

The importance of resources in determining butterfly population abundance at multiple scales

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This dissertation is submitted for a Research Degree at
University College London



Declaration

I, Robin Curtis confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis

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Abstract

Long term monitoring has revealed that butterfly populations vary dramatically between years, among sites and across species. This PhD investigates the importance of biotic and abiotic resources in determining butterfly abundance at multiple scales, using long term data from intensive studies on the Glanville fritillary and from the extensive UK Butterfly Monitoring Scheme.

The most important resource at local scales is the 'suitability' of the larval hostplant: only plants within a certain temperature range are likely to be utilised for oviposition.

Laying eggs on warmer plants maximises the probability of successful larval development within restricted seasonal temperature constraints. Analysis of Glanville fritillary population time-series reveals that populations are more abundant in those habitat types providing suitable microclimates for larval development, and in years following warm spring temperatures (i.e. during oviposition). These factors were also important when comparing abundance across sites, as were patch area and isolation. This landscape-scale analysis also revealed a significant negative interaction between habitat quality and temperature, suggesting that microsites for oviposition are less restricted in warm than cool years.

Across regional scales (southeast England), the availability of both host and nectar plants are important in determining butterfly abundance, both across and within species. However, hostplant availability is a stronger predictor of abundance than nectar, and is most pronounced on sites with a northerly aspect. Trait analysis revealed that species with restricted diets, low mobility and habitat specialism are most sensitive to variation in foodplant availability.

Taken together, the results suggest that many UK butterfly species are limited at small scales by the availability of hostplants in warm microclimates, but at large scales by dispersal limitation and climatic tolerance. Site management can therefore increase the abundance of key species of conservation concern by creating thermally diverse habitats and maximising the biomass of their hostplants.

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Introduction

Why abundance varies between species and populations is a fundamental question in ecology (Krebs 1978; Andrewartha & Birch 1984). For any species, the abundance or density (defined as numbers per area) of a population is determined by variation in the four main population parameters of natality, mortality, immigration and emigration (Begon *et al.* 1986), but the mechanisms which underpin such changes remain poorly understood (Storch & Gaston 2004; McGill *et al.* 2007). Therefore, explaining why a species has a particular abundance is the 'embarrassing and obvious question that ecology cannot yet answer' (McGill 2006).

Certainly, the abundance and distribution of a species is a reflection and response to environmental conditions (Brown 1995), and population growth can be restricted by both abiotic factors, for example, climate and temperature, as well as biotic interactions with other species through competition or predation and limitations in resources (Newton 1998). However, understanding the importance of the separate factors which determine abundance (and particularly specific resources) is not straightforward (Hanski 1994a; Bartoń & Zalewski 2007), as many environmental components are inter-related (May 1975; Gaston *et al.* 2000). Furthermore, the significance of a specific factor may also depend on the scale at which the species or population is studied (Hengeveld & Haeck 1982; Blackburn & Gaston 1996; Smallwood & Schonewald 1996).

Resources encompass any component of the environment that can be utilised by a species and can vary in both quality and quantity (Lincoln 1982), although food availability is often considered the primary resource (Odum 1963). Within terrestrial ecosystems, several broad scale studies on mammals and birds have demonstrated that populations limited by food availability increase abundance with increases in edible biomass (Lack 1954; Carbone & Gittleman 2002) or habitat productivity (McLoughlin *et al.* 2000; Pettorelli *et al.* 2009). However, the strength of relationship between the amount of resources, abundance and population growth rates also varies with temperature (Savage *et al.* 2004; Melis *et al.* 2006), and is further complicated by different species requiring different resources or allocation (Ford 1990; Gregory & Gaston 2000). The amount of resource used per individual will therefore directly determine the number of individuals that can be supported by a particular site (Carbone & Gittleman 2002; Brown *et al.* 2004), and so the importance of resources may also vary depending on species traits (Brown & Maurer 1987). For example, differences in body size

and metabolic demands determine how food energy is converted into biomass, and hence population size (Peters 1983; Siemann *et al.* 1996; Brown *et al.* 2004; White *et al.* 2007).

Resources are also of paramount importance to insects, with food availability explaining both species richness (Murdoch *et al.* 1972; Kelly & Southwood 1999; Fleishman *et al.* 2005; Novotny *et al.* 2006; Dapporto & Dennis 2008) and structuring of populations (Strong *et al.* 1984; Potts *et al.* 2003). However, the importance of resources in determining insect abundance remains equivocal (Thomas *et al.* 2011). At local (site level) scales, resource abundance has been shown to correlate with insect abundance from a strong positive relationship (Dempster 1971; Marques *et al.* 2000) to a weak or inverse relationship (Thomas 1983b; Kelly & Debinski 1998). At landscape (multisite) scales, resources have also shown to range from extremely important (Dennis *et al.* 2003; Yamamoto *et al.* 2007), to insignificant (Hanski & Meyke 2005; Rabasa *et al.* 2008), and at large (regional) scales the evidence is both limited and mixed, with single studies suggesting positive (Gutierrez & Menendez 1995) and negative (Kuussaari *et al.* 2000) relationships between the amount of resource and abundance. Indeed, Gaston and Lawton (1988) demonstrate that widespread insect species are generally more abundant than rarer species, and this is often regarded as one of the few most persuasive patterns in ecology (Lawton 1999). However, other studies have demonstrated a negative density distribution relationships in insects (Paivinen *et al.* 2005), although the strength of this relationship could also vary on size of the region studied (Cowley *et al.* 2001a).

Fundamentally, it is axiomatic that food availability can potentially limit population growth through competition for limited resources or by constraining reproductive ability (Blackburn & Gaston 1999; Brown *et al.* 2004). However, different taxa and species vary considerably in their environmental associations and so respond differently to fluctuations in resource availability, often posing unique conservation problems (Thomas 1995c). Given that habitat degradation, fragmentation and climate change continue to pose serious threats to biodiversity (Millennium Ecosystem Assessment 2005; Lawton *et al.* 2010), it is essential to clarify the determinants of population abundance at all scales, as only then can we attempt to mitigate the increasing pressures on the landscape from a cumulative human population (Rands *et al.* 2010).

Insects and butterflies as study organisms

Insects are one of the most successful and numerous groups on the planet, comprising > 50% of all known animals and plants (Groombridge 1992), with estimates of between four million (May 2000) and ten million extant species (Gaston 1992; Godfray *et al.* 1999; Mora *et al.* 2011). They are an essential component to the functioning of most terrestrial ecosystems (Odum 1963; New 2009) and understanding their requirements, movements, interactions (with their own and other species), has significant consequences for conservation, agriculture, forestry, diseases, ecosystem services and ultimately humanity (Biesmeijer *et al.* 2006; Haslett 2008; Potts *et al.* 2010). However, understanding insect biodiversity patterns is complicated compared with vertebrates, because adults and larvae have fundamentally different resource requirements (Williams 1960; Murdoch *et al.* 1972; Hardy *et al.* 2007).

All insect populations fluctuate in response to environmental changes over time (Varley *et al.* 1974; Wolda 1988), and the responses of individuals to environmental conditions will also determine whether populations of successive generations will remain relatively constant, increase or decline towards extinction (Southwood 2003). With extinction rates in insects exceeding those of plants, birds and mammals (Thomas *et al.* 2004; Dunn 2005) clarifying the importance of the various factors which determine species abundance remains a fundamental requirement for developing a successful conservation strategy (Jones 2011; Fox 2012).

Like most ectothermic insects, butterflies are extremely sensitive to changes in temperature and restricted by both climatic restraints (Thomas 1995c; Bryant *et al.* 2002; Davies *et al.* 2006) and limitations in resources (Dennis 2010). The high degree of specialisation required to successfully utilise both differing temperature gradients and resources within the smallest habitats means that many butterflies are short lived thermophilous species, often showing rapid and clear responses to changes in the environment making them ideal indicators to gauge the health of habitats and ecosystems (Erhardt & Thomas 1991; Oostermeijer & van Swaay 1998; Thomas *et al.* 2004). Indeed, they have long attracted population biologists as convenient model organisms (Ford 1945; Ehrlich 1983), and are one of the few insect groups for which annual abundance monitoring is possible (Roy *et al.* 2007).

Within the U.K., butterflies are monitored as part of the Butterfly Monitoring Scheme. This scheme was initiated in 1976 across 34 sites whereby observers walk a set route (transect) once a week, under favourable weather conditions throughout the main butterfly flight period (April – September), recording all butterfly species encountered within a 5 metre box (Asher *et al.* 2001). The aim of the scheme was to provide a standardised annual measure of the

changing status of butterfly species, and an index of abundance is calculated for each species from each site, simply by summing the mean weekly counts, and the trends can then be analysed across sites and years (Pollard & Yates 1993). By 2004, the number of transect sites had risen to 134, although several hundred transects were being walked outside of this scheme as part of the Butterfly Conservation Transect project (Fox *et al.* 2006). In spring 2006, these two schemes merged to incorporate data from all of the transect routes, and the UK Butterfly Monitoring Scheme (UKBMS) was established. This long term monitoring of butterfly populations has shown that populations fluctuate both regularly and dramatically (Botham *et al.* 2009). However, researchers have been more proficient at describing the changes in distribution and abundance than in understanding the mechanisms behind the underlying causes of change (Thomas *et al.* 2011).

This is probably because the mechanics driving butterfly population fluctuations are complex and interacting, for example, climate and weather (Pollard 1988; Roy *et al.* 2001; Dennis & Sparks 2007), resources (Dempster & Pollard 1981; Hardy *et al.* 2007; Dennis 2010), quality of habitat (Thomas & Morris 1994; Clarke *et al.* 1997; Dennis & Eales 1997; Thomas *et al.* 2001; Fleishman *et al.* 2002), geometry (area and isolation) of habitat patches (Hanski *et al.* 1995; Hanski 1998b) and enemies including predators, parasitoids and pathogens (Lei *et al.* 1997; Laine 2004; Harvey *et al.* 2005; van Nouhuys & Hanski 2005). All of these factors can influence the birth, death, immigration and emigration rates, and therefore a species chance of survival and breeding could be said to theoretically depend on the whole environment. However, in reality just one or two factors usually turn out to be important enough to account for most of the variability in population abundance (Thomas *et al.* 2011), and both resource availability and temperature are considered two of the most important factors which influence the distribution and abundance of nearly all species (Odum 1963; Krebs 1978; Begon *et al.* 1986).

More specifically, increases in temperature have been observed to increase population size (Pollard 1988; Pollard & Moss 1995), larval growth (Porter 1982), advance emergence dates (Roy & Sparks 2000; Sparks *et al.* 2006), induce range shifts (Hill *et al.* 2002; Hellmann *et al.* 2008; Chen *et al.* 2011), as well as increase flight activity (Howe *et al.* 2007; Wikstrom *et al.* 2009) and movement (Sparks *et al.* 2005; Sparks *et al.* 2007), although a more recent study has also shown an inverse relationship with temperature (Isaac *et al.* 2011b).

However, butterfly populations are also frequently observed to be restricted by limitations in resources (Dennis 2010). Within butterfly biology, several authors divide resources into consumables and utilities (Shreeve *et al.* 2004; Dennis *et al.* 2006b; Hardy & Dennis 2007);

consumables are resources which can be eaten or absorbed by both adults and larvae, for example hostplants, oxygen, water, minerals, salts, nectar, pollen and sap, whereas utilities describe conditions for existence and persistence, for example thermoregulation, pupation and mate location sites (Dennis *et al.* 2003). For clarification, throughout this thesis I use the word 'resources' to mean consumable resources, more specifically foodplants (i.e. host and nectar plants), unless otherwise stated.

British butterflies are also often sub-divided into two main groups depending on their degree of resource specialisation (Asher *et al.* 2001; Dennis 2010). Species which are limited in resource use are described as specialists, whereas species which have more catholic tastes are described as generalists (or non-specialists). In reality, this classification represents a continuum of ecological strategies and encompasses a variety of traits: specialist species tend to feed on just one species of hostplant (i.e. they are monophagous), be restricted to particular habitat types, have limited mobility, patchy distributions and discrete populations (Fox *et al.* 2006; Dennis 2010), with the opposite traits being exhibited by generalists. For this reason, the term 'colonial' or species with 'closed' populations (Pollard & Yates 1993) is nearly synonymous with 'specialist' as defined by Asher *et al.* (2001). Likewise, generalist butterfly species are also described as 'wider countryside species' (Asher *et al.* 2001), or as having 'open populations'.

Certainly, the more resources that a species can utilise then the greater potential there is for survival across a multitude of environmental conditions and sites (McNaughton & Wolf 1970; Brown & Maurer 1987). Climate and resources are only two (albeit important) of many limitations acting upon a species which defines its potential living space or 'niche' (Hutchinson 1957). The 'fundamental' niche is the potential living space which a species could occupy given a lack of any limitations. Therefore, in theory, *any* area which has sufficient resources coupled with a suitable climate could allow indefinite persistence of a particular butterfly species. However, the area that a species can actually occupy is typically a fraction of the potential niche. Further limitations from utilities (e.g. nectar or roost sites), competition or parasitoids and a combination of these factors will result in further reductions in the space that can be actually occupied, until all limitations are considered and the definitive species distribution is reflected by its 'realised' niche. For example, the ability to use additional or supplementary hostplants will generally broaden the niche as different species of plants will differ in distribution (within as well as between sites), and occur in different environmental conditions (e.g. soil types). Understanding niche breadth can help to explain where species occur, and

how common they are, with narrower niche species normally being more restricted in habitats or distribution (Oliver *et al.* 2009).

It has long been appreciated that widely distributed species are generally found to be more locally abundant than species with a more restricted distribution (Darwin 1859), although this has only been quantified relatively recently (Hanski 1982; Brown 1984). However, among butterflies in northern Europe this 'interspecific abundance occupancy relationship' is weak and sometimes negative, although this can also depend on the scale of study (Cowley *et al.* 2001a; Paivinen *et al.* 2005). This is probably because species with small distributions are generally habitat specialists and tend also to exhibit low mobility (compared to generalists) (Asher *et al.* 2001). However, many of these life history traits are not mutually exclusive (Ockinger *et al.* 2010; Betzholtz & Franzen 2011; Sekar 2011; Stevens *et al.* 2012), and so it is often difficult to explain the mechanism which underpins patterns of both distribution and abundance (Paivinen *et al.* 2005; Kearney & Porter 2009). Furthermore, the distinction between specialists and generalists is not straightforward (see above) and lacks consistency, further complicating the understanding of the link between resources and abundance. For example, some species may be both nectar (the adult resource) and hostplant (the larval resource) specialists (Tudor *et al.* 2004; Hardy *et al.* 2007), while others are larval host plant specialists but nectar generalists (Dennis 2010), and so uncertainty remains as to their classification (i.e. species' degree of specialisation may be measured on more than one axis). Moreover, there is still a lack of data on adult nectar preferences, for example, within the U.K. 29 butterfly species (half the total) have less than fifty records for adult feeding (Dennis *et al.* 2008b).

So generally, rarer species tend to be highly sedentary in an extremely localised habitat and are therefore unlikely to have any interactions with the nearest colony. Individuals living within these highly isolated populations with little interactivity are often described as 'closed' (Warren *et al.* 2001), and face several problems. At low density females may have reduced lifetime fecundity because it takes longer to mate or might fail to mate (Gilpin & Soule 1986; Lande 1987). Breeding within small populations is also likely to reduce genetic fitness and increase the likelihood of inbreeding depression due to the Allee effect (Allee 1949; Saccheri *et al.* 1998), thus many small populations may have to rely on the 'rescue effect' in order to persist (Brown & Kodricbrown 1977). However, there is the possibility that population structure will vary depending on the scale of the study (Harrison 1994) and furthermore, there are increasing numbers of sporadic records of individuals of what are perceived as highly sedentary species being recorded miles away from the nearest known colony (Fox *et al.* 2006),

so again, the definition of 'open' and 'closed' are somewhat arbitrary. Fundamentally, the ability of a species to adapt to current environmental conditions will determine its population structure (Thomas & Kunin 1999). Some species may exist within discrete colonies dotted across the landscape, bounded by restraints of a particular temperature or habitat, other species may be much more widespread and therefore the distinction between colonies is much more diffuse (Hanski 1998b).

Consequently, a species realised niche will depend on the climate, and the quality of both the habitat and the resources it contains. Understanding the importance of separate resources is not straightforward, as like many insects, butterflies go through definitive life cycle stages in order to develop; egg; larvae; pupa and finally adult. The requirements for each stage of the life cycle may be reliant on totally different temperature or resource needs than the previous stage, for example, most larvae feed on plant tissues but adults often feed on nectar. Therefore, due to the variation in life history stages, evidence remains mixed as to the significance of different types of resources in determining butterfly population abundance.

Adult butterflies are the most conspicuous stage of the life cycle and are therefore the easiest to study (Ehrlich *et al.* 1975). Floral nectar is by far the most common food source (Boggs 1987), and although its quality depends on flower age, time of day, weather and activities of previous nectar feeders (Gottsberger *et al.* 1990), many studies suggest that nectar contributes to longevity and reproductive success (Boggs & Ross 1993; Boggs & Freeman 2005; Erhardt & Mevi-Schutz 2009). Several studies have also demonstrated a positive relationship between adult abundance and amount of nectar (Clausen *et al.* 2001; Summerville & Crist 2001; Bergman *et al.* 2008; Kubo *et al.* 2009), and in the Åland islands patches which contained a lot of nectar sources had reduced emigration rates for *Melitaea cinxia* (Kuussaari *et al.* 1996; Moilanen & Hanski 1998).

However, more significantly, nectar failed to predict occupancy and abundance within these same habitat patches (Hanski 1998b) and no scientific study has yet to show nectar as a key driver in population change (Thomas *et al.* 2011). Furthermore, many authors also suggest that nutrients acquired during larval development are believed to be primary determinant of longevity and fecundity in butterflies (Labine 1968; Boggs 1987; Baylis & Pierce 1991; Hughes 2000), potentially reducing the importance of nectar as a determinant of abundance.

As no external feeding occurs while inside the egg, or during pupation, then the only remaining possibility for biotic resources to act as a limiting factor are during the larval stage. The availability of the host foodplant is certainly very important (Leon-Cortes *et al.* 2003; Dennis *et*

al. 2004), and is often considered a more effective predictor of abundance than nectar (Auckland *et al.* 2004; Eichel & Fartmann 2008), principally because a species cannot persist without the host plant being present to facilitate successful reproduction.

In a pioneering study, Dempster (1971) showed that abundance of the cinnabar moth was determined by the biomass of a foodplant to the extent that predictions on future population size were relatively accurate (Lakhani & Dempster 1981). However, more recent studies show that while the amount of host plant is closely linked to the abundance of several butterfly species (Munguira *et al.* 1997; Haddad & Baum 1999; Luoto *et al.* 2001; Matter & Roland 2002; Krauss *et al.* 2004b; Betzholtz *et al.* 2006; Nowicki *et al.* 2007), this relationship is often weaker than predicted (Kelly & Debinski 1998), with many other studies on single species showing no significant relationship (Kuussaari *et al.* 2000; Kuussaari *et al.* 2004; Hanski & Meyke 2005; Fred *et al.* 2006; Rabasa *et al.* 2008; Stasek *et al.* 2008), or even an inverse one (Thomas 1984; Thomas *et al.* 1986).

Additionally, in a recent meta-analysis using British butterflies Thomas *et al.* (2011) demonstrated that for over 20 species recorded on the UK Butterfly Monitoring Scheme (UKBMS), host plant abundance was not significantly related to butterfly abundance at local scales. Thus, the simple presence of a suitable host plant rarely provides sufficient conditions for survival (New 1995; Dennis *et al.* 2003), and the critical factor is not the overall amount or abundance of host plant, but the number of plants growing in suitable locations for egg laying and larval development (Dennis 2010; Thomas & Lewington 2010).

This is because the larval stages of butterflies have considerably more exacting ecological habitat requirements, and so they can be described as occupying a narrower realised niche than adults (Thomas 1995b; Roy & Thomas 2003). While adult butterflies can fly between flowers searching for nectar, or seeking shelter during inclement weather, most larvae are restricted to spending the majority of their lifetime within a few square metres of habitat, predominantly feeding on the oviposition foodplant or a close neighbour. This lack of mobility will reduce the ability to control for variations in temperature, weather, or lack of resources, and so the constraints faced by larvae (compared to adults) are more acute. Certainly, any larvae which fail to locate a suitable plant on which to feed will starve, and so the selection of oviposition site is of considerable importance (Doak *et al.* 2006; Bonebrake *et al.* 2010).

Many female butterflies will therefore restrict oviposition to a host plant growing within a suitably warm microclimate (Thomas 1983a; Weiss *et al.* 1988), of a particular size or shape (Bourn & Thomas 1992; Gripenberg & Roslin 2005), or select hostplants based on chemical

composition for use as larval defence (van Nouhuys & Hanski 1999; Goverde *et al.* 2008; Talsma *et al.* 2008). Therefore, butterflies may only use a subset of the host plants available to them (Thomas *et al.* 2001), with rarer species in particular only using a fraction of the available larval resource (Dennis & Shreeve 1991). Hence the distribution of a particular growth *form* of the plant may be considerably more important than its total abundance. However, the strength of relationship between a species and its foodplants may also vary depending on other factors, for example, life history traits (Boggs & Ross 1993; Garcia-Barros 2000; Mattila *et al.* 2009; Poyry *et al.* 2009a), niche breadth (Thomas 1995c; Hughes 2000; Roy & Thomas 2003; Komonen *et al.* 2004; Summerville *et al.* 2006; Anthes *et al.* 2008; Friberg *et al.* 2008; Mattila *et al.* 2009; Oliver *et al.* 2009) or local site characteristics (Hanski *et al.* 1995; Moilanen & Hanski 1998; Kuussaari *et al.* 2000; Holt *et al.* 2004; Dennis & Sparks 2005; Dennis *et al.* 2006b; Grundel & Pavlovic 2007; Pettis & Braman 2007; Rabasa *et al.* 2008; Rundlof *et al.* 2008; Sjodin *et al.* 2008; Poyry *et al.* 2009b; Lindell & Maurer 2010).

The relationship between butterflies and their host plants is therefore not straightforward (Quinn *et al.* 1998). Certainly, at a highly localised level, the presence of a butterfly species at a particular site may depend on a wide range of factors including amount of heat, light and shelter, weather, abundance of food plants, the profusion and quality of flowers for adult feeding, and the abundance of predators and parasitoids and prevalence of diseases (Dennis 2010). Consequently, local populations are undoubtedly influenced due to vegetation and floristic differences between sites, and abundance is often found to be highest on sites which have both an ample supply of nectar and a high density of host plants (Fred *et al.* 2006; Bergman *et al.* 2008; Stasek *et al.* 2008).

Therefore, while the limits of species distributions of butterflies is likely to be determined by climatic constraints (Heath *et al.* 1984; Gaston 2003), their abundance is likely to be influenced by local resource levels (Gutierrez & Menendez 1995). The concept of resources limiting abundance is not new, with Milne (1957, 1962) suggesting that because of the variability of nature, only competition for resources acts in a sufficiently consistent density dependent way to provide a limit to the size of populations. Pollard and Yates (1993) also suggest that a resource limit or 'ceiling' (Dempster 1983) is likely to produce the synchrony observed across both species and sites, as no other factor is likely to limit population growth in such a consistent way. Since resources are both spatially or temporally limited, density dependent processes can regulate populations across all sites and habitats (Dennis & Taper 1994; Nowicki *et al.* 2009), because each site has a 'carrying capacity' which allows it to support a population of a certain size but no larger (Sawchik *et al.* 2002). At or near carrying capacity, resource

limitation affects population growth rate through intraspecific competition (Thomas *et al.* 1997). Thus, the frequently observed dramatic population increases are probably because the previous year's numbers were low relative to the carrying capacity of the site, and when populations are low there remains large areas of unexploited food plants providing potential for population growth (Dempster & Pollard 1981). Although density dependence is not easy to detect over short periods, long term datasets suggests that it is widespread in Lepidoptera (Hanski & Woiwod 1991).

Indeed, this 'resource limitation hypotheses' can potentially explain the fluctuations observed within the UKBMS dataset, as monitoring has shown that the patterns of fluctuations can be very similar from site to site, and the variation in abundance remains very similar from year to year (Pollard 1991; Botham *et al.* 2009). The high degree of synchrony between populations over a large area for many years would certainly suggest the same factor operating on all populations, and many studies have alluded to weather as the most important factor in determining abundance (Pollard *et al.* 1995; Sutcliffe *et al.* 1996; Roy *et al.* 2001; Hanski & Meyke 2005; Guiney *et al.* 2010), possibly because weather (particularly rainfall, sunshine or temperature) could influence resource availability which in turn limits population growth (Dennis & Sparks 2006). Nonetheless, it is also plausible that fluctuations in both abundance of the food plant and the insect host could be responding to the same environmental factor with no causal relationship between the two (Dempster & Pollard 1981). Therefore, a key unanswered question remains whether the relationship between resources and population abundance is universal, or instead contingent on the spatial scale, timeframe and species under investigation.

The advent of landscape ecology

It has been recognised for a long time that currently occupied areas may become vacant tomorrow and reoccupied next week or next year (Andrewartha & Birch 1954), and the advent of both the Theory of Island Biogeography (MacArthur & Wilson 1967), examining the importance of spatial configuration of real islands, and metapopulation theory (Levins 1970), which uses habitat islands within terrestrial fragmented landscapes, both re-orientated research away from conserving species within single reserves to the importance of conserving interacting populations across entire landscapes. Indeed, these concepts remain influential in modern nature conservation policy, which often emphasise the importance of size and structural connectivity of landscapes (Boitani *et al.* 2007; Hodgson *et al.* 2009).

Metapopulation theory was founded on a pioneering study in 1967 which used real islands to suggest that both area and isolation were the most important characteristics for determining occupancy (MacArthur & Wilson 1967). The underlying principle was that the larger the distance between islands, the fewer individuals will move between them resulting in lower occupancy rates. Shortly after this, Levin's (1970) conceived the concept of the metapopulation, originally devised as a mathematical term describing a population of populations. This term was later used to neatly describe a network of terrestrial habitat patches which persisted as a population through a continual balance of colonisations and extinctions of local populations (Hanski 1994b; Hastings & Harrison 1994). More specifically, the term metapopulation became synonymous with the long term study of the Glanville fritillary butterfly in the Åland Islands (Hanski 1999b) which supported the importance of area and isolation in determining patch occupancy (Hanski *et al.* 1994; Hanski *et al.* 1995; Hanski 1998b).

The main tenet of metapopulation studies is that areas with aggregations of resources may lead to a clustering of individuals within certain habitat 'patches' (Southwood 1977), with unfavourable areas between patches containing very few resources described as a 'matrix' (Hanski 1999b), which remains predominantly unoccupied (Moilanen & Hanski 1998). As inhabited habitat patches become distinct from the surrounding matrix, or as isolation between colonies increases, populations form distinct units in which abundance varies depending on patch characteristics and associated biotic and abiotic factors (Hanski 1994a). It is this degree of separation (or connectivity) which defines populations, ranging from multi-partite populations which contain overlapping interacting groups with indistinct boundaries to patchy populations with no interactions (Hanski 1999a). However, when suitable patches become separated by relatively short distances (e.g. close enough to allow re-colonisation) they may still be connected by regular transfer of individuals – hence the whole metapopulation persists – but only as a network of vacant and occupied habitat patches. Each habitat patch can thus be described as a source, in equilibrium, pseudosink or sink depending on the number of emigrants it provides or the average number of immigrants it receives (Hanski *et al.* 1995).

On the assumption that most patches in a network are occupied, Levins (1970) suggested a minimum of some 15 – 20 well connected patches are required for long term persistence, a concept which was also supported by Thomas and Hanski (1997). Although, some authors suggested that the Levins or 'classic' population structure was deemed unrealistic within real landscapes (Harrison & Taylor 1997), it is believed to be a reasonable description of the

population structure of many butterflies, including approximately half of resident Finnish (Hanski *et al.* 1995) and British butterfly species (Hanski & Thomas 1994). Many of these butterflies are 'specialist' species and so they tend to be monophagous with limited dispersal capabilities, hence they are often restricted to rarer habitats and exhibit patchy distributions. Consequently, specialists also tend to include the rarer, most rapidly declining species, and priority is often given to their conservation (Fox *et al.* 2011).

Therefore, metapopulation theory had important consequences for butterfly conservation in Europe, with research suggesting that the priority for land managers should be preserving large, interconnected habitats (regardless of the quality of the habitat within them), thereby distracting from the more important (but less interesting) problem of habitat management (Thomas *et al.* 2001). The debate then became polarised as to which factors were more important at explaining the dramatic disappearance of butterflies across modern landscapes, with advocates of metapopulation theory explaining extinction as a result of too few, small and isolated populations to allow continued persistence (Hanski 1994b, 1998b), and those suggesting that local extinctions are caused by temporary or more permanent change in habitat quality (Harrison 1994; Thomas 1994). However, concrete explanations of the determinants of abundance and persistence remained elusive. Both camps moved only slightly towards middle ground, with habitat quality advocates suggesting that as most landscapes change as 'shifting mosaics' over long periods of time (Boorman & Likens 1979), and that as changing habitat quality inevitably contributes to population turnover, metapopulation persistence is possible but more likely in successional habitats (Harrison 1994).

Metapopulation advocates also incorporated a habitat quality factor into their research. The importance of habitat, specifically host plant abundance, was evaluated by Kuussaari (2000) who compared host plant density with *Glanville* fritillary density on the Åland Islands, but like many previous autecological studies found no relationship. However, resources could certainly influence adult movements, with high host plant abundance shown to increase immigration, and low numbers increasing emigration (Brommer & Fred 1999; Hanski & Singer 2001; Kuefler & Haddad 2006).

Given that the amount of host plants within a habitat patch did not explain variation in population abundance (Hanski & Meyke 2005), metapopulation studies continued to focus on the importance of isolation and size of habitat patches.

Principally, research demonstrated that the more isolated a site, the more likely it is to be unoccupied (Hanski *et al.* 1994; Hill *et al.* 1996; Dennis 1998; Wilson *et al.* 2002; Betzholtz *et*

al. 2006; Bauerfeind *et al.* 2009), support smaller populations (Aviron *et al.* 2007; Lenda & Skórka 2010; Rosin *et al.* 2011) have lower persistence times (Hanski 1998b; Thomas *et al.* 2001) and the individuals within them possessing lower genetic fitness (Ehrlich 1983; Saccheri *et al.* 1998; Haag *et al.* 2005; Austin *et al.* 2011) resulting in increased extinction risk (Haikola 2003). More isolated patches are therefore likely to receive fewer immigrants, because increasing isolation may result in patches being beyond the dispersal capabilities of individuals (Mennechez *et al.* 2003; Junker & Schmitt 2009; Leidner & Haddad 2011). Furthermore, larger patches are more likely to be occupied (Thomas *et al.* 1992; Hanski *et al.* 1995; Bauerfeind *et al.* 2009), support more individuals than smaller ones (Luoto *et al.* 2001; Krauss *et al.* 2004b; Lenda & Skórka 2010; Rosin *et al.* 2011) and produce a larger number of emigrants, and receive more immigrants (Hill *et al.* 1996; Kuussaari *et al.* 1996; Wahlberg *et al.* 2002), and so extinction risk is considerably lower (Thomas 2000; Hanski & Ovaskainen 2002; Ovaskainen *et al.* 2002; Drechsler *et al.* 2003).

However, there is a caveat with the isolation effect, in that several studies suggest that many species are moving greater distances than originally suspected (Asher *et al.* 2001; Baguette 2003) and other studies have shown no or very weak relationships between population size and isolation (Krauss *et al.* 2003b; Krauss *et al.* 2005), with individuals from isolated patches showing no genetic differentiation from non-isolated individuals (Krauss *et al.* 2004a). Additionally, as patch size increases, it is likely to encompass more heterogeneous habitat and variations in topography, and less likely to be uniform in resource type, quality and quantity (Dennis 2010). Therefore, larger patches may also contain a disproportionate increase in matrix habitats, and this probably explains why several studies have shown that abundance does not increase proportionally with area (Steffan-Dewenter & Tschardt 2000; Rabasa *et al.* 2008). Furthermore, area has also been found to be a poor predictor for a wide variety of species on both occupancy (Prugh *et al.* 2008), and explaining extinction rates (Pellet *et al.* 2007), so it is highly likely that the importance of area depends on the way that habitat patches are defined or delimited (Pautasso & Gaston 2006).

Fundamentally, metapopulation theory suggests that species persistence is a function of patch number and spatial arrangement of patches, and their size and isolation (Hanski *et al.* 1994; Hanski 1998a). The probability of extinction for individual patches is related to small patch size, demographic stochasticity, emigration exceeding immigration, asynchrony in emergence of sexes, and inbreeding depression (Hanski *et al.* 1995; Haikola 2003). Although increased habitat heterogeneity had been shown to result in decreased population variability (Hanski & Woiwod 1991), one of the main criticisms of metapopulations was that they were mainly

habitat homogeneous, and within most metapopulation studies habitat quality had always been subsumed by patch area (Nieminen *et al.* 2004). However, patch area makes no reference to the composition and structure of resources which comprise habitat patches or resource connectivity, although large increases in patch size (by orders of magnitude) revealed that resource quantity can partly offset reductions in resource quality (Dennis 2010).

Metapopulations are also frequently considered to be too simplistic because doubts remain as to what is defined as a colony, patch, and matrix, and the distinction between an area containing resources and one without is becoming more and more blurred (Dennis & Hardy 2007). Indeed, our understanding as to what is considered to be an important resource has broadened, and the more resources which are taken into account in defining habits in butterfly biology, for example, roost, thermoregulation, and hibernation sites (as well as hostplants), then the greater the number of resources that will be found within the matrix (Dennis *et al.* 2006b). The importance of the matrix habitat is therefore frequently understated, despite Ovaskainen (2004) observing that individual butterflies often spend more than fifty per cent of their time within it, and that it also affects survival, maintenance and reproduction within metapopulations as well as direction, distance and speed of movements (Dennis 2010). Additionally, the real-world distinction between 'patches' and 'matrix' is often unclear, and the boundaries between them change over time, so defining patch boundaries is problematic (Meeting & McCullough 1996; Thomas & Kunin 1999).

Hence, several authors have questioned the usefulness of metapopulations in conserving species within real landscapes (Baguette 2004), as inevitably real systems rarely match their purely theoretical definitions (Harrison & Taylor 1997). For example, a key assumption in metapopulations is that the individual habitat patches should have asynchronous population dynamics so that simultaneous extinctions are unlikely (Sutcliffe *et al.* 1996; Mousson *et al.* 1999). However, shorter distances between colonies, correlated environmental conditions and increasing dispersal can all greatly enhance population synchrony (Sutcliffe *et al.* 1997), particularly on marginal populations experiencing climatic constraints (Powney *et al.* 2010). Furthermore, any strong tendency for species to persist at sites weakens the validity of much of classical metapopulation theory (Levins 1969) and fundamentally, modelling is only reliable if considerable information exists on habitat quality and distribution, population sizes, dynamics and dispersal behaviour (Sutherland 1998).

Despite this, metapopulations have greatly enhanced our understanding of how patch geometry influences rates of colonisation, extinction, immigration and emigration, and

highlighted the importance of landscape characteristics in conserving species existing within fragmented landscapes (Jones 2011). However, area and isolation appear to have little role in determining whether species within occupied patches occur at high or low abundance (Hanski 1999b), and so an unanswered question remains to what extent do resources affect abundance over both landscape and regional scales.

There have been relatively few studies examining the importance of resources on butterfly abundance at regional scales. Certainly, the distribution of the hostplant can determine a butterfly's range at larger scales (Brandle *et al.* 2002), but understanding the relationship between resources and abundance is more complex, probably because of the difficulty in measuring resource availability over large areas (Gaston *et al.* 2004; Paivinen *et al.* 2005). Despite this, the amount of hostplant (edible biomass) has shown to have a positive relationship with abundance for 23 of 39 butterfly species inhabiting small islands (areas of 0.15, 0.76, 1.45, 0.56, and 0.15km²) in Japan (Yamamoto *et al.* 2007) and at the regional scale (170km²) abundance of the larval food plants family was also related to butterfly abundance in northern Spain (Gutierrez & Menendez 1995). Similarly, Cowley *et al.* (2001b) collected data on the density and distribution of adult butterflies and all associated host plants within a 35km² area in the U.K. (North Wales), and found that butterfly species whose hostplants occur at high density also tend to be locally abundant.

However, Hughes (2000) found no relationship between hostplant and lycaenid abundance across seventeen (50 x 50m) sites in Colorado, America, and on a much larger scale Kuussaari (2000) found no relationship between host plant and *Glanville fritillaria* abundance in the Åland Islands (an area of 3500km²), although this result is perhaps unsurprising over such a large area given that the condition of the hostplant is often considered to be more important than its abundance (Thomas *et al.* 2011).

Therefore, at localised scales (within sites), both the strength and direction of the relationship between resources and butterfly abundance can depend on species traits and site characteristics (Isaac *et al.* 2012). At the landscape scale, the persistence and abundance of interacting populations can also depend on the geometric properties of habitat patches as well as the resources they contain (Hanski 1999b; Dennis 2010). However, at broader scales there remains the potential to answer how resources determine both intra and interspecific abundance across entire regions (Gaston 1992), especially with the scarcity of previous research. Furthermore, given the severity of butterfly declines across Europe from habitat degradation (van Swaay *et al.* 2010; Thomas *et al.* 2011), fragmentation (Hanski 2011a;

Ockinger *et al.* 2012) and climate change (Morecroft *et al.* 2011; Wilson & Maclean 2011) all three approaches could be useful in suggesting ways to increase butterfly abundance, from site specific management recommendations (depending on species and location), through to understanding the importance of habitat management, size, and connectivity of populations within fragmented landscapes, and finally understanding the broad scale patterns from which general recommendations could be incorporated within regional conservation policy or biodiversity action plans.

Thesis outline

In this thesis, I address the issues and complexities of determining species abundance at local (Chapter 1), landscape (Chapter 2) and regional (Chapter 3) scales. Fundamentally, I have taken a ‘bottom up’ approach to explaining butterfly abundance, rather than top – down (predators and parasitoids). This is because for the majority of butterfly species, resource availability is the major factor which limits population growth and determines mean population size (Pollard & Yates 1993; Dennis 2010; Thomas *et al.* 2011). The frequent synchrony observed in disparate butterfly populations would suggest that interactions with local predators and parasitoids are relatively insignificant (Rausher 1981; Pollard & Yates 1993), to the extent that predation was not even considered as a factor within a review of drivers of population change (Thomas *et al.* 2011). The importance of parasitoids also remains equivocal, despite evidence from a limited number of species; *Melitaea cinxia* (Lei *et al.* 1997), *Euphydryas aurinia* (Porter 1981) and *Celastrina argiolus* (Revels 2006). However, while parasitism may be a potentially synchronising mechanism (Nicholson & Bailey 1935; Hassell *et al.* 1991), it is not an important mechanism in explaining variation in host abundance, with more recent studies on the same species contradicting the findings of earlier studies e.g *Melitaea cinxia* (Hanski & Meyke 2005).

Therefore, in Chapter 1 I assess the importance of temperature and variation in microhabitats as determinants of abundance. In Chapter 2, I compare habitat quality with landscape parameters and test whether the strength of each parameter varies with temperature. In Chapter 3, I explore the determinants of inter and intra specific abundance at a regional scale, examining the importance of species traits and site characteristics.

Chapter 1

I use the Glanville fritillary as a study organism as it is a specialist butterfly species at the northern margin of its range within the U.K., and therefore highly likely to be sensitive to changes in the environment. Additionally, its population levels are easy to monitor as the

larvae are relatively conspicuous within 'webs'. Indeed, I have been monitoring population levels of this species since 1996, originally under the guidance of Jeremy Thomas, and found the dramatic population fluctuations so intriguing that I continued to monitor it annually to the present day. Furthermore, it has been intensively studied in previous research on which much evidence for butterfly conservation has been derived.

In this chapter, I explore the key factors which determine oviposition preferences at localised scales, and assess whether small scale variation in habitat and temperature can be correlated with changes in population abundance between years and experimental plots on a small (<1km²), isolated site. I also suggest implications for site management given that many butterfly species inhabit unnatural early successional habitats at northern latitudes.

Chapter 2

In this chapter I again use population data from the Glanville fritillary, derived from 8 sites (containing 70 habitat patches) along the south coast of the Isle of Wight, thereby encompassing spatial variation of approximately 30km.

I use a measure of the amount of suitable habitat within patches (habitat quality) as a surrogate of suitable resource availability, and also incorporate the geometric properties of habitat patches (metapopulation parameters of area and isolation) and ambient air temperature to assess the most important determinants of abundance at the landscape scale. I also examine the importance of temperature variation as an interactive effect with the other parameters.

The results suggest that all of these parameters are important, and I discuss the significance of each with relevance to conserving species within fragmented habitats.

Chapter 3

Finally, in this chapter I use UKBMS population data for 30 butterfly species from 54 sites across southeast England, combined with population specific estimates of resource availability (host and nectar plant abundance) to test a suite of hypotheses about the variation in population abundance both between and within species at a regional scale. I also examine species traits and site characteristics to explain species' sensitivity to changes in resource abundance.

Taken together, this research aims to show that despite contradictory results as to the importance of resources within many previous studies, general patterns do emerge at a broader scale which could be used to manage butterfly populations within sites. I also reassess conservation priorities while accounting for differences in species, sites and scales.

Chapter 1) The Effects of Temperature, Microclimate and Habitat Quality on Abundance of the Glanville fritillary on the Isle of Wight.

Abstract

Clarifying the mechanisms which underpin species distributions and abundance remains a key question in ecology, and both climate and resources have been implicated in many studies as constraining factors at a range of temporal and spatial scales.

The number of Glanville fritillary larval 'webs' was monitored on five adjacent habitat plots on a small, isolated site on the south coast of the Isle of Wight from 1997 - 2010. Ground temperatures beneath the various habitat successional stages were measured and compared, and the relationship between butterfly distribution and hostplant and habitat temperatures was examined. Temporal variation in abundance was correlated with habitat quality (calculated from the distribution of successional stages in each plot), plot aspect and ambient air temperature. Larval hostplant and habitat preferences were also compared from 1980 and 2011 to assess any changes over the 30 year period.

Comparisons of ground temperatures beneath habitats showed that earlier successional stages were considerably warmer than later successional stages, and the distribution of Glanville fritillary larval 'webs' within plots was restricted to these warmer habitats and the hostplants within them. I also demonstrated that hostplants selected for oviposition by gravid females (whilst not directly compared against plants not laid on) were considerably warmer than ambient temperature.

The most important factor in predicting abundance was habitat quality, more specifically the availability of hostplants in short turf which provides favourable microclimatic conditions for oviposition. However, annual variation in web abundance was also related to ambient temperature, although the importance of plot aspect remained inconclusive. A comparison of the spatial distribution of webs in 1980 and 2011 showed changes in oviposition preference towards larger hostplant size but no difference in habitat (successional stage).

The amount of suitable habitat and ambient temperature during the flight period both determine larval abundance. Furthermore, recent rises in spring temperatures have increased the carrying capacity of this site probably because previously unsuitable (cooler) areas have become warm enough to allow oviposition - thereby causing dramatic increases in Glanville fritillary abundance.

The importance of habitat quality reinforces the concept that sites should be managed to create thermally diverse environments, as many butterflies within the U.K are restricted to warmer microclimates due to temperature constraints. Furthermore, sites with varied topography and managed for habitat heterogeneity are more likely to support viable insect populations as climate warming increases.

Introduction

The abundance and distribution of a species is a reflection and response to environmental conditions (Brown 1984). All species populations fluctuate in response to environmental changes over time (Andrewartha & Birch 1954), and the direction and scale of the response can be influenced by many factors, for example, climate, resources, predators and diseases and often the complex interactions between them (Begon *et al.* 1986). Clarifying the importance of the various factors that determine species distributions and abundance is a key question in ecology (Whittaker 1975; MacArthur 1984), as although there are general patterns, the mechanistic explanations do not yet appear to be definitive (Storch & Gaston 2004; McGill 2006; Mattila *et al.* 2011). However, there are key drivers of these processes, and temperature and resource availability influence both the distribution and abundance of nearly all species (May 1975; Krebs 1978).

Butterflies, like most insects, are highly responsive to changes in the environment (Oostermeijer & van Swaay 1998; Thomas 2005), but are particularly sensitive to changes in temperature (WallisDeVries & Van Swaay 2006). Indeed, it is of such importance that an increase in temperature has been observed to increase range and distribution (Crozier 2004; Wilson *et al.* 2005), population size (Pollard 1988; Pollard & Moss 1995) advance emergence dates (Roy & Sparks 2000; Sparks *et al.* 2006) as well as increase flight activity (Howe *et al.* 2007; Wikstrom *et al.* 2009) and movement (Sparks *et al.* 2005; Sparks *et al.* 2007), but see Isaac *et al.* (2011b) for a counter-example. However, the magnitude of response to changes in temperature is likely to depend on geographic location (Thomas 1993), site characteristics (Sutherland & Hill 1995; Cozzi *et al.* 2008) as well as species life history traits (Heikkinen *et al.* 2009; Diamond *et al.* 2011).

Butterflies are frequently constrained by climatic limitations at a range of spatial scales (Heath *et al.* 1984; Dennis & Shreeve 1991; Bryant *et al.* 2002). Geographical location, in particular latitude, is important as regional butterfly distribution is limited by climatic tolerances of species (Gutierrez & Menendez 1995; Dennis *et al.* 2008a), mainly because the time available in which to complete the life cycle is a primary constraint (Andrewartha & Birch 1954).

Butterfly species richness therefore declines from the equator to the poles, and because temperature is a key driver in determining distribution, northern Europe is the range limit for many butterfly species (Dennis 1977). However, site altitude, slope and aspect, will all influence the local thermal microclimate and thereby influence distribution patterns over smaller scales (Thomas *et al.* 1998; Storch *et al.* 2003).

Within sites, small variation in vegetation structure and topography creates thermal gradients across the landscape, forming microclimates where patches of ground become considerably hotter or cooler than the ambient temperature (Rosenberg 1974). This is particularly important to butterflies, as the temperature of a hostplant within a microclimate is often crucial to optimise larval development (Renwick & Chew 1994; Doak *et al.* 2006). Therefore, within species, individuals can control for variations in temperature by choosing to oviposit on hostplants on different aspects or within vegetation of different heights (Dennis 2010). For example, temperatures are often considerably higher on south facing slopes (Bennie *et al.* 2008), and so aspect can have an important influence on whether a particular hostplant is utilised for oviposition (Weiss *et al.* 1988). Certainly, within the U.K., many species are restricted to warmer south facing slopes to counteract the reduction in time available to complete the life cycle (Bryant *et al.* 1997; Burke *et al.* 2005). However, in warmer latitudes, oviposition sites can vary depending on altitude. For example, in Spain, *Aporia crataegi* lays eggs on cooler north facing slopes at low elevations, but only on warm south facing slopes at higher altitudes (Merrill *et al.* 2008).

Similarly, the structure and height of vegetation will also determine ground temperature (Waterhouse 1950), and is a principle determinant of oviposition locations (Thomas & Lewington 2010). At warmer latitudes species may utilise different habitats depending on altitude. For example, in Spain, *Parnassius apollo* chooses relatively warmer microclimates at higher elevations to counteract a decrease in temperature (Ashton *et al.* 2009). However, many butterflies at the northern edge of their range survive by inhabiting earlier (hotter) successional stages of habitats opposed to their conspecifics living within the (warmer) centres of their range (Thomas 1993; Thomas *et al.* 1999). This could explain why, at cooler latitudes as in the U.K., butterflies may only utilise a fraction of hostplants available to them (Quinn *et al.* 1998), probably because many are not within a suitable temperature which is required for completion of the life cycle (Oliver *et al.* 2009).

Therefore, many species of butterfly at higher latitudes lay their eggs within suitably warm areas to expedite larval emergence and development (Labine 1968; Fleishman *et al.* 1997; Bonebrake *et al.* 2010), and so the local distribution of populations is frequently restricted by microclimates within habitats (Thomas 1995c). Indeed, in a recent meta-analysis Thomas *et al.* (2011) demonstrated that the relationship between the availability of habitat which provides a suitable temperature for larval development and butterfly density was significant for 97% of species studied. This has important ramifications for conservation management, particularly in the cool climate of the UK, where many butterflies reach the northern limit of their distribution (Dennis 1977). Hence, research on habitat requirements at greater spatial and ecological detail remains a priority for conservation (Kearney & Porter 2009).

Furthermore, with recent increases in global temperatures as a result of climate change, several studies have identified notable shifts occurring in butterfly phenology (Roy & Sparks 2000; Dell *et al.* 2005; van Strien *et al.* 2008) and distribution (Hill *et al.* 2002; Franco *et al.* 2006; Hickling *et al.* 2006; Chen *et al.* 2011). However, temperature driven changes in habitat associations remain largely ignored (Davies *et al.* 2006; Turlure *et al.* 2010), yet understanding such changes is essential for adaptive conservation management (Sutherland 1998; Roy & Thomas 2003).

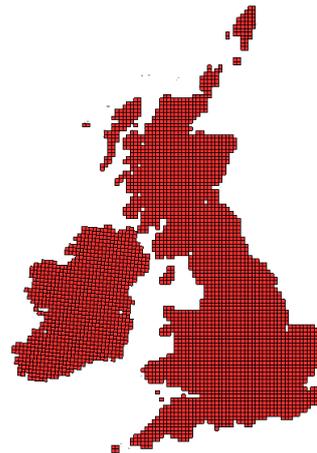
In this study, the Glanville fritillary *Melitaea cinxia* is used to test the role of both temperature and habitat quality on distribution and abundance. It is an excellent model as;

- i. The Glanville fritillary is a univoltine, monophagous species and thus it is a simple system to study. Its U.K. distribution is restricted to early-successional habitat on south-facing slopes on the Isle of Wight, yet the hostplant (Ribwort plantain, *Plantago lanceolata*) is widespread (Figure 1.1), implying a strong role for temperature and microclimate as limiting factors. As a specialist species with highly limited distribution and narrow niche breadth it is also predicted to be extremely sensitive to changes in temperature (Diamond *et al.* 2011). Furthermore, its autecology and metapopulation biology is understood (Hanski 1999b; Thomas *et al.* 2001).
- ii. The larvae form conspicuous webs, making it possible to conduct accurate population counts within just a couple of weeks each year (Thomas & Simcox 1982).

Figure 1.1 Map Showing 10km squares with records for the Glanville Fritillary *Melitaea cinxia* and Ribwort Plantain *Plantago lanceolata* in Great Britain and Ireland. The information used here was sourced through the NBN Gateway website and included the following resources. Butterfly and plant distributions for Great Britain for the period 1690-2009 were from Butterfly Conservation, the Biological Records Centre and the Botanical Society of the British Isles. Accessed 20/10/2011. The data providers and NBN Trust bear no responsibility for the further analysis or interpretation of this material, data and/or information.



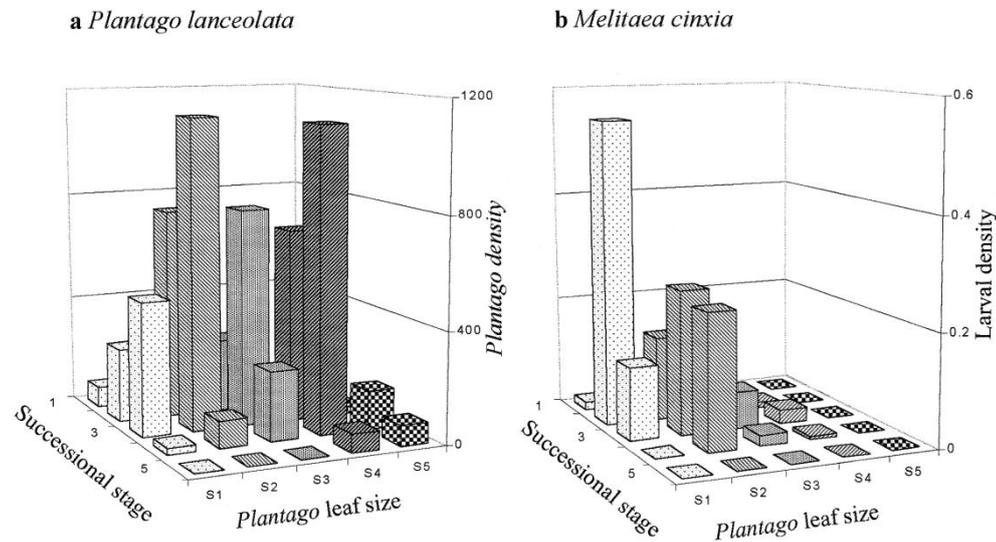
10km squares with records for *Melitaea cinxia* (Glanville Fritillary) in Great Britain and Ireland.



10km squares with records for *Plantago lanceolata* (Ribwort Plantain) in Great Britain and Ireland.

Research on the Glanville fritillary within the U.K., has demonstrated that females are highly selective and choose to oviposit only on the smallest plants which are located in one of the earliest successional stages (Figure 1.2). Thomas *et al* (2001) used this oviposition preference to estimate habitat quality across 72 patches, finding that patch quality was highly correlated with both occupancy (presence – absence in patches) and population abundance (the density of larval webs per plantain on occupied sites). See Chapter 2 for an exploration of apparent differences in results from Finnish and UK populations.

Figure 1.2 (reproduced from Thomas *et al.* 2001). a) Distribution of *Plantago lanceolata*, larval foodplant of *Melitaea cinxia*, in five successional stages of grassland and in five classes of mean plant leaf size. b) Density of larval webs of *Melitaea cinxia* in the same samples measured for *Plantago lanceolata* (n = 368 larval webs). Habitat preference is given by the difference in relative bar height between a) and b). Adult females prefer to oviposit in successional stages 2 and 3 and on leaf sizes 1 and 2.



Thomas *et al.* (2001) concluded that habitat quality played a crucial role in the distribution and abundance of the Glanville fritillary, although this study was based on field data for two years (1996 -7) and did not account for the variation in habitat quality among years. Such variation is likely to be important because of the early successional nature of the preferred habitat, and a key variable in explaining inter-annual variations in abundance is likely to be temperature (Pollard 1988; Roy *et al.* 2001). The increase in summer temperatures during this decade could also instigate ecological changes and influence both distribution and abundance. Indeed, Thomas *et al.* (2011) demonstrated that long term climate change or successional changes that effect microclimate can change the carrying capacity of a site by two orders of magnitude for non-migratory species.

In this chapter, I describe the distribution of larval ‘webs’ within plots and model Glanville fritillary larval abundance over 14 years as a function of temperature, habitat quality and aspect among five adjacent plots of occupied habitat on the Isle of Wight.

I record the temperature of hostplants utilised for oviposition and demonstrate that the temperature of microclimates at the ground surface vary depending on the height of vegetation above it. I use also site characteristics measured in the field to assess the importance of both habitat and aspect, and I use data obtained from the nearest meteorological weather station to test the importance of air temperature on oviposition

locations and temporal abundance. I also compare larval hostplant and habitat preferences which were recorded in 1980 (Thomas *et al.* 2001) to preferences recorded during field surveys in 2011.

In particular I test the following hypotheses;

H1: Temperature is predicted to be a principle determinant in suitability of oviposition locations.

- i. I predict that hostplant (*Plantago lanceolata*) choice or 'suitability' is explained by variation in temperature, in that hotter plantains will be utilised more frequently for oviposition than cooler plantains.
- ii. I also predict that the ground temperature or 'microclimate' of earlier successional stages will be considerably warmer than later ones. Therefore, hostplants distributed within hotter microclimates will be used for oviposition more frequently than those situated within cooler successional stages and thus I attempt to explain the larval habitat preferences described in Thomas *et al* (2001).

H2: Plot characteristics, as in habitat (spatial extent of suitable microclimates) and aspect, as well as annual variations in ambient temperature will also be important determinants of abundance. I also assess the significance of each predictor.

- i. I predict that incidence of Glanville fritillary larval webs should be higher in plots containing higher percentages of earlier (warmer) successional habitat and lower in plots containing higher percentages of later (cooler) successional habitat.
- ii. I also expect plots with south facing aspects to contain higher numbers of webs than plots which are flat or have more northerly aspects.
- iii. I predict that butterfly abundance (recorded as number of larval 'webs') will be higher in warmer years than cooler ones, as hostplants (located in cooler microclimates) will become 'suitable' for oviposition with increases in ambient temperature.
- iv. I assess the relative importance of these parameters and predict that habitat quality will be the strongest determinant of abundance, followed by fluctuations in annual temperature and finally aspect.

H3: I compare larval preferences in hostplant size and habitat associations in 1980 and 2011.

- i. I test whether larval preferences in both hostplant size and habitat successional stage were different in 1980 and 2011.

Methods

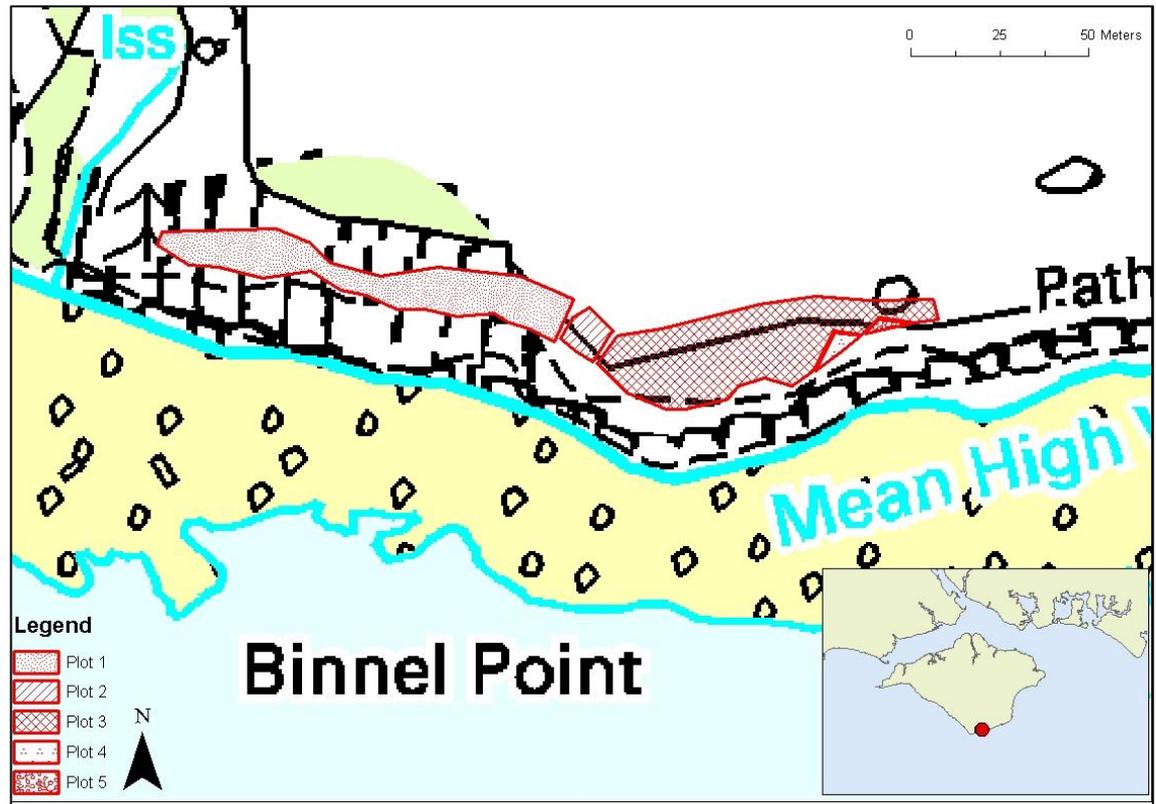
Study species

The Glanville fritillary is a univoltine species in the U.K., with a typical flight period lasting from May to July. Eggs are laid in clusters on the underside of a Ribwort plantain leaf, with most oviposition occurring in June. During summer the larvae live and feed gregariously and spin a silken web around the plantain leaves. They enter diapause within the web during early autumn, and emerge the following spring, when they again feed communally and spin a conspicuous web around plantains before pupating in April.

Study Site

Binnel Point is approximately 2.5km east of the southern tip of the Isle of Wight, just south of the village of St Lawrence. It supports a relatively small population of Glanville fritillaries and is isolated from the next nearest population (St Catherine's Point) by over 2km. The site contains a mix of predominantly semi-permanent grassland on the cliff edges flanked on the northern edge by impenetrable scrub. The area used for breeding and oviposition by Glanville fritillaries remains extremely small with the cliff top grassland habitat covering an area of approximately 200m x 20m, with a total study area of 0.4 hectares (see Figure 1.3).

Figure 1.3. A map of study plots surveyed at Binnel Point, on the south coast of the Isle of Wight.



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In order to test the importance of variation in habitat and aspect on larval web numbers, the study area was divided into adjacent plots. A previous mark-recapture study had demonstrated that female *Glanville fritillaries* could roam the entire site (unpublished data) and so isolation was not considered a limiting factor in determining web abundance. The plots were therefore defined on the basis of clear differences in habitat and topography (Table 1.1 & 1.2), which a priori were expected to explain some variation in butterfly abundance, and allowed plots to be easily identifiable on repeated surveys.

Table 1.1: Characteristics of plots surveyed at Binnel Point 1997 – 2010.

Plot Number	Aspect	Area (m ²)
1	South	1175
2	None (flat)	122
3	North	1375
4	South	62
5	South	45

Larval Survey

Glanville fritillary larval webs were recorded by walking briskly along a series of imaginary lines 5 metres apart across each plot until the entire area had been surveyed. They were recorded within a 2.5 metre imaginary box, perpendicular to the observer in the way that most adult butterflies are recorded (Pollard & Yates 1993; Botham *et al.* 2009).

Between 1997 and 2010, I counted the number of webs (annually) in each plot during late March (when the webs are most conspicuous), following methodology which has been shown to be both accurate and robust (Thomas & Simcox 1982). Survey data was also incorporated from counts conducted by the Isle of Wight Natural History and Archaeological Society (IWNHAS), using the same methodology on the same site from 1983 to 1996 (although not stratified by plot, nor accompanied by habitat quality estimates). These data are included for a long term context but not included in statistical models.

Environmental variables

Local Temperature Data

A hand held laser thermometer was used to record hostplant temperatures that were utilised for oviposition [H1:i]. Temperatures were acquired by following 60 gravid females during 6th – 25th June 2010 and recorded whilst oviposition was occurring. A note was made of time of oviposition, and this time was then matched to ambient temperature of a Tiny tag data logger which was set to record ambient air temperature every five minutes during the same day. If times did not exactly match then differences of two minutes or less were rounded down to the nearest five minute recording, and three minutes and above were rounded up to the next recording. Air temperatures varied very little between five minute intervals.

Tiny tag data loggers were also placed just below the ground surface of each habitat category (see Table 1.2 for definitions) and in shade to record ambient air temperature, and were set to record temperature every 10 minutes from 15th to 17th May 1998. This was to assess ground temperature differences between the various successional stages [H1:ii].

Habitat Quality

At each survey, plots were scored by the percentage cover in five categories (successional stages from bare ground to long grass) based on the amount of bare ground and mean turf height (Table 1.2). These data were converted into estimates of habitat quality by multiplying the area in each category by the habitat preference score for that category. Habitat preference scores are the relative probabilities of occurrence within each habitat type, summed to 1. We used scores derived from Thomas *et al* (2001), who compared the distributions of 368 larval webs and hostplants among five habitat categories, each representing a different successional stage (Figure 1.2).

Table 1.2: Definitions of successional stages contained within a typical succession from bare ground to scrub and habitat preference scores associated with each stage (after Thomas *et al.* 2001).

Habitat category (successional stage)	% Bare Ground	Mean Turf Height (cm)	Habitat preference scores (after Thomas <i>et al.</i> 2001)
1	>90	<5cm	8%
2	90 - >0	5 < 15cm	54%
3	0	15 < 20cm	35%
4	0	20 - 25cm	3%
5	0	>25cm	0%

Plot – year combinations with a high proportion of habitat category 2 would therefore have the highest measured habitat quality. Plots with 100% cover of habitat 2 would score 54 on the habitat quality scale. These estimates of quality were used to assess the strength of relationship between amount of suitable habitat and butterfly abundance [H2:i].

Aspect

Aspect was assessed for each of the five plots by recording its orientation as ‘south’, ‘north’ or ‘none’ (flat) to evaluate the importance of variations in plot orientation on butterfly abundance [H2:ii]. Plot aspects did not change throughout the study period.

Regional Annual Temperature Data

Weather data were obtained from the nearest Meteorological Office station, which was just over 2km from Binnel Point (St Catherine’s Point Lighthouse SZ497753). The June mean

maximum temperature was used in the analysis (i.e. the mean of the daily maxima; a measure of the warmth of June days), as June coincides with the peak adult emergence and egg laying period. This data was used to assess the relationship between temporal variation in ambient air temperature and butterfly abundance [H2:iii].

Larval preferences

Thomas *et al* (2001) assessed larval preferences in 1980 within 246 random 1m² quadrats containing 368 webs on 3800 plantains across six occupied sites. Each plantain was classified as growing in one of five successional stages (Table 1.2), and the mean leaf size was measured and assigned to one of five classes (S1: < 120mm²; S2: 120-500mm²; S3: 501-1800mm²; S4: 1801-3910mm²; S5: > 3910mm²). The density of Glanville fritillary larval webs was recorded in the same samples, and the successional stage and plantain leaf size they used was also measured.

I repeated this methodology across five (different) occupied sites during March 2011, assessing larval preferences within 700 random 25cm² quadrats containing 991 plantains and 145 larval webs.

Larval preferences were compared between years to assess any changes in hostplant sizes and habitat associations [H3:i].

Statistical Analysis

The aim of this study was to assess the importance of temperature in determining both larval abundance and larval hostplant and habitat preferences of the Glanville fritillary butterfly.

H1: Temperature is predicted to be a principle determinant in suitability of oviposition locations.

I used a paired t-test to compare temperatures between hostplants chosen for oviposition and matching ambient air temperature [H1:i]. Temperature estimates from the data loggers were approximately normally distributed. To describe microclimate preferences, I examined the temperature differences between successional stages of habitats to explain habitat preferences described in Thomas *et al* (2001) [H1:ii].

H2: Assessing the importance of habitat quality, temperature and aspect as determinants of abundance.

The data used in this analysis was derived from 14 years of surveys on 5 habitat plots. The sample size is therefore $14 \times 5 = 70$ web counts: one for each year- plot combination, each of which has a matching estimate of habitat quality. There is only one air temperature value per year. Prior to analysis, the plots were coded values according to aspects; plots with southerly aspect were attributed a score of 1, plots with northerly or no aspect scored zero. All tests of this hypothesis used generalised linear models (GLMs) with quasipoisson errors (since the abundance estimates were over-dispersed), with the number of webs as the response variable. Since the data comprised of actual counts, this approach is more appropriate than using normal errors on log-transformed counts (O'Hara & Kotze 2010).

Initially, butterfly abundance (number of larval webs) was regressed against plot area. The model results showed that area was significant ($b=0.86$, $se=0.25$, $t=3.49$, $p<0.001$). However, because the estimate was close to (and not significantly different from) 1, this suggested that a doubling of area would equate to an approximate doubling of larval web numbers. Therefore, area was included as an offset in subsequent models. Glanville fritillary abundance (number of webs) was then modelled as a function of habitat successional stage [H2:i] and aspect [H2:ii] (from the same year) and June temperatures (of the *previous* year, when those eggs were laid)[H2:iii], using separate, single predictor models.

Next, abundance was modelled against all parameters from the previous step, in a multi-predictor GLM, to assess which parameter was most important in determining abundance [H2:iv]. Plot identity was included as a categorical 'nuisance variable' (to control for variation among plots that cannot be attributed to our hypotheses). Significance was assessed by removing terms and comparing the goodness-of-fit of nested models using Chi-squared, with $\alpha=0.05$. I estimated the effect size for each predictor variable as the fitted difference in web numbers over the observed range of variation of that predictor. All models were fitted in R (R Development Core Team 2010).

H3: Comparison of larval preferences in hostplant size and habitat associations in 1980 and 2011.

Preferences are defined as the relative probability of a larval web occurring within a particular habitat successional stage and on a particular sized plantain. I therefore constructed a statistical model to compare the distribution of probabilities between the years. I first

converted web density (per plantain) from the Thomas *et al* (2001) data back into counts of webs and plantains. I then fitted a set of generalised linear models to the combined set of 50 pairs of counts (5 plantain size class, 5 habitat category, 2 years), with quasibinomial errors (as the data were overdispersed). First, I fitted the saturated model, containing the main effects (plantain, habitat and year) and all interaction terms, as recommended by Crawley (2007), pages 552-3. I then simplified this model by removing terms sequentially, starting with the three-way interactions then removing two-way interactions. At each step I compared the fit of each set of models using a Chi-squared test. This process continued until all remaining terms were significant at $\alpha=0.05$. Significant two-way interactions between year and either habitat category or plantain size would indicate a change in preferences (in one or both dimensions) from 1980 - 2011 [H3:i].

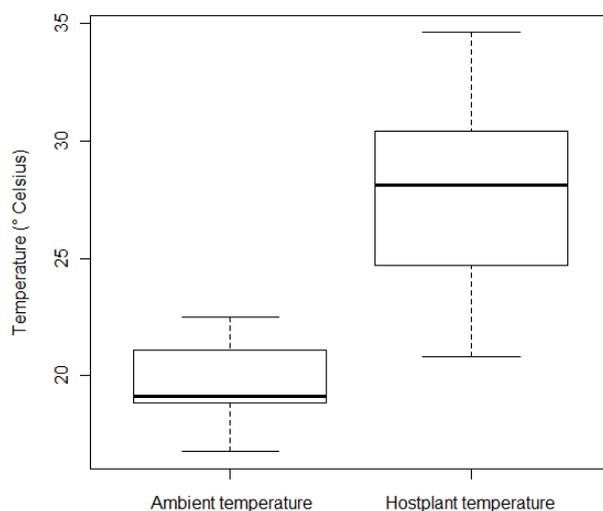
Results

The Importance of Temperature in Determining Oviposition Locations [H1]

Hostplant temperatures

Mean temperature of hostplants during oviposition was 27.70 degrees Celsius (S.D = 3.47, Figure 1.4). Although not directly compared with hostplants on which oviposition did not occur, simultaneous ambient air temperature was just 19.79 degrees (S.D = 1.64). The difference is highly significant: $t(59) = 20.754$, $p < 0.001$.

Figure 1.4. A boxplot illustrating the differences between ambient air temperature recorded by Tiny tag temperature loggers (left) and temperature of a ribwort plantain leaf used for oviposition by the Glanville fritillary (right) recorded using a laser thermometer by following gravid females ($n=60$). Temperatures were recorded in degrees Celsius on seven dates from 6th - 25th June 2010. Boxplot shows median (thick line), upper and lower quartiles (box), and minimum and maximum values.



The temperature of plants on which females were observed to oviposit was therefore on average 8 degrees hotter than ambient air temperatures. Thus, Glanville fritillary females show a clear preference for hostplants which are significantly hotter than ambient temperatures [H1:i].

Habitat microclimate temperatures

The temperature beneath the various successional stages of habitats (see Table 1.2 for definitions) was recorded by five Tiny tag temperature loggers placed beneath the soil surface, with another recording ambient air temperatures from 15th to 17th May 1998 (Figure 1.5).

Figure 1.5. A comparison of temperatures between habitat successional stages 1 – 5 (see Table 1.2), and ambient air temperature over three days in May 1998, recorded by Tiny tag temperature loggers.

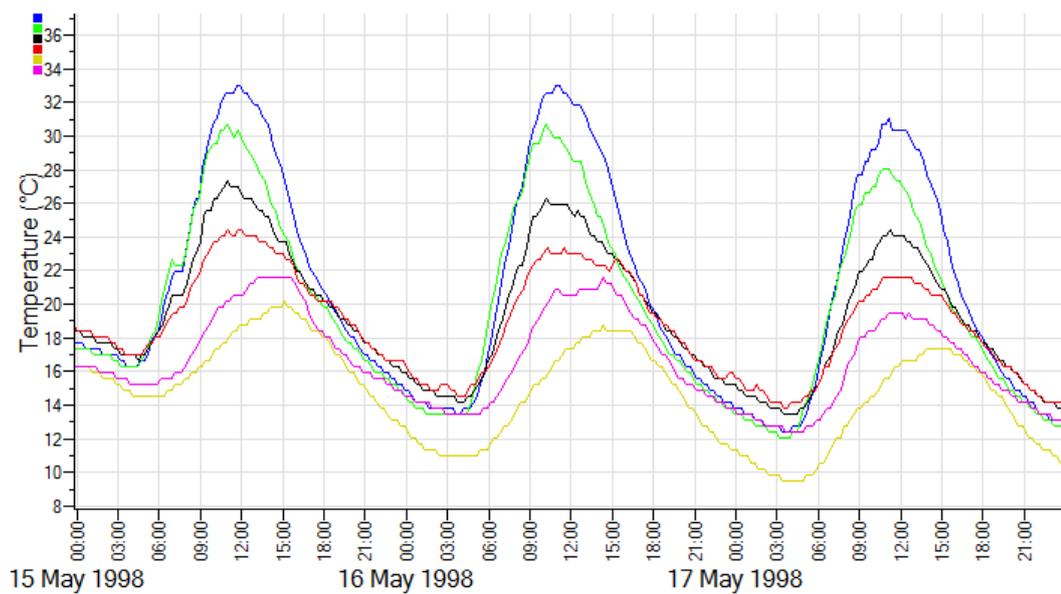


Figure 1.5. Legend

	Habitat 1
	Habitat 2
	Habitat 3
	Habitat 4
	Habitat 5
	Air Temperature

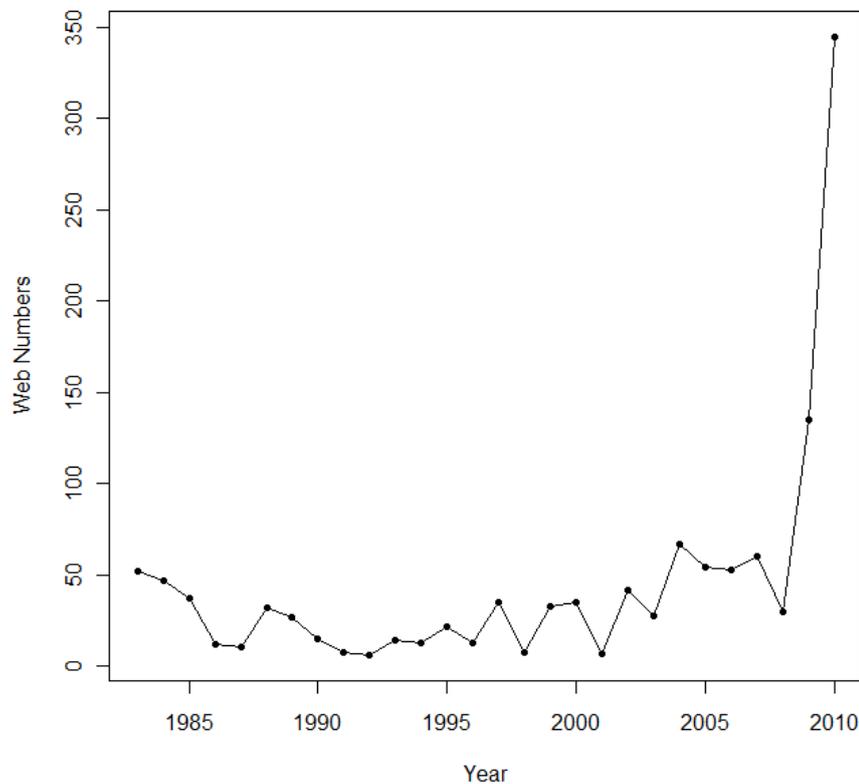
There is a clear decrease in ground temperature between the earliest successional stage (1) and the last (5) of approximately two degrees per stage around the warmest time of day – midday. The preferred habitat categories (2 and 3, see Table 1.2) are eight and ten degrees warmer than ambient air temperature, i.e. approximately the same as the difference between ambient temperature and oviposition sites (Figure 1.4).

Population Time Series

Given the importance of temperature in determining larval distribution within habitats (see above), the spatial extent of suitably warm habitat or microclimates, plot aspect and annual variation in ambient temperatures could also be important predictors of abundance.

Annual monitoring has shown a high degree of variation between years and although the number of webs recorded has been steadily increasing since 1997, since 2008 the population has increased dramatically. The inclusion of IWNHAS data illustrates that up until early 1990's the population was declining (Figure 1.6).

Figure 1.6. Binnel Point larval web counts 1997 – 2010, summed across plots 1-5, combined with IWNHAS larval web counts 1983 – 1996.

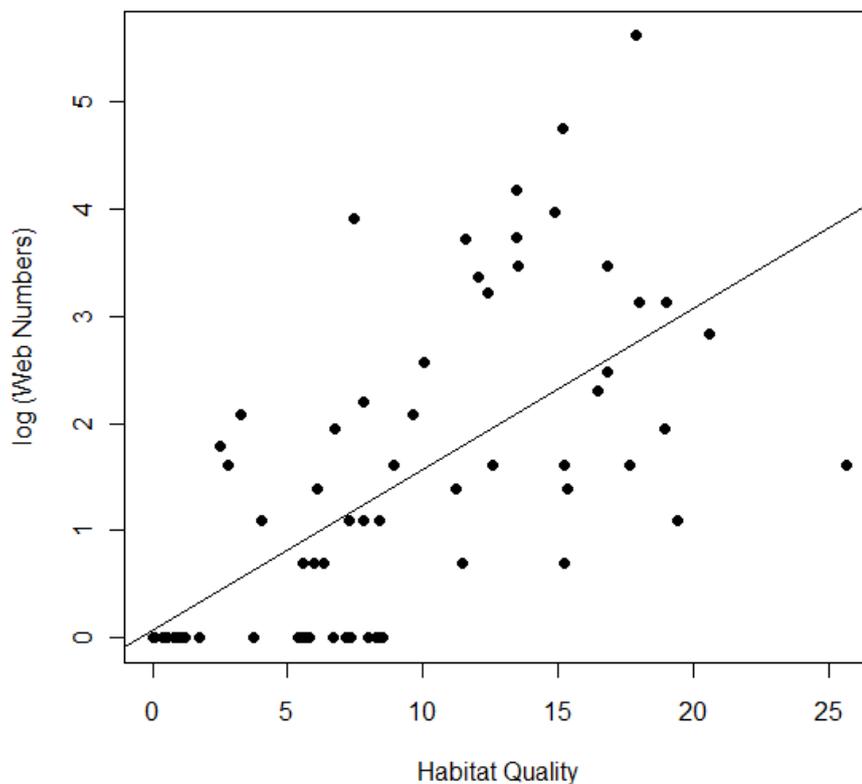


The Importance of Site Characteristics in Determining Abundance [H2:i]

Since 1997, plot area, habitat quality (percentage of various successional stage habitats within each plot) and aspect were recorded annually for each of the five plots within the site.

To test the importance of the spatial extent of successional stages (variations in microclimate), butterfly abundance was regressed against habitat quality. The results showed that there is a strong, statistically significant, positive relationship between butterfly abundance and habitat quality ($b=0.19$, $se=0.035$, $t=5.38$, $p<0.001$). This implies that across plots, each point increase on the habitat quality scale is associated with an increase in web abundance of 19% (Figure 1.7) [H2:i]. Across the observed range of variation (0 - 25.65), this corresponds to a 31 fold increase in fitted abundance from the lowest to highest quality habitat.

Figure 1.7. The relationship between web numbers recorded in each plot ($\log_e x$) and matching estimate of habitat quality from 1997 - 2010 at Binnel Point with least squares regression line (not the GLM used in hypothesis testing).

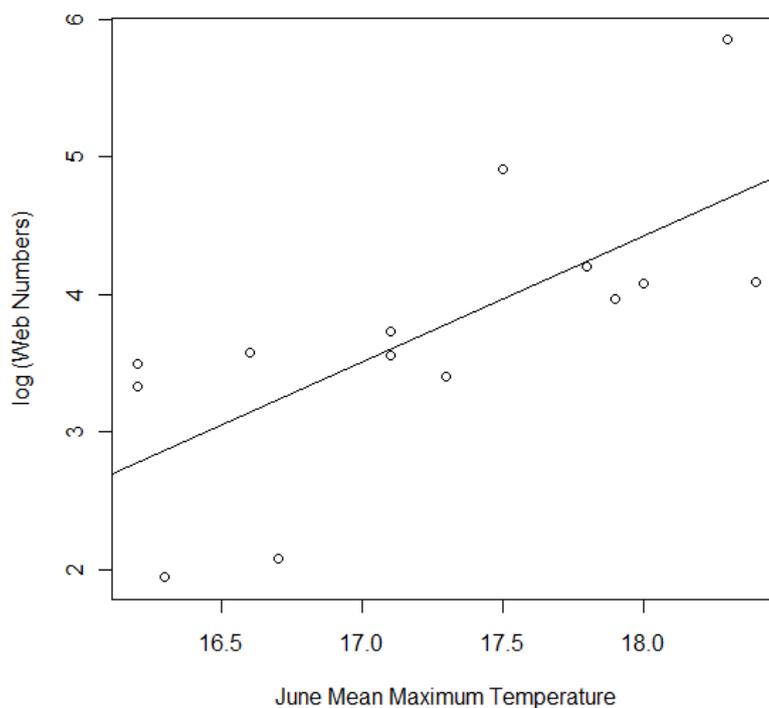


Aspect also appears to be an important predictor of abundance, with model results also suggesting a strong, statistically significant, positive relationship between butterfly abundance and plots with southerly aspect ($b=1.80$, $se=0.488$, $t=3.68$, $p<0.001$). However, due to the small variation between plots and years (e.g. low statistical power as aspect does not change over time, and the sample size is small - 3 plots are south facing, 1 is flat and 1 north facing), there remains a degree of uncertainty about the importance of aspect on abundance [H2:ii]. This is explored in further detail below.

The Importance of Ambient Temperature in Determining Abundance [H2:iii]

Model results suggest there is a strong, statistically significant, positive relationship between butterfly abundance and temperature ($b=1.04$, $se=0.263$, $t=3.96$, $p<0.001$). This implies that across plots, an increase of 1 degree of temperature will increase abundance by 104% (Figure 1.8) [H2:iii].

Figure 1.8. The relationship between web numbers summed across plots ($\log_e x$) and June mean maximum temperature (degrees Celsius) from 1997 – 2010 at Binnel Point with least squares regression line (not the GLM used in hypothesis testing).



Ambient air temperature therefore appears to be an extremely important predictor of abundance, probably because it influences both hostplant suitability and microclimate choice at more localised scales.

Assessing the Importance of Parameters in Determining Abundance [H2:iv]

All parameters were included in a multiple regression (area was offset and quasipoisson errors) along with plot identity (as a fixed effect) which would determine which was the most significant parameter in determining abundance [H2:iii].

Progressive simplification of the model, and comparing goodness-of-fit using Chi-squared showed there was no change in deviance or degrees of freedom when aspect was omitted from the model. This occurs because patch identity is also included in the model. More importantly this suggests that the evidence that aspect is an important predictor of abundance is inconclusive.

However, there is a strong and significant role for both temperature and habitat quality. Web counts were significantly higher following relatively warm June weather ($b=0.935$, $se=0.166$, $t=5.63$, $p<0.001$) and when large areas of high quality habitat were available ($b=0.103$, $se=0.04$, $t=2.819$, $p<0.05$). A Chi-squared test also showed that both temperature and habitat quality are independent effects, with no significant relationship between the two parameters ($p=0.25$).

To compare the effect sizes of each parameter, I estimated the difference in fitted abundance across the range of observations for both temperature and habitat quality. For temperature, the parameter estimate means that each degree of warmth is associated with an increase in web counts by a factor of $e^{0.935} = 2.5$. Thus, across the range of temperatures observed (2.2 degrees C), the fitted difference in abundance varies by $e^{(0.935 \times 2.2)} = 7.83$ fold from the coldest to warmest years. Each point increase (percentage) on the habitat quality scale is associated with an increase of webs by $e^{0.103} = 11\%$, and across the range of qualities (0 - 25.65) the fitted difference in abundance varies by $e^{(0.103 \times 25.65)} = 14.04$ fold from the poorest to highest quality habitats.

Therefore, despite the estimate for temperature being considerably higher than habitat quality, the fitted differences in abundance would suggest that habitat quality is almost twice as important as temperature in determining butterfly abundance.

Comparison of larval preferences between 1980 – 2011 [H3:i]

Thomas *et al* (2001) described the Glanville fritillary larval preferences (hostplant size and habitat successional stage) in 1980 (see Figure 1.2). Using similar methodology (700 random 25cm² quadrats containing 991 plantains and 145 larval webs), I describe hostplant and habitat

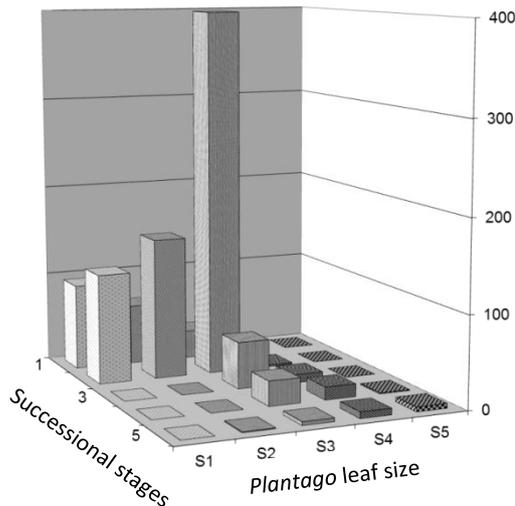
preferences across five occupied sites (although different to those sampled in 1980) in March 2011 (see Figure 1.9).

Figure 1.9 (see Figure 1.2 for direct comparison of Thomas et al (2001) preferences)

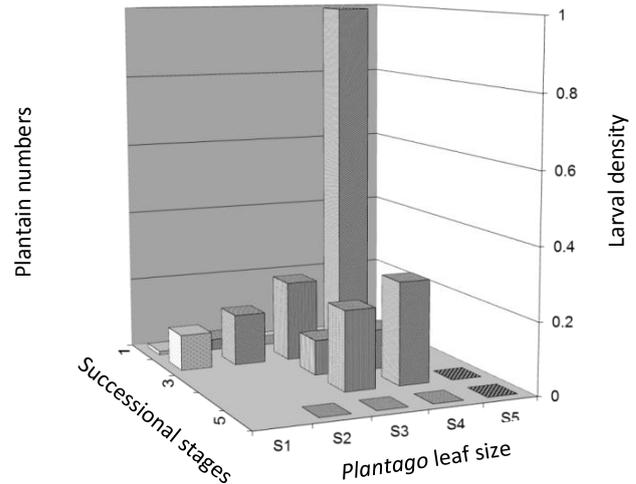
a) Distribution of *Plantago lanceolata*, larval foodplant of *Melitaea cinxia*, in five successional stages of grassland and in five classes of mean plant leaf size in 2011. Therefore, almost 400 plantains occur in *Plantago* size class 3, successional stage 2. b) Density of larval webs of *Melitaea cinxia* in the same samples measured for *Plantago lanceolata* (n = 145 larval webs).

Habitat preference is given by the difference in relative bar height between a) and b). Adult females prefer to oviposit in successional stage 2 and on leaf size 4.

a) *Plantago lanceolata*



b) *Melitaea cinxia*



Therefore, most plantains are distributed within successional stages 1 and 2, but adults prefer to oviposit on larger hostplants (which are also in successional stage 2). The largest bar reflects the fact that there are very few plantains occurring of size group 4 within habitat stage two, yet they are highly likely to be used for oviposition.

A Chi-squared test comparing the distributions between 1980 and 2011 showed that the habitat-year interaction is not significant ($p=0.097$), but the plantain-year interaction was significant ($p<0.001$), indicating that preferences have not changed for habitat successional stage, but larvae are now feeding on significantly larger hostplants compared to 1980.

There is a considerable difference in mean maximum June temperatures (of the previous year) between when the preferences were described in 1980 (15.3 degrees) and 2011 (18.3 degrees). Given our knowledge about temperature differences between the habitat successional stages (approximately two degrees per stage - Figure 1.5), it could have been expected that larval webs would have shifted into a cooler successional stages (3 or 4) to counteract the recent increase in temperatures. However, while there is no evidence to support this, there is

clear shift towards utilising larger plantains possibly because larger plants tend to occur within marginally longer turf and are therefore slightly cooler.

Discussion

The aim of this study was to determine how significant the parameters of temperature, habitat quality and aspect were in explaining distribution and abundance of the Glanville fritillary, on an isolated site over time on the south coast of the Isle of Wight.

The results showed that oviposition was restricted to warmer hostplants and habitats, and both habitat quality (percentage of warmer successional stages present within each plot) and ambient air temperature were highly significant in determining butterfly abundance. Comparison of larval preferences showed a tendency to use larger hostplants, but no change in habitat successional stage. Taken together, these results reveal the fundamental importance of temperature in determining both the Glanville fritillary niche and carrying capacity of sites.

The Importance of Temperature in Determining Oviposition Locations

Selection of Hostplants [H1:i]

Female Glanville fritillaries show a clear preference for hostplants which are considerably warmer (on average 8 degrees) than the ambient air temperature (Figure 1.4 and results from t test). This is because the temperature of a hostplant is crucial to optimise larval development (Renwick & Chew 1994; Doak *et al.* 2006). Therefore, as the Glanville fritillary is at the northern edge of its distribution within the U.K., females will invest considerable effort in finding suitably warm locations for oviposition which will expedite larval growth and maximise chances of successful development (Thomas 1991; Merrill *et al.* 2008).

Selection of Habitat Successional Stage [H2:ii]

Temperatures recorded by the Tiny tag data loggers (Figure 1.5), demonstrate the differences in ground temperatures between successional stages (depending on the height of vegetation and the amount of bare ground) within soft cliff habitat on the south coast of the Isle of Wight. It has long been realised that temperatures vary among nearby habitats (Odum 1963), but it is the subtle differences in temperature within vegetation that creates various microclimates (Suggitt *et al.* 2011), which are of paramount importance to the survival of ectotherms with limited mobility such as butterfly larvae (Thomas 1995c; Turlure *et al.* 2010).

Although it is not possible to directly compare between hostplant temperatures (Figure 1.4) and microclimate temperatures (Figure 1.5), because of differences in dates between temperature recordings, it seems likely that temperature is a key factor in determining oviposition locations. I have demonstrated that Glanville fritillaries, on average, choose hostplants that are considerably warmer than ambient temperatures (Figure 1.4). It would therefore follow that most oviposition locations (and larval webs) would occur within warmer locations within sites - and this neatly matches the larval habitat preferences described by Thomas *et al* (2001) – see Figure 1.2.

Warmer microclimates are therefore favoured by gravid females because within earlier successional habitats hostplants are likely to be much warmer than ambient air temperature, and thus more likely to be utilised for oviposition (see selection of hostplants). Although a comparison of temperatures beneath successional stages (Figure 1.5) shows that the earliest stage (1) is the warmest, this stage is predominantly bare ground interspersed with very short turf. The clear preference for habitat successional stage 2 can be explained in that it is sufficiently warm to allow efficient thermoregulation (see below), yet it is the first successional stage which provides a sward structure capable of supporting a larval web complete with inner chambers, and more importantly a hibernaculum which is essential for overwintering survival. Furthermore, temperature demarcation above habitat stage 2 is so acute, that hostplants are unlikely to be of a suitably warm temperature (and thus utilised), unless they are within locations which are warm for reasons other than habitat structure, for example, because they are sheltered due to topography or on south facing slopes. Therefore, larval numbers remain quite low in the earliest (warmest) successional stage (although larvae often feed on plantains in this habitat), and this is because the limited amount of very short grass is not capable of supporting web structures which are essential for thermoregulation.

The Importance of Microclimatic Temperature in Larval Thermoregulation

Within the U.K., many species of butterfly lay their eggs on or close to the ground (Thomas & Lewington 2010). A suitable temperature is crucial for larval development and completion of the life cycle (Thomas 1991), and it is the efficiency of larval thermoregulation which is often the primary mechanism that underpins survival (Bryant *et al.* 1997).

The Glanville fritillaries preference for warmer hostplants and earlier successional stages can also be explained by examining the larval ecology, and particularly the reliance on effective thermoregulation. Glanville fritillary larvae are gregarious, which is much more effective at

raising body temperature than basking individually (Porter 1982; Bryant *et al.* 2000). As the air temperature reaches 13 degrees Celsius, the larvae can actively increase their body temperature by up to a further 20 degrees by basking within a group (Thomas & Lewington 2010). At a critical 33 – 34 degrees the larvae become active and start feeding on the surrounding plantains (Thomas & Lewington 2010). By leaving a basking group and commencing solitary feeding, the body temperature starts to decrease and continues to drop while feeding. The caterpillar therefore feeds in short bouts and then resumes basking. This post-feeding basking is believed to be important in maximising the efficiency of a gut enzyme, which can digest plantains most effectively at 34 degrees centigrade (J. Thomas pers comm). Thus, microclimatic temperature is crucial for the metabolism and development of Glanville fritillary larvae.

Eggs are laid on hostplants within the warmest habitats to maximise thermoregulation and metabolic efficiency, thus expediting development time (Bryant *et al.* 2002). Furthermore, in this particular species, fast larval development may also be important to minimise the risk of attack from host specific parasitoids, as synchronicity between parasitoid and host is much greater during cooler years, when larvae are unable to utilise the warmer temperatures to develop at a faster rate (van Nouhuys & Lei 2004).

The Importance of Site Characteristics in Determining Abundance

Habitat Quality [H2:i]

The amount of suitable habitat or spatial extent of warmer thermal microclimates (habitat quality) is an important determinant of butterfly abundance [H2:i], with estimates ranging from 10% (within the multiple regression) to 19% (within a single predictor model). Thus abundance increases from 14 to 31 fold from the worst habitats to the best (or 10% – 19% with each point increase on the habitat quality scale).

Plots with greater spatial extent of warmer successional stages (both within and between years) are thus more likely to contain higher numbers of larval webs. Given the importance of temperature on the distribution of the Glanville fritillary (see above), this result is not surprising. For conservation, habitat quality can be controlled by management - unlike both aspect or ambient temperatures (Thomas *et al.* 2011). Therefore, based on the results of this study, increasing the amount of earlier successional habitats within plots would increase abundance of the Glanville fritillary butterfly. Furthermore, the abundance of many butterfly species within the U.K are likely to increase with the availability of early successional habitats,

given that they are often restricted to warmer microclimates within habitats (Thomas 1993). Hence, the lack of management within sites can often explain the demise of many thermophilous butterfly species (Thomas 1991), and the initiation of appropriate management within sites can also explain the dramatic recovery of others (Thomas 1983a, 1995b; Thomas *et al.* 2011).

Aspect [H2:ii]

The temperature of south facing sites is often considerably warmer than sites with more northerly aspects (Bennie *et al.* 2008), and this can be an important factor in determining oviposition locations (Weiss *et al.* 1988). Indeed, within the U.K., Warren (1993) demonstrated distinct aspect preferences for British butterflies, with most preferring south and south-west facing slopes because they are warmer.

The results from this study are inconclusive, in that within single predictor models aspect seems to be extremely significant in determining butterfly abundance ($b=1.80$, $se=0.488$, $t=3.68$, $p<0.001$), yet within the multiple regression containing all parameters its explanatory power is considerably weaker, probably because it becomes confounded with plot identity.

Therefore, aspect is probably important in determining butterfly abundance, but within this study the results remain inconclusive. However, aspect has been shown to be an important influence on butterfly distribution in several other studies (Davies *et al.* 2006; Turlure *et al.* 2010), and so it remains plausible that plots with warmer aspects support higher abundances of the Glanville fritillary.

The Importance of Ambient Temperature in Determining Abundance [H2:iii]

Temperature is often considered a principle constraint on the distribution and abundance of all species (Krebs 1978), and more specifically, the selection of oviposition sites used by butterflies is often temperature related (Dennis 1993; Thomas 1993; Ashton *et al.* 2009).

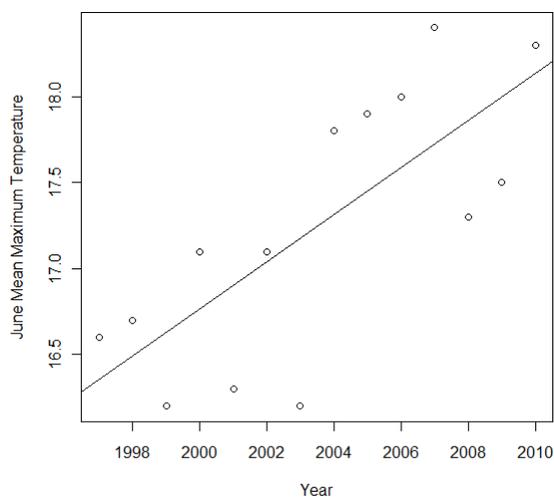
Several studies have shown that in general butterfly abundance is related to temperature (Pollard 1988; Kwon *et al.* 2010; WallisDeVries *et al.* 2011). Results from this study suggest that variation in Glanville fritillary abundance is highly correlated with mean maximum June temperature, and this concurs with the results of Roy *et al.* (2001) who showed positive relationships between population growth rates and ambient temperature for most U.K. butterflies (out of 31 species studied), but that the most important period of the year varied according to species. Hence, this study also supports the findings of Diamond *et al.* (2011) who

suggest that species with both narrower ranges and dietary niche breadth are likely to be most sensitive to temperature changes.

The strength of temperature as a predictor of abundance can be explained by two mechanisms; First, adult activity is highest during June, and most oviposition occurs during this month. Oviposition sites are often determined by temperature (Thomas 1995b) and female Glanville fritillaries have a preference for hostplants in warmer locations (see selection of hostplants). Therefore, hostplants that are located within microclimates which, in a year of normal temperature are too cool, can be utilised for oviposition during warmer years. Thus an increase in temperature is likely to increase spatial distribution using hostplants within cooler aspects (Davies *et al.* 2006) and slopes (Weiss *et al.* 1988). Secondly, many species at the northern edge of their range are often restricted to areas with unusually warm microclimates (Thomas 1993), thus, in warmer years, it may be possible to use hostplants situated within later successional stages, for example in longer turf.

Both these mechanisms can also explain why species at northern limits of their range often experience dramatic population fluctuations, as cooler locations can be utilised for oviposition in warmer years resulting in a population boom before temperatures return to normal (Thomas *et al.* 1994). However, there has recently been a dramatic increase in Glanville fritillary abundance (Figure 1.6). This can be attributed to a period of increased warming (Figure 1.10), although factors such as density dependence (Hanski *et al.* 1996; Nowicki *et al.* 2009) and resource depletion (Dennis 2010) would suggest this rate of increase is unlikely to continue.

Figure 1.10. June mean maximum temperatures from 1997 – 2010 at St Catherine’s Point lighthouse, Isle of Wight, with least squares regression line.



Assessing the Importance of Parameters in Determining Abundance [H2:iv]

Both temperature and habitat quality were highly significant in determining abundance of the Glanville fritillary butterfly. Furthermore, estimates from the model initially suggested that temperature was the most important parameter, but fitted difference abundance values (accounting for variation in range of habitat qualities and temperatures) would suggest that habitat quality is actually almost twice as important as ambient air temperature.

This is probably because the key factors determining oviposition are the presence and suitability of the hostplant, the vegetation structure and the microclimate (Fartmann 2006). Assuming that the distribution of hostplants is relatively constant across habitats (as Thomas *et al* (2001) suggests), then individual females can select suitably warm hostplants by adjusting habitat preferences *despite* variations in ambient air temperature. Temperature demarcation between habitat successional stages is so acute, that even a two degree difference in ambient air temperature between years would not influence oviposition locations compared to an increase of turf height of only a few centimetres. Indeed, the importance of habitat quality has possibly been understated in this study, in that it does not reflect the abundance of suitable hostplants within microclimates, as this will vary depending on site and weather conditions (Dobkin *et al.* 1987). Nor does it account for the size of the butterfly population in the previous year which may also have reduced the number of hostplants (Dempster & Pollard 1981). Furthermore, variations in site conditions, for example aspect or management, are also likely to be extremely important in whether successional stage is an appropriate measure of habitat quality. Therefore, in an extreme example, a north facing grazed area will have a high value for habitat quality yet is highly unlikely to contain any larval webs because of temperature constraints.

Fundamentally, both air temperature and habitat quality are thermal measurements across different scales; habitat quality as defined by Thomas *et al* (2001) and used in this study equates to a measure of variation in ground temperature or 'microclimate', whereas air temperature is measured at a greater (less precise) scale. Hence, habitat quality is more significant than air temperature because it operates at a much more localised scale, where it exerts a strong influence on both the distribution and abundance of small species like insects, especially those which inhabit cooler latitudes where temperature constraints are more acute. However, ambient air temperature remains an important predictor of abundance, and it is no coincidence that a majority of British butterfly species, including the Glanville fritillary, increase after warm summers (Pollard 1988; Roy *et al.* 2001).

Comparison of larval preferences between 1980 – 2011 [H3:i]

Comparing larval preferences between the years 1980 and 2011 showed significant changes in hostplant size but not in habitat successional stage. Given the differences in mean maximum June temperatures (of the previous year) between when the preferences were described in 1980 (15.3 degrees) and 2011 (18.3 degrees) it would have been expected to have observed a shift in habitat preferences, for example, from shorter to longer turf to compensate for higher temperatures.

It is possible that the significant shift in hostplant size preferences could be a subtle effect of climate warming, in that the soil and vegetation around larger plants is cooler than around smaller plants which could facilitate more effective thermoregulation. Alternatively, the preferences for smaller plants observed during 1980 may be because of a drought effect, and so the larger (older) plants were avoided because they were less palatable than fresh young growth. However, although the aim was to compare preferences between years, the preferences were actually described from different sites, with no consideration given to variations in site characteristics (e.g. aspect or management) or hostplant densities, all of which could affect oviposition preferences. Therefore, although there appears to be a significant increase in size of hostplant preference between the years, this could be for site differences which have not been accounted for, for example grazing or soil type, and in reality preferences could therefore vary depending on variation in spatial landscape characteristics rather than temporal differences. Nonetheless, the lack of any significant in habitat preferences between years gives us confidence in the derived estimates of habitat quality that we used for modelling abundance.

Recommendations for Site Management

Results from this study suggest that the amount of suitable habitat within an area (habitat quality) is of paramount importance in determining both the distribution and abundance of the Glanville fritillary butterfly.

Although the most important sites for this butterfly occur within soft cliff habitats where management is not an option, it also often occurs in fields adjacent to core colonies where, with the introduction of light grazing, abundance of this species could be increased dramatically. The clear larval preference for early successional stages means that creating a mosaic of (mainly short) turf heights interspersed with longer areas of vegetation which provide shelter and structure for hibernacula should provide suitable areas for oviposition.

Indeed, several downland areas (e.g. Compton and Brook Down) which are close to core sites and owned and grazed by the National Trust have recently been colonised by Glanville fritillaries, probably due to recent rises in June temperatures facilitating range expansion into these marginally cooler locations. Furthermore, many landowners keep livestock in areas adjacent to several Glanville fritillary colonies, although butterfly populations within such sites tend to be ephemeral due to fluctuations in grazing intensity, with overgrazed sites removing longer grasses which are essential for supporting hibernacula. Although it would appear straightforward to reduce grazing intensity to the benefit of butterflies, there remain financial incentives for landowners to maximise numbers of livestock, especially as production levels are predicted to increase in order to provide food for a growing population (Border 2012).

However, there are two important caveats to the management recommendations of increasing the availability of shorter turf habitats; First, it should be remembered that the Glanville fritillary is probably the most thermophilous butterfly species in the U.K., and thus while maximising the spatial extent of warm microclimates would benefit this particular species, it could be at the detriment of others. This question remains an important priority for future research, as while the Glanville fritillary is within a group of one sixth of butterfly species which could benefit from the availability of early successional habitats (Thomas 1993), this also implies that five sixths may not, and so the trade-off between maintaining species diversity and increasing (general) butterfly abundance remains complex.

Secondly, and more importantly, summer temperatures are predicted to continue to increase (IPCC 2007), and so while there is currently no upper temperature threshold for oviposition, at some point larval preferences may shift into slightly cooler microclimates to counteract the increasing temperatures. Indeed, this reinforces the concept that research at greater spatial and ecological detail remains a priority to understand the impact of climate change (Kearney & Porter 2009). Nonetheless, the creation (and maintenance) of thermally diverse habitats is of paramount importance in conserving many butterfly species, especially those at the northern edge of their range within the U.K. where temperature constraints are more acute (Thomas *et al.* 2011). Certainly, the relatively high losses observed in insects populations compared to other species groups are often due to inappropriate or lack of management thereby reducing the spatial extent of early successional or suitably warm habitats (Thomas & Morris 1994; Thomas 1995c; Thomas *et al.* 2004).

Creating a mosaic of vegetation within sites therefore remains a priority in butterfly conservation, as oviposition sites are often determined by temperature (Shreeve 1986; Dennis

2010; Turlure *et al.* 2010). Variation in turf heights will provide a degree of flexibility which can counteract ambient temperature fluctuations (Roy & Thomas 2003) and furthermore, patches of longer turf will provide shelter which can be important during periods of inclement weather (Dennis & Sparks 2006) and provide oviposition locations for less thermally restricted species thus maximising butterfly diversity within sites (New 2009).

Conclusions

The Glanville fritillary is at the northern edge of its range within the U.K., where temperature is a principle constraint. Most eggs and larvae occur in the (earlier) warmer successional stages, although a caveat is that vegetation must be present with a sward height that is capable of supporting larval web structures.

The Glanville fritillary is extremely sensitive to fluctuations in both the amount of suitably warm habitat within plots and ambient air temperature, and therefore both habitat quality and temperature are highly significant predictors of population abundance.

To maximise abundance within sites, management creating a range of thermally diverse habitats is recommended. Areas which contain more heterogeneous habitats will also allow a degree of flexibility in choice of oviposition locations, in that variations in turf height can counteract year-to-year fluctuations in ambient temperatures. This could be particularly important for conserving insect populations if temperatures continue to increase due to climate warming.

Chapter 2) The Effects of Area, Isolation, Habitat Quality and Temperature on the Abundance of the Glanville fritillary along the South Coast of the Isle of Wight.

Abstract

In the last chapter I examined the importance of quality of suitable habitat and temperature in determining abundance of the Glanville fritillary butterfly on a single, isolated site over time. Both factors were significant, although the parameter of habitat quality was considerably more important than ambient temperature, increasing abundance 14 to 31 fold from the worst habitats to the best.

However, most species rarely exist within discrete populations in total isolation from their neighbours. The movement of individuals from one population to another through immigration or emigration can potentially influence the abundance of a population, although the quality of the habitat and its size are also likely to be important.

These landscape parameters inevitably operate over wider spatial scales than within a single, localised population, so in this chapter the number of Glanville fritillary larval 'webs' was monitored from 1996 – 2010 across 70 habitat patches along the entire south coast of the Isle of Wight, thereby encompassing an area which supports over 95% of its population within the U.K.. Web abundance was correlated with habitat quality (calculated from the distribution of successional stages in each patch), patch area, isolation (from the nearest occupied patch) and ambient air temperature. The significance of each parameter was examined, and the interaction between the three landscape parameters and temperature was also assessed to test whether the strength of relationship varied between cooler and warmer years.

The most significant factor in predicting abundance was area, with web abundance increasing 17 - 26 fold from the smallest patches to the largest. Habitat quality was also highly significant, with the best quality habitats supporting 9 – 17 fold increases in abundance compared to the poorest habitats. There was a significant negative relationship between isolation and abundance, with a decrease of 4 - 5 fold from the patches with the nearest occupied neighbours to the most isolated, and temperature was also a significant determinant of Glanville fritillary abundance, with web numbers increasing 1.88 to 3.5 fold from the coldest to the warmest years. Only habitat quality had a significant (negative) interaction with temperature, thus, as temperature increases habitat quality becomes a weaker predictor of abundance.

Understanding the importance of area, isolation and habitat quality is paramount to the development to an effective conservation strategy within an increasingly fragmented landscape. By examining these results I suggest how to maximise abundance within sites, and assess conservation priorities in the likelihood of increasing land fragmentation and rising temperatures.

Introduction

Organisms are not distributed randomly, nor evenly spaced across the surface of the planet (Krebs 1978). Differences in climate, geology, topography and land management will all influence the structure and composition of the surface vegetation creating different biotopes and habitats (Odum 1963). Within habitats, individuals go to areas where the rewards are highest (Sutherland 1996), and so locations with favourable local climates or aggregations of resources may lead to clustering of individuals facilitating the formation of discrete spatial populations with varying population densities (Begon et al. 1986). The advent of both the Theory of Island Biogeography (MacArthur & Wilson 1967), examining the importance of spatial configuration of real islands, and metapopulation theory (Levins 1970), which uses habitat islands within terrestrial fragmented landscapes, have both re-orientated research away from conserving species within single reserves to the importance of conserving interacting populations across entire landscapes.

Within terrestrial ecosystems, butterflies, having high fecundity rates and varying dispersal capabilities, have been essential to understanding the importance of the size and spatial arrangement of habitat patches within fragmented habitats (Brown & Ehrlich 1980; Hanski 1991; Ehrlich & Hanski 2004). Several studies have demonstrated that populations occupying larger, less isolated sites have longer persistence times (Thomas *et al.* 1992; Hanski 1998b; Wilson *et al.* 2002), because despite discrete populations becoming extinct, they are often re-colonised and so the whole population can persist as a balance between extinctions and colonisations of separate populations (Hanski 1994b). The geometric properties of habitat patches within fragmented landscapes and in particular the importance of both area and isolation have formed the basis of metapopulation theory (Hanski 1998b), which has recently steered landscape ecology and is frequently cited for use in conservation policy, especially in attempting to maximise biodiversity within remaining habitat fragments (Ross *et al.* 2008; Johst *et al.* 2011; Jones 2011; Leidner & Haddad 2011).

However, explaining the mechanisms behind changes in population density across landscapes are much more complex than comprehending the factors which determine occupancy (Hanski 1999b). This is probably because species abundance can be determined by a multitude of factors, principally the distribution of resources (Dennis 2010), but also the habitat quality (Thomas *et al.* 2011) as well as area and isolation (Hanski 1998b) of habitat patches.

The importance of habitat quality, in particular, has proved divisive. Research on the Glanville fritillary in the Åland Islands has suggested it is relatively unimportant (Moilanen & Hanski 1998), where average population size is related to the area of habitat, although weather, more specifically precipitation, is also important (Hanski & Meyke 2005). However, studies in the U.K. have shown that habitat quality is significantly more important than both area or isolation in explaining abundance of the Glanville fritillary (Thomas *et al.* 2001), although results were based on surveys conducted only over two years. Similar contradictions have been demonstrated in other studies, with the importance of habitat quality ranging from extremely important (Clarke *et al.* 1997; Dennis & Eales 1997; Luoto *et al.* 2001; Fleishman *et al.* 2002; Poyry *et al.* 2009b) to insignificant (Rabasa *et al.* 2008; Bauerfeind *et al.* 2009; Matter *et al.* 2009). One explanation for these inconclusive results is that the definition of habitat quality used within different studies is inconsistent (Mortelliti *et al.* 2010).

Indeed, the contrasting importance of habitat quality observed from studies on the Glanville fritillary in the Åland Islands and the U.K. is probably because the definitions of habitat quality used in both studies differ so considerably. Moilanen and Hanski (1998) defined habitat quality by using modified patch area and isolation to create a value of extinction risk, and combined this with a habitat heterogeneity factor derived from vegetation classes obtained from Geographical Information Systems (G.I.S). Hence the value of habitat quality was the degree to which different habitats affected both immigration and emigration rates between patches, thereby affecting extinction risk. By contrast, Thomas *et al.* (2001) used a precise description of the species larval preferences to estimate habitat quality (see Chapter 1). Furthermore, although the proponents of metapopulation ecology (principally the importance of area and isolation) and habitat quality (amount of suitable habitat within sites) acknowledge the cogency of other landscape parameters (Thomas 1991; Hanski & Ovaskainen 2000), studies of metapopulation dynamics have often ignored habitat quality, and vice versa. Indeed, the simplification (or the disregarding) of the importance of habitat quality within metapopulation studies is probably because patch geometric properties are mathematically less complex to measure and incorporate within statistical models (Mortelliti *et al.* 2010), although the length of time (e.g. field seasons) required to measure variation in habitats is an additional problem

(Thomas *et al.* 2001). However, it is imperative to clarify the importance of habitat quality within real landscapes, as both the metapopulation and habitat quality viewpoints suggest different solutions to the problems of species decline within modern landscapes (Harrison & Taylor 1997). Metapopulation theory advocates the importance of conserving species within networks of habitat patches, each patch being within dispersal range which allows persistence of the whole population despite some patches being intermittently vacant (Thomas & Jones 1993; Hanski & Thomas 1994; Thomas 1995a; Meeting & McCullough 1996). The alternative (habitat quality) view would suggest that it is considerably more important to manage sites correctly, regardless of the number or proximity of other patches (Clarke *et al.* 1997; Thomas *et al.* 2001; Fleishman *et al.* 2002).

There have also been disparities in the importance of other landscape factors in determining population size. Many studies have shown that larger areas support more individuals (than neighbouring smaller areas) (Luoto *et al.* 2001; Krauss *et al.* 2004b; Lenda & Skórka 2010; Rosin *et al.* 2011), probably because they contain more resources (for both larvae and adults) within them (Dennis 2010). This is also evident from studies on the Glanville fritillary on the Åland Islands (Nieminen *et al.* 2004), from which considerable evidence for the importance of maintaining larger areas to conserve populations within fragmented landscapes has been derived.

However, several other studies have shown that abundance increases less than proportionally with area (Steffan-Dewenter & Tschardt 2000; Rabasa *et al.* 2008). Thomas *et al.* (2001) found no relationship between population density (i.e. abundance/area) in the Glanville fritillary in the U.K., in line with several other studies (Matter *et al.* 2003; Poyry *et al.* 2009b). Therefore, the relationship between area and numbers is not straightforward, possibly because of differences in the way that habitat patches have been defined and delimited (Pautasso & Gaston 2006).

Additionally, while the evidence for reduced occupancy with increased isolation is well established (Thomas *et al.* 1992; Hanski 1999b), the effect of isolation on abundance is less clear. Several studies have shown that population numbers are lower on more isolated sites (Aviron *et al.* 2007; Lenda & Skórka 2010; Rosin *et al.* 2011) possibly because the probability of local extinction increases with isolation (Thomas & Jones 1993), and the chances of re-colonisation declines with distance from nearest occupied patch (Baguette *et al.* 2000). Increasing isolation may also lead to inbreeding depression (Saccheri *et al.* 1998) or reduced genetic fitness (Hanski & Saccheri 2006), also resulting in increased extinction risk (Haikola

2003). However, other studies have shown very weak (Krauss *et al.* 2005) or no relationship between isolation and population size (Krauss *et al.* 2003b), with individuals from isolated patches showing no genetic differentiation from non-isolated individuals (Krauss *et al.* 2004a).

It is vital to clarify the importance of these three parameters, particularly as habitat destruction poses the single greatest threat to the long term survival of species (Barbault & Sastrapradja 1995; Rands *et al.* 2010). Indeed, the majority of insect losses are seen as a direct result of biotope destruction and habitat loss (Thomas 1995b; May 2007). Most remaining natural communities are now significantly more fragmented than they once were (Thomas *et al.* 2004), and current rates of human population growth suggest that this trend will continue unabated (Reid & Miller 1989). Within the U.K., 80% of the land surface is under agriculture (of which 21% is arable) compared to 0.8% which are designated nature reserves (Barr 1993), and so very little of the U.K. is covered in semi-natural habitats (Lawton *et al.* 2010). Additionally, specific conservation measures are frequently recommended on the basis of the strength of metapopulation parameters in research on specific species (Drechsler *et al.* 2003; Fred & Brommer 2003; Bauerfeind *et al.* 2009; Guiney *et al.* 2010; Rosin *et al.* 2011), despite the fact the importance of each parameter could vary between species, sites (subject to landscape characteristics) or over time depending on climatic conditions. Given the importance of temperature in determining the attractiveness of individual microsites to egg laying females, we might expect a positive relationship between annual temperature and the proportion of any given patch that is suitable for oviposition (i.e. a positive interaction between temperature and area in determining abundance). Additionally, habitat quality could become a less significant predictor with increases in temperature, as oviposition locations are not restricted to such thermally constrained microclimates, and so the suitability of patches of low and intermediate quality is likely to be higher (i.e. a negative interaction between temperature and habitat quality in determining abundance).

Therefore, in this study, I examine the importance of area, isolation and habitat quality and their interactions with temperature on the abundance of the Glanville fritillary across 70 habitat patches along the south coast of the Isle of Wight from 1996 to 2010. In particular I test the following hypotheses;

- 1) I determine which of the parameters of air temperature, habitat quality, area or isolation are most important in determining abundance of Glanville fritillary larval webs across 803 observations (patch – year combinations) over time, along the south

coast of the Isle of Wight. I predict that air temperature, habitat quality, and area will be positive, and patch isolation negatively related to abundance.

- 2) The importance of habitat quality, area and isolation is predicted to vary with annual temperature. These effects are expected to be expressed as i) a positive interaction between patch area and annual temperature and ii) a negative interaction between patch habitat quality and temperature. Isolation is not expected to have any significant interaction with temperature.

Methods

To summarise, I monitored the number of Glanville fritillary larval ‘webs’ and compiled site characteristics (area, isolation and habitat quality) from 803 observations (patch – year combinations) across the south coast of the Isle of Wight from 1996 to 2010, following protocols described in the previous chapter. Temperature data was acquired from the Meteorological Station at St Catherine’s Point to provide a matching annual estimate for ambient air temperature for each year.

All parameters (area, isolation, habitat quality and ambient air temperature) were initially modelled against butterfly abundance within both multiple regression and mixed effect models (with random effects) to determine the significance of each parameter and to assess which factor was most important. Secondly, variability in ambient temperature is predicted to influence the importance of landscape factors and so the interactive relationship between area, isolation and habitat quality and matching annual ambient temperatures were also evaluated within separate multiple regression and mixed effect models.

Study Species

The Glanville fritillary is a univoltine species in the U.K., with a typical flight period lasting from May to July. Eggs are laid in clusters on the underside of a Ribwort plantain leaf, with most oviposition occurring in June. During summer the larvae live and feed gregariously and spin a silken web around the plantain leaves. They enter diapause within the web during early autumn, and emerge the following spring, when they again feed communally and spin a conspicuous web around plantains before pupating in April.

Study Sites

A survey of Glanville fritillary larval webs in 1979 (Simcox & Thomas 1979) repeated in 1996 (Thomas *et al.* 2001) established that over 95% of the British population of Glanville fritillaries occurred on 8 sites along the south coast of the Isle of Wight (see Figure 2.1 and Table 2.1), between Compton Bay in the west, and Red Cliff at the south-eastern end of the Island (Asher *et al.* 2001).

Figure 2.1. A map of study sites on the Isle of Wight.

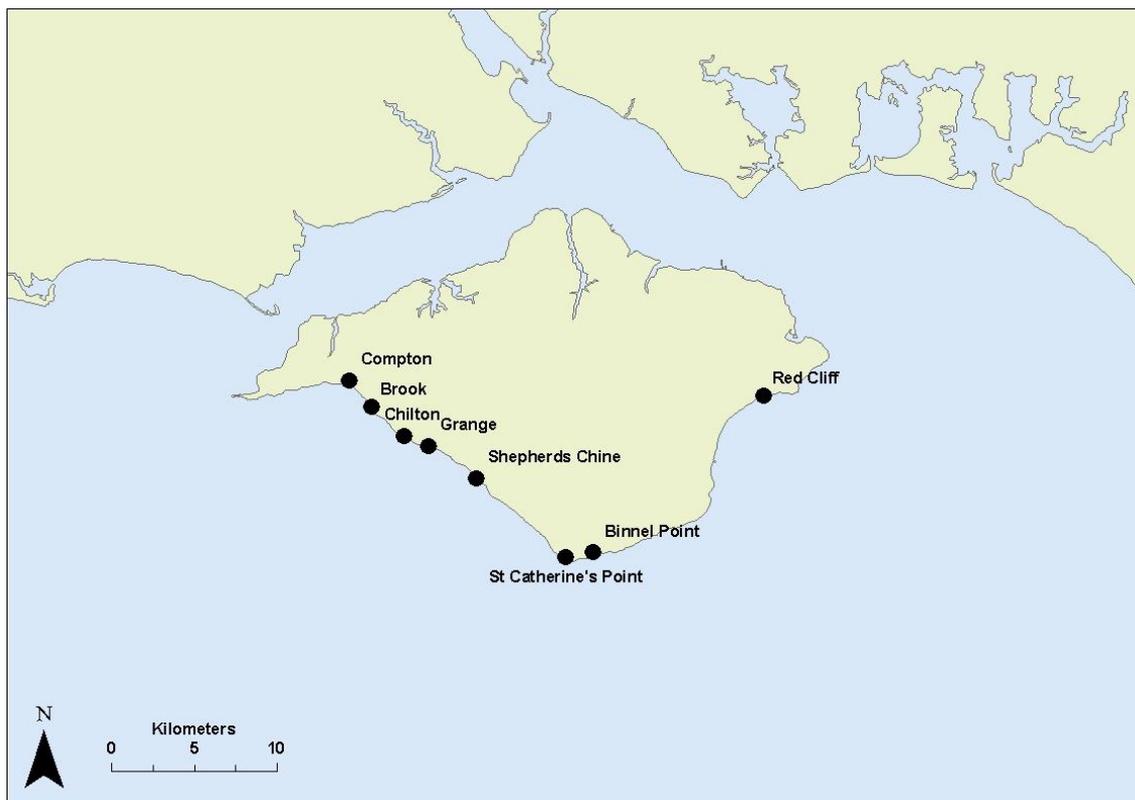


Table 2.1. A list of study sites, mean number of patches per year and their location on the south coast of the Isle of Wight. Sites listed from west to east.

Site	Mean Number of Patches per Year	Easting	Northing
Compton	9.1	371	848
Brook	4.9	387	831
Chilton	8.9	410	821
Grange	3.8	421	817
Shepherds Chine	11.5	447	798
St. Catherine's Point	5.6	499	753
Binnel Point	5	525	758
Red Cliff	4.7	620	854

Four of these sites (Brook, Chilton, Grange and Shepherds) are centred on chimes or riverine valleys, where small land slippages and erosion produce patches of bare ground which create ideal breeding habitat for Glanville fritillaries. However, other sites (Compton and Red Cliff) are comprised of more dynamic and larger landslips, which often create and remove suitable habitat patches between years. Finally, two sites (St Catherine's Point and Binnel Point) contained large areas of semi-permanent grassland.

Sites were defined as any area which contained Glanville fritillary populations in both 1979 (Simcox & Thomas 1979) and 1996 (Thomas *et al.* 2001), and were separated in space from other sites by areas in which larval webs did not usually occur (non-breeding habitat). The dramatic fluctuations of the Glanville fritillary population at Binnel Point (see Chapter 1), meant that in occasional population 'boom' years very small numbers of larval webs occurred within this non-breeding habitat, but this occurred infrequently enough (≤ 2 years out of 15) to identify 'sites' as areas where breeding is normally restricted and continuous throughout the study period. The exception is the most isolated site, Red Cliff, which is included as a site throughout this study (as it contains suitable habitat) despite the Glanville fritillary population going extinct there in 2000, and only being recolonized in 2006.

Patch Delimitation

To facilitate accurate monitoring, each site had been sub-divided into habitat patches during previous surveys (Simcox & Thomas 1979; Thomas *et al.* 2001). Boundaries between patches were defined in terms of discontinuities in geomorphology, aspect and habitat, such that individual patches were more-or-less homogenous in these features (Simcox & Thomas 1979). However, the number of patches deemed to be in existence varied each year due to the dynamic nature of the habitat, as regular landslips can both create and destroy patches as well as making some unsafe to survey.

Furthermore, due to recent increases in spring temperatures (see Figure 1.10, Chapter 1), many unoccupied patches in previous surveys (i.e. too cool in aspect or areas containing high percentages of habitats with longer turf heights), are increasingly occupied (also see Davies *et al.* 2005). Therefore, the distance between occupied patches has decreased, and so within this survey, a high percentage of occupied patches are adjacent. This patch definition is comparable with Hanski's *et al.* (1994) study, but at odds with Thomas *et al.* (2001), who used 75 metres isolation distance as the criterion for recognising a patch (i.e. many occupied patches recognised here would have been considered the same patch by Thomas *et al.*).

Glanville fritillary larval 'web' survey

Since 1996, every patch (area of potentially suitable habitat) was surveyed for the presence of Glanville fritillary larval webs by walking briskly along a series of imaginary lines 5 metres apart until the entire area had been surveyed (as in Chapter 1). Webs were recorded within an area of approximately 2.5 metres square, estimated by eye, perpendicular to the observer in the way that most adult butterflies are recorded (Pollard & Yates 1993; Botham *et al.* 2009).

Glanville fritillary abundance was calculated by counting the total number of larval 'webs' observed within each habitat patch during March, because this is when the webs are largest and most conspicuous (Simcox & Thomas 1979). It is not possible to conduct accurate population surveys during the summer (when the eggs are laid) due to detectability issues as early larval instars create small, inconspicuous webs (e.g. Hanski *et al.* (1995) estimated detectability of larval webs at 35% during the summer in Åland).

Landscape variables

Area

Each patch was mapped and its area measured during 1996 and 1997. Throughout subsequent annual surveys, area was re-measured for patches whose dimensions had clearly changed due to cliff falls or land slippages. In 2010, patch areas were re-measured using a G.P.S. The perimeter of each habitat patch was walked with a G.P.S. and the route recorded. This route was then downloaded into ArcGIS as a shapefile, producing a patch outline. The area was calculated for each patch (in metres squared) by tracing over the outline using the measuring tool within the ArcGIS toolbox. Patch area ranged from 45m² (the smallest) to 2500m² (the biggest) with a mean patch size of 3340m² and median of 1800m².

Isolation

Isolation was calculated as the distance to the nearest occupied patch (following Hanski 1998b; Thomas *et al.* 2001) by measuring the distance from nearest edge to edge in metres, using the measuring tool within the ArcGIS toolbox. Isolation distances therefore vary annually depending on number of patches occupied within any particular year. Pairs of patches (as defined in Patch Delimitation above) where the edges abutted were considered to be isolated by 1 metre. Isolation ranged from 1m to 10000m with a mean of 489.3m separating occupied patches (and median of 1m).

Habitat Quality

Habitat quality was defined and estimated from Thomas *et al.* (2001) – see Chapter 1 (Table 1.2), based on the percentage cover of each of five successional stages. The time taken to estimate the amount of each successional stage within each patch depended on its size, ranging from several minutes for smaller patches (<100m²) to up to 30 minutes for larger patches. Percentage cover was estimated during March, but prior to the larval survey so that habitat quality scores remained uninfluenced by the number of larval webs recorded within each patch. Patch habitat quality ranged from a score of 0 (for the lowest quality habitats) to 48 (for the best) with a mean quality score of 10.48 and median of 9.05.

Regional Temperature Data

Weather data were obtained from the Meteorological Office station at St Catherine's Point Lighthouse (SZ497753). The June mean maximum temperature was used in the analysis (i.e. the mean of the daily maxima; a measure of the warmth of June days), as June coincides with the peak adult emergence and egg laying period. This data was used to assess the relationship between temporal variation in ambient air temperature and larval web abundance, and to test interactions with other parameters. Air temperature ranged from 16.2 degrees (1998 and 2002) to 18.4 degrees (2006), with a median of 17.3 degrees.

Statistical Analysis

The data comprise 803 estimates (patch-year combinations) of larval web abundance on 70 patches at 8 sites over 15 years. Habitat quality, area and isolation all vary among patch - year combinations, although the inter-annual variation in all three variables is small. Ambient temperature varies among years only.

The aim of this study was to determine Glanville fritillary abundance (number of larval webs) as a function of annual variations in temperature (mean maximum June temperature *from the previous year* - i.e. the temperature at the time the eggs were laid), area, isolation and habitat quality and assess which factor was most important. Additionally, variation in annual temperature was tested as an interaction with the other parameters, by using both multiple regression and mixed effect models. Prior to the analysis, both the parameters of area and isolation were transformed by natural logarithm.

Initially, abundance was modelled as a linear function of temperature, area, isolation and habitat quality using General Linear Model (GLM) with quasipoisson errors as the data were overdispersed. Significance for each parameter was assessed using an F-test ($\alpha=0.05$) to compare pairs of nested models (with and without the parameter of interest). Secondly, as the data comprises repeated measures across 803 patch – year combinations (with temperature a constant between patches and sites), all parameters were included in a Generalised Linear Mixed Effects (GLME) model with patch, site and year as random effects to allow for a lack of independence among individual abundance estimates (Cowlshaw *et al.* 2009; Isaac *et al.* 2011b), and to control for variation among patches not accounted for by the landscape parameters. Patch identity is nested within site, and year is crossed with the other random effects. The models also included a random effect at the observation level (repeat measures on the same patch), to control for the fact that abundance data were overdispersed (Roy *et al.* 2012). Poisson errors were used in the mixed effect model as the data comprised of actual counts of larval webs, rather than using normal errors on log-transformed counts (O'Hara & Kotze 2010). Significance for each parameter was also assessed using p values ($\alpha=0.05$) from Wald Z tests, as recommended by Bolker *et al.* (2009). These models assessed the importance of each parameter in determining butterfly abundance [H1]. All models were fit in R, with GLMEs employing the lme4 package (Bates & Maechler 2010; R Development Core Team 2010).

Secondly, to the models above I added an interaction between temperature and each of the other three fixed effects (area, isolation, quality) as single, separate predictors, to ascertain whether the strength of the relationship of the three landscape factors varied depending on air temperature [H2]. As in the previous chapter, I estimated the effect sizes as the range of fitted abundances over the range of observed variation in the parameter of interest.

Therefore, I ran a total of eight models: a GLM and a GLME model, both including temperature, area, isolation and habitat quality as explanatory variables [H1]. A further three GLMs (one for each landscape parameter – area, isolation and habitat quality) and three GLMEs models were fitted to explore interaction effects between landscape parameters and temperature [H2].

Results

The results show that there are statistically significant, strong positive relationships between number of Glanville fritillary larval webs and habitat quality, ambient temperature and area. There is also a statistically strong negative relationship between web numbers and isolation (Figure 2.2 and Tables 2.2 & 2.3).

Figure 2.2. A scatterplot showing the relationship between Glanville fritillary numbers ($\log_{e}x$) and habitat quality, temperature (mean maximum June temperature at the time the eggs were laid), area ($\log_{e}x$) and isolation ($\log_{e}x$).

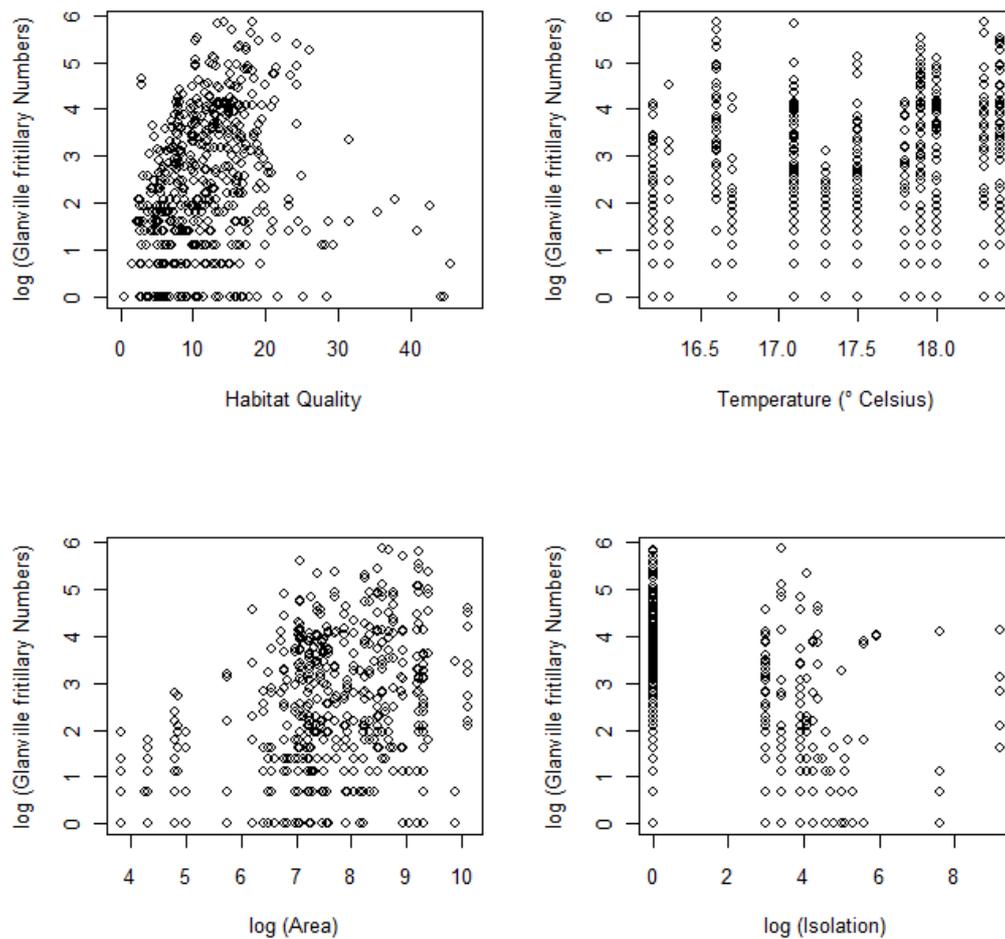


Table 2.2. The results of a multiple regression (GLM) of Glanville fritillary web numbers against habitat quality, temperature, isolation and area (with quasipoisson errors). Dispersion parameter = 57.1.

	Estimate	Std. Error	t value	P value
Intercept	-5.917	1.686	-3.508	<0.001
Habitat Quality	0.046	0.006	7.267	<0.001
Temperature	0.288	0.095	3.033	<0.001
log(Isolation)	-0.152	0.032	-4.773	<0.001
log(Area)	0.453	0.055	8.202	<0.001

Table 2.3. The results of a linear mixed model of Glanville fritillary web numbers against habitat quality, temperature, isolation and area (with poisson errors and observation-level random effect).

	Estimate	Std. Error	z value	P value
Intercept	-13.453	4.918	-2.735	0.006
Habitat Quality	0.060	0.012	5.156	<0.001
Temperature	0.574	0.274	2.099	0.036
log(Isolation)	-0.174	0.041	-4.220	<0.001
log(Area)	0.513	0.180	2.842	0.004

Web abundance was higher in areas of better quality habitats in both the GLM (Table 2.2) and GLME (Table 2.3). This suggests that for the Glanville fritillary on the ‘average’ site, an increase of 1 on the habitat quality scale is associated with an increase of 4.7% ($e^{0.046} = 1.047$) in the GLM or 6.2% ($e^{0.06} = 1.062$) in the GLME, corresponding to a 9 - 18 fold difference in fitted in abundance between the highest and lowest quality habitat (observed range 0-48).

An increase in ambient air temperature also increases web abundance within both the GLM and GLME. Thus, across the range of temperatures (2.2 degrees) web counts increase by a factor of $e^{0.288*2.2} = 1.88$ (in the GLM) or $e^{0.574*2.2} = 3.5$ (in GLME) fold fitted difference in abundance from the coldest to the warmest years.

Area also shows a strong, positive relationship within the GLM and the GLME. Thus, an increase of 1 on the ln(area) scale corresponds to an increase in abundance, on the ‘average’ site, of between $e^{0.45} = 57\%$ (GLM) and $e^{0.51} = 67\%$ (GLME), or 45% - 51% for a doubling of area. From the smallest patch (45 m²) to the largest (25000 m²), this corresponds to an increase of over 17-26 fold increase in web abundance.

Isolation has a strong negative influence on abundance within the GLM and GLME. An increase of 1 on the ln(isolation) scale corresponds to an change in abundance on the ‘average’ site of between $e^{-0.15} = -14\%$ (GLM) and $e^{-0.17} = -16\%$ (GLME), or 15% - 17% decrease for a doubling of isolation. From the most isolated patch (10000 m) to the least isolated (1 m), this corresponds to a 4-5 fold difference in web abundance.

The results from the GLME also suggest that the largest component of variation is patch within site (50% of the total), site contributes 16% and year just 9%, with the remainder attributable to observation-level variance. Therefore, the inter-annual variation (modelled in Chapter 1) is the smallest proportion of the variance total, and by substantially increasing the number of sites, and particularly patches within sites, this multisite study can explain a considerably higher proportion of the variation in abundance of the Glanville fritillary.

Interactions with Temperature

Although area and isolation showed no significant interactions with temperature, habitat quality did show a significant negative interaction both within the GLMs (Table 2.4) and GLMEs (Table 2.5).

Table 2.4. Results of separate interactions models between temperature and other parameters using GLMs, with quassipoisson errors.

	Estimate	Std. Error	t value	P value	Dispersion
Temperature: Habitat Quality	-0.054	0.013	-4.106	<0.001	70.5
Temperature: log(Isolation)	0.003	0.056	0.055	0.956	85.4
Temperature: log(Area)	-0.002	0.092	-0.018	0.986	70.5

Table 2.5. Results of separate interactions between temperature and other parameters using GLMEs, with poisson errors and observation-level random effects.

	Estimate	Std. Error	z value	P value
Temperature: Habitat Quality	-0.076	0.014	-5.304	<0.001
Temperature: log(Isolation)	0.033	0.041	0.810	0.418
Temperature: log(Area)	0.052	0.061	0.846	0.397

The abundance – habitat quality relationship is approximately 9% shallower during warmer years (cooler years: $b=1.105$ (GLM) and $b = 1.44$ (GLME), warmer years: $b=1.00$ (GLM) and $b = 1.292$ (GLME)). Therefore, habitat quality is a weaker predictor of abundance in warm years than cold ones.

The results from the GLME also suggest that the largest component of variation in abundance (from the temperature – habitat quality interaction model) is patch within site (51% of the total), then observation (21%), site (20%) and finally year (8%).

Discussion

The aim of this study was to determine which of the landscape characteristics of habitat quality, area and isolation as well as air temperature were the most important in determining abundance of Glanville fritillary larval webs across eight sites along the south coast of the Isle of Wight, and to assess any interactions between temperature and the other parameters.

The Glanville fritillary has previously been intensively studied in both the Åland Islands and the U.K.. Both studies have suggested contrasting results as to the importance of these landscape parameters. However, this study uses a much longer time series (15 years) than previous studies. The results show that area is the most important parameter in determining abundance, then habitat quality, isolation and finally temperature.

Due to the parameter of regional air temperature operating at higher hierarchical scales than the more localised factors of area and habitat quality, it was predicted that these landscape parameters would show an interactive effect with temperature. In particular, because temperature determines oviposition locations (Chapter 1), we predicted that the slope of area would be closer to one in warmer years, as hostplants within cooler areas of the patch could be utilised. We also suggested that habitat quality would be a weaker predictor in warmer years, as oviposition would not be primarily restricted to the earliest (warmest) successional stages. However, the results showed that only habitat quality had a significant (negative) interaction (i.e. quality is less important in warm years).

Area

Area is the most significant parameter in determining abundance within this study. Glanville fritillary larval web abundance increase 17-26 fold from the smallest patches to the largest, with a doubling of area equating to an increase of 45% - 51%. Thus, if the conservation aim

were to double the number of individuals within a habitat patch, then this could theoretically be achieved by extending patch size by four times its original size.

The results from this study show that there is a strong positive relationship between abundance and area ($0.45 < b < 0.51$). Previous research has often shown a positive area – abundance relationship for many species (Simberloff 1976; Hanski & Gyllenberg 1997; Matter *et al.* 2002), but within butterfly studies the strength of this relationship can probably be explained by the importance of larval host plants, and in particular their ‘suitability’ (Dennis 2010). The abundance of many butterfly species increases with larger amounts of larval host plant at local scales (Munguira *et al.* 1997; Luoto *et al.* 2001; Matter & Roland 2002; Auckland *et al.* 2004; Krauss *et al.* 2004b; Eichel & Fartmann 2008) hence bigger patches (containing a relatively even distribution of hostplants) will support larger populations. However, because several butterfly species select hostplants on the basis of temperature (Thomas 1983a; Ashton *et al.* 2009; Thomas *et al.* 2011), then encompassing a larger area is likely to contain more heterogeneous habitat and thus some host plants are likely to be in locations that are unsuitably cool to utilise (Chapter 1). As a result, abundance increases less than proportionally with area ($b < 1$), except in areas where temperatures are relatively spatially constant e.g. within homogeneous habitat or on south facing slopes. The strength of the area – abundance relationship is therefore likely to depend on local site characteristics or the species studied, also explaining why specialist species may be more sensitive to increases in area (Krauss *et al.* 2003a) and more vulnerable to extinction within smaller patches than generalists (Krauss *et al.* 2003b).

In this study, we suggest that the strength of the area - abundance relationship is because many of the habitat patches are on south facing soft cliff early successional habitats which (more importantly) are areas where the temperature is suitably warm, and so the majority of host plants within these patches are suitable for oviposition (see Chapter 1). We would not expect such a strong relationship if the sites encompassed more topographically heterogeneous areas, as variations in thermal gradients would reduce the likelihood of oviposition within cooler areas, thus producing a shallower area – abundance slope.

There was no significant interaction between temperature and area. If such a relationship does exist, we might have failed to detect it primarily because many of the habitat patches are south facing, early successional habitats, and so temperature is unlikely to be restrictive factor in determining suitability of host plants.

Habitat Quality

Results from this study suggest that habitat quality is also important, with the best quality habitats supporting 9 – 17 fold increases in population abundance compared to the poorest habitats. Therefore, abundance of the Glanville fritillary is considerably higher in patches which contain larger amounts of earlier (warmer) successional stages. This is because the temperature of the hostplant is of paramount importance in determining oviposition locations (Weiss *et al.* 1988; Renwick & Chew 1994), and so female Glanville fritillaries actively seek out warmer habitats and microclimates in which to lay their eggs (see Chapter 1).

The spatial extent of warmer microclimates is important because they facilitate the effective thermoregulation and development of larvae (Bryant *et al.* 2002; Burke *et al.* 2005; Ashton *et al.* 2009), particularly in more northerly latitudes where temperature constraints are more acute (Thomas 1993). Indeed, the importance of habitat quality may actually have been understated in this study, as it only describes the availability of successional stages within a patch and does not account for variations in aspect which could reduce temperature sufficiently to discourage oviposition (Weiss *et al.* 1988). Therefore, patches could have a high habitat score, yet be of a northerly aspect and so unlikely to contain larval webs. Aspect, combined with extinction on the most isolated site (Red Cliff), can explain why several patches have high habitat quality scores but no larval webs (Figure 2.2).

Habitat quality has often been omitted or ignored in many studies, possibly because it can be difficult to define or describe objectively (Mortelliti *et al.* 2010). However, there is increasing evidence that habitat quality (availability of suitable microclimates) is of paramount importance in determining abundance (Turlure *et al.* 2010; Chouff *et al.* 2011; Smee *et al.* 2011). Indeed, the fact that the abundance of so many species can be correlated to spatial extent of suitable larval habitat (Thomas *et al.* 2011), would suggest that increasing habitat quality remains a priority for conserving remaining populations within fragmented habitats. Certainly, the decline of many butterfly species can be attributed to a lack of management within sites, thus reducing the availability of earlier, warmer successional stages on which many larvae depend for effective development (Thomas 1991, 1995c). Despite this, the conservation policy for fragmented landscapes often focuses on the structural connectivity of landscapes (Boitani *et al.* 2007; Hodgson *et al.* 2009), often overlooking the detrimental effect of habitat degradation within sites (Thomas *et al.* 2001).

The results also showed a significant negative interaction between temperature and habitat quality. Therefore, habitat quality becomes a weaker predictor of abundance (the abundance – habitat quality relationship is approximately 9% shallower) during warmer years.

This supports evidence from previous studies that species may shift oviposition locations within habitats depending on ambient temperature (Roy & Thomas 2003). Furthermore, it also suggests that Glanville fritillaries choose oviposition sites in marginally longer turf to counteract increasing temperatures, but the strength of the relationship is shallow enough not to observe a noticeable shift in habitat preferences (Chapter 1), probably because temperature declines with increases in turf height are so acute.

This has conservation implications for many species which are thermally limited, in that as temperatures are predicted to increase (IPCC 2007), the management recommendations prescribed several decades ago (when summers were cooler) to increase specific species abundance within sites may not need to be so thermally restrictive (e.g. Thomas 1983a). However, it would be premature to advocate a universal relaxation of grazing regimes on the basis of this evidence, and creating habitat mosaics within sites remains the current priority. Heterogeneous habitats are more likely to allow species to compensate for extremes in temperature for both oviposition and nectaring locations, and also more likely to provide shelter during inclement weather (Dennis 2010). Therefore, because of the significance of temperature to invertebrate distribution and abundance, it should be of paramount consideration in any long term management strategy, although research at greater spatial and ecological detail remains a priority to determine the likely implications of climate change (Kearney & Porter 2009).

Isolation

Glanville fritillary larval web abundance decrease 4 -5 fold from the patches with the nearest occupied neighbours to the most isolated patches, with a doubling of isolation distance equating to a decrease of 15% - 17%. Thus, if the conservation aim were to double the number of individuals within a habitat patch, then this could theoretically be achieved by reducing isolation by six times its proximity to an occupied patch.

Although the evidence for increased isolation of habitat patches resulting in decreased occupancy is well established (Dennis 1998; Hanski 1998b; Betzholtz *et al.* 2006; Lenda & Skórka 2010), the effect of isolation on abundance remains equivocal. Several studies have shown isolation to have a negative effect on abundance (WallisDeVries & Ens 2010; Rosin *et al.*

2011), although other studies have shown that isolation has no effect (Krauss *et al.* 2004b; Krauss *et al.* 2005).

In this study, we suggest that the observed (negative) isolation - abundance relationship could be partly explained because many of the habitat patches are approximal, with over half of the patches having edges that abutted other occupied patches. Additionally, the importance of isolation may have been amplified by the extinction at Red Cliff, in that all patch-year combinations within this site between 2000 – 2005 had high isolation (10,000m), and contained no larval webs, such that the abundance and isolation data are not wholly independent. Certainly, the strength of isolation as a parameter will vary depending on patch definition and delimitation (Bowler & Benton 2005), and describing isolation as distance to nearest occupied patch (as opposed to nearest patch) could compromise the independence of isolation from abundance. However, a measure of distance to nearest patch (whether occupied or unoccupied) is normally only used when the aim is to predict occupancy (Moilanen & Nieminen 2002), and more importantly, both previous studies on the Glanville fritillary have concurred that higher numbers occur in the least isolated patches, regardless of whether distance to nearest patch or occupied patch measurements were used (Hanski *et al.* 1994; Thomas *et al.* 2001). Therefore, the results from this study are consistent with research on several other butterflies (WallisDeVries & Ens 2010; Rosin *et al.* 2011), as well as previous intensive studies of the Glanville fritillary in both the U.K. and the Åland Islands.

Temperature

Temperature is also a significant determinant of Glanville fritillary abundance, with web numbers increasing 1.88 to 3.5 fold from the coldest to the warmest years.

The importance of air temperature can be explained by examining the adult preference for ovipositing on hostplants in the warmest locations (Chapter 1). An increase in ambient temperature is likely to improve the suitability of hostplants growing in cooler areas, for example in longer turf or cooler aspects. However, the importance of temperature is weaker than expected for several reasons; first, air temperature is recorded at St Catherine's Lighthouse which is located up to 13 kilometres away from several of the sites, thus it may not be an accurate reflection of air temperature at these more distant locations. Second, a difference of 2.2 degrees is unlikely to cause a major shift in habitat preferences (see temperature beneath habitat stages Fig 1.5, Chapter 1), and so females could select hostplants

of a suitable temperature by adjusting habitat preferences by a couple of centimetres (within the same successional stage) – as the effect of turf height is more acute than air temperature.

Furthermore, this study does not account for variation in hostplant abundance (Gutierrez & Thomas 2000; Krauss *et al.* 2004b; Bauerfeind *et al.* 2009), local site characteristics or density dependence (Dempster & Pollard 1981; Dobkin *et al.* 1987; Dennis 2010), all of which will determine the size of the population on a patch at a particular time. The degree of synchrony in population abundance between patches and sites is therefore likely to vary considerably. Certainly, numbers are significantly higher in warmer years, but inter-annual variance in web numbers (the only variation that can be attributed to temperature) only accounts for a small amount of variation in abundance (9%), the majority of which can be explained by variation in patch characteristics (50%).

Recommendations for Site Management

Habitat destruction is undoubtedly the greatest threat to invertebrates worldwide and habitat fragmentation is highly detrimental to remaining invertebrate populations (Haslett 2008).

The results from this study demonstrate that to maximise abundance for the Glanville fritillary butterfly, sites should be as large as possible, be managed to create microclimates warm enough to allow successful development of larvae, and to a lesser extent be within proximity of other occupied sites. Fundamentally, the evidence from this study supports the conservation principle of “MORE, BIGGER, BETTER AND JOINED” as advocated by Lawton *et al.* (2010).

Therefore, the recommendations from this study are not purely specific to conserving the Glanville fritillary, but are often seen as a conservation panacea to minimise invertebrate losses and maximise abundance within all fragmented landscapes. However, within the U.K and particularly in southeast England, most reserves are already established within a predominantly agricultural landscape, and so advising to increase site area or reduce site isolation is of limited value. Nonetheless, it remains desirable to encompass as large an area as possible, as larger sites, incorporating topographically diverse areas, are likely to provide a greater spatial extent of both consumable and ancillary resources which are likely to support larger populations (Hodgson *et al.* 2009; Dennis 2010). In this study, the parameter of area was the most important factor in determining abundance. The strength of this relationship can partly be explained by the high degree of homogeneity of patches, in that most are south facing and so temperature constraints are less likely to influence hostplant suitability, so a

relatively high proportion of the patch will be suitable for oviposition. Conversely, larger areas containing various slopes and aspects are likely to exhibit a shallower area – abundance slope, but the benefit will be that species can use resources in various locations depending on temperature or weather, thus the likelihood of population stability and persistence times are increased (Holt *et al.* 2004; Oliver *et al.* 2010). Indeed, species which can utilise all consumable resources within a patch may exhibit boom and bust population cycles due to resource depletion (Dempster & Pollard 1981).

As well as being spatially heterogeneous, it is also important for sites to contain thermally diverse environments within habitats, or more specifically variations in microclimates (Dobkin *et al.* 1987). In this study, there is a strong relationship between habitat quality (particularly availability of the earlier successional stages) and Glanville fritillary abundance. However, many species within the U.K are restricted to early successional stages, and the demise of many species can be correlated to the decline of management within sites which prevents succession from reducing ground temperatures sufficiently to discourage oviposition (Thomas 1991). Despite the evidence that the importance of habitat quality varies considerably between studies, there has recently been increasing substantiation for its inclusion within landscape studies (Turlure *et al.* 2010; Chouff *et al.* 2011), particularly as different organisms exploit and perceive their environment at different spatial scales. As invertebrates are so small, they often exist within very small localised populations occupying areas less than two hectares in size (Thomas 2005), so evidently variation in habitat should also be measured at this scale. Despite this, most studies do not include fine scale habitat information (Suggitt *et al.* 2011), and therefore research at greater spatial and ecological detail remains a priority (Kearney & Porter 2009).

The small size of most invertebrates can also inhibit movement between habitats. Hence, even small distances across 'non-habitat' (for example between 1 metre and 1 kilometre) can act as significant barriers and be prohibitive to dispersal (Thomas 1991). The results from this study would also suggest, with certain caveats (see above), that habitat patches in close proximity to other occupied patches are more likely to support higher abundances, although the strength of this relationship is also likely to depend on how habitat patches are defined and delimited (Bowler & Benton 2005). Certainly, the evidence for longer persistence times within less isolated sites is unequivocal (Thomas & Harrison 1992; Thomas *et al.* 1992; Hanski *et al.* 1995; Thomas *et al.* 2001; Johst *et al.* 2002; Wilson *et al.* 2002; Baguette *et al.* 2003). Thus, ideally sites should be within a species dispersal distance for several reasons. First, a degree of genetic variability from immigrants will reduce the likelihood of inbreeding depression and increase

'fitness' (Hanski 2011b; Severns *et al.* 2011), and secondly, if a population does become extinct then close proximity to other occupied patches will increase the probability of re-colonisation (Vandewoestijne *et al.* 2004; Leidner & Haddad 2011). However, there is a caveat to this advice in that the importance of isolation as a determinant of abundance is considerably less than either area or habitat quality, and so priority should be given to these first. Additionally, it is possible that isolation is less significant within larger sites as intra-patch movements may reduce the need for inter – patch movements, and this question remains an important priority for future research.

Climate change is also a serious threat to many species, but is particularly relevant to invertebrate conservation due to their sensitivity to changes in temperature (Thomas *et al.* 2006; Heikkinen *et al.* 2009; Wilson & Maclean 2011). Although current estimates to the amount of warming vary, for example depending on emissions, most researchers now agree that global temperatures will continue to increase and therefore needs to be considered in future conservation policy (Morecroft *et al.* 2011).

Temperature increases are predicted to induce range shifts (Hill *et al.* 2002; Hellmann *et al.* 2008; Chen *et al.* 2011), and alter habitat associations (Davies *et al.* 2006; Ashton *et al.* 2009; Oliver *et al.* 2009), but a key question remains whether species will be able to keep track of changes within an increasingly fragmented landscape (Hill *et al.* 2001; Warren *et al.* 2001; Franco *et al.* 2006). Therefore, increasing landscape connectivity has been perceived as the best solution to ameliorate the impact of climate change (Crooks & Sanjayan 2006; Heller & Zavaleta 2009). However, given that isolation is often a weaker predictor of abundance compared to area and habitat quality (as in this study), the effectiveness of focussing purely on connectivity as a remedy to climate change remains debateable (Hodgson *et al.* 2009). Indeed, this illustrates the need to evaluate the processes which allow population persistence at both small and large scales, as over-generalisations could lead to both costly and inappropriate conservation measures.

Certainly, the results from this study would advocate increasing the size of protected areas, and maintaining and in some cases increasing heterogeneity within (well managed) habitats as a priority. This would not only mitigate the effects of climate change, but is also likely to increase abundance, as well as enhancing population stability and persistence within fragmented landscapes.

Conclusions

Comprehending the various factors that determines species abundance within fragmented habitats remains a priority for conservation.

In this study, the landscape parameters of area, isolation and habitat quality and ambient air temperature were correlated against abundance of Glanville fritillary larval webs within 803 habitat – patch observations along the south coast of the Isle of Wight, thereby encompassing 95% of its British distribution. The interaction between these landscape parameters and temperature was also assessed.

The results suggested that area was the most important parameter, followed by habitat quality, then isolation and finally temperature. Only habitat quality had a significant interaction with temperature, which suggested that as temperature increased habitat quality became a weaker predictor of abundance. This was probably because as temperature increases oviposition locations are not restricted to such thermally restrictive successional stages.

To maximise abundance within fragmented habitats we suggest the priority is for sites to be as large as possible, and to be managed to create heterogeneous, thermally diverse habitats. Not only is this likely to increase abundance, but also encourage population stability and persistence, and may also ameliorate the impact of climate warming.

Chapter 3) Defining the Principle Determinants of Butterfly Abundance on Chalk Grassland across Southeast England.

Abstract

Why abundance varies between species and populations is a fundamental question in ecology. Food availability has been shown to limit population density for many terrestrial species, but the evidence for insects remains mixed. This is probably due to differing stages of the life cycle requiring different food resources, with most insect larvae feeding on plant tissues and adults feeding on nectar. This is further complicated by adults restricting oviposition to a subset of foodplants within a 'suitable condition'.

In this chapter, I examine the importance of the principle food resource for both larvae (host foodplants) and adults (nectar plants), by comparing mean adult butterfly abundance with percentage cover of host and nectar plants across 54 grassland sites in southeast England.

There was a significant positive relationship between butterfly abundance and both host and nectar plant abundance. However, host plant abundance was more important than nectar in determining population density.

The strength of relationship between butterfly and plant abundance also depends on other factors, including species' life history traits and variations in site conditions. For host plants, the relationship with abundance was stronger for species that use fewer host and nectar plants (narrower dietary niche breadth), were habitat specialists and species with low mobility. The hostplant-abundance relationship is also steeper on sites with cooler aspects. However, there were no significant interactive relationships between butterfly abundance and nectar plants.

By further understanding the relationship between butterflies and their associated plants we can propose management advice to maximise butterfly abundance within sites. These results show that the abundance of virtually all butterfly species could be increased through management for their hostplants. On this evidence, we suggest the priority should be managing sites to attain a maximum number of host plants (preferably within suitably warm conditions), although areas of longer turf will also provide nectar sources (which are important for several species), and compensate for extremes in temperature fluctuations that determine oviposition locations.

Introduction

Within any species distribution, the abundance or density (defined as numbers per area) of a population is determined by variation in the four main population parameters of natality, mortality, immigration and emigration (Odum 1963). No population increases without limits, with growth primarily restricted by temperature, limitations in resources and interactions with other species through competition or predation (May 1975). Understanding the mechanisms which determine population density is a fundamental question in ecology (Krebs 1978), and can facilitate why some populations of particular species are smaller or larger than others.

Abundance varies in response to environmental constraints over time (Southern 1970), or across space (Hengeveld & Haeck 1982) depending on both species traits (Brown 1995) and site characteristics (Sutherland 1998). However, while changes in density have been well described, the mechanisms which restrict population growth have been less well understood (Hanski 1994a). The pioneering work of Andrewartha and Birch (1954) suggested that the numbers of animals within a population were limited by i) a shortage of material resources (e.g. food) ii) inaccessibility of these resources relative to the animals dispersal and iii) shortage of time when population growth is positive. More recently, both metapopulation theory and autecological research have developed these concepts also providing evidence as to the importance of area, isolation (Hanski 1998b), and habitat quality (Thomas *et al.* 2001) of occupied patches within species distributions, and the relative importance of these landscape characteristics has dominated current research in insect population ecology (New 2009; Poyry *et al.* 2009b; Hodgson *et al.* 2011). However, as nutritional resources are essential for species persistence (Begon *et al.* 1986), proponents of metabolic theory suggest that a species metabolic rate will determine the efficiency at which food can be converted into energy (Peters 1983), and so food availability could underlie limitations in population growth by constraining reproductive ability or through competition for limited resources (Blackburn & Gaston 1999; Brown *et al.* 2004). It is therefore important to clarify all the determinants of population density, as only then can we suggest management advice to maximise species abundance within sites.

Within terrestrial ecosystems, food availability has been shown to be important in determining density of carnivores (Carbone & Gittleman 2002) and birds (Lack 1954), yet the evidence for insects remains mixed (Thomas *et al.* 2011). This could be because unlike most species, many insects go through definitive life cycle stages in order to develop; egg; larvae; pupa and finally adult. The requirements for each stage of the life cycle may therefore be reliant on different

nutritional needs than the previous stage, for example, most insect larvae feed on plant tissues but adults often feed on nectar (Ehrlich & Raven 1964). Butterflies, like most insects, require the presence of the hostplant on which to oviposit and is an essential food for larval growth and survival (Frohawk 1934). Nectar can also form a vital part in the life history of butterflies (Vane-Wright & Ackery 1984; Hardy *et al.* 2007; Erhardt & Mevi-Schutz 2009) as adult feeding can contribute to longevity and reproductive success (Boggs & Ross 1993; Boggs & Freeman 2005; Erhardt & Mevi-Schutz 2009), although its quality depends on flower age, time of day, weather and activities of competing nectar feeders (Gottsberger *et al.* 1990). Therefore, due to the variation in foodplant use throughout the life cycle, the importance of both larval and adult food resources in determining insect population density remains inconclusive (Dennis 2010).

Consequently, while several studies have demonstrated a positive relationship between adult abundance and amount of nectar available at local scales (Clausen *et al.* 2001; Summerville & Crist 2001; Bergman *et al.* 2008; Kubo *et al.* 2009), other studies have concluded that the importance of nectar as a determinant of population density is minimal (Thomas *et al.* 2011). Similarly, several studies have also shown that higher densities of butterflies are found in areas containing larger amounts of larval host plants (Munguira *et al.* 1997; Haddad & Baum 1999; Luoto *et al.* 2001; Matter & Roland 2002; Auckland *et al.* 2004; Krauss *et al.* 2004b; Betzholtz *et al.* 2006; Nowicki *et al.* 2007; Eichel & Fartmann 2008), but this relationship is often weaker than predicted (Kelly & Debinski 1998) with many other studies showing no significant relationship (Kuussaari *et al.* 2000; Kuussaari *et al.* 2004; Hanski & Meyke 2005; Fred *et al.* 2006; Rabasa *et al.* 2008; Stasek *et al.* 2008), or even an inverse one (Thomas 1984; Thomas *et al.* 1986). Furthermore, in a recent meta-analysis using British butterflies Thomas *et al.* (2011) demonstrated that for over 20 species recorded on the UK Butterfly Monitoring Scheme (UKBMS), host plant abundance was not significantly related to butterfly abundance at local scales (i.e. butterflies do not tend to be more abundant on sites with more hostplants). However, at a regional scale (North Wales) Cowley *et al.* (2001b) collected data on the density and distribution of adult butterflies and all associated host plants to assess whether abundance of butterflies and host plants was correlated. The results demonstrated that butterfly species whose hostplants occur at high density also tend to be locally abundant. However, some species only occupied a small proportion of the host plant range (see Quinn *et al.* 1998) and some pairs of species which shared the same hostplant also had contrasting distributions (Gutierrez *et al.* 2001).

The variation in importance of resources both between and within species can also be influenced by local site characteristics (Hanski *et al.* 1995; Moilanen & Hanski 1998; Kuussaari *et al.* 2000; Holt *et al.* 2004; Dennis & Sparks 2005; Dennis *et al.* 2006b; Grundel & Pavlovic 2007; Pettis & Braman 2007; Rabasa *et al.* 2008; Rundlof *et al.* 2008; Sjodin *et al.* 2008; Poyry *et al.* 2009b; Lindell & Maurer 2010). For many butterfly species the critical factor is not the total amount of hostplant, but the availability of plants growing in 'suitable condition' (Thomas 1991; Dennis 2010). For example, females of many butterfly species restrict oviposition to host plants growing within a suitably warm microclimate to expedite growth (Thomas 1983a; Ravenscroft 1994; Fartmann 2006) or within narrow limits of light and shade (Pollard 1979; Shreeve 1986; Warren 1987) or of a particular size or shape (Bourn & Thomas 1992; Gripenberg & Roslin 2005), high in nitrogen (Dennis 1984; Pullin 1987) or containing chemicals which can be utilised as a larval defence (van Nouhuys & Hanski 1999; Goverde *et al.* 2008; Talsma *et al.* 2008). Discrepancies in the strength of relationship between host plant abundance and butterfly density may therefore depend on, for example, how much of a site has southerly aspect, or managed by grazing thereby reducing the turf height and increasing the temperature of the hostplant increasing likelihood of oviposition (Thomas & Lewington 2010). Thus, both abiotic and biotic factors could increase the percentage of plants within 'suitable condition' within a site, producing very different results at local scales, yet these effects could be ameliorated over larger scales incorporating many sites.

Additionally, certain species are likely to be more or less sensitive in changes in foodplant abundance due to phylogenetic factors. Differences in life history traits (Boggs & Ross 1993; Garcia-Barros 2000; Mattila *et al.* 2009; Poyry *et al.* 2009a) and niche breadth (Thomas 1995c; Hughes 2000; Roy & Thomas 2003; Komonen *et al.* 2004; Summerville *et al.* 2006; Anthes *et al.* 2008; Friberg *et al.* 2008; Mattila *et al.* 2009; Oliver *et al.* 2009) may influence how many plant species a butterfly can utilise, or its effectiveness at locating suitable foodplants. Species which have increased 'choice' in foodplants, for example by having higher mobility, or feeding on more than one hostplant (polyphagous species) in theory could have higher abundances as the environmental constraints they face are less restrictive. However, while species distributional extent may be linked to an ability to utilise a wider range of resources (Brown 1984), it is less clear why species with broad resource requirement should occur at higher densities (Hanski *et al.* 1993).

There is considerable evidence implicating weather and climate (Pollard & Moss 1995; Sutcliffe *et al.* 1996; Roy *et al.* 2001; Hanski & Meyke 2005; Wikstrom *et al.* 2009; Guiney *et al.* 2010), landscape factors of area, isolation and habitat quality (Hanski 1998b; Moilanen & Hanski

1998; Thomas *et al.* 2001), and to a lesser extent predators, parasitoids and pathogens (Lei *et al.* 1997; Laine 2004; Harvey *et al.* 2005; van Nouhuys & Hanski 2005) as determinants of butterfly density within species, and some evidence to suggest that life history factors distinguish rare and common species (Cowley *et al.* 2001a; Paivinen *et al.* 2005). Food availability (hostplants and nectar) vary along both axes: each species has a different preference and each site contains a different plant community. Therefore, to understand more deeply the role of food availability on butterfly populations, we should explore how the variation in abundance co-varies with food availability across sites and across species simultaneously.

Recently, Isaac *et al.* (2012) tested 23 predictor variables including traits of species, sites and populations. The most important predictors of abundance were climate, position in range, larval diet breadth and population structure, although surprisingly most correlations were in the opposite direction to that predicted, perhaps reflecting bias in the way sites are selected on the UKBMS. In Finland Paivinen *et al.* (2005) found that both adult habitat breadth and larval diet breadth were negatively related to butterfly density, whereas in the U.K. Cowley *et al.* (2001a) showed that mobility was a key trait in influencing density, with more widely distributed species having lower abundances, but niche breadth (larval host plant specificity and larval feeding specificity – the parts of plants eaten and larval association with ants) was not important. Several studies have also shown that species which are restricted to few hostplants are more sensitive to climatic temperature change (Diamond *et al.* 2011), or that nectar specialists tend to be rarer than nectar generalists (Tudor *et al.* 2004), or that species with lower mobility are less able to colonise areas containing apparently suitable foodplants within fragmented landscapes (Gutierrez & Thomas 2000; Cowley *et al.* 2001a; Komonen *et al.* 2004; Betzholtz & Franzen 2011). An unanswered question is whether these species traits determine the degree to which food resources limit abundance.

To date, no study has examined the relationship between butterfly population density and foodplant abundance both among and within species. Understanding both axes of variation, and the causes thereof, could allow land managers to target species which are most likely to respond positively towards (foodplant) management.

In this paper, we determine whether adult butterfly abundance within grassland communities is significantly related to abundance of host plants and nectar plants. We also test species 'sensitivity' to host and nectar plants as the strength of relationship between food and adult butterfly abundance. We also assess whether the correlation between butterfly abundance

and food availability is mediated by life history, niche and site traits. In particular, we include traits significant in previous multi-species studies; mobility (Cowley *et al.* 2001a; Komonen *et al.* 2004) and also include other life history (habitat specificity, population structure and larval duration), and niche traits (larval and adult dietary breadth). We also include some site characteristics (aspect and turf height) in an attempt to validate whether the relationship between butterfly and hostplant is stronger when a higher percentage of host plants are more likely to be in 'suitable condition'. By further understanding the determinants of population density, we also aim to suggest management advice to maximise butterfly abundance within sites.

In particular I test the following hypotheses;

H1) Is adult butterfly population density correlated to the amount of food resources? Furthermore, which food resource is most limiting - larval or adult?

The total amount of foodplant is predicted to be positively correlated with adult butterfly population density. However, as hostplants are essential for larval development, whereas nectar probably prolongs adult lifespan but has little impact on fecundity, it is predicted that hostplants will have greater explanatory power in adult butterfly density than nectar plants.

H2) Particular species, or species groups, are more sensitive to changes in host and nectar plant abundance depending on life history or niche traits.

- i) Niche Breadth: The ability to utilise one or only a few species of host or nectar plant could enhance sensitivity to changes in food abundance. Species which have the ability to utilise a wide variety of foodplants are predicted to be less sensitive to variations in food abundance, as increased foodplant choice could act as a buffer against scarcity of preferred foodplants.
- ii) Mobility: How does species dispersal ability influence sensitivity to foodplants? Species with lower mobility cannot migrate to areas with higher-quality food resources, and are therefore predicted to be more sensitive to how much foodplant is available locally. In contrast, wider ranging species can sample a range of patches before choosing where to oviposit, and are therefore predicted to be less sensitive to foodplant abundance (i.e. show a shallower relationship with food availability across sites).

- iii) Larval duration: Is there a time constraint on the larval resource? Larvae that undergo rapid development must consume all the resources for growth in a short period of time, which could potentially exhaust the edible biomass of their hostplant. Thus, rapidly developing larvae risk starvation unless their hostplant is locally abundant. By contrast, larvae of species whose development is spread over longer time periods exert a lower herbivore load on their hostplant, and are therefore predicted to be less sensitive to variation in hostplant abundance.

H3) Populations which exist on sites with more northerly aspect or little or no grazing are predicted to be more sensitive to changes in foodplant abundance.

Temperature is a primary factor in determining the suitability or 'quality' of foodplants, therefore populations inhabiting cooler microclimates are predicted to be more sensitive to changes in foodplant abundance.

To examine the effect of temperature we assess the importance of;

- i) Aspect: Temperature of the microclimate in which the foodplant is located is important in determining suitability for oviposition (and probably nectaring). Species which occur on more southerly sites are therefore predicted to be less sensitive to changes to foodplant abundance. This is because more of the foodplant on south facing slopes is considerably warmer (e.g. temperature is less restrictive in oviposition choice) and thus within suitable condition. Species on more northerly (cooler) slopes are predicted to be more sensitive to foodplant amounts as only a fraction of foodplant will be within suitable condition depending on ambient daytime temperatures.
- ii) Turf height: Site management can potentially increase food plant suitability by reducing the turf height and increasing foodplant temperatures by controlling the amount of grazing. Species inhabiting sites with shorter turf are therefore predicted to be less sensitive to changes in foodplant abundance due to a higher percentage of plants being within suitable temperatures, and species on sites with longer turf more sensitive as a lower percentage of foodplant will be within suitable condition.

Methods

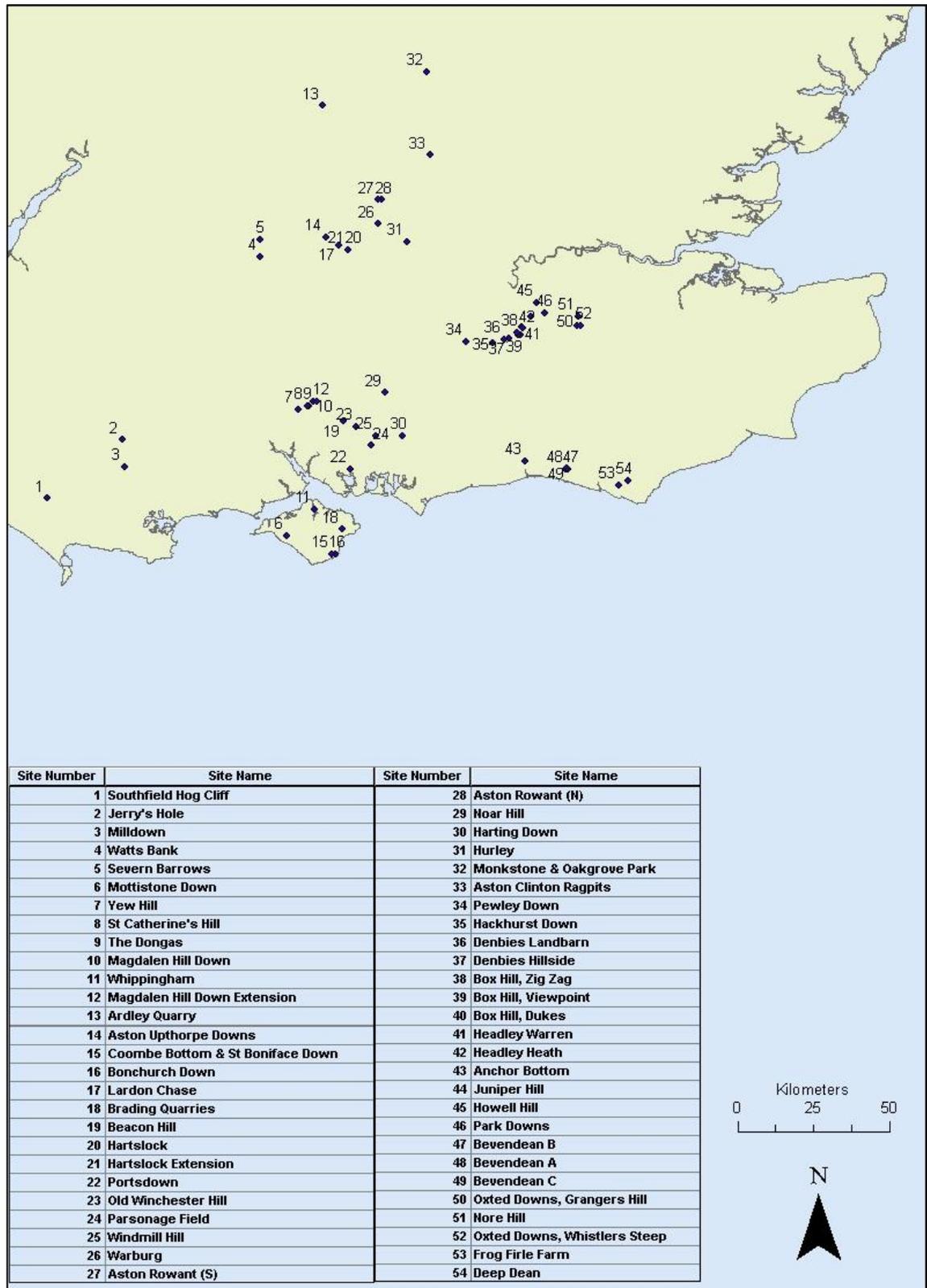
To summarise, I sampled foodplant abundance and compiled site characteristics from 54 U.K. Butterfly Monitoring Scheme (UKBMS) grassland study sites across southeast England during 2008 – 2009. This was then correlated with mean population density for 30 butterfly species recorded on the same study sites during 2006 – 2010 by UKBMS transect walker volunteers. Life history and niche traits were also acquired from other studies (references below) to assess interactive effects with foodplant abundance.

Selection of study sites

Within the U.K., calcareous grassland is one of the most important habitats for butterflies supporting approximately 50 % of British butterfly species (Dennis 1977), most of which breed predominantly within this habitat (Thomas & Lewington 2010). However, grassland is a plagioclimax community and needs to be continually managed to prevent natural succession into scrub and woodland (Odum 1963). Many species of butterflies and other wildlife are therefore reliant on livestock grazing, mowing, burning or scrub removal for their survival (Sutherland & Hill 1995). Currently, over half of threatened Lepidoptera in Europe occur on grassland habitats (van Swaay 2002).

Within the U.K., many of these sites are protected areas, and several of the butterfly populations have been monitored as part of the UKBMS for several decades (Botham *et al.* 2009). The majority of these grassland sites are in southeast England, and 54 UKBMS sites were selected on the basis that they contained > 50% grassland and had been regularly monitored (Figure 3.1).

Figure 3.1. A map of the 54 UKBMS study sites included in this study, numbered from west to east.



Estimates of vegetation abundance and resource availability

Vegetation surveys were conducted on 54 UKBMS sites between May to September 2008 – 2009. For each site, the transect route had been subdivided into a number of sections on establishment (depending on transect length) to distinguish between habitat types and to facilitate recording. Each of the sections were walked with a regular transect walker and mapped with a GPS. The vegetation was surveyed in four x 1m² quadrats per section in order to obtain a representative sample of the vegetation along each transect route. To create random points for quadrat locations at a particular site, the transect route (comprised of separate sections) was initially downloaded into ArcMap as a shapefile. Using the buffer tool, a 5 metre area was then created each side of the section route. This distance was chosen because transect walkers record butterflies within a 5 metre ‘box’ perpendicular to the observer, therefore in most instances 2.5 metres either side of them. However, many of the section routes walked were often on gravelled paths or sheep trails, and so by doubling the width of the route ‘buffer’ this increased the likelihood of avoiding the heavily trampled areas which were unlikely to represent the vegetation at that site. Therefore, the vegetation was sampled from the area immediately around the transect route, rather than the entire study site, as the latter is difficult to define objectively. Similarly, the buffer was not extended to more than 5 metres in order to prevent quadrat locations occurring in areas not within the site, for example, many semi-natural grassland transects border farmland which is not only likely to be private but contain few plant species relevant to butterfly abundance within a reserve.

By using Hawth’s tools (Beyer 2004) random points were created within this buffered area – and these points were then uploaded back to the GPS to give locations for each 1m² vegetation quadrat.

Using the GPS, points for random quadrats were located, and each quadrat was assigned a unique identification number. Before placing a quadrat, fundamental site and section details were recorded (site name, site BMS number, section number and date).

The vast majority of 1m² plots (frame quadrats) contained high percentages of relatively short grassland, and I therefore employed a methodology that has been widely used in national vegetation surveys of these habitats (e.g. Carey *et al.* 2008). The basic vegetation structure was recorded as a percentage layer (grass, herb and woody), and visual estimates were made of the percentage cover of each species of higher plant. Additionally, the percentage cover of the

seven principle grass species that are used for oviposition by grassland butterflies was also recorded: *Holcus lanatus*, *Festuca rubra*, *Festuca ovina*, *Brachypodium sylvaticum*, *Brachypodium pinnatum*, *Dactylis glomerata*, and *Elytrigia repens*. Cover was recorded as the 'area of ground occupied by a perpendicular projection on to it of the foliage and stems of individuals of a particular species' (Shimwell 1972). The summed percentage covers of individual species nearly always exceeded 100% because of the layering and overlapping of species.

To calculate foodplant abundance associated with each butterfly species at each site, we summed the percentage cover of the relevant plant species at each site. Relevant plant species were defined as those recorded as larval host plants and nectar sources, using preferences obtained from Dennis (2010). Host plants were listed for each butterfly species as both 'main' and 'secondary', the latter which also included foodplants consumed in captivity. We therefore used 'main' hostplants to calculate hostplant abundance, although the very similar estimates of hostplant availability were derived by also including 'secondary' sources (not shown). There was no distinction for use of nectar plants, and so all nectar plants on which a species had been observed feeding were included in the first nectar analysis. However, within the 30 species of butterflies included in the analyses, ten species also use their associated hostplant as a nectar sources. Therefore, to ensure nectar was tested as an independent effect, we generated a second estimate of nectar availability that ignored the contribution of nectar sources that were also recorded as hostplants.

To estimate the amount of food available at each site (plant cover), a total of 1624 quadrats were surveyed from 406 transect sections across 54 sites (four quadrats per section). This gave a total of 16,720 separate estimates of plant abundance across all quadrats, corresponding to 2934 plant – site abundance combinations. A total of 165 different plant species were recorded, with a mean number of 54.3 species per site.

Site Characteristics

Turf height was recorded for each quadrat as a direct measurement from the ground to the base of the crown of the vegetation as described in Shimwell (1972). The mean turf height for each site was calculated by excluding all quadrats containing less than 75% grass or over 50cm high, because most grassland butterflies only utilise vegetation below this height (Nature Conservancy 1986) and so only variation below this threshold is biologically interesting. Aspect was assessed for any quadrat where the ground surface inclined in a constant direction, and its

orientation was recorded to the nearest five degrees. A site level figure for aspect was produced by aggregating the section means.

Life history and niche traits

For each species, diet breadth estimates (number of main larval host plants utilised) were obtained from Dennis (2010), and degree of nectar specialism characterised as the number of species of nectar plants utilised by adults were obtained from Hardy *et al* (2007). Habitat specialism is a categorical variable, distinguishing wider countryside species, migrants and specialists restricted to specific habitats (Botham *et al.* 2009). Mobility scores were derived from Dennis *et al* (2005) who ranked species mobility on a scale from 1 – 9, from low to high dispersal capabilities. Population structure values were extracted from Warren *et al* (2001) and based on a seven point score with the most sedentary species having lower scores and the most dispersive species scoring highly. Larval duration periods were calculated from life history tables (Frohawk 1934), ignoring any period of inactivity caused by dormancy throughout the winter months (i.e. average number of days feeding on host plant during March – October). Thus larval duration is the amount of time (in days) which is spent as an actively feeding caterpillar. See Table 3.1 for a description of diet breadth, life history and site traits included in this study.

Table 3.1. Description of diet breadth, life history and site traits.

Trait	Measure	Definition	Source
Diet breadth			
Larval niche breadth	Number of larval Core Host Plants (CHP)	Records of only main host plants including prominent regional ones	Dennis (2010)
Adult niche breadth	Degree of adult nectar specialism (RanS)	Monte Carlo estimated number of nectar sources (from mean number of nectar sources per 100 records)	Hardy <i>et al</i> (2007)
Life history traits			
Habitat specialist	Degree of adult habitat specialism	Habitat preferences as wider countryside species and migrants or specialists restricted to specific habitats	Botham <i>et al</i> (2009)
Mobility	Degree of dispersal capabilities	Dispersal capabilities (1-9, low to high)	Dennis <i>et al</i> (2005)
Population structure	Measurement of colony structure	Defined as 'open' or 'closed' population (1-7, open to closed)	Warren <i>et al</i> (2001)
Larval duration	Duration of larval stage calculated from life history tables	Average number of days spent feeding on hostplant during March - October	Frowhawk (1934)
Site Traits			
Turf Height	Mean turf height (cm)	Mean turf height measured from ground level to crown of vegetation	This study
Aspect	Aspect (to nearest five degrees)	A measure of ground orientation	This study

Estimates of butterfly abundance

I used data from the Butterfly Monitoring Scheme (UKBMS) to provide estimates of butterfly abundance.

The Butterfly Monitoring Scheme was initiated in 1976 whereby observers walk a set route (transect) once a week, under favourable weather conditions throughout the main butterfly flight period (April – September), recording all butterfly species encountered within a 5 metre box (Asher *et al.* 2001). Although the primary aim of the UKBMS is to provide information at regional and national levels on changes in species status (Botham *et al.* 2009), more recently this data has been used to assess the determinants of species abundance (Isaac *et al.* 2012), and to demonstrate variances in species sensitivity to factors such as temperature and niche breadth (Diamond *et al.* 2011).

The UKBMS is well described (Pollard 1977), robust (Gross *et al.* 2007), and butterfly abundance has shown to correlate with population estimates obtained by mark – release – recapture for a wide range of species (Thomas 2005). Although the accuracy of transects can depend both on species and time of day (Harker & Shreeve 2008) due to bias in detectability (Dennis *et al.* 2006a; Pellet *et al.* 2012), the UKBMS data provide a good reflection of relative abundance for most species and of large scale trends in abundance (Isaac *et al.* 2011a).

I used the annual site index (based on the sum of weekly counts) from the UKBMS dataset as a measure of the abundance of a species at a particular site. For populations surveyed every week from April to September, the site index is equal to the total number of adult butterflies recorded. Of the ~60 species of butterflies recorded regularly in the British Isles, 46 species were recorded by UKBMS volunteers transect walkers across the 54 study sites. Of these, 4 wide-ranging species were excluded from the analysis because their host foodplant was not recorded within any of the study sites (*Anthocharis cardamines*, *Pieris brassicae*, *Pieris napi* and *Pieris rapae*), such that our models have no power to predict their abundance. We also excluded 12 species that occurred on 7 sites or fewer (*Euphydryas aurinia*, *Hamearis lucina*, *Boloria euphrosyne*, *Boloria selene*, *Limenitis camilla*, *Melitaea cinxia*, *Apatura iris*, *Satyrrium w-album*, *Neozephyrus quercus*, *Thecla betulae*, *Plebejus argus*, and *Leptidea sinapsis*). Therefore, a total of 30 species were included within the analysis (see Table 3.2).

The geometric mean of abundance from 2006 – 2010 was calculated for each of these 30 species across 54 sites, producing a total of 1250 individual measures of abundance. The total

number of butterfly species recorded on each site varied between a minimum of 3, and a maximum of 34 species, with a mean of 27.6 butterfly species per site.

Table 3.2. A list of species included within the analysis, and the number of sites on which they occurred. Species listed in alphabetical order.

Species	No of Sites	Species	No of Sites
<i>Aglais urticae</i>	49	<i>Lycaena phlaeas</i>	51
<i>Aphantopus hyperantus</i>	50	<i>Maniola jurtina</i>	53
<i>Argynnis aglaja</i>	34	<i>Melanargia galathea</i>	52
<i>Argynnis paphia</i>	21	<i>Ochlodes sylvanus</i>	51
<i>Aricia agestis</i>	53	<i>Pararge aegeria</i>	50
<i>Callophrys rubi</i>	44	<i>Polygonia c-album</i>	53
<i>Celastrina argiolus</i>	49	<i>Polyommatus bellargus</i>	26
<i>Coenonympha pamphilus</i>	50	<i>Polyommatus coridon</i>	41
<i>Colias croceus</i>	39	<i>Polyommatus icarus</i>	54
<i>Cupido minimus</i>	24	<i>Pyrgus malvae</i>	38
<i>Erynnis tages</i>	42	<i>Pyronia tithonus</i>	52
<i>Gonepteryx rhamni</i>	50	<i>Thymelicus lineola</i>	12
<i>Hesperia comma</i>	18	<i>Thymelicus sylvestris</i>	32
<i>Inachis io</i>	50	<i>Vanessa atalanta</i>	50
<i>Lasiommata megera</i>	12	<i>Vanessa cardui</i>	50

Statistical Analysis

The data used in the analyses were derived from the geometric mean population density for 30 species of butterfly (from 2006 – 2010) and the availability of host and nectar plants (from 2008 – 2009) sampled across the same 54 grassland sites in southeast England. Prior to the analysis, most of the predictors were transformed in order to improve normality. Natural logarithm transformations were performed on both measures of niche (diet) breadth (number of core host and nectar plants), mobility, population structure and larval duration. Aspect was cosine transformed so sites with southerly aspect had scores approaching 1, northerly aspects scored -1 and east and west-facing aspects zero.

The aim was to explain the variation in butterfly abundance by correlating population density (log of (abundance / transect length)) - against foodplant abundance to determine the significance of this relationship, and to assess which was more important - host or nectar plants (H1). To also assess the importance of three groups of predictors; niche, life history and

site level traits, and their interactive effect with plant abundance to evaluate which species show the strongest and weakest relationships to changes in foodplant abundance (H2 and H3).

Initially, the independence of the two key explanatory variables (host and nectar plants) was tested by Pearson's product moment correlation to explore the relationship between the two types of foodplants. Secondly, the relationship between mean butterfly density and food availability (H1) was modelled across all species using both linear regression and mixed effects models, with separate models for hostplant and nectar abundance (nectar models were repeated with the exclusion of nectar sources that are also hostplants). Mixed effect models included Site and Species identity as crossed random effects (Cowlshaw *et al.* 2009; Isaac *et al.* 2011b) to allow for a lack of independence in abundance estimates (site and species effects). Next, I ran separate linear regressions for each species (60 models in total) in order to explore the variation in species-specific responses to hostplant and nectar abundance.

Butterfly population density was then modelled as a function of six species traits and two site characteristics (turf height and aspect) as separate interactions with hostplant and nectar abundance (i.e. a total of 16 models; 6 species and 2 site traits and 8 models each for nectar and hostplants) to ascertain the strength of these variables in predicting butterfly population density (H2 and H3 – see Table 3.1). All models included site and species as random effects, as above.

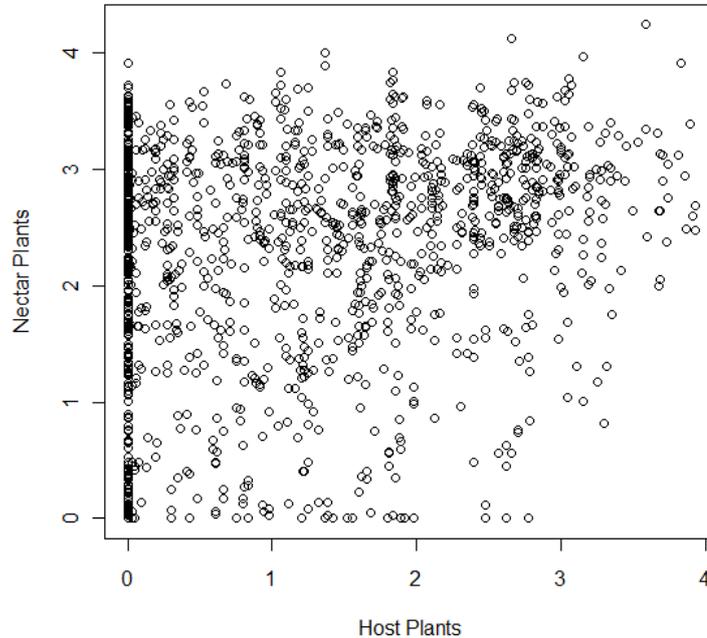
Significance of fixed effects in mixed models was assessed using the Wald t-test, as recommended by Bolker *et al.* (2009). All models were fit in R, with GLMEs employing the lme4 package (Bates & Maechler 2010; R Development Core Team 2010).

Results

1. Testing the relationship between host and nectar plants.

The relationship between host and nectar plants was tested using Pearson's product moment correlation. There was a significant positive relationship between the two key variables ($r = 0.324$, $t = 13.247$, $p < 0.001$, see Figure 3.2). However, the R squared value of 0.105 is weak enough that the explanatory power of both host and nectar plants can be considered to be independent effects.

Figure 3.2. A scatterplot of the relationship between the logarithm of host and nectar plants obtained from 1495 plant species – quadrat combinations recorded across 54 UKBMS sites during 2008 – 2009.



Abundance of host plants is therefore correlated with the abundance of nectar plants, but the relationship is weak enough to validate the independence of both host and nectar plants as predictors of butterfly population density.

2. Butterfly population density and hostplant availability

There is a strong, statistically significant, positive relationship between butterfly population density and abundance of their associated hostplants both in the linear regression across all species ($b=0.441$, $se=0.0449$, $t=9.82$, $p<0.001$), and linear mixed effect model ($b=0.333$, $se=0.0389$, $t=8.56$, $p<0.001$). The slope of the mixed model is less steep than for linear regression, but is more precisely estimated. These models imply that, for the 'average' species on an 'average' site, an increase of 1 log unit of hostplant abundance is associated with an increase of 0.33-0.44 log units in butterfly population density, i.e. a doubling of hostplant availability leads to an increase in butterfly abundance of 33 - 44%.

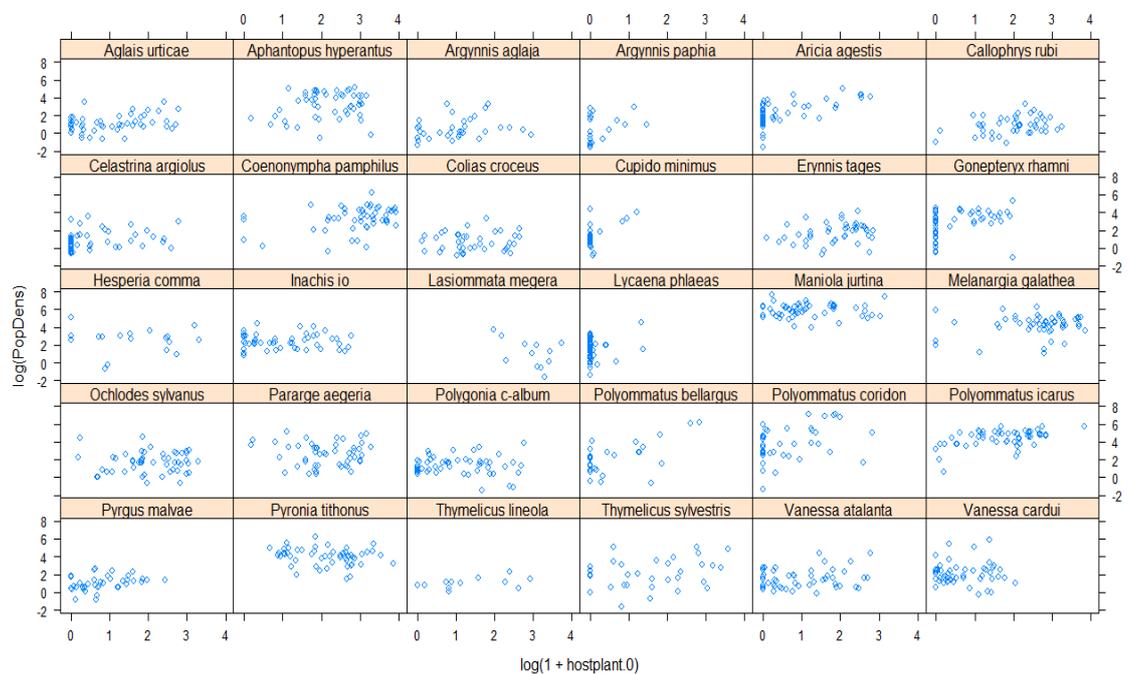
Table 3.3. Results of species-specific linear regressions between the logarithmic geometric mean of density for each of the 30 butterfly species recorded across 54 UKBMS sites during 2006 – 2010, against abundance of associated hostplants for the same sites recorded during 2008 – 2009, in alphabetical order.

	Estimate	Std. Error	t value	Pr(> t)	Rsq
<i>Aglais urticae</i>	0.337	0.148	2.267	0.028	0.099
<i>Aphantopus hyperantus</i>	0.385	0.281	1.372	0.176	0.038
<i>Argynnis aglaja</i>	0.387	0.244	1.582	0.124	0.073
<i>Argynnis paphia</i>	1.048	0.738	1.420	0.172	0.096
<i>Aricia agestis</i>	0.960	0.177	5.425	<0.001	0.366
<i>Callophrys rubi</i>	0.433	0.190	2.284	0.027	0.111
<i>Celastrina argiolus</i>	0.318	0.167	1.901	0.063	0.071
<i>Coenonympha pamphilus</i>	0.485	0.188	2.579	0.013	0.122
<i>Colias croceus</i>	0.102	0.226	0.454	0.653	0.006
<i>Cupido minimus</i>	2.333	0.667	3.498	0.002	0.357
<i>Erynnis tages</i>	0.373	0.230	1.620	0.113	0.062
<i>Gonepteryx rhamni</i>	0.723	0.294	2.459	0.018	0.112
<i>Hesperia comma</i>	-0.030	0.324	-0.092	0.928	0.001
<i>Inachis io</i>	0.023	0.133	0.173	0.863	0.001
<i>Lasiommata megera</i>	-1.391	0.808	-1.720	0.116	0.228
<i>Lycaena phlaeas</i>	0.785	0.544	1.443	0.155	0.041
<i>Maniola jurtina</i>	0.014	0.123	0.114	0.910	0.000
<i>Melanargia galathea</i>	0.180	0.171	1.054	0.297	0.022
<i>Ochlodes sylvanus</i>	0.024	0.208	0.115	0.909	0.000
<i>Pararge aegeria</i>	-0.053	0.242	-0.219	0.828	0.001
<i>Polygonia c-album</i>	-0.040	0.164	-0.242	0.810	0.001
<i>Polyommatus bellargus</i>	1.259	0.344	3.660	0.001	0.358
<i>Polyommatus coridon</i>	0.790	0.361	2.187	0.035	0.109
<i>Polyommatus icarus</i>	0.529	0.135	3.931	<0.001	0.229
<i>Pyrgus malvae</i>	0.422	0.201	2.103	0.043	0.109
<i>Pyronia tithonus</i>	-0.245	0.163	-1.507	0.138	0.043
<i>Thymelicus lineola</i>	0.275	0.168	1.633	0.134	0.210
<i>Thymelicus sylvestris</i>	0.392	0.262	1.494	0.146	0.069
<i>Vanessa atalanta</i>	0.171	0.170	1.005	0.320	0.021
<i>Vanessa cardui</i>	-0.057	0.299	-0.192	0.848	0.001

For the species-specific models, the median of the estimate suggests that doubling the amount of hostplants would increase butterfly population density by 44% (Table 3.3). The estimate ranges from -1.391 to 2.333, and R squared scores range from 0.3% to a maximum of 37%. Most of the relationships between hostplants and butterfly abundance are positive (Figure 3.3).

Of the 30 species, only six have a negative correlation (none of which are significant), with the remaining 24 species all showing a positive relationship (ten of which are significant). Even after accounting for the fact that a large number of tests have been conducted, this suggests that the abundance for many butterfly species is affected by the availability of hostplants. For the three species showing strongest relationships, hostplant abundance explains around 35% of the variation in adult butterfly density across sites (*Aricia agestis*, *Polyommatus icarus* and *Polyommatus bellargus*).

Figure 3.3. A scatterplot of the logarithmic geometric mean of density for each of the 30 butterfly species recorded across 54 UKBMS sites during 2006 – 2010, against abundance of associated hostplants for the same sites recorded during 2008 – 2009.



2. Butterfly population density and nectar plant availability

As with hostplants, there is a strong, statistically significant, positive relationship between butterfly population density and nectar abundance in both the linear regression ($b=0.435$, $se=0.0503$, $t=8.65$, $p<0.001$) and linear mixed effect model ($b=0.284$, $se=0.0532$, $t=5.34$, $p<0.001$). For the ‘average’ species on an ‘average’ site, an increase of 1 log unit of hostplant abundance is associated with an increase of 0.28 - 0.43 log units in butterfly population density, i.e. a doubling of nectar plant availability leads to an increase in butterfly abundance of 28 - 43%. Thus, the magnitude of the effect size is very similar to that for hostplants (see above). Very similar results were returned after the contribution of nectar sources that are

also hostplants was removed: the results for the linear regression were almost identical ($b=0.443$, $se=0.0450$, $t=9.85$, $p<0.001$) but the mixed model returned a much shallower and less significant relationship ($b=0.180$, $se=0.0490$, $t=3.66$, $p<0.001$).

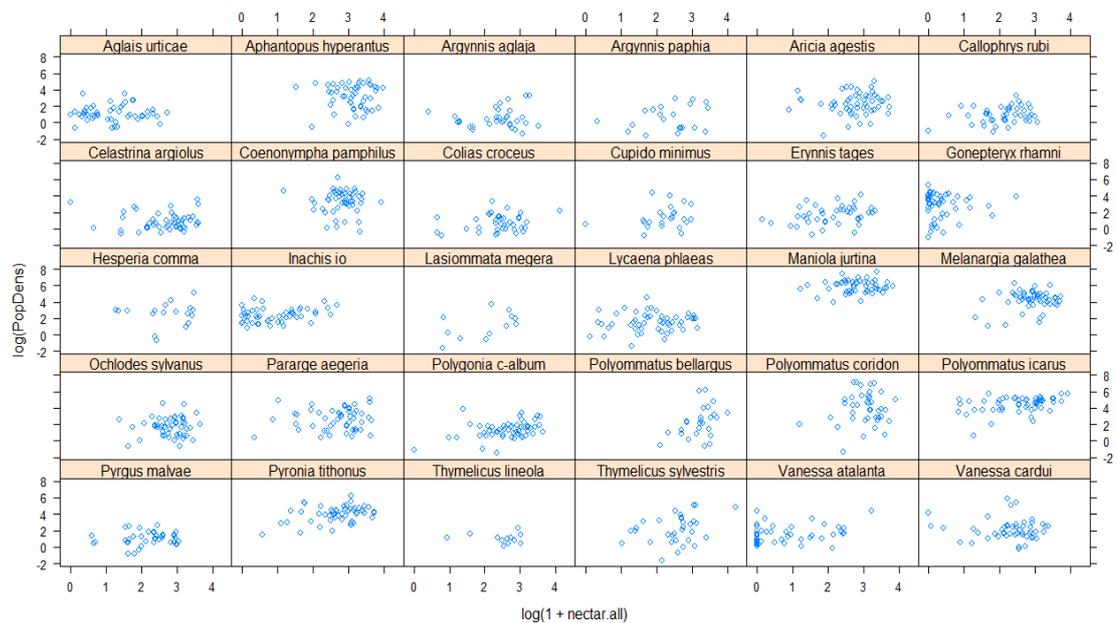
Table 3.4. Results of species-specific linear regressions between the logarithmic geometric mean of density for each of the 30 butterfly species recorded across 54 UKBMS sites during 2006 – 2010, against abundance of associated nectar plants for the same sites recorded during 2008 – 2009, in alphabetical order.

	Estimate	Std. Error	t value	Pr(> t)	Rsqr
<i>Aglais urticae</i>	0.000	0.191	-0.002	0.999	0.000
<i>Aphantopus hyperantus</i>	0.026	0.415	0.062	0.951	0.000
<i>Argynnis aglaja</i>	0.182	0.291	0.624	0.537	0.012
<i>Argynnis paphia</i>	0.430	0.412	1.044	0.310	0.054
<i>Aricia agestis</i>	0.146	0.282	0.516	0.608	0.005
<i>Callophrys rubi</i>	0.391	0.216	1.808	0.078	0.072
<i>Celastrina argiolus</i>	-0.024	0.189	-0.127	0.899	0.000
<i>Coenonympha pamphilus</i>	-0.096	0.440	-0.217	0.829	0.001
<i>Colias croceus</i>	0.256	0.235	1.089	0.283	0.031
<i>Cupido minimus</i>	0.479	0.430	1.114	0.277	0.053
<i>Erynnis tages</i>	0.441	0.211	2.089	0.043	0.098
<i>Gonepteryx rhamni</i>	0.006	0.419	0.015	0.988	0.000
<i>Hesperia comma</i>	0.169	0.488	0.346	0.734	0.007
<i>Inachis io</i>	0.300	0.151	1.987	0.053	0.076
<i>Lasiommata megera</i>	1.008	0.528	1.908	0.086	0.267
<i>Lycaena phlaeas</i>	0.152	0.197	0.771	0.444	0.012
<i>Maniola jurtina</i>	0.143	0.186	0.771	0.444	0.012
<i>Melanargia galathea</i>	0.426	0.298	1.431	0.159	0.039
<i>Ochlodes sylvanus</i>	0.137	0.347	0.396	0.694	0.003
<i>Pararge aegeria</i>	0.164	0.246	0.666	0.508	0.009
<i>Polygonia c-album</i>	0.553	0.186	2.971	0.005	0.148
<i>Polyommatus bellargus</i>	1.780	0.796	2.235	0.035	0.172
<i>Polyommatus coridon</i>	0.480	0.616	0.779	0.440	0.015
<i>Polyommatus icarus</i>	0.420	0.154	2.733	0.009	0.126
<i>Pyrgus malvae</i>	0.151	0.204	0.744	0.462	0.015
<i>Pyronia tithonus</i>	0.483	0.180	2.691	0.010	0.127
<i>Thymelicus lineola</i>	-0.076	0.297	-0.257	0.802	0.007
<i>Thymelicus sylvestris</i>	0.784	0.428	1.830	0.077	0.100
<i>Vanessa atalanta</i>	0.300	0.159	1.890	0.065	0.069
<i>Vanessa cardui</i>	-0.125	0.231	-0.539	0.593	0.006

The species-specific models show that the effect of hostplants range from -1.125 to 1.78 and R squared scores range from <0.001% to a maximum of 27% (Table 3.4). Most of the relationships between hostplants and butterfly abundance are positive (Figure 3.4).

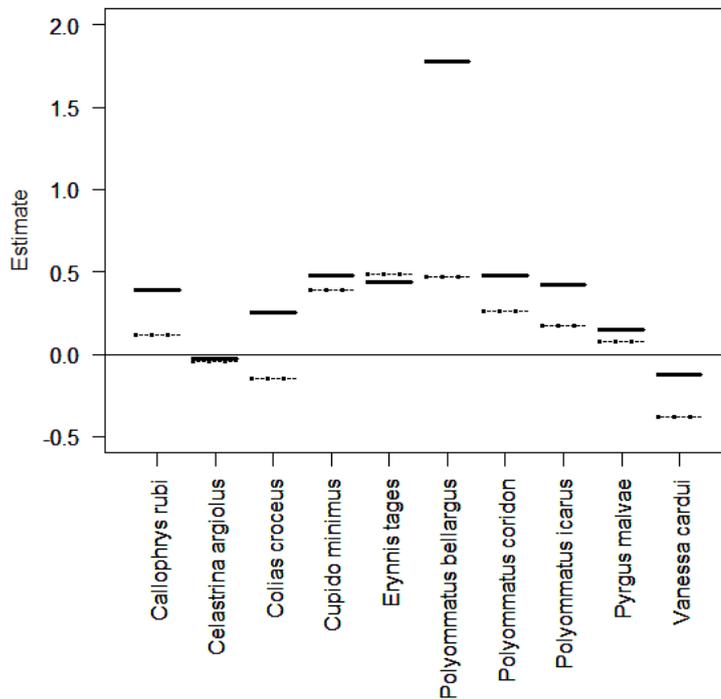
Of the 30 species, only five have a negative correlation (none of which are significant), with the remaining 24 species all showing a positive relationship (five of which are significant). This suggests that nectar availability may be important to several species, and for the three species showing strongest relationships (*Pyronia tithonus*, *Polyommatus icarus* and *Polygonia c-album*) nectar plant abundance explains around 13% of the variation in adult butterfly density across sites.

Figure 3.4. A scatterplot of the logarithmic geometric mean of density for each of the 30 butterfly species recorded across 54 UKBMS sites during 2006 – 2010, against abundance of associated nectar plants for the same sites recorded during 2008 – 2009.



Ten butterfly species also use their associated hostplant as a nectar source. Therefore, to ensure nectar was tested as an independent effect, the hostplants used by these ten species were removed from their list of associated nectar sources and the models re-run (Figure 3.5 & Table 3.5).

Figure 3.5. Estimates for the ten butterfly species affected by the removal of hostplants from nectar abundance. Original estimate with hostplants included (solid lines), adjusted estimate without hostplants (dashed lines), species listed in alphabetical order.



Only one species has a higher estimate without hostplants (*Erynnis tages*), one species changes from a positive to negative estimate (*Colias croceus*), and *Polyommatus bellargus* shows a considerable reduction in significance. See Table 3.5 for importance of hostplants as nectar sources.

Table 3.5. Original estimate, adjusted estimate with hostplants removed from associated nectar sources, the difference between the two and % of nectar records that are hostplants obtained from Dennis (2010). Numbers in brackets are number of nectar feeding records, species listed in alphabetical order.

Species	Original Estimate	Estimate without hostplants	Difference	% Nectar records that are hostplants
Callophrys rubi	0.391	0.113	0.278	6.4 (46)
Celastrina argiolus	-0.024	-0.044	0.020	22.1 (269)
Colias croceus	0.256	-0.152	0.408	12.7 (82)
Cupido minimus	0.479	0.390	0.089	40 (15)
Erynnis tages	0.441	0.487	-0.045	21.2 (33)
Polyommatus bellargus	1.780	0.466	1.314	8.7 (25)
Polyommatus coridon	0.480	0.259	0.221	6.9 (33)
Polyommatus icarus	0.420	0.174	0.246	27.3 (344)
Pyrgus malvae	0.151	0.077	0.074	12.1 (33)
Vanessa cardui	-0.125	-0.385	0.260	14.9 (484)

3. Effect of species traits and site characteristics

Particular species, or species groups, are more sensitive to changes in host and nectar plant abundance depending on life history, niche traits or site characteristics (H2 and H3) – see Table 3.6.

Table 3.6. Results of separate linear mixed models between the logarithmic geometric mean of density for all 30 butterfly species recorded across 54 UKBMS sites during 2006 – 2010, against site and species traits as an i) interaction with host plants and ii) interaction with nectar. The results in the table are therefore obtained from 16 separate models (8 for both nectar and host plants) and the results of the main effect have been omitted.

Independent variable	i) Interaction with host plants				ii) Interaction with nectar plants			
	Estimate	Std. Error	t value	p value	Estimate	Std. Error	t value	p value
Diet breadth								
Larval niche breadth	-0.068	0.025	-2.715	0.007	-0.022	0.029	-0.766	0.444
Adult niche breadth	-0.010	0.003	-3.053	0.002	-0.003	0.004	-0.733	0.463
Life history traits								
Habitat specialist	0.475	0.155	3.073	0.004	0.248	0.154	1.608	0.258
Mobility	-0.336	0.073	-4.574	<0.001	-0.179	0.092	-1.945	0.052
Population structure	-0.047	0.049	-0.959	0.337	-0.055	0.061	-0.915	0.360
Larval duration	0.045	0.069	0.652	0.514	0.107	0.089	1.206	0.228
Site traits								
Turf height	0.032	0.039	0.808	0.419	-0.066	0.050	-1.317	0.188
Aspect	-0.164	0.069	-2.395	0.017	-0.082	0.077	-1.066	0.286

i. Life History Traits

Larval niche breadth (Number of core host plants)

There is a weak but significant negative interaction effect between larval niche breadth and abundance ($b=-0.068$, $se=0.025$, $t=-2.715$, $p<0.01$), so species which utilise fewer hostplants (monophagous) tend to be more sensitive to changes in hostplant abundance than species which can utilise a wider number of hostplants - which is as predicted. The butterfly – hostplant relationship is almost twice as steep for species which use a single hostplant ($b=0.577$) compared to species which use four or more hostplants ($b=0.373$). There is no significant interaction with nectar plants.

Adult niche breadth

There is no significant interaction between adult niche breadth and nectar abundance. However, interestingly, there is a weak significant negative interaction with hostplants ($b=-0.01$, $se=0.003$, $t=-3.053$, $p<0.005$), so species which utilise fewer species of nectar plant are likely to be more sensitive to changes in host plant abundance.

Habitat Specialist

There is a strong, significant positive interaction between degree of habitat specialism and hostplant abundance ($b=0.475$, $se=0.155$, $t=3.073$, $p<0.005$). Species which are restricted to more specialist habitats are therefore considerably more sensitive to changes in hostplant abundance – which is as predicted. Indeed, the butterfly – hostplant relationship becomes weakly negative for wider countryside species ($b=-0.005$). There is no significant interaction with nectar plants.

Mobility

There is also a strong significant negative interaction between mobility and hostplant abundance ($b=-0.336$, $se=0.073$, $t=4.574$, $p<0.001$), and species which are less dispersive are more than twice as sensitive to changes in the amount of hostplant. For sedentary species, the butterfly – hostplant relationship is 1.15, yet only 0.48 for more dispersive species. There is also a negative interaction with nectar plants, but this relationship is not significant.

Population structure

There are no significant interaction effects between population structure and either host or nectar plants.

Larval duration

There are no significant interaction effects between larval duration and either host or nectar plants.

ii. Site Characteristics

Turf height

There are no significant interactions between turf height and either host or nectar plants.

Aspect

There is a significant negative interaction between aspect and host plant abundance ($b=-0.164$, $se=0.069$, $t=-2.395$, $p<0.05$), suggesting that butterfly populations on sites with cooler aspects are more than twice as sensitive to changes in host plant abundance, as predicted. For north-facing sites (aspect=-1), the butterfly-hostplant relationship approaches 0.57 and a mere 0.25 for south facing slopes (aspect=+1). The direction of the interaction is the same with amount of nectar plants, but the result is not significant.

Discussion

Research at this regional scale allows us to understand the broader implications of the importance of consumables resources both within and between butterfly populations. Additionally, including both species life traits and site characteristics within this study allows us to assess which species or sites may respond more positively to conservation management.

The results showed that both the abundance of hostplant and nectar were significantly related to the size of butterfly populations across sites. The amount of hostplant was generally a stronger predictor than nectar, but several species were correlated more strongly with nectar than hostplants. Furthermore, species which possessed 'specialist' traits of narrower dietary niche breadth, habitat specialism and lower mobility were more sensitive to changes in the amount of resource, as were individuals which occupied cooler sites.

This suggests that generally, land managers should give more priority to managing for host, rather than nectar plants to maximise butterfly abundance within sites. It also suggests that in general, specialist species should show the strongest response to increases in resources, which could be of benefit to conservation as they are often the rarest, most rapidly declining species.

The relationship between host and nectar plants

There is a significant positive correlation between host and nectar plants, although the explanatory power of relationship is low ($R^2 = 0.11$). The fact that there is a weak correlation is expected, as many of the sites surveyed in this study are high quality well managed habitats with high floristic diversity. Therefore, quadrats comprising a large number of plant species are likely to contain high numbers of both host and nectar plants. However, the correlation between these two key variables is weak enough not to undermine their independence as separate predictors of butterfly population density.

The importance of host and nectar plants in determining abundance

The fact that food plant abundance is significantly related to butterfly density suggests a similarity to other species groups, for example, mammals (Carbone & Gittleman 2002) and birds (Lack 1954) in that the amount of food available within sites is indeed a limiting resource. Both hostplants and nectar are highly significant, although the regression coefficient and variance explained by host plants is considerably higher than nectar plants. This result is expected, given that hostplants are essential for larval survival, while nectar can prolong adult longevity increasing the chances of mate location and egg laying duration (Boggs 1987; Jervis & Boggs 2005; Morris *et al.* 2008), however, it has little impact on fecundity.

The positive relationship between adult butterfly abundance and host plants is in accordance with earlier research conducted on British butterflies within North Wales (Cowley *et al.* 2001b). Within the species specific models, although only 10 species show significant relationships with hostplants, a total of 24 species show a positive relationship suggesting a general underlying trend. It is also noteworthy that two of the most significantly positive species (*Gonepteryx rhamni* and *Cupido minimus*) have shown strong dependence on host plants in previous studies (Gutierrez & Thomas 2000; Krauss *et al.* 2004b). The most sensitive species (to their hostplants) are not restricted to a single family, although interestingly six out of the ten most significant species are lycaenids. This can probably be explained by two of the key hostplants used by these species (*Helianthemum nummularium* and *Hippocrepis comosa*) being restricted to regions where the mean July isotherm exceeds 20 degrees centigrade (Pigott *et al.* 1992), and furthermore, the limit to the distribution of *Hippocrepis comosa* is associated with high summer temperatures essential for its reproduction (Hennenberg & Bruelheide 2003). Therefore, it may be that the local density and distribution of resources is generating the same pattern in the consumer (Hanski *et al.* 1993; Gaston 1994). Additionally,

this may be because many lycaenids are also reliant on ants for their survival (Thomas & Lewington 2010), and so the presence of the associated hostplant within chalk grassland may also coincide with high ant abundances, particularly of the genus *Lasius* and *Myrmica*. Thus lycaenid butterfly abundance is more likely to reflect hostplant abundance, although the fact that there are also positive relationships for species whose larvae feed on nettles (*Aglais urticae*), shrubs (*Gonepteryx rhamni*) and grasses (*Coenonympha pamphilus*) suggests a more general phenomenon.

Therefore, despite many species having extremely precise ecological requirements (e.g. Thomas *et al.* 2001) our results suggest that the quantity of host foodplant (as well as quality) is an important determinant of butterfly abundance for species with widely differing requirements, and across a large number of sites. Principally, this suggests that for conservation it is important to maximise hostplant abundance within sites, and furthermore, this evidence is based on a large sample size along two axis of variation – both between and within species. The sites included within this study are of varying quality, and so there is a large range in values for both butterfly population density and hostplant abundance. Indeed, it is possible that these results contrast with more local studies because the majority of those studies only examined a small range of variation in hostplant availability. However, it is also possible that the strength of relationship may be because many of the sites within this study were composed mainly of high quality well managed habitats (several of which are reserves managed specifically for butterflies), and therefore a high percentage of hostplants are likely to be in suitable condition. Certainly, other studies in poorer quality habitats, for example farmland (Smart *et al.* 2000) have shown no correlation of butterfly abundance with amount of host plant. However, an underlying assumption of most previous macroecological studies (and this one) is that hostplant cover equates to availability, with little or no consideration given to the suitability of the hostplant. Therefore, an unanswered question remains the importance of habitat quality (as demonstrated in Chapters 1 and 2) across broader scales. Although some indication of the importance of the quality of habitat is suggested in this study by examining site conditions (e.g. aspect and turf height), other habitat quality parameters (e.g. microclimate) should be incorporated in future studies to further understand the robustness of the relationship between butterfly and hostplant abundance.

It is certainly interesting to note that many of the species showing a negative or weak correlation with hostplants feed on grasses (e.g *Maniola jurtina* and *Pyronia tithonus*). Most of these grass feeding butterflies occupy mid-successional habitats and occur in wider countryside habitats that are rarely the target of conservation management within reserves (Thomas & Lewington 2010). Thus, grassland plant species will occur within some of the tightly grazed well managed chalk grassland (but will be too short to utilise) as well as within darker scrubby areas or rides (the majority of which will be too long and dark to utilise). This would also explain why some of the chalk speciality species show some of the strongest positive relationships, in that many of the study sites are managed for their benefit, for example *Cupido minimus*, *Aricia agestis*, *Polyommatus bellargus*, *Pyrgus malvae* and *Polyommatus coridon*.

Although less important than hostplants, the abundance of nectar sources is also significantly related to the size of butterfly populations across sites. However, within species specific models, only 5 species show a significant relationship with nectar plants; *Erynnis tages*, *Polyommatus bellargus*, *Pyronia tithonus*, *Polyommatus icarus* and *Polygonia c-album*, although 26 species show a positive relationship suggesting a more general underlying pattern. However, after removing hostplants from associated nectar sources this number drops to just three significant species *Erynnis tages*, *Pyronia tithonus* and *Polygonia c-album*. Therefore, for the other two significant species, we cannot rule out the possibility that the correlation with nectar is an artefact of high hostplant abundance. For example, *Polyommatus bellargus* uses *Hippocrepis comosa* (the core hostplant) as a nectar source, but it is not an important one forming only 8% of feeding records (Table 3.5). Once this hostplant is excluded as an associated nectar source, *Polyommatus bellargus* drops from 4th most significant species to 17th. However, the possibility remains that given the small number of feeding records (25 records – see Table 3.5), the importance of *Hippocrepis comosa* as a nectar source may have been understated. This is plausible, but unlikely, because in reality the number of nectar sources will tend to increase with number of nectar feeding records (Tudor *et al.* 2004), rather than a dramatic increase in usage of a particular species which is likely to be encountered regularly while searching for oviposition and mate locations.

So, with hostplants removed, it appears that the amount of nectar available within sites for *Erynnis tages*, *Pyronia tithonus* and *Polygonia c-album* is important. This is interesting, especially as the latter two species also show two of the weakest relationships with hostplants.

The reason that species are expected to show stronger relationships with hostplants (than nectar) is primarily because within most sites, virgin females are normally discovered and mated within hours of emergence, laying some eggs late on the first day, but the majority on the second, and to a lesser extent third day of life (Cushman *et al.* 1994; Wahlberg 1995). Therefore, adult survival – which is probably prolonged by nectar – may be of limited benefit as reproduction and subsequent egg laying has usually been accomplished within the first few days of life. Furthermore, many authors also suggest that nutrients acquired during larval development are believed to be the primary determinant of longevity and fecundity in butterflies, as opposed to nectar (Labine 1968; Boggs 1987; Baylis & Pierce 1991; Hughes 2000). Despite this, it is apparent from this study that nectar can be of importance to some species, and concurs with the evidence suggesting that butterfly abundance is often found to be highest on sites which have both an ample supply of nectar and a high density of host plants (Fred *et al.* 2006; Bergman *et al.* 2008; Stasek *et al.* 2008). Furthermore, it remains plausible that as in hostplants, in this study nectar plant cover equates to availability, with little or no consideration given to its suitability. Therefore, grazing animals could reduce nectar availability while not reducing its percentage cover, and so the importance of nectar within sites which contain livestock (of which this study included many), may be underestimated.

Life history and niche traits

Of the nine traits included within the model, five show significant interactions with host plants and none show any significant interactions with nectar plants. The strength of these interactions again suggests that hostplants are more important predictors of population density than nectar plants. Although some of these traits are intercorrelated, the patterns that emerge give some insights into the ecological mechanisms linking resource availability with population abundance.

Larval niche breadth

There is a weak negative interaction between larval niche breadth and host plant abundance, which implies that species which can utilise several different species of host plant are less sensitive to changes in host plant abundance. This is as expected, as the more hostplants (or any resource) that a species can utilise then the greater potential there is for survival across a multitude of environmental conditions and sites (Brown 1984; Dennis 2010). However, more pertinently, this suggests that monophagous species are more sensitive to changes in

hostplant abundance. Therefore, it follows that by increasing abundance of an associated hostplant through management, it should be possible to increase population density of certain target species. This is important, given that the most rapidly declining species are often monophagous e.g many lycaenids and several nymphalids (Fox *et al.* 2011), and furthermore it should be easier to manage for one particular hostplant than a suite of plant species required by polyphagous species. Indeed, it may actually be considerably more difficult to manage sites for polyphagous species, given that their interaction with hostplants is weaker.

Adult niche breadth

There is no significant interaction between adult niche breadth and nectar plants. However, interestingly, there is a significant but weak negative interactive effect between adult niche breadth and host plants. This suggests that species which feed on a broad range of nectar plants are less sensitive to changes in host plants, or more specifically that species which are more restricted in host plant choice are more likely to be specialist adult feeders as well. Similar conclusions have been demonstrated for woodland butterflies by Tudor *et al.* (2004), which showed that specialism in flower use was also related to larval host range and biotope occupancy. Furthermore, many woodland nectar specialists were species of conservation concern, and results from this study would suggest that this is applicable to chalk grassland butterfly species as well. However, unlike Tudor, the evidence from this study would not advocate that management of chalk grassland sites should give as much emphasis to nectar sources as hostplants.

Habitat specialism

There is a strong, positive significant interactive relationship between habitat specialism and hostplants suggesting that more widely distributed species are less sensitive to changes in hostplants. Thus species restricted to more specialist habitats (e.g. chalk grassland) are more sensitive to changes in foodplants (within those sites) than species which can survive in more heterogeneous habitats. There are two possible reasons for this, first, the associated hostplants for these specialist species may also be restricted to these rarer habitats, and so it remains possible that the local density of resources can also dictate the population density of the consumer (Hanski *et al.* 1993). Secondly, the trait of habitat specialism may also be closely linked to other life history traits (Kearney & Porter 2009; Ockinger *et al.* 2010), for example, narrower dietary niche breadth or lower mobility, hence species grouped as habitat specialists may be sensitive to changes in hostplants because they possess multiple (or additional more important specialist traits) rather than solely because of their habitat preferences. However,

habitat specialism has such a strong interactive relationship with host plants that it is likely that it is a trait of paramount importance.

Mobility

Mobility is important for survival, as dispersal will determine the probability whether individuals will have the ability to move and locate individual plants or habitats. A species mobility is primarily driven by resource distributions, in particular, the resource aggregation, frequency and abundance (Dennis *et al.* 2003). There is a strong interaction with host plants suggesting that species with higher mobility are less sensitive to changes in host plant abundance. These results concur with previous studies (Cowley *et al.* 2001b; Komonen *et al.* 2004) and are expected – mobility can enhance a species potential to colonise new habitats and discover new host plants. Again, species with limited mobility may also possess other specialist traits (Betzholtz & Franzen 2011; Sekar 2011; Stevens *et al.* 2012), although the interaction with hostplants is strong enough to suggest that mobility as an independent trait is of paramount importance.

Population structure

There are no significant interactions between population structure and host and nectar plants, which is surprising as a result similar to mobility traits could have been expected. However, the definitions of population structure and mobility differ in that population structure is linked specifically to metapopulation structure definitions. Therefore, it remains possible that the weakness of interaction effects may be due to uncertainty as to the accuracy and contradictions of species assignment to 'open' or 'closed' populations, and the divisions therein, compared to the measurement of flight distances recorded by mobility. Although many British species are perceived to exist within classic metapopulations (Hanski & Thomas 1994), metapopulation structure can vary among landscapes (Singer & Thomas 1996), regions (Thomas & Harrison 1992) and fundamentally in reality metapopulation structures are not easily categorised (Harrison & Taylor 1997). Furthermore, many mark recapture studies have now shown that many species which were originally perceived to be sedentary are dispersing much further than previously thought (Baguette 2003), and so perhaps the boundaries between 'open' and 'closed' remain inconclusive. The advent of field based estimates of dispersal using genetic markers would help resolve this issue.

Larval duration

There was a weak positive interaction with both hostplants and nectar plants. However, neither of these results was significant, and so it is unlikely that the rate of resource consumption is an important factor in the relationship between butterfly population density and foodplant abundance.

Site Characteristics

Turf height

Turf height can be an important factor in determining the ground temperature which in turn can influence oviposition locations (Nature Conservancy 1986; Roy & Thomas 2003). Turf height shows a weak positive relationship as an interaction with host plants, and a weak negative interaction with nectar plants although neither result is significant. The general effect of turf height is probably weaker than predicted because of the nature of sampling sites using random quadrats; the turf height of a tightly grazed meadow would increase dramatically if one of the quadrats were located within scattered gorse bushes or nettle patches, and conversely, the turf height of scrubby areas could be reduced dramatically by randomly locating nettles or grassy clearings.

Aspect

Aspect is an important factor determining ground temperature (Bennie *et al.* 2008), which can be important for oviposition (Thomas & Lewington 2010). Aspect has a strong negative interaction with host plants. This suggests that populations inhabiting sites with cooler aspects (e.g. not a southerly) are considerably more sensitive to variation in hostplant abundance. This is predicted, as temperature is a key driver of whether a hostplant is within suitable condition (Thomas 1983a; Renwick & Chew 1994), and so more hostplants can be utilised within hotter aspects, thus changes in hostplant abundance are of less importance than to those species inhabiting cooler aspects. There is a similar, but insignificant effect with nectar plants but the underlying cause of the relationship is almost certainly the same - as species may restrict feeding to nectar plants of a certain temperature (Weiss *et al.* 1988; Comba *et al.* 1999), then nectar plant abundance will be less important to species inhabiting warmer sites.

Recommendations for Site Management

At local scales, intensive field studies of single species on a limited number of sites has shown that the strength of correlation between abundance of butterflies and their associated foodplants can vary tremendously (Thomas *et al.* 2011). We do not dispute the results from these studies, but suggest that the relationship between butterflies and food plants will vary depending on the species studied, their associated life history traits and often the environmental conditions of the site on which they were studied.

Based on the results from this study, we suggest that in general, management for specific hostplants can increase butterfly population abundance. More specifically, species which are monophagous, are restricted to more specialist habitats and have lower mobility are more sensitive to changes in hostplant abundance, and therefore increasing the amount of hostplant within sites should increase their population density. Many of the species which possess these life history traits are some of the rarest and rapidly declining species, for example the ten year population trend for *Polyommatus coridon* and *Aricia agestis* show declines of 26% and 38% respectively (Fox *et al.* 2011). However, their sensitivity towards changes in hostplant abundance would suggest that by targeting increasing abundance of their associated hostplant within sites through management, for example by planting 'plugs' of hostplants, could increase population levels. Additionally, on the evidence from this study, species which are polyphagous and are more mobile – wider countryside species – are more difficult to manage for as regards hostplant abundance. However, these species tend to be commoner, and so their conservation priority is not as high.

Furthermore, within sites, hostplant suitability can depend on temperature, and so we recommend focussing on areas where favourable aspects may ensure that a higher percentage of plants are likely to be within 'suitable condition'. Within the U.K., Warren (1993) demonstrated distinct aspect preferences for British butterflies, with most preferring south and south-west facing slopes because they are warmer. However, this does not mean to abandon management in areas deemed unsuitable, for even parts of sites which are less intensively grazed or with northern facing aspects can be valuable as refuges during poor weather (Dennis 2010), and can also contain nectar sources which are of importance to a number of species.

Due to the variation in sensitivity to the amount of hostplant both between and within species and across sites, it is challenging to produce a conservation panacea which could benefit all species. However, the current recommended management for most grassland sites would be

to create a mosaic of turf heights with small patches of scrub inter-dispersed between the grassland. There are several reasons why managing sites in this way remains important for conservation; a mixture of turf height creates suitable oviposition and nectaring locations for a broad range of species, so this is likely to maximise both species richness and population density within sites (Fred *et al.* 2006; Bergman *et al.* 2008; Stasek *et al.* 2008). Second, longer turf and scrubby areas will also provide shelter during inclement weather and furthermore, a more heterogeneous turf height, particularly on the hottest slopes, may compensate for extremes in temperature fluctuations which determine oviposition locations, especially with climate warming predicted to increase (IPCC 2007). However, it is also important to realise that some species which are more sensitive to changes in hostplant abundance can be targeted by increasing hostplant abundance within a site, and this knowledge could be especially beneficial in conserving some of the most rapidly declining butterfly species.

Conclusions

This is the first large scale study, to our knowledge, which has correlated abundance for hundreds of butterfly populations against percentage cover of foodplants on a large number of sites. We can now be confident that consumable resources are a limitation on population size, both within and between species. This study has also clarified the relative importance of differing food plants in explaining butterfly abundance at regional scales, which can also be influenced by species traits and site characteristics. On the basis of these results, we can now recommend broad scale conservation measures to increase butterfly abundance, as well as suggesting on which species and sites may respond most positively to management.

We conclude that both the amount of host and nectar plants are important determinants of butterfly population density. However, we also suggest that in this study hostplants are considerably more important than nectar plants, with a higher number of significant species, and higher R squared values than nectar plants. Nonetheless, nectar does appear to be important, and with hostplants removed from associated nectar sources it still explains considerable variation in abundance for several species.

We therefore suggest that despite many species having precise oviposition requirements, and restrict host plant choice to a subset of plants in 'suitable condition,' larger amounts of hostplants do support larger populations. However, the significance of this relationship may in part be because our choice of study sites contains many high quality habitats including reserves managed specifically for chalk specialist butterflies.

Several life history and niche traits show interactive effects with host plants, but not with nectar plants, again suggesting host plants are more important in determining abundance. Both broader dietary and habitat requirements and higher mobility allow species a greater flexibility for survival across environmental conditions and sites, reducing their sensitivity to changes in foodplant abundance. Therefore, the results from this study suggest that it is now possible to make informed decisions regarding management for specific butterflies, as sensitivity towards changes in host and nectar plant abundance is likely to be predictable based on species traits. This could have important ramifications for conservation, as many of the most sensitive species are also some of the rarest, and so are highly likely to respond positively to increases in hostplant abundance. However, it is also highly likely that temperature is a key factor in determining 'suitable condition' of hostplants, as species which inhabit sites of predominantly southerly aspect are significantly less sensitive to changes in hostplant abundance.

Generally therefore, we suggest that land managers should place considerably more emphasis on managing sites for butterfly host plants than for their associated nectar sources. We also advise that achieving a suitable condition of hostplants is a priority, although maximising spatial extent across different aspects will be beneficial as variations in location and microclimate of plants are likely to buffer against climatic fluctuations which influence oviposition choice. However, nectar plants should not be entirely ignored, as many studies suggest that abundance is higher on sites which have an ample supply of nectar and a high density of host plants, and evidence from this study would suggest that nectar is important for several species.

General Discussion

This thesis addressed several gaps in our knowledge regarding the importance of resources and other abiotic factors in determining butterfly abundance at multiple scales. In particular, using data collected on the Glanville fritillary on the Isle of Wight and population abundance data extracted from the UKBMS, I assessed the factors which; i) determine abundance of a single species at a local scale over time ii) determine abundance of a single species throughout space at the landscape scale and iii) explored the determinants of inter and intra specific abundance at a regional scale. I also reassessed conservation priorities while accounting for differences in species, sites and the likelihood of continued climate warming.

Summary of key findings

In Chapter 1, I attempted to explain the observed distribution of Glanville fritillary larvae described by Thomas *et al* (2001) which show a clear preference for earlier successional stages and smaller hostplants, and explained the mechanisms behind fluctuations in population levels over a 14 year timescale, on a small (<1km²), isolated site.

I demonstrated that hostplants selected for oviposition by female Glanville fritillaries were considerably warmer than ambient air temperature. I also established that ground temperatures beneath successional stages of grassland decreased with increasing turf height. Taken together, this suggested that temperature was of primary importance in determining oviposition locations, hence providing a mechanism to explain the preference for earlier successional stages as shown by Thomas *et al* (2001). Furthermore, this was reinforced by demonstrating that abundance was significantly higher both in plots which contained higher percentages of early successional habitats, and following years when the temperature during the flight period (June) was warmer.

In Chapter 2, I assessed which factors were most important in determining abundance of a single species throughout space at the landscape scale. I used a measure of habitat quality as a surrogate of suitable resource availability, and included the metapopulation factors of area and isolation as well as ambient air temperature as predictors of abundance. I also tested temperature as an interactive effect against the other parameters.

The results showed that all predictors were significant, but area was most important, followed by habitat quality, isolation and temperature. Thus, two of the parameters important at local scales are also important at the landscape scale, although the inclusion of many more sites has

reduced the importance of temperature, probably because inter-annual variation only accounts for a small amount of variation in abundance (9%), the majority of which is attributable to variation among patches (50%). This suggests that metapopulation factors do have key role in determining species abundance at the landscape scale (Hanski 1998b), but that habitat quality is also an essential component which should not be overlooked (Thomas *et al.* 2001). Only habitat quality showed a significant negative interaction with temperature, suggesting that in warmer years the precise definition of 'suitable' habitat became weaker, probably because thermal constraints on oviposition locations are not as acute.

Both of these chapters highlight the importance of the 'condition' (in this case microclimate) of the hostplant, although the geometric properties of habitat patches are also important.

The Glanville fritillary is therefore among the 16% of British butterfly species that inhabit unnatural early successional stages in the U.K. because they are warmer, and laying eggs on warmer plants maximises the probability of successful larval development within restricted seasonal temperature constraints (Thomas 1993).

In Chapter 3 I used UKBMS population data for 30 butterfly species from 54 sites across southeast England, combined with site specific estimates of resource availability (host and nectar plant abundance) to explain the variation in population abundance both between and within species at a regional scale. I also examined species traits and site characteristics to explain species' sensitivity to changes in host and nectar plant abundance.

The results showed that both the abundance of hostplant and nectar were significantly related to the size of butterfly populations across sites. The amount of hostplant was generally a stronger predictor than nectar, but several species' abundance was correlated more strongly with nectar than hostplants. In addition, species which possessed 'specialist' traits of narrower dietary niche breadth, habitat specialism and lower mobility were more sensitive to changes in the amount of resource, as were populations on cooler sites.

This suggests that generally, land managers should give more priority to managing for hostplants of key butterfly species, over providing nectar. It also suggests that specialist species should respond well to managed increases in their resource base, which could be of benefit to conservation as they are often the rarest, most rapidly declining species (Fox *et al.* 2011).

Taken together, the results of this thesis show that specialised butterfly species are probably limited at small scales by the availability of hostplants in suitable condition, but at large scales by dispersal limitation and thermal tolerance. They also demonstrate how sensitive butterflies can be to changes to both the amount of suitable habitat and temperature, as well as landscape characteristics, and emphasise how important management is to maximise butterfly population abundance.

Therefore, my results are broadly congruent with the 'resource limitation hypothesis' in that finite amounts of resources can restrict population growth over time and throughout space. Clarifying the importance of resources at multiple scales can therefore further our understanding as to why butterfly populations fluctuate both within and across sites, thereby facilitating a more effective conservation strategy.

Study limitations

While the research presented in this thesis advances our knowledge of the importance of resources in determining abundance, it has several limitations.

The determinants of abundance are often complex and interacting (McGill 2006). In this study, I focussed primarily on the importance of consumable resources (host and nectar plants), also suggesting that their 'condition' was often as important as their abundance. However, no consideration was given to the importance of utility resources, for example thermoregulation, pupation and mate location sites (Dennis *et al.* 2003), nor the many other factors which could affect a species abundance, including predators, parasitoids and pathogens (Lei *et al.* 1997; Laine 2004; Harvey *et al.* 2005; van Nouhuys & Hanski 2005), or weather (apart from temperature), all of which can undoubtedly influence butterfly population abundance at multiple scales.

For the Glanville fritillary research I considered each larval web to constitute a population unit of one, and did not account for variation in numbers of larvae within each web. Theoretically, therefore, it is possible that smaller numbers of webs could produce more individuals than a slightly larger number of webs, although previous research by Simcox and Thomas (Simcox & Thomas 1979) did suggest that numbers of larvae within webs were relatively consistent. Furthermore, I did not account for bias in web counts between habitats, in that webs could have been more conspicuous within earlier successional stages. However, when possible, counts were conducted early in the morning when dew was still present, or after light rain which increased web visibility due to water droplets covering the silk, in order to minimise this

error. Additionally, many of the sites containing more heterogeneous terrain were surveyed twice, both at the start and end of the survey period to ensure that late emerging individuals were accounted for.

I also made no consideration of recording bias within the UKBMS dataset, so I assumed that each species had as much chance of being recorded as another, despite research suggesting that wing colour determines detectability (Dennis *et al.* 2006a). I also did not account for variation in transect walker ability at butterfly identification, eyesight or walking speed, all of which could affect both the number and species of butterflies recorded within a set transect route. However, generally, the UKBMS method for monitoring butterflies is well described, extensively tested and scientifically sound (Pollard 1977; Pollard & Yates 1993; Gross *et al.* 2007; Isaac *et al.* 2011a). In other words, the error in abundances estimated by the UKBMS is small in comparison with the total variation in abundance that exists.

Finally, research on the significance of resources at multiple scales has both benefits and limitations in scope for conservation. For example, results from broader scale studies can highlight general patterns between resources and butterfly populations, but it is difficult to assess the importance of resource condition (e.g. is the hostplant in a suitable microhabitat?). Likewise, the results from more local studies could highlight the importance of resource condition on a specific species at a particular site, yet this specific knowledge could be of limited value in advocating general management regimes for increasing abundance of multiple species across regions. Finally, the factors which determine abundance at all spatial scales are complex and interacting, and resources are just one (albeit important) component. Therefore, conservation measures based purely on resource availability are unlikely to be definitive, and I have tried to be explicit in the limitations of conservation recommendations advocated on the evidence from these studies.

Conclusions

Understanding abundance is essential for assessing the potential impact of environmental change and is crucial for conservation (McGill 2006).

The importance of resources within landscape and macroecological studies has been overlooked in the literature, probably because of the difficulty in measuring resource availability over large areas (Gaston *et al.* 2004; Paivinen *et al.* 2005). Results from my Chapter 3, in which I used hostplant abundance as a surrogate for resource availability, demonstrate that resources are equally important in determining abundance over large scales (including

across species) as over small scales. While this would appear unsurprising (Dennis 2010), this suggests that priority should be given to increase resource abundance within sites, although particular attention should be given to their 'condition'. The importance of resource condition varies between species (niche breadth) and site characteristics, and so the creation or maintenance of heterogeneous habitats throughout the landscape would increase the likelihood of providing resources in suitable condition for many species.

In addition, much of the autecological research conducted on (mostly 'specialist') butterflies at local scales during the 1980's highlighted the importance of temperature of local microclimates in determining population abundance, because of the constriction of the larval niche (Thomas 1983b, a; Thomas *et al.* 1986). In this study, the importance of temperature is evident at all scales; it influences the suitability of the host foodplant at local scales and thereby restricts oviposition to earlier successional stages, and the availability of warmer habitats also determines abundance at the landscape scale. At regional scales, species which inhabit cooler sites are also likely to be more sensitive to changes in resource availability. Therefore, the importance of managing habitats to create thermally diverse environments cannot be understated, particularly in more northerly altitudes where temperature constraints are more acute.

Disregard for both the importance of resource condition and temperature can also potentially explain why during a period of rising global temperatures (IPCC 2007), insects have declined at faster rates than homeothermic species (Thomas & Morris 1994). The inappropriate or lack of management within sites is certainly a contributory factor (Warren *et al.* 2001; Haslett 2008), and has reduced the availability of sufficiently warm habitats (and particularly warm microclimates within them) which are necessary for provide suitable resources which facilitate successful larval development (Thomas 1995c). Current losses suggest that the natural world is experiencing the sixth major extinction event in its history (Thomas *et al.* 2004), and we ignore these declines at our peril.

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