tested and they must be applied to systems of genuine conservation concern.

1.2.2 Metapopulation theory, modelling and application

The main tenets of metapopulation theory are population size-dependent extinction and isolation-dependent colonisation rates. Small populations, which usually occupy small habitat areas, have a higher probability of extinction than larger populations of the same species due to demographic or environmental stochasticity (Diamond 1984; Harrison 1991, Hanski 1994c). A small population will be more vulnerable to demographic variation (birth and death processes) and to increased rates of inbreeding which reduce fecundity and increase mortality (Saacheri *et al.* 1998). At extremely low densities individuals may face the further problem of the Allee effect, which refers to a decrease in population growth rate due to difficulties in finding mates, decreased foraging efficiencies and reduced defences against predators. Kuussaari *et al.* (1998) found that the probability of mate location decreased with decreasing population density in the smallest populations of *Melitaea cinxia*. Per capita emigration rates are often found to be higher in small populations (Hill *et al.*1996; Kuussaari *et al.* 1996; Sutcliffe *et al.* 1997a; Kindvall 1999; Hanski *et al.* 2000; Petit *et al.* 2001). As a consequence, the loss of individuals through emigration may increase extinction risk in smaller populations (Thomas C. D. *et al.* 1998a; Hanski *et al.* 2000) and can increase overall mortality for the whole metapopulation (Hanski & Zhang 1993).

Environmental variation contributing to the increased risk of extinction in small populations include, unusual weather events (Harrison *et al.* 1988) and habitat change, such as a change in grazing pattern (Warren 1993a; Gutiérrez *et al.* 1999). Environmental stochasticity may cause local and even metapopulation-level extinction if there is inadequate habitat heterogeneity to buffer the effects of, for example, extreme climatic effects (Sutcliffe *et al.* 1996, 1997b).

The assumption is made that, habitat quality being equal, a linear relationship exists between population size and habitat area. Many empirical examples exist which support the theory of an increased risk of extinction to small populations inhabiting small patches. For example, the European nuthatch *Sitta europaea* (Verboom *et al.* 1991), the bush cricket *Metrioptera bicolor* (Kindvall, & Ahlén 1992), the butterflies *Euphydryas editha bayensis* (Harrison *et al.* 1988) and *Melitaea cinxia* (Hanski *et al.* 1994, 1995b) all show this pattern. Thomas & Harrison (1992) surveyed patches of *Plebejus argus* butterfly in one year and repeated this seven years later. Turnover rate was as low at 10% in large patches (>0.9ha) compared to 35% in medium patches (0.2 to 0.9ha) and as great as 80% in the smallest patches (<0.2ha).

Patch size is often measured as a proxy for population size for use in metapopulation models based on the assumption, stated above, that patch and population size are correlated. Patch size may be more accurately measured than population size because population size will vary from year to year within a patch, making a single census an unreliable estimate of average population size in a given year. However patch quality varies and no patch is completely homogeneous. If the quality of a patch is low then the size of the population it supports may be much lower than would be predicted from patch size. The importance of habitat quality for the regional persistence of species has been suggested to be important in many studies (Verboom *et al.* 1991; Litvaitis & Villafuerte 1996; Nieminen 1996; Dennis & Eales 1997; Wettstein & Schmid 1999). This has recently been quantified by Thomas J. A. *et al.* (2001), who showed that among-site variation in habitat quality predicted patch occupancy and population density more strongly than patch area and to some extent isolation in three butterfly species. This remains a metapopulation approach, but implies that factors other than habitat area may represent the main predictor of extinction risk (Thomas C. D. 1994).

The probability of colonisation is dependent on distance. If a population becomes extinct from a patch, then the chance of it being re-colonised will depend on the distance to the nearest local populations. Habitat patches that are isolated will have the lowest probabilities of re-colonisation and well connected patches will have the highest probabilities of colonisation, as the number of immigrants decreases with increasing distance (Hanski 1994c; Thomas & Hanski 1997). There is a wealth of empirical data to support this such as for the European nuthatch *S. europaea* (Verboom *et al.* 1991) and the bush cricket *M. bicolor* (Kindvall, & Ahlén 1992). The butterfly *Hesperia comma* was found to colonise large patches close to exiting populations (Thomas & Jones 1993; Davies *et al.* 2001; Thomas C. D. *et al.* 2001). Other butterfly species exhibiting the same patterns include *P. argus* (Thomas & Harrison 1992), *Mellicta athalia*, *Thymelicus acteon* and *Strymonidia pruni* (Thomas C. D. *et al.* 1992).

For highly isolated populations few immigrants will arrive (loss of the 'rescue effect', Brown & Kodric-Brown (1977)), and the most dispersive individuals may emigrate. These factors may result in the evolution of reduced mobility. Dempster (1991) measured museum specimens of *Papilio machaon* and hypothesised that mobility was linked to thoracic size. The thoracic width to length ratio of individuals from a highly isolated population of *P. machaon* from Wicken Fen was found to be significantly smaller than individuals from a less isolated population of the Norfolk Broads. Dempster hypothesised that since the thorax contained the muscles responsible for flight then a narrower thorax would result in weaker fliers, with reduced mobility.

Patch isolation is often measured by distance alone. However, distance between suitable patches may not be the only factor involved. Recent work by Conradt *et al.* (2000) gives evidence of non-random dispersal patterns in the butterfly *Maniola jurtina* in which butterflies may systematically search and actively orientate to distant habitat. If individuals behaviourally adjust their movements in the context of specific landscapes, then the assumption that colonisation is dependent on distance alone is too simplistic. How the intervening landscape is perceived by the focal species will influence to some extent which vacant patches are more likely to be colonised (Ricketts 2001). Nonetheless, over the range of isolation values found in most habitat networks of rare species, the conclusion that fewer immigrants arrive in the more isolated patches is likely to be robust.

Landscape structure has significant effect on movement. Matrix habitat (unsuitable habitat surrounding suitable habitat patches) varies greatly and this will have an impact on the way a species moves through the landscape (Wiens 1997; Ricketts 2001). The probability of reaching an unoccupied but suitable habitat patch is probably dependent on more aspects than just its isolation. The intervening landscape was found to affect dispersal by *Parnassius smintheus*, which inhabits alpine meadows in Canada. Dispersal declined with distance, but declined more rapidly through forest and with elevational changes than through the more open, but unsuitable, meadows (Roland *et al.* 2000).

Metapopulation models use the theoretical basis of area-dependent extinction and isolation-dependent colonisation (supported by the empirical evidence given above) to model the distributional patterns and dynamics of species within fragmented landscapes. This may be an oversimplification, as metapopulation theory generally leaves out habitat quality, for example. In a conservation context, metapopulation models should be used as a tool to help understand and predict the persistence of species in real fragmented landscapes and model the effects of increased fragmentation. For this to work, the models must be simple. To incorporate many parameters is incredibly time consuming (e.g. Thomas J. A. *et al.* 2001 took 11 field seasons to complete). The area and spatial distribution of suitable habitat patches are much quicker to collect and have been shown empirically, to be good predictors of metapopulation persistence, and are therefore more commonly used. It is the nature of models that they are simplifications of the real world. When interpreting the results from such models, the assumptions behind them must be taken into consideration, and their implications considered. When further parameters and complexities are added to make models more biologically 'real', they may become less predictive possibly because they do not reflect the more important biological predictors. Hanski & Thomas (1994) and Moilanen & Hanski (1998) found that adding complexity did not improve the predictive accuracy of the model to any great extent.

Many metapopulation models have been developed (Hanski & Simberloff 1997); from spatially implicit models (Levins 1969, 1970) to spatially realistic ones (Hanski 1994a; Hanski & Thomas 1994). The latter are most applicable to conservation of species within real landscapes, as these models allow the inclusion of the specific geometry of particular habitat networks, such as the number of patches, their size and exact locations. An example of such a model is the Incidence Function Model (IFM) (Hanski 1994a,b, 1997a,b), as used in chapter three, which has created a useful link between models and empirical studies. The IFM was developed and successfully applied to the well-studied butterfly *Melitaea cinxia* (Hanski *et al.* 1995a; Kuussaari *et al.* 1996; Kuussaari 1998). Hanski *et al.* (1996c) used the IFM to predict the distribution of *M. cinxia* within suitable habitat patches on the Åland Islands, off the SW coast of Finland. The model was parameterised using data from a small part of the study area and then modelled over the rest of the study area, to predict the dynamics of the butterfly. Over most of the study area the model predictions agreed with the observed fractions of occupied habitat. However, in the south-eastern area there was some discrepancy attributed to differences in habitat quality as a result of different grazing levels.

The IFM has also been applied to other butterfly species *Melitaea diamina* (Wahlberg *et al.* 1996), moth assemblages (Nieminen 1996), the grasshopper *Oedipoda caerulescens* (Appelt & Poethke 1997), the American pika *Ochotona princeps* (Moilanen *et al.* 1998) and the field vole *Microtus agrestis* (Crone *et al.* 2001). However, it has rarely been directly applied to answer specific conservation questions about persistence or decline of species within fragmented landscapes, which is often used to justify the development of such models. I found only one example in the literature where the IFM was used to derive the minimum viable metapopulation size, for the frog hopper *Neophilaenus albipennis* (Biedermann 2000).

The IFM is one of the most applicable metapopulation models for conservation purposes, as it is possible to parameterise the model for existing metapopulations with readily available data. Once parameterised, it may be used to predict the persistence of species metapopulations in specific networks of habitat patches and investigate persistence under different landscape scenarios, levels of fragmentation or management actions. Quantitative questions can be asked about the lifetime of a species in a current patch network and the consequences for the species, if further fragmentation and habitat loss occurs. This is the first time, to my knowledge, that the IFM has been applied to multiple independent networks. Where the focal species currently persists in comparison to networks where the species has become extinct recently, to quantify the threshold habitat area required for long-term species persistence.

Metapopulation models have been used to calculate the minimum viable metapopulation size (MVM), which is defined as the minimum number of interacting local populations necessary for long-term persistence of a metapopulation. Similarly the minimum amount of suitable habitat (MASH) is defined as the minimum density of suitable habitat patches necessary for long-term persistence (Hanski *et al.* 1996a).

The metapopulation capacity (Hanski & Ovaskainen 2000) has recently been developed, as a measure of the capacity of a highly fragmented landscape to support a given species. It has been derived from metapopulation theory and can be calculated for real networks of known spatial configuration and patch area, to allow comparisons to be made in the relative ability of different landscapes to support a metapopulation. The metapopulation capacities of the independent networks have been calculated, in addition to the IFM results, to aid the estimation of a minimum network area for metapopulation persistence.

1.2.3 Non-equilibrium metapopulations and extinction debt

The majority of metapopulation models are based on the assumption that systems are at equilibrium, where local population extinctions are balanced by local population colonisations. However, this is probably not the case for most real metapopulations at least when one is concerned with declining species (Harrison 1991). The distribution of suitable habitat does not remain constant over time (Thomas & Hanski 1997) and with continued habitat fragmentation and destruction such perturbations will result in a non-equilibrium system (Hanski 1997a). Following such a perturbation, the metapopulation may not have had time to reach the new equilibrium generating a 'debt of extinctions' (Hanski 1994b). Many occupied networks are likely to become extinct, but have not become so yet because it takes time to reach the new equilibrium.

Hanski *et al.* (1996b) demonstrated non-equilibrium dynamics with *M. cinxia.* Within a 25km^2 area, the reduction in habitat area over 20 years was quantified using aerial photographs. The total area of suitable habitat declined to one-third and the number of patches decreased from 55 to 42. The metapopulation of *M. cinxia* was predicted to have closely followed this decline (Hanski *et al.* 1996a) probably because the amount of remaining habitat was large. With further habitat loss (each patch was reduced by 50% in area in the simulations, over 20 years), the patch network would be considerably smaller, less than the minimum amount of suitable habitat for metapopulation persistence. However, extinction (the equilibrium state) was predicted to take hundreds of years to occur. This time lag to extinction probably occurs because the last populations to go are the largest populations with the smallest probability of extinction. If many metapopulations of conservation concern are not at equilibrium and predicted to succumb to the 'extinction debt' (Tilman *et al.* 1994), then the estimated network size necessary for long-term persistence is actually an underestimate. Conservationists will fail by just conserving the current patch network. The notion that a given species will survive through protecting the current habitat network is probably insufficient for long-term survival.

1.3 Parasitoids

Parasitoid larvae develop by feeding on the bodies of other arthropods, usually insects, with larval development resulting in the death of the parasitoid's host (Godfray 1994). Insect parasitoids are an important group, recent estimates indicating that host insects are on average attacked by five to six parasitoid species (Hochberg & Hawkins 1994). Parasitoids are widely recognised to have regulatory effects on their host population dynamics (Dempster 1983; Hassell 1985; Hawkins & Sheehan 1994; Lawton 1994; Hassell 2000). A wealth of literature exists on the biology of parasitoids and their behavioural and evolutionary ecology (Godfray 1994; Godfray & Shimada 1999) and on their economic importance in the biological control of pests (Hassell 1980; Biever 1992).

More recently, attention has focused on the effects of space on dynamic interactions between parasitoids and hosts on a local scale (Hassell 1982; Jones *et al.* 1993; Godfray & Hassell 1997; Hassell 2000). Huffaker's classic experiments demonstrated the effect of heterogeneity on population dynamics. In a simple environment (with few oranges), the prey and predatory mite populations became extinct rapidly. When the environment was made more complex (120 oranges) the populations persisted (Huffaker 1958; Huffaker *et al.* 1963). Hassell & May (1973, 1974) developed models with discrete patches of host over which the parasitoid roamed. They concluded that persistence is promoted by increased parasitoid aggregation in patches where the host is at higher densities, with stabilisation occurring because the lower density patches act as refugia for the host. Many empirical and theoretical studies resulted from this and contributed to the still unresolved debate concerning the role of density-dependence in predator-prey interactions (Hassell *et al.* 1991; Pacala & Hassell 1991; Hassell 2000 and references therein).

The spatial interactions described above are mainly at the local scale where complete mixing of both host and parasitoid is assumed. Fewer studies have extended host-parasitoid dynamics to the metapopulation scale (Hassell 2000). At this larger spatial scale it appears that patchiness, generated for example through habitat fragmentation, actually has a de-stabilising effect on host-parasitoid dynamics (Kareiva 1987; Roland & Taylor 1997) probably through decoupling of the host from its natural enemy.

Lei (1997) investigated the host-parasitoid dynamics in the metapopulation of *M. cinxia* in Finland. Ten species of parasitoid were found to be associated with the butterfly (primary parasitoids and hyperparasitoids) with *Cotesia melitaearum* being the most important, as it is gregarious and produces three generations of adult per host generation (Lei *et al.* 1997). The parasitoid appears to have a metapopulation structure like its host; the incidence of *C. melitaearum* increased with increasing host population size and decreased with increasing isolation (Lei & Hanski 1997). The risk of extinction for local populations of *M. cinxia* was found to increase with parasitoid population size. Parasitoid attack had a significant effect on local extinction of the host (Lei & Hanski 1997). It appears that the parasitoid drives the host to extinction in some local populations and as a result becomes extinct itself. *C. melitaearum* is absent from the smallest host populations. Long-term persistence of the host and parasitoid apparently only occurs at the metapopulation scale.

The decline of many butterflies has been widely documented (van Swaay & Warren 1999; Asher *et al.* 2001), but even more endangered must be the specialist parasitoids attacking these butterflies (Thomas & Elmes 1993) about which relatively little is known (Shaw & Fitton 1989; Shaw 1990).

The parasitoids of *E. aurinia* were investigated by Porter (1979, 1981, 1983, 1984). He suggested that rates of mortality, caused by the parasitoid, might depend on spring weather conditions that affect the relative development rates of the host and parasitoid (Porter 1983). In cool but sunny weather conditions larvae are able to thermoregulate (Porter 1982), the host is able to develop more quickly and it can pupate before adult parasitoids emerge. This loss in synchrony results in a low parasitism rate (7.7% in 1979). Under cloudy conditions, host larval development is synchronised with parasitoid emergence and thought to result in an increased incidence of parasitism (74.5% in 1980). However, this survey was restricted to one site in Oxfordshire, occupied by a small population of *E. aurinia.* The dynamics of this butterfly and its parasitoids have not been investigated at a larger spatial scale.

1.4 Habitat restoration and re-creation

The main reasons for the decline in the distribution of *E. aurinia* are unsuitable habitat management practices and the destruction and fragmentation of existing habitat (Warren 1994a; van Swaay & Warren 1999; Asher *et al.* 2001). Metapopulation theory and empirical studies both lead to the conclusion, that species are most likely to persist in regions with large areas of good quality habitat and where habitat patches are close together. Where species persist in partially degraded landscapes, there is the potential to increase the chance of persistence through habitat restoration and re-creation. For the purpose of this thesis, habitat restoration is defined as a process that brings back, through a certain grazing regime for instance, a former ecological state that may be considered to be preferable. Habitat re-creation also seeks to reinstate some former preferable habitat, but through more active human intervention such as seed-mix application, to habitat that has been more fundamentally altered (e.g. improved agricultural land). If such methods are developed then action can be taken to halt and reverse this decline (Dobson *et al.* 1997).

The habitat requirements of *E. aurinia* are generally understood (Warren & Bourn 1997; Warren 1994a), but populations have become extinct from many sites through changes in land use (Hobson *et al.* 2001). If habitat restoration methods can be developed then there is the potential to restore *E. aurinia* habitats. If existing populations can be increased through enlarging the habitat area and improving the habitat quality, then populations are likely to be at a reduced risk of extinction.

The current focus of habitat restoration tends to be in re-introduction programs (Thomas J. A. 1995b; Pullin *et al.* 1995; Pullin 1996), or when only a few populations of the target species of concern remain (Martila *et al.* 2000; O'Dwyer & Attiwill 2000). With research now emphasising the importance of habitat area (Hanski 1999a) and the problem of extinction debt, habitat restoration should be a vital component in conservation programs. Indeed, it may be much more practical to increase the likelihood of long-term persistence in habitat networks, that are only partially degraded and where species still persist, than to restore habitat quantity and quality in severely degraded networks, where species have already become extinct.

1.5 Scope of thesis

The remainder of this thesis is made up of five chapters. Chapter two provides the context of this study, describing and analysing the widespread national decline of *E. aurinia* that has taken place between two major survey periods, spanning 30 years. The decline is quantified, at a 10km scale. On the basis of this, the predicted distribution for 2020 is presented, assuming that the current causes and patterns of decline continue. Chapter three examines the distribution and persistence of the butterfly at a regional scale, in one large and well-studied area in Dorset. The factors that determine occupancy in this system are examined. Metapopulation modelling, through the Incidence Function Model, is used as a tool to examine and predict the persistence of *E. aurinia* in Dorset and other independent habitat networks elsewhere in England and Wales. The threshold network area for 95% probability of persistence is calculated.

Chapter four begins to explore the complex relationship between *E. aurinia* and the specialist parasitoid *C. bignellii* by investigating parasitism rates at four sites in Dorset and presents preliminary data on the spatial distribution of the parasitoid in relation to its host.

In light of the results of chapter three, which clearly shows that there is not enough remaining habitat in some networks to sustain metapopulations of *E. aurinia*, chapter five experimentally investigates various methods of restoring habitat quality in unmanaged habitat and re-creating habitat in improved pasture.

Chapter six provides a general discussion, outlines the conservation implications of this work and gives recommendations for future research.

1.6 Introduction to study species

1.6.1 Distribution, status and ecology of *Euphydryas aurinia*

The range of *Euphydryas aurinia* Nymphalidae (Rottemburg)[1] (plate 1.1) extends from Europe, Morocco and Algeria to temperate Asia and Korea (Emmet & Heath 1990; Tolman & Lewington 1997). However, it is in serious decline across much of its range. In Europe the butterfly is present in 38 countries and extinct in one (van Swaay & Warren 1999) with the distribution across Europe decreased to between 20 and 50% of its former area of occupancy in the last 25 years. The main threats are from agricultural improvement and abandonment, and through changes in habitat management, which cause habitat either to be destroyed or rendered unsuitable for *E. aurinia*. The butterfly is protected under the 1979 Bern Convention (Annexe II) and the EC Habitats and Species Directive (Annexe II).

The UK is a stronghold of the species, supporting 5-15% of the European distribution (van Swaay & Warren 1999). Within Britain the butterfly has experienced a substantial and rapid decline (figure 1.1) (Warren 1994a; Barnett & Warren 1995; Fox *et al.* 2001 and chapter two), with a 55% loss in 10km recorded distribution since 1970 (Asher *et al.* 2001). These documented declines took place despite full legal protection under the Wildlife and Countryside Act (1981 plus amendments). Incomplete historical records mean that the observed pattern is undoubtedly an underestimate of the true level of decline. The specific causes of decline in Britain are attributed to the loss and fragmentation of semi-natural grassland and changing grazing patterns (Asher *et al.* 2001). Lowland flower-rich grassland has declined by 97% in Britain and Ireland since 1940 and chalk and limestone grassland by 80% over the same time period (Department of the Environment 1995).

The map (figure 1.1) shows the current distribution in Britain. Extinctions have occurred in the eastern half of Britain with contractions of the species towards the core areas of the south, the south-west, Wales and western Scotland (Asher *et al.* 2001; Heath *et al.* 1984). But even in these strongholds, colonies are estimated to be disappearing at a rate of 11.5% per decade (Warren 1994a). However, a few

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[1] Nomenclature follows Karsholt & Razowski (1996).

populations still occur in fragmented landscapes, such as in parts of north Wales and Cumbria.

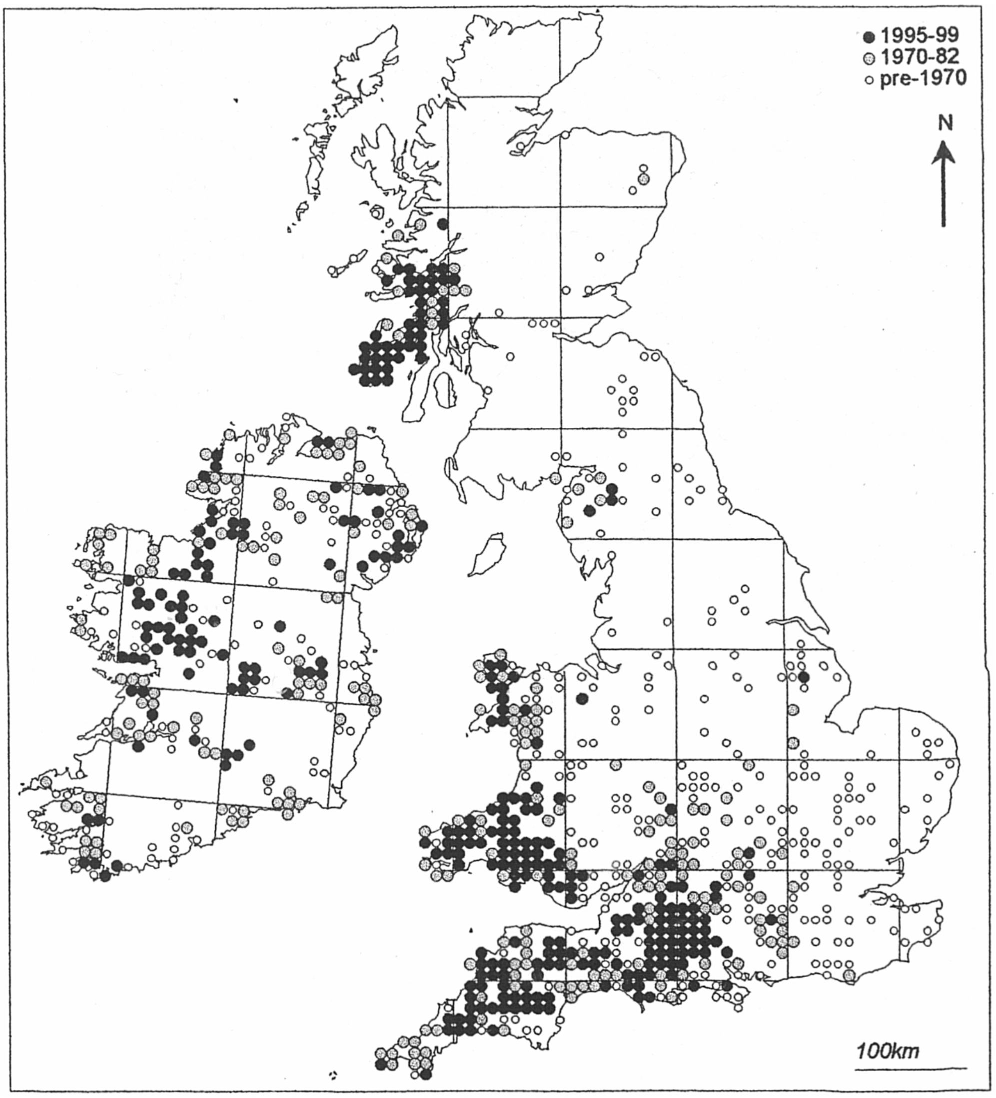

Figure 1.1 The British distribution of *Euphydryas aurinia* plotted by 10km squares of the National Grid. 1995-99 records are shown as black circles, 1970-82 records, shown as grey circles, are now presumed to be extinct 10km squares (i.e. no 1995-99 records. The small, open circles are pre-1970 records, where the species is now extinct (source: Asher *et al.* 2001).

Plate 1.1 Adult *Euphydryas aurinia.*

Plate 1.2 Principal host plant, *Succisa pratensis.*

Euphydryas aurinia breeds in damp, acidic grassland where the host plant, *Succisa pratensis* (plate 1.2), is abundant. These habitats are normally quite tussocky pastures dominated by *Molinia caerulea* or, on more neutral soils, by *Deschampsia cespitosa*. The butterfly also occurs on dry, calcicolous grasslands, mainly on the chalk downs of Dorset and Wiltshire, where colonies breed in much shorter turf (5-10 cm). In both habitats, it prefers swards that are either cattle grazed or un-grazed by domestic stock. Grazing by sheep tends to be detrimental because sheep remove the larger plants that are chosen for egg laying (Warren 1994a).

After mating, females lay an egg cluster on the underside of relatively larger leaves of *S. pratensis*, adjacent to the central rib. The egg batches, which contain up to 500 eggs, hatch within 30 to 40 days (Porter 1981), and change colour from cream when first laid, darkening to orange-brown and then leaden grey prior to eclosion.

Freshly emerged first instar larvae immediately use silk to bind the leaf on which they were laid to an adjacent leaf, to form a feeding web. As the larvae grow, the web is extended. They moult to the second instar after 20 to 30 days of feeding (Porter 1981). A new web is then formed and gregarious feeding continues. After approximately 25 days (Porter 1981) the larvae enter the third instar and the web is extended over large areas of host plant, as the feeding requirements increase. The third to fourth instar moult takes place after about 20 days and occurs in a specially spun web. In early September the fourth instar black larvae construct a dense hibernaculum web around themselves at the base of the vegetation layer and over-winter in this state (Porter 1981).

During sunny days in February larvae begin to emerge from the hibernation web to bask and feed. By early April the larvae fragment into clusters of between 20 and 60 individuals and then moult to the fifth instar. As the larvae develop, feeding groups fragment, eventually becoming solitary feeders in the later stages due to their increased resource requirements, and eventually moult to the final sixth instar. By early May, the larvae are fully-grown and seek suitable pupation sites in the vegetation (Porter 1981).

Adults emerge from mid May and fly until mid July, with males tending to emerge first. Once mating is completed the female searches for a suitable oviposition site, usually near to emergence site. The butterfly is relatively sedentary; Porter (1981) recorded average movements of less than 100m within one site. Work in Finland has shown mean dispersal ability to be 645m (±69) and 467m (±43) for males and females respectively (Wahlberg 2000). Colonisations have been recorded some distance from known populations, between 5 and 20km in distance, which suggests that at least some individuals of the species may be more mobile than previously thought (Warren 1994a).

1.6.2 Larval parasitoids of *E. aurinia*

Porter (1979, 1981, 1983 & 1984) conducted research on the parasitoid species that attack the larval stage of *E. aurinia*. Two *Cotesia* (=*Apanteles*) parasitoids were found to be specific to *E. aurinia*. *Cotesia bignellii* Braconidae (Marshall) has been documented to have a mainly southerly distribution and *C. melitaearum* (Wilkinson), to have a northerly distribution. Two generalist parasitoid flies (Tachinidae) have also been reported from *E. aurinia*. The two *Cotesia* species were hyperparasitised by several unidentified *Gelis* species. I briefly outline the ecology of *C. bignellii* only, as this parasitoid is specific to its host, is one of the most important parasitoids that attacks *E. aurinia*, and is the only species to be dealt with in chapter four.

Three generations of *C. bignellii* occur in one host generation, with parasitoids emerging from late third instar hosts in late August, from late fourth instar hosts in March (the parasitoid over-wintering within the host) and from final instar hosts in June. When the parasitoid larva emerges from its host, it begins to spin a white, silken cocoon with the adult emerging after about four weeks, depending on temperature. Adult parasitoids resulting from early instar hosts are ideally placed within the larval web to re-infect *E. aurinia* larvae.

1.6.3 Ecology of larval host plant *Succisa pratensis*

Euphydryas aurinia larvae feed almost exclusively on *Succisa pratensis* Dipsaceae (Moench)[2] (plate 1.2) in Britain, although the use of alternative resources has occasionally been noted, such as *Lonicera periclymenum* (Ford & Ford 1930; Warren 1993c; Bulman pers. obs.), *Knautia arvensis* (Dunk 1952; Warren 1986), *Scabiosa columbaria* (Palmer 1995) and *Plantago* spp. (Lavery 1993; Palmer 1995; Bealey pers. comm.). These plants are very rarely used for egg laying. They are generally utilised in years of high larval abundance when *S. pratensis* is in short supply, when usually late instar larvae wander in search of alternative food plants. Therefore, *S. pratensis* was the only larval host plant considered in this work. In Spain, the two sub-species of *E. aurinia* use either *L. periclymenum* (Munguira *et al.* 1997) or *L. etrussca* (Warren 1994b). In Alpine regions the butterfly is reported to use *Gentiana* spp. and *Primula vixcosa* (Warren 1994b) and in southern France uses *Lonicera implexa* and *Cephalaria leucantha* (Singer pers. comm.).

Succisa pratensis is found across the British Isles (figure 1.2) and most of continental Europe with the exception of the extreme North and parts of the Mediterranean (Grime *et al.* 1988). It is a rosette-forming, perennial herb associated with moist habitats and mainly found in unimproved or partially improved damp pastures, wood margins and calcareous soils, where the pH is intermediate (Adams 1955; Grime *et al.* 1988). The species is relatively tolerant of light grazing and trampling. Flowering occurs from July to October, with the fruit maturing within one month. The seed viability is limited to one year, as no permanent seed bank has been found (Adams 1955; Grime *et al.* 1988; Bühler & Schmid 2001). Recruitment occurs mainly by seedling establishment, which germinate in the spring. Vegetative spread through the production of lateral shoots occurs occasionally (Adams 1955; Grime *et al.* 1988; Bühler & Schmid 2001). The plant is a poor coloniser of new habitat due to poor seed dispersal mechanisms. The majority of seed falls around the parent plant and is thereby restricted to semi-natural vegetation (Grime *et al.* 1988). A full account of the species phenology and ecology can be found in Adams (1955), and Grime *et al.* (1988) further describes its ecology and habitat.

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[2] Nomenclature follows Stace (1997).

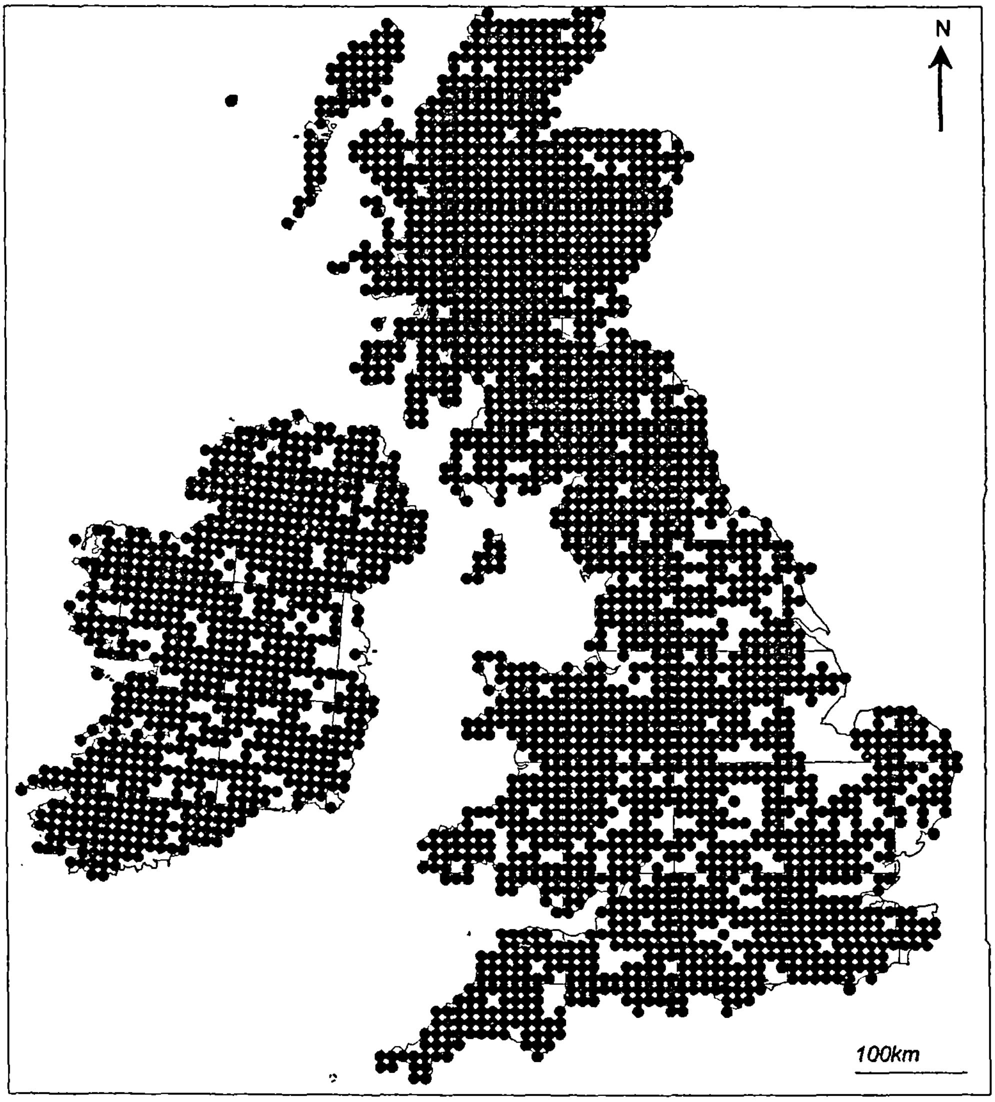


Figure 1.2 The British distribution of *Succisa pratensis* plotted by 10km squares of the National Grid (source: Perring & Walters 1962).

1.7 Introduction to the study areas

Work presented in this thesis has been carried out in various parts of England and Wales across the range of *E. aurinia*. In chapter three, results are presented from data collected in Dorset, Devon, Cornwall, Somerset, Ceredigion, Anglesey and Cumbria. In chapter four the parasitoid larval collections were undertaken in Dorset and reared at the University Gardens in Leeds. In chapter five the habitat experiments were established at Rhos Llawr Cwrt NNR in Ceredigion, Wales.

1.7.1 Dorset

The main study area, located in north Dorset (England, UK), was 25km by 25km (625 square kilometres) in size (figure 1.3). This large area encompassed the two types of habitat occupied by *E. aurinia*; chalk downland stretching from Cerne Abbas in the south-west to Fontmell Down in the north-east and wet grasslands on the clay soils of the Blackmoor Vale in the north-west of the region (figure 1.3). This area was selected due to the variation in habitat quantity, quality and isolation across the region. This large area was necessary to detect any isolation effects, given the dispersal power of the butterfly (Warren 1994a; Wahlberg 2000), but was still a manageable area to cover.

1.7.2 4km by 4km independent networks

Five pairs of 4km by 4km squares (16 square kilometres) were located across the range of *E. aurinia* in England and Wales with a final sixth pair from within the Dorset study area. The location of each of these study squares is shown in Figure 1.4. Of the pairs, one square is centred on a surviving or extant *E. aurinia* population and the corresponding square centred on a recently extinct population (within the last 15 years). Both members of each pair are located within the same habitat type.

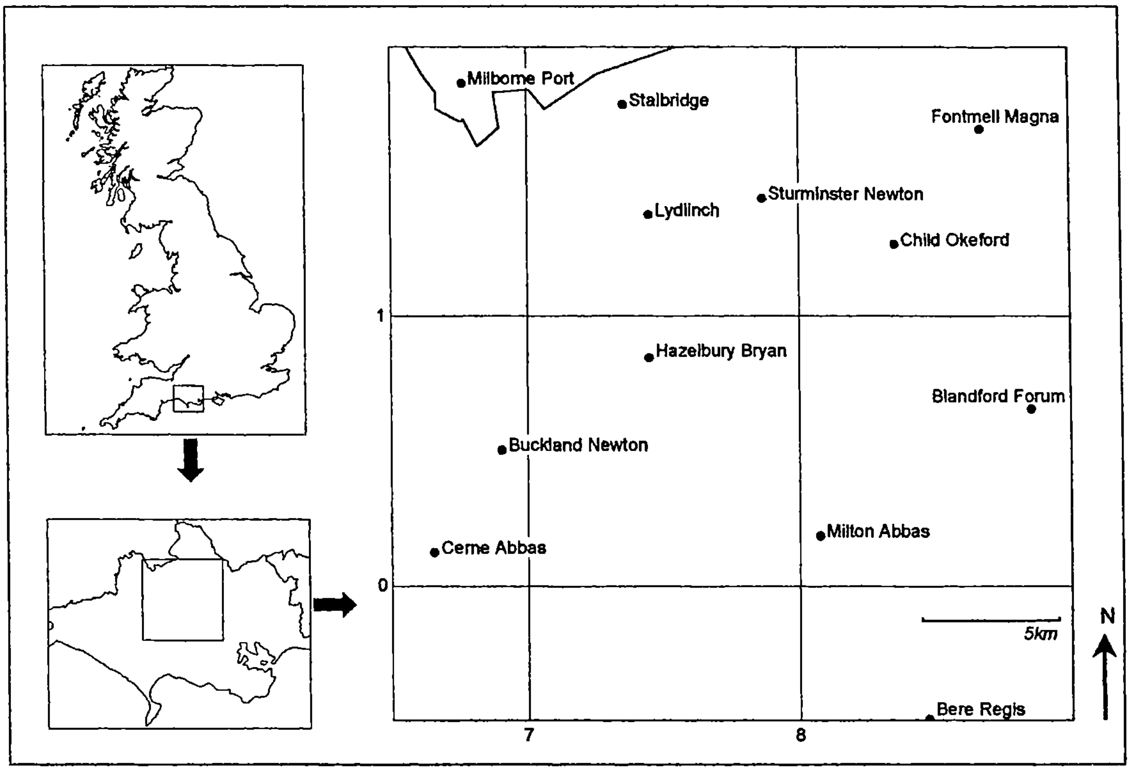


Figure 1.3 Location of the study area in the county of Dorset, UK, with detailed map showing main towns and villages within the 25km by 25km area (Wiltshire/Dorset border shown in north west).

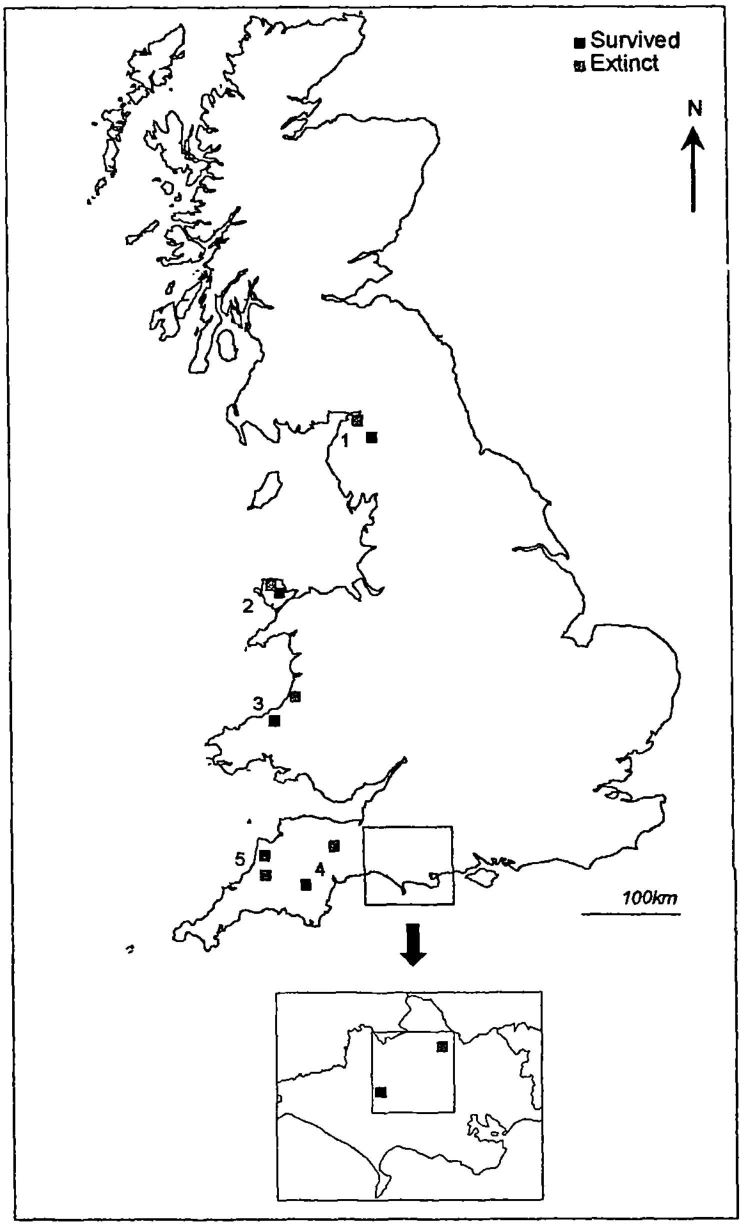


Figure 1.4 Study sites across England and Wales. The small squares (not to scale) indicate the position of the 4km by 4km paired squares across the range of *E. aurinia*, (black survived and grey extinct: 1 Cumbria, 2 north Wales, 3 mid Wales, 4 south-west A, 5 south-west B). The large square and inset indicate the 25km by 25km study area in Dorset with the 4km by 4km squares shown.

1.7.3 Rhos Llawr Cwrt NNR

Rhos Llawr Cwrt is an area of largely unimproved marshy grassland situated in the district of Ceredigion in Wales (figure 1.5). The site comprises of a large area of wet *Molinea caerulea* and *Juncus* spp. pasture with associated wet heath and mire communities. A major reason for notification and designation was the large population of *E. aurinia* present on the site in addition to the species-rich unimproved pasture across the reserve referred to as 'rhos'.

This was the location of habitat restoration and re-creation experiments (chapter four) in locations where the butterfly was not present, but adjacent to the main reserve and within dispersal range of the existing population.

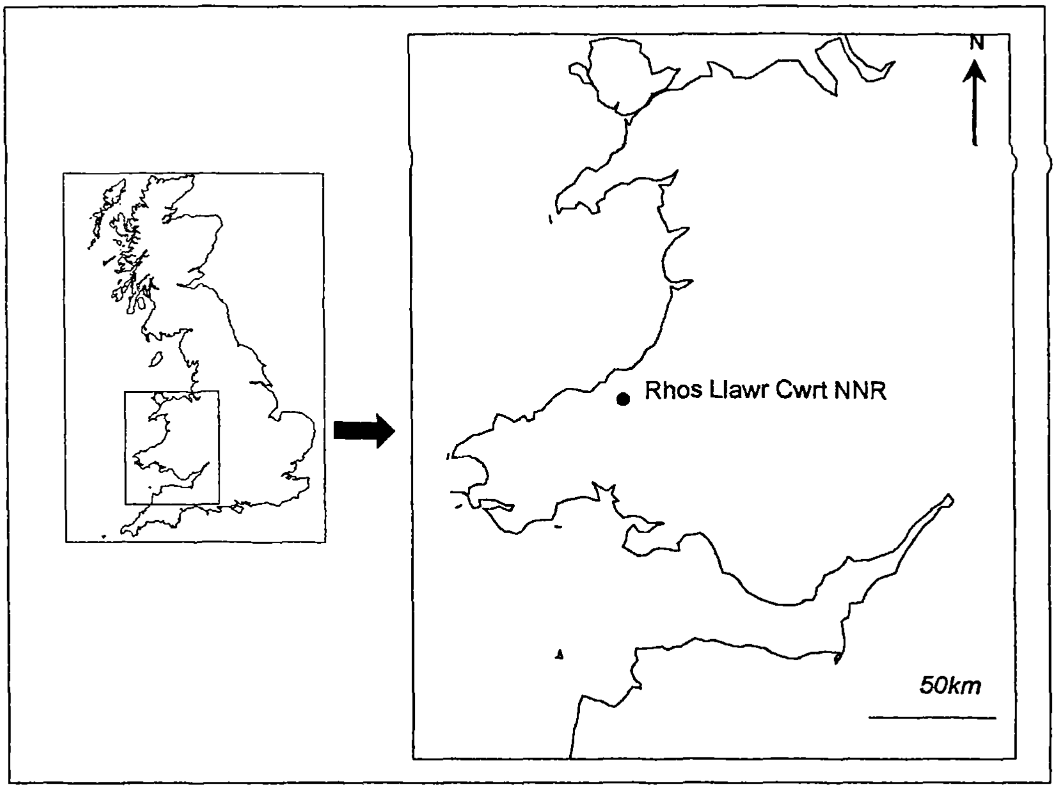


Figure 1.5 Location of Rhos Llawr Cwrt National Nature Reserve in Ceredigion, Wales.

2.0 NATIONAL DECLINE IN THE DISTRIBUTION OF *EUPHYDRYAS AURINIA*

2.1 Introduction

Mapping the distribution of species is a common method used by biologists for conservation purposes, such as establishing a species distributional range, identifying diversity 'hot spots', monitoring increases or decreases in distributions and targeting conservation strategies (Groombridge 1992; Prendergast *et al.* 1993; Firbank *et al.* 1994; Thomas & Abery 1995; Heads 1997; Warren *et al.* 1997; Cowley *et al.* 1999; Dennis & Hardy 1999). The traditional method is to map the distribution of a species recorded as present or absent on a grid-based system. These vary in scale from 1km or tetrad (2km) level (Thomas J. A. 1998), 10km nationally (Heath *et al.* 1984; Asher *et al.* 2001) up to 50km at a continental level (Mitchell-Jones 1999).

If these mapping surveys are carried out repeatedly over a number of years, then estimates may be made as to how the distribution of a particular species has changed over time. If patterns can be discerned from a decline or increase in distribution, then predictions can be made for the future distribution (Buckland *et al.* 1996), if the processes that caused the original change continue to operate.

This chapter uses 10km grid square data from two major national surveys of UK butterflies, one carried out in 1970-82 (Heath *et al.* 1984), and the other in 1995-99 (Asher *et al.* 2001), which reveal a dramatic decline in the distribution of *E. aurinia* (figure 2.1). During the 1970-82 survey period 252 grid squares (10km scale) were recorded to contain populations of *E. aurinia* in Britain. This declined to 224 squares in 1995-99 despite 110 new squares being added during the recent survey period through increased recorder effort. The decline in the distribution of *E. aurinia* is estimated to be a 55% loss of grid squares occupied in 1970-82 (Asher *et al.* 2001). A more conservative estimate calculated by equalising the recorder effort in both survey periods gives a decline of 37% in 10km grid squares between the two periods (Warren *et al.* unpublished data). Both approaches reveal a severe decline, between 37 and 55%, in occupied 10km grid squares for *E.* aurinia in Britain.

Initial inspection of the distribution maps suggests that the more isolated 10km grid squares have become extinct. These isolated records probably represent areas where the butterfly is rare and isolated within the 10km square (Kunin 1998; Kunin *et al.* 2000) and that are unlikely to be re-colonised due to the lack of surrounding populations in the neighbouring grid squares. Analysis was carried out to identify the pattern of decline by comparing the datasets from the two distribution atlases, and using this to predict the future distribution of the butterfly.

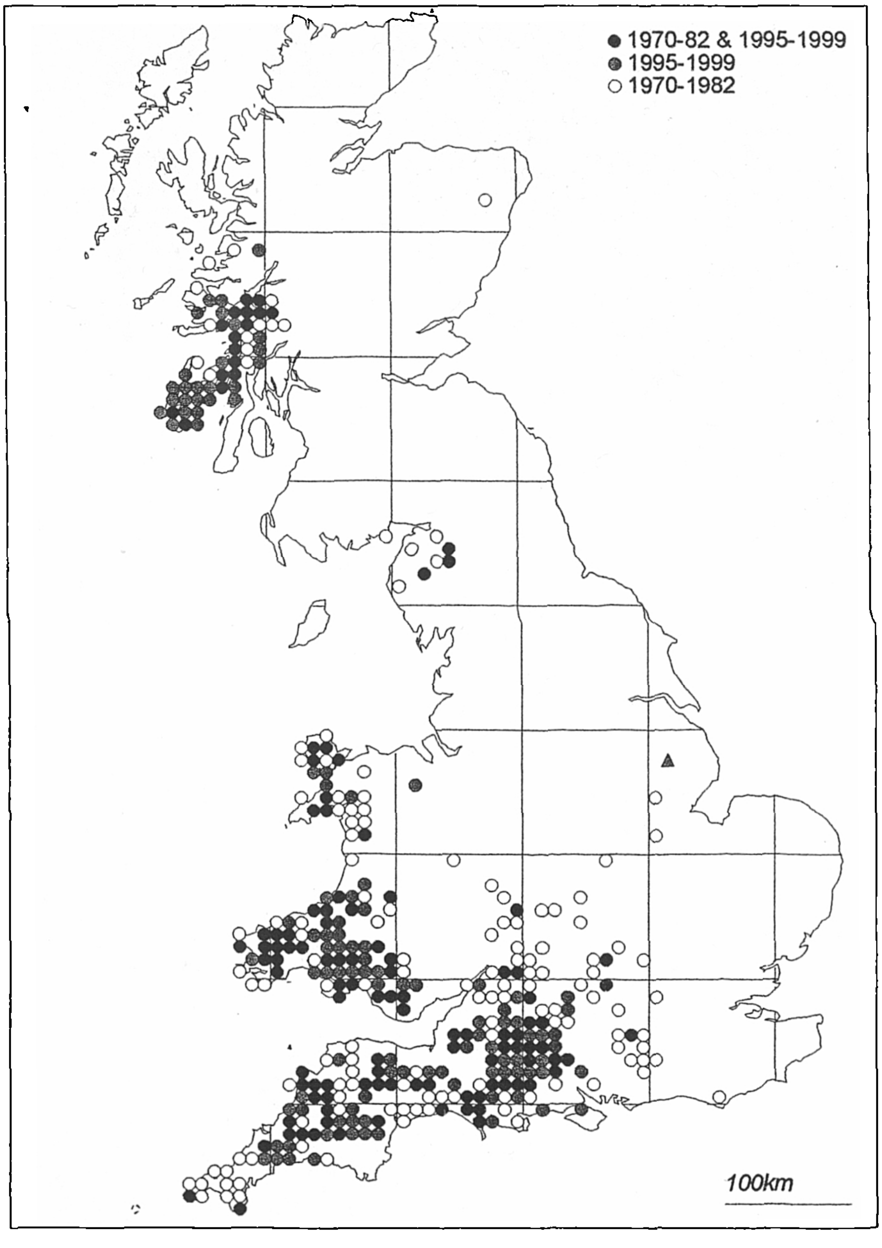


Figure 2.1 Distribution of *E. aurinia* in England, Wales and Scotland (10km grid square). White symbols are records from 1970-82, which were not recorded in 1995-99 and therefore presumed extinct. Black symbols are records in both recording periods; grey symbols are records from 1995-99 and not previously recorded (assumed to be the result of increased recording effort).

2.2 Methods

Changes in the distribution of *E. aurinia* were examined using the 10km by 10km national grid. Two datasets were used to quantify declines over the last 30 years, the first covering a 13-year survey period (1970-1982) and published in Heath *et al.* (1984). The second dataset covered a 5-year period (1995-1999), recently published in Asher *et al.* (2001). Many of the 10km grid squares occupied in the 1970-82 survey were not occupied in the 1995-99 survey and presumed to be extinct. There was a much higher recorder effort in 1995-99, with a 6.65 fold increase in records received relative to the period 1970-82 (Warren *et al.* unpublished). As a result, some new 10km square records for *E. aurinia* were found. Given the background of a national decline in the species (37 to 55% in 10km grid squares), it is unlikely that many colonisations of new grid squares occurred. These might possibly be colonisations or unknown introductions, but it is more probable that almost all of them are the result of increased recorder effort and the targeting of under-recorded areas (Asher *et al.* 2001). For the purpose of this analysis, all new records were assumed to have been present during the 1970-82 recording period, but had remained unrecorded for various reasons. Scotland was excluded from the analysis because of the lower level of recorder effort compared to England and Wales.

Each 10km square occupied in 1995-99 was assessed for its degree of isolation, by calculating the number of neighbouring squares occupied by *E. aurinia* in a 20km band outside of the focal square. This was expressed as a proportion of the number of 10km squares occupied out of the potentially available squares (24 potential squares in a 20km surrounding area). The number of occupied grid squares neighbouring each focal grid square was calculated using the Neighbourhood Analysis (counts in squares) function of SAFE (Spatial Analysis For Ecologists, Hartley 2001).

Logistic regression (Norusis 1998) was used to calculate the probability of occupancy in each 10km square as a function of isolation. The presence or absence of the butterfly in each 10km grid square occupied in 1995-99 was used as the dependent variable. The independent variable was the proportion of neighbouring squares in a 20km radius that were occupied in 1970-82 (or deemed to be occupied then because of a subsequent record in 1995-99). The equation derived from this was used to determine the probability of occupancy ($e^z/1+e^z$) of each 10km grid square in 20 years time, as a function of its isolation in 1995-99. Note that each dependent grid square cannot be regarded as truly spatially independent. For example, it is possible that single populations may sometimes lie across grid boundaries, and adjacent 10km squares will share over half of their neighbourhood squares with each other. The purpose of this chapter is simply to identify the overall pattern and project this pattern into the future.

2.3 Results

Of the 10km grid squares occupied by *E. aurinia* in 1970-82 in England and Wales, 124 were not recorded as occupied in 1995-99 and therefore presumed to be extinct, 181 squares were occupied (figure 2.2). Core areas for the species are in the south and south-west of England and south-west Wales (and also in Western Scotland but not considered in this chapter). A few 10km squares remain occupied in north Wales, Cumbria and central southern England. Extinctions appear to have occurred in the more isolated 10km squares, that have few occupied neighbouring squares. In a logistic regression, the number of occupied 10km squares in a 20km radius of the focal square was found to have a positive effect on survival (table 2.1), with 70% of cases classified correctly by the model.

The logistic regression equation (table 2.1) was used to predict the 1995-99 distribution of *E. aurinia* in England and Wales, starting from the presumed 1970-82 distribution. A very similar pattern was found (figure 2.3), with the core regions remaining occupied. Extinctions were predicted to occur in the more isolated 10km squares. As expected a few of the 10km squares with a relatively low probability of persistence (<50%) were observed to persist, for example in north Wales, Gloucestershire, Buckinghamshire, Oxfordshire, Hampshire and Cornwall. However, some of these grid squares are now empty due to the extinction of the one or two remaining populations within the square recently (Hobson *et al.* 2001).

The logistic regression equation (table 2.1) was used to predict the future distribution of *E. aurinia* (assuming current rate of decline) from the actual distribution in 1995-99, as a function of the proportion of occupied neighbouring squares in a 20km radius (figure 2.4). The model predicted 94 grid squares to survive in 2020, and of these, only 39 had a probability of surviving >0.75. The squares predicted to survive are in the core areas of the south and south-west of England and south-west Wales. However, many of the grid squares in the south-west England core have only an intermediate probability of survival of between 0.5 and 0.75. The model predicts a 48% decline in occupied 10km grid squares by 2020. Populations in Cumbria, north Wales and Somerset are predicted to have very low survival probabilities ($p<0.5$) per 10km square and many or even all of these are likely to become extinct.

These modelling results suggest that *E. aurinia* is being lost from the isolated squares, it was hypothesised that this was due to small areas of habitat available and population isolation. To investigate this, the number of 1km square records (not including multiple records) per 10km square were analysed from the 1995-99 database. (This was not possible for the 1970-82 data as not enough records were at 1km resolution). A significant correlation (figure 2.5) was found between the number of 1km records/10km grid square and the proportion of neighbours in a 20km radius (Spearman Rank Correlation $r_s=0.24$, $P=0.001$, $n=182$). The mean number of 1km records/10km grid square generally increased with the proportion of occupied neighbours (figure 2.6). Occupied 10km grid squares contained an average of 8.4 one-km records when >80% of the neighbouring 10km squares were occupied, dropping to only 1.9 one-km squares when <20% of neighbouring 10km squares were occupied. Grid squares with increased numbers of 1km square records were assumed to have a greater quantity of occupied habitat than those grid squares with very few 1km records. Those grid squares that contained a greater area of occupied habitat were found to also have a greater proportion of neighbouring grid squares occupied by the butterfly. Grid squares are surviving where the area of suitable habitat within them is greater (reducing the extinction risk) and where more neighbouring populations are present (increasing the likelihood of re-colonisation if extinction does occur).

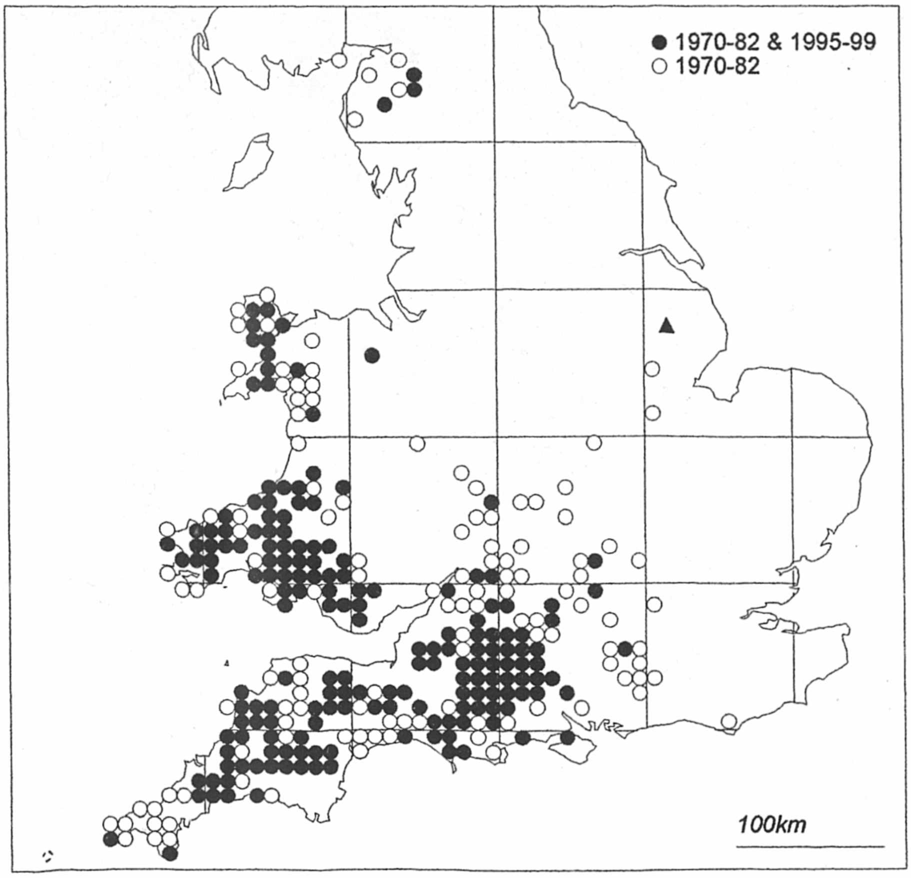


Figure 2.2 Distribution of *E. aurinia* in England and Wales (10km grid square), with all 1995-99 records presumed to be extant in 1970-82. Black symbols are records in 1995-99 and 1970-82, white symbols are records from 1970-82, not recorded in the recent survey and presumed to be extinct. The known introduction in Lincolnshire is shown with a triangle.

Table 2.1 Logistic regression of survival as a function of the proportion of occupied neighbours in a 20km area of each 10km grid square.

	Model if term removed			
Variable	**Effect**	**-2 Log LR**	***df***	***P***
Neighbours (20km radius)	+	62.47	1	<0.00001

-2 log likelihood=349.96, Goodness of Fit=297.02, Model χ^2=62.15, df=1, P<0.00001.

$n_{occupied}$=181, $n_{extinct}$=124, 70% of cases were classified correctly by the model.

Z=-1.8534 + 4.8163 (proportion of neighbours in 20km radius)

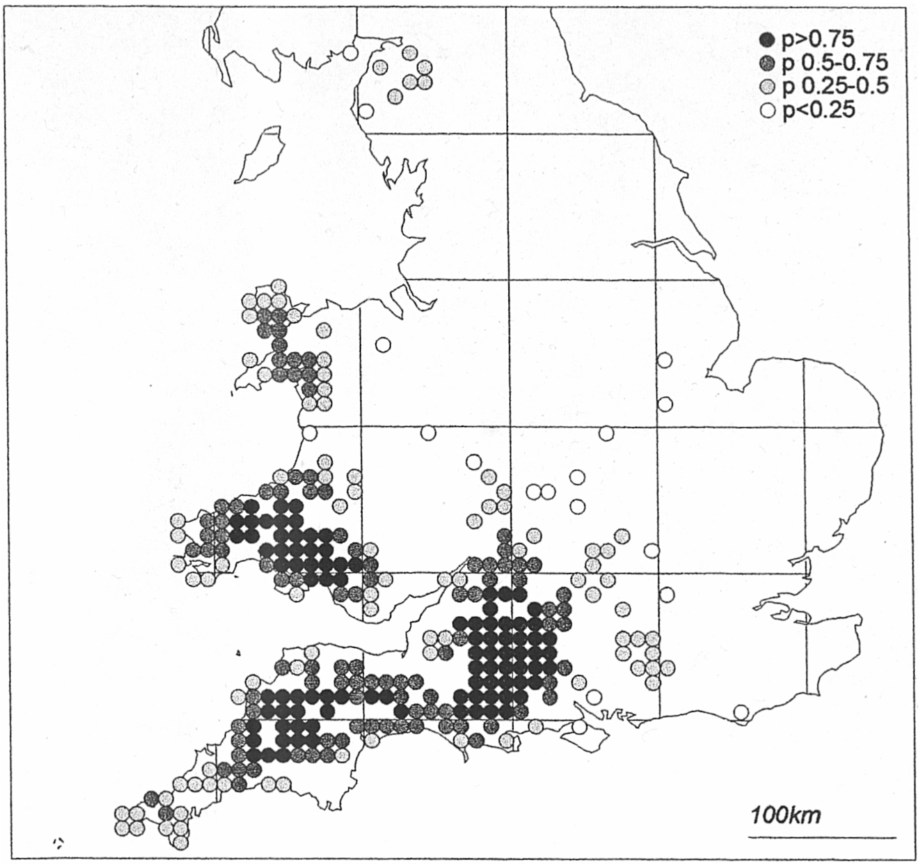


Figure 2.3 Predicted 10km distribution of *E. aurinia* in 1999, based on the probability of survival (p) as a function of the proportion of neighbours in a 20km surrounding area in 1970-82, calculated using the logistic regression equation in table 2.1. Black symbols represent grid squares predicted to remain occupied (p >0.75), dark-grey symbols have a high probability of remaining occupied (p =0.5-0.75). The light-grey symbols are more likely to become extinct (p =0.25-0.5) and white symbols are very likely to become extinct (p <0.25).

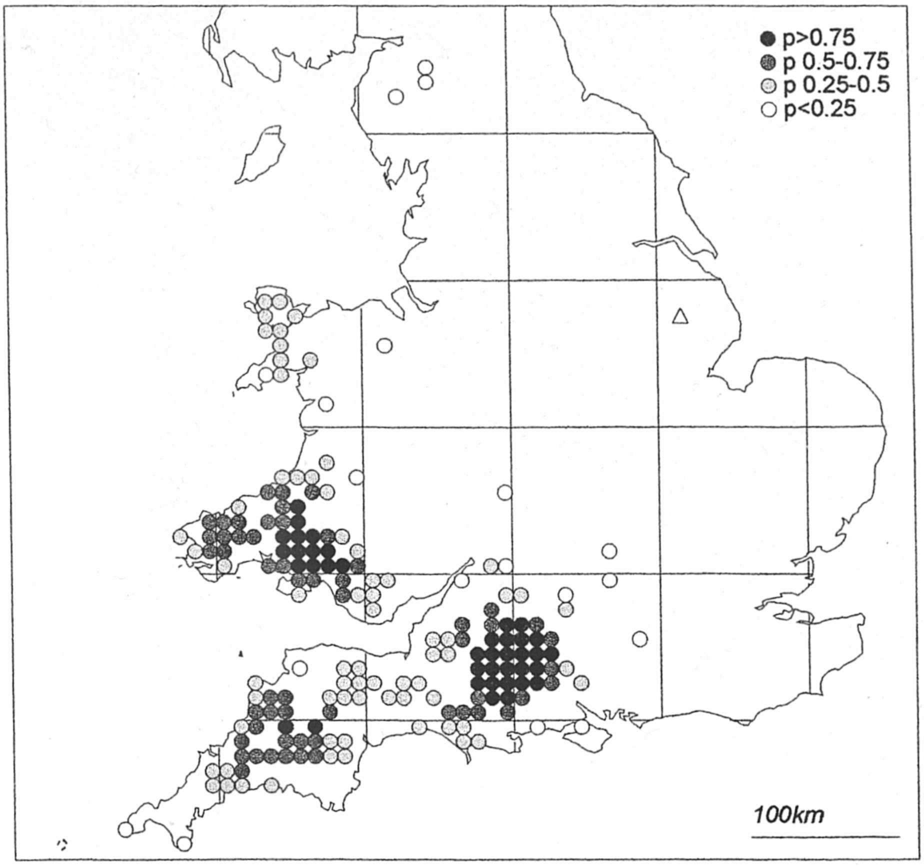


Figure 2.4 Predicted 10km distribution of *E. aurinia* in 2020, based on the probability of survival (p) as a function of the proportion of neighbours in a 20km surrounding area in 1995-99, calculated using the logistic regression equation in table 2.1. Black symbols represent grid squares predicted to remain occupied (p >0.75), dark-grey symbols have a high probability of remaining occupied (p =0.5-0.75). The light-grey symbols are more likely to become extinct (p =0.25-0.5) and white symbols are very likely to become extinct (p <0.25). The triangle represents the known introduction in Lincolnshire and has a probability of occupancy of <0.25.

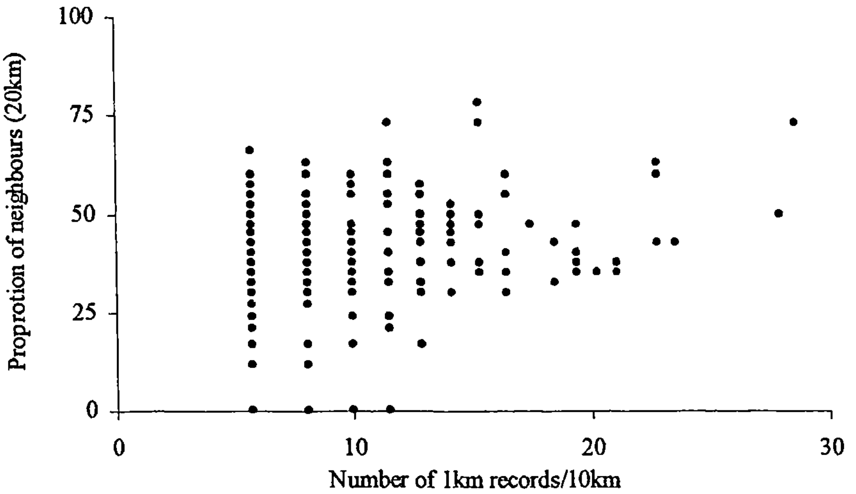


Figure 2.5 Relationship between number of 1km records/10km grid square and the proportion of neighbours in a 20km radius of each grid square. (Data for each axis was arcsine transformed for the analysis). Spearman Rank Correlation r_s=0.24, *P*=0.001, n=182.

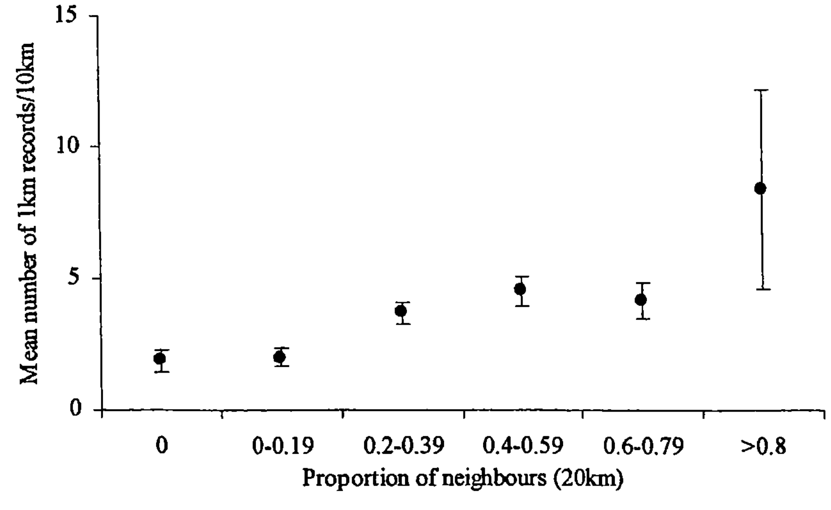


Figure 2.6 Mean number of 1km records/10km grid square (± 1 S.E.) by category of proportion of neighbours within a 20km area.

2.4 Discussion

If the decline in *E. aurinia* distribution continues at the same rate that has been observed recently then the status of the butterfly in Britain is under serious threat. The predictions presented here suggest that the butterfly is likely to become restricted to three core regions in its range with populations on the fringes of these areas becoming extinct with time. Overall decline is projected to be 48% by 2020. Of course the butterfly is much rarer than it appears to be from the distribution maps because it only occupies a very small area within each grid square. The actual flight area occupied by the species has been estimated to be 0.01% of the British land surface (Cowley *et al.* 1999).

There could be two major biases in these projections of decline even assuming that the processes operating between 1970-82 and 1995-99 are repeated into the future. First, the projected decline rate may be over estimated slightly if some of the 'new' 10km records for the 1995-99 period do represent genuine colonisations. On the other hand, a much larger bias is likely to underestimate the decline rate. 10km squares were relatively under-recorded in 1970-82 so, for this analysis, the 1970-82 distribution was reconstructed as the 1970-82 distribution plus additional 10km squares recorded in 1995-99. However, this is likely to be an underestimate of the true 1970-82 distribution because grid squares that were occupied at this time and not recorded and became extinct by 1995-99, were excluded. In any case, future land use changes are uncertain and the projections should not be over-interpreted. The point is that one might expect a substantial fraction of the 1995-99 distribution to be lost by 2020.

Distribution map data have been used to investigate declines in less specialised species. In widespread generalist species distributions at a 10km resolution appear stable or exhibit only a very slight decline. For such species, 10km grid cells generally contain many local populations, so losses from entire squares are only detected at very high levels of decline (Thomas & Abery 1995). Inspection at finer scales highlight dramatic reductions in population level decline, estimated at 89% for *Lycaena phlaeas* (León-Cortés *et al.* 2000) and 75% for *Polyommatus icarus* (León-Cortés *et al.* 1999) over a 100 year period in one landscape. Declines in such widespread non-specialised species are 'masked' at the 10km scale and not exhibited in the extinction of 10km grid squares. Grid square losses at the 10km scale also underestimate population-level declines for rare species, although the problem is not quite so great as for more common species (Thomas & Abery 1995). Therefore, the 37 and 55% rates of decline that have taken place between1970-82 and 1995-99, and the projected 48% loss by 2020, are likely to underestimate population-level declines over the same period. The potential role of scale in estimates of decline can be deduced from figure 2.6. An isolated 10km square contains populations in less than two of its 1km grid squares, whereas the most connected 10km squares contain populations in eight of the available 1km grid squares. If the probability of a 1km square becoming extinct over the time period was for example 0.8, the probability of extinction from a 10km square containing two occupied 1km squares would be 0.64, but the extinction risk from one containing eight occupied 1km squares would be 0.17. The probability of all populations becoming extinct within a 10km square decreases with increasing number of records, so, population level rates of loss are expected to be even higher as these are not revealed by coarse scale mapping.

2.5 Conclusion

Isolated grid squares appear to be at greatest risk from extinction. These squares contain relatively few 1km records, which is presumably correlated with the amount of occupied habitat, and they are less likely to be re-colonised as there are very few or no neighbouring populations producing potential colonists. The pattern of losses from the more isolated 10km squares could lead to very different approaches in conservation terms. With finite resources, where should the limited resources available to conservation be targeted? Two options arise; whether to (a) target resources in the areas most at risk, i.e. the more isolated grid squares with few extant populations and which may be genetically different (Joyce & Pullin 2001). Or (b) target the core regions in order to maintain the substantial populations extant in these areas and halt any further decline. Chapter three in particular attempts to address these issues by investigating the dynamics of the species at a regional scale.

3.0 THE PERSISTENCE AND EXTINCTION OF *EUPHYDRYAS AURINIA* IN FRAGMENTED LANDSCAPES

3.1 Introduction

Habitat destruction and fragmentation caused by the expansion and intensification of human land use is widely documented to have detrimental effects on biodiversity. Many species have declined drastically in recent years, (Diamond 1984; Saunders *et al.* 1991; Groombridge 1992; Pimm *et al.* 1995; Brooks *et al.* 1997) and now occupy very small areas of habitat (Cowley *et al.* 1999; Kareiva 1985; Kunin 1998; Asher *et al.* 2001; Fox *et al.* 2001). It is necessary to understand the effects of habitat loss and fragmentation (loss of original habitat and increasing isolation and reduction in size of the remaining patches (Andrén 1994)) on these species to understand their persistence in such landscapes.

To mitigate against the negative effects of habitat fragmentation it is necessary to understand how species persist within these changing landscapes in order to conserve them (Harrison & Bruna 1999). One particular approach is through metapopulation theory (Hanski & Gilpin 1997; Hanski 1998; Hanski 1999a,b), which considers small local populations at greater risk from extinction than larger ones (Thomas & Harrison 1992), and isolated populations to be less likely to be colonised than well-connected populations.

Metapopulation studies require detailed investigation into the distribution and dynamics of species on a large scale (Thomas & Kunin 1999). However, most species in most parts of their distribution cannot be studied in such great detail due to resource constraints (Baguette *et al.* 2000). A key question is to ask whether exemplar species studied on this larger scale can be used to predict or understand the status of species in decline.

The butterfly *E. aurinia* was studied across one landscape to investigate the influence of habitat quantity, location and resource quality, on occupancy and persistence of the species within a fragmented landscape. Past studies investigating a combination of factors such as habitat size, spatial location and quality have shown them to be important predictors of habitat occupancy (Verboom *et al.* 1991; Hanski *et al.* 1996b; Hill *et al.* 1996; Dennis & Eales 1997; Thomas J. A.1995b and Thomas J. A. *et al.* 2001).

When species inhabit a fragmented and patchy landscape, where extinction and colonisation events occur, the metapopulation approach can be a productive and useful way to understand distributions (Harrison 1991, Harrison 1994; Harrison & Taylor 1997; Hanski 1998).

The practical and simple spatially explicit Incidence Function Model (Hanski 1994a) enables parameter estimation with field data, to facilitate its application to real metapopulations (Hanski & Simberloff 1997). This modelling technique has been successfully applied to butterflies (Hanski *et al.* 1996b; Wahlberg *et al.* 1996); other insects (Nieminen 1996; Eber & Brandl 1996; Appelt & Poethke 1997; Biedermann 2000); birds (Hanski 1998) and mammals (Moilanen *et al.* 1998; Crone *et al.* 2001).

The model takes into account the two main assumptions of metapopulation theory to predict patch occupancy. That of area dependent extinction, where local extinction is determined by the size of the respective habitat patch, which assumes a positive relationship between expected population size and patch area (Kindvall & Ahlén 1992; Hanski *et al.* 1995b). And distance dependent colonisation, where the colonisation probability of unoccupied patches decreases with distance from occupied patches (Harrison *et al.* 1988; Thomas & Jones 1993; Hill *et al.* 1996; Kuussaari *et al.* 1996; Sutcliffe *et al.* 1997a; Hanski 1999a,b) and is based on a negative exponential function.

The basic premise of the model is as follows; the long-term probability of patch i being occupied, called the incidence J_i (Hanski 1994a) is given by:

$$Ji = \frac{Ci}{Ci + Ei - CiEi}$$

Where C_i and E_i are the colonisation and extinction probabilities (based on the above assumptions), with C_iE_i accounting for the rescue effect (Brown & Kodric-Brown (1977). C_i and E_i are derived from patch area (proxy for population size), distances between patches and the estimated colonisation ability of the species in question. The equation can then be applied to empirical data to estimate model parameters that are used to simulate the dynamics of the species in the original and/or other patch networks (Hanski 1994a).

The aim of this study was to investigate the main factors behind the observed occupancy pattern in Dorset. These results were used to generate parameters for the Incidence Function Model. The parameters were then applied to a series of independent networks to predict the persistence of the butterfly in habitat of differing levels of fragmentation and in different regions; some of which contained surviving populations and others where the species had become extinct. Network areas were then manipulated in the model to estimate a threshold habitat area that could be applied to the long-term conservation of *E. aurinia.*

3.2 Methods

3.2.1 Model System – Dorset

The area chosen for this large-scale study was located in north Dorset (England, UK), and selected due to the variation in habitat quantity, quality and isolation across the region. The study area was 25km by 25km (625 square kms) in size. This was large enough to detect any isolation effects in operation (Thomas & Kunin 1999), and large enough relative to the dispersal power of the butterfly (Warren 1994a; Wahlberg 2000), but still a manageable area to cover with the help of a field assistant. (See section 1.7.1 for further details.)

The square encompassed the two types of habitat occupied by *E. aurinia*, chalk downland stretching in a band from south-west to north-east; and wet grasslands on the clay soils in the north-west of the region.

3.2.1.1 Habitat patch mapping

The distribution of the host plant, *Succisa pratensis*, was mapped across the Dorset study area during 1998. Due to the size of the study area, and the tendency of the plant to be found in both semi- and unimproved grassland habitats (Adams 1955; Grime *et al.* 1988), it was necessary to refine the search to suitable habitat. This was achieved using Phase I survey maps (English Nature 1982), which provided accurate information on the distribution of both semi- and unimproved grasslands of acid, neutral and calcareous types. In addition, Dorset Environmental Records Centre (DERC) and Dorset Wildlife Trust provided a list of sites where *S. pratensis* had been recorded, which provided a basis for the search.

All suitable areas were systematically searched for *S. pratensis*. When the plant was encountered a search was made to find the extent of the patch, and if greater than ten plants were found, recording was undertaken. The area of the patch was mapped onto 1:25 000 maps (Ordnance Survey 1997a and b, 1998) with larger areas subdivided for recording. The distribution of the plant was recorded to a 1 hectare (0.01km^2) resolution. Slope and aspect were measured using a compass clinometer. The vegetation characteristics of host plant cover and leaf length were recorded by stratified random sampling across the patch using a 1m² quadrat. Between 30 and 40 measurements were made depending on the size of the patch. Vegetation height was recorded using a metre rule and drop disc (BUTT 1986, Stewart *et al.* in press). If no *S. pratensis* was encountered in any 1m² then the vegetation height alone was noted. A general estimate of the frequency of *S. pratensis* based on the DAFOR scale (Kent & Coker 1992) was made for each patch and sub-division.

Discrete patches, containing all necessary resources for the persistence of a local population (Fahrig & Merriam 1994; Jonsen & Fahrig 1997), were defined as areas separated by 50m or more of habitat where the host plant was absent, or by 25m or more if a scrub or woodland barrier existed. These distances are similar to those used in other butterfly metapopulation studies (Thomas & Jones 1993; Hill *et al.* 1996; Lewis & Hurford 1997 and Wilson 1999).

Due to the size of the study area unsuitable habitat such as improved grassland, arable land and urban areas were not intensively searched for host plant, as *S. pratensis* was very unlikely to be found in these localities. To test this assumption, *20 one-km* squares, of the squares not already searched within the study area, were randomly selected for intensive searches. No host plant or suitable habitat was found.

3.2.1.2 *E. aurinia* distribution and density

The distribution of *E. aurinia* was mapped across the Dorset study area to establish the occupancy status of each habitat patch. Surveys for adults were carried out during the flight period when weather conditions permitted. Confirmation of sites as suitable for breeding was achieved through egg and larval web searches in late July and August. This thorough survey was executed in 1998, but due to bad weather during the flight period, the completeness of this survey was questionable. Therefore, the survey was repeated in the following year. The very similar results mean that I can be confident that the recorded distribution reflects the actual breeding distribution of the butterfly across the study area.

To establish the abundance of *E. aurinia* at each of the occupied sites, butterfly transects were carried out using a standard method (Pollard 1977; Pollard *et al.* 1986; Pollard & Yates 1993). This involves the recorder walking a fixed route at a uniform pace and counting the number of butterflies seen within an imaginary box 2.5m either side and 5m in front. Counts were made between the hours of 10.45 and 15.45 BST when conditions were suitable for butterfly activity (temperature range of 13°C to 17°C if >60% sunshine, and under sunny or cloudy conditions if the temperature is >17°C).

Fixed transects were walked at two sites within the study area at Rooksmoor (Ordnance Survey grid reference ST 739108) and Giant Hill (ST 670020), completed once a week during the whole flight period of *E. aurinia*. At all other sites when *E. aurinia* was encountered a transect was carried out irrespective of the time during the flight period, as the fixed transect data was available to adjust numbers to the figure predicted to be present on the day of peak numbers (Thomas J. A. 1983). Estimates of population density measured using this method have been shown to correlate well with population density as measured by mark-release-recapture methods for all species for which this has been attempted, including *E. aurinia* (Thomas J. A. 1983; Pollard & Yates 1993).

3.2.1.3 Patch analysis

The characteristics of the habitat patches were analysed to investigate their effects on patch occupancy. Stepwise Multiple Logistic Regression (Norusis 1998) procedures were used to test the influence of the above habitat characteristics on the presence or absence of *E. aurinia*. The independent variables were entered into the model by forward stepwise selection, with the significance level for inclusion set at 5% and removal of variables set at 10%.

Patch connectivity (S_i), which is the degree of isolation of a habitat patch, was measured using the following equation (Hanski 1994a; Moilanen 2000):

$$S_i = \sum_{i \neq j} p_j e^{-adij} A_j^b$$

Where S_i is the measure of connectivity for patch i, where patch i receives immigrants from patch j and all other surrounding patches. The number of immigrants to patch i increases with the area of patch j but decreases with its distance from patch i. P_j is the incidence of the species in patch j (0 or 1). The constant α determines the effect of distance on colonisation by describing how fast the number of migrants from patch j

decline with increasing distance. d_{ij} is the Euclidean distance between patches *j* and *i*, A_j is the area of patch *j* and *b* is a parameter that transforms patch area to expected emigration rate (Moilanen & Nieminen, unpublished manuscript; Hanski 1999a,b). Two measures of connectivity were calculated. Firstly, connectivity to all *E. aurinia* populations, including those populations within a 5km radius of the study area boundary (connectivity A). Secondly, connectivity to all habitat patches (connectivity B).

3.2.1.4 Parameterisation and testing of the model

The Incidence Function Model was parameterised using 'snap shot' patterns of occupancy and extinction observed during 1998 and 1999. Past colonisation and extinction events are necessary for the model to estimate accurate parameters. This was supplied using survey data from Martin Warren to construct the pattern of patch occupancy in 1981. The Monte Carlo Markov Chain method was used for the final estimation of parameters (Moilanen 1999), with 1000 Function evaluations in initiation, and 4000 Function evaluations in estimation. As there was a low incidence of occupancy over the patch network for the three recording years of this study, it was difficult to be confident that the system was at equilibrium, the violation of this assumption being a problem in the model (Hanski 1994a; Moilanen 2000). Therefore, a small sub-set (7km by 5km, fraction of occupied patches=0.2) of the Dorset landscape was used for parameterisation. By selecting a sub-set with a concentration of occupied and unoccupied patches I could be more confident that the system would be at equilibrium, due to the lack of historical factors which could be responsible for absence from some areas.

Set parameters were $\alpha=2$, which describes the colonisation ability of the species, i.e. how fast the number of migrants from patch *j* decline with increasing distance. This value is consistent with the biology of the species (Porter 1983; Warren 1994a) and has been used for species with similar dispersal abilities (Wahlberg *et al.* 1996). The minimum patch area (A_0) where the extinction probability equals 1 was set at 0.1ha (1000m^2) which is approximately the minimum size of the occupied patches. Remote colonisation probability was included and set at 0.001, which means that each patch has a 1 in 1000th chance of being colonised from outside the study area in one year. This was a necessary component to include because of the known occupied patches within 5km of the study area boundary. Other set parameters were B=0.5, an estimate of emigration rate, where the per capita emigration rate tends to be greater in smaller patches (Kareiva 1985; Hill *et al.* 1996; Kussaari *et al.* 1996; Sutcliffe *et al.* 1997a; Kindvall 1999; Hanski *et al.* 2000; Petit *et al.* 2001). Regional stochasticity was included in the model by default, with evar=0.0005 derived from the estimation process. The IFM also assumes homogeneity in patch quality. To meet this assumption all patches with vegetation height equal to or <4cm, were removed from the parameterisation process.

Once the parameters were estimated these were applied to the whole of the Dorset network to test how well the derived parameters predicted the occupancy patterns. 100 iterations of the model were run for 200 generations (years). The initial occupancy status was either set at the observed occupancy in 1999 or that of 1981. Parameters generated from other butterfly systems were also applied to the Dorset network, these being *Melitaea cinxia* (Hanski *et al.* 1996b; Wahlberg *et al.* 1996) and *E. aurinia* from studies in Finland (Wahlberg 2000) to test how these parameters performed in the Dorset system.

3.2.2 Test system – 4km by 4km independent networks

The findings from Dorset concerning patch occupancy and the IFM parameters were tested in a series of independent 4km by 4km networks distributed across the species range (see section 1.7.2) to test the accuracy of the model. These were non-randomly selected to be the best available habitat within each sub-region. By modelling *E. aurinia* in these independent networks quantitative questions could be asked about the persistence of the butterfly in these differing fragmented landscapes. Such as, does the model predict the species to survive in those networks where it is still present and predict extinctions where this has occurred in reality?

The same methods as described above (section 3.2.1.1) were adopted for the field surveys of the 4km paired squares.

The parameter estimates were used to run 100 simulations of up to 200 generations (years) in both the survived and extinct independent networks. Because the occupancy status of the extinct networks was not available, all patches were set as occupied at the start of the simulations in both the extinct and survived networks. The survived networks were also simulated starting with the real patch occupancy status in 1999.

3.2.2.1 Scenario modelling in the independent networks

A further step is to explore how the persistence of a particular metapopulation is affected by increasing the available habitat area or by simulating further decreases in patch size.

The relationship between species persistence and patch size was investigated in four extant networks: mid Wales, South-west A, South-west B and Cumbria. Increasing the patch size was assumed to be conceptually similar to improving habitat quality. Individual patch sizes were increased by 25%, 50%, 75% and 100% to examine effects on persistence, with additional increases of 200% and 400% in the case of Cumbria. With the South-west B network, the patch sizes were reduced by 25%, 50% and 75% of the original area. The IFM model was run using the Dorset parameters as before.

3.2.3 Metapopulation capacity

A new and alternative method of determining whether networks will support metapopulations is the metapopulation capacity of a landscape (Hanski & Ovaskainen 2000). This has been derived from metapopulation theory and can be applied to real networks of known spatial configuration and patch area. It allows the comparison of different landscape capacities to support metapopulations by combining habitat quantity and configuration. Less information is required concerning the population dynamics of the species inhabiting the network and may be useful to conservation. The metapopulation capacity (λ_M) was calculated for the Dorset network and each of the 4km by 4km independent networks.

3.3 Results

3.3.1 Model system – Dorset

Succisa pratensis was found in 938 of the 100m (1ha) squares across the study area, with habitat ranging from chalk downland to wet, marshy grasslands (figure 3.1). Contiguous records were classified into 123 habitat patches (total area of 408.46ha). Of these patches 14 were occupied (total area 83.69ha) by *E. aurinia* in 1998, 1999 or 2000 (figure 3.2). Since 1981, ten patches have become extinct and four patches have been colonised (Warren, unpublished data).

The mean density of *E. aurinia* in each patch over the three years is shown in table 3.1, where the mean density is adjusted for peak using the fixed transect at Giant Hill or Rooksmoor. The mean estimated number at peak was estimated from density and patch area. The relationship between the corrected density/100m and the habitat variables of vegetation height, host plant cover, leaf length and connectivity was investigated to see if a relationship existed between patch quality and population density. The multiple regression showed only a very weak correlation and was not statistically significant (adjusted R^2=0.28, F=0.779, P=0.569). There was much variation in density within patches from year to year, large fluctuations in population density are typical in this species (Warren 1994a) and may account for this.

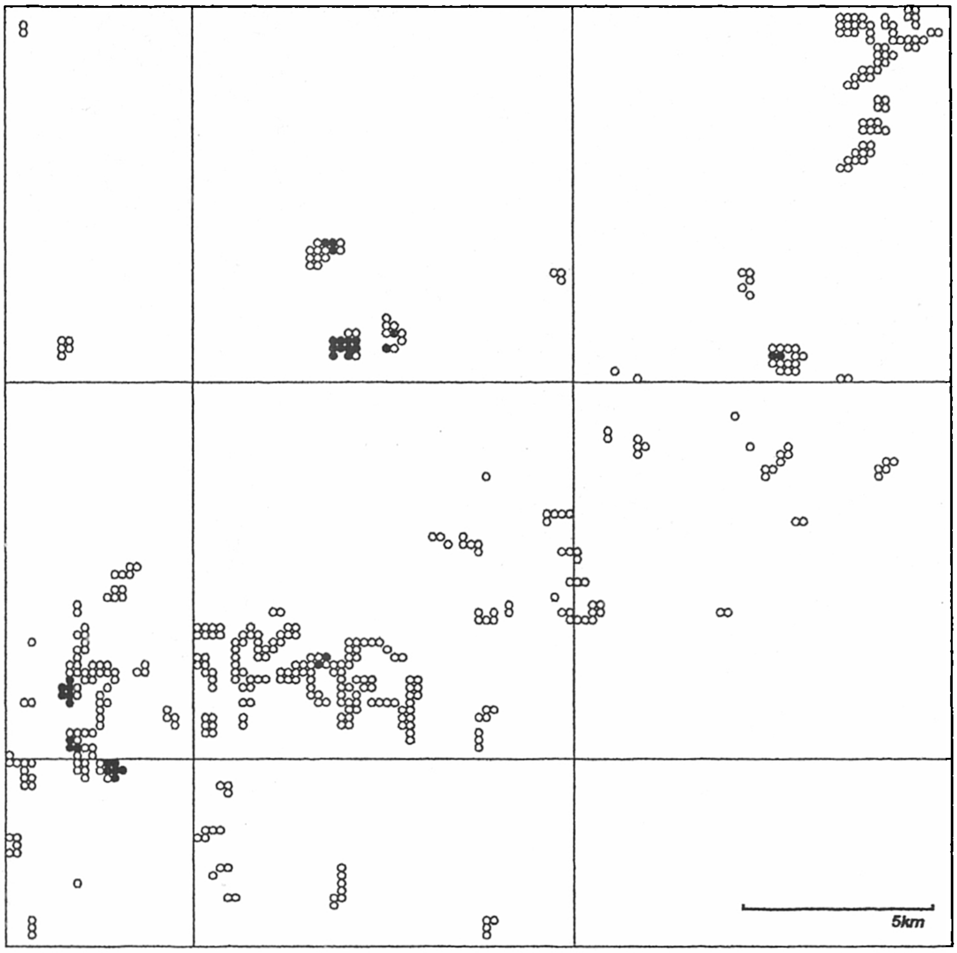


Figure 3.1 Distribution of *S. pratensis* across the 25km by 25km study area at a 200m scale (records were made at a 100m resolution). White circles are unoccupied by *E. aurinia* and black circles are occupied by *E. aurinia*.

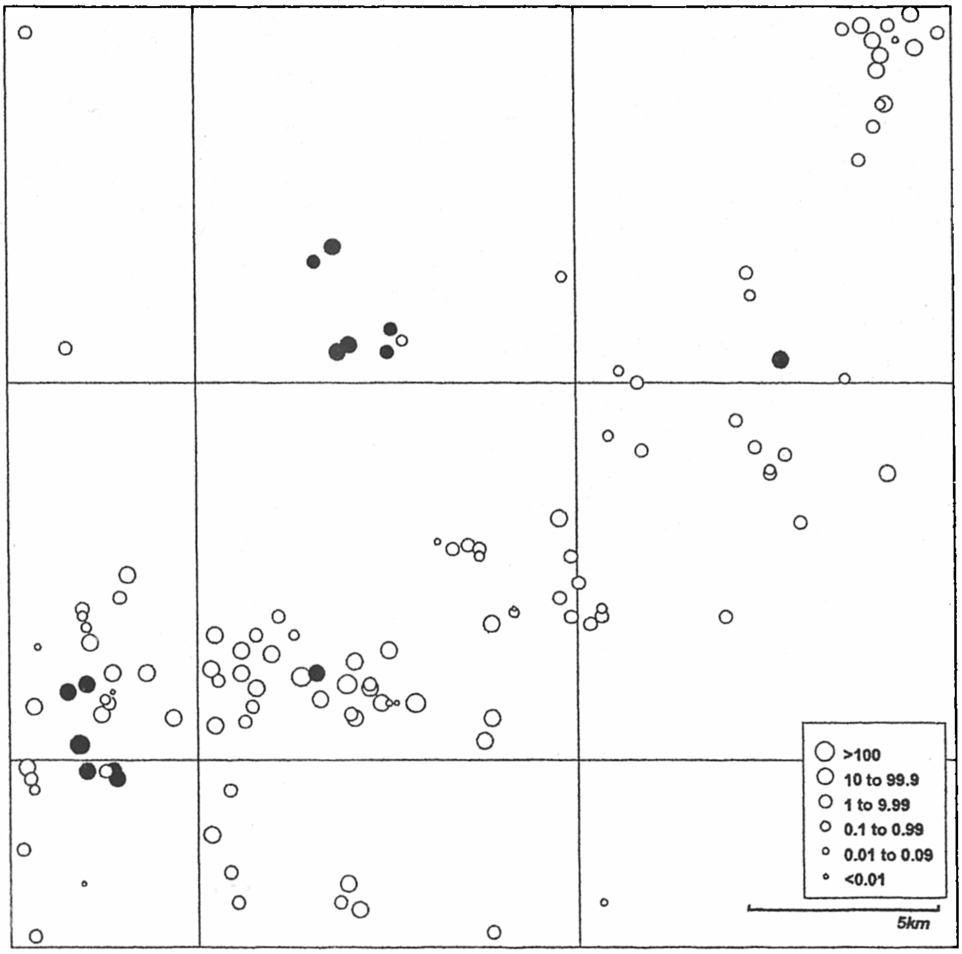


Figure 3.2 Distribution of *S. pratensis* across the 25km by 25km study area, patches are scaled by resource area (ha). Black circles indicate those patches that are occupied by *E. aurinia* and the white circles show the vacant patches.

Table 3.1 Mean transect density per 100m and mean population estimate based on habitat area, corrected for peak (1998 to 2000).

Site	Area (ha)	Mean corrected density/100m	Mean estimated number at peak
Giant Hill	8.42	6.77	527
Giant Hill East	14.35	1.00	166
Bramble Bottom A	4.00	1.94	110
Bramble Bottom B	2.98	0.96	68
Black Hill	12.15	0.63	109
Hod Hill	2.61	0.97	66
Lyscombe Down	10.76	3.28	344
Rooksmoor A	2.50	1.26	71
Rooksmoor B	12.00	1.91	239
Deadmoor A	0.90	11.03	128
Deadmoor B	1.12	1.97	63
Lydlinch D	8.95	1.17	133
Lydlinch A	1.15	2.27	66

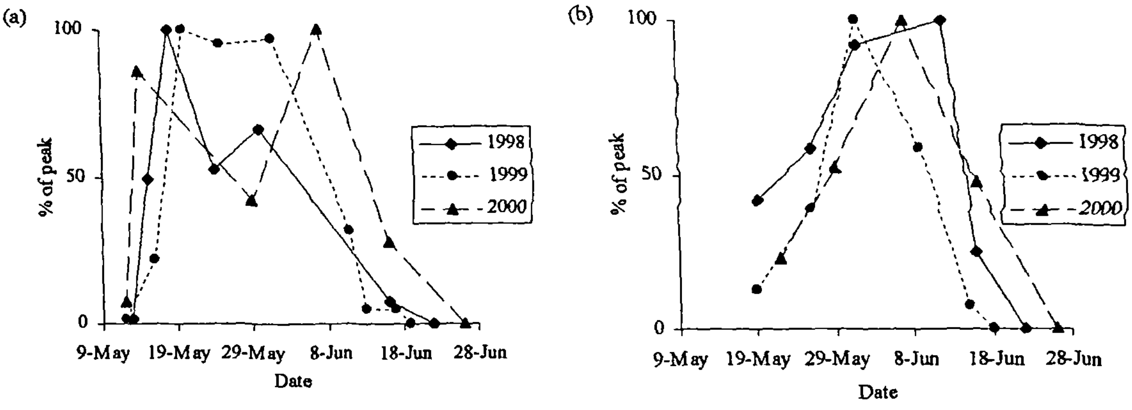


Figure 3.3 Phenology graphs for the fixed transects at (a) Giant Hill and (b) Rooksmoor from 1998 to 2000.

3.3.1.1 What factors determine the observed occupancy of *E. aurinia* across the Dorset landscape?

From initial inspection of the distribution map (figure 3.2) a large number of patches contain the host plant, but only 11.4% of patches are actually occupied by the butterfly. *E. aurinia* probably requires more than just the presence of the larval host plant. What attributes do the occupied patches have that make them suitable for occupancy, and why are so many patches unoccupied in the study area?

Stepwise logistic regression was used to investigate which of the patch variables that had been measured explained the observed occupancy patterns. Host plant cover and patch area were positively correlated ($R_S=0.248$, $P<0.01$) (table 3.2) and therefore multiplied together to produce a variable to represent extent of resource to *E. aurinia* termed 'resource area'. Patch area and host plant cover as separate variables did not explain any more variation in the model than the combined variable.

Vegetation height and host plant leaf length were highly correlated ($R_S=0.754$, $P<0.0001$) (table 3.2). When these variables were tested separately in a logistic regression the model containing vegetation height was nearly as successful as that containing leaf length, the two models only differing by two patches in the number of patches classified correctly. Because of the practical utility of vegetation height in conservation management, this variable was used over leaf length in the logistic regression model.

The result of the logistic regression is shown in table 3.3. Connectivity to all *E. aurinia* populations, vegetation height and resource area have positive effects on patch occupancy, with 92% of cases correctly classified by the model (model correctly predicted a patch to be occupied or vacant). Patches are predicted to be occupied if the resource area is high (large patch area and abundant host plant), the vegetation height is tall and they are well connected to other occupied patches. Isolated patches that are small in area, with little host plant and short vegetation are less likely to be occupied. With resource area being a significant variable, it is interesting to note that a large patch with a low density of host plant may be no more suitable than a smaller patch with a high density of host plant.

Table 3.2 Spearman Rank Correlation matrix (n=123 patches). A critical probability of P=0.003 is required to attain statistical significance with Bonferroni correction.

	Patch area (ha)	**Vegetation height (cm)**	**Host plant cover**	**Leaf length (cm)**	**Resource area**	**Connectivity A**	**Connectivity B**
Patch area (ha)	-						
Vegetation height (cm)	R_S=0.117 NS	-					
Host plant cover	R_S=0.248 P<0.01	R_S=0.035 NS	-				
Leaf length (cm)	R_S=0.037 NS	R_S=0.754 P <0.0001	R_S=0.134 NS	-			
Resource area	R_S=0.915 P <0.0001	R_S=0.125 NS	R_S=0.570 P <0.0001	R_S=0.101 NS	-		
Connectivity A	R_S=0.197 P <0.05	R_S=0.187 P <0.05	R_S=0.177 NS	R_S=0.140 NS	R_S=0.237 P <0.01	-	
Connectivity B	R_S=0.230 P <0.01	R_S=-0.17 NS	R_S=0.040 NS	R_S=-0.075 NS	R_S=0.222 P <0.05	R_S=0.504 P <0.0001	-

Connectivity A calculated to all occupied patches. Connectivity B calculated to all habitat patches.

Table 3.3 Logistic regression of connectivity A, vegetation height and resource area on patch occupancy. Only significant variables are shown. Z is the logistic regression equation.

	Model if term removed			
Variable	**Effect**	**-2 Log LR**	***df***	***P***
Connectivity A	+	16.801	1	<0.00001
Vegetation height	+	14.985	1	<0.0001
Resource area	+	9.175	1	<0.01

-2 log likelihood=48.674, Goodness of Fit=106.655, Model χ^2=38.516, df=3, P<0.00001.

$n_{occupied}$=14, n_{vacant}=109, 92% of cases were classified correctly by the model.

Z=-6.2568+1.920(connectivity A)+0.2512(vegetation height)+0.0313(resource area)

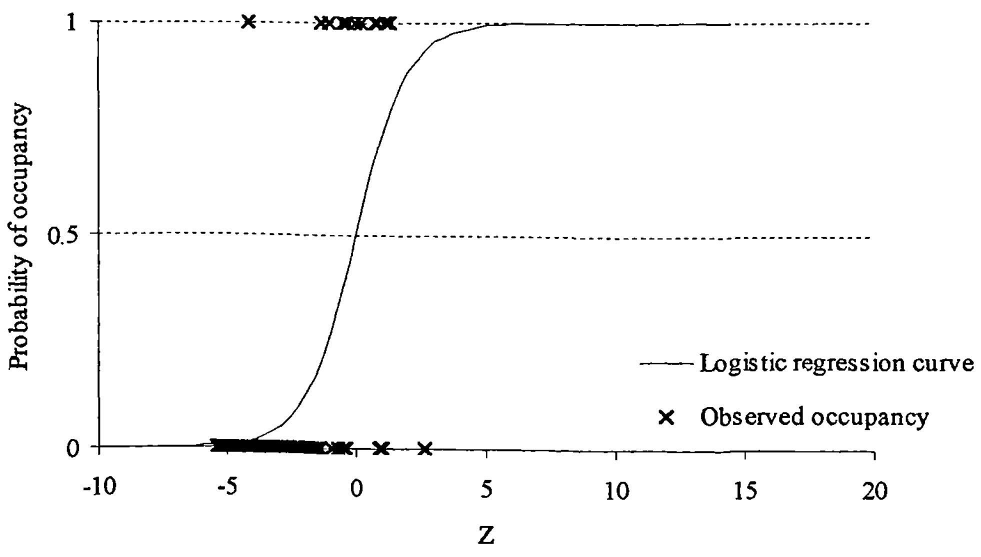


Figure 3.4 Logistic regression curve of the probability of occupancy as a function of connectivity A, vegetation height and resource area (from equation in table 3.3). The probability of occupancy = $e^z/1+e^z$. Each cross represents one patch, which is either occupied (1) or vacant (0).

Table 3.4 Logistic regression of vegetation height, connectivity A, host plant cover and patch area on patch occupancy. Only significant variables are shown. Z is the logistic regression equation.

	Model if term removed			
Variable	**Effect**	**-2 Log LR**	***df***	***P***
Vegetation height	+	22.76	1	<0.00001
Connectivity A	+	15.58	1	<0.0001
Host plant cover	+	7.596	1	<0.05
Patch area	+	5.851	1	<0.05

-2 log likelihood=44.268, Goodness of Fit=70.179, Model χ^2=42.922, df=4, P<0.00001.

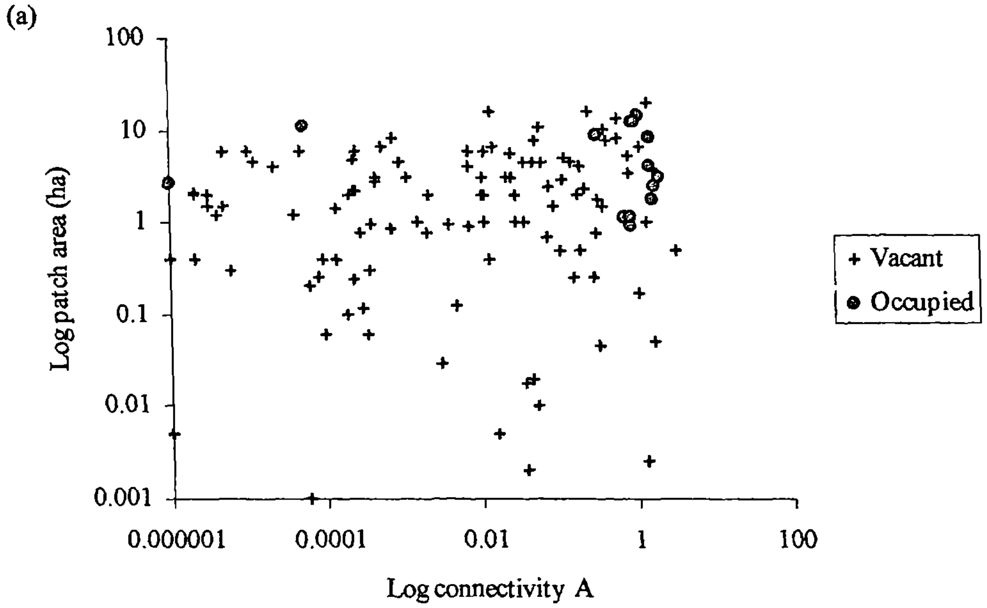
$n_{occupied}$=14, n_{vacant}=109, 92% of cases were classified correctly by the model.

Z=-9.4814+0.3191(vegetation height)+1.8382(connectivity A)+0.4794(cover)+0.1780(area)

The total model containing patch area, instead of resource area also classified 92% of patches correctly. This model is shown in table 3.4, and can be applied to landscapes where host plant density in each patch is not known.

In Dorset both the spatial arrangement of patches (proximity to occupied patches and patch area) and habitat quality are important variables for occupancy by *E. aurinia*. The following graphs illustrate these patterns well (figure 3.5), where the occupied patches are scattered in the top right part of the graphs. The species has a low occupancy of apparently suitable habitat and it is probable that this species is particularly sensitive to habitat fragmentation.

Anecdotal evidence has suggested that aspect, and to a lesser extent slope, may influence occupancy of certain patches by the butterfly. *E. aurinia* appears to have a preference for westerly-facing chalk sites (Warren 1993b). The influence of aspect and slope on occupancy in the chalk sites was tested using logistic regression. Wet grassland sites were not included in the procedure as these are generally flat sites with no slope or aspect associated with them. The aspect for each patch was converted to degrees from west and slope entered in degrees ($n_{occupied}=8$, $n_{unoccupied}=108$). No significant relationship was found between aspect and slope and the occupancy status of the patch.



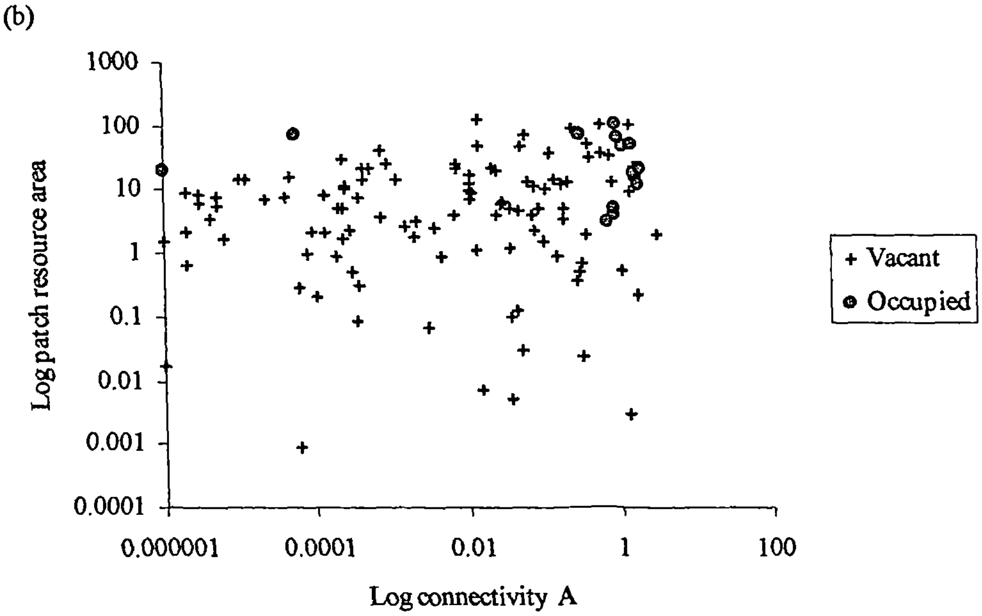
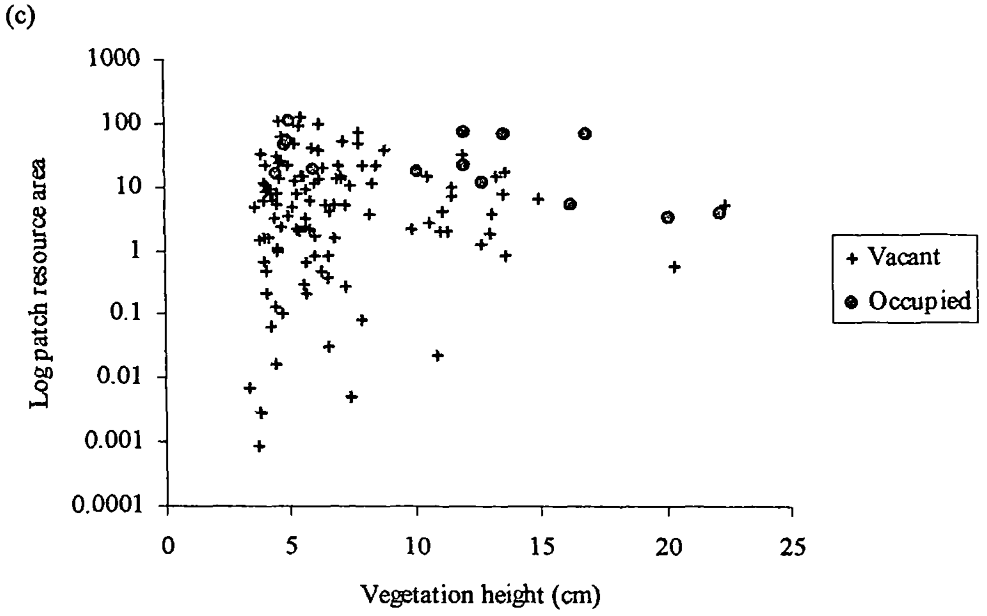


Figure 3.5 Pattern of occupancy in each of the 123 patches against patch area (ha), connectivity and resource area. Grey circles represent occupied patches and crosses vacant patches. (a) patch area and connectivity A (b) patch resource area and connectivity A.



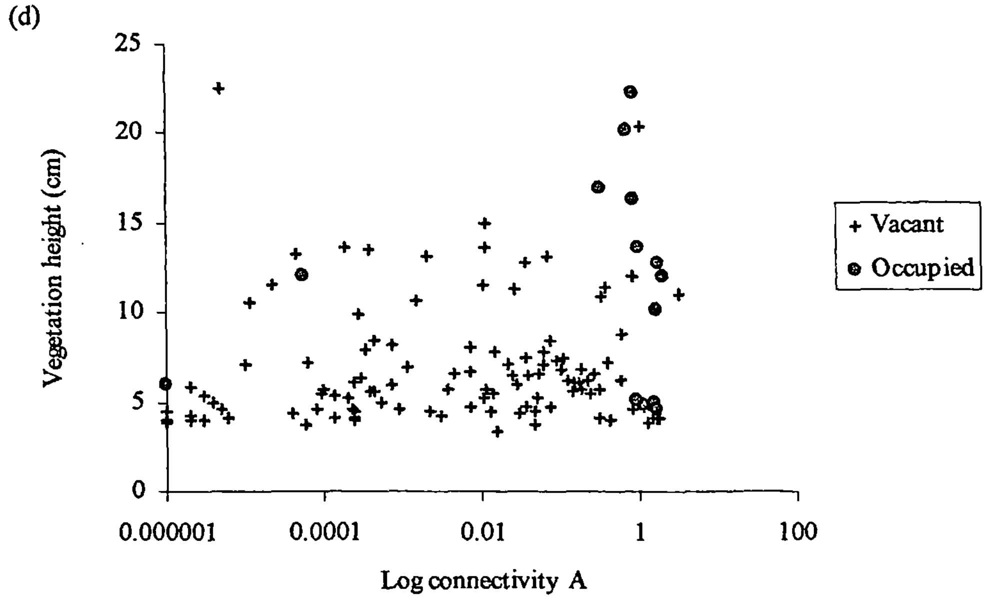


Figure 3.5 contd. Pattern of occupancy in each of the 123 patches against resource area, connectivity and vegetation height (cm). Grey circles represent occupied patches and crosses vacant patches. (c) patch area and connectivity A (d) patch resource area and connectivity A.

3.3.1.2 Historical occupancy in Dorset

The current occupancy pattern of *E. aurinia* across the Dorset landscape is influenced by patch size, the spatial distribution of habitat and quality within patches. The historical changes in patch occupancy was known from documented colonisation and extinction events that have been recorded in Dorset since the early 1980's. Twenty patches were extant in 1981, with ten extinctions taking place and four new patches colonised to date. The relative influence of patch size and spatial location on the historical pattern of occupancy was investigated.

A stepwise logistic regression was used to test the influence of patch area and connectivity on the present occupancy of patches that were occupied in 1981. The connectivity of patches occupied by *E. aurinia* in 1981 was measured, but patch area alone explained the pattern of occupancy (table 3.5). Of all patches occupied in 1981, the larger patches were more likely to be occupied in 1999, with smaller patches becoming extinct. Those patches still occupied in 1999 tended to be the larger patches (Mann-Whitney U test, $n_{survived}=14$, $n_{extinct}=10$, $U=22$, $P<0.01$) (figure 3.6).

However, a few patches are small and remain occupied. When the above logistic regression was repeated, with the inclusion of connectivity A (measure of connectivity to all currently occupied patches), past and present connectivity became significant with patch area no longer included in the model. The relatively smaller patches remain occupied because of their close proximity to occupied patches (verified by running a logistic regression including connectivity A). Even though connectivity (to occupied patches in 1981) was not detectable as a factor in the extinction of these patches, the trend is nonetheless strong, and this factor may well be important in maintaining the occupancy, possibly through the rescue effect (Brown & Kodric-Brown 1977).

With resource area, connectivity and habitat quality being significant factors in the occupancy of patches, the metapopulation approach was adopted and modelled using the Incidence Function Model.

Table 3.5 Logistic regression of patch area on present occupancy in those patches occupied in 1981.

	Model if term removed			
Variable	**Effect**	**-2 Log LR**	***df***	***P***
Patch area	+	7.554	1	<0.01

-2 log likelihood=25.701, Goodness of Fit=23.169, Model χ^2=6.90, df=1, P<0.01.

$n_{occupied}$=14, $n_{extinct}$=10, 71% of cases were classified correctly by the model.

Z=-0.7672+0.3453 (patch area)

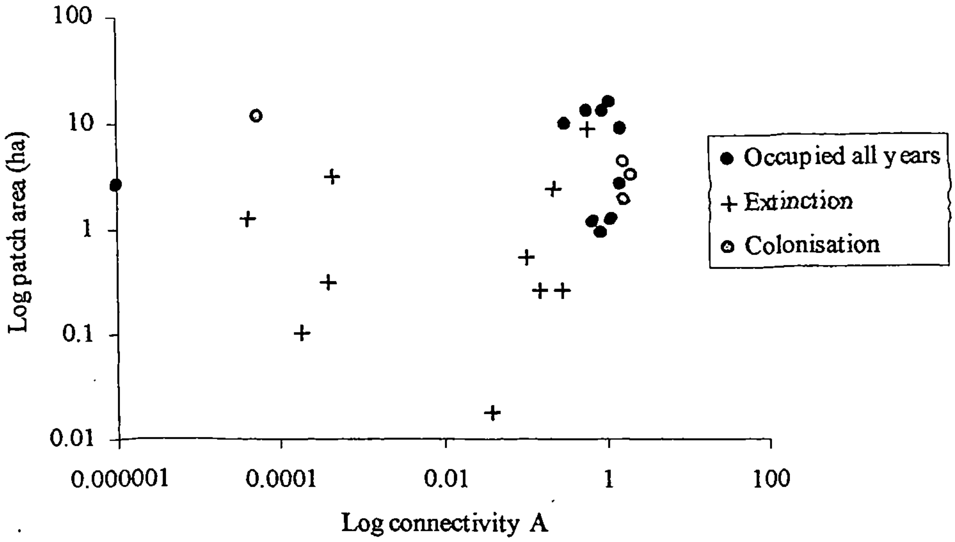


Figure 3.6 Occupancy status of patches against area (ha) and connectivity A, only patches that were occupied during recording years or where turnover was detected are shown. Black circles are patches occupied in 1981 and 1998-2000. Crosses indicate extinctions since 1981 and grey circles are patches colonised since 1981.

3.3.2 Incidence Function Model results – Dorset

The parameters estimated from the sub-set of Dorset patches are given in table 3.6. The table includes the parameters estimated from *M. cinxia* (Hanski *et al.* 1996b; Wahlberg *et al.* 1996) and *E. aurinia* (Wahlberg 2000) in Finnish systems which were also applied to the Dorset network.

The parameter estimates were used to run 100 iterations of 100 generations (years) in the Dorset study area. The changes in fraction of patches occupied are shown in figure 3.7. The first graph (a) was initiated with the patches set as occupied in 1999. The metapopulation persists at a level of approximately 16 to 20% occupancy, slightly higher than the observed proportion of patches occupied, with 6% of iterations becoming extinct. The graph (b) shows the fraction of patches occupied for 100 simulations using the Dorset parameters, with the 1981 occupancy pattern. Between 1981 and 1999, 50% of the occupied patches became extinct; the simulations reflect this observed pattern with a decrease in the fraction of patches occupied over time.

M. cinxia parameters (Hanski *et al.* 1996c) were simulated in the Dorset network, with patches set at the present occupancy. The change in fraction of patches occupied is dramatically different (c), with an increase to between 60 and 80% in patches occupied, with no extinctions occurring. *E. aurinia* parameters estimated in Finland (Wahlberg 2000) were also simulated in the Dorset network. As with *M. cinxia*, the fraction of patches occupied is overestimated with a jump to >75% after less than five years, dramatically different to the observed situation.

Table 3.6 Table of parameter values from the Incidence Function Model used to estimate the metapopulation dynamics in Dorset and the independent networks. (Parameter explanations: α describes the colonisation ability, x the strength of environmental stochasticity, y speed at which the colonisation probability approaches unity with increasing immigrants, e describes the probability of extinction per unit time in a patch of unit size).

Parameter	***E. aurinia*** **(Dorset sub-set)**	***M. cinxia*** **(Hanski *et al.* 1996b)**	***E. aurinia*** **(Wahlberg 2000)**
α	2	1	0.4204
x	0.679100	0.952	1.3001
y	4.483450	3.970	4
e	0.209071	0.010	0.0849

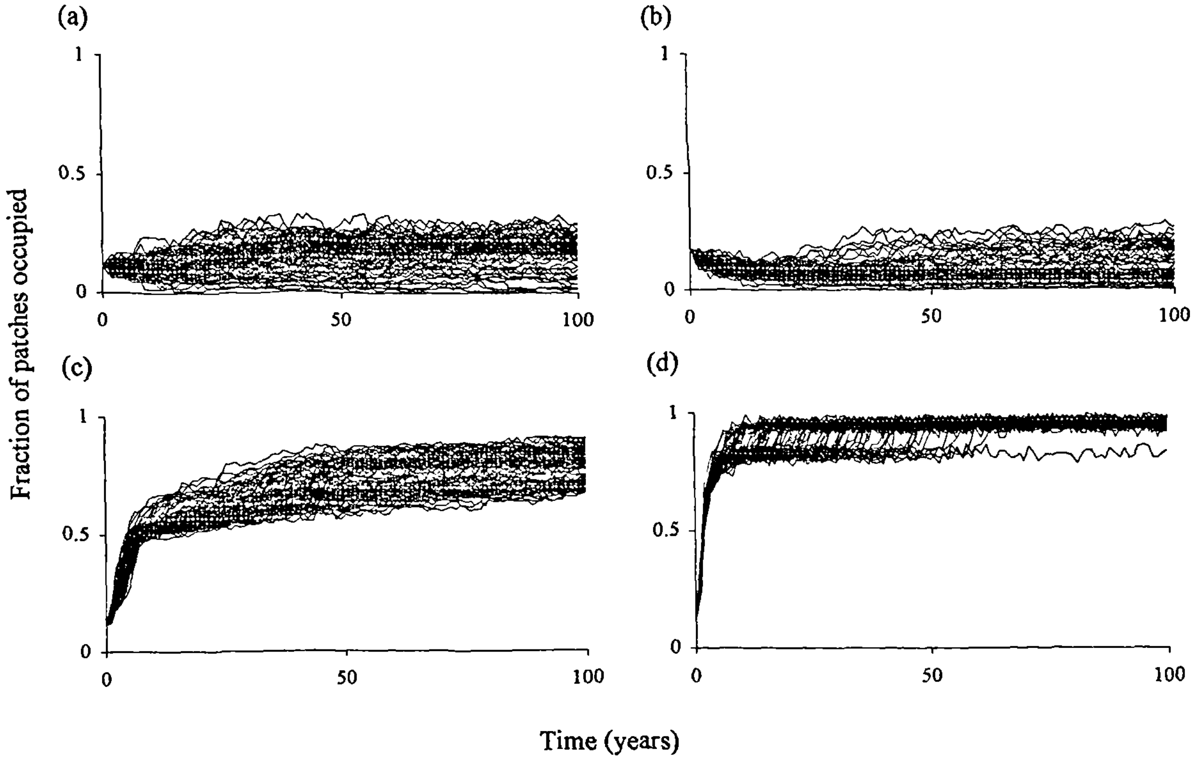


Figure 3.7 The predicted dynamics of fraction of patches occupied within the Dorset 25km by 25km study area over 100 years. (a) Dorset sub-set *E. aurinia* parameters, 1999 occupancy; (b) Dorset sub-set parameters, 1981 occupancy; (c) *M. cinxia* parameters and 1999 occupancy; (d) *E. aurinia* (Finland) parameters and 1999 occupancy.

3.3.3 4km by 4km independent networks

The patch networks in each of the 4km by 4km independent squares show similar patterns to Dorset. The distribution and occupancy patterns are shown in figure 3.8. In general the survived networks (those with *E. aurinia* extant), have more patches with greater total area in comparison to the extinct networks (table 3.7). Mann-Whitney U tests were carried out to look at the differences between the patch variables and the status of the network ($n_{extinct}$=6, $n_{survived}$=6) (figure 3.9). A statistically significant difference was found between the number of patches (*U*=3, *P*=0.015); connectivity of habitat patches (*U*=5, *P*=0.041) and total patch area (*U*=2, *P*=0.009). Median patch area was not significant, but the difference was highly significant when an outlier (Cumbria extinct) was removed (*U*=0, *P*=0.004). This was also the case for resource area. With removal of the outlier, the difference became highly significant (*U*=0, *P*=0.004).

A logistic regression was carried out to test network occupancy against these network variables. Total area was found to be the best predictor of network occupancy (table 3.8, figure 3.10). The model correctly classified 11 of the networks. Cumbria survived is misclassified because it contains only two patches. Because the variables were highly correlated (table 3.9) a separate logistic regression was carried out on each variable. The test statistic (–2 log likelihood) was less with 'total area' than for the other variables tested (patch number, resource area and connectivity) and therefore is the better predictor of occupancy in each of the 4km networks. Using the equation, the habitat area of a network must be >21ha to attain a 50% probability of network occupancy.

The same patterns found in Dorset are found more widely across the distribution of *E. aurinia*. The butterfly is occupying only the larger networks where the habitat patches are less isolated.

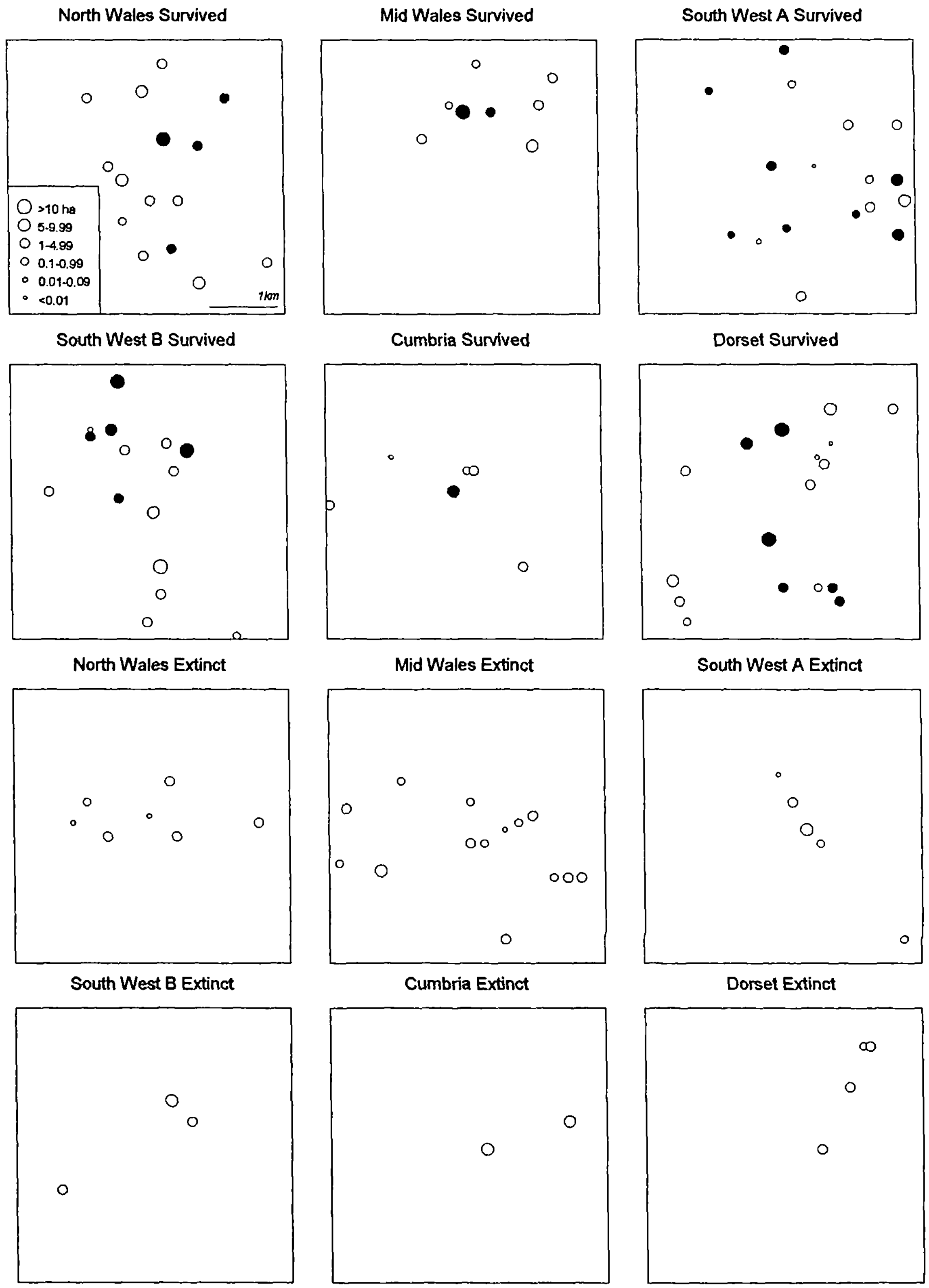


Figure 3.8 Spatial location and size of patches (ha) in each 4km by 4km independent network. Black circles are occupied patches and open circles are vacant patches.

Table 3.7 Patch characteristics for the 4km by 4km independent networks, with Dorset pairs included. Connectivity values are calculated to all *habitat* patches. The date of the last known record is given in brackets for the extinct networks.

Network	# of patches	Total patch area (ha)	Patch area Mean (±1 S.E.) *Median (IQR)*	Resource area Mean (±1 S.E.) *Median (IQR)*	connectivity A Mean (±1 S.E.) *Median (IQR)*
Survived					
North Wales	15	114.88	7.66 (3.76)	31.39 (17.67)	3.18 (0.33)
			3.6 (2.25-5.95)	*10.64 (5.13-22.85)*	*3.52 (2.31-4.15)*
Mid Wales	8	40.98	5.12 (1.90)	23.61 (11.08)	2.55 (0.34)2.35
			3.92 (1.64-5.77)	*16.12 (5.01-23.30)*	*(1.79-2.89)*
South-west A	17	32.53	1.91 (0.43)	10.51 (2.78)	1.78 (0.26)
			1.8 (0.4-2.62)	*10.05 (1.48-11.01)*	*1.51 (0.89-2.81)*
South-west B	15	116.12	7.74 (2.92)	23.96 (9.68)	3.50 (0.44)
			3.5 (1.52-6.75)	*8.09 (3.84-20.11)*	*3.50 (1.88-4.93)*
Cumbria	6	14.12	2.35 (1.10)	12.19 (5.36)	0.97 (0.35)
			1.55 (0.46-3.15)	*10.34 (1.24-18.49)*	*0.74 (0.31-1.42)*
Dorset	18	79.79	4.43 (1.00)	25.26 (6.56)	2.37 (0.23)
			3.24 (1.12-7.56)	*16.73 (3.76-35.69)*	*2.32 (1.74-2.79)*
Extinct					
North Wales	7	10.30	1.47 (0.56)	3.65 (1.42)	0.81 (0.16)
(1986)			*1.5 (0.14-2.25)*	*3.82 (0.31-5.49)*	*0.81 (0.58-0.90)*
Mid Wales	14	19.54	1.39 (0.39)	2.96 (1.25)	1.47 (0.19)
(1987)			*0.92 (0.32-1.78)*	*1.31 (0.25-2.68)*	*1.51 (0.82-1.93)*
South-west A	5	9.46	1.89 (1.16)	6.95 (4.22)	0.95 (0.24)
(1989)			*0.3 (0.12-3)*	*1.06 (0.56-11.19)*	*1.06 (1.01-1.12)*
South-west B	3	7.50	2.50 (1.26)	10.78 (8.37)	0.52 (0.26)
(1994)			*1.5 (1.25-3.25)*	*3.15 (2.42-15.32)*	*0.54 (0.29-0.75)*
Cumbria	2	16.65	8.32 (1.42)	26.15 (5.82)	0.22 (0.01)
(1992)			*8.32 (7.61-9.03)*	*26.15 (23.24-29.06)*	*0.22 (0.21-0.23)*
Dorset	4	5.9	1.47 (0.56)	7.56 (2.83)	0.90 (0.32)
(1981)			*3.24 (1.12-7.56)*	*16.73 (3.73-35.69)*	*2.32 (1.74-2.79)*

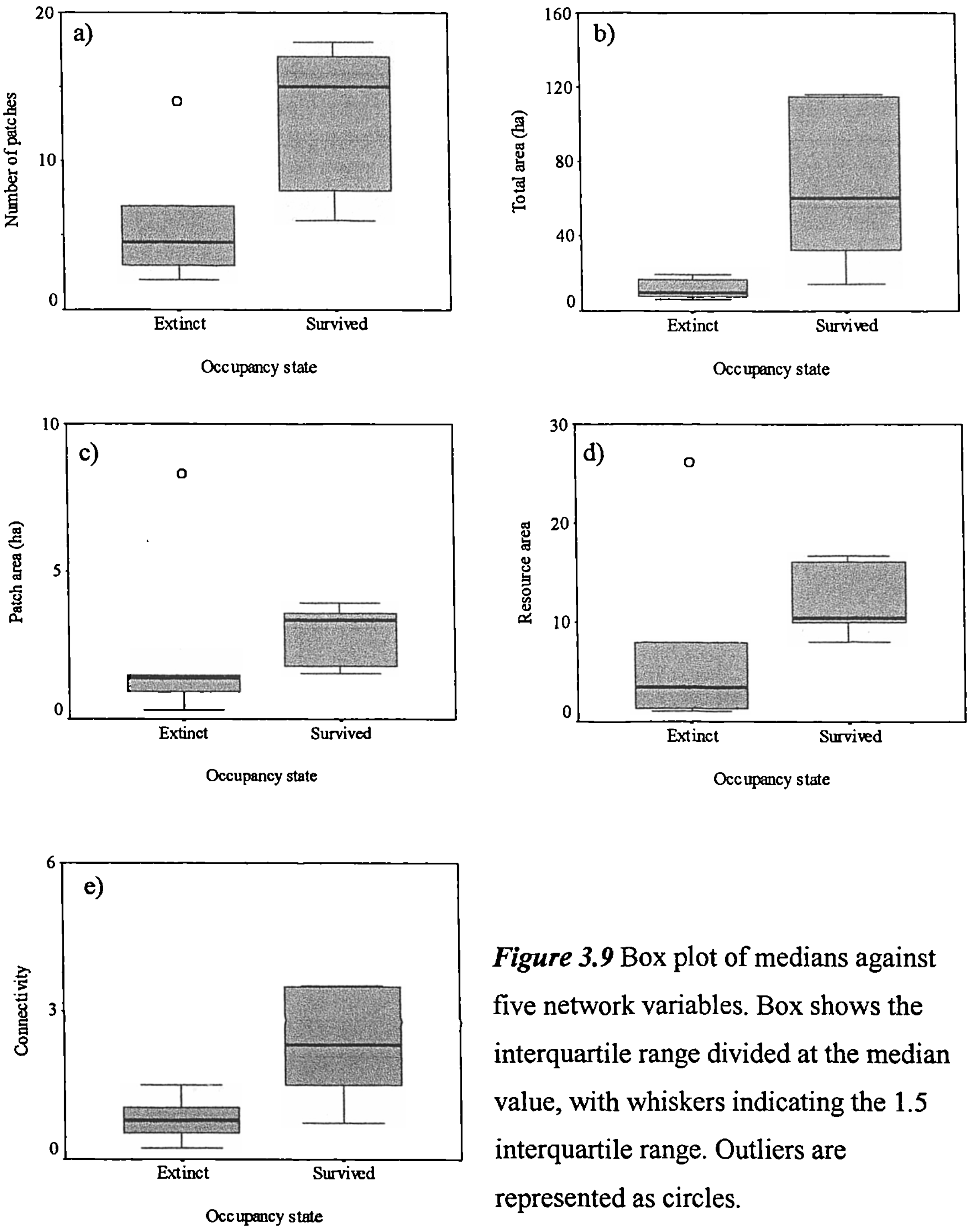


Figure 3.9 Box plot of medians against five network variables. Box shows the interquartile range divided at the median value, with whiskers indicating the 1.5 interquartile range. Outliers are represented as circles.

Table 3.8 Logistic regression of network total area (ha) on network occupancy.

	Model if term removed			
Variable	**Effect**	**-2 Log LR**	***df***	***P***
Total area (ha)	+	13.62	1	<0.001

-2 log likelihood=5.846, Goodness of Fit=6.162, Model χ^2=10.789, df=1, P<0.001.

$n_{survived}$=6, $n_{extinct}$=6, 92% of cases were classified correctly by the model.

Z=-4.6874+0.2216 (Total area)

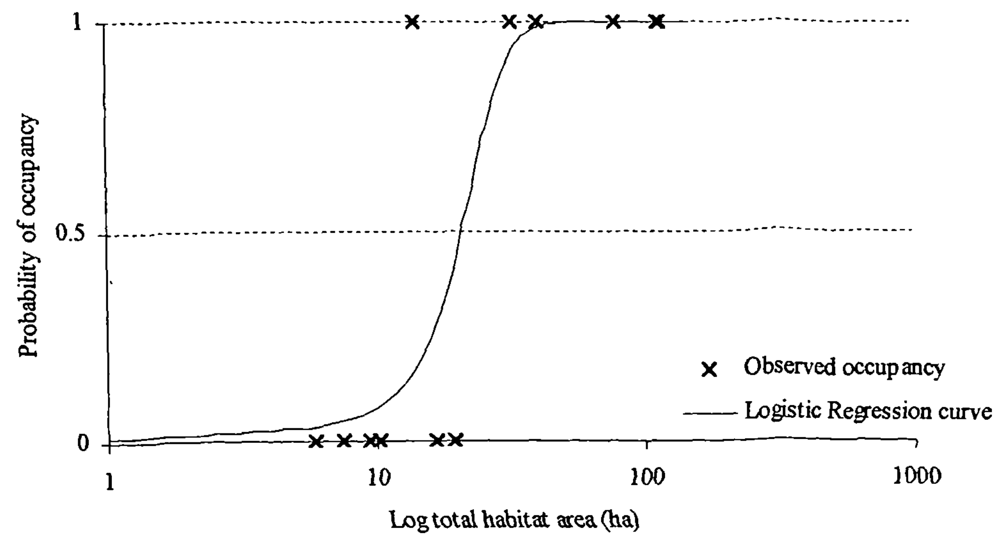


Figure 3.10 Logistic regression curve of the probability of occupancy as a function of total network area (from equation in table 3.8). Probability of occupancy =$e^z/1+e^z$. Each cross represents one network, which is either occupied (1) or vacant (0).

Table 3.9 Spearman Rank Correlation matrix (n=12). A critical probability of *P*=0.005 is required to attain statistical significance with Bonferroni correction.

	Number of patches	Total area (ha)	Mean patch area (ha)	Resource area	Connectivity
Number of patches	-				
Total area (ha)	$R_S = 0.78$ $P < 0.002$	-			
Mean patch area (ha)	$R_S = 0.53$ NS	$R_S = 0.57$ NS	-		
Resource area	$R_S = 0.18$ NS	$R_S = 0.60$ $P < 0.05$	$R_S = 0.94$ $P < 0.0001$	-	
Connectivity	$R_S = 0.83$ $P < 0.001$	$R_S = 0.85$ $P < 0.0001$	$R_S = 0.31$ NS	$R_S = 0.36$ NS	-

3.3.4 Incidence Function Model results – 4km by 4km networks

In these independent 4km by 4km networks, it is probable that the butterfly is persisting as a metapopulation, with habitat area being a crucial factor in persistence, therefore the Incidence Function Model is a useful approach to take. The parameters generated from Dorset were applied to the independent networks, firstly to test the applicability of the model and secondly, to simulate the persistence of *E. aurinia* in the future (Wahlberg *et al.* 1996). The model was used as a tool to predict the persistence of *E. aurinia* in these independent networks where it remains extant and where the butterfly has become extinct, and to predict persistence times in these networks.

The Dorset parameter estimates were used to run 100 simulations of 200 generations (years), in every independent network. The change in fraction of patches occupied is shown in the following graphs (figure 3.11) which give the results for each network, with the model set at full patch occupancy in year zero. This unrealistic situation was modelled to allow comparison between the survived and extinct networks. The occupancy status of each patch was known for the survived networks but only partial information on the historical occupancy of the extinct patches was available. In the survived networks, a few simulations became extinct, in particular in Cumbria and South-west A, but most persisted for greater than 200 generations, reflecting the real situation. In the extinct networks all simulations became extinct in less than 100 years, with the exception of South-west A.

Figure 3.12 shows the changes in fraction of patches occupied in the survived networks, where each patch was set at its known occupancy in 1999. Similar patterns are displayed, but with extinction equilibrium occurring sooner.

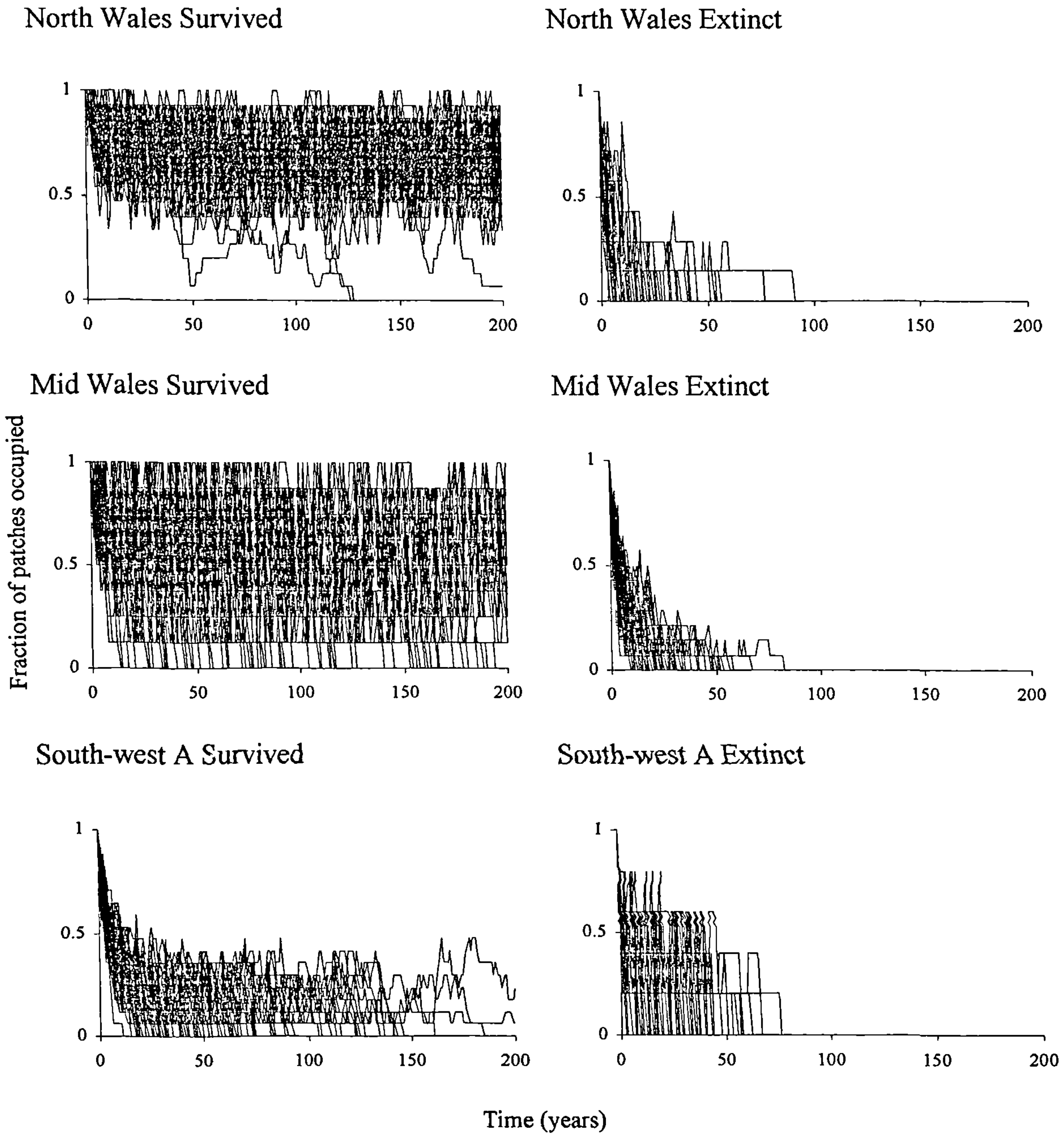
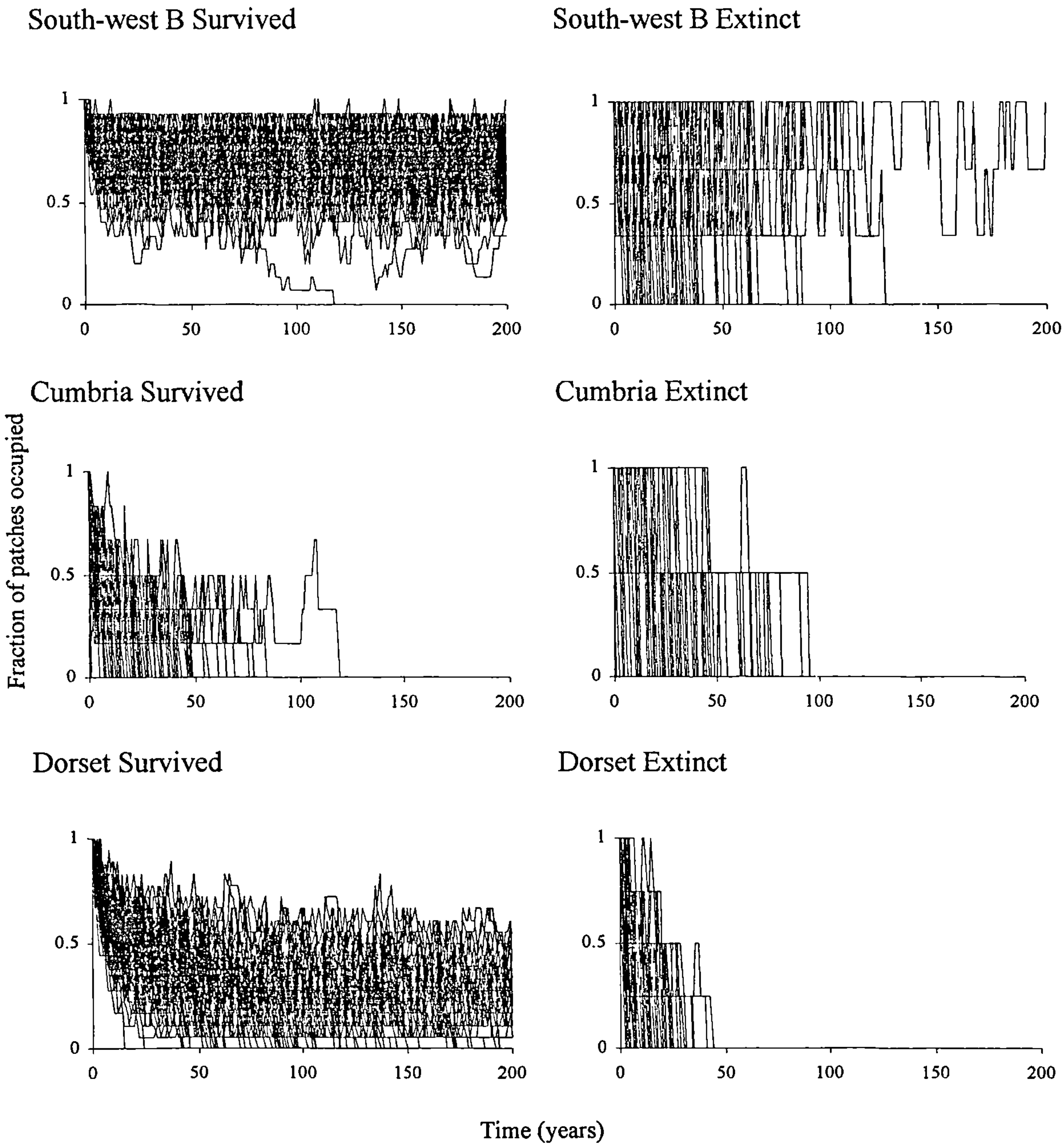


Figure 3.11 The predicted dynamics of fraction of patches occupied within the independent networks over 200 years. 100 simulations were run with each line representing one simulation.



South-west B Survived

South-west B Extinct

Cumbria Survived

Cumbria Extinct

Dorset Survived

Dorset Extinct

Figure 3.11 contd. The predicted dynamics of fraction of patches occupied within the independent networks over 200 years. 100 simulations were run with each line representing one simulation.

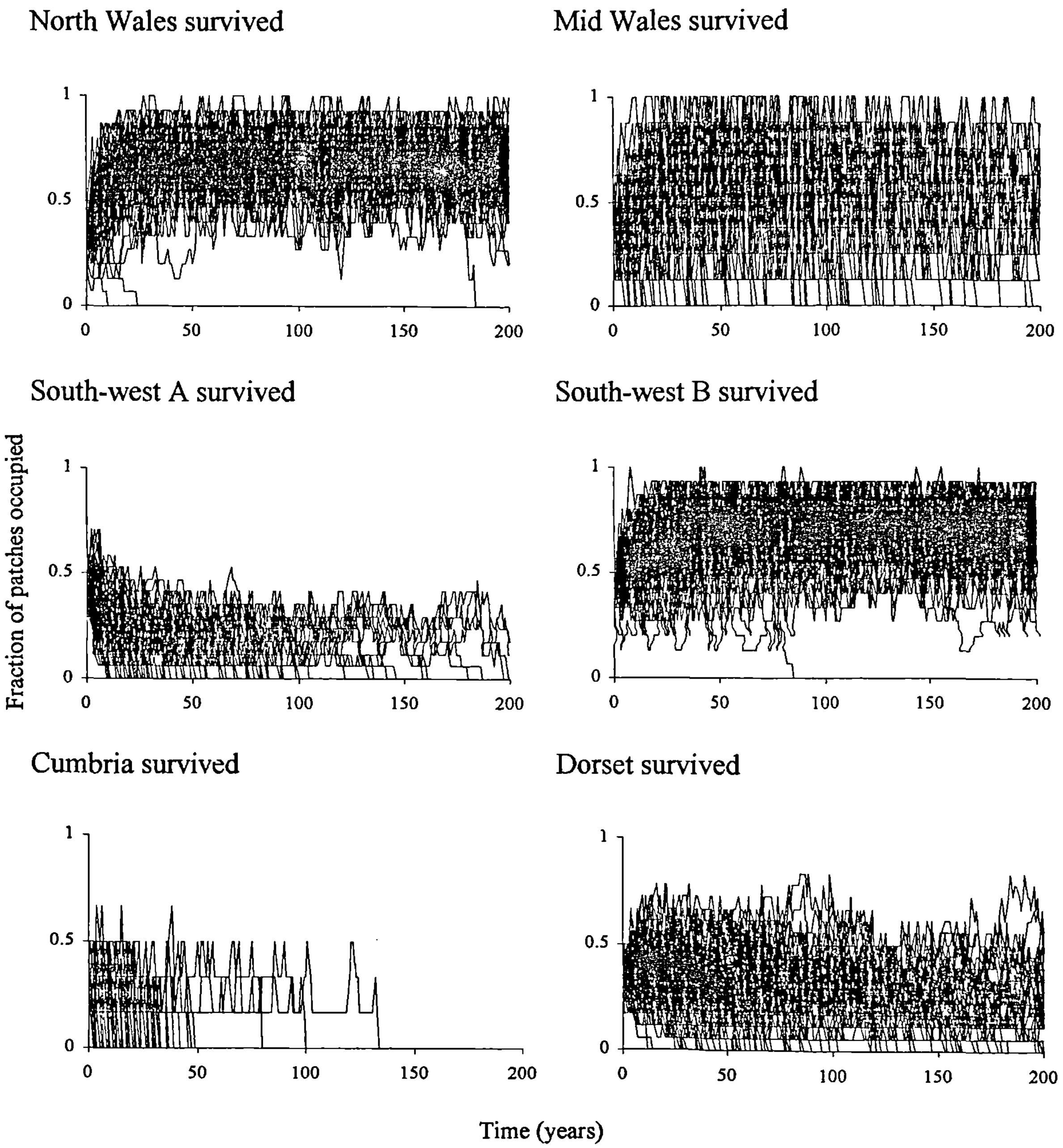


Figure 3.12 The predicted dynamics of fraction of patches occupied within the independent networks over 200 years. 100 simulations were run with each line representing one simulation with patches set as occupied in 1999.

Figure 3.13 compares the fraction of simulations or iterations surviving for each network. In general the extinct simulations reach extinction quicker than in the survived networks (Mann-Whitney U test, $n_{survived}=6$, $n_{extinct}=6$, $U=4$, $P<0.05$). *Two of* the survived networks (north Wales and south-west B) persist extremely well for >200 years. The model results successfully predicted the species to have become extinct in fragmented landscapes where it has indeed gone extinct. Table 3.10 gives the median times to extinction (when 50 simulations became extinct) for each network. The values in the first column were simulated with all patches set as occupied; therefore the predicted outcomes are optimistic. Four of the currently occupied networks have a substantial probability of becoming extinct in the near future, with one having a median time to extinction of only 21 years (Cumbria). The second column gives the results for the networks simulated with the real occupancy pattern. The north Wales and south-west B networks again persist well, but the median time to extinction in the remaining networks is reduced by up to 28%.

It is interesting to note the fate of the two mid Wales simulations. Despite the extinct network containing more patches than the survived network (table 3.7), the species still persists for less time than in the survived network. Even though there are more patches, these are small due to high fragmentation (mean patch area of 1.91ha) and therefore have a higher probability of extinction than the larger, but fewer, patches in the survived network.

The modelling results are likely to have useful applications for the conservation of *E. aurinia* in fragmented landscapes. The results can be used to understand which networks of habitat are better at maintaining metapopulations of *E. aurinia*. The most useful predictor of occupancy appears to be total area of the networks (logistic regression table 3.8). This relationship between habitat area and median time to extinction may be used to predict the threshold habitat area for persistence, and is shown in figure 3.14 (note that the two variables are not completely independent). Following log transformation a linear regression produced the equation: $y=0.959x+0.296$, adjusted $R^2=0.858$. To attain a median time to extinction of 100 years, the total area in a network must exceed approximately 60ha. The relationship between median time to extinction and the other variables was not as significant. (Number of patches $y=0.037x+1.164$, $R^2=0.278$; resource area $y=0.03x+1.086$, $R^2=0.481$; connectivity A $y=0.396x+0.982$, $R^2=0.658$).

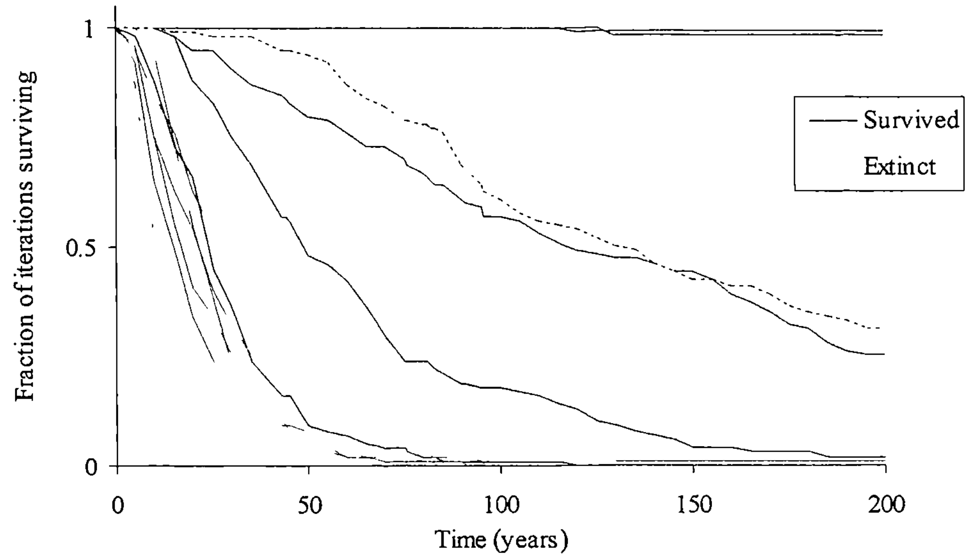


Figure 3.13 Fraction of iterations surviving for the survived (black) and extinct (red) networks, where all patches are set as occupied. Dorset networks are differentiated by the dashed lines.

Table 3.10 Median time to extinction for simulations in the survived and extinct networks. First column for simulations with all patches set as occupied and second column for simulations with survived networks set at 1999 occupancy.

	Network	**Median time to extinction[1] (years)**	**Median time to extinction[2] (years)**
Survived	North Wales	>200	>200
	Mid Wales	116	97
	South-west A	50	45
	South-west B	>200	>200
	Cumbria	24	15
	Dorset	130	126
Extinct	North Wales	15	
	Mid Wales	21	
	South-west A	17	
	South-west B	22	
	Cumbria	26	
	Dorset	11	

[1] All patches set as occupied [2] Patches set at 1999 occupancy status.

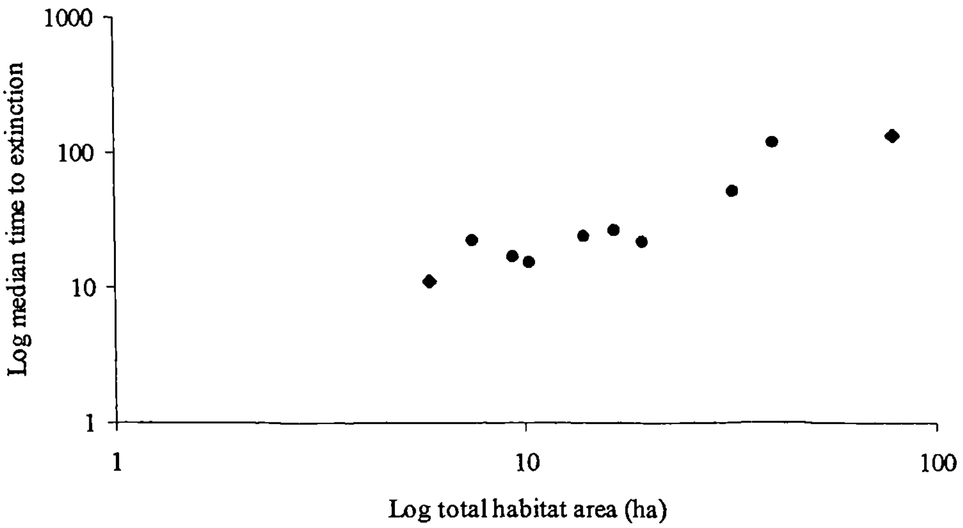


Figure 3.14 Linear relationship between total habitat area (ha) of each network (Dorset networks indicated by diamond symbol) and the median time to extinction from the IFM. Linear regression y=0.959 (total habitat area) +0.296, adjusted $R^2=0.858$. (Note that the two axes are not independently derived).

Given that many metapopulations are already extinct, and others are apparently on borrowed time, is there any opportunity to enhance the probability of persistence through habitat restoration? In contrast, how much further habitat loss would threaten one of the best networks, south-west B?

The concept of a minimum viable population (MVP) size (Soulé 1987) can be applied to metapopulations (Hanski *et al.* 1996a; Hanski 1999a). The IFM simulations can be utilised to investigate the habitat area requirements to meet the conventional MVP criteria of >95% survival for 100 years. From the IFM simulations, only the north Wales and south-west B networks would achieve this level of persistence. For the remaining networks it would be necessary to increase habitat area to achieve the same level of persistence. What increase in habitat area is required for these networks and for the best networks and what level of habitat loss would decrease persistence below this level?

With each increase in area the proportion of iterations persisting increased for those networks tested, as would be expected. The mid Wales network required an increase from 40ha to between 61 and 71ha to attain a 95% or greater probability of persistence for 100 years. A doubling of habitat area from 32ha to 65ha was required to achieve this in the south-west A network. For Cumbria, the survived network, predicted to become extinct in less than 50 years, achieved only 72% persistence with an increase in area to four times its existing size (table 3.11).

When habitat loss was simulated in the south-west B network (one of the best networks). A 25% reduction in habitat area to 87ha caused persistence to decrease to 90% survival in 100 years; when half the habitat area was destroyed only 41 iterations persisted for 100 years in the IFM simulation (table 3.12).

The relationship between increasing habitat area and % persistence for 100 years is shown in figure 3.15. A linear regression was carried out to investigate the general relationship in these networks. The data for the linear regression was arcsine transformed (for proportions) due to the sigmoid relationship, resulting in the equation $y=1.24x-10.641$, adjusted $R^2=0.887$, this is transformed back to produce the curve in figure 3.15.

Table 3.11 Changes in % persistence of iterations for 100 years with increasing habitat area in mid Wales, south-west A and Cumbria survived networks. The Spearman Rank Correlation Coefficient and *P* values are indicated.

	Persistence with % area increase								
Network	**0**	**25**	**50**	**75**	**100**	**200**	**400**	**R_S**	***P***
Mid Wales	57	85	90	99	97	-	-	0.90	<0.05
South-west A	15	50	65	85	95	-	-	1	<0.0001
Cumbria	1	5	2	10	15	26	72	0.96	<0.0001

Table 3.12 Changes in % persistence of iterations for 100 years with decreasing habitat area in south-west B survived network. The Spearman Rank Correlation Coefficient and *P* value are indicated.

	Persistence with % area decrease					
Network	**0**	**25**	**50**	**75**	**R_S**	***P***
South west B	99	90	41	2	-1	<0.0001

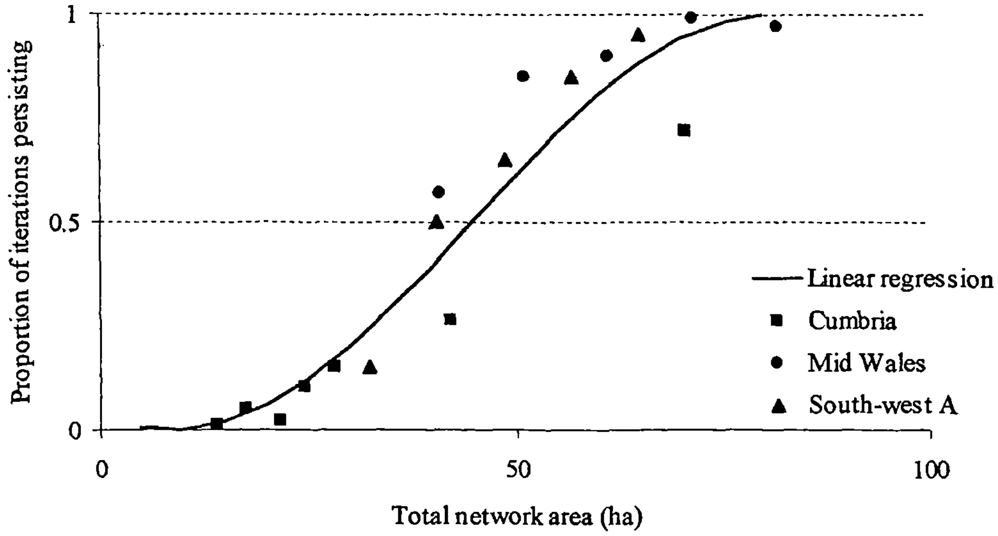


Figure 3.15 Proportion of iterations persisting for 100 years against total network area in three of the survived networks where the patch areas were increased, by increments of 25%.

When total habitat area was increased in the survived networks, an average area of 71ha was required to achieve a 95% persistence of the metapopulation over 100 years within a 4km by 4km area (4.42% of the total area). From the analysis presented here, this threshold area for persistence is possibly larger than current areas in some networks.

3.3.5 Metapopulation Capacity

The calculated metapopulation capacity for the Dorset study area and the independent networks are shown in table 3.14. The metapopulation capacity of the survived networks is greater than for the extinct networks (Mann-Whitney U test, U=2, P=0.01, $n_{survived}$=6, $n_{extinct}$=6). In a logistic regression metapopulation capacity was found to be a good predictor of network occupancy, with 92% of cases classified correctly by the model (table 3.13 and figure 3.16).

There was a positive correlation between metapopulation capacity and total network area (Spearman Rank Correlation R_S=0.853, P<0.0001, n=12), those networks with larger patches had greater metapopulation capacities. The metapopulation capacity for each network reflects the same conclusions that can be drawn from the IFM simulations. Those networks with high metapopulation capacity also persisted well in the IFM and had greater median times to extinction (figure 3.17), (Spearman Rank Correlation R_S=0.879, P=0.001, n=10 (excludes networks with median time to extinction >200 years)).

Table 3.13 Logistic regression of metapopulation capacity on occupancy in each network.

	Model if term removed			
Variable	**Effect**	**-2 Log LR**	***df***	***P***
Metapopulation Capacity	+	12.173	1	<0.001

-2 log likelihood=5.977, Goodness of Fit=5.987, Model χ^2=10.658, df=1, P<0.01.

$n_{occupied}$=6, n_{vacant}=6, 92% of cases were classified correctly by the model.

Z=-5.2371+2.5512(metapopulation capacity)

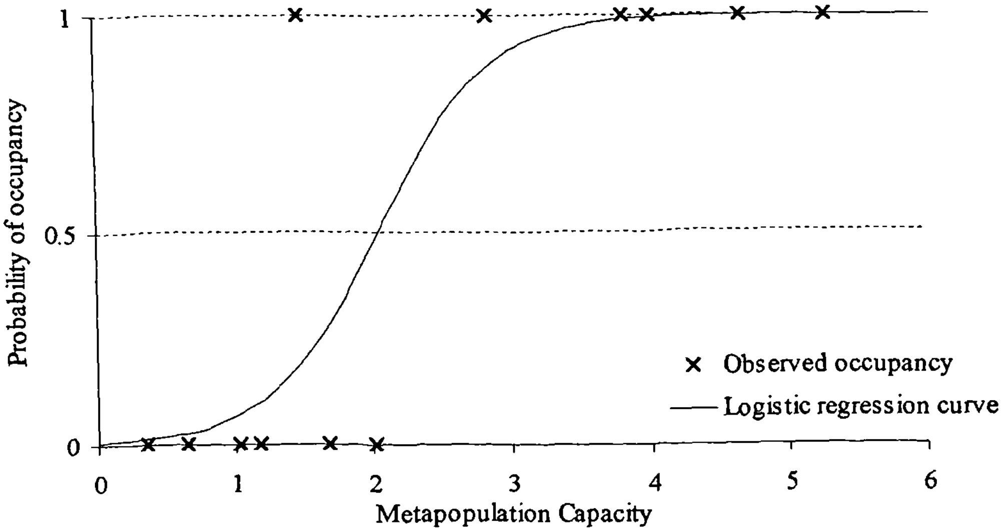


Figure 3.16 Logistic regression curve of the probability of occupancy as a function of metapopulation capacity. Probability of occupancy $=e^z/1+e^z$. Each cross represents one network, which is either occupied (1) or vacant (0).

Table 3.14 Calculated metapopulation capacities for all the independent networks and the Dorset study area.

	Network	Metapopulation Capacity (λ_M)
Survived	North Wales	5.30
	Mid Wales	3.83
	South-west A	2.84
	South-west B	4.68
	Cumbria	1.48
	Dorset	4.02
Extinct	North Wales	0.64
	Mid Wales	1.03
	South-west A	2.00
	South-west B	1.17
	Cumbria	1.68
	Dorset	0.35
	Dorset (25km)	4.93

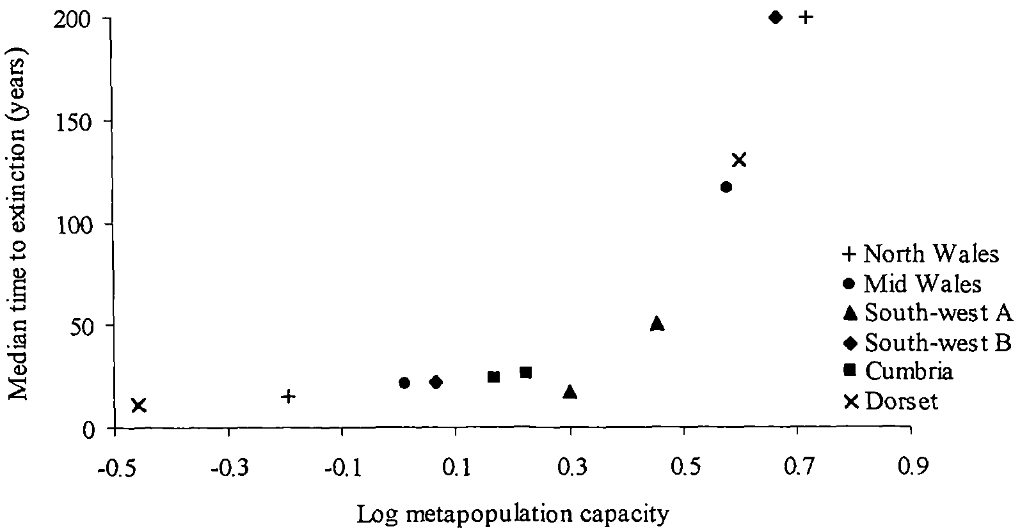


Figure 3.17 Log metapopulation capacity (λ_M) and median time to extinction for all independent networks, black symbols are the occupied networks and red symbols are the extinct networks. (NB. North Wales and south-west B median time to extinction is >200 years but shown as 200 years here).

3.4 Discussion

The distribution of *E. aurinia* across fragmented landscapes appears to be determined by the combination of patch area, isolation and quality. Such a pattern of occupancy means that a metapopulation approach may provide insight into the species persistence across the landscape. The Incidence Function Model suggests that *E. aurinia* is particularly sensitive to habitat fragmentation and requires a large amount of highly connected habitat to secure persistence in the future.

3.4.1 What factors determine occupancy?

The host plant *S. pratensis* is described as ubiquitous and found widely across the British Isles (Grime *et al.* 1988). However, in the study area it appeared to be mainly restricted to steep chalk downland, and unimproved marshy grassland on clay soils. The butterfly was recorded in fewer sites than was expected from the existing distribution records (Thomas & Webb 1984; Thomas. J. A. *et al.* 1998). It was originally thought that this could be due to the bad weather during the flight period in 1998. However, the same distribution was found in the subsequent surveys, and therefore these results reflect the actual distribution of the butterfly across the study area. Additional distribution records, where no breeding populations are found, probably represents occasional single sightings of dispersive individuals.

It is evident that other processes, rather than just the presence of host plant, are responsible for the observed distribution of the butterfly (Thomas J. A. 1984; Quinn *et al.* 1998), and the understanding of these processes is necessary for the effective conservation of the species (Lawton & Woodroffe 1991).

Habitat patch size and proximity to other patches influenced the occupancy pattern of *E. aurinia* in Dorset. The butterfly was more likely to persist in large patches that were well connected to other occupied patches. Figure 3.5 shows two interesting outlying data points, these represent patches that are relatively isolated, however they are large in area which may explain their continued persistence. Patch turnover data (figure 3.6) showed habitat area to be highly significant, with populations inhabiting the smaller patches, more likely to become extinct. Colonisations occurred most frequently in the least isolated patches. These patterns are consistent with the interpretation that *E. aurinia* has a metapopulation structure (Thomas & Kunin 1999).

Many species have been found to have a metapopulation structure, where local patch extinction is dependent on population size and isolation-dependent colonisation rates (Hanski 1999a, b). Small populations occupying small habitat patches have higher probabilities of becoming extinct because they are more vulnerable to extinction from demographic or environmental stochasticity (Diamond 1984; Schoener & Spiller 1987; Kindvall & Ahlén 1992;Thomas C. D. *et al.* 1992; Cook & Hanski 1995; Hanski *et al.* 1995b). Per capita emigration rates in small populations are often higher in small patches than in larger patches (Hill *et al.* 1996; Kussaari *et al.* 1996; Sutcliffe *et al.* 1997a; Kindvall 1999; Hanski *et al.* 2000; Petit *et al.* 2001). As a result, the loss of individuals through emigration increases the extinction risk (Thomas C. D. *et al.* 1998a; Hanski *et al.* 2000). Small populations are also susceptible to the Allee effect, such as reduced growth rate at low densities due to fewer mating opportunities (Kindvall *et al.* 1998; Kuussaari *et al.* 1998), or to increased rates of inbreeding which results in reduced fecundity and increased mortality (Saccheri *et al.* 1998).

When patches become extinct, the most isolated have the lowest probability of re-colonisation, as the number of immigrants decreases with increasing distance (Harrison *et al.* 1988; Kindvall & Ahlén 1992; Thomas & Harrison 1992; Thomas C. D. *et al.* 1992; Thomas & Jones 1993; Hanski *et al.* 1994; Hill *et al.* 1996). Isolated patches, if occupied, are less likely to receive immigrants and therefore be 'rescued' from imminent extinction (Brown & Kodric-Brown 1977).

In addition to the spatial properties of a patch discussed above, the quality of that habitat is vital for *E. aurinia*. Patches with a high density of host plant (incorporated with patch size in the 'resource area' term) and tall vegetation, had the highest probabilities of being occupied. Other studies have shown that female *E. aurinia* prefer to breed in areas of longer vegetation where the host plants are abundant and the leaves are larger for egg laying (Porter 1983; Warren 1994a; Lewis & Hurford 1997; Hobson 1997). Specific habitat quality requirements necessary to maintain persistence have been demonstrated in other butterfly studies. For example, *Aricia agestis* requires lush host plants for egg laying (Bourn & Thomas 1993; Wilson 1999). *Maculinea arion* depends on a specific host plant and on the ant *Myrmica sabuleti* (Thomas J. A.

1995b). *Mellicta athalia* requires early successional habitats in which to breed (Warren 1987), as does *Plebejus argus* (Thomas C. D. 1985a, 1985b & 1991). The restricted distribution of *Erynnis tages*, despite the widespread nature of its host plant, was explained by the need of the butterfly for ungrazed oviposition sites with plentiful bare ground to provide a warm microclimate (Gutiérrez *et al.* 1999). Cowley *et al.* (2000) demonstrated that habitat association is an effective predictor of species distributions.

Many metapopulation studies have been criticised because they focus attention on area and isolation effects, ignoring resource quality within patches (Thomas J. A. *et al.* 2001). I have shown here, that habitat area, connectivity and quality are all important for persistence in *E. aurinia*, and a combination of all factors should be incorporated in metapopulation models. However, this is difficult to achieve and it was not possible to include habitat quality within the Incidence Function Model. Moilanen & Hanski (1998) showed that the additional complexity of adding habitat quality did not necessarily improve the predictive power of the metapopulation model, whilst involving a great deal more effort. The area and spatial distribution of suitable habitat patches are much quicker and easier to collect and have been widely demonstrated to be good predictors of metapopulation persistence. The absence of habitat quality parameters may not be too critical, providing that suitable habitat has been defined accurately. Despite this deficiency, the IFM was considered to be a useful tool in this study and care was taken to ensure that only those habitats suitable for *E. aurinia* were considered in the model, by removing those patches with vegetation height <4cm. Figure 3.5(c) shows that there is little or no relationship between vegetation height and occupancy above this threshold height.

Evidence that patch area and isolation effects (as discussed above) are in operation within the Dorset study area suggested that *E. aurinia* exhibits metapopulation dynamics (Warren 1994a; Lewis & Hurford 1997; Munguira *et al.* 1997). A metapopulation approach to modelling the system should therefore, provide insight into the persistence of the species in a fragmented landscape (Harrison 1994; Hanski 1999a,b).

3.4.2 Incidence Function Model – Dorset

The Incidence Function Model predicted the fraction of patches occupied in the whole of the study area to be approximately 16 to 20%. This is slightly higher than the observed occupancy and may be explained by the presence of large areas of habitat which the model perceives to be suitable and therefore should be occupied by the butterfly, but in reality are vacant. These areas may not be occupied because the butterfly has not colonised them yet or that current (or past) management has been unsuitable.

One proposed advantage of the IFM is the possibility of applying rigorously tested parameters, generated from a well-studied butterfly species, to simulate patch occupancy when data is unknown for a rare or endangered congeneric species (Wahlberg *et al.* 1996). However, this approach failed in the present study. When published parameters from *M. cinxia* (Hanski *et al.* 1996b) and *E. aurinia* (Wahlberg 2000), which occur in quite different habitats in Finland, were simulated in the Dorset network, the pattern of patch occupancy was dramatically different.

These differences may be explained by the differences in the parameters. The parameters related to extinction (x and e) produce higher extinction rates for *E. aurinia* than for *M. cinxia* and *E. aurinia* in Finland. Parameter x describes the strength of environmental stochasticity as a function of patch size: when x is small (<1), even large populations in large patches have a substantial risk of extinction (Hanski 1994a). This appears to be the case in Dorset, where *E. aurinia* is apparently more vulnerable to environmental stochasticity. Parameter x for the other two cases is larger, resulting in a lower risk of extinction. Parameter e describes the probability of extinction per unit time in a patch of unit size. *Euphydryas aurinia* in Dorset has an increased risk of extinction due to the large value of e compared to the others.

The parameters concerned with colonisation also differ. Parameter y determines how fast the colonisation probability approaches unity with an increasing number of immigrants. For *E. aurinia* in Dorset the value is slightly larger in comparison to the others and therefore isolation has a greater effect on the colonisation ability. *Melitae cinxia* and *E. aurinia* (Finland) are less affected by isolation, which is reflected in the higher proportion of patches occupied. Alpha (α) describes the colonisation ability of the species, i.e. how fast the number of migrants from one patch declines with increasing distance. The value of alpha in the other two cases modelled allows for greater dispersal, which again explains the increased proportion of occupied patches using the *M. cinxia* and *E. aurinia* (Finland) parameter sets in the Dorset network.

It is interesting that despite the similarities in the species, the parameters produce widely different simulation results. This may be due to different habitats that the species occupy. *Euphydryas aurinia* in Finland occurs in a highly dynamic system of meadows and woodland clearcuts. The butterfly regularly moves between these habitats, which become overgrown and unsuitable over short periods of time (Wahlberg 2000). These results suggest that model parameters, generated for one butterfly, cannot be applied safely to a network occupied by a different species or to the same species when the habitats are radically different.

The main message is that *E. aurinia* (Dorset) requires much larger habitat patches than for the other well-studied cases. These results suggest that Wahlberg *et al.*'s (1996) conclusion, that parameter sets derived from relatively common species can be applied to rarer ones, is premature. In the Dorset system, *E. aurinia* (for some reason) is experiencing a higher level of stochasticity and a lower rate of population increase than *M. cinxia* (in Finland), which increases the risk of local extinction (Foley 1997). This translates into a requirement for larger habitat patches.

3.4.3 Application of the IFM to the independent 4km networks

When the survived and extinct networks were compared, area and isolation effects were found to be significant. The survived networks tended to contain significantly greater number of patches; larger total area, larger mean patch area and patches were less isolated than in the extinct networks. The Incidence Function Model was applied to these networks.

The IFM simulations closely predicted the real situations in the independent networks. All the survived networks persisted better than the extinct networks, with the exception of Cumbria. However this was expected, as only a few small patches are present in this small and isolated network. The networks that in reality are extinct were predicted to become so in the model. When the median times to extinction are compared, even starting with the unrealistic situation of full patch occupancy, many of the networks are predicted to become extinct rapidly.

Total network area was found to be both the simplest and most accurate predictor of network occupancy. However, this conclusion is based on only 12 systems. Median time to extinction in the simulations was also positively correlated with total habitat area, but less so with connectivity, resource area and patch number. Hanski *et al.* (1995a) investigated the network-level effects of average patch area and isolation. Hanski *et al.* divided their study area into 4km^2 'semi-independent networks' and found that the fraction of occupied patches increased with increasing patch size and increasing number of patches in the squares.

The IFM appears to be a useful conservation tool. It suggests that habitat fragmentation and loss is likely to be a major cause of decline throughout much of the species' range and reveals the possible worry that a number of surviving systems are living on borrowed time.

Some of the network simulations may be exhibiting an 'extinction debt' (Tilman *et al.* 1994; Hanski 1994b; Tilman & Lehman 1997), where metapopulations occur in habitat patch networks insufficient for long-term persistence. A time lag occurs between habitat change and the resulting extinctions and, in the worst case, the new equilibrium will be metapopulation extinction. The model results have shown that some of the survived networks may be exhibiting such a phenomenon (figure 3.13). For example, the networks in mid Wales and south-west A, are predicted to persist, but the simulations for the next 200 years show that they are susceptible to extinction even if no further habitat loss occurs.

Hanski *et al.* (1996b) used the IFM to model a 50% loss of habitat area for *M. cinxia* over a 20 year period. This resulted in a network inadequate for long-term persistence, but ultimate extinction of the metapopulation was predicted to take many years. Hanski (2000) also modelled a hypothetical species inhabiting old-growth forest in Finland. With no further change in forest structure, extinction occurred within 100 years representing an extinction debt. A time-lag between deforestation and extinction has been proposed as an explanation as to why few endemic bird species have become extinct from rainforests in South America following the destruction of nearly 90% of the habitat (Brooks & Balmford 1996).

Extinction debt may be occurring in isolated remnants of scrub habitat in California, where plant species diversity decreased with time since isolation (Soulé *et al.* 1988, 1992). Delayed extinctions have also been predicted for primates in African forest fragments (Cowlishaw 1999). Species-area curves, based on the current extent of forest habitat, predict extinctions to have occurred due to deforestation in the last 50 years if extinctions occur simultaneously with habitat loss. None of these extinctions have yet taken place and the consequences of any further habitat loss may be dramatic. Gonzalez (2000) found evidence of extinction debt occurring in bryophyte-based micro-landscapes after fragmentation. There was a delay in loss of species richness of six months in the small patches and eight months in the larger patches.

Petit & Burel (1998) proposed the existence of a time-lag between landscape change and response in the ground beetle (*Abax parallelepipedus*), as its current distribution was significantly related to the hedgerow network 50 years ago, rather than the present one. This does not necessarily indicate extinction debt but highlights the slow response of species to habitat destruction and isolation. We must not be fooled into thinking that extinctions will stop if there is no further habitat loss. It is probable that some metapopulations are only persisting because they have not yet had time to reach extinction due to the time lag (Hanski 1999a).

In the independent networks, total area appears to be the most useful predictor of occupancy. Having established this, the probability of persistence can be enhanced through increasing habitat area. If the assumption is made that increasing the patch area is equivalent to increasing patch quality, when they both increase carrying capacity by the same amount, the simulation results illustrate the potentially beneficial consequences of metapopulation-scale habitat management. Given that even the surviving networks are in decline, it is clear that the total habitat and its quality must be increased if persistence is to be attained in the future.

By modelling increases in network area and testing persistence of *E. aurinia* within such modelled landscapes, it is possible to estimate the threshold network area to achieve a 95% probability of persistence for 100 years. This is estimated to be at least

71ha, within a 4km by 4km area. The maximum habitat area in any network was 116ha, so even the 'most persistent' networks could easily come under threat with further habitat loss.

A complication arises if the Dorset system is not at equilibrium, where extinction and colonisation events are unbalanced. The figure of colonisation and extinction events (figure 3.6), shows that ten extinctions and four colonisation events have occurred since 1981, suggesting that Dorset may not be at equilibrium. By definition, the IFM assumes equilibrium (Moilanen 2000). If Dorset is not at equilibrium, but still declining, the IFM will give an optimistic picture (i.e. prediction of colonisation rates that are too high and of extinction rates that are too low). The problem was minimised by parameterising in a sub-area of Dorset, where the butterfly has declined less. However this assumption will affect the modelling result predictions when applied to other networks. If Dorset is not at equilibrium and still declining the estimated network size necessary for long-term persistence is actually an underestimate. The real threshold network area is probably in excess of 71ha. Given the maximum observed network area of 116ha, this is very worrying.

3.4.4 Metapopulation capacity

Metapopulation capacity (Hanski & Ovaskainen 2000) appears to be a useful measure of landscape structure allowing networks to be ranked by their relative ability to support a metapopulation. Metapopulation capacity was closely correlated with habitat area and the time to extinction. Together, these measures reinforce the importance of conserving all habitat patches in habitat networks. The calculation of metapopulation capacity does not require patch turnover data; the capacity of a landscape to support a metapopulation is calculated using the amount of good quality habitat and its spatial configuration. Therefore, it is not necessary to make as many assumptions about species dynamics if the spatial arrangement, quality and quantity of patches are known, in order to rank the suitability of different landscapes. Therefore, this approach may be a more applicable method for use by conservation managers as fewer data are required. However, user-friendly software is not yet available to do this, and for now, a conservation manager may be better to stick with simpler measures, particularly total habitat area.

3.5 Conclusions

The survival of *E. aurinia* metapopulations in fragmented landscapes is dependent on patch size and the spatial arrangement and quality of patches. The focus must be towards the metapopulation-scale. Habitat management needs to be targeted at maintaining and improving the quality of habitat patches throughout habitat networks. Further fragmentation should be minimised, as this would reduce patch size and increase the isolation of populations.

The Incidence Function Model is a useful predictive tool for directing conservation action. Simulations suggest that few networks are sufficiently large to maintain populations in the long term and many occupied networks apparently have substantial probabilities of extinction. Conservation action must be directed at securing the largest of these networks so as to eliminate further risk from fragmentation. The long-term aim must be to increase the total network area to greater than 71ha, and probably 100ha, necessary for 95% persistence for 100 years. Options are to protect existing habitat and potentially to restore habitat that is currently available.

The IFM has proved to be useful in predicting the fate of metapopulations within fragmented landscapes. However, caution must be taken when applying parameters generated for one species to another. The likelihood that the Dorset system is not at equilibrium means that the threshold network areas presented here, may actually be an underestimate.

Re-introductions to already extinct networks should not be contemplated when conservation action in surviving networks is so much more important. In any case, re-introductions should only be contemplated once the patch network has been restored.

4.0 PARASITOIDS AND *EUPHYDRYAS AURINIA*

4.1 Introduction

Parasitoid larvae feed on the bodies of other arthropods, usually insects, with the feeding and larval development resulting in the death of the host (Godfray 1994). Most insect species are attacked on average, by five to six parasitoids (Hochberg & Hawkins 1994) with some occasionally being host to 20 or more (Jones *et al.* 1994) and therefore can have a major impact on the population dynamics of their host (Berryman 1996). Ecological interest in parasitoids was initiated because they were found to be important in controlling pest species (Hassell 1980; Biever 1992). The scope of these studies eventually broadened to parasitoid behaviour, ecology and evolution (Godfray 1994; Hawkins & Sheehan 1994; Godfray & Shimada 1999).

Much research has concentrated on how spatial patchiness affects the population dynamics of the parasitoid and host. Modelling and empirical evidence appears to suggest that parasitoids can have a regulatory effect on their host dynamics (Hassell 1982; Jones *et al.* 1993; May 1994; Hassell 2000). But this has been at a very local scale, for example using host plants as patches, where complete mixing of the dispersing individuals is assumed (Hassell 2000). Rarely has the scale of host-parasitoid dynamics been investigated at a metapopulation scale, where distances involved are greater relative to the dispersal rates of the organisms. At this spatial scale, effects such as habitat fragmentation may promote less stable dynamics (Kareiva 1987, Roland & Taylor 1997). Studies on *Cotesia melitaearum* attacking *Melitaea cinxia* suggest, that the parasitoid has a strong impact on the host, which often leads to the extinction of local populations of the host (Lei & Hanski 1997; Lei 1997).

Metapopulation theory has been utilised to explain the distribution and decline of butterflies in increasingly fragmented landscapes. Parasitoids that are specialists on such species will therefore also have a metapopulation structure, as the host acts as a 'patch' of suitable habitat. Their parasitoids are probably even rarer and more endangered, than their hosts (Thomas & Elmes 1993; Lei 1997), but little is known about this (Shaw & Fitton 1989; Shaw 1990).

Past research has been undertaken on the parasitoids attacking Melitaeinae butterflies. Stamp (1981a,b, 1982a,b) studied the behavioural interactions between *Euphydryas phaeton* and its larval parasitoid *Cotesia* (=*Apanteles*) *euphydryidis*. She found that high host densities were preferentially used by parasitoids, with the lower host densities escaping the attention of the dispersing parasitoids. Moore (1989a,b) investigated dynamics between *Euphydryas editha* and the larval parasitoid *Cotesia koebelei*. Post-diapause larval mortality was very variable and was positively correlated with parasitism rates.

Much research has been conducted on the parasitoid complex attacking *M. cinxia* in Finland. Ten species of parasitoid (primary parasitoids and hyperparasitoids) were found to be associated with the host butterfly (Lei *et al.* 1997; Lei & Hanski 1998), with *C. melitaearum* having the most impact on the host dynamics (Lei & Hanski 1997). The parasitoid was found to have a metapopulation structure similar to its host, with the incidence of the parasitoid increasing with increasing host population size, patch size, and with decreasing isolation (Lei & Hanski 1997). The parasitoid was absent from the smallest host populations. Their results suggested that the parasitoid contributes to, and may cause the extinction of local host populations, particularly if hyperparasitoids were at low densities or absent. van Nouhuys & Tay (2001) suggested that the parasitoid appears to be at a greater risk from extinction than its host and therefore of greater conservation concern. They found 59% of parasitoid populations became extinct with the probability of extinction declining with host population size.

The foraging behaviour and movement patterns of *C. melitaearum* were analysed by Lei & Camara (1999), who found that parasitoids were aggregated in high density host patches. They suggested that immediate dispersal of attacked hosts and high mobility of the parasitoid, combined to produced high parasitism rates and decreased the local stability of the host.

Porter (1979, 1981, 1983 & 1984) researched the parasitoids of *Euphydryas aurinia* at one small site in Oxfordshire. At this site, *E. aurinia* was attacked by *C. bignellii*, which has three generations per host generation. Adult parasitoids emerge from third instar hosts in late August, late fourth instar hosts in March, where the parasitoid larva overwinters within its host, and from final instar hosts in June. The parasitoid larva emerges as its host moults from one instar, when the host's cuticle is at its weakest.

The larva spins a white silken cocoon, usually next to the dead host, emerging after approximately four weeks. Adults are then ideally placed to re-infect remaining larvae in the web.

Populations of *E. aurinia* are well known for their great variation in abundance, which has been attributed to larval parasitism (Ford & Ford 1930; Porter 1981). Porter (1983) suggested that rates of mortality caused by the parasitoid might depend on spring weather conditions that affect the relative development rates of the host and parasitoid. In cool but sunny weather conditions larvae thermoregulate to temperatures >30°C (Porter 1982), such that the host is able to develop faster and reach pupation before the adult parasitoids emerge, resulting in a low parasitism rate (7.7% in 1979). When spring conditions are cloudy, larval development is synchronised with parasitoid emergence and thought to result in an increased incidence of parasitism (74.5% in 1980). Porter's work was restricted to one small population of *E. aurinia* and concentrated on the biology of two parasitoid species. The spatial dynamics of the host and parasitoid were not explored.

This study attempts to establish the incidence of parasitism at a spatial scale greater than one site, by investigating four populations of *E. aurinia* in Dorset. The incidence of *C. bignellii* only was investigated, as this species is specific to *E. aurinia* and probably has the most important impact on the hosts population dynamics, similar to that found in *M. cinxia-C. melitaearum* systems, because the parasitoid has three generations per host generation. Other parasitoid species appear to be generalists with limited impact on *E. aurinia* population dynamics. The aims were to investigate incidence of parasitism, changes in adult and parasitoid abundance and spatial differences and patterns. Butterfly abundance was very low over the duration of this study resulting in small sample sizes; therefore the conclusions are tentative. However, this preliminary work highlights some interesting areas for further investigation.

4.2 Methods

In order to detect the presence of parasitoids at each site, a sample of larvae was collected from every larval web that was encountered. Post-diapause fourth instar larvae were collected from four sites in the Dorset study area in 1999 and 2000, at Giant Hill (ST665018), Lydlinch (ST735134), Rooksmoor (ST739109) and Deadmoor (ST751110). These were chosen because they were the largest *E. aurinia* populations within the Dorset study area. Larval web searches (Thomas & Simcox 1982; Lewis & Hurford 1997) had been carried out in the previous August/September, which aided the location of larval groups. All larval groups that were found were sampled, with fifteen larvae removed randomly from each group using entomological forceps, which had no detrimental effect on the larvae, and placed in plastic boxes containing leaves of the larval host plant *Succisa pratensis*.

The larvae were reared in poly-tunnels at the University Experimental Gardens. Each group of larvae was reared on potted *S. pratensis* with each pot containing three plants. Caging was erected around each plant using two plastic loops that clipped onto the sides of the plant pot to form a frame. A stocking (10 denier 'natural') was placed over the pot to form a cage around the plant. This enclosed the larvae and prevented them from escaping whilst allowing natural light conditions and the free flow of air.

The larvae were checked daily for host plant supply and signs of parasitism. Any individuals that appeared to be sick or not eating were removed and placed singly in plastic containers. Individuals with characteristic *Cotesia* parasitoid cocoons adjacent to the host were removed along with the parasitoid cocoons and placed in plastic containers. Parasitoids were reared to emergence in constant temperature incubators at 15°C. Samples were retained for identification. All remaining larvae were returned to their original habitat patches when they had reached the final instar or entered the pupal stage.

The collection, rearing and release were undertaken in accordance with English Nature licence agreements, (reference numbers 19990323 and 20000341).

4.3 Results

4.3.1 General observations

Parasitoids were only found in larvae collected from Giant Hill and Lydlinch. No parasitoids were found at Deadmoor or Rooksmoor in either sampling years. The number of webs found increased at Giant Hill and Lydlinch between 1999 and 2000, an increase in abundance which is reflected in the adult counts (estimated population at peak at Giant Hill increased from 500 to 535 and at Lydlinch from 168 to 358 between 1999 and 2000). This increase resulted in a slight decrease in the observed percentage parasitism rate (percentage of webs with parasitoids detected). Of the 15 larvae sampled per web, the mean number of larvae parasitised per web was 1.43 (± 0.29) at Giant Hill and 1.8 (± 0.37) at Lydlinch in 1999 with a slight increase detected in 2000 to 2.17 (± 0.65) at Giant Hill and 2.62 (± 0.42) at Lydlinch. These increases were not statistically significant. The number of cocoons found per larva was found to range between 1 and 5 in 1999, with a mean of 2.40 (± 0.34) at Giant Hill and 3 (± 0.44) at Lydlinch. In 2000 the number of cocoons per larva ranged between 1 and 12 with a mean of 4.38 (± 0.75) at Giant Hill and 3.48 (± 0.34) at Lydlinch (table 4.1). These differences were not statistically significant.

The change in adult butterfly abundance at the four sites between 1998 and 2000 is shown in figure 4.1. Parasitoids may have influenced this pattern. Giant Hill appears to have remained constant during the three years. In contrast Lydlinch, Deadmoor and Rooksmoor appear to have increased in abundance.

Table 4.1 Summary of parasitoid results from larvae collected at Giant Hill and Lydlinch in 1999 and 2000.

1999	**Number of webs sampled**	**Number of webs with parasitoids**	**% web parasitism rate**	**Mean number of larvae parasitised per sample**	**Mean % parasitism rate per web**	**Mean number of cocoons per larva**
Giant Hill	26	7	26.92	1.43 (± 0.29)	9.52 (± 1.98)	2.40 (± 0.34)
Lydlinch	8	5	62.50	1.8 (± 0.37)	12.89 (± 2.15)	3 (± 0.44)
2000						
Giant Hill	29	6	20.69	2.17 (± 0.65)	14.44 (± 4.36)	4.38 (± 0.75)
Lydlinch	14	8	57.14	2.62 (± 0.42)	17.5 (± 2.79)	3.48 (± 0.34)

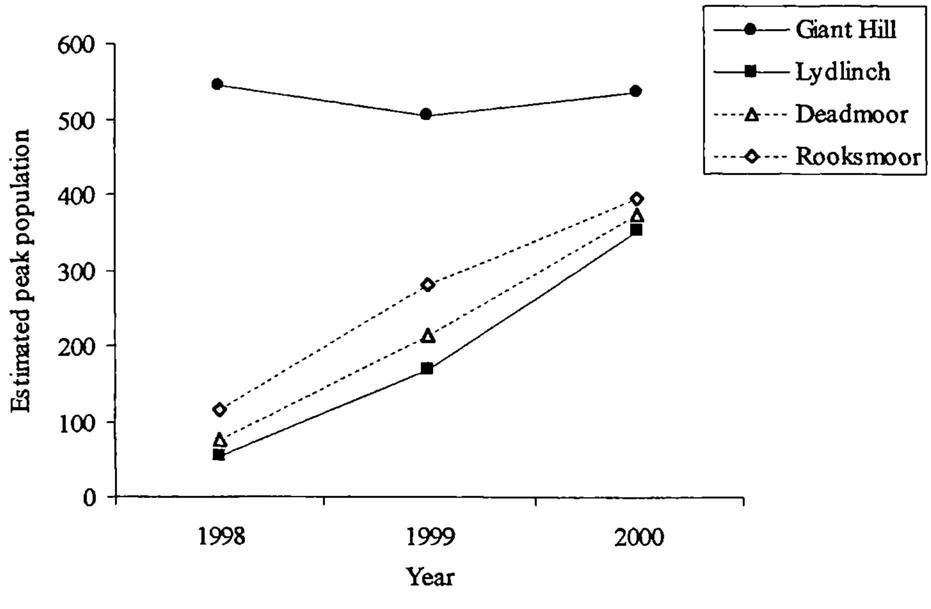


Figure 4.1 Change in estimated adult peak population (see 3.2.1.2 for method) between 1998 and 2000 for the butterfly. Sites without parasitoids are shown with dashed lines.

4.3.2 Observations on the small-scale distribution of host and parasitoid

At Lydlinch in 1999 only eight larval groups were found during a thorough search of the whole site. The majority of webs were found in the northern part of the site (area D), with one larval web found in the southern part (area A). A distance of 700m separates these two areas, see figure 4.2. *Cotesia bignellii* parasitoids appeared to be restricted to area D, with six of the larval groups parasitised. No parasitoids were found in area A, although only one web was found (Figure 4.3a).

In 2000 the number of larval groups found at Lydlinch increased to 14. In area A, four webs were present, with no evidence of parasitoids. In area D eight larval webs were present, of which seven were parasitised. (Fisher's exact test, $df=1, P=0.01$). Webs were found in two new areas. One web in area C which was 75m away from area D and was found to have been parasitised and a second web in area B which was 200m to the west of area D, but no evidence of parasitoid attack was found (figure 4.3b).

The sample sizes are unfortunately small, reflecting the very small size of the host population. Nonetheless, they suggest that the parasitoid may be patchily distributed at Lydlinch, with the butterfly increasing in abundance in sub-sites where the parasitoid does not occur, such as area A relative to area D, where parasitoids were found to infect most of larval webs.

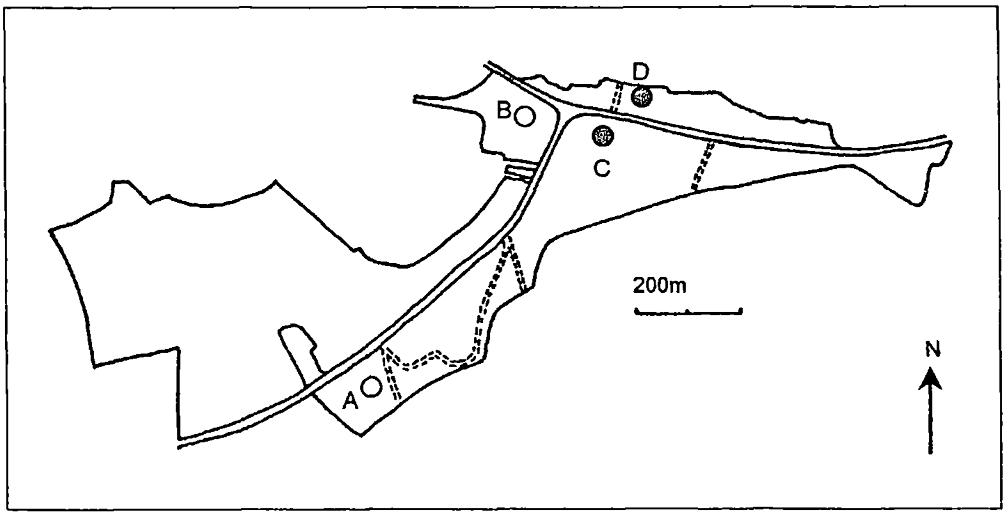
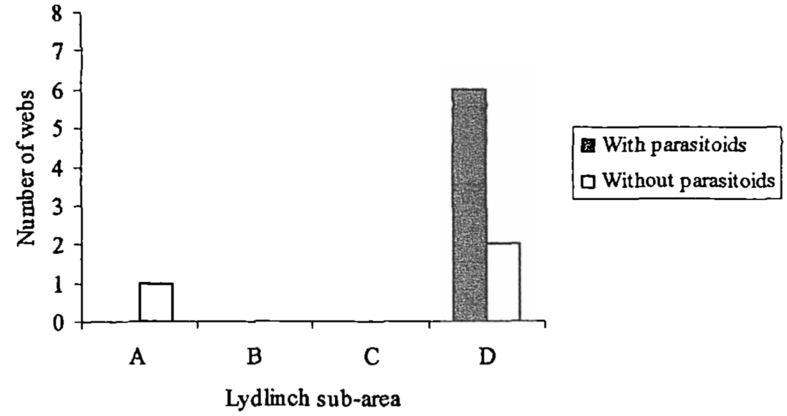


Figure 4.2 Map of Lydlinch showing location of sub-areas where larval webs were sampled (A to D). Shaded circles are sites with parasitoids and un-shaded circles are sites without parasitoids.

(a) 1999



(b) 2000

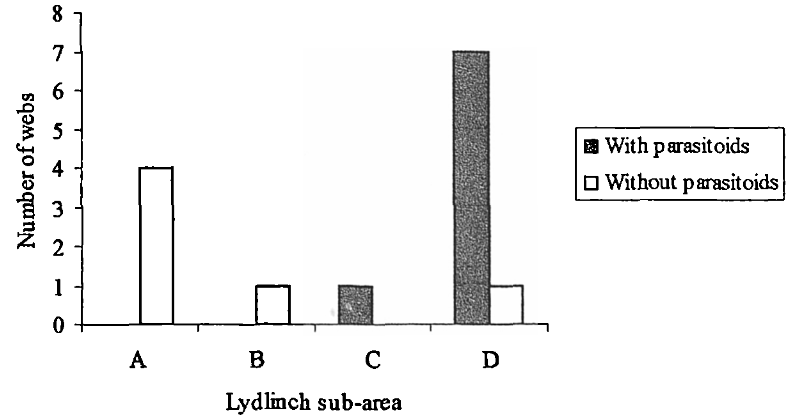


Figure 4.3 Number of larval webs present in each area (coded A to D) at Lydlinch in 1999 and 2000, webs with parasitoids are shaded and webs without are un-shaded.

4.4 Discussion and conclusion

Parasitoids were only found in larvae at two of the four sites investigated in Dorset. The population size of *E. aurinia* was very low at Lydlinch, Rooksmoor and Deadmoor during this study. The absence of parasitoids at Rooksmoor and Deadmoor suggest that the local population of parasitoids at these sites may have been lost, at some point in the past, perhaps when the population crashed to low adult numbers prior to the start of this study. Lei & Hanski (1997) found that the decline in *C. melitaearum* was associated with a decline in the number of host populations. Even if the host remained extant, parasitoid extinction occurred either as a result of hyperparasitism or for stochastic reasons. This may have occurred at Rooksmoor and Deadmoor.

It was hoped that a pattern could be found between *E. aurinia* abundance and the incidence of parasitoids. From the changes in adult populations in figure 4.1, Giant Hill has generally remained constant, which is reflected in the similar number of webs found and number of webs parasitised in both years. In contrast the population size at Lydlinch increased at a similar rate to the other wet grassland sites of Deadmoor and Rooksmoor. There are two possible explanations. Either the parasitoid has no effect on population size or the presence of parasitoids has suppressed the population increase at Lydlinch and that the observed increase at Lydlinch, is not as great as it would otherwise have been.

The distribution of larval webs and parasitoids at Lydlinch suggest that the host and parasitoid have a patchy distribution at a local scale. The structure at Lydlinch suggests, that larval groups of *E. aurinia* are perhaps able to 'escape' parasitoid attack in some areas and therefore increase in abundance in comparison to those areas where parasitoids are present (Kareiva 1987; Roland & Taylor 1997). The patchy nature of Lydlinch may explain the increase in adult numbers; the increase in the butterfly population was largely in the sub-area that lacked parasitoids. These locations may exist because of the limited dispersal ability of the parasitoid. No data exists on the dispersal ability of *C. bignellii*, but work by Lei & Camara (1999) on the similar parasitoid *C. melitaearum* attacking *M. cinxia*, found that the maximum distance moved by marked wasps was 70m, with recolonisation of host patches documented up to 200m away from a source population. The distance between the two sites at

Lydlinch was approximately 500m, probably greater than the normal dispersal ability of *C. bignellii*, if it is similar to *C. melitaearum*. In addition, adult parasitoids tend to remain in large host groups where more larvae are available (Stamp 1981b; Lei & Camara 1999) when searching for hosts. Adult parasitoids are less likely to move away from such an abundant resource and are less likely to find small host groups if they disperse. As a result, in areas where the butterfly larvae are not attacked by parasitoids, the population increase is probably greater due to the absence of one factor that contributes to its mortality.

In contrast the population of *E. aurinia* at Giant Hill is distributed across the hillside as one continuous population. It is likely that there is a much greater degree of free mixing between host and parasitoid at this site, as no spatial sub-division appears to exist. It is possible that the parasitoid is having a density-dependent regulatory effect at this site, demonstrated by the relatively constant population size between 1998 and 2000 in comparison to that at Lydlinch.

With three generations of parasitoid per host generation, the parasitoid can potentially reduce a population to very low numbers. Relatively low parasitism rates in the generation studied may lead to higher rates later because parasitoids may re-infect other larvae in the same group. For example, a web may contain 50 host larvae with a 14% parasitism rate. If an average of three parasitoids emerge from each host, producing 21 adult parasitoids, then a large proportion of the remaining hosts maybe attacked, with the population severely depleted. In the similar species, *C. melitaearum* Lei (1997) found that adult females were able to deplete a host group in a very short time, with handling time never exceeding ten seconds. One female parasitoid was able to oviposit in 40 sixth instar larvae in one group in approximately 120 minutes.

The absence of *C. bignellii* from two populations in Dorset and its patchy distribution at Lydlinch suggest that the parasitoid is rarer than its host, *E. aurinia*. Parasitoids possibly help to explain the variable dynamics of *E. aurinia* and its requirements for large habitat networks.

5.0 HABITAT RESTORATION FOR *EUPHYDRYAS AURINIA*

5.1 Introduction

Habitat restoration seeks to reinstate, renew or replace some former ecological state that may be considered preferable (Anderson 1995). The need for habitat restoration is justified by the documented losses and fragmentation of many terrestrial habitats through human activity (Groombridge 1992; Saunders *et al.* 1991; Asher *et al.* 2001). With the reduction in habitat size and increasing isolation from remnant habitat elsewhere, species occupying these habitats will become increasingly prone to extinction, due to reduced population sizes, genetic effects and increased emigration. Habitat restoration is one approach to improve the prospects for endangered species (Fahrig 1997).

Habitat restoration is seen as a potential tool to mitigate the effects of habitat destruction and fragmentation (Anderson 1995). Many studies of species persistence in fragmented landscapes (chapter three, Kindvall & Ahlén 1992; Hill *et al.* 1996; Zschokke *et al.* 2000) have demonstrated the need for large areas of suitable habitat. Habitat restoration offers the potential to increase the size of existing patches of habitat (Huxel & Hastings 1999), thus increasing the patch carrying capacity, with a larger population size being less vulnerable to extinction (Diamond 1984; Thomas C. D. *et al.* 1992). Restoration also has the potential to create new patches to reduce the detrimental effects of isolation, by reducing distances between extant populations and thereby increase the probability of re-colonisation (Dobson *et al.* 1999). A useful option for conservation is the restoration of neglected and unsuitable habitat and the creation of new habitat that increases area and decreases isolation. Immigration will be the key to successful restoration attempts; the priority must be given to restoring habitat within the colonisation distance of extant populations (Huxel & Hastings 1999).

Chapter three introduced the concept of extinction debt (Tilman *et al.* 1994) and provided modelled evidence of its existence. In the recent past, landscape change has occurred at such a rapid rate that many metapopulations will be far from equilibrium. In many cases, such as *E. aurinia*, many current patch networks are likely to be too small and fragmented to support a viable metapopulation, and will eventually become extinct unless habitat loss is halted and most importantly reversed (Hanski 1999a). If protection is limited to the currently occupied habitat, then in many cases this will fail. For the long-term survival of many species it is necessary to begin to increase and expand the amount of suitable habitat through restoration (Dobson *et al.* 1997; Huxel & Hastings 1999) as well as maintain existing good quality habitat (as demonstrated in chapter three).

Habitat restoration is usually attempted when a species is to be re-introduced to an area where it has been extirpated. Examples include the successful re-introduction of *Maculinea arion* to suitably restored grassland habitat (Thomas J. A. *et al.* 1989; Thomas J. A. 1995b) and the on-going work to meet the habitat requirements for the re-introduction of *Lycaena dispar* to fen habitat (Pullin *et al.* 1995; Pullin 1996, 1997). Or when only a few remnant populations remain (Marttila *et al.* 1997; Marttila *et al.* 2000; O'Dwyer & Attiwill 2000). Restoration ecology has developed mainly through this kind of reactive conservation work. Perhaps the use of restoration could be considered in conservation programs at an earlier stage, alongside good habitat management (Dobson *et al.* 1997) and on a large spatial scale (Simberloff *et al.* 1999), if it is to be cost-effective.

Euphydryas aurinia is declining rapidly, and the situation is still precarious in areas where the butterfly remains, with some and perhaps most networks predicted to become extinct in less than 100 years. For the long-term persistence of *E. aurinia*, this study has shown that networks of habitat must be large (exceed at least 71ha), be well connected to other populations of the butterfly and be managed to produce good quality habitat (see chapter three). The modelling presented in chapter three predicts that many networks have insufficient areas of good quality habitat to maintain the species in the long-term. Therefore conservation action is required to initiate the restoration of neglected and inappropriately managed habitat and agriculturally improved grasslands, in particular those areas surrounding and adjacent to existing populations (Huxel & Hastings 1999).

The extent of grassland habitat has markedly declined in Britain with a 97% loss of lowland flower-rich grassland and 80% loss of chalk and limestone grassland since the 1940's (Asher *et al.* 2001). In England and Wales the current extent of wet grassland of high conservation value, is estimated to be between 9000 and 17500ha (Blackstock *et al.* 1999). Including the estimates for calcicolous, neutral and acidic grassland, this estimate only represents one to two percent of the cover of permanent lowland grassland in England and Wales (Blackstock *et al.* 1999). The potential for good quality habitat restoration remains. A recent study by Hobson *et al.* (2001) has shown that 74% of sites with *E. aurinia* records between 1990 and 1998, but extinct at present, are in an unfavourable condition. 37% of sites are over-managed, 36% are under-managed or not managed at all, and 1% has been lost through improvement. There is an urgent need to restore these habitats to increase the habitat resource available for the butterfly. These total quantities of wet grassland with *Succisa pratensis* provides some optimism for the long-term conservation of *E. aurinia* in some core areas, but only if it is properly managed and sufficient quantities of it occur in individual landscapes.

This research work and other studies have demonstrated the importance of appropriate habitat management to maintain populations of *E. aurinia*, which is now relatively well understood (see Warren 1994a; Barnett & Warren 1995; Warren & Bourn 1997; Hobson *et al.* 2001). In marshy grasslands the aim is to maintain an uneven sward of between 8 and 25cm through extensive cattle grazing, where the host plant grows in abundance. The techniques of managing existing habitat are relatively well known, although little research has been conducted on habitat restoration, which is often required for many species (Sheail *et al.* 1997). Little research has been undertaken to establish the best methods for restoration of habitats that are no longer suitable through under-management and neglect, and for the re-creation of suitable habitat from agriculturally improved grassland.

The first experiment aimed to restore unimproved marshy grassland for *E. aurinia*, which had become dominated by coarse grasses such as *Molinia caerulea* and a variety of *Juncus* species. These dominant species had out-competed *Succisa pratensis* and reduced the density of host plant to such a low level that the butterfly no longer used the area for breeding. Figure 5.1 shows the density of *S. pratensis* at all sites studied in England and Wales. The density of host plant on the main reserve (R on the graph) is much greater than the density in the experimental field (E), which may explain why the field is not utilised by the butterfly despite its close proximity to the reserves large population. Differences in the densities are likely to be due to differences in management. The vegetation height and sward structure was also unsuitable, as it was too tall and overgrown. The objective was to restore habitat suitability via cutting at different times of the year combined with pony grazing. Figure 5.1 also suggests that there may be considerable opportunities to increase habitat quality on existing sites for *E. aurinia*, by establishing management that increases *S. pratensis* density.

The second experiment aimed to investigate the feasibility of re-establishing *S. pratensis* in an improved field of low productivity. A common method for habitat re-creation on improved grassland is the use of seeds to introduce the required plant species (Anderson 1995; Smith *et al.* 1996b). Given the probable low dispersal rate of *S. pratensis* (Grime *et al.* 1988), the re-establishment of high host plant densities in improved pastures, is likely to be very slow without active intervention. This experiment involved sowing locally collected seed onto experimental plots that had been treated in different ways.

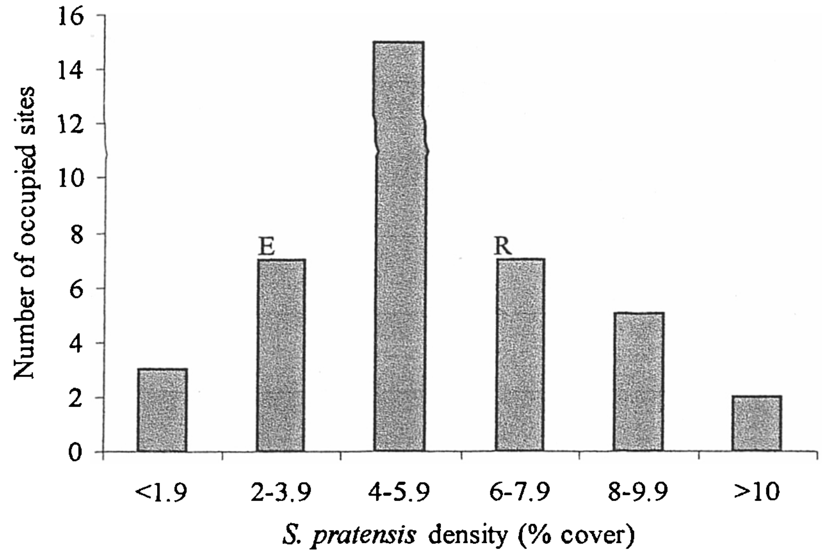


Figure 5.1 Variation in density of *S. pratensis* (% cover) at all sites occupied by *E. aurinia* (data from Dorset and 4km by 4km networks, see chapter 3). E indicates the density of host plant in the experimental field (3.24% cover) and R the density in the main reserve at Rhos Llawr Cwrt (6.07% cover).

5.2 Methods

Two experiments were established in November and December 1997 at Rhos Llawr Cwrt NNR, an area of largely unimproved marshy grassland in Ceredigion, Wales (see chapter one for further description), where *E. aurinia* occurs.

5.2.1 Habitat restoration experiment

The aim was to restore habitat that had become unsuitable for the butterfly through under-grazing. In a large and moderately homogenous field, sixteen 20m by 20m plots were established, with two treatments and control plots. The treatments were (a) one cut during March and (b) two cuts occurring in March and June/July. A BCS Power Scythe with 1m cutter bar was used to cut the plots and the cut material was removed from the site. Each treatment was replicated six times, with the control plots, where no cutting occurred, replicated four times. Because parts of the field were unsuitable for the experiment, I was limited to 16 plots in total, increased replication of the treatments was carried out because it was important to detect whether these differed from one another. (See figure 5.2 for diagram of experimental design). Light grazing using Welsh mountain ponies occurred across all the plots at a density of 0.5 lu/ha/yr, the recommended level for the maintenance of *E. aurinia* habitat (Warren 1994a) and the maximum that any grazier was prepared to stock on this type of vegetation. Cutting or mowing is not a recommended method for habitat management on occupied sites as it produces an even sward (Hobson *et al.* 2001) and depending on timing may damage larval groups. However, mowing was deemed to be a suitable alternative restoration technique to grazing because a stocking level of >0.5 lu/ha/yr, necessary to reduce the dominance of target plant species, would have incurred animal welfare problems. In addition, the butterfly had not bred in this field for a number of years (Wheeler pers. comm.) and it was hoped that the grazing ponies would develop the necessary uneven sward after cutting had taken place.

To measure the change in vegetation, twelve fixed quadrats (1 m^2) were randomly located in each of the plots. Each plot was searched for *S. pratensis*, and the plot was stratified into areas with and without the host plant. Six quadrats were randomly placed in areas with *S. pratensis* and six in areas without. Quadrat positions were mapped, and marked with a post and aluminium label in the south-west corner. This was done to measure changes in the density of *S. pratensis* and the spread of the plant in response to the different treatments. No recording was undertaken in a two metre wide buffer strip within the perimeter of each plot, allowing for vehicle movement between each plot and to remove any edge effects in vegetation, due to proximity to a different plot or treatment.

These quadrats were surveyed in November 1997, prior to any treatment, and then in September/October 1998 and 1999.

To measure changes taking place in the vegetation, the cover of different vegetation categories were recorded, including: cover of *S. pratensis*, *Juncus* spp., *M. caerulea*, other herbs, grasses, sedges, non-angiosperms (non-angiosperms), bare ground and standing water. Four vegetation height measures were taken within each quadrat, using a drop disk (Stewart *et al.* in press). Additional vegetation height measures (25) were taken across the whole plot.

5.2.2 *Succisa pratensis* seeding experiment

Experimental plots were established in a partially improved field at Rhos Llawr Cwrt where no *S. pratensis* occurred, with the aim of investigating the feasibility of re-establishing *S. pratensis* by five methods. Each plot was 4m^2, with five treatments and control, replicated six times (36 plots in total). Four posts with aluminium labels marked the corners of each plot. The treatments applied were as follows:

C	Control, with no seed
SC	Seed, no pre-treatment of the substrate
SH	Seed, vegetation pre-removed by herbicide (Roundup)
SD	Seed, vegetation disturbed using a spade prior to seeding
SP	Seed, plots with simulated poaching (4 minute stamping in boots)
TC	Transplant one 20cm by 20cm *S. pratensis* turf from the species-rich grassland.

Seed was gathered from the site in September 1997 and sown once the plots had been established in November of the same year. Those plots where herbicide was applied were left for one month before seeding, so that the herbicide did not affect the germination. Seed was sown evenly over the plot at a density of $50m^{-2}$ (i.e. 200 seeds per plot). The experimental design is shown in figure 5.3. These plots were surveyed in October 1998, 1999 and 2000 to investigate seedling recruitment and survival. Each plot was 'fingertip' searched for any *S. pratensis* seedlings. The total number of seedlings was recorded, along with length and width of longest leaf, number of leaves in the rosette, seedling condition and evidence of flowering.

5.2.3 Statistical analysis

The habitat restoration experiment data was analysed using multivariate ANOVA and multivariate repeated measures ANOVA to assess the effect of treatment on target species or plant categories that occurred frequently in the sward. 'Plot' was nested within 'treatment' as the between-subjects factor. 'Year' was the within-subjects repeated measure. Two replicates of the cut treatments were removed randomly to balance the design to four replicates for each treatment (Underwood 1997). The measured data was tested for homogeneity of variance using Levene's test and for normality using a Kolmogorov-Smirnov test (Norusis 1998). Quadrat data was arc-sine square root transformed. Where repeated measures ANOVA was used, homogeneity of covariance was tested using the Mauchly's Test of Sphericity; if the data failed this sphericity test ($p<0.05$) the more conservative Greenhouse-Geisser method for calculating the F value was used (Kinnear & Gray 2000).

The seeding experiments were analysed using one-way ANOVA and repeated measures ANOVA. The data were tested for the assumptions as outlined above. Seedling data were arc-sine square root transformed because these were proportions. The mean proportion of seeds established is only tested in those treatments where seedlings were found.

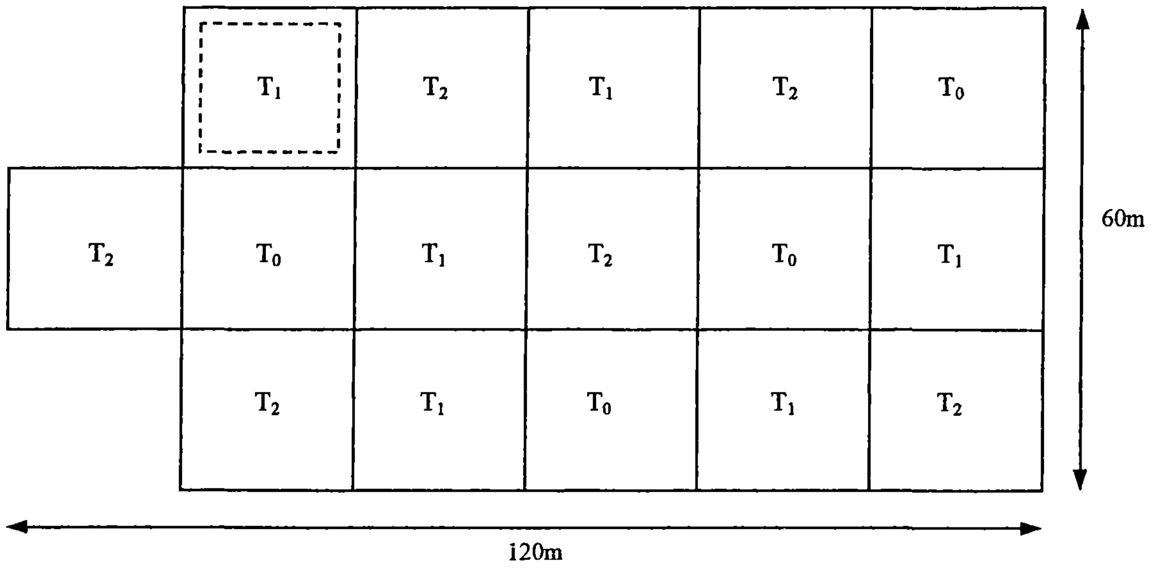


Figure 5.2 Experimental design of the habitat restoration experiment, with treatment code for each 20m by 20m plot. Inner dashed box illustrates the 2m buffer strip within each plot. Treatments are labelled as: T_0 control (4 replicates), T_1 March cut (6 replicates), T_2 March and June/July cut (6 replicates).

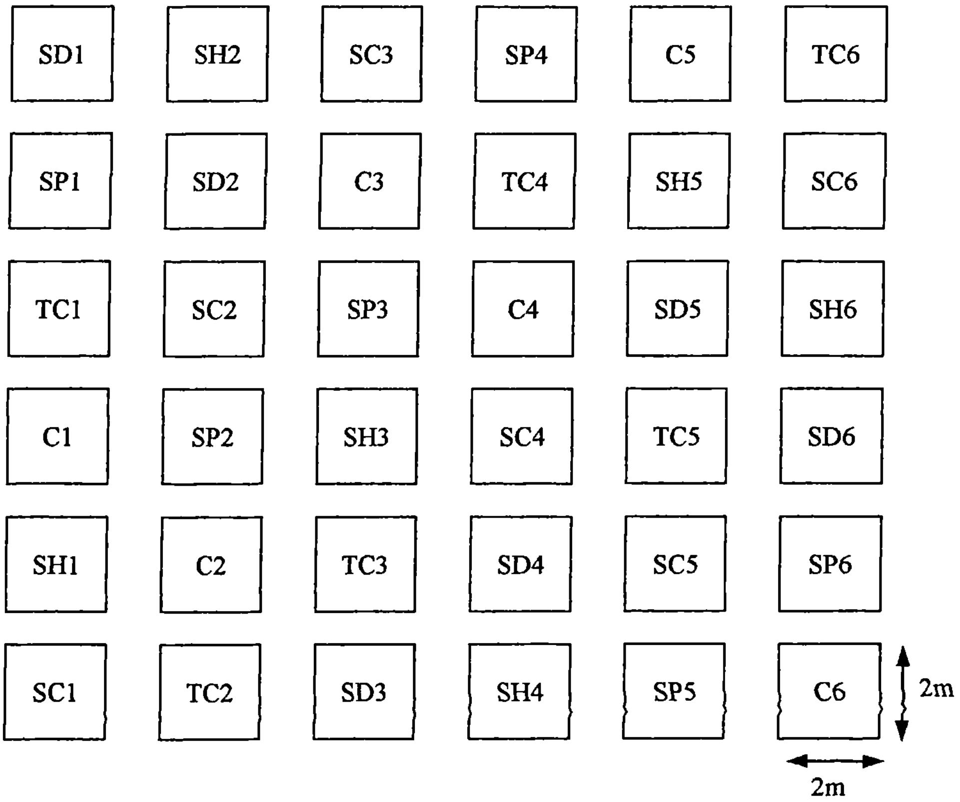


Figure 5.3 Habitat seeding experimental design, with treatment code. Treatments were allocated using a latin square layout. (C) substrate control, no seed; (SC) substrate control + seed; (SH) substrate removed with herbicide (Roundup) + seed; (SD) substrate disturbed + seed; (SP) simulated poaching of substrate + seed; (TC) 20cm by 20cm *S. pratensis* turf transplant.

5.3 Results

5.3.1 Habitat restoration experiment

A baseline survey was completed before any treatments were applied. Differences in the two types of quadrat were assessed (table 5.1). In those quadrats that contained *S. pratensis* there was greater cover of fine grasses (*Festuca* spp.) and non-angiosperms such as moss species. The vegetation height also tended to be shorter in these areas. In comparison, those quadrats not containing *S. pratensis* tended to have greater cover of *Juncus* spp. and *M. caerulea*. Due to these initial differences in vegetation cover and height with quadrat, changes in cover with treatment application were then analysed separately for the two quadrat types, referred to as '*S. pratensis*' and 'random' quadrats. The goal of restoration would be to replicate those characteristics found in the *S. pratensis* quadrats in the random quadrats, and to increase the density of host plant in those quadrats containing it, and decrease the density of *M. caerulea* and *Juncus* spp.

The vegetation cover and height measured in 1997, before the cutting treatments were applied, was tested to see if any natural variation existed. There was no significant difference among treatments in the *S. pratensis* (table 5.2a) or random quadrats (table 5.3a). Any differences that were found subsequently would be mainly due to treatment effects.

Table 5.1 Differences in cover (%) and vegetation height (cm) between the '*S. pratensis*' and 'random' quadrats, at the start of the experiment, before the cutting treatments were applied. Values are means ± 1 S.E. n=72. Final column gives *F* values, *df* and significance levels * $P<0.05$; ** $P<0.01$; *** $P<0.001$; **** $P<0.0001$; NS = not significant.

	Quadrat type		
Variable	***S. pratensis***	**Random**	$F_{1,142}$
Molinia caerulea	32.68 (1.73)	49.25 (2.94)	21.86****
Juncus spp.	26.43 (2.08)	33.34 (2.51)	4.05*
Other herbs	2.77 (0.42)	2.64 (0.51)	0.03 ^{NS}
Fine grasses	5.81 (0.85)	0.75 (0.22)	70.11****
Non-angiosperms	22.08 (1.90)	5.27 (1.39)	68.69****
Vegetation Height (cm)	14.18 (0.42)	18.23 (0.78)	20.86****

Table 5.2 Effects of cutting treatments on vegetation cover (%) and height (cm) in '*S. pratensis*' quadrats, in each year. Part (a) shows the state of plots prior to any treatment, (b) after one year and (c) after two years. Values are means ± (1 S.E.) n=4, multivariate two-way ANOVA. Significance of treatment and interaction (plot within treatment) are shown. Means followed by different letters are significantly different within each response across the row. * $P<0.05$; ** $P<0.01$; *** $P<0.001$; **** $P<0.0001$; NS = not significant.

	Control	**One- cut**	**Two-cuts**		
(a)	**1997**			**Effect**	
	Treatment 0	**Treatment 1**	**Treatment 2**	**Treatment**	**Interaction**
Succisa pratensis	3.35 (0.36)a	4.04 (0.53)a	3.83 (0.68)a	NS	NS
Molinia caerulea	28.02 (3.89)a	37.94 (0.78)a	32.08 (1.37)a	NS	NS
Juncus spp.	29.80 (3.76)a	23.18 (2.06)a	26.30 (6.66)a	NS	NS
Other herbs	3.53 (1.23)a	2.25 (0.84)a	2.54 (0.77)a	NS	**
Fine grasses	6.10 (2.50)a	5.08 (1.89)a	6.28 (1.92)a	NS	*
Non-angiosperms	23.06 (2.96)a	20.78 (3.04)a	22.39 (7.79)a	NS	*
Vegetation height (cm)	14.81 (1.05)a	14.72 (1.28)a	13.02 (0.39)a	NS	*
(b)	**1998**			**Effect**	
	Treatment 0	**Treatment 1**	**Treatment 2**	**Treatment**	**Interaction**
Succisa pratensis	5.09 (0.30)a	6.27 (1.18)a	4.87 (0.62)a	NS	NS
Molinia caerulea	29.28 (7.77)a	27.86 (3.95)a	13.09 (1.47)b	****	***
Juncus spp.	24.03 (1.86)a	25.49 (2.69)a	9.48 (1.25)b	****	NS
Other herbs	5.61 (1.15)a	4.64 (0.51)a	7.43 (2.04)a	NS	***
Fine grasses	6.15 (1.70)a	5.88 (0.70)a	11.43 (3.19)b	***	***
Non-angiosperms	17.35 (4.34)a	13.95 (3.33)a	28.78 (10.07)b	***	***
Vegetation height (cm)	16.07 (1.56)a	20.67 (0.68)a	7.80 (0.57)b	****	NS
(c)	**1999**			**Effect**	
	Treatment 0	**Treatment 1**	**Treatment 2**	**Treatment**	**Interaction**
Succisa pratensis	4.42 (0.43)a	7.26 (1.76)b	4.64 (0.46)a	**	NS
Molinia caerulea	39.45 (7.68)a	18.82 (1.91)b	11.61 (1.53)c	****	*
Juncus spp.	22.83 (3.79)a	4.89 (0.94)b	4.41 (0.18)b	****	NS
Other herbs	6.87 (2.46)a	9.75 (1.29)a	9.88 (1.78)a	NS	NS
Fine grasses	5.11 (2.26)a	12.77 (2.17)b	11.80 (4.06)b	****	***
Non-angiosperms	11.17 (3.47)a	18.77 (2.66)b	36.77(9.83)c	****	***
Vegetation height (cm)	25.34 (2.35)a	8.24 (0.11)b	8.93 (0.35)b	****	NS

Table 5.3 Effects of cutting treatments on vegetation cover (%) and height (cm) in 'random' quadrats, in each year. Part (a) shows the state of plots prior to any treatment, (b) after one year and (c) after two years. Values are means (±1 S.E.) n=4, multivariate two-way ANOVA. Significance of treatment and interaction (plot within treatment) are shown. Means followed by different letters are significantly different within each response across the row. * $P<0.05$; ** $P<0.01$; *** $P<0.001$; **** $P<0.0001$; NS = not significant.

	Control	**One- cut**	**Two-cuts**		
(a)	**1997**			**Effect**	
	Treatment 0	**Treatment 1**	**Treatment 2**	**Treatment**	**Interaction**
Succisa pratensis	–	–	–	–	–
Molinia caerulea	41.21 (8.62)a	58.26 (8.23)a	48.28 (5.98)a	NS	***
Juncus spp.	37.96 (6.42)a	27.37 (4.99)a	34.67 (10.27)a	NS	***
Other herbs	3.61 (1.77)a	2.29 (0.55)a	2.03 (0.46)a	NS	NS
Fine grasses	1.35 (0.71)a	0.62 (0.39)a	0.29 (0.11)a	NS	NS
Non-angiosperms	8.41 (4.22)a	4.72 (1.94)a	2.67 (2.47)a	NS	NS
Vegetation height (cm)	16.82 (1.26)a	20.53 (0.67)a	17.34 (2.88)a	NS	*
(b)	**1998**			**Effect**	
	Treatment 0	**Treatment 1**	**Treatment 2**	**Treatment**	**Interaction**
Succisa pratensis	–	–	–	–	–
Molinia caerulea	41.84 (7.26)a	47.51 (5.08)a	17.14 (2.27)b	****	NS
Juncus spp.	30.67 (4.39)a	28.06 (2.87)a	17.29 (1.10)a	NS	NS
Other herbs	5.57 (0.42)a	4.07 (0.83)a	11.11 (1.76)b	****	**
Fine grasses	1.19 (0.33)a	1.22 (0.73)a	4.98 (0.72)b	****	NS
Non-angiosperms	6.13 (3.49)a	4.88 (2.01)a	6.54 (2.09)a	NS	NS
Vegetation height (cm)	22.55 (2.92)a	26.01 (2.80)a	9.31 (0.67)b	**	**
(c)	**1999**			**Effect**	
	Treatment 0	**Treatment 1**	**Treatment 2**	**Treatment**	**Interaction**
Succisa pratensis	–	0.04	–	–	–
Molinia caerulea	48.40 (8.75)a	25.58 (5.27)b	15.04 (0.92)b	****	NS
Juncus spp.	36.41 (10.07)a	6.49 (0.44)b	8.83 (0.84)b	****	*
Other herbs	3.51 (1.06)a	15.62 (3.26)b	16.86 (2.55)b	****	*
Fine grasses	0.76 (0.37)a	8.47 (1.12)b	6.04 (1.16)b	****	NS
Non-angiosperms	4.75 (3.60)a	16.59 (3.10)b	13.51 (2.55)b	****	NS
Vegetation height (cm)	36.37 (1.11)a	9.92 (0.72)b	10.59 (1.15)b	****	NS

Repeated measures ANOVA showed a significant change in cover of vegetation over time and between treatments over time in both the *S. pratensis* (table 5.4) and random (table 5.5) quadrats. In the *S. pratensis* quadrats, cover of the host plant, other herbs and fine grasses increased over time whereas cover of *M. caerulea* and *Juncus* spp decreased. Change in cover of non-angiosperms and in vegetation height was not significant over time. With time x treatment factors most differences were highly significant. Cover of *M. caerulea* in control plots actually increased over time, in contrast to the cut treatments where cover decreased over time, most significantly in treatment 2. *Juncus* spp. cover decreased in all treatment plots over time especially in year 2, with the decrease in treatment 1 and 2 being significantly greater than in the control. There were increases in cover over time for fine grasses and other herbs in the cut treatments. Cover of non-angiosperms decreased in the control and also slightly in treatment 1, but significantly increased in treatment 2. Vegetation height changed with time x treatment, with an increase in the control (probably due to very wet weather) and a decrease when cut, as would be expected.

Some plot-specific changes may reflect slight differences in the original vegetation in the soil, and/or in soil water. This highlights the need to monitor the consequences of applying any management to other sites where the precise vegetation and soil conditions may differ.

Similar patterns were observed over time in the random quadrats (table 5.5). Cover of *M. caerulea* and *Juncus* spp. decreased over time with the two cutting treatments, in the control plots *M. caerulea* appeared to increase in cover and *Juncus* spp. decreased slightly. The cover of fine grasses, other herbs and non-angiosperms increased over time in treatment 1 and 2, with decreases detected for fine grasses and non-angiosperms in the control plots with other herbs remaining stable. Overall, vegetation height did not change significantly with time, because height increased in the control plots and decreased in both cut plots, giving rise to a significant time x treatment interaction.

Table 5.4 Effects of cutting treatments on vegetation cover and vegetation height in the '*S. pratensis*' quadrats between 1997 and 1999. Values are means (± 1 S.E.) n=4. Multivariate repeated measures ANOVA. Within subject effect is time (repeated measures); between subject effect is treatment; interaction is plot nested within treatment. * $P<0.05$; ** $P<0.01$; *** $P<0.001$; **** $P<0.0001$; NS = not significant.

	Treatment 0			Treatment 1			Treatment 2			Within subject Effects			Between subject effects	
Response	1997	1998	1999	1997	1998	1999	1997	1998	1999	Time	Time x Treatment	Time x treat. x plot	Treatment	Interaction
Succisa	3.35	5.09	4.42	4.04	6.27	7.26	3.83	4.87	4.64	****	*	NS	NS	NS
pratensis	(0.36)	(0.30)	(0.43)	(0.53)	(1.18)	(1.76)	(0.68)	(0.62)	(0.46)					
Molinia	28.02	29.28	39.45	37.94	27.86	18.82	32.08	13.09	11.61	****	****	NS	***	*
caerulea	(3.89)	(7.77)	(7.68)	(0.78)	(3.95)	(1.91)	(1.37)	(1.47)	(1.53)					
Juncus spp.	29.80	24.03	22.83	23.18	25.49	4.89	26.30	9.48	4.41	****	****	***	***	NS
	(3.76)	(1.86)	(3.79)	(2.06)	(2.69)	(0.94)	(6.66)	(1.25)	(0.18)					
Other herbs	3.53	5.61	6.87	2.25	4.64	9.75	2.54	7.43	9.88	****	**	*	NS	*
	(1.23)	(1.15)	(2.46)	(0.84)	(0.51)	(1.29)	(0.77)	(2.04)	(1.78)					
Fine grasses	6.10	6.15	5.11	5.08	5.88	12.77	6.28	11.43	11.80	****	****	***	*	**
	(2.50)	(1.70)	(2.26)	(1.89)	(0.70)	(2.17)	(1.92)	(3.19)	(4.06)					
Non-	23.06	17.35	11.17	20.78	13.95	18.77	22.39	28.78	36.77	NS	****	NS	**	***
angiosperm	(2.96)	(4.34)	(3.47)	(3.04)	(3.33)	(2.66)	(7.79)	(10.07)	(9.83)					
Vegetation	14.81	16.07	25.34	14.72	20.67	8.24	13.02	7.80	8.93	NS	****	NS	****	NS
height (cm)	(1.05)	(1.56)	(2.53)	(1.28)	(0.68)	(0.11)	(0.39)	(0.57)	(0.35)					

Table 5.5 Effects of cutting treatments on vegetation cover and vegetation height in the 'random' quadrats between 1997 and 1999. Values are means (± 1 S.E.) n=4. Multivariate repeated measures ANOVA. Within subject effect is time (repeated measures); between subject effect is treatment; interaction is plot nested within treatment. * $P<0.05$; ** $P<0.01$; *** $P<0.001$; **** $P<0.0001$; NS = not significant.

	Treatment 0			Treatment 1			Treatment 2			Within subject Effects			Between subject effects	
Response	1997	1998	1999	1997	1998	1999	1997	1998	1999	Time	Time x Treatment	Time x treat. x plot	Treatment	Interaction
Succisa pratensis	–	–	–	–	–	0.04	–	–	–	–	–	–	–	–
Molinia caerulea	41.21 (8.62)	41.84 (7.26)	48.40 (8.75)	58.26 (8.23)	47.51 (5.08)	25.58 (5.27)	48.28 (5.98)	17.14 (2.27)	15.04 (0.92)	****	****	*	**	NS
Juncus spp.	37.96 (6.42)	30.67 (4.39)	36.41 (10.07)	27.37 (4.99)	28.06 (2.87)	6.49 (0.44)	34.67 (10.28)	17.29 (1.10)	8.83 (0.84)	****	****	***	**	*
Other herbs	3.61 (1.77)	5.57 (0.42)	3.51 (1.06)	2.29 (0.55)	4.07 (0.83)	15.62 (3.26)	2.03 (0.46)	11.11 (1.76)	16.86 (2.55)	****	****	*	***	*
Fine grasses	1.35 (0.71)	1.19 (0.33)	0.76 (0.37)	0.62 (0.39)	1.22 (0.73)	8.47 (1.12)	0.29 (0.11)	4.98 (0.72)	6.04 (1.16)	****	****	NS	***	NS
Non-angiosperm	8.41 (4.22)	6.13 (3.49)	4.75 (3.60)	4.72 (1.94)	4.88 (2.01)	16.59 (3.10)	2.67 (2.47)	6.54 (2.09)	13.51 (2.55)	****	****	NS	NS	NS
Vegetation height (cm)	16.82 (1.26)	22.55 (2.92)	36.37 (1.11)	20.53 (0.67)	26.01 (2.80)	9.92 (0.72)	17.34 (2.88)	9.31 (0.67)	10.59 (1.15)	NS	****	**	****	NS

Repeated measures ANOVA does not reveal differences between treatments at each time period, therefore, multivariate two-way ANOVA was carried out at each recording period (table 5.2 and 5.3). As discussed above, no statistically significant differences were found in 1997 between treatments for the vegetation characteristics measured in either the *S. pratensis* or 'random' quadrats, although there were a few significant differences among plots within treatments.

In 1998 in the *S. pratensis* quadrats (table 5.2b), significant differences were found among treatments, which could be attributed to treatment 2, that had received two cuts, with no significant differences between treatment 1 and the control plots. The cover of *M. caerulea* and *Juncus* spp. was much reduced in these plots (treatment 2) in contrast to treatment 1, which did not differ from the plots where no cutting had occurred. The cover of fine grasses and non-angiosperms was higher with treatment 2. No significant difference was detected in the cover of *S. pratensis* or other herbs, species that perhaps take longer to increase in density through reproduction. Vegetation height was much reduced in the plots that had received two cuts.

In the random quadrats, similar patterns were found in 1998 (table 5.3b). *Molinia caerulea* cover was much reduced in treatment 2, with no significant difference between cover in treatment 1 and the control plots. No significant difference was found in the cover of *Juncus* spp. between treatments or in the cover of non-angiosperms. Other herbs and fine grasses cover was greater in treatment 2. Vegetation height was again much reduced in the plots that had received two cuts.

Problems occurred in 1999 with the application of a second cut for treatment 2 plots. Due to the very wet spring and summer only one cut was possible in late May/June, which may explain why significant differences between the two cutting treatments were rarely found. *Succisa pratensis* cover differed with treatment, cover was higher in treatment 1 with no significant difference between treatment 2 and control plots (table 5.2c). There was no significant difference in cover of other herbs, which was the case in the previous year. *Molinia caerulea* cover differed significantly with all treatments, remaining higher in the control, 50% less in treatment 1 and further reduced in treatment 2. The cover of *Juncus* spp. was dramatically less in both treatments 1 and 2 compared to the control plots. The cover of fine grasses was greater in treatment 1 and 2 than in the control. Cover of non-angiosperms was significantly different between all treatment plots, with the greatest cover occurring in treatment 2. Vegetation height in treatment 1 and 2 was significantly shorter than the control plots. In the random quadrats vegetation response in treatment 1 and 2 was statistically similar, with both being significantly different to the cover in control plots. The presence of *S. pratensis* was also recorded in one quadrat, indicating possible spread of the host plant. The main trends were the reduced cover of *M. caerulea* and *Juncus* spp. in the cut plots and an increase in other herbs, fine grasses and non-angiosperms. Vegetation height was lower in the cut plots, as expected.

5.3.2 *Succisa pratensis* seeding experiment

Table 5.6 summarises the proportion of seedlings germinated in each treatment of the seedling experiment between 1998 and 2000. After one year of the experiment seeds had germinated and become established in plots receiving the herbicide and poaching treatment and in the seed-control plots. No seedlings were found in plots where the vegetation had been disturbed prior to seeding. The proportion of seedlings germinated in the herbicided plot was statistically significantly different than in the other plots with seedlings.

After two years, seedlings were found in two of the 'disturbed' plots, where seedlings had not previously been found, but were significantly less than in any other seeded treatment. There was a slight increase in proportion of seedlings established in the seed only and poached plots, but a decrease in proportion of seedlings in the herbicided plots, the differences no longer significant.

After three years the proportion of seedlings established in the plots that had initially been herbicided remained higher than in all the other plots, despite this having decreased slightly over time. The proportion of seedlings also decreased in the seed only and poached plots, and in contrast the proportion of seedlings established increased slightly from the previous year in the disturbed plots. No significant differences were found.

Any change in proportion of seedlings established over time and with treatment was not significant (repeated measures ANOVA).

At the end of the experiment no seedlings were found in the control plot. As these plots had not received any seed, this is not surprising and, it confirms that the possibility of transportation of seed from other parts of the reserve by wandering grazing animals is negligible. No seedlings were found in the area adjacent to the transplanted turf. Flowering and seed set of the plants in the transplanted turf was observed however no seedlings were found. This may be due to a combination of the relatively short duration of the experiment and the inability of the plant to disperse seeds for any distance greater than the area below the seed head.

These results show that *S. pratensis* can be established without prior treatment of the substrate. However, quicker and increased establishment can be achieved by treating the substrate, particularly through herbicide application (Milligan *et al.* 1999), which drastically reduces the dominance of potential competing species. The simulation of poaching the ground, which creates openings and pockets in the soil for seed to gather, appears to be useful.

Table 5.6 Mean proportion of seeds established in the six replicate plots of each treatment over the three years of the experiment. Values are means (±1 S.E.) n=6, univariate two-way ANOVA. *F* values are given for the effect of treatment. Means followed by different letters are significantly different within each row. * P<0.05; ** P <0.01; *** P <0.001; **** P <0.0001; NS = not significant.

Proportion of seedlings established	**Treatment**						$F_{3,20}$ **Treatment**
	C	**SC**	**SH**	**SD**	**SP**	**TC**	
1998	–	0.002a	0.043b	0a	0.009a	–	9.75****
		(0.001)	(0.01)		(0.007)		
1999	–	0.007ab	0.035a	0.002b	0.011ab	–	3.81*
		(0.005)	(0.01)	(0.001)	(0.006)		
2000	–	0.003a	0.027a	0.003a	0.007a	–	2.83^{NS}
		(0.001)	(0.01)	(0.002)	(0.004)		

5.4 Discussion

5.4.1 Habitat restoration experiment

The habitat restoration experiment aimed to restore unimproved marshy grassland, by decreasing the dominance of *M. caerulea* and *Juncus* spp. and increasing cover of the host plant and other plant species that it appeared to be associated with. This seems to have been achieved.

After one year, the main trend was a reduction in *M. caerulea* and *Juncus* spp. cover and increase in fine grass and lower plant cover in the plots receiving two cuts. In both quadrat types there was some change in treatment 1, but this was not significant and vegetation cover remained similar to that in the control plots. Cutting twice a year with low levels of grazing reduced the dominance of the coarser species and opened up the vegetation sward, encouraging the growth of fine grasses, some herbs and non-angiosperms. The vegetation height had also been reduced to a more favourable level.

After two years and possibly due to the problems with cutting frequency, the vegetation characteristics in treatment 1 and 2 became similar and were significantly different to the controls. Despite treatment 1 plots being cut only once the reduction in cover of *M. caerulea* and *Juncus* spp. and increase in fine grasses and non-angiosperms had been maintained. Both *M. caerulea* and *Juncus* spp. required two cuts (treatment 2 after 1 year, treatment 1 after two years) to bring about substantial reductions in cover. *Succisa pratensis* cover only increased in the plots receiving one cut, perhaps due to the lower frequency of cutting. It is encouraging that signs of host plant spread were detected in the random quadrats, where seed has germinated in the more open sward. No buried seedbank is reported in the literature and vegetative spread is rare (Adams 1955; Grime 1988), so regeneration is almost entirely by seed germinating in the spring.

Changes in the control plots may be due to natural responses in weather conditions. For example wetter than average springs may have increased the vegetation height. Changes may also have occurred due to increased levels of grazing by the ponies. Sections of the field being cut probably encouraged the ponies to wander into the control plots and graze, or at least trample these preferentially over the rest of the uncut field.

This experiment demonstrates that two cuts, with associated grazing, in the first year is necessary to reduce the dominance of target species and open up the sward, with one cut in the second year with grazing, necessary to maintain these conditions. If only one cut is possible in the first year then the same conditions can be achieved by cutting again in the second year with the maintenance of grazing. Although not specifically tested for in this experiment, it is probable that grazing has maintained the conditions that the cutting created, with the ponies preferentially grazing the re-growth in the cut plots (personal observations). When accumulated dead material is removed by cutting, then *M. caerulea* dominated communities can provide suitable levels of nutrient intake for grazing animals (Common *et al.* 1997). Selective grazing can influence the species balance in unimproved grasslands (Grant *et al.* 1996b).

There have been few experimental studies conducted on the effect of cutting on vegetation cover for restoration or conservation purposes. Most papers concentrate on grazing, burning and cutting treatments to improve sward quality for livestock (Grant *et al.* 1981; Armstrong *et al.* 1997; Common *et al.* 1997; Kramberger & Gselman 2000). Studies that have used a combination of cutting and grazing treatments to improve species richness have demonstrated that management, such as spring or autumn grazing has a positive effect on species richness (Smith & Rushton 1994; Smith *et al.* 1996a; Peet *et al.* 1999).

Much has been reported on the control of *M. caerulea* due to concern about the increase of this species in upland moorland communities at the expense of *Calluna vulgaris* (Taylor *et al.* 2001). It is also of concern due to the relatively low palatability for grazing stock and the monotonous, species-poor landscapes which result from *M. caerulea* dominated moorland (Chambers *et al.* 1999).

The main method of control is through manipulating grazing levels or controlled burning, as cutting would not be an appropriate method of control over large areas. However, the effect that cutting had on cover of *M. caerulea* in this experiment is similar to those experiments testing grazing treatments. Grant *et al.* (1996a) investigated the effect of heavy and light grazing levels. The higher rate of grazing by cattle reduced the rates of leaf extension in *M. caerulea*, reduced biomass production by 86% and decreased cover. General floristic diversity on all grazed plots was increased compared to ungrazed areas. *Molinia caerulea* was shown to be highly sensitive to defoliation and the dominance of the species could be reduced through heavy grazing (Torvell *et al.* 1988; Grant *et al.* 1996a).

5.4.2 *Succisa pratensis* seeding experiment

The seeding experiment has demonstrated that *S. pratensis* can be established within an improved field, most effectively by reducing the competitive ability of other species through herbicide treatment or creation of gaps through for example, poaching. The number of seedlings tended to decrease over time (however this was not statistically significant). This decrease may be due to the lower competitive ability of *S. pratensis* in a relatively high nutrient status field (Grime *et al.* 1988) and in the longer term it may become out-competed. *Succisa pratensis* is a relatively slow growing plant, an adaptive characteristic under conditions of low nutrient supply, but when such species encounter concentrations of nutrients the species generally does not benefit as it is usually out competed by other vegetation (Pegtel 1986).

Work on reducing the nutrient status of improved grassland is currently being undertaken at Rhos Llawr Cwrt, for the restoration of rhos pasture (Roughley 1996). Three treatments were applied with the aim of decreasing soil pH and reducing the nitrogen and phosphorus status of the soil. Aluminium sulphate application has changed the specific soil chemical properties, which resemble the unimproved soil more than the control improved soil (Adams *et al.* 1999; Adams & Young 2001). Top soil removal has been shown to be an effective method to reduce soil fertility, in particular phosphorus levels, for the restoration of *Cirsio-Molinietum* wet meadows (Tallowin 2000; Tallowin & Smith 2001). It would be important to reduce the nutrient status in improved grassland prior to seeding, to reduce the competitive ability of plants commonly found in improved grassland (Manchester *et al.* 1999). It would be very valuable to combine treatments in future to examine the effects on the re-establishment of *S. pratensis* from seed. However, the rate of loss of small *S. pratensis* plants in the seeding experiment is relatively low and not statistically significant, and may be no higher than in other (unimproved) parts of Rhos Llawr Cwrt.

The decline in seedling establishment is unlikely to be due to a self-thinning effect (density dependent mortality), which has been found in *S. pratensis* (Kotorová & Lepš 1999) as this was only exhibited at much higher densities in laboratory experiments. Similar results of the effect of litter layer and moss layer on seedling establishment have been found, establishment was higher in plots where above-ground vegetation had been removed and in plots that had been mown and the moss layer removed (Kotorová & Lepš 1999).

Because the overall rate of establishment of plants from seed was rather low (and not atypical of plants in general), a larger number of seed or greater replication would be desirable to identify which treatments differ from each other. Nonetheless, the results were clearly significant in year one, and the same pattern was observed in later years. Even in the final year, the poached treatment had just over twice the density of *S. pratensis* plants as the seed-control and disturbed treatments, and the herbicide plots had four times the density of the poached treatment. This is encouraging, with further work there is real potential to restore such semi-improved pastures to *E. aurinia* habitat.

5.5 Conclusions

The objective of the habitat restoration experiment was to open up the vegetation dominated by *M. caerulea* and *Juncus* spp., in order to restore conditions suitable for *S. pratensis* to increase and subsequently for the butterfly to re-colonise. This appears to have been achieved. Observations at the site (September 2000) revealed the vegetation to have remained open with good cover of *S. pratensis* which was flowering in abundance, with finer grasses, mosses and other herbs. No cutting had occurred for over a year and the pony grazing had controlled the dominance of *M. caerulea* and *Juncus* spp. Six larval webs of *E. aurinia* were found, five in the cut plots and one at the edge of a control plot. These were the first records of breeding in this part of the field (Woolley pers. comm.) and demonstrate that the restoration experiment has been a success. If the habitat management is maintained and *S. pratensis* increases in density, there is the potential to establish a much larger *E. aurinia* population in the future.

Habitat restoration is feasible for sites that have become overgrown through a combination of cutting and grazing. Two cuts in the first year and one cut in the second year have shown that the desired vegetation characteristics can be achieved, combined with extensive grazing.

The seeding experiment has demonstrated that establishment is possible in improved grasslands by decreasing competition from other plants, for example, through herbicide application. However, to achieve long term establishment of *S. pratensis*, and other plants characteristic of unimproved habitats, it is probable that changes in the nutrient load of the soil will be necessary (Smith *et al.* 1996b; Blackstock *et al.* 1998). Further research is required to identify the best way to do this, but the results presented here and in Adams *et al.* (1999) suggest that there is room for optimism. Nonetheless, restoration of currently unmanaged and overgrown wetland sites is likely to be faster, cheaper and more effective, and should be carried out widely before such sites become increasingly degraded.

6.0 GENERAL DISCUSSION

This discussion initially summarises the findings and implications that have been raised and discussed in the preceding chapters. It will then consider the more general implications from this study for the conservation of *Euphydryas aurinia*, other butterflies and species in general, which inhabit fragmented landscapes, highlighting some areas for further research.

6.1 Summary of results

6.1.1 Metapopulation dynamics

The national distribution of *E. aurinia* has undergone severe decline since 1970, as has clearly been demonstrated in the distribution maps presented in chapter two. The 10km grid squares that have become extinct in the past were found to be the most isolated, with few occupied neighbouring squares. If the current causes and patterns of decline continue, the national distribution of *E. aurinia* at a 10km scale is predicted to decline by 48% by 2020 (from 1995-99 levels). The species is predicted to have the highest probability of surviving in the core regions of south and south central England, south west England and south Wales (and probably also western Scotland), with populations on the fringes of these areas progressively becoming extinct.

The metapopulation approach (chapter three) was found to be useful in understanding the occupancy pattern and persistence of *E. aurinia* within fragmented landscapes. Analysis at a regional scale in Dorset found that occupancy of habitat patches was determined by patch connectivity (isolated patches were less likely to be occupied), vegetation height and resource area (patch area multiplied by host plant cover). Therefore, a habitat patch was most likely to be occupied if it was well connected to other occupied patches, had tall vegetation and a high resource area value. Both the spatial arrangement and quality of habitat patches are important for *E. aurinia*. Such patterns of occupancy (and known population turnover) are consistent with the interpretation that the butterfly persists as a metapopulation. This permitted the use of the metapopulation concept to investigate *E. aurinia* persistence in fragmented landscapes.

Although it is simplistic, the Incidence Function Model (IFM) has advantages for conservation purposes because it is possible to parameterise the model for real, existing metapopulations (Hanski 1994a; Wahlberg *et al.* 1996; Moilanen *et al.* 1998; Biedermann 2000). It was a useful tool to explore the possible fate of *E. aurinia* in fragmented landscapes. It suggests that habitat loss and consequent fragmentation is likely to be a major cause of decline and highlights the problem of extinction debt. According to IFM simulations, the threshold network area (or minimum viable metapopulation size) was predicted to be 71ha, to achieve a 95% probability of persistence for 100 years for a network within a 4km by 4km area. Relatively small losses of habitat in the future may greatly reduce persistence time for networks where long-term persistence is currently predicted. However, 71ha is likely to be an underestimate of the area required, if the distribution of *E. aurinia* was not at equilibrium in the Dorset landscape where the model was parameterised.

6.1.2 Parasitoids

Cotesia bignellii appears to have a metapopulation structure, which must be superimposed on the dynamics of its host. At a local scale, the parasitoid has a patchy distribution at Lydlinch, where the host may be able to 'escape' parasitoid attack in areas where the parasitoid is absent, in contrast to Giant Hill, where the butterfly and parasitoid populations are probably more panmictic. The presence of parasitoids and their effect on population dynamics, may be a major cause of variation in *E. aurinia* abundance and metapopulation dynamics and may help to explain the butterfly's species requirement for large habitat patches.

6.1.3 Habitat restoration and re-creation

Many current habitat networks have insufficient suitable habitat to ensure long-term persistence of *E. aurinia*. Habitat restoration is an important conservation option in such areas. The restoration experiments have shown that unmanaged habitat can be quickly restored to conditions suitable for the butterfly, through a combination of cutting and grazing treatments. Habitat restoration is feasible for such sites that have become overgrown but still contain some *Succisa pratensis*. Habitat re-creation of improved grassland is also potentially feasible, but more fundamental changes in the soil nutrient status are probably necessary, to achieve the long-term persistence of

S. pratensis. This is likely to be more time consuming and expensive than the restoration of overgrown, but unimproved sites.

6.2 Implications for conservation and future research

The findings of this study have wider implications for the conservation of species that inhabit increasingly fragmented landscapes. This will be discussed, including possible areas for further research.

From this study, the key factors for *E. aurinia* persistence are habitat patch size, connectivity to other occupied patches and habitat quality, although interactions with parasitoids and other natural enemies may be just as important (see below). Such patterns of occupancy are consistent with the interpretation that species persist as metapopulations. Comparable patterns have been documented in other butterfly species (Harrison *et al.* 1988; Thomas & Harrison 1992; Thomas, C. D. *et al.* 1992; Hanski *et al.* 1995a, 1996c; Hill *et al.* 1996; Kuussaari 1998), insects (Appelt & Poethke 1997; Biedermann 2000) and mammals (Moilanen *et al.* 1998). In such patchy and fragmented landscapes, small populations are the most likely to become extinct and increasingly isolated habitat patches are the least likely to be colonised (Hanski 1997a; Hanski 1999a). Long-term conservation will require the protection of networks of large, well connected areas of habitat.

Larger patches are usually more heterogeneous and may decrease the risk of population extinction because of the variation in habitat conditions (Thomas & Hanski 1997). Environmental stochasticity, such as summer drought, may cause some microhabitats to become inhospitable (Thomas C. D. 1995; Sutcliffe *et al.* 1997b), but large patches that contain a variety of microhabitats, may contain some locations that allow survival during such events. In addition, large heterogeneous patches may allow local escape from attack by natural enemies (Taylor 1998).

In addition to the spatial properties of a patch, the quality of the habitat is also important for occupancy. Many early successional butterfly species have been shown to have very specific habitat requirements (Bourn & Thomas 1993; Thomas J. A. 1995b; Warren 1987, 1991; Gutiérrez *et al.* 1999; Thomas J. A. *et al.* 2001). This work (chapter three and five) has shown that *E. aurinia* is more likely to occupy suitable habitat patches that have longer vegetation and where the host plant is abundant. These findings support by earlier work (Porter 1981; Warren 1994a), showing that *E. aurinia* preferentially breeds in areas of longer vegetation (between 5 and 20 cm), where the host plant is abundant and leaves are large for egg-laying. Thus, habitat quality is clearly important in determining the presence or absence of the butterfly, in as much as that the butterfly is periodically absent from low-quality habitat. But it is far less clear that variation in quality is important in determining presence/absence or population density within a broad range of 'suitable' habitat conditions. This study found no correlation between patch quality and adult butterfly density, which suggests that some other factors, in addition to habitat quality, are influencing population density. Natural enemies are one possibility (Dempster 1983; Webb & Pullin 1996) and have often been suggested to cause the fluctuations in abundance that are characteristic of *E. aurinia* populations (Ford & Ford 1930; Porter 1981; Warren 1994a; Lewis & Hurford 1997). It is evident that a certain threshold of habitat quality is necessary for occupancy, as demonstrated in this study. However, further research is required to understand the relationship between density and improving habitat quality, if such a relationship exists for *E. aurinia*. This will be difficult to interpret due to natural fluctuations in abundance, as mentioned above. If natural enemies determine density, then increasing habitat quality above a certain threshold may have no beneficial effects. The preliminary findings presented here and in work by Lei (1997), suggest that parasitoids significantly increase the risk of local extinction of the host butterfly, by reducing the population to a small size. The impact of natural enemies, such as parasitoids, on population density requires further research. It would be useful to develop a method suitable for *in situ* sampling, so that metapopulation-scale assessments can be made. It would also be interesting to re-introduce the butterfly into a suitable habitat network without the parasitoid and examine subsequent abundance, dynamics and habitat range.

Regardless of the exact situation for *E. aurinia* and its parasitoids, this raises a general issue. When abundances and distributions are set by variation in habitat quality (Thomas J. A. *et al.* 2001), it is generally easy to identify species requirements and to suggest conservation actions. When they are set by natural enemies, identifying conservation actions is likely to be far harder and the consequences less predictable.

The modelling reinforces the point that much larger habitat patches are required for *E. aurinia* persistence than for other well-studied butterflies (Wahlberg *et al.* 1996; Hanski *et al.* 1996b) whose (imaginary) dynamics were also modelled in the Dorset landscape. Relative to the parameter estimates for other butterfly species, *E. aurinia* in the Dorset system is experiencing a higher level of stochasticity that results in an increased risk of local extinction. One possible cause is parasitoids (Lei 1997).

This has wider implications for modelling species in fragmented landscapes. Parameter sets derived from one species may not be applicable to other species, or even for the same species in very different habitats. Radically different conclusions about the habitat network requirements for *E. aurinia* would have been made if, for example, predictions were based on the parameters generated for *M. cinxia* only. To apply one parameter set to a different species can be misleading (Wahlberg *et al.* 1996). This makes it very difficult to make general predictions about groups of species in fragmented habitats, as different species respond differently to levels of fragmentation, and of course they differ in their habitat requirements. Conservation recommendations must be based on species-specific analysis (Wilson 1999; Baguette *et al.* 2000; Gutiérrez *et al.* 2001).

Many systems that have been affected by habitat destruction and fragmentation in the past may not yet have reached a new equilibrium and some or many of these may be subject to the phenomenon known as extinction debt (Tilman *et al.* 1994). The simulation results of this study suggest that several of the extant metapopulations may be susceptible to extinction even if there is no further habitat degradation. This effect has been proposed as a possible explanation for delayed extinction in a number of systems (Soulé *et al.* 1988, 1992; Brooks & Balmford 1996; Petit & Burel 1998; Cowlishaw 1999; Gonzalez 2000). Biedermann (2000) modelled a reduction in patch number for the froghopper *Neophilaenus albipennis* using the IFM and found a similar delay. If this time-lag to extinction is a common phenomenon in fragmented systems, then our estimates of minimum viable metapopulation size based on observed occupancies will be underestimated for many species. Hence, the protection of current habitat networks may often be insufficient for long-term persistence. Where the dynamics of systems are not at equilibrium it is very complicated to assess minimum viable metapopulation size, or even the habitat quality requirements of a species. It is difficult to obtain unequivocal empirical evidence of extinction debt, due to the time scales involved, but this is certainly an area for further research.

Where habitat networks are already small, habitat restoration must become an integral part of conservation if the species is to be maintained within these networks. Increasing evidence (discussed above) suggests that current network size in many cases is insufficient for long-term persistence. Where species persists in partially degraded landscapes, with unsuitable but potential habitat, metapopulation persistence may be increased through restoration. Habitat management that improves unsuitable habitat for occupancy is important, for example by increasing grazing on ungrazed sites and reducing such pressures on overgrazed sites. Increasing habitat network size up to or exceeding a threshold level for persistence will be difficult in the smaller networks, as the amount of habitat available for such action will be much reduced. To be most effective, sites targeted for restoration should be close enough to existing occupied habitat to allow natural colonisation (Dobson *et al.* 1999).

Much of this work poses the question of where scarce conservation resources should be targeted for species conservation in fragmented landscapes. There are two options. Firstly, concentrate effort in the core regions to ensure that no further habitat is lost and ensure that species will survive in at least these areas. This is probably the most cost-effective option, protecting all habitat patches within a network from further degradation and enhancing metapopulation size through habitat restoration. There will then be little need for more expensive habitat re-creation.

The second alternative is to concentrate efforts on the periphery, in the areas most at risk from extinction. This has some attractions, as there is concern that different populations across a species range may contain evolutionary distinct populations (Thomas *et al.* 1999; Joyce & Pullin 2001). However, peripheral populations, which possibly consist of small and isolated populations, are more prone to loss of genetic diversity through inbreeding (Saccheri *et al.* 1998) and the greatest diversity is probably maintained within the largest metapopulations. To conserve metapopulations at greatest risk from extinction would require a great increase in habitat area. For some networks, this may mean at least a doubling of habitat area. This is possible if sufficient habitat is available to be restored, but very unlikely for most species in most current landscapes. Habitat re-creation would be necessary in many networks, but will be the most expensive option, requiring manipulation of the nutrient status of improved habitats (Adams *et al.* 1999) and a vast amount of suitable seed. In most biological systems, habitat re-creation is more expensive, more difficult and less likely to be successful than maintaining existing habitats. It is an option of last resort when no viable systems remain.

In conclusion, conservation research must consider the relative contribution of patch size, spatial location, habitat quality and interaction with other species, such as natural enemies, on the occupancy and persistence of species in fragmented landscapes. However, the observed pattern of occupancy may be further complicated by extinction debt and non-equilibrium systems, which may mean that our estimates of minimum viable metapopulation size are insufficient to secure long-term persistence.

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