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The marsh fritillary butterfly in the Avalon Marshes, Somerset: A study on habitat restoration and the re-establishment potential

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The Marsh Fritillary butterfly in the Avalon Marshes, Somerset: A study on habitat restoration and the re-establishment potential

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Saving butterflies, moths and their habitats

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Summary

The purpose of this study is to investigate the re-establishment potential for the Marsh Frtillary in the Avalon Marshes. Furthermore, the aim is to identify measures that achieve restoration of the vegetation at Shapwick Heath National Nature Reserve (NNR) to "favourable condition" *and* habitat restoration for the Marsh Fritillary butterfly, and to identify any bottlenecks during habitat restoration or when maintaining habitat conditions in the future.

Re-establishment potential for the Marsh Fritillary butterfly

To enable a successful re-establishment of the Marsh Fritillary butterfly, it is necessary to restore the former habitat on Shapwick Heath NNR in the areas known as the Lows north and south and on Ashcott plot, and to restore/create habitat in other overgrown areas and re-profiled peat excavations on this reserve. This viable meta-population can be further extended to include the former colony on Catcott Heath, and the colony on Street Heath with the aid of stepping-stone patches on Ham Wall NNR. Re-establishment of the Marsh Fritillary butterfly will be most successful when all conservation bodies in the area contribute to providing Marsh Fritillary habitat, thus ensuring that the amount of available habitat in the meta-population is maximized.

Habitat restoration experiments

Conclusions can only be drawn after certain experiments have been monitored for at least three years, but the experiments have already put forward important points.

Bottlenecks in the restoration phase
A necessity to realize re-establishment of the Marsh Fritillary is increase in cover and re-establishment of the butterfly's host plant Devil's-bit Scabious. This study has shown that patches where the plant is now present have higher fine grasses cover, are more species-rich, drier and less acidic and have a lower percentage of Purple Moor-grass and competitors in the species composition than patches were the species is absent. However, fine grass patches without Devil's-bit Scabious also occur, suggesting that re-colonization of suitable patches is limited, probably because of the species' poor dispersal capacity and absence of a seed bank.

The aim of the current intensive grazing regimes is to restore the vegetation to "favourable condition". However, it is likely that they will not result in increase in cover or re-establishment of Devil's-bit Scabious. This study has shown that the high stocking rates prevent flowering and seed setting of the few remaining plants, thus hindering dispersal and increase in cover. If English Nature wants to restore the vegetation to "favourable condition" *and* restore the habitat of the butterfly, additional measures are necessary to realize the required re-establishment and increase in cover of the host plant. Optional measures are sowing and planting of Devil's-bit Scabious, and management regimes under which planting and sowing of the host plant are most successful are being investigated as part of this study.

The seeds sown in this first year of the study have not germinated. It is thought that this can be attributed to the viability of the seeds and not to the conditions created by application of the treatments. It is thought that subsequent sowings will be more successful.

Establishment of Devil's-bit Scabious transplants has been successful during the first six months of the study. All transplants protected from grazing established and the majority flowered. Most of the transplants that were grazed established, but almost none flowered. The

establishment success can however not be judged from this short period of time only as similar studies on other species recorded considerable mortality in the subsequent three years.

Bottlenecks in the habitat maintenance phase
Restoration management in one of the study areas consists of sheep grazing. The results of the study investigating the effects of grazing on Devil's-bit Scabious suggest that even at low stocking rates, sheep select for the fine grass patches containing the host plant and possibly also select for the species itself. This selective grazing results in small plants with a low biomass, while the female butterfly requires large host plants with a high biomass for egg laying. If sheep grazing is to be continued in the future after the site has been sufficiently restored, this might hinder re-establishment of the Marsh Fritillary butterfly because of the effect sheep grazing would have on the butterfly's host plant.

Recommendations

Re-establishment potential for the Marsh Fritillary butterfly

Firstly, it should be emphasized that re-establishment of the Marsh Fritillary butterfly will be most successful when all conservation bodies in the area contribute to providing Marsh Fritillary habitat, thus ensuring that the amount of available habitat in the meta-population is maximized.

To enable a successful re-establishment of the Marsh Fritillary butterfly, it is recommended that:

- The former habitat in the Lows north and south and on Ashcott plot at Shapwick Heath NNR is restored, with additional habitat restoration/creation in other overgrown areas and re-profiled peat excavations on this reserve.

- This viable meta-population is further extended to include the former colony on Catcott Heath and Street Heath. To realize this, habitat restoration is necessary on Catcott Heath and on Street Heath, as well as further habitat restoration/creation in re-profiled peat excavations on Ham Wall NNR.

Habitat restoration experiments

To continue the initiated experiments and to further investigate the habitat restoration potential, future work should comprise:

- application of the treatments in the experimental plots for at least three consecutive years, with monitoring of the vegetation in June. The timing of the hay cuts should be June for one hay cut and June and September for two hay cuts. Furthermore, grazing on the Lows and on Ashcott plot south should ideally commence as early in spring as possible;
- reseeding half of each sown plot in a density of 5kg seeds per hectare, coinciding with the natural seed fall in autumn, and subsequent monitoring of germination and establishment of Devil's-bit Scabious for at least three consecutive years;
- experiments that investigate factors that influence viability and germinability of Devil's-bit Scabious seeds;
- monitoring of the survival and condition of the Devil's-bit Scabious transplants.

Furthermore, consideration should be given to the possibilities of protecting some patches where Devil's-bit Scabious is present from grazing, in order to encourage dispersal and increase in cover of the host plant.

Contents

1 Introduction

The extent of semi-natural grassland in England and Wales has declined considerably during the second half of the 20th century. Fuller (1987) estimated that by 1984, unimproved or semi-natural grasslands dominated by indigenous species covered only 600,000 hectares, a loss of 92% since 1932. Moreover, he stressed that much of the grassland recorded as unimproved may not be of special value for nature conservation. Indeed, Blackstock and others (1999) have shown that of the 600,000 hectares estimated by Fuller, only 50,000-100,000 hectares are of particular conservation value; communities of special floristic interest represent only 1-2% of the permanent lowland grassland cover. The main causes for the decline are changes in hydrological conditions (drainage), resulting in desiccation; eutrophication and acidification; ploughing; application of artificial fertilizers and abandonment of sites (Fuller 1987; Bakker & Berendse 1999).

Furthermore, a lot of the vegetation communities are represented in small fragmented and often isolated stands and conservationists are concerned that small patch size, fragmentation and remoteness of remnant grasslands pose a threat to the survival of specialist species associated with these habitats (Blackstock and others 1999). In particular habitat specialist butterfly species which are thought to function as meta-populations, and which can be used as ponderous indicators for the health of ecosystems (New and others 1995; Oostermeijer & van Swaay 1998; Griffis and others 2001), suffer from the increasing fragmentation of their habitats and are declining rapidly as a result (Asher and others 2001).

Blackstock and others (1999) have estimated the extent of semi-natural grassland communities in England and Wales based on several studies. Notably damp grasslands are now highly fragmented within their remnant heartlands in western Britain. They have estimated that there are some 9000-17,500 hectares of wet lowland grassland of conservation interest remaining in England and Wales and the mean extent per site does not exceed 2 hectares. The predominantly low cover estimates for certain communities stresses the need for continued protection of surviving stands, mitigation of the effects of severe depletion, restoration of swards and, where practicable, expansion of stands (Blackstock and others 1999). Purple Moor-grass and Rush pastures deserve particular attention, as they are often overlooked in conservation programmes (Blackstock and others 1999).

The subject of this study is a M25 *Molinia caerulea – Potentilla erecta* mire community[1]. Of this community, about 4000-8000 hectares remain in England and Wales, with a mean extent of 2.2 hectares per site (Blackstock and others 1999). Three subcommunities can be distinguished; the *Erica tetralix* sub-community M25a which is more heathy, the *Anthoxanthum odoratum* M25b subcommunity which is more grassy, and the *Angelica sylvestris* M25c subcommunity which is more herb-rich (Rodwell 1991; Averis and others 2004). Although Purple Moor-grass can be very dominant, these communities are not devoid of interest for nature conservation. Notably at lower altitudes the vegetation can be species-rich (Averis and others 2004) and contain plants like Lesser Butterfly Orchid (*Platanthera bifolia*), Bog Asphodel *Narthecium ossifragum* and Ivy-leaved Bellflower (*Wahlenbergia hederacea*). Endangered invertebrates associated with the community are for example Narrow-bordered Bee Hawk-moth (*Hemaris tityus*) and the Marsh Fritillary butterfly (*Euphydryas aurinia*).

Encroachment of Purple Moor-grass is a considerable problem in certain vegetations. A lot of factors are thought to be linked to the advance of Purple Moor-grass, notably desiccation, eutrophication, acidification, inappropriate burning and/or grazing regimes (Milligan and others 2004), abandonment of sites, and in The Netherlands atmospheric deposition of

[1] See Rodwell (1991; 1992) for NVC communities and codes.

nitrogen (Berendse & Aerts 1984). The overwhelming dominance of Purple Moor-grass results in species-poor stands. Restoration measures aimed at recovering a species-rich vegetation in these Purple Moor-grass stands often comprise highly intensive management like grazing with high stocking rates, burning, mowing and/or scrub clearance over short timescales (Hobson and others 2001), which is known to have a detrimental impact on invertebrates (Kirby 2001; Sheppard 1999). For example, "over-enthusiastic" restoration management is thought to be strongly linked to the recent decline of the Marsh Fritillary butterfly on nature reserves (Hobson and others 2001). However, habitat restoration can be effective (e.g. Bulman 2001) and might not harm the present invertebrate community as long as drastic management measures are not taken across the whole site at the same time (Sheppard 1999). Restoration management will be most effective when areas are targeted where aggregations of similar grasslands occur (Blackstock and others 1999) especially when re-establishment of associated invertebrate communities that function at a metapopulation level is desirable (Thomas and others 1992; Thomas 1994; Thomas 1995; Bulman 2001).

In the Avalon Marshes, extensive areas of M25 mire occur in close vicinity to each other. The areas have suffered severely from drainage caused by neighbouring peat excavations resulting in Purple Moor-grass and scrub encroachment, and the areas are now in "unfavourable condition". As part of English Nature's Public Service Agreement, the objective is that the areas are in "favourable condition", or "unfavourable recovering condition" by 2010[2]. The mire vegetations used to form suitable habitat for the Marsh Fritillary butterfly, however, Purple Moor-grass encroachment, scrub invasion and subsequent management regimes implemented to counteract these problems, coupled with environmental stochasticity and demographic stochasticity that played an enlarged role in the dwindling Marsh Fritillary populations, resulted in local extinction in 1995 (Borsje 2004b). A sustainable re-establishment of the butterfly in the Avalon Marshes is desirable, and the extensive, well connected areas of mire vegetations on and around Shapwick Heath NNR might offer opportunities to realize this. Restoration management (grazing, burning, topping) aimed at achieving "favourable condition" for the mire vegetations has already been applied for an number of years in the areas.

However, vegetation communities, like the M25 *Molinia caerulea-Potentilla erecta* community and subcommunities, exhibit a wide range of variation in composition and structure (Blackstock and others 1999). Several rare and declining grassland species, among which the Marsh Fritillary, are dependent on certain specific properties within these vegetation communities in terms of the species composition (eg plentiful large, lush host plants available) and structure of the sward (eg a patchwork of short vegetation and long tussocky grasses). Therefore, restoring the vegetation to "favourable condition" does not necessarily imply habitat restoration for the Marsh Fritillary butterfly. Bottlenecks might arise, and the implemented restoration measures might be unsuccessful in achieving both objectives.

To be able to identify any bottlenecks, or to evaluate the successfulness of the implemented measures, it is important to clarify the conditions that have to be met for both aims to be achieved, because evaluation and monitoring can only take place if targets are clearly defined (Bakker and others 2000). The next section describes the objectives for the study area, followed by section 1.2 that discusses the aims of this study.

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[2] For more information on the Public Service Agreement, and the designation of sites in the condition categories, see appendix I

1.1 The bilateral objectives in the study area

The two objectives in the study area are:

I - Restoration of vegetation

In order to realize restoration of the vegetation to "favourable condition", the following targets have to be achieved[3]:

- A decrease in cover of Purple Moor-grass
- A decrease in cover of scrub and tree species
- An increase in species-richness
- An increase in indicator species[4]

The **aim after restoration** is:

- An extensively grazed poor fen and heath system

II – Restoration of habitat for the Marsh Fritillary butterfly

In order to realize the re-establishment of a viable meta-population of the Marsh Fritillary butterfly, habitat restoration is necessary. The following targets have to be achieved:

- An increase in abundance of the host plant Devil's-bit Scabious where the plant is still present and re-establishment and subsequent increase in cover of the plant in compartments where it is now absent.

The **aim after restoration** is to have:

- Extensive cattle grazing, aimed at creation and maintenance of a patchwork of short vegetation and tussocky grasses (vegetation height between 8-25 cm) where large lush host plants suitable for egg laying are present in abundance.

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[3] Targets, practical in the frame of this study, have been extracted from the Common Standards Monitoring (CSM) targets for lowland purple moor grass and rush pastures. For CSM targets, see Joint Nature Conservation Committee (2004)

[4] See Joint Nature Conservation Committee (2004) for positive indicator species for M25 mire communities.

1.2 Aim of the study, research questions & structure of the report

The aim of this study is to answer the following questions:

Is a sustainable re-establishment of the Marsh Fritillary feasible in the Avalon Marshes?

What are suitable measures to achieve both restoration of the vegetation and habitat restoration for the Marsh Fritillary butterfly, and do any bottlenecks occur during the habitat restoration phase or will they arise when maintaining the habitat conditions in the future?

These questions will be answered by carrying out a number of studies and experiments, aimed at answering the following research questions:

1. Is suitable Marsh Fritillary habitat present on Shapwick Heath NNR and what areas on the reserve have a high potential for the species?

2. Is a sustainable re-establishment of the Marsh Fritillary butterfly in a viable meta-population structure feasible in the Avalon Marshes?

3. Is it possible to realize favourable conditions for germination and/or establishment of Devil's-bit Scabious by means of different management regimes and the resulting differences in habitat characteristics at micro-scale?

4. Is it possible to significantly reduce the cover of Purple Moor-grass and scrub species in favour of forbs and fine grasses by means of different management regimes?

5. Are viable Devil's-bit Scabious seeds present in the soil seed bank of the mire vegetations?

6. What factors are associated with the presence and/or abundance of Devil's-bit Scabious in the mire vegetations?

7. How do the restoration grazing regimes affect the Devil's-bit Scabious plants in the mire vegetations?

8. Is establishment of Devil's-bit Scabious by means of transplants a possibility in the mire vegetations and what factors influence the success rate?

The study will give insight in the re-establishment potential for the Marsh Fritillary butterfly in the Avalon Marshes, and the measures necessary to achieve this. Moreover, the study yields valuable knowledge about habitat restoration for the Marsh Fritillary and restoration of mire vegetation suffering from Purple Moor-grass and scrub encroachment in general.

The studies and experiments carried out to answer the research questions are discussed in separate sections. In some of these sections, these research questions are treated as main questions with their subsequent research questions.

2 Context, the study species and study area

2.1 Species diversity, habitat management and habitat restoration

Species communities, species strategies and species diversity

A plant community can be defined as a collection of species growing together in a particular location that show a definite association or affinity with each other. The species are found growing together in certain locations and environments more frequently than would be expected by chance (Kent & Coker 1992).

The reason that certain species grow together in particular environments is because they have similar requirements for existence in terms of environmental factors such as moisture, pH, nutrients availability, or they may all be able to tolerate factors such as grazing, burning, cutting or trampling. Plant species have a certain need (minimum requirement) and tolerance (maximum permissibility) for all these factors and the optimum abundance for a certain species is often reached in between of the two extremes. The resulting curve often approximates a normal curve and is known as the ecological amplitude. Width, height and the form of the curve for each species will be different, as their tolerance ranges differ. The occurrence and abundance of different plant species enables ecologists to make statements about the prevailing environmental conditions (Schaffers & Sykora 2000). An extensively used system of indicator values is that of Ellenberg (Ellenberg and others 1992) which is widely used in vegetation assessment, both to estimate soil variables from vegetation relevés as well as to predict vegetation composition from given soil variables (Wamelink and others 2002).

Other important factors determining the composition of a vegetation are the properties of the plants themselves. Through evolution, a plant species has evolved a set of characteristics that enable it to survive in certain environments. Numerous components of the life history of a plant vary to produce different strategies. Grime and others (1988) has developed the C-S-R model, which proposes that the vegetation that develops in a particular place and at a particular time is the result of an equilibrium between the intensities of stress, disturbance and competition. Stress consists of phenomena that restrict photosynthetic production, such as shortages of light, water and mineral nutrients. Disturbance is associated with the partial or total destruction of the plant biomass, eg burning, cutting and grazing. These two factors are thought to form the basis for the evolution of three plant strategies in plants; *competitors* exploit conditions of low stress and low disturbance, *stress-tolerators* are associated with high stress and low disturbance while *ruderals* are characteristic of low stress and high disturbance. Others exploit the various intermediate conditions (Grime and others 1988). Stress and disturbance control the intensity of competition by restricting the density and vigour of the vegetation. This results in immediate impacts on the present plants, while on the longer-term control occurs by means of selective effects on extinctions and immigrations. Where stress and disturbance are low, highly competitive plants will become dominant; diversity is suppressed by the explosive development of biomass of the dominant species. Most species-rich swards of high botanical interest have developed in nutrient-poor conditions that have reduced growth rates that allow a rich variety of slow-growing stress-tolerant plants to coexist. Vegetation management maintains these species-rich plant communities by sustaining the nutrient poor conditions, by carrying off nutrients and by suppressing potential dominants, through grazing, cutting or burning. In the absence of vegetation management, swards can become dominated by coarse grasses and a litter layer builds up which smothers smaller plants and reduces the availability of gaps in the sward available for germination. The build-up of litter often results in an increase in nutrient levels and organic matter in the soil, thereby further promoting competitors to the detriment of the species-richness of the sward.

Maintenance and restoration vegetation management

High species and community diversity are associated with a high degree of constancy in environmental factors, and management practices like burning, grazing and cutting with a regular frequency and constant intensity are considered to be system-inherent environmental factors (Bakker 1989). Therefore, when the nature conservation interest is already high, maintenance management is required, preferably of the type, intensity and timing the site has received before. When the nature conservation interest of a site has decreased significantly, restoration management is required aimed at restoring an area so that it matches the vegetation community that existed previously at that site (Bakker & Berendse 1999). Restoration management includes both practices carried out only once (like disturbance) and regular management practices (like grazing and cutting). The regular management types are discussed below.

Grazing

There are three major components of the grazing process (Crofts & Jefferson 1999): defoliation, trampling and manuring. Defoliation is the removal by animals of some or all of the above ground parts of plants, which may be dead or alive. Except at high stocking densities, grazing is a gradual form of vegetation removal. Grazing is selective, and effects the species composition and structure of the sward. The quantity of more palatable species is reduced, while grazing resistant plants like rosette forming herbs and unpalatable forbs and grasses become more frequent. At higher stocking rates grazing is often less selective and older tougher plant material and coarse grasses are also eaten, which can be useful during restoration management. Grazing prevents dominance of competitive species by continually removing their additional biomass. Extensive grazing creates and/or maintains a varied vegetation structure consisting of a mosaic of different grassland types and heights (Bakker 1989; Ausden & Treweek 1995).

Grazing also creates physical disturbance to the vegetation and soil, which is important in providing suitable conditions for seedling germination and for invertebrates that require bare, sparsely vegetated or disturbed ground. Most of the nutrients removed by grazing are returned to the grassland through urine and dung (Bakker 1989), and the distribution of dung will determine where these nutrients are returned. As well as causing local nutrient enrichment, the avoidance of grazing around these areas results in local patches of taller vegetation (Ausden & Treweek 1995). Long-term dunging is thought to have no net enrichment effect beyond these localised latrines (Crofts & Jefferson 1999).

Stocking density influences the quantity of the vegetation removed, which influences the species composition of the sward and its structure. Conservation objectives generally require stocking levels that are lower than the carrying capacity of the grassland. This makes a significant proportion of the biomass available to other food chains like invertebrate herbivores and decomposer communities, and also enhances the structured diversity of the habitat (Crofts & Jefferson 1999). Stocking levels are often expressed in Livestock Units per hectare (LU/ha), a system that takes the quantity of vegetation removed for different types of stock into account.

Different animal species differ in their grazing behaviour and selectivity and this grazing behaviour and selectivity influences both the species composition and structure of the sward.

Cattle prefer to eat longer grass, which they pull into their mouth with their tongue before it is bitten off using the incisors. They cannot graze very close to ground level; they graze and maintain longer swards. Cattle have thick, wide immobile lips and cannot manipulate the vegetation effectively. As a result, they do not graze selectively; they cannot select for certain species growing within a fine mixture and do not select for flowerheads (Ausden & Treweek 1995; Crofts & Jefferson 1999). Cattle do utilize rough tall and tussocky swards and also dead material and litter is taken (Crofts & Jefferson 1999). Cattle are most suitable for creating and maintaining a structurally diverse sward of benefit to invertebrates (Crofts & Jefferson 1999; Kirby 2001). Through most of the United Kingdom, the traditional management of the damp grasslands used by the Marsh Fritillary is extensive cattle grazing (Warren 1994) and it is thought to be the most suitable management to maintain the habitat of the butterfly (Butterfly Conservation 2004).

Sheep move more slowly over the sward and nibble the grass; they graze right down to close to ground level and produce very short swards. They have thin and mobile lips and as a result graze very selectively. They can select certain species growing in a fine mixture with other less preferred species and do also select for flowers. Sheep avoid rough and tussocky areas, while concentrating on the more herb-rich, palatable fine grass patches (Crofts & Jefferson 1999; Warren 1994). Sheep do browse low scrub from selected bushes. Heavy grazing by sheep produces a very short and even sward, which is poor for most invertebrates (Kirby 2001). Sheep grazing is thought to be unsuitable for managing Marsh Fritillary habitat, as sheep select for the fine grass patches containing Devil's-bit Scabious and possibly also for the host plants themselves, reducing them to small rosettes which are unsuitable for egg laying, while producing a short tight sward without the structure required by the butterfly (Butterfly Conservation 2001).

Goats graze or browse, but most goats are by preference browsers eating both trees and shrubs (Ausden & Treweek 1995). Goats can be of great benefit in neglected sites containing much scrub. It is thought that goats will browse more when kept mixed with sheep (Crofts & Jefferson 1999). Goats prefer Willow *Salix* spp, Alder *Alnus glutinosa* and Gorse *Ulex* spp, but avoid Birch *Betula* spp, and at high stocking rates they will eat Thistle *Cirsium* spp and rushes *Juncus* spp. The suitability of goat grazing for maintaining Marsh Fritillary habitat has not been studied, but it might be a useful grazing animal as Kirby (2001) and Ausden & Treweek (1995) mention that goats do create a varied structure when they graze a sward.

Cutting

Cutting differs from grazing in being a sudden and largely unselective form of vegetation removal, resulting in a sward of relatively uniform height and structure. Compared with grazing it encourages tall, bulky palatable herbs and other species usually intolerant of grazing, and those that depend on early seed set (Ausden & Treweek 1995). Aftermath grazing is thought to be important in hay meadows, as the hooves of livestock produce gaps providing sites for regeneration (Crofts & Jefferson 1999). Like grazing, regular mowing prevents the dominance of robust competitive grasses, herbs and the establishment of shrubs and trees, maintaining the vegetation as a grassland. If cuttings are removed, cutting will reduce soil nutrient levels, however, in restoration experiments this has proven to be a slow process (Bakker 1989). Bakker (1989) suggests that short-term changes in species composition resulting from cutting are largely due to changes in the structure of the sward as a consequence of timing and frequency of cutting. Hay cutting dates are principally dictated by the growth stage of the grass crop and the weather conditions, however, cutting should not take place before breeding birds have hatched or characteristic annual, biennial or short-lived perennial species have had a chance to set seed. In practice, cutting dates in conservation areas range from late June to late July. An occasional late cut (August/September) might be beneficial for late flowering species (Crofts & Jefferson 1999).

Constraints in the restoration of ecological diversity

Restoration management practices attempt to re-establish the often species-rich original plant communities by the removal of nutrients or the suppression of dominants through grazing, cutting or sod cutting after eutrophication, rewetting after severe drainage, and scrub removal after bush encroachment (Bakker and others 1996). However, in many short- and long-term studies in restoration management, most of the target species (rare and often endangered species characteristic of the concerning community) did not establish after years or even decades even though appropriate soil conditions were restored. Biotic constraints seem to be the main problem; often target species do not appear as they are lacking from the seed bank while seed banks often contain large amounts of non-target species such as Soft Rush *Juncus effuses* and Bulbous Rush *Juncus bufonius*. When seeds of target species are not present in the established vegetation or in the soil seed bank, they need to be dispersed from elsewhere. Nowadays however, the chances for target species to arrive at the concerning site are strongly reduced because of the extensive fragmentation of the landscape, resulting in a lack of local unimproved species-rich grassland to act as propagule emigration sources (Gibson and others 1987; Bakker & Berendse 1999). In order to aid the establishment of species-rich communities which include rare and endangered target species, it may be necessary to introduce these species by means of seeds or transplants (Bakker 1989; Davies and others 1999; Bakker and others 2002; Pywell and others 2002; Matus and others 2003). In studies involving sowing, inability to provide species-specific conditions for seedling recruitment seems to be one of the major factors limiting establishment (Isselstein and others 2002). Further research is necessary on practical methods to increase the successful establishment of poor-performing, but desirable target species (Pywell and others 2003).

Factors affecting seedling germination and establishment

Successful sexual regeneration by a plant depends upon its seeds being dispersed where they can germinate and establish seedlings. A large variety of structures and dispersal types of seeds exist among plant species (Bakker and others 1996). The transport of the ripened seeds away from the parent plant often involves an external agent such as wind, water, or animals such as sheep or birds. After dispersal, most seeds undergo a period of dormancy, which may last from a few days to many decades. In some species, a proportion of the seeds become incorporated in the seed bank (Fenner 1985). A seed bank is an aggregation of ungerminated seed potentially capable of replacing adult plants (Bakker 1989). Some generalizations can be made; if the environment is spatially unpredictable and rare, species have to feature long-distance dispersal, for example pioneer species in primary successions. If the environment is moderately predictable on a time scale and confined spatially, a persistent seed bank is a common strategy (Bakker and others 1996).

When seeds are dispersed from the parent plant they are scattered into a very heterogeneous environment in which few sites are suitable. Dormancy is a delaying mechanism, which involves a resting condition of the seed with reduced metabolic rate (Allaby 1998). This mechanism prevents germination under unsuitable conditions for establishment (Fenner 1985). In response to favourable external conditions, most notably warmth, moisture and oxygen, germination, the beginning of growth of the seed, does occur (Allaby 1998). Each species has its own characteristic set of germination requirements.

Regeneration from seed in most plant communities is dependent upon the occurrence of gaps in the vegetation because the conditions in closed vegetation are too harsh for the recruitment of new individuals; they are unable to capture enough resources to compete with the established plants. Gaps provide conditions in which competition is reduced or even absent. Gaps can arise because of outside factors like landslides, floods, fires, storms or the activities of burrowing or trampling animals, or an opening may be created by the death of a plant within the system itself (Fenner 1985). Factors such as light, temperature and moisture regimes are radically different in gaps compared to closed vegetation. It is thought that many of the responses that seeds make to specific germination cues are adaptations for gap detection. For example a lot of seeds require fluctuating temperatures to break their dormancy. A cover of vegetation acts as a very effective temperature buffer, while the temperature fluctuations in a gap can be considerable (Fenner 1985; Probert 1992).

After a seed has germinated, the seedling's growth is largely dependent on its own stored food reserves. As the growth of the root and shoot proceeds, dependence on internal resources is gradually reduced and external resources are being exploited. A seedling is considered to be established when it has become independent of its seed reserves (Fenner 1985). The hazards encountered during the process of establishment are numerous, but the main cause of death in seedlings seems to be desiccation. Other hazards are biotic factors such as predation, disease and competition. Competition from neighbouring plants, whether from contemporary individuals or pre-existing vegetation, is also a major hazard faced by colonizing seedlings and this is illustrated by the fact that mortality is highest in the growing season, especially in closed vegetation. One of the most effective adaptations plants have developed to ensure successful establishment of its seedlings is the possession of large seeds (Fenner 1985). This provides the seedling with an ample reserve of nutrients during the period immediately after germination, useful in achieving a certain critical size, and the position to capture external resources in competition with other plants. Furthermore, it is thought that mycorrhizal infection of the root system may be a significant phenomena in the process of seedling establishment on infertile soils. It has been found that within some herbaceous communities of infertile soils, the roots of individual plants of the same, or even different, species may become connected through a common network of investing hyphae through which assimilate appears to move from source to sink plants (Grime and others 1988; Kitajima & Fenner 2000).

2.2 Ecology of the Marsh Fritillary butterfly

Introduction

The Marsh Fritillary *Euphydryas aurinia* is a butterfly from the family *Nymphalidae* and the genus *Eurodryas* (Emmet & Heath 1990). The adult butterfly is very variable, with the ground colour of the upper side ranging from dirty yellow to bright orange or brick-red. It is heavily marked with pale-yellow spots and black cross-lines (Chinery 1998). Females tend to be a little larger and slightly less bright than males, but otherwise the sexes are alike (Chinery 1998; Emmet and Heath 1990).

Life cycle

Adults fly between May and mid July, with a peak period end of May to mid June. The males emerge first, often several days before females (Barnett and Warren 1995). Males survive an average of four days, and females three days (Emmet and Heath 1990). After mating, females search for prominent plants of Devil's-bit Scabious in a slow ponderous flight (Emmet and Heath 1990). The first batch is typically laid in the natal habitat patch because the females are so egg-laden that they are not able to fly long distances (Porter 1981). Females lay an egg cluster on the underside of relatively large leaves of Devil's-bit Scabious, adjacent to the central rib (Emmet and Heath 1990). The egg batches contain up to 350 eggs, subsequent batches are smaller (about 50-150 eggs) (Asher and others 2001). The eggs hatch within 30 to 40 days, and the freshly emerged pale ochreous first instar larvae immediately create a 'sandwich', a feeding web made by spinning together two leaves of Devil's-bit Scabious. The earliest signs of feeding are brown patches on the upper surface of the leaf as the larvae consume the lower epidermis. Second-instar larvae feed together inside a silken web spun over part of the foodplant (Emmet and Heath 1990). After approximately 25 days, the larvae enter the third instar and the web is extended over large areas of host plant, as the feeding requirements increase (Porter 1981).

The fourth, fifth and sixth instars exhibit a basking behaviour on sunny days. In applying the strategy of basking, larvae of Marsh Fritillaries are thought to be relatively independent of ambient temperatures. They enhance their growth rate in a low temperature environment by reaching their optimum temperature faster. As a result the peak metabolic rate is reached sooner and food assimilation rate can be maximised. This allows them to develop faster than would be predicted from looking at ambient temperatures (Porter 1982). Background is a prominent feature of the basking behaviour; dry, dead vegetation such as oak leaves and grasses are chosen on the basis of their solar radiation absorbance-reflection characteristics (Porter 1982).


Marsh Fritillary adult


Marsh Fritillary egg batch

In early September the fourth instar larvae construct a dense hibernaculum web at the base of the vegetation and over-winter in this state (Porter 1981). The larvae emerge from this ball of silk on sunny days in February, often returning to dormancy if weather conditions deteriorate. In March they are feeding together in discrete groups, spinning webs and basking in sunshine. In early April they change into the fifth instar and start feeding in small groups of 5-20 and by late April they feed alone and moult a final time (Emmet and Heath 1990). The pupa is 12-15 millimetres long and is often attached to a leaf or stick. The duration of this stage is 16-26 days, depending upon ambient temperature.

Colonies of the species fluctuate tremendously in size from year to year (Emmet & Heath 1990). It is suggested by Porter (1983) that, next to the direct influence of weather, the indirect influence of weather on the pupal development of the parasitoid *Cotesia bignellii* contributes towards these population fluctuations. This parasitic wasp is specific to the Marsh Fritillary, and has several generations in one generation of the butterfly. The parasitoid is very dependent upon synchrony with its host. If synchronisation was always perfect, Marsh Fritillary populations would be held at very low levels, or might even be driven to extinction. The vulnerable phase in the maintenance of synchrony is thought to occur when spring generations of *Cotesia bignellii* have to oviposit in late instar hosts. When spring weather is cool but sunny, the larvae of the butterfly develop faster through their basking behaviour than the parasitoid, resulting in the host having already pupated before the majority of female parasitoids have emerged (Porter 1983). The parasitoid probably occurs in a meta-population structure, as the host acts as a 'patch' of suitable habitat and these parasitoids are possibly even more rare and endangered than their hosts (Bulman 2001).

Marsh Fritillary larvae

Marsh Fritillary habitat, Goss Moor, Cornwall

Mobility

Males and females do not wander far from their emergence ground until late in the flight period, by which time most females have finished egg laying (Emmet and Heath 1990). Porter (1981) recorded average movements of less than 100 metres within a site. Wahlberg and others (2002) found average movements of 645 metres (±69, maximum 1300) for males and 467 metres (±43, maximum 510) for females in Finland. However, colonisation has been recorded some distance from known populations (between 5 and 20 kilometres) which suggests that at least some individuals may be more mobile than generally thought (Warren 1994).

Habitat & ecological requirements

In the United Kingdom, the Marsh Fritillary occurs in two main biotopes; damp, neutral or acidophilous grasslands and dry, calcicolous grasslands (Barnett and Warren 1995). Only damp grassland habitats are discussed here.

The Marsh Fritillary breeds in discreet areas of unshaded, flower-rich damp grasslands, containing a mixture of rushes, marshy grassland and in the south west of England, wet heathland (Butterfly Conservation 2001). The National Vegetation Classification communities associated with these damp grasslands are shown in table 2.1 (Warren 1994).

Table 2.1 The National Vegetation Classification communities in which Marsh Fritillary habitat can be found.

NVC communitues	Region
Mosaics of fen meadow (M24) and/or mire (M25 sometimes with M6) with wet heath (M16) and/or rush pasture (M23)	Cornwall, Devon, Somerset
Mosaics of fen meadow (M24) and/or mire (M25) with neutral grasslands (MG5) and their imtermediates	Dartmoor, Somerset, Cumbria
Mosaics of mire (M25) and acid grasslands (U4) with Bracken	Cornwall and Dartmoor

The best breeding areas seem to be a patchwork of short vegetation and long tussocky grasses such as Purple Moor-grass on more acidic soils, or Wavy Hair-grass *Deschampsia flexuosa* on more neutral soils (Warren 1994). A study by Hobson (1997) showed that the majority of the occupied compartments had a sward height of between 12-25 centimetres. Bulman (2001) also found vegetation height to be an explanatory variable for patch occupancy. Her conclusion was that patches with taller vegetation have a higher probability of being occupied. When managing grasslands for the Marsh Fritillary butterfly, the recommendation is to aim for an uneven sward between 8-25 centimetres (Butterfly Conservation 2004).

The relative abundance of the larval host plant Devil's-bit Scabious is also an important factor determining habitat suitability. Hobson and others (2001) showed that a vast majority of occupied compartments had at least patchy, locally abundant Devil's-bit Scabious. Wahlberg and others (2002) and Anthes (2002) also found that density of flowering Devil's-bit Scabious (number of plants per hectare) partly explained the occupancy of a patch, as did Bulman (2001). She combined this factor with another important explanatory variable; patch area, naming this combined variable 'resource area' (% cover of Devil's-bit Scabious x patch area). She mentions that as a result of resource area being a significant variable, a large habitat patch with a low density of host plant may be no more suitable then a smaller patch with a high density of host plant. Patch area was also found to be an important explanatory variable by Wahlberg (2002), and Anthes (2002).
Since Marsh Fritillary colonies function as meta-populations as described by Hanski (1999), connectivity (the degree of isolation of a habitat patch) is an important factor in explaining habitat occupancy (Anthes 2001; Bulman 2001). Wahlberg and others (2002) used the same equation for connectivity as was used by Bulman and Anthes, but they found that this variable did not significantly improve their model for predicting the occurrence of the butterfly.

Distribution and status

The range of the Marsh Fritillary extends from south Scandinavia to north Africa and from the west of France and the United Kingdom via the temperate zone of Asia to Korea (Ebert & Rennwald 1991; Maes & Van Dyck 1999). Within its European range the butterfly is declining rapidly (Asher and others 2001); it is extinct in Flanders in Belgium since 1959 (Maes & Van Dyck 1999), and in The Netherlands since 1984 (Wynhoff and others 1999). It has a major stronghold in the United Kingdom with more than 20% of the north-western European colonies probably located here (Barnett and Warren 1995; Warren 1994). However, the results of a recent survey indicate an accelerating rate of decline for Marsh Fritillary populations; between 1970-1990 the estimated rate of decline was 29% (Warren 1994), in the period between 1990 and 1999/2000 a decline rate of 66% has been identified, a doubling in just ten years (Hobson and others 2001). This trend is mirrored by the findings in the Millennium Atlas of Butterflies in Britain and Ireland (Asher and others 2001) that identified a continued range contraction. The butterfly has disappeared from 55% of the 10 kilometre squares recorded in 1970-1982. It is now extinct in the eastern half of Britain (Asher and others 2001), although it is still quite widespread in parts of southwest England and Wales (Barnett and Warren 1995). However, colonies are disappearing fast; an overall population loss of 56% has been recorded over 1990-1999/2000. Moreover, 63% of these populations were classified as small and only 20% as large or above (Hobson and others 2001). Bulman (2001) has shown that, assuming the rate of decline as observed continues, a 48 % decline in occupied 10 kilometre grid squares can be expected in 2020, with the surviving grid squares located in the south and south-west of England and south-west Wales. The conservation status of the species is high; it is listed in the UK Biodiversity Action Plan as a Priority Species and it is a high priority species for Butterfly Conservation. The European status is vulnerable; it is listed in the Bern Convention (Annexe II) and in the EC Habitats and Species Directive (Annexe II).

Factors affecting the butterflies habitat

According to Asher and others (2001), the decline of the Marsh Fritillary is linked to three main factors. As a result of ploughing and agricultural improvement there has been a massive loss of unimproved grassland. For example in south-west England, the area of damp pasture was reduced by 92% (Asher and others 2001). The Marsh Fritillary has also suffered greatly from changes in management in the fragments that remain; much habitat is not managed at all or managed too intensively. The species requires light grazing by cattle or ponies, and cannot tolerate heavy grazing, especially during summer. Hobson and others (2001) found that a lot of sites that lost Marsh Fritillaries recently are in an unfavourable condition for the species. 37% of the sites are over-managed, 36% are under-managed or not managed at all, and 1% has been lost through improvement. This indicates that potential exists for habitat restoration. Marsh Fritillary populations function at a landscape scale (Bulman 2001); the species is extremely prone to local extinctions, which can be balanced by its ability to colonize sites, but only within a certain range. It seems to have survived in areas where numerous habitat patches still exist; in many areas, potential habitat patches are too small and isolated to support the species (Asher and others 2001; Bulman 2001).

The decline and extinction of the Marsh Fritillary in the Avalon Marshes

When considering the history of the Somerset Levels, it seems likely that large areas of suitable Marsh Fritillary habitat must have existed in the area in the past. The Levels were drained from the 13th century onwards, resulting in extensive areas of marshy pasture and meadow. These large areas of extensively used, unimproved grasslands must have offered excellent habitat for the Marsh Fritillary. From the 18th century onwards, drainage became more intensive when rivers were straightened and channels were dug to ‘improve’ the land. Furthermore, farmers started fertilizing and using the meadows and pastures intensively, which made the areas unsuitable for the Marsh Fritillary. Finally, the amount of habitat for the butterfly was significantly reduced as a result of the commercial peat excavations that took place in the area from the 1960s onwards.

A large meta-population of Marsh Fritillaries must have existed in the Avalon Marshes, but unfortunately, by the 1960s, the meta-population was reduced to three colonies on Shapwick Heath NNR (two colonies in the Lows and one on Ashcott plot), and one on each of the nature reserves Street Heath, Westhay Moor NNR and Catcott Heath. The species persisted until the early 1990s. Then, management problems arose; because of neighbouring commercial peat excavations, it was not possible to maintain a high water table on the nature reserves and the habitats suffered from desiccation. This resulted in Purple Moor-grass and scrub encroachment, which left parts of the habitat unsuitable for the species. Other parts of the habitat were managed too intensively, or in a way that was unsympathetic to the needs of the butterfly, for example regular cuttings. These factors, together with environmental stochasticity and demographic stochasticity that played an enlarged role in the dwindling populations, probably caused the butterfly’s local extinction in 1995. The nearest extant populations of the butterfly are located more than 25 kilometres away in the Blackdown Hills near Taunton. This is too far away to allow re-colonisation through natural means.

Fourth instar larvae spinning a hibernaculum web

Former overgrown Marsh Fritillary habitat in the Lows north, Shapwick Heath NNR.

2.3 Ecology of the host plant Devil's-bit Scabious

Devil's-bit Scabious is a polycarpic perennial with a short vertical rhizome bearing a rosette of leaves in opposite pairs and fused at the base (Grime and others 1988; Adams 1955). The plant is wintergreen and flowers from July to October. The flowers are purple and normally insect-pollinated although self-pollination is possible (Grime and others 1988). The fruits mature within one month (Grime and others 1988). The seeds are surrounded by a persistent calyx, which is dry and hairy and increases the surface area of the seed. The species has no well-defined dispersal mechanism (Grime and others 1988). Wind dispersal has been observed but this only occurs over short distances (Soons & Heil 2002). Adams (1955) and Bakker and others (2002) mention that the species can also be dispersed by livestock. In general, the species is poorly dispersed and most seeds fall close to the parent plant, resulting in clusters of seedlings (Adams 1955; Grime and others 1988). No buried seed bank has been reported (Grime and others 1988). Seedlings have been found to appear on permanent quadrats at almost all times of the year by Adams (1955), though Grime and others (1988) found that the species regenerates almost entirely by seed in spring. Next to reproducing sexually, the species also reproduces asexually by means of lateral emerging new rosettes (Adams 1955; Grime and others 1988, Hartemink and others 2004), however, effective reproduction seems to be mainly by seed, as lateral shoot production only occurs occasionally and does not cause spreading to more than a few centimetres (Adams 1955). The roots of the plants are thought to be infected with mycorrhizas (Grime and others 1988).

Flowerhead of Devil's-bit Scabious.

Rosettes of Devil's-bit Scabious.

Devil's-bit Scabious is a slow growing herb which exploits sites where the growth of potential dominants is restricted by a low level of soil fertility and often also by grazing and/or hay cutting. The species is strongly associated with continuously moist habitats, however, it is also, though rarely, found in waterlogged sites other than in soligenous mire or on tussocks of other species (Grime and others 1988). In unproductive grasslands, the species is characteristic of soils of intermediate pH, with maximum frequency reached in the 5.5-6.5 range. However, it is also found on a wide range of other soil types, including calcareous mineral soils (Grime and others 1988). In grazed habitats, the flattened rosettes of Devil's-bit Scabious often escape predation and they are fairly resistant to trampling (Adams 1955; Grime and others 1988). Bühler and others (2001) have shown that in a fen, the type of management, either mowing or grazing, was relatively unimportant for explaining the density and population structure of Devil's-bit Scabious, but the intensity of management significantly affected the population structure. In heavily grazed areas seed set and seedling recruitment was hindered by continuous removal of flowering stalks by livestock. Early mowing might also result in removal of the flowering stalks, thus preventing seed set (Bühler and others 2001). However, after mowing Devil's-bit Scabious often forms new flowering stalks and these might set seed if they are not grazed down during aftermath grazing (Crofts & Jefferson 1999).

Several studies have shown that Devil's-bit Scabious is a consistently poor-performing species during ecological restoration experiments (Bakker and others 2002; Warren and others 2002; Hooftman and others 2003; Matus and others 2003; Pywell and others 2003). In most cases, the species is absent from the seed bank and there are no extant populations nearby, which makes re-establishment by natural means not possible. Even when extant populations are present in the vicinity of the concerning site, the chances on natural colonization are low because of the poorly developed dispersal mechanisms of the seeds. Low germination percentages and considerably varying germination percentages per year may partly explain problems encountered during restoration experiments involving sowing of the species (Hooftman & Diemer 2002; Hooftman and others 2003; pers. comm. P. Vergeer). Another important factor is possibly that restored grasslands often develop into closed, productive communities, dominated by generalist, competitive, vegetatively vigorous species in which less competitive and more specialist species are excluded. These grasslands seem to offer relatively few opportunities for seedling recruitment after the initial seeding stage (Pywell and others 2003). Establishment of these less competitive species, which are often stress-tolerators, might require the creation of specific microhabitats or the phased introduction of species several years after restoration (Pywell and others 2003).

Adams (1955) mentions that Devil's-bit Scabious is often found in areas that have been disturbed some time ago, and on the margins of well-worn paths and in the centre of those less used, suggesting that recruitment of the species is associated with disturbance. In accordance with this Isselstein and others (2002) found that soil disturbance was a significant factor influencing Devil's-bit Scabious seedling emergence, and Pywell and others (2003) also found that cultivation of the experimental area caused a significant increase in frequency of Devil's-bit Scabious. Increased germination of the species has also been found on irrigated plots and plots that are more sheltered because of the presence of the existing vegetation cover, suggesting that the seeds have a particular high moisture requirement for germination However, the key factor controlling seedling establishment was the competitive strength of the existing vegetation and soil disturbance was of minor importance (Isselstein and others 2002).

A large number of studies have shown the negative effects of small population size on plant performance of Devil's-bit Scabious. Hooftman & Diemer (2002) found a 80% decrease in proportion of seedlings present in small habitats. They assume this is due to lower seedling recruitment as a result of reduced fitness, and they contribute this to genotypic differences. Vergeer and others (2003) have also found reduced plant performance in combination with increased inbreeding coefficients and loss of genetic variation in smaller populations of Devil's-bit Scabious. Germination percentage, germination rate, seed weight, seed production and the percentage of flowering plants producing germinable seedlings were all positively correlated with population size. For example, total germination was very low in small populations compared with nearly 80% in some of the large populations, and a highly significant negative correlation was found between population size and seedling mortality (Vergeer and others 2003; Vergeer and others 2004). Vergeer and others (2004) have also demonstrated the risk of inbreeding in populations of Devil's-bit Scabious by showing strong reductions in seed production, seed weight, germination, germination rate and flowering percentage after selfing.

2.4 The study area & the study site

In this section, the study area the Avalon Marshes, and the study site Shapwick Heath NNR will be discussed briefly.

The Avalon Marshes

The Avalon Marshes area consists of 1,600 ha of internationally important wetland habitat situated on the peat working areas of the Brue Valley to the west of Glastonbury, Somerset. It was created by the extensive reclamation of exhausted peat workings. The Avalon Marshes incorporate Shapwick Heath NNR managed by English Nature, Westhay Moor NNR, Street Heath and Catcott Heath managed by Somerset Wildlife Trust and Ham Wall NNR managed by the RSPB. The location of these nature reserves is shown in figure 2.1 below.

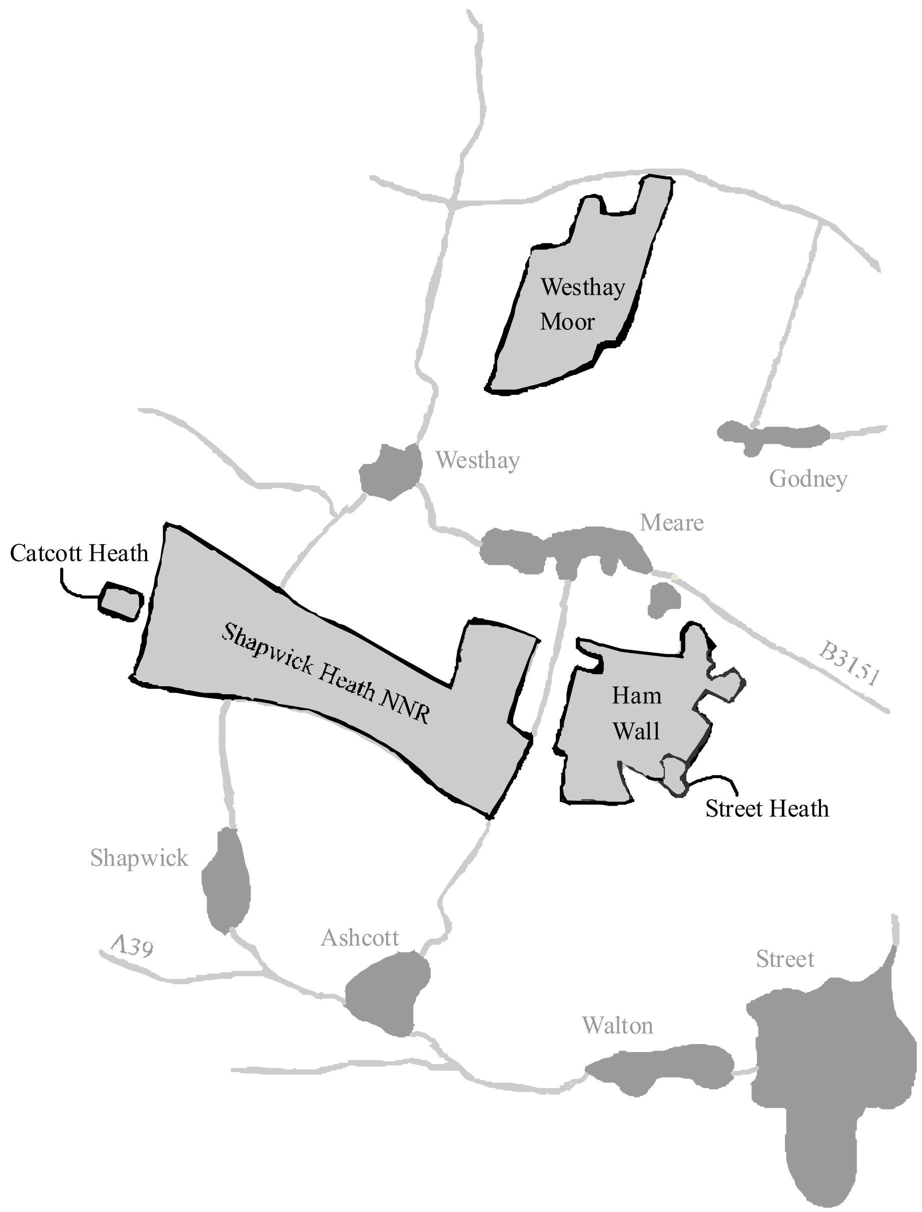

Figure 2.1 The location of the nature reserves Shapwick Heath NNR, Westhay Moor NNR, Street Heath, Catcott Heath and Ham Wall NNR, all present within the area known as the Avalon Marshes.

Shapwick Heath NNR

Shapwick Heath National Nature Reserve is located approximately half a mile to the north of the village Shapwick, near Glastonbury in Somerset. The reserve has an area of roughly 400 hectares and comprises a wide diversity of habitats. Large parts consist of re-profiled peat excavations that have been restored to wetlands. Furthermore, a considerable area of herb-rich meadows and herb-rich grazing fen is present on the reserve. Large parts of these latter habitats, which are declining rapidly in Britain, have suffered from drainage caused by the neighbouring peat excavations. The two areas where the experiments have been conducted are the Lows south and Ashcott plot. In both the Lows south and Ashcott plot, colonies of the Marsh Fritillary were present until the species became locally extinct in 1995. The two areas are described shortly below.

The Lows south

The vegetation on the Lows south has been classified as M25 *Molinia caerulea – Potentilla erecta* mire, in places grading to M16 *Erica tetralix – Sphagnum compactum* wet heath (Prosser & Wallace 2000). The area has suffered severely from drainage caused by nearby peat excavations. The hydrological state of the Lows has been stabilized about 10 years ago by placing a clay bank around the area, which prevents further drainage. However, the effects of drainage combined with lack of grazing and vegetation management have resulted in the area being in "unfavourable condition". Large parts of the vegetation are dominated by Purple Moor-grass and Bog Myrtle *Myrica gale*. Species like Greater Birdsfoot Trefoil *Lotus pedunculatus*, Meadow Thistle *Cirsium dissectum*, Cross-leaved Heath *Erica tetralix,* Carnation Sedge *Carex panicea* and Devil's-bit Scabious are rather rare, but they do still occur, notably in patches with fine grasses like Creeping Bent *Agrostis stolonifera,* Common Bent *A. capillaris*, Sweet Vernal Grass *Anthoxanthum odoratum* and occasionally Red Fescue *Festuca rubra*. Restoration management has been applied for a few years now, and consists of cattle grazing and topping (pers. comm.. M. Yeandle).

Red Devon cattle in the Lows south (June 2004).

Ashcott Plot

Ashcott Plot is a remnant of a raised bog. The vegetation on the ancient bog surface has been classified as a mosaic of M25 Purple Moor-grass – *Potentilla erecta* mire, M16 *Erica tetralix* – *Sphagnum compactum* wet heath and M24 Purple Moor-grass – *Cirsium dissectum* fen meadow (Prosser & Wallace 2000). Ashcott Plot has also suffered severely from drainage caused by neighbouring peat excavations. As a result of drainage combined with lack of grazing and vegetation management, the area has become almost completely overgrown with scrub consisting of Bog Myrtle, Downy Birch *Betula pubescens* and Creeping Willow *Salix repens* in the recent past, while the more open areas have become dominated by large tussocks of Purple Moor-grass. In contrary to the Lows, the water levels have not been restored on Ashcott Plot to date and desiccation of the habitat is still a considerable problem. It is thought that the scrub contributes significantly to the drying out of the bog surface, and large areas of scrub have been cleared in recent years. Currently, the vegetation consists mainly of large tussocks of Purple Moor-grass, however, some patches with species like Red Fescue, Cross-leaved Heather, Devil's-bit Scabious and more rare species like Ivy-leaved Bellflower and Bog Pimpernel *Anagallis tenella*, still exist. To counteract Purple Moor-grass and scrub encroachment, sheep and goat grazing has been introduced to the site in May 2004 while scrub removal is ongoing (pers. comm.. M. Yeandle).

Shetland sheep on Ashcott Plot (September 2004).

3 Habitat availability on Shapwick Heath NNR

This section discusses the habitat availability assessment that was carried out on Shapwick Heath NNR.

Main question
Is suitable Marsh Fritillary habitat present on Shapwick Heath NNR and what areas on the reserve have a high potential for the species?

3.1 Methods

All fields on Shapwick Heath NNR were systematically searched for Devil's-bit Scabious plants. Where the plant was encountered, a search was made to find the extent of its occurrence, and if more than 10 plants were found, recording was undertaken in the concerning field.

The vegetation characteristics host plant cover and vegetation height were recorded by random sampling across the field using a 1 square metre quadrat. Vegetation height (centimetres) was measured using a 1.5 metre graduated pole and a drop disc (polystyrene foam, diameter 10 centimetres, weight 5 grammes). Host plant cover was estimated as the percentage cover of Devil's-bit Scabious in the quadrat. Depending on the area of the field, between 20 and 220 measurements were taken. Vegetation communities were read off maps enclosed with the report "Shapwick Heath, Ashcott Heath and Seventy Acres NVC survey" (Prosser & Wallace 2000). Information about the present and future management originates from discussions with the site staff.

After all fields had been recorded, patches were defined. Discrete patches were defined according to Bulman (2001) as areas separated by 50 metres or more of habitat where the host plant was absent, or 25 metres or more if a scrub or woodland barrier existed. From the measurements, means for the variables host plant cover and vegetation height were calculated for all patches. Often, two or more fields could be considered as one patch when following Bulman's guidelines. The measurements for the fields were then merged and an overall mean for the patch was calculated. The patches were mapped onto 1:10,000 maps of the nature reserve. The habitat conditions in the patches and the present management determines whether the patches are suitable or unsuitable for the butterfly. The criteria that have to be met for a patch to be classified as suitable are presented in table 3.1. For further information on the criteria, see Borsje (2004a). The potential of the patches for the Marsh Fritillary was also assessed based on the proposed future management.

Table 3.1 Habitat requirements Marsh Fritillary butterfly (for further information on the criteria, see Borsje 2004a).

Variable	values
Vegetation community	M23, M24, M25, M6, M16, MG5
Patch area	≥0.02 hectares
Host plant cover	≥4.4%
Vegetation height	8-25 centimeters
Management	Extensive cattle or pony grazing

3.2 Results

In 27 fields on Shapwick Heath NNR, more than 10 Devil's-bit Scabious plants were encountered. These fields were merged to 10 habitat patches. Most patches were present in the west of the reserve, with one patch designated in the east of the reserve (see appendix II). The data recorded in all patches is summarized in table 3.2. The patches can be roughly divided into hay meadow patches and mire patches. Both categories are briefly discussed below.

The hay meadow patches Of the hay meadow patches Head Drove 1 and 2, Brickyard and Canada Farm, Station road and Sweet Track 1 and 2, the patches Head Drove 2 , Brickyard Farm and Canada Farm have a host plant cover that would qualify these areas a suitable (see figure 3.1). However, in most of these patches, the majority of the vegetation is too high for the patch to be qualified as suitable. Based on their botanical and cultural value, the hay fields that form the hay meadow patches have been designated as a Site of Special Scientific Interest (SSSI). The management in these patches, a hay cut in July, is aimed at maintaining and enhancing the botanical interest of these fields. The management of these hay meadow patches severely limits their potential as Marsh Fritillary habitat since it results in a uniform sward without the structure required by the butterfly.

The vegetation in the hay meadow patch Brickyard Farm, with a high cover of the host plant Devil's-bit Scabious.

The habitat in the mire patch the Lows north has suffered severely from drainage caused by neighbouring peat excavations, resulting in Purple Moor-grass encroachment.

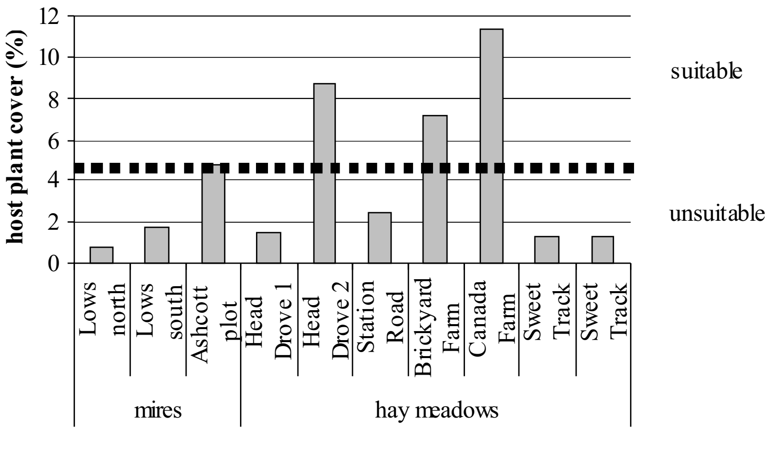

Figure 3.1 Mean host plant cover recorded in the patches. The dotted line represents the limiting value of 4.4% under which the host plant cover is insufficient for the butterfly.

The mire patches The mire vegetations on the reserve have suffered severely from drainage caused by neighbouring peat excavations. There used to be Marsh Fritillary colonies present in all three designated mire patches. However, Purple Moor-grass and scrub encroachment and subsequent management regimes implemented to counteract these problems, coupled with environmental stochasticity and demographic stochasticity that played an enlarged role in the dwindling colonies resulted in local extinction in 1995. Nowadays, Purple Moor-grass domination is still a major problem, and the cover of the considerably less competitive host plant Devil's-bit Scabious has declined significantly (see figure 3.1). The host plant cover is very low in The Lows north and, with a mean of 62 centimetres, the vegetation height is far too high (see figure 3.2). Restoration management (cutting in July) has only recently started in part of this patch, but will hopefully result in a rapid increase in host plant cover. The Lows south has been grazed with Red Devon cattle for a number of years now, and although the host plant cover is recovering, it is presently still only 1.7%. Grazing has had a positive effect on the vegetation height, which, with a mean of 16 centimetres, is classified as suitable for the Marsh Fritillary.

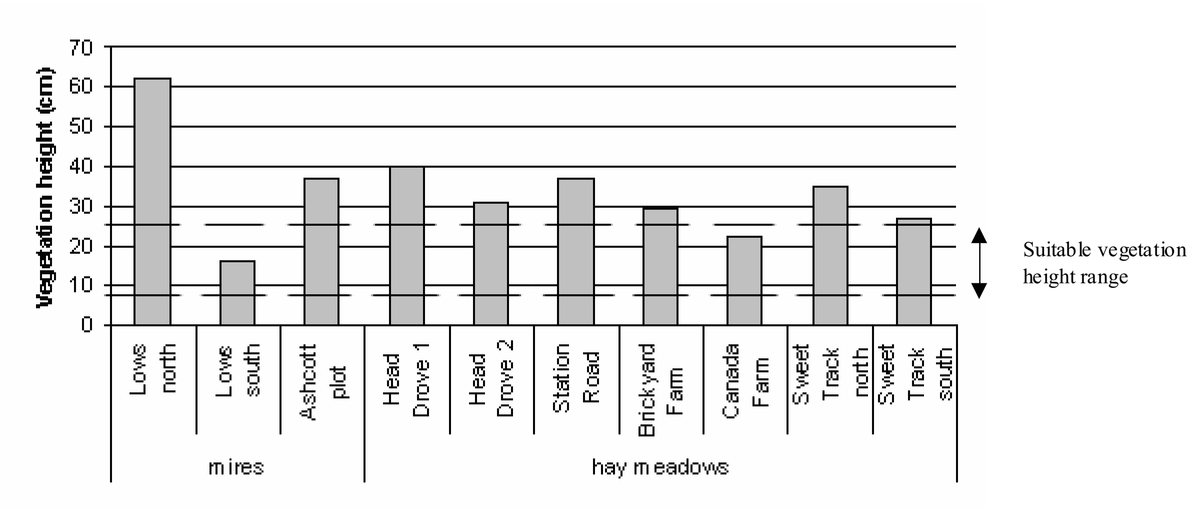

Figure 3.2 Mean vegetation height recorded in the patches.

The patch Ashcott plot consists of two fields; one with a very high host plant cover, and one that is a remnant of raised bog that has suffered severely from drainage. This raised bog remnant is now overgrown with Purple Moor grass and scrub. The host plant can still be found, but only in a few discrete patches. The host plant cover in the second field of the patch Ashcott plot is very high, resulting in the high score for host plant cover for the total patch. Due to the large Purple Moor-grass tussocks and the unmanaged state of the patch, the vegetation in the majority of the patch is too high at the moment (see figure 3.2). In the year after this habitat assessment was carried out, sheep and goat grazing was introduced to the site.

When the mire patches have been sufficiently restored, the aim is to maintain their favourable condition by means of extensive cattle grazing.

Table 3.2 The designated patches and the data for the variables NVC community, area, host plant cover, vegetation height, present management and future management. When the value of a particular variable is shaded, this means that the value for that variable renders the patch unsuitable in terms of that variable. The column suitability judges the suitability of the patch based on the present conditions. The column compatibility compares the compatibility of the future management with the management requirements of the butterfly. The column potential assesses the future potential of the patch for the butterfly based on all variables.

Habitat patch	NVC Community[5]	Area (ha)	HP cover[6]	Vegetation height	Present management	Suitability	Future management	Compatibility	Potential
The Lows north	M23, M24, M25	10.7	0.7%	62 cm	Restoration: cut in July	Unsuitable	Extensive grazing	Compatible	**High**
The Lows south	M24, M25, M16	6.6	1.7%	16 cm	Restoration: cattle grazing and topping	Unsuitable	Extensive grazing	Compatible	**High**
Head Drove 1	M23, M24, MG5	0.8	1.5%	40 cm	Cut in July	Unsuitable	Cut in July	Incompatible	Low
Head Drove 2	M23, M24, MG5	1.7	8.7%	31 cm	Cut in July	Unsuitable	Cut in July	Incompatible	Low
Station road	M22, MG8	1.9	2.5%	37 cm	Cut in July	Unsuitable	Cut in July	Incompatible	Low
Brickyard Farm	M23, M24, MG5	9.9	7.1%	29 cm	Cut in July	Unsuitable	Cut in July	Incompatible	Low
Canada Farm	M23, M24, MG5, MG8	6.7	11.4%	22 cm	Cut in July	Unsuitable	Cut in July	Incompatible	Low
Sweet Track North	M23, M24, MG8	2.2	1.3%	35 cm	Cut in July	Unsuitable	Cut in July	Incompatible	Low
Sweet Track South	M22, M23, MG5, MG1	3.1	1.3%	27 cm	Cut in July	Unsuitable	Cut in July	Incompatible	Low
Ashcott plot	M23, M24, M25, M16	4.9	4.8%	37 cm	Restoration: Partly topped, partly grazed with sheep	Unsuitable	Extensive grazing	Compatible	**High**

[5] National Vegetation Classification Community
[6] Host Plant cover

3.3 Discussion & Conclusion

The patches on Shapwick Heath NNR can be divided in hay meadow patches and mire patches. When all habitat criteria are taken into account, none of the designated patches on the reserve consist of suitable habitat for the Marsh Fritillary butterfly.

Although some of the hay meadow patches meet the host plant cover criterion, the main problem for the Marsh Fritillary is the management of the fields, which consists of hay cutting in July. This type of management results in a uniform sward without the structure required by the butterfly. In addition, the hay cut removes the host plant when the larvae are still actively feeding, as well as causing high mortality during the actual cut. As long as these fields are cut for hay, they can not be suitable habitat for the Marsh Fritillary. Based on their botanical and cultural value, the fields that form the hay meadow patches have been designated as a Site of Special Scientific Interest (SSSI). Their management is aimed at maintaining or enhancing the botanical interests. As species-rich hay meadows are rare nowadays, it is not advisable to change the management regime in these fields in favour of the Marsh Fritillary. Therefore, the hay meadow patches can not be suitable for the butterfly.

The patches that do have potential for the butterfly are the mire patches. Until the butterfly became locally extinct in 1995, Marsh Fritillary colonies existed in all three mire patches. The local extinction is thought to be the result of Purple Moor-grass and scrub encroachment, and subsequent management regimes implemented to counteract these problems. Purple Moor-grass domination is still a considerable problem in the mire patches. The Lows south has been cattle grazed for a number of years now, and as a result the host plant density is increasing. In the Lows north, restoration management (burning, and cutting in July) has only commenced in the past year. On Ashcott plot, scrub-cutting is ongoing and the site is now grazed by sheep and goats. Although it will take a number of years before the mire patches are restored to Marsh Fritillary habitat, their potential for the species is high. Once restored, the patches comprise a considerable area of continuous Marsh Fritillary habitat, while the future management of the patches, extensive cattle grazing, is sympathetic to the needs of the butterfly.

Purple Moor-grass dominated vegetation on Ashcott plot

4 Re-establishment potential in the Avalon Marshes

This section explores whether a sustainable re-establishment of the Marsh Fritillary in the Avalon Marshes is feasible.

Main question
Is a sustainable re-establishment of the Marsh Fritillary butterfly in a viable meta-population structure feasible in the Avalon Marshes?

4.1 Methods

The Incidence Function Model (IFM) (Hanski 1999) has been used to assess the potential for re-establishment of the Marsh Fritillary in the Avalon Marshes. The model has been successfully applied to the Glanville Fritillary *Melitaea cinxia* (Hanski and others 1996), the False Heath Fritillary *Melitaea diamina* (Wahlberg and others 1996), the Marsh Fritillary in England (Bulman, 2001) and in Finland (Wahlberg and others 2002). The IFM is spatially explicit and incorporates patch area and isolation effects into a basic meta-population model. It allows numerical simulation of extinction-colonization dynamics in any meta-population structure, by independently assigning area-dependent extinction and isolation-dependent colonization for each patch in each generation, using the probabilities given by the model. The model is based on a first-order linear Markov chain and yields the long-term probability on occupancy of a patch (the incidence J_i). The basic premise of the model is as follows:

$$J_i = C_i / (C_i + E_i - C_i E_i)$$

where C_i and E_i are the colonization and extinction probabilities. For further information on the Incidence Function Model, see Hanski (1999). Parameters are estimated by considering the patterns of patch occupancy of individual patches. Bulman (2001) has shown that it is very important to use parameters that have been specifically estimated for the concerning species inhabiting similar habitats. Application of parameters estimated for the Glanville Fritillary and even for the Marsh Fritillary in Finland which occurs in quite different habitats there, proved unsuccessful in a network in Dorset. During this study, parameters for the Marsh Fritillary estimated by Bulman (2001) have been used. Bulman has used these Marsh Fritillary parameters successfully to predict persistence in five pairs of networks throughout the butterfly's range in England and Wales. The Avalon Marshes are situated close to two of these five networks and is also close to the area in Dorset where the parameters were estimated. The model parameters and settings of the model are shown in table 4.1. For more information on the parameters and the parameter estimation for the Marsh Fritillary, see Hanski (1999) and Bulman (2001). With the model parameters known, it is possible to numerically simulate extinction-colonization dynamics in any meta-population by assigning area-dependent extinctions and isolation-dependent colonisations independently for each patch in each generation using the probabilities given by the model. In order to do this, information about the area of the patches, the spatial coordinates of the patches, and the pair wise distances between the centre points of the patches in the network has to be available. The output of the model gives information on the proportion of occupied patches, the occupied area in the meta-population over a given period of time and the long-term probability of a patch being occupied (Incidence J_i). With this data, the chances on survival of the meta-population over a given period of time (persistence) and the mean time to extinction can also be assessed.

Table 4.1 Parameter and model settings used during IFM simulations. Parameters estimated by Bulman (2001).

Parameter	setting
α	-2
x	0.6791
y	4.4835
e	0.2091
Minimum patch area	0.1
b	0.5
Remote colonization probability	0
evar	0.0005

Two hundred iterations of the model were run for 100 years, and a meta-population was classified as viable when a 95% chance on persistence in 100 years was achieved (Soulé 1987).

The patches that have been used during the modelling study include the patches that have a high potential for the Marsh Fritillary as defined during the habitat assessment (the mire patches, see section 3.2), patches on neighbouring nature reserves where the butterfly was breeding in the past and other potential areas that have been assigned in consultation with the site manager of Shapwick Heath NNR and the site managers of the neighbouring nature reserves Catcott Heath, Street Heath, Westhay Moor NNR and Ham Wall NNR. These latter potential areas are present in re-profiled peat excavations where acidic vegetations are developing, and rough undergrazed meadows that could be restored to Marsh Fritillary habitat. It is likely that these areas consisted of suitable habitat for the butterfly in the past, but nowadays the host plant Devil's-bit Scabious is not present any more. Nevertheless, these areas have a high potential for the butterfly if re-establishment in a viable meta-population structure is desirable.

In figure 4.1 below, a map is given that represents the study area showing the location of all patches used during simulations (for further information about the patches, see Borsje 2004a). The grid reference of the south-west corner of this map is ST340380, the grid reference of the north-east corner is ST480460. The area comprises 8 by 8 kilometres. The grid lines divide the area in 1 kilometre squares. In the results section, this map will be shown again, then only showing the spatial arrangement of the patches of the meta-population that is being discussed. The dots in these figures are scaled to the size of the concerning patch and the colour of the dot will refer to the long-term probability of the concerning patch being occupied in that particular meta-population structure (Incidence J_i ; black >50%, grey 25-50%, white <25%). Simulation graphs that show the proportion of patches that were predicted to be occupied during simulations, will also be presented.

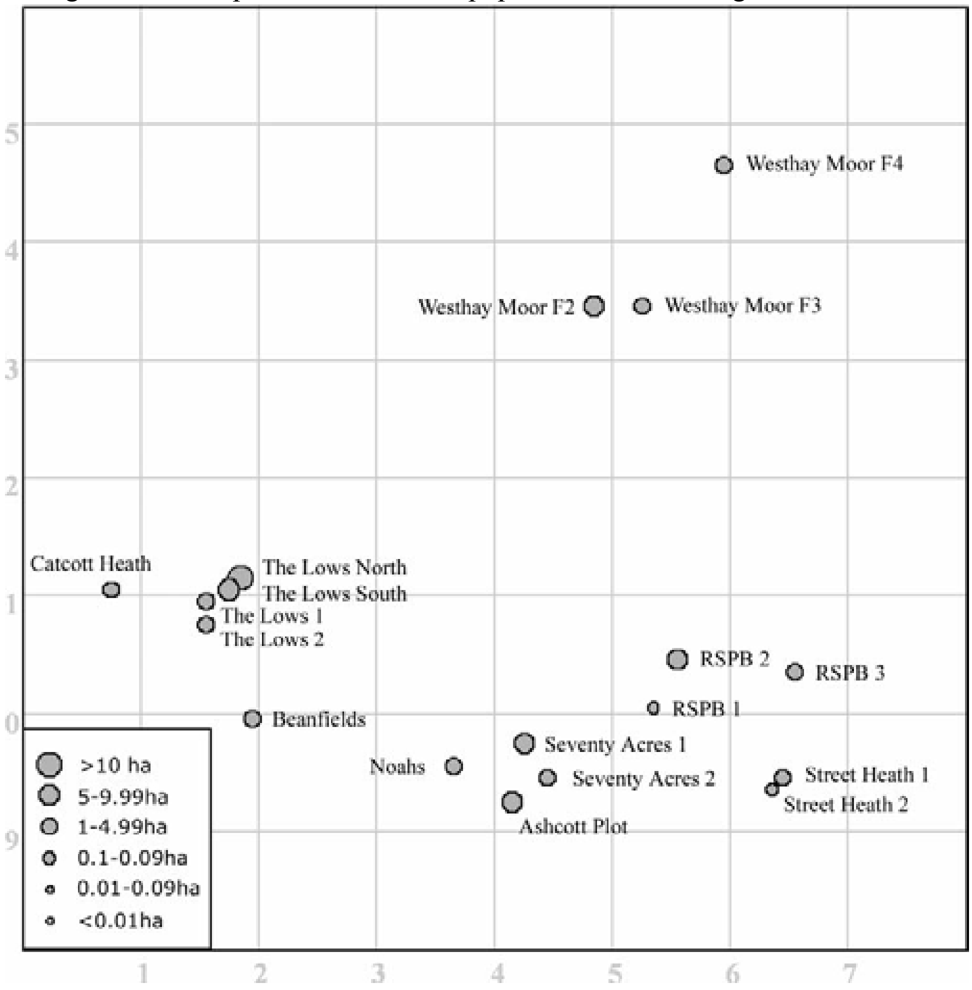

Figure 4.1 Map of the 8 by 8 kilometre study area showing the name and location of the patches used during simulations.

4.2 Results

The potential on Shapwick Heath NNR

The model results suggest that restoration of Marsh Fritillary habitat in the mire patches the Lows north, the Lows south and Ashcott plot is not sufficient to realize a sustainable re-establishment of the butterfly in the area. The patch Ashcott plot is too isolated from the patches in the Lows, and has a low long-term probability on occupancy of only 23% as a result. The chance on persistence of the whole network is only 62% in 100 years.
However, two areas near the Lows, the Lows 1 and 2, currently overgrown with scrub and Purple Moor-grass, could be restored to Marsh Fritillary habitat. Furthermore, an extensive area of re-profiled peat excavations is present near Ashcott plot. Natural colonization of the host plant Devil's-bit Scabious in this area indicates the potential for development of Marsh Fritillary habitat. Three potential patches have been designated here, namely Seventy Acres 1 and 2 and Noahs. The meta-population consisting of all these abovementioned areas is shown in figure 4.2. This network would consist of 42 hectares, and the model predicts it to be viable with a 99.5% chance on persistence in 100 years and a mean time to extinction of 99.9 years with only one iteration going extinct (see figure 4.3). All patches in the network have a long-term chance on persistence higher than 70%. Even when the area of each patch is reduced by a quarter, to account for application of rotational cutting or topping management and/or the realistic assumption that a patch almost never completely consists of suitable habitat due to microclimatic differences, the decrease in chance on persistence is negligible. Therefore, this Shapwick meta-population offers a realistic opportunity to re-establish the Marsh Fritillary on Shapwick Heath NNR in a viable meta-population structure. The network could be further extended with the patch Beanfields (see figure 4.1 for the location of the patch), an area of arable land that has recently been acquired by English Nature. Although the high nutrient levels might limit the possibilities of establishing a species-rich vegetation with Devil's-bit Scabious in the near future, the large area of this patch (5 hectares) and its position suggest that it could be very valuable in bridging the gap between the habitat patches in the west and east of the proposed meta-population.

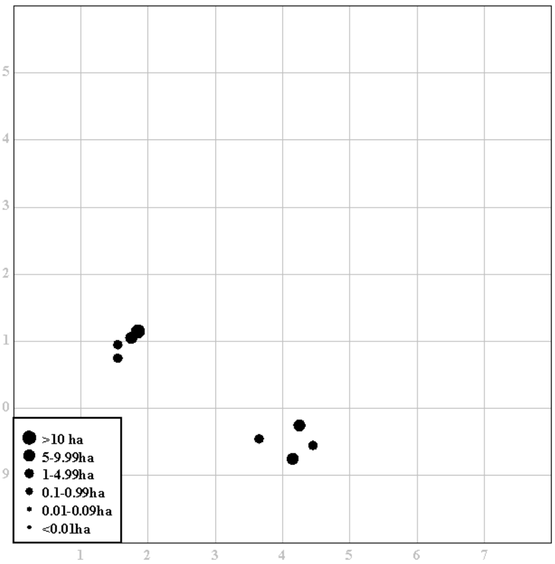

Figure 4.2 The Shapwick meta-population. The long-term probability on occupancy of all patches is higher than 70%.

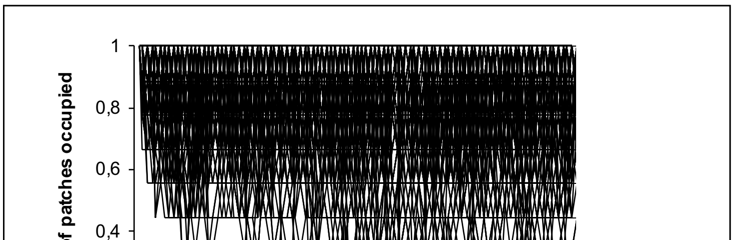

Figure 4.3 The predicted dynamics of fraction of patches occupied in the Shapwick meta-population over 100 years. Each line represents one iteration.

The potential in the Avalon Marshes

Marsh Fritillary records from roughly the 1960s until present in databases at Butterfly Conservation and the Somerset Environmental Records Centre give insight in the historic occurrence of the Marsh Fritillary in the Avalon Marshes. The data suggests that colonies used to be present on three nature reserves around Shapwick Heath, namely on Street Heath, Westhay Moor NNR and Catcott Heath. It is assumed that they used to form one meta-population with the areas where the butterfly used to occur on Shapwick (see figure 4.4). This meta-population was present until the early 1990s, when the colonies became extinct one by one resulting in local extinction in 1995. The results of input of this 'historic meta-population' in the IFM suggests that these patches were too isolated from each other to be able to form a meta-population. The former colonies on Westhay Moor NNR, Street Heath and Ashcott plot have very low long-term probabilities on persistence, and the chance on persistence of the network as a whole is only 64% with 72 iterations predicted to become extinct (see figure 4.5). Only Catcott Heath benefits from the proximity of the two large colonies on the Lows resulting in a long-term probability on occupancy of 45% for this patch.

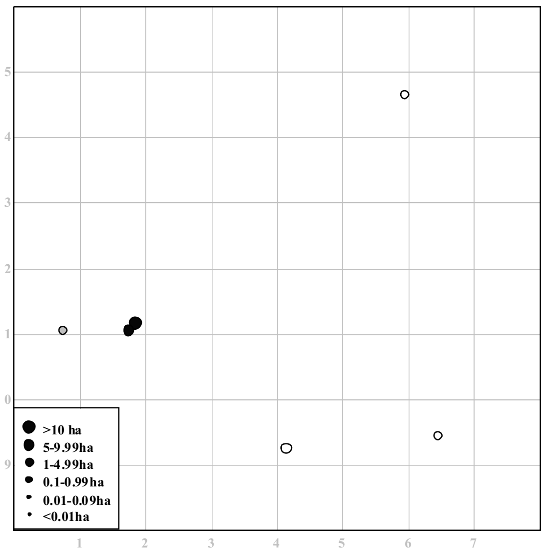

Figure 4.4 The 'historic meta-population. Only the patches in the Lows have a long-term probability on occupancy higher than 50%.

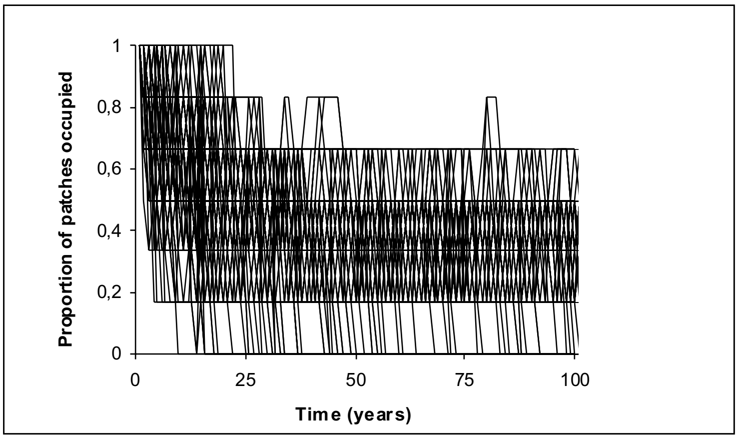

Figure 4.5 The predicted dynamics of fraction of patches occupied in the 'historic meta-population' over 100 years. Each line represents one iteration.

Although inappropriate habitat management probably was the final blow for the butterfly in the area, the simulation has shown that, at least from the 1960s onwards, the amount of habitat in the network was reduced in such a way that the Marsh Fritillary was destined to become extinct, as the landscape had already long ago lost its ability to support the species. It seems likely that the patches that were occupied until the early 1990s were only a remnant of a larger, viable meta-population that once existed in the Avalon Marshes. Many of the patches of this extensive network have probably been lost to peat excavations or agricultural improvement. The colonies that stood ground until the early 1990s were all located on nature reserves, and were therefore protected against these threats. The simulation also suggests that sustainable re-establishment on Westhay Moor NNR and Street Heath is unlikely unless additional habitat restoration nearby these patches is possible.

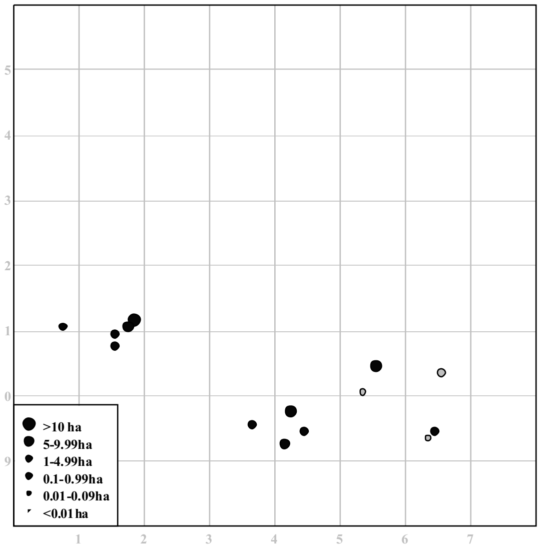

Figure 4.6 The Shapwick meta-population extended to include Catcott Heath, and Street Heath by means of stepping stone patches on Ham Wall NNR.

With the aid of stepping stone patches on RSPB's Ham Wall NNR and a small additional patch on Street Heath, it is possible to bridge the gap between the Shapwick meta-population and the patch on Street Heath, thus extending the meta-population to include this former colony (see figure 4.6). Old maps of Ham Wall NNR suggest that before the peat excavations, the vegetation on the reserve was very similar to that on Street Heath. Moreover, there is one Marsh Fritillary record known from the area, although this could be a wanderer from Street Heath or Ashcott plot. The patches on Ham Wall NNR consist of re-profiled peat excavations where some of the old peat surface is still present. The acidic character of the developing vegetation in these areas indicates the potential for the Marsh Fritillary.

Model results suggest that it is not advisable to re-establish the Marsh Fritillary in its former habitat patch on Westhay Moor NNR. Even though two undergrazed rough grasslands totalling 11 hectares could be restored to Marsh Fritillary habitat nearby the former habitat patch, the long-term probability on occupancy is lower than 32% for all three patches. Further modelling has indicated that even if all mire vegetations on Westhay Moor NNR would be Marsh Fritillary habitat, this meta-population would only be marginally viable. Most of these areas have other conservation priorities which require management regimes that are incompatible with the needs of the butterfly. Moreover, model results have shown that the distance between the two networks is so large that the networks on Shapwick Heath and Westhay Moor NNR would function independently, i.e. no regular migration would occur between the two networks. Therefore, re-establishment of the Marsh Fritillary on Westhay Moor NNR would require the restoration of a second meta-population, independent from the meta-population on and around Shapwick Heath NNR (see figure 4.7).

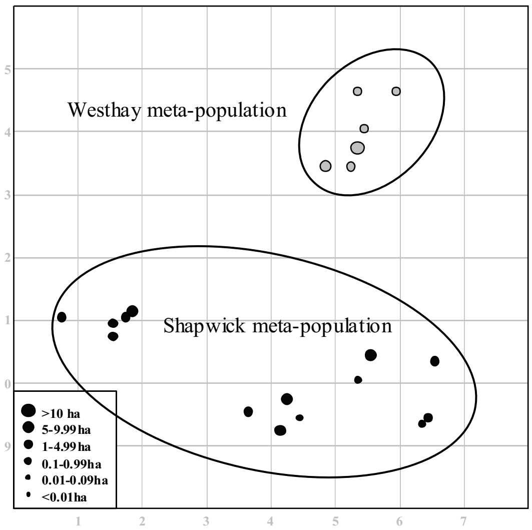

Figure 4.7 Sustainable re-establishment of the Marsh Fritillary on Westhay Moor NNR would require a second, independent meta-population.

4.3 Discussion & Conclusion

The aim of this study was to investigate whether re-establishment of the Marsh Fritillary in a viable meta-population structure is feasible in the Avalon Marshes. A meta-population was classified as viable when a 95% chance on persistence in 100 years was achieved. However, discussion is possible about on what time-scale one should think, what chance on persistence is acceptable, and consequently what amount of habitat is necessary to realize this. In addition, although the Incidence Function model that has been used to assess the viability of potential networks during this study, has been successfully applied during a number of other studies, it is a model, a simplification of reality. A simplification can never give completely accurate predictions, and the modelling results are guidelines only.

Nevertheless, the scenario studies carried out in the frame of this research have clearly shown that Shapwick Heath NNR and the surrounding nature reserves have a high potential for realizing the re-establishment of the Marsh Fritillary butterfly in a viable meta-population structure.
Re-establishment requires that the former habitat in the Lows and on Ashcott plot is restored. In addition, further habitat creation is necessary near Ashcott plot. The habitat creation would be in areas that have been re-profiled after peat excavation, and natural colonization of the host plant Devil's-bit Scabious in these areas indicates the potential of these areas for the butterfly. The viable Shapwick meta-population can be further extended to include the former colony on Catcott Heath, and the former colony on Street Heath, with the aid of stepping stone patches in re-profiled peat excavations on Ham Wall NNR.

A viable meta-population is only viable to the extend that sympathetic habitat management is guaranteed in the patches. Several studies have shown the detrimental effects of unsuitable management regimes (overgrazing, undergrazing, sheep grazing and cutting) on Marsh Fritillary colonies (eg Warren 1994; Hobson 2001). All habitat in the Avalon Marshes meta-population would be owned and managed by conservation bodies who can ensure that management in the habitat patches is sympathetic to the needs of the Marsh Fritillary.

It is rare that an entire viable Marsh Fritillary meta-population can be present within a single nature reserve, with possibilities for further extension to neighbouring nature reserves. The model results have clearly indicated that the Avalon Marshes could be one of the key areas for the conservation of the Marsh Fritillary in the United Kingdom if all conservation bodies in the area contribute to providing Marsh Fritillary habitat.