The habitat preferences and phenology of a generalist butterfly species, Melanargia galathea (marbled white), at multiple spatial and temporal scales, within the British Isles

BETHAN JANE HINDLE

How to cite:

HINDLE, BETHAN JANE (2014) The habitat preferences and phenology of a generalist butterfly species, Melanargia galathea (marbled white), at multiple spatial and temporal scales, within the British Isles. Masters thesis, Durham University.

The habitat preferences and phenology of a generalist butterfly species, *Melanargia galathea* (marbled white), at multiple spatial and temporal scales, within the British Isles

Bethan Jane Hindle

Master of Science by Research

School of Biological and Biomedical Sciences

Durham University

2014

Abstract

The climate is undergoing unprecedented rates of change, altering species' abundances, phenologies and distributions and providing a huge challenge to conservation biology. I look at the distribution of a generalist British butterfly, *Melanargia galathea*, at multiple temporal and spatial scales, to provide detailed knowledge on this species' ecology useful for its conservation under a changing climate.

At a broad spatial scale I estimated demographic parameters for six generalist British butterflies. Carrying capacities differed between occupied habitats, with estimates varying from 7 (*P. c-album*; heathland/moorland) to 279 (*P. tithonus*; neutral grassland) butterflies per hectare per year. Average intrinsic growth rates in newly colonised sites varied from 0.26 (*P. c-album*) to 0.56 (*P. tithonus*). I suggest that these differences should be incorporated into species distribution models to increase the accuracy of predictions of future ranges.

Phenological asynchrony may occur when interacting species differ in the rate at which they respond to climate change. I show that some *M.galathea* individuals may be emerging before a key nectar source, *Centaurea scabiosa* is available. However, topographical diversity lengthened the flowering period of two key nectar species by up to 14 days and could therefore decrease the likelihood of phenological asynchrony.

The diverse microclimates provided by topographically heterogeneous sites may also affect *M.galathea* behaviour. Using scan samples and point counts I show that the abundance and behaviour of *M.galathea* differs between microhabitats, with a mean five minute point count of 0.18 butterflies in flat sheltered areas compared with 1.32 in flat exposed areas.

Effective monitoring methods are vital to accurately assess the success of conservation strategies and to estimate demographic parameters. I compared estimates of emergence and population sizes obtained from transect data and mark release recapture data and suggest that an inability to sex individuals during transects could cause bias.

Contents

List of Figures

Chapter 2 **Page**

Chapter 3

Chapter 4

Chapter 5

List of Tables

Chapter 2 **Page**

Chapter 3

Chapter 4

Chapter 5

Abbreviations

AIC	Akaike’s Information Criterion
ANOVA	Analysis of variance
FE	Flat exposed
FS	Flat sheltered
GLM	Generalised Linear Model
IUCN	International Union for the Conservation of Nature
MRR	Mark Release Recapture
NE	North East
S	South
SE	South East
SW	South West
UK	United Kingdom
UKBMS	United Kingdom Butterfly Monitoring Scheme

Statement of copyright

Acknowledgements

Firstly I would like to thank my primary supervisor Steve Willis for his help and support over the past year. I’d also like to thank Shane Richards, my secondary supervisor for his guidance and statistical expertise.

I’d also like to thank my lab group for their support. Particular thanks must go to those that helped with my fieldwork that is Alke, Amy, Hagen, Jamie, Martin, Sam, Tom and my mum. In addition I’d like to thank Chantelle Kerr for the use of her fieldwork data and George Palmer for her help and patience this year.

I’d also like to thank Durham City Council for allowing me to carry out my research at their site, with particular thanks to the Countryside Ranger, Gary Whitton.

Data were supplied by the UK Butterfly Monitoring Scheme (UKBMS) and Yorkshire Wildlife Trust. The UKBMS is operated by the Centre for Ecology & Hydrology and Butterfly Conservation and funded by a multi-agency consortium including the Countryside Council for Wales, Defra, the Joint Nature Conservation Committee, Forestry Commission, Natural England, the Natural Environment Research Council, and Scottish Natural Heritage. The UKBMS is indebted to all volunteers who contribute data to the scheme.

Funding was provided by the Grevillea Trust.

Chapter 1

Conserving British butterflies under climate change: range shifts and phenological changes

1.1 Introduction

The scale of recent biodiversity loss has led to suggestions that the planet is on the edge of a sixth mass extinction event (Thomas et al., 2004b, Wake and Vredenburg, 2008, Barnosky et al., 2011), with recent extinction rates estimated to be between 100 and 1000 times that of pre-human rates (Pimm et al., 1995). According to the International Union for Conservation of Nature (IUCN) criteria 10-50% of well studied higher taxonomic groups are under threat of extinction (Millennium Ecosystem Assessment, 2005). There are numerous causes of biodiversity loss, including habitat loss and degradation, pollution, unsustainable harvesting and climate change (Millennium Ecosystem Assessment, 2005).

Rapid warming has occurred in the 20th century, with an estimated increase in the average global land surface temperature of 0.19-0.32°C decade^{-1} from 1979 (Hansen et al., 2001, Smith and Reynolds, 2005, Brohan et al., 2006) and simulations suggesting that mean global temperatures could rise by up to 6°C by the end of the century (IPCC, 2007). Whilst changes of a similar magnitude have been experienced in the past, the rate of change is unprecedented; warming of 4-7°C between the glacial and interglacial periods in the past occurred over approximately 5,000 years (IPCC, 2007). Regionally specific changes in precipitation are also predicted with, for example, annual precipitation levels expected to increase in northern Europe and decrease in the south (IPCC, 2007).

With the impacts of 20th century climate change already apparent for many taxa (Walther et al., 2002, Parmesan and Yohe, 2003, Root et al., 2003), and the unprecedented rates of change predicted, climate change is expected to be one of the key drivers of changes in biodiversity this century (Sala et al., 2000, Thomas et al., 2004a, Maclean and Wilson, 2011). The rate of change is expected to constrain the ability of many species to respond adequately to avoid extinction (Thomas et al., 2004a). Ecological responses will also be affected by the predicted increase in the frequency of extreme weather events (Easterling et al., 2000, Parmesan et al., 2000), which may also increase extinction risks (Andrello et al., 2012). Active conservation will be necessary to prevent the wide scale loss of biodiversity and ecosystem functioning (Millennium Ecosystem Assessment, 2005, Rands et al., 2010).

The funds available for conservation are limited however, increasing the pressure for the available money to be used efficiently and effectively, using evidence based methods

(Thomas et al., 2011). A lack of knowledge of the ecology of species can often act as a barrier to the design of appropriate conservation strategies (New et al., 1995, Thomas et al., 2009). In order to effectively conserve species under climate change it is necessary to understand their habitat and resource requirements and their biotic interactions (Thomas et al., 2009). It is also necessary to have effective population monitoring methods to be able to assess the risk of extinction and the success of conservation strategies (Sutherland et al., 2010).

1.2 The use of butterflies as indicators

Many species of butterfly are declining in Britain (Fox et al., 2011b) and across Europe (van Swaay et al., 2006, van Swaay et al., 2011). In Britain 37% of species are listed as either regionally extinct or threatened (IUCN critically endangered, endangered or vulnerable; Fox et al., 2011b). A lack of understanding of the ecology of species has hindered the conservation of British butterflies, such as *Maculinea arion* (large blue), in the past (Thomas, 1980, Thomas et al., 2009), suggesting that an increased understanding of the ecology of this taxa may be crucial in preventing further declines.

Due to constraints in time, funds and expertise it is not possible however to study all species in such detail, especially given that many species remain unknown to science (Mora et al., 2011). This has necessitated the development of indicator taxa, which are thought to be representative of a wider taxon or community (Brown and Freitas, 2000, Brereton et al., 2011). Insects are a highly diverse class, with most estimates suggesting global richness of 5-10 million species (Stork, 1988, Stork, 1993, Odegaard, 2000). Despite this, and the important role played by insects in many ecosystems, they are notoriously understudied, with extinction risks often underestimated due to a lack of data (McKinney, 1999, Thomas et al., 2004b). Furthermore there is evidence that recent extinction rates in invertebrates have been higher than those in other taxa (Thomas et al., 1994, Thomas et al., 2004b). This increases the necessity of understanding the ecology of insects in order to predict how these species will respond to climate change and the potential wider effects of these responses on ecological communities.

Butterflies have been widely used as an indicator group for insects (e.g. Thomas, 2005), as, partly due to their charismatic appearance, they have been studied extensively. They are particularly well recorded in the United Kingdom (UK), with abundance data from the UK Butterfly Monitoring Scheme (UKBMS) available from 1976. Despite some criticism of the use of butterflies as indicators for other insects (Hambler and Speight, 2004, Fleishman and Murphy, 2009), they are often considered reasonably representative (Kerr et al., 2000, Thomas and Clarke, 2004, Thomas, 2005) and, perhaps more importantly, are often the only group for which sufficient data are available.

Butterflies are also used as indicators of wider ecological change, including by the UK government (Brown and Freitas, 2000, Brereton et al., 2011). As poikilotherms, they are expected to be highly affected by small changes in climate (Pollard, 1988). Their high levels of fecundity and short generation times mean that the effects of change are more likely over short time periods than for longer lived species. Responses of British butterflies to climate change have been more pronounced than other taxonomic groups such as birds; such changes seen in butterflies may be indicative of future responses in other taxa (Thomas et al., 2004b, Devictor et al., 2012).

1.3 The effects of climate and habitat on the abundance and distribution of British butterflies

The warming climate is predicted to cause increases in abundance for most British butterfly species, with strong correlations between summer temperatures and both abundance (Pollard, 1988, Roy et al., 2001) and diversity (Turner et al., 1987). However, it appears that recent temperature increases have not been sufficient for many species to overcome the negative effects of habitat fragmentation and degradation (Warren et al., 2001). Whilst there has been a general increase in butterfly species richness in Britain, the observed increase is not as large as would be expected given climate change (Menendez et al., 2006).

The distributions of many species are currently shifting polewards as the climate changes (Parmesan and Yohe, 2003, Hickling et al., 2006). Butterflies are no exception, with the ranges of European butterflies generally extending northwards and to higher altitudes, as temperatures increase (Parmesan et al., 1999, Konvicka et al., 2003, Mitikka et al., 2008, Devictor et al., 2012). The distribution of 63% of 35 non-migratory European butterflies studied showed a recent northerly shift, whilst only 3% shifted south (Parmesan et al., 1999). There has also been an increase in the abundance of migrant species in Britain with increasing temperatures in mainland Europe (Sparks et al., 2005). As northern range boundaries extend in Britain there is evidence of local extinctions due to climate change at the range edge of three of the four species with a southern range boundary in Britain (Franco et al., 2006). Whilst southern range boundaries appeared to have remained static for two-thirds of European butterfly species studied that extended their northern boundaries (Parmesan et al., 1999), a failure to take altitude into account could help to explain this result. In Spain the lower elevational boundary of 16 butterfly species rose by an average of 212m over 30 years (Wilson et al., 2005).

Whilst summer temperatures appear to have the largest effect on butterfly abundance they are not the only climatic factor that affects butterflies (Pollard, 1988). In the UK precipitation is predicted to increase during the winter and decrease during the summer

(Murphy et al., 2009), with decreases in summer precipitation expected to positively affect butterfly abundance (Dennis and Sparks, 2007). The effects of precipitation on butterflies may be complicated however as they may be direct or indirect, through changes to the growth of hostplants (Pollard, 1988, Dennis and Sparks, 2007). Additionally, the increasing variability of temperatures and precipitation predicted to occur may have larger effects on populations than changes to the means of these climatic variables (Murphy et al., 2009, Bauerfeind and Fischer, 2014). An increase in the variability of precipitation levels is already thought to have caused population extinctions in *Euphydryas editha bayensis* in America (McLaughlin et al., 2002a).

Despite the widespread changes in species distributions recorded recently, the majority of species have been unable completely track climate change (Warren et al., 2001), suggesting that climate is not the only determinant of species distributions. The European butterfly community composition was estimated to have lagged an average of 135km behind climate change between 1990-2008 (Devictor et al., 2012), whilst many species in southern Britain have decreased in range size despite the predicted positive effects of climate change in this area (Hill et al., 2002). The ability of species to track climate change will affect their probability of extinction (Thomas et al., 2004a). Other factors which may limit the ability of species to track climate include habitat availability (Hill et al., 1999), dispersal ability (Warren et al., 2001) and biotic interactions (Pelini et al., 2010b). The range of *Pararge aegeria* (speckled wood), has expanded more quickly in areas with higher habitat availability despite smaller increases in climatic suitability in these areas (Hill et al., 2001).

The effects of climate change on abundance and species distributions appear to be highly dependent on species traits; habitat specialists are less likely to be able to track changes, partly as their habitat is likely to be more isolated (Dennis and Shreeve, 1991, Warren et al., 2001). Whilst generalist species richness is predominantly affected by the direct effects of climate, specialist species show a higher dependence on the availability of suitable habitat and host plants (Menendez et al., 2007). Habitat specialists in the UK have been undergoing long term declines, whilst there has been little or no change in the abundance of habitat generalists (Brereton et al., 2011), resulting in communities containing an increasing proportion of generalist species (Warren et al., 2001, Menendez et al., 2006).

Additionally the ability of species to track changes in suitable climates may be affected by the climate itself, through changes to their dispersal ability. As butterflies are ectothermic increasing temperatures may increase the amount of time individuals spend in flight (Shreeve, 1984), potentially increasing dispersal (Mitikka et al., 2008, Cormont et al., 2011). Dispersal has also been shown to be affected by cloud levels and wind in some species (Mitikka et al., 2008, Cormont et al., 2011); cloud cover has been predicted to decrease during summer in the UK in the future (Murphy et al., 2009), which may increase dispersal in some butterflies. Although it should be noted that the effect of climatic variables on dispersal may depend on habitat fragmentation, with evidence that temperature had a higher effect on dispersal in more fragmented habitats in *Maniola jurtina* (meadow brown) (Delattre et al., 2013a).

Many butterfly species are reliant on specific plant species for larval food plants and for nectar sources as adults (Asher et al., 2001). Butterflies may therefore be restricted by the distribution of their host plants (Merrill et al., 2008, Pelini et al., 2010a), for example *Phengaris alcon* (Alcon blue) is dependent on the presence of its only host plant *Gentiana pneumonanthe* (Cormont et al., 2013). Local adaptation to particular host plants may prevent some species from spreading under climate change, if their host plants are not able to shift their ranges as quickly (Pelini et al., 2010b). However, some species may be able to switch host plants as the climate changes. *Aricia agestis* (brown argus) was originally largely restricted to *Helianthemum nummularium* in Britain, but in recent years has begun to use *Geranium molle* as well, allowing rapid range expansion (Thomas et al., 2001, Pateman et al., 2012). Additionally asynchrony with species that have a negative impact may increase the abundance or distribution of the focal species. In *Aricia agestis* lower rates of parasitism were found in newly colonised sites, allowing higher growth rates and therefore the potential for faster expansion (Menendez et al., 2008).

As poikilotherms the distribution of many butterflies may be more constrained by microclimate than the presence of hostplants (Eilers et al., 2013, Wick et al., 2014). In many species host plant distribution appears to only become a constraining factor in distribution in stressful environments (Hanspach et al., 2014). Differences in microclimate can affect survivorship and will therefore have important consequences for species distributions (Weiss et al., 1988, Bennie et al., 2013). The microclimate of an area will be affected by the habitat and local topography (Bennie et al., 2008, Suggitt et al., 2011). A species' habitat associations may differ with time of year (Roy and Thomas, 2003), altitude or latitude (Thomas et al., 1998, Oliver et al., 2009, Ashton et al., 2009). Changes in regional climate may alter the microclimate of a habitat type sufficiently to allow colonisation of a previously unsuitable habitat (Thomas et al., 1999, Thomas et al., 2001). Some species have already undergone alterations in microhabitat preferences under climate change; for example, *Hesperia comma* (silver-spotted skipper) is no longer confined to southerly facing slopes in Britain (Thomas et al., 2001, Davies et al., 2006). It is estimated that this increase in the habitat niche breadth has tripled the expansion rate of this species (Thomas et al., 2001), showing the importance of changes in habitat associations for distribution changes. Many British butterfly species are declining; having been unable to increase their habitat breadth despite increasing temperatures. This is probably mainly due to habitat degradation (Oliver et al., 2012).

1.4 Phenological responses to climate change

The timing of many biological events is governed at least partly by climatic variables. As such it is no surprise that recent climate change has seen the advancing of many spring events, including flowering in plants (Menzel and Fabian, 1999, Fitter and Fitter, 2002), egg laying in birds (Crick et al., 1997, Crick and Sparks, 1999) and the migration of a range of taxa (Marra et al., 2005, Cherry et al., 2013). In butterflies earlier and longer flight periods have been recorded across Europe (Roy and Sparks, 2000, Stefanescu et al., 2003). Between 1976 and 2008, 32 out of 44 British species showed a significant advancement in their day of first appearance (Diamond et al., 2011) and there is evidence of correlations between temperature and appearance date (Roy and Sparks, 2000, Diamond et al., 2011). A warming of 1°C could make the first and the peak appearances of most British butterfly species earlier by as much as 2-10 days (Roy and Sparks, 2000), whilst warming of 3°C could advance their appearance by as much as two or three weeks (Sparks and Yates, 1997). Although it should be noted that these predictions assume a linear response between temperature and emergence dates, which may be unlikely in practice. An increase in voltinism has also been recorded, which may increase the ability of butterflies to adapt to climatic change by decreasing generation times (Altermatt, 2010). Phenology does not appear to be affected by precipitation in most butterfly species (Polgar et al., 2013).

Whilst phenological responses to climate change are common across multiple taxa the rate of change may differ (Thackeray et al., 2010). If interacting species differ in their reaction rates to climate change there is the potential for temporal mismatches between dependent species, for example between butterflies and larval host plants or adult nectar sources, which may in turn affect their abundance and distribution (Parmesan, 2007, van Asch and Visser, 2007). Both temporal and spatial asynchrony between interacting species can therefore have important consequences for the persistence of populations and for determining whether a species will be able to spread under climate change.

In addition the effects of climate change discussed above will not be independent of each other, for example those species which are able to track climate changes effectively may be less likely to undergo changes in phenology. This is supported by species with larger ranges showing smaller advancements in the day of their first appearance as the climate warmed (Diamond et al., 2011).

1.5 Conclusion

The effects of climate change on ecological communities has the potential to be catastrophic (Thomas et al., 2004a). Predicting the impacts of climate change on species, populations and communities is necessary for the implementation of appropriate conservation policies (Hannah et al., 2002), including the management of networks of protected areas (Araujo et al., 2011, Wise et al., 2012), increasing connectivity (Vos et al., 2008) and undertaking assisted colonisations (Carroll et al., 2009). As previous conservation strategies were often static, the scale of predicted range shifts may necessitate the redesign of many conservation initiatives, as for example protected areas may no longer contain the species they were designed to protect (Pressey et al., 2007, Bull et al., 2013).

Many British butterflies reach their northern range boundaries in Britain and as such they may be expected to be positively affected by the predicted increase in temperatures associated with climate change. However, climate is not the only variable that will affect butterflies and as such it is also important to understand how a species interacts with the rest of its environment. Factors such as habitat availability, biotic interactions, behaviour and demography may limit the ability of species to respond to climate change. Therefore it is necessary to study these factors in order to gain a full understanding of how butterflies' abundances, distributions and phenologies will change under future climate change.

1.6 Thesis Plan

In this thesis I attempt to address areas that may prevent the effective conservation of species under climate change, focusing primarily on the generalist British butterfly *Melanargia galathea* (marbled white). I consider the temporal and spatial distributions of this species at multiple scales, and the implications of these for the conservation of this species and other insects.

Chapter 2

Knowledge of demography and the broadscale habitat preferences of species is necessary for many conservation strategies, including planning translocations and the designation of reserves and wildlife corridors. In this chapter I consider the broadscale habitat preferences of six species of British butterfly that have shown spread in recent years. I estimate two demographic variables, population growth rates and carrying capacities in occupied habitats. I suggest that habitats with lower densities may have been important in allowing these species to have spread in recent years.

Main hypothesis: Estimates of the carrying capacity and intrinsic growth rate will differ between habitat types and species for six species of generalist butterfly.

Chapter 3

Climate change is affecting the phenology of many species, with the advancing of many biological events. In this chapter I look at how the timing of *M. galathea*'s flight period has changed over recent years across Britain. I focus on three sites, one in the core of its range, one towards the edge of its natural distribution and one introduced population, outside of the species' natural range. The rates of phenological change may differ between taxonomic groups, with consequences for the abundance and extinction risk of interacting species. I relate the timing of *M.galathea*'s flight period to that of the flowering period of a key nectar source, *Centaurea scabiosa*.

Main hypotheses:

- The timing of the flight period of *M.galathea* and flowering period of a key nectar source, *C.scabiosa* will have advanced in recent years and will be earlier at sites further south.
- The rate at which the flight period of *M.galathea* has advanced will be faster than the rate at which the flowering period of *C.scabiosa* has advanced.

Chapter 4

A key challenge in the conservation of species is monitoring endangered populations. Estimating population sizes and demographic parameters can be vitally important for conservation management. The timing of emergence may be of particular importance to estimate given the possibility of phenological mismatches described in Chapter 3. In this chapter I compare parameter estimates using a mark release recapture method and a new method for estimating these variables using more readily available transect data. I consider whether an inability to sex individuals during transects may affect the accuracy of parameter estimates using this method.

Main hypothesis: Estimates of population size and demographic parameters from transect data will differ from those estimated from mark release recapture data.

Chapter 5

Finally I consider habitat preferences and phenology at a finer scale, demonstrating how spatially heterogeneous sites may be important for supporting populations under climate change. I look at whether the presence of topographical diversity within a site affects the flowering period of two of *M.galathea*'s main nectar sources, as this could reduce the chance of a phenological mismatch occurring. I also look at individual site use by *M.galathea*, by studying movement across the site and the use of different aspects at different times of day.

Main hypotheses:

- Topographical diversity will increase the length of the site wide flowering period of *C.scabiosa* and *C.nigra*.
- *M.galathea* abundance and behaviour will differ among aspects and with time of day and season.
- *M.galathea* mobility will differ between the sexes.

Chapter 6

In this final chapter I make final conclusions from the previous chapters and provide an insight on future challenges in the area.

Chapter 2

Estimating intrinsic growth rates and carrying capacities for six British butterfly species

Abstract

Background: The distribution of climatically suitable areas for species is expected to change under climate change. Whether species are able to track these changes will depend on species specific demographic parameters and the availability of suitable habitats. I estimate carrying capacities and intrinsic growth rates for six species of generalist butterfly species that have recently expanded their UK ranges, using UK Butterfly Monitoring Scheme (UKBMS) data.

Methods: Carrying capacities were estimated for occupied habitat types using the mean density across years at sites with stable populations. Maximum likelihood models were used to estimate intrinsic growth rates at newly colonised sites. Kruskal Wallis tests were used to determine whether carrying capacities and intrinsic growth rates varied between habitat types and species.

Results and Conclusions: Densities differed significantly ($p<0.05$) between occupied habitats for four out of the six study species, with estimates ranging from 7 to 279 butterflies per hectare per year. Intrinsic growth rate estimates differed significantly among species (Kruskal Wallis; $\chi^2=13.09$, $p=0.02$), varying from 0.26 (*P. c-album*) to 0.56 (*P. tithonus*). I show that demographic variables differ between species and habitat types and suggest these estimates should be included in species distribution models to improve the accuracy of range predictions under climate change.

2.1 Introduction

Many taxa, including butterflies, are undergoing extensive alterations in their ranges under climate change (Parmesan and Yohe, 2003, Hickling et al., 2006, Parmesan, 2006). There has been much debate over how to adequately conserve species whose ranges are changing. However, a lack of knowledge of a species' broad habitat requirements and demography can hamper these efforts, including by producing inaccurate predictions of possible future distributions.

The distributions of species are dependent on a number of factors, including climate and habitat availability. The distribution of the majority of species of butterfly have lagged behind recent changes in climate (Warren et al., 2001, Willis et al., 2009a, Devictor et al., 2012), suggesting that climate is often no longer the constraining variable at their northern range boundaries. Britain underwent significant changes in land use during the 20th century, and the impacts of this, such as habitat fragmentation and degradation, may have limited the spread of species (Warren et al., 2001, Hill et al., 2002). In addition the rate at which species can spread under favourable environmental conditions will be dependent on dispersal ability and demographic variables including fecundity, survival rates and population densities (Thuiller et al., 2008, Altwegg et al., 2013).

To understand how future climate change will affect species distributions it is necessary to consider these additional variables and how they will affect a species' ability to spread. Knowledge of these factors will help to predict which species may struggle to track climate change and may provide useful information on which habitats are able to support different species. The density of individuals an area can support will differ across the species' distribution, dependent upon habitat quality (Underwood, 2007). In a previous study, three out of four butterfly species studied showed significantly different densities among habitat types (Pocewicz et al., 2009). Despite having relatively wide habitat requirements generalist butterflies still differ in habitat preferences (Asher et al., 2001). Thus, when estimating demographic variables it is necessary to distinguish between habitat types.

In this chapter I estimate carrying capacities and intrinsic growth rates for six generalist butterfly species. I use UK Butterfly Monitoring Scheme (UKBMS) data from across Britain to determine whether carrying capacities and intrinsic growth rates differ among habitat types and species.

2.2 Methods

2.2.1 Study species

The following six species were selected for these analyses: *Polygonia c-album* (comma), *Pyronia tithonus* (gatekeeper), *Melanargia galathea* (marbled white), *Aphantopus hyperantus* (ringlet), *Thymelicus sylvestris* (small skipper) and *Pararge aegaria* (speckled wood). These species have all shown spread over recent decades; between 1970-82 and 1995-9 their distributions at a 10km grid square level increased by between 33% (*P. tithonus*) and 79% (*P. c-album*) (Asher et al., 2001). The study species are generalists, however they have different demographic traits and habitat preferences (Pollard and Yates, 1993, Asher et al., 2001). They utilise relatively widespread host plants, which minimises the importance of biotic interactions on both their population dynamics and distributions (Asher et al., 2001). As *P. aegaria* is a multivoltine species (the remaining study species are univoltine), values for this chapter were calculated annually to allow comparisons between the species.

2.2.2 UK Butterfly Monitoring Scheme (UKBMS) Data

UKBMS transects are walked weekly between April and September every year, depending on pre-defined weather criteria being met (Pollard and Yates, 1993). The transects are walked at a steady pace and all butterflies seen within the transect are recorded. The transects are typically 5m wide and between 2 and 4 km long, and are classified into broad habitat types (Table 2.1). Annual abundance indices are calculated for each species at each site. For further details on the data collection methods see Pollard and Yates (1993).

Table 2.1: Shortened classifications used to refer to the UKBMS habitat classifications in this chapter.

UKBMS habitat classification	Shortened classification
Dry semi/unimproved (flower rich) chalk/limestone grassland	Chalk grassland
Dry semi/unimproved (flower rich) neutral grassland	Neutral grassland
Dry semi/unimproved acid grassland	Acid grassland
Mature broadleaved woodland	Broadleaved wood
Mature mixed broadleaved and coniferous woodland	Mixed wood
Wet and dry heathland/ dry heather moorland	Heathland/moorland
Intensive arable crops	Arable crops

2.2.3 Estimating carrying capacities

Carrying capacities were estimated for each study species using the mean population density at sites with a stable population. Sites were selected from those classified by the UKBMS as having a stable population and this was checked using a linear regression of the natural log of the annual abundance index against year. Densities were calculated by dividing the abundance by the transect area. For this reason, sites with transects of unknown length were discarded from the analysis. Where the transect width was not recorded it was assumed to be 5m, as this is the standard width in the UKBMS guidelines (Pollard and Yates, 1993). Sites with no broad habitat classification and those with less than 5 years of abundance data were also discarded. The mean density across years was taken for each site, with missing years excluded from the analysis. All available years of data were used, unless the index of abundance dropped to 0 during this time, in which case data from that year onwards was excluded.

All species-habitat combinations with ≥10 stable population sites were used to estimate habitat specific carrying capacities for individual species. A maximum of 20 sites per habitat classification were used due to time constraints; where more than 20 stable sites existed for any species-habitat combination, included sites were selected at random. Kruskal Wallis tests were used to determine whether densities differed significantly between habitat types for each species, as the data were not normally distributed and did not improve sufficiently under transformation.

2.2.4 Estimating intrinsic growth rates

Initial population growth rates (Pollard et al., 1996, Pollard and Yates, 1993) were estimated for each study species using newly colonised sites (defined as sites with absence for ≥1 year followed by presence for ≥2 years (Willis et al., 2009b)). Growth rates were calculated using the first 10 years of abundance data since colonisation or until the annual abundance index dropped to 0, whichever was sooner, following Willis et al. (2009b). Sites with less than five years of data were excluded. Increasing populations were confirmed using linear regression of the natural log of the annual abundance index against year. As there were insufficient study sites for individual habitats that fit the above criteria a single estimate of r for each species was produced.

Maximum likelihood models were used to estimate intrinsic growth rates (Equation 2.1) using data from 10 sites per species. The solver add-in in Microsoft Excel 2007 was used estimate r, N_0 and, where applicable, K, assuming a negative binomial distribution. Density at year *t* is calculated using

$$N_\mathrm{t} = \begin{cases} e^{r(t-1)} & \text{if } N_0 e^{r(t-1)} < K; \\ K & \text{if } N_0 e^{r(t-1)} > K; \end{cases}$$

Equation 2.1

where N_t is the abundance at time t, N_0 is the abundance at time 0, r is the intrinsic growth rate and K is the carrying capacity. The log-likelihood of observing i butterflies when you expect to see μ, with a variance parameter φ is

$$\mathrm{LL}(i|\mu,\varphi) = \ln\Gamma(1+a) - \ln\Gamma(i+1) - \ln\Gamma(a) + a\ln\left(\frac{b}{b+1}\right) - i\ln(1+b),$$

Equation 2.2

where $a = \frac{\mu}{\phi}$ and $b = \frac{1}{\phi}$.

As the carrying capacities appeared to vary with habitat type for most species and there was insufficient data available to test whether this was the case for the intrinsic growth rate, where carrying capacities were included in best model sets, a Spearman's rank correlation of intrinsic growth rate against carrying capacity was undertaken to determine whether there was a relationship between the two parameters. It was not always possible to estimate the carrying capacity using this method, as not all of the populations had started to level off; however as the carrying capacities were estimated separately using sites with stable populations this was not considered to be a problem.

2.3 Results

2.3.1 Carrying capacities

The estimated carrying capacities for each species differed between occupied habitats by up to 189 butterflies per hectare per year (*M.galathea*), with statistically significant differences between habitat types for four of the six study species (Table 2.2). It was not possible to carry out post-hoc tests to determine which habitat types differed in density as non-parametric Kruskal Wallis tests were used. The number of habitats each species was recorded in ranged from three (*M.galathea*) to seven (*P. tithonus*) (Figure 2.2; Table 2.2). The carrying capacity estimates varied from 7 (*P. c-album*; heathland/moorland) to 279 (*P. tithonus*; neutral grassland) butterflies per hectare per year.

Habitat preferences varied among the species, although all of the study species occurred on chalk grassland, neutral grassland and in broadleaved woods. *P.tithonus* used the widest range of habitat classes and had the highest density of any species in any habitat (Figure 2.1; Table 2.2). It was found in highest densities on neutral grassland and in mixed woodland habitats; however, the differences in density between habitats were not significant for this species. *M. galathea* occurred predominantly on chalk grasslands, as expected from the literature (Asher et al., 2001); however, it also occurred at lower densities on neutral grassland and in broadleaved woods. *P. aegeria* is predominantly a woodland species (Figure 2.3; Hill et al., 1999, Asher et al., 2001), although it also occurred at lower densities on grasslands and heathland/moorland. *P. c-album* was found at lower densities than the other study species; it occurred on grassland, wooded areas and heathland/moorland. *A. hyperantus* occurred predominantly in the woodland habitats, although it was also present on chalk and neutral grasslands and heathland/moorland. *T. sylvestris* was found at relatively high densities in mixed wood and neutral grasslands, and at lower densities in broadleaved wood and chalk grasslands, although this difference was not significant.

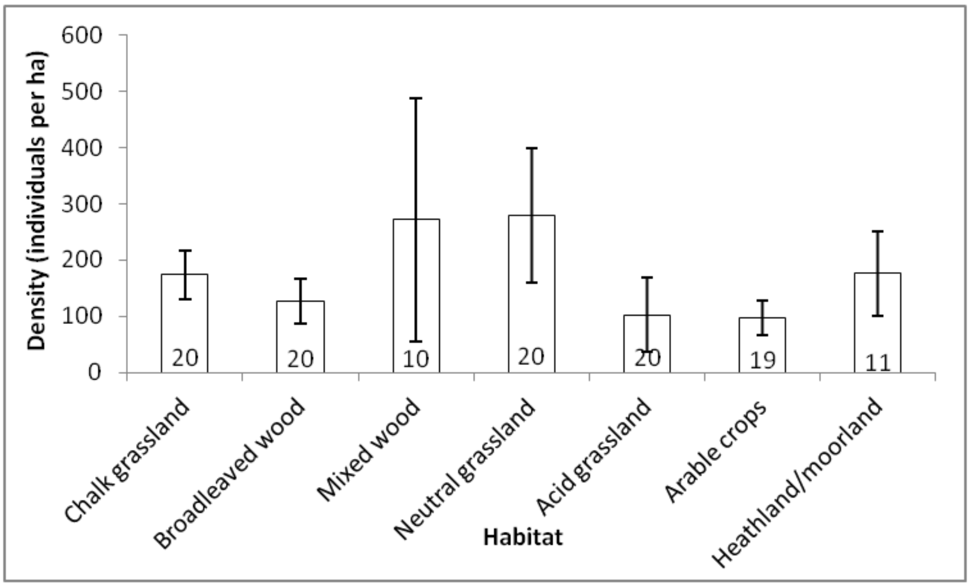


Figure 2.1: Density of *P. tithonus* per hectare per year in occupied habitat types. Error bars show 95% confidence intervals. Sample sizes for each habitat are shown by the data labels on the bars.

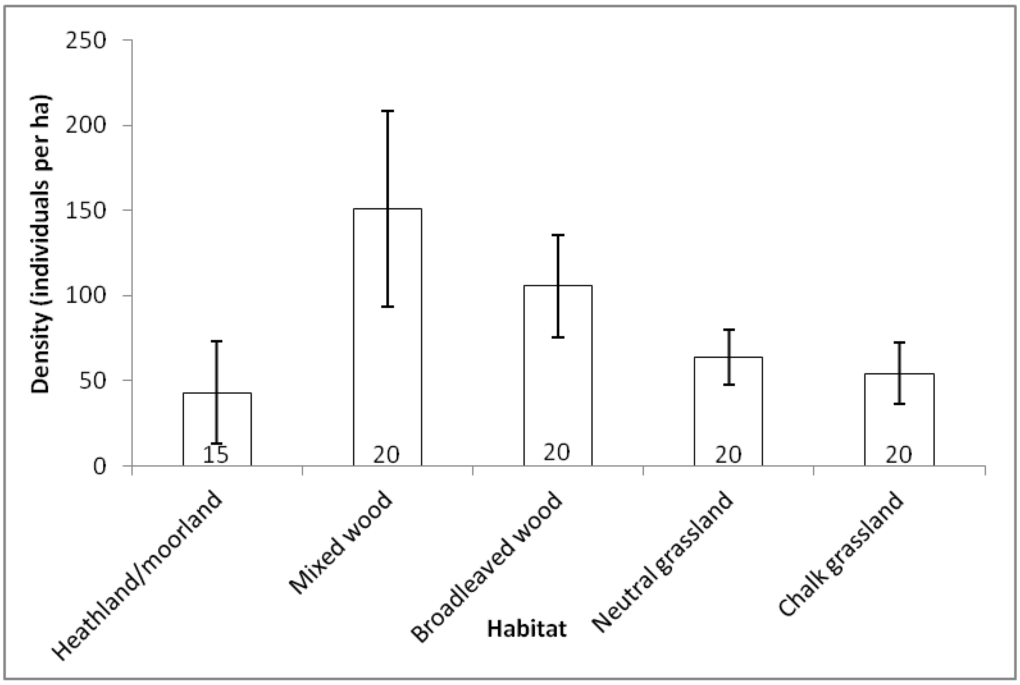


Figure 2.2: Density of *P. aegaria* per hectare per year in occupied habitat types. Error bars show 95% confidence intervals. Sample sizes for each habitat are shown by the data labels on the bars.

Table 2.2: Estimates of density per hectare per year for each occupied habitat type for each study species. See Table 2.1 for UKBMS habitat classifications. The *p* values are associated with the null hypothesis that all occupied habitats for each species support the same density of individuals.

Species	Habitat classification	Density (Individuals per ha)	95% CI	n	*P* value
Aphantopus hyperantus	Chalk grassland	103	68-138	20	0.002
	Neutral grassland	168	60-276	17	
	Broadleaved wood	184	115-253	20	
	Mixed wood	238	181-295	20	
	Heathland/moorland	54	27-81	10	
Melanargia galathea	Chalk grassland	233	141-325	20	0.003
	Neutral grassland	128	67-189	13	
	Broadleaved wood	44	11-77	11	
Pararge aegaria	Chalk grassland	54	36-72	20	<0.001
	Neutral grassland	64	48-80	20	
	Broadleaved wood	106	77-135	20	
	Mixed wood	151	94-208	20	
	Heathland/moorland	43	14-72	15	
Polygonia c-album	Chalk grassland	9	5-13	20	0.009
	Neutral grassland	15	11-19	20	
	Broadleaved wood	20	10-30	20	
	Mixed wood	18	12-24	20	
	Heathland/moorland	7	3-11	12	
Pyronia tithonus	Chalk grassland	174	131-217	20	0.067
	Neutral grassland	279	161-397	20	
	Acid grassland	102	37-167	10	
	Broadleaved wood	127	88-166	20	
	Mixed wood	271	55-487	20	
	Heathland/moorland	176	102-250	19	
	Arable crops	98	69-127	11	
Thymelicus sylvestris	Chalk grassland	42	20-64	20	0.071
	Neutral grassland	79	50-108	12	
	Broadleaved wood	30	8-52	10	
	Mixed wood	86	19-153	11	

2.3.2 Intrinsic growth rates

The intrinsic growth rate differed significantly among species (Kruskal Wallis; χ^2=13.09, *p*=0.02), with estimates from 0.26 (*P. c-album*) to 0.56 (*P. tithonus*) (Figure 2.1). Spearman's rank tests showed no significant relationship between the carrying capacities included in the maximum likelihood models to estimate intrinsic growth rates, and the intrinsic growth rates for any of the species (*p*>0.2 for all species).

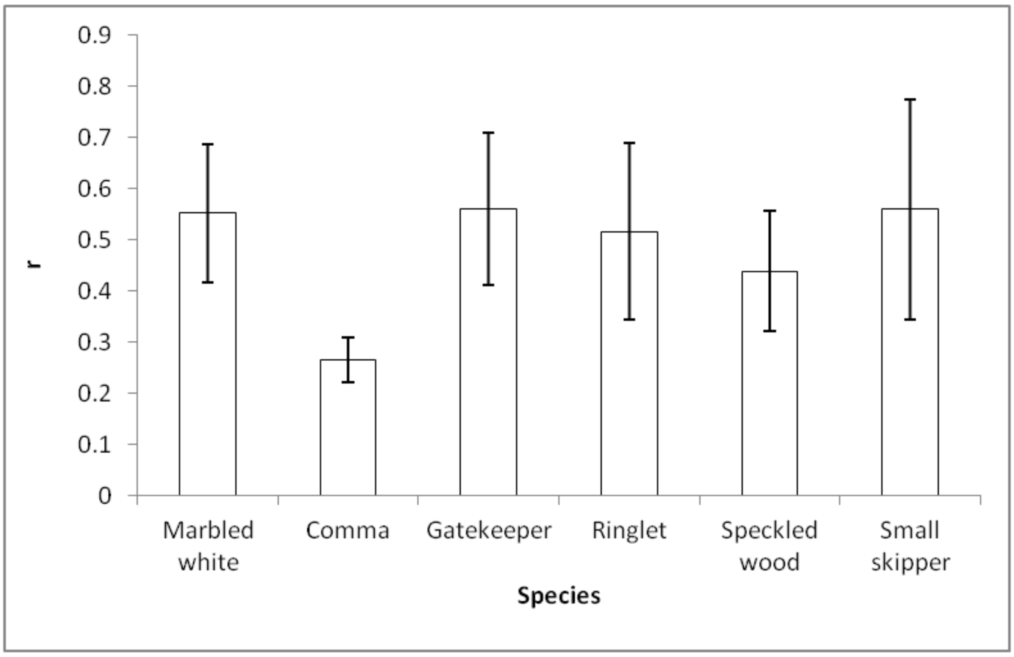


Figure 2.3: Estimates of intrinsic growth rate, *r*, per year for each of the study species. Error bars show 95% confidence intervals. N=10 for all species. The intrinsic growth rates were estimated using Equation 2.1.

2.4 Discussion

The differences in intrinsic growth rate among species are expected to affect the rate at which they can alter their range under climate change (Willis et al., 2009b). However, although it was not possible to perform a post-hoc test to confirm which species differed significantly, the results show little interspecific variation, with only *P.c-album* appearing considerably lower than the other species. *P.c-album* is a very mobile species which is able to spread quickly (Asher et al., 2001), but is often found at relatively low densities, as shown by the carrying capacity estimates. The small sample size and number of species in this study necessitates further studies however, possibly comparing how growth rates differ among and within taxonomic groups.

Despite being thought of as habitat generalists, the densities of most of the study species differed significantly among habitat types. This variation in density is similar to that recorded in other studies (Warren, 1994, Pocewicz et al., 2009), occurrences in these low density habitats could be vital in connecting high quality habitat patches and facilitating spread. Spread may even be more rapid through areas which are unable to support high densities, if dispersal increases significantly once a carrying capacity has been met (Nowicki and Vrabec, 2011). Whilst most British butterflies are expected to extend their northern boundaries under climate change, the majority of specialist species have undergone range contractions, whilst some generalist species have expanded their range (Warren et al., 2001). The ability of generalists to colonise and persist in a wide range of habitat types may be integral to their ability to spread as the climate becomes more favourable at their northern range boundaries. Generalists also tend to be more mobile than specialists however; it is difficult to separate the effects of these traits on their ability to spread (Warren et al., 2001).

Population dynamics may also be affected by variables such as altitude and latitude. Due to data limitations and time constraints it was not possible to explore these effects, or to consider how intrinsic growth rates differ among habitat type. There was no significant relationship between the intrinsic growth rate and carrying capacity at the newly colonised sites for any of the species. As carrying capacity was shown to differ for the majority of the species this could suggest that the growth rate may not be affected by habitat type. However, this rather indirect method also has a small sample size and further research is necessary to confirm whether intrinsic growth rates differ with habitat type. Furthermore the carrying capacities in this study were calculated for broad habitat types and did not consider the effects of neighbouring habitats, which may contain source populations.

In this chapter I have shown that six generalist species were found in a range of broad habitat types. The densities differed significantly between occupied habitat types for the majority of the study species. Studying species' broad habitat requirements can provide useful information for conservation, including for the selection of appropriate translocation sites (e.g. Willis et al., 2009a). Loss of appropriate habitat is thought to be preventing the range expansion of many British butterfly species (Warren et al., 2001). Quantifying habitat associations may therefore be particularly useful for predicting future spread under climate change (Hill et al., 2001). Intrinsic growth rates may affect the ability of species to spread under climate change (Willis et al., 2009b); however there appeared to be little difference among the intrinsic growth rates of most of the species studied here.

Chapter 3

The phenology of a generalist butterfly, *M.galathea*, and its principal nectar source, *C. scabiosa*

Abstract

Background: The phenologies of many biological events are advancing as the climate changes; however the rate of change varies widely among taxonomic groups. Phenological asynchrony between interacting species may result in changes in distribution, abundance and extinction risk with implications for the wider ecosystem also possible. Here I look at differences in the flight phenology of *M.galathea* and the flowering period of a key nectar source, *C.scabiosa,* across recent years at three sites within the UK.

Methods: Data on knapweed emergence were collected by counting the number of developing, open and spent flowers on up to 240 plants every 2-3 days. Regular transects throughout the flight season were used to collect data on *M.galathea* abundance. Log likelihood models were used to determine whether the timing of the flowering period and flight period differed among years and sites.

Results and Conclusions: The flight period of *M.galathea* and flowering period of *C.scabiosa* both appeared to differ among study sites and years, with both emerging later at the northernmost study site. The start of *C.scabiosa*'s flowering period has become later over time (Spearman's rank; ρ_7=0.81, p=0.01), whilst there has been no consistent trend over time in the start of *M.galathea*'s flight period (Spearman's rank; ρ_7=0.12, p=0.76). This has resulted in a decrease in the length of time between the start of *C.scabiosa*'s flowering period and the start of *M.galathea*'s flight period over recent years (Linear regression; R^2=0.59, p=0.02), suggesting that some *M.galathea* individuals may be starting to emerge before a key nectar source was available. Differences in the cues used to determine the phenology of butterflies and their nectar sources may result in phenological asynchrony, which may be exacerbated under a changing climate.

3.1 Introduction

Climate change is affecting the phenology of many species (Parmesan and Yohe, 2003, Parmesan, 2006). Whilst a wide range of taxa are showing phenological advancements the rate and direction of change may not be constant between species (Thackeray et al., 2010). Differences in the rate or direction of change between interacting species could lead to phenological mismatches, with consequences for the abundance and extinction risk of the interacting species (Memmott et al., 2007, Fabina et al., 2010). It is therefore necessary to consider the effects of environmental change on interdependent species when planning conservation measures (Visser and Both, 2005).

Butterflies may be limited by the availability of hostplants, climatic conditions or interactions between these two variables (Cormont et al., 2013, Hanspach et al., 2014) . It is therefore important to consider the indirect effects of the changing climate on butterflies, mediated through changes in hostplant availability, as well as the direct effects of climatic variables. Despite the important roles insects play in ecosystem functioning and crop pollination there has been little research on potential phenological mismatches in these species and the wider impacts these could have (though see Bartomeus et al., 2011, Rafferty and Ives, 2011, Kudo and Ida, 2013). Earlier flight periods (Roy and Sparks, 2000, Forister and Shapiro, 2003) and increased levels of voltinism (Altermatt, 2010) have been recorded in many butterfly species, and these effects are expected to increase under further climate change. The rate of larval development in butterflies is often constrained by environmental variables with, for example, faster development seen under higher temperatures (Garcia-Barros, 2000, Briscoe et al., 2012). Most adult butterflies are dependent on a restricted number of plant species for nectar sources (Asher et al., 2001). Whilst the flowering periods of many plants have also become earlier under climate change (Fitter and Fitter, 2002, Primack et al., 2004, Calinger et al., 2013), there is evidence that butterflies may be showing higher levels of advancement (Gordo and Sanz, 2005, Parmesan, 2007). In addition there is evidence in some species that the climatic cues used by butterflies differ from those used by plants (Doi et al., 2008), which may increase the chance of a phenological mismatch occurring.

In this chapter I look at how the timing of *Melanargia galathea*’s flight period has changed over recent years and between sites across the UK. A previous study found its flight period to be later with increasing altitude (Gutierrez and Menendez, 1998). As such I expect the timing of *M. galathea*’s flight period to be affected by climate and, as such, to be later at sites further north. I relate the timing of *M.galathea*’s flight period to that of the flowering period of one of its main nectar sources, *C.scabiosa* (Figure 3.1; Asher et al., 2001).

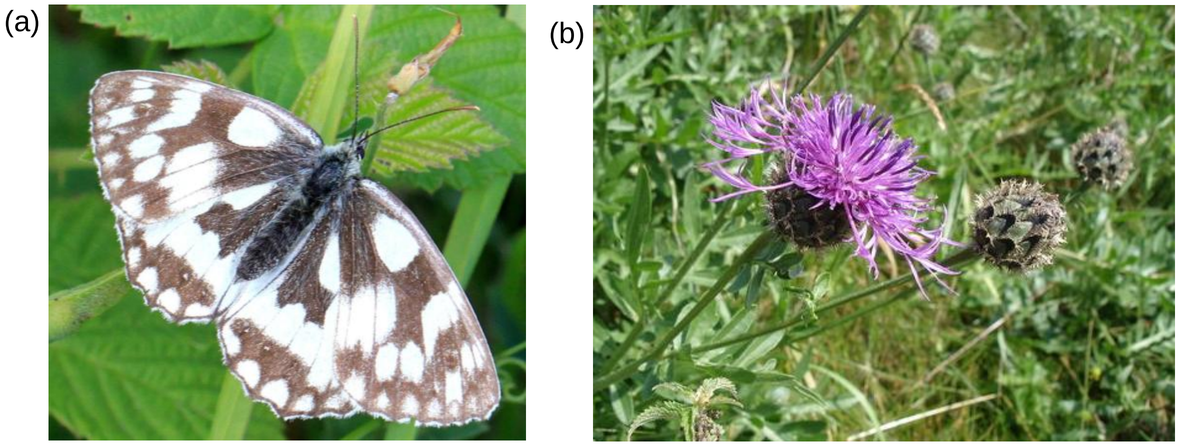


Figure 3.1: Photographs of the two study species: (a) adult *Melanargia galathea* (b) developing and flowering *C.scabiosa* flower heads. Photograph credit: Andrina Laidler and Ian Cunliffe.

3.2 Methods

3.2.1 Flowering phenology of *C.scabiosa*

Data on the flowering phenology of *C.scabiosa* were collected at Wingate Quarry Local Nature Reserve, County Durham, in 2013. Data were collected by counting the number of developing (flower buds), flowering (those with bright inflorescences and pollen present) and past flowers (those with withering flowers, and developing or spent seed capsules) on each plant. Plants were surveyed on 21 days between 25/06/2013 and 23/08/2013, with between 180 and 240 plants selected on each survey date.

Data were also collected (by Dr. S.G.Willis and students under his supervision) using the same methods in eight previous years (2001, 2003-6, 2008, 2011 and 2012) at Wingate and at two additional sites in 2011 (Brockadale Nature Reserve and Totternhoe Chalk Quarry Reserve; Figure 3.2). Brockadale is in North Yorkshire and, as such, is close to *M. galathea'*s natural northern range boundary. Totternhoe is located in Bedfordshire, in the core of *M. galathea*'s UK range.

Figure 3.2: Map showing the location of the three study sites, Wingate, Brockadale and Totternhoe (from North to South).

Statistical Analysis

The sum of flowering and past flowers is herein referred to as the cumulative number of flowers. The expected cumulative proportion of flowers by day x is approximated by

$$p(x) = \frac{e^{\beta(x-\bar{x})}}{1+e^{\beta(x-\bar{x})}}, \qquad \text{Equation 3.1}$$

where $\bar{x}$ is the day by which 50% of flowers are open and β is a parameter negatively related to the length of the flowering period (Kerr, 2013). In order to allow the length and timing of the flowering period to differ between sites and years two additional parameters were added to the equation. The number of open flowers by day x in year y is given by $p_y(x)$where

$$p_y(x) = \frac{e^{(\beta+b_y)(x-\bar{x}+a_y)}}{1+e^{(\beta+b_y)(x-\bar{x}+a_y)}}. \qquad \text{Equation 3.2}$$

$\bar{x}$ and β were allowed to vary between sites, whilst a_y and b_y varied between years (Table 3.1). I assumed that the variation in open flowers about the expected proportion is described by a beta-distribution such that when the mean is $p(x)$ the variance is $p(x)\big(1 - p(x)\big)\phi/(1+\phi)$. This assumption implies that the number of open flowers among plants is described by a beta-binomial distribution. The likelihood of observing *n* flowers being open by day x when *N* flowers were present on a plant is given by

$$L(\boldsymbol{\theta}|N,n) = \frac{\Gamma(N+1)\Gamma(a+b)\Gamma(n+a)\Gamma(N-n+b)}{\Gamma(n+1)\Gamma(N-n+1)\Gamma(a)\Gamma(b)\Gamma(N+a+b)}, \qquad \text{Equation 3.3}$$

where $a = p(x)/\phi$ and $b = (1 - p(x))/\phi$.

A set of models (Table 3.1) was parameterised to determine whether the timing and length of the flowering period differed between sites or years or both. It was assumed that the variation between plants was constant between sites and years and, as such, φ was kept constant within each model. The Microsoft Excel add-in Solver was used to find the parameter estimates which maximised the log-likelihood value. Parsimonious models were selected using AIC values (Burnham and Anderson, 2002, Richards, 2008). The most parsimonious model (lowest AIC value) was used to calculate the flowering period, which was defined as the number of days during which between 5% and 95% of the flowers had opened.

Table 3.1: Parameterisations of the model (Equation 3.2). *K* is the number of parameters estimated in each model. Parameters refer to those which were allowed to vary between sites $(\bar{x}, \beta)$ or years $\left(a_y, b_y\right)$ in each model.

Model	*K*	Parameters	Description
M1	3	-	Timing and length of flowering period (FP) constant between sites and years
M2	5	$\bar{x}$	Timing of FP differs between sites
M3	7	$\bar{x}, \beta$	Timing and length of FP differ between sites
M4	21	a_y, b_y	Timing and length of FP differ between years
M5	14	$\bar{x}, a_y$	Timing of FP differs between sites and years
M6	25	$\bar{x}, \beta, a_y, b_y$	Timing and length of FP differ between sites and years

3.2.2 Variation in the *M. galathea* flight period among years and sites

Data were collected every 2-3 days from a 1,550m long and 5m wide transect around Wingate Local Nature Reserve, using the standard UKBMS guidelines (Pollard and Yates, 1993). Data from this transect were also available from eight other years between 2001 and 2012. Similar transect data from Brockadale and Totternhoe were also analysed to investigate the effect of site on the timing of the flight period. These data were collected by the UKBMS and the Yorkshire Wildlife Trust respectively, following the same UKBMS transect guidelines adopted for surveying at Wingate (Pollard and Yates, 1993).

Statistical Analysis

The expected number of individuals seen on a transect on day *t* is given by

$$y(t) = y_{max} e^{-\frac{1}{2}\left(\frac{t-\bar{t}}{\sigma}\right)^2}, \qquad \text{Equation 3.4}$$

where the peak abundance (y_{max}) is reached on day $\bar{t}$ and the expected duration of the flight period is given by 2σ (Kerr, 2013). These three parameters are allowed to vary between years. Additional parameters are added to the equation as follows to allow variation in the peak abundance (a_s) and the timing (b_s) and length (c_s) of the flight period between sites (Table 3.2)

$$y(t) = (y_{max} + a_s)e^{-\frac{1}{2}\left(\frac{t-\bar{t}-b_s}{\sigma+c_s}\right)^2}. \qquad \text{Equation 3.5}$$

Variation about the expected counts was assumed to have a negative-binomial distribution (Equation 2.2). The variance term (φ) is kept constant within each model, thus it is assumed that variation is constant between sites and years. The equation was maximised using Solver to find the maximum-likelihood parameter estimates. Parsimonious models were selected using AIC values (Burnham and Anderson, 2002); models with a ΔAIC ≤6, where there was no simpler model with a lower AIC value, were retained (Richards, 2008). The flight period was defined as the number of days during which ≥1 butterfly is predicted to be alive and was calculated using the most parsimonious model (lowest AIC value).

Table 3.2: Parameterisations of the model (Equation 3.3). *K* is the number of parameters predicted by each model. Parameters refer to those which were allowed to vary between sites or years in each model.

Model	*K*	Parameters	Description
M1	4	-	Peak abundance, day of peak abundance and flight period constant between sites and years
M2	24	$y_{max}, \bar{t}$	Peak abundance and day of peak abundance differed between years
M3	24	y_{max}, σ	Peak abundance and length of flight period differed between years
M4	34	$y_{max}, \bar{t}, \sigma$	Peak abundance, day of peak abundance and flight period differ between years
M5	13	a_s, b_s, c_s	Peak abundance, day of peak abundance and flight period differ between sites
M6	43	$y_{max}, \bar{t}, \sigma, a_s, b_s, c_s$	Peak abundance, day of peak abundance and flight period differ between sites and years

3.3 Results

3.3.1 Flowering phenology of *C. scabiosa*

The most parsimonious model allowed the timing ($\bar{x}$) and the length (β) of the flowering period to differ between both years and study sites (Table 3.3). For 2011, where data were available from all three sites, the flowering period was earliest at the southernmost site (Totternhoe) and latest at the most northern site (Wingate; Table 3.4; Figure 3.3) as expected. At Wingate, where multiple years of data were available, the start of the flowering period was increasingly delayed over time (Spearman's rank; ρ_7=0.81, *p*=0.01) and the length of the flowering period had decreased (Spearman's rank; ρ_7=-0.80, *p*=0.01).

Table 3.3: Model selection results for the *C.scabiosa* model (Table 3.1). Models with a ΔAIC≤6 without a simpler model with a lower AIC value are retained (Richards, 2008); these models are marked with an *.

Model	K	LL	ΔAIC
M1	3	-18863.01	4424.97
M2	5	-17463.16	1629.26
M3	7	-17440.03	1587.00
M4	21	-17089.64	914.23
M5	14	-16676.61	74.16
M6	25	-16628.5	0.00*

Table 3.4: Julian day by which 5 and 50% of the flowers are expected to be open by, and the expected length of the flowering period (FP) for each year and site. These are calculated using the best fitting model (M6), using Equation 3.2.

Year	Brockadale			Totternhoe			Wingate		
	5%	50%	FP	5%	50%	FP	5%	50%	FP
2001	-	-	-	-	-	-	159	207	97
2003	-	-	-	-	-	-	172	199	55
2004	-	-	-	-	-	-	167	208	83
2005	-	-	-	-	-	-	179	211	64
2006	-	-	-	-	-	-	179	205	53
2008	-	-	-	-	-	-	201	220	40
2011	165	190	52	163	186	47	178	203	51
2012	-	-	-	-	-	-	205	226	43
2013	-	-	-	-	-	-	189	214	52

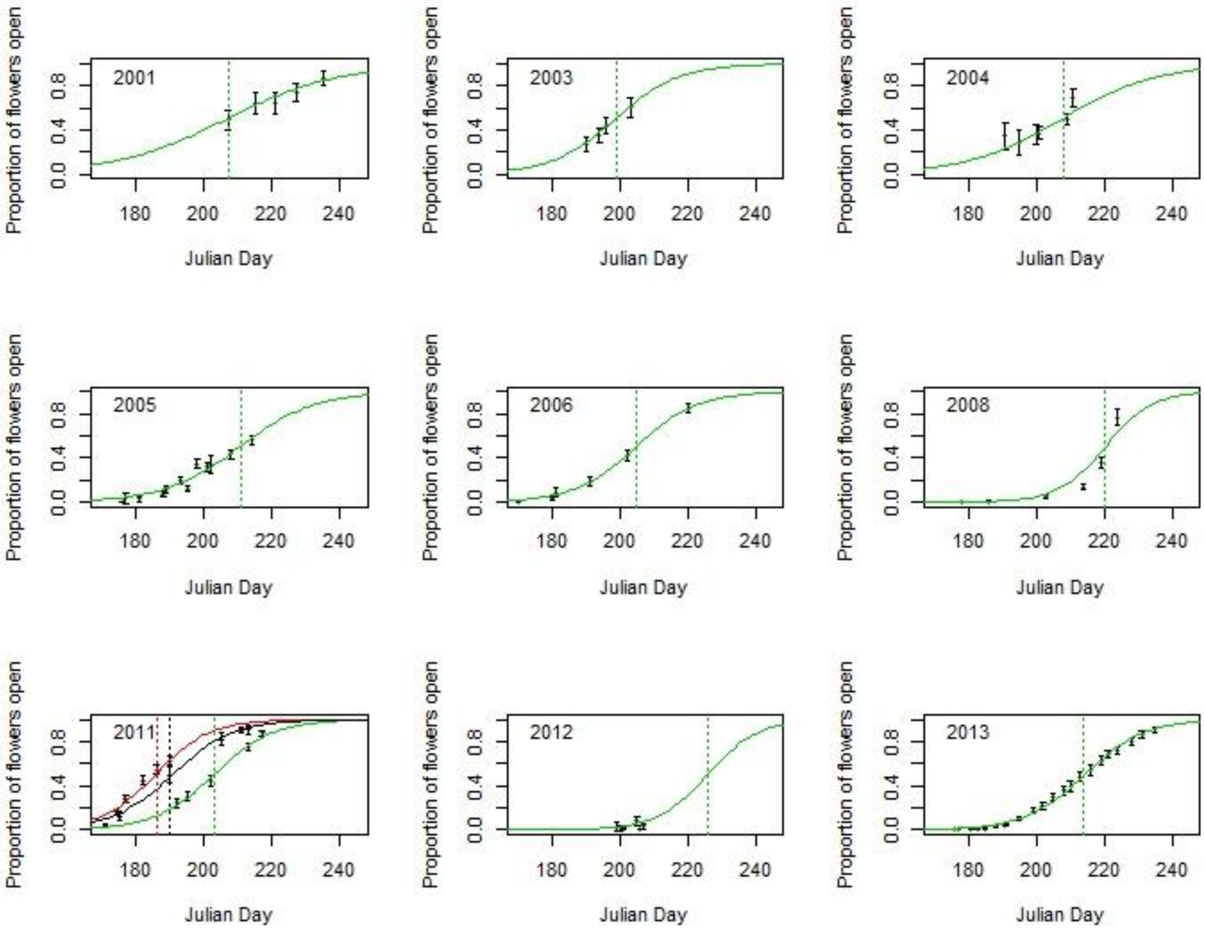


Figure 3.3: Proportion of open flowers on each plant over time, for nine years and three study sites. The data from Wingate are in green, those from Brockadale are black and Totternhoe are red. Each point is the mean for that day, calculated from 30-40 plants. Error bars show 95% confidence intervals. The solid lines show the predicted proportion of flowers open according to the best fitting model (Table 3.3) for each year and site. The dotted lines show the estimated day on which 50% of the flowers are open for each site each year.

3.3.2 Inter-site and inter-annual differences in *M. galathea* flight period

The most parsimonious model (M6) allowed the peak abundance, the day of peak abundance and the length of the flight period to differ with year and site (Table 3.5). Wingate had the latest predicted day of peak abundance and the shortest predicted flight period (Table 3.6; Figure 3.4). At Wingate, the start (Spearman's rank; $\rho_7=0.12$, $p=0.76$) and length (Spearman's rank; $\rho_7=-0.10$, $p=0.81$) of the flight period have not changed significantly with year. Whilst the model generally appeared to fit reasonably well this was not the case for all site year combinations, particularly in 2009 and 2012 in Totternhoe and in 2008 in Brockadale. This may be a result of fitting a mean year effect across the sites and suggests that site and year are not the only factors affecting the abundance of butterflies and the timing of the flight period.

Table 3.5: Model selection results for the *M.galathea* model (Table 3.2). Models with a ΔAIC≤6 without a simpler model with a lower AIC value are retained (Richards, 2008); these models are marked with an *.

Model	*K*	LL	ΔAIC
M1	4	-650.41	136.82
M2	24	-618.71	113.42
M3	24	-639.68	155.36
M4	34	-609.31	114.62
M5	13	-602.32	58.65
M6	43	-543.00	0*

Table 3.6: Estimates of peak abundance (y_{max}), day of peak abundance $(\bar{t})$ and flight period (FP) for different years and sites, according to the most parsimonious model (Table 3.5; M6). Flight period (FP) is calculated as the predicted number of days where ≥1 butterfly is expected to be on the wing.

Year	Brockadale			Totternhoe			Wingate		
	Y_{max}	$\bar{t}$	FP	Y_{max}	$\bar{t}$	FP	Y_{max}	$\bar{t}$	FP
2001	-	-	-	50	196	56	18	207	43
2002	-	-	-	-	-	-	18	202	35
2004	-	-	-	-	-	-	35	202	29
2006	-	-	-	88	193	60	56	204	51
2007	123	187	63	42	189	58	10	200	41
2008	129	195	72	48	197	67	16	209	52
2009	99	187	79	18	190	65	-	-	-
2010	175	189	49	94	191	49	-	-	-
2011	161	183	50	80	185	49	48	197	40
2012	-	-	-	46	196	46	14	207	33
2013	-	-	-	-	-	-	42	205	36

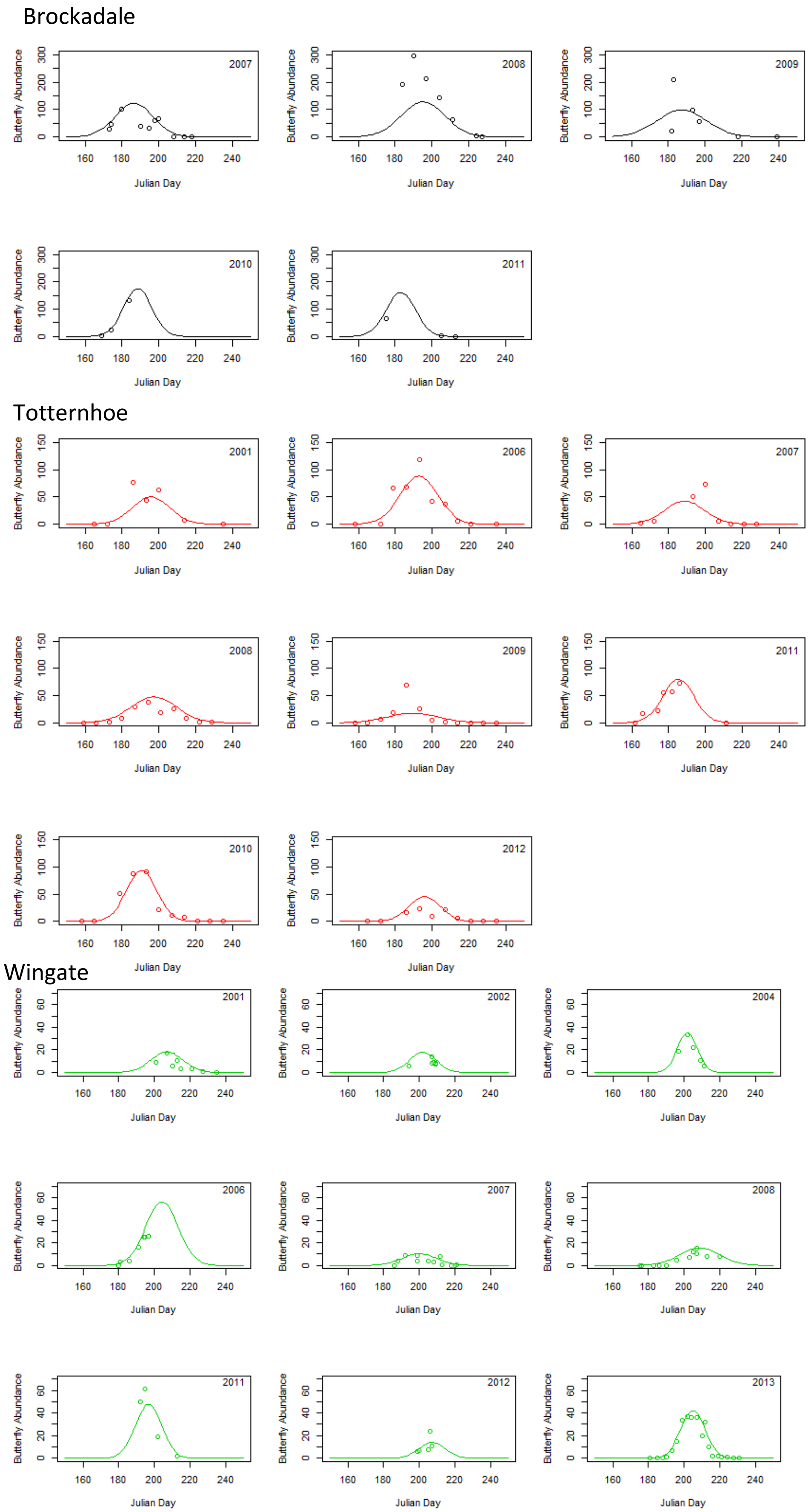


Figure 3.4: Number of butterflies seen per transect over the season at the three study sites. The lines show predicted number of butterflies according to the most parsimonious model (Table 3.5; M6).

There was no significant correlation between the timing (Figure 3.5; Spearman's rank; ρ_5=0.51, p=0.16) or length (Spearman's rank; ρ_5=-0.49, p=0.18) of *C.scabiosa*'s flowering period and the timing and length of *M. galathea*'s flight period respectively. There was evidence that the amount of time between the start of *C.scabiosa*'s flowering period and the start of *M.galathea*'s flight period had decreased over time (Figure 3.6; Linear regression; R^2=0.59, p=0.02).

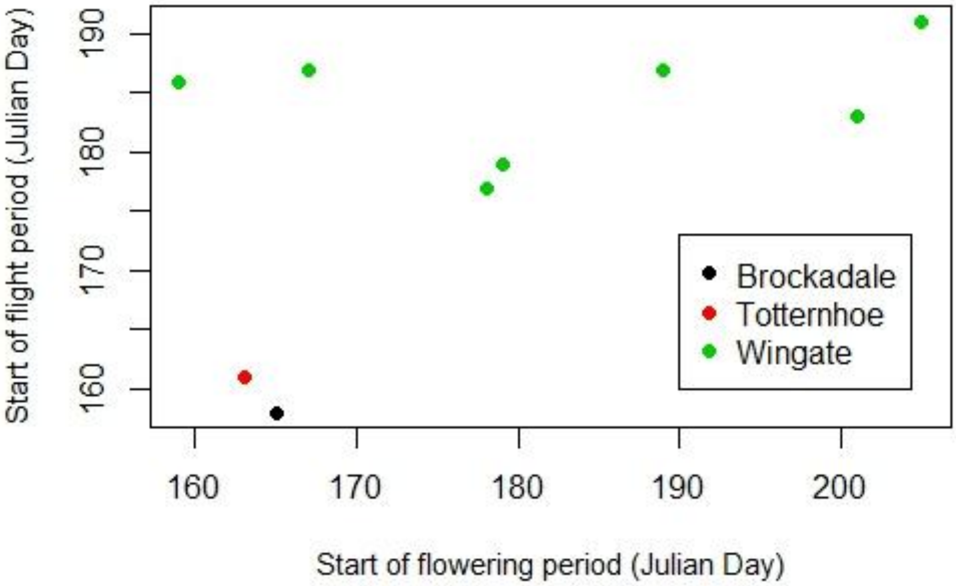


Figure 3.5: The estimated start of *M.galathea*'s flight period plotted against the estimated start date for *C.scabiosa*'s flowering period. Each point represents one year's data at one of the three study sites.

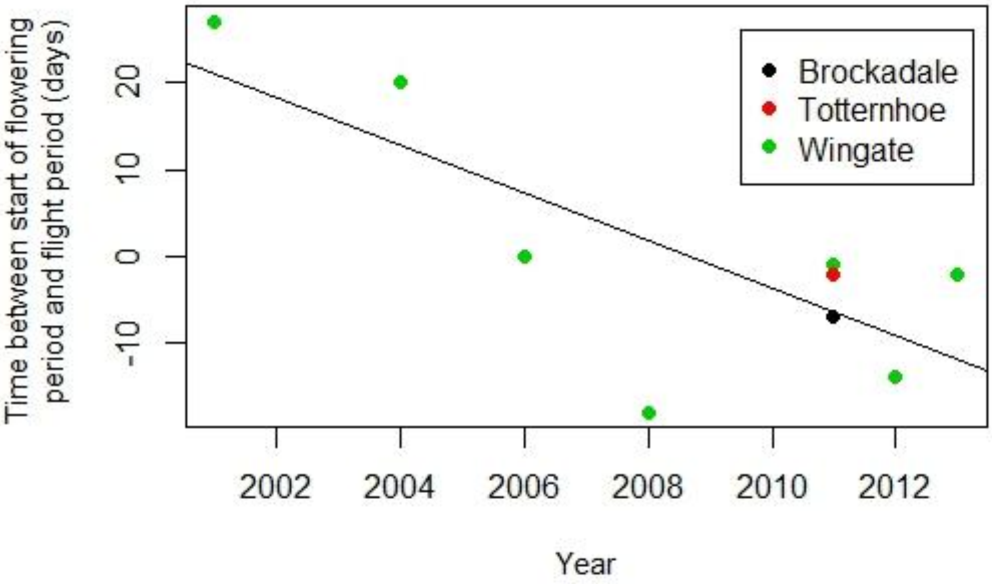


Figure 3.6: Difference between the start date of *M.galathea*'s flight period and *C.scabiosa*'s flowering period. Each point represents one year's data at one of the three study sites. The line shows the linear regression fitted to the data.

3.4 Discussion

The timing of the flowering period of *C.scabiosa* and flight period of *M.galathea* both differed between sites and years. This is unsurprising as the phenology of both flowering plants (Fitter and Fitter, 2002) and butterflies (Roy and Sparks, 2000, Sparks and Yates, 1997, Westgarth-Smith et al., 2012) have often been linked to environmental variables, such as temperature, which will vary spatially and temporally. Over recent years the flowering period of *C.scabiosa* appears to have been increasingly delayed at Wingate, which is surprising given the general trend for earlier emergence of flowering plants in the UK (Fitter and Fitter, 2002). However, this was a relatively short term study and there were several unusually late summers during the latter part of the study. The length of *C.scabiosa*'s flowering period decreased over time, which may be due to the delayed start of the flowering period. Although the timing of the flight period of *M.galathea* differed between years this has not resulted in a trend in a particular direction over time at Wingate. Again this may be surprising given the earlier flight periods recorded in many British species (Sparks and Yates, 1997, Roy and Sparks, 2000). I do not link the phenology of either species directly to climate; further studies are needed in order to see whether how the phenologies of both species have been affected by climate in recent years and to predict how they may change under the rapid rates of climate change expected.

Over recent years the timing of *M.galathea*'s flight period appears to have become less well correlated with the flowering period of a key nectar source, with the possibility of some individuals starting to emerge before the start of *C.scabiosa*'s flowering period. This suggests that *C.scabiosa* emergence is not driving the phenology of *M.galathea*; instead the phenology of both species is likely to be driven by climatic variables. This is the case in other interactions between butterflies and their nectar sources, such as *Anthocharis cardamines (*orange tip) and its two host plants, where the butterfly's phenology was better predicted by temperature than by the phenology of the flowering of either host plant (Phillimore et al., 2012). Whilst the majority of the flight period does still overlap with the flowering period complete mismatches are not needed for community effects to occur (Fabina et al., 2010). The flight period decreased in length at the sites closer to the edge of the natural range (Gutierrez Illan et al., 2012), which could have consequences for the ability of species to expand at range edges, as a shorter flight period will presumably increase the chance of a phenological mismatches occurring. Additionally there was evidence that the flowering period of *C.scabiosa* may be decreasing over time, which could also increase the likelihood of phenological asynchrony.

A loss of phenological synchrony may have catastrophic effects on populations, suggesting that there will be a strong selection pressure on maintaining synchrony between interacting species (Fabina et al., 2010). The sensitivity of a species' demography to phenological asynchrony will depend however on the importance of that interaction and how likely the mismatch is to occur (Miller-Rushing et al., 2010). The selection pressure for *M.galathea* to time its emergence to that of *C.scabiosa* may depend therefore on the diversity of nectar sources that are available, and the phenology of these other plants (Gilman et al., 2012, Bartomeus et al., 2013). *C.scabiosa* is not the only nectar source used by *M.galathea* (Asher et al., 2001); in order to predict how phenological changes will affect the population dynamics of *M.galathea* it will be necessary to consider the phenology of other nectar sources. Furthermore plant pollinator interactions are not necessarily constant through time (Alarcon et al., 2008); some butterfly species such as *Aricia agesti* (brown argus), have recently undergone changes in host plant use (Thomas et al., 2001, Pateman et al., 2012). The potential for *M.galathea* to use previously unexploited nectar resources should also be considered. Additionally it should be noted that, in some species at least, phenological asynchrony occurred prior to anthropogenically caused climate change, suggesting that the selection pressure for synchrony may not be large (Singer and Parmesan, 2010).

The availability of nectar plants is not the only biotic interaction necessary for a butterfly species such as *M.galathea*. These species may also be affected by changes in the phenology and distribution of larval food plants, whilst some butterfly species also have specialist interactions with other organisms (Thomas et al., 2009). Conversely, biotic interactions are not only positive and phenological mismatches with species that have negative impacts, through competition, predation or parasitism, could have positive effects on the abundance of these insects.

Climate change is expected to have huge impacts on many species, communities and ecosystems (Parmesan and Yohe, 2003), yet too often studies focus on how single species will be affected, without considering the effects of biotic interactions, and how dependent species will be affected by the environmental change. Whilst biotic interactions are slowly being included into species distribution models (Araujo and Luoto, 2007, Cormont et al., 2013), there has been a lack of research on how the phenologies of insects and the species they interact with will be affected. Here I suggest that the phenology of a generalist butterfly may be starting to become out of sync with the flowering period of a key nectar source. Phenological mismatches have the potential to disrupt ecosystem functioning, with consequences not only for the species which have become asynchronous (Fabina et al., 2010, Nakazawa and Doi, 2012). Further research is necessary on the phenological cues used by interacting species in order to predict the effects of future climate change on communities.

Chapter 4

Comparing emergence and population estimates of *M.galathea* from mark release recapture and transect data.

Abstract

Background: Effective methods of monitoring populations are vital in evaluating the success of conservation strategies, however there is often a trade off between the accuracy and cost and intensity of methods. In Lepidoptera transect data have been widely used to inform conservation management. I compare estimates of population size over the season and demographic variables using more intensive mark release recapture data and transect data from Wingate quarry.

Methods:

Mark release recapture data were collected by walking the entire site every 2-3 days throughout the flight season and catching all encountered individuals with a net. These data were analysed using a POPAN model in MARK. A 1,550m by 5m transect was also walked every 2-3 days and butterflies were recorded according to the standard UKBMS guidelines. Estimates of population size and demographic parameters were obtained using a recently developed method of analysing transect data (Soulsby and Thomas, 2012).

Results and conclusions: The most parsimonious POPAN model allowed emergence, survival and capture rate to differ between the sexes and over the course of the season. Allowing differences between the sexes resulted in a different emergence curve to that produced from the transect data. Transect data should be used with caution, particularly if individuals cannot be easily sexed and the data is being used to compare populations that may differ in sex ratios or levels of protandry.

4.1 Introduction

Estimating population sizes and demographic parameters such as survival can provide vital information for monitoring populations of endangered species (Fox et al., 2011b, van Swaay et al., 2011). This includes determining the threat risk of a population or species and assessing the success of conservation management strategies. Additionally, as the emergence of adult butterflies, including *M.galathea* may be becoming asynchronous with the availability of nectar resources (see Chapter 3) being able to estimate the timing of emergence may help to determine whether species are likely to undergo phenological mismatches. Mark release recapture (MRR) methods can be used to estimate population sizes, demographic rates and to study dispersal, however as they require high levels of effort they are not always practical (Collier et al., 2008, Harker and Shreeve, 2008).

Transect data have been widely used to inform and evaluate conservation strategies, through estimating demographic parameters, relative abundance (Swengel and Swengel, 1997) and population sizes (Krauss et al., 2004). Transect data can be collected at large scales, using the help of amateur volunteers and requires much less intensive effort than mark release recapture experiments. In the UK butterflies have been widely monitored using transects, with data from sites across the country collated by the UK Butterfly Monitoring Scheme (UKBMS) since the 1970s. By comparing these data to that of more intensive methods it is possible to compare demographic parameters estimated from both approaches and assess the most relevant ways these data may be used (Haddad et al., 2008). Numerous studies have compared MRR data to transect data; some have shown close correlations between the data types (Bergman, 2001, Collier et al., 2008) whilst others have found little evidence that transects provide an accurate estimate of relative abundance or emergence patterns (Harker and Shreeve, 2008, Shuey and Szymanski, 2012).

There are several potential sources of error in transect data that could bias estimates of population size and emergence. The behaviour and spatial distribution of a population may differ both within and among days due to variation in the weather conditions, which could lead emergence patterns being wrongly identified (Harker and Shreeve, 2008). In addition, the statistical methods used to estimate population sizes from transect data often make what may be unrealistic assumptions, including that survival and other demographic parameters do not vary across the season (Calabrese, 2012).

I suggest that a further potential cause of bias in transect methods may arise due to the difficulty of sexing individuals when carrying out surveys. Detectability differs between species and sites (Isaac et al., 2011), with evidence that the abundances recorded may be dependent on behaviour, as well as wing pattern (Dennis et al., 2006). As wing pattern and colour, behaviour and microhabitat preferences may differ between the sexes (Slamova et al., 2011), it seems likely that detectability may also differ between the sexes. In addition, protandry is often found in butterfly populations, with males emerging before females (Schtickzelle et al., 2002). If protandry occurs in a population and one sex has a higher detectability then the transect data may show the emergence only of the more visible sex. It is often much easier to sex individuals in the hand, as happens during MRR experiments, which means that these experiments can be used to determine emergence differences between the sexes.

In this chapter I compare estimates of population size and emergence for *Melanargia galathea* from a MRR experiment to those from a recently developed method of analysing transect data (Soulsby and Thomas, 2012). I compare the fit of MRR models that allow selected parameters to differ across the season to others that remain fixed, and compare both to estimates derived from transect data. An inability to record the sex of individuals in transect data may affect resultant population size and emergence estimates from transect methods. Here I compare transect parameter estimates from transect data to the most parsimonious MRR model and a MRR model that does not allow emergence, detectability and survival variation between the sexes.

4.2 Methods

4.2.1 Study population and study site

The study site was Wingate Quarry Local Nature Reserve, County Durham (OS grid reference NZ3737). The site is 26.5 hectares in extent and the *M.galathea* study population was introduced to the site in 2000 as part of a study on the feasibility of using climate models to predict where suitable climate occurred for assisted colonisation (Willis et al., 2009a). Approximately 500 individuals were released and the population has since increased in size and dispersed across the study site, according to annual transect data (Willis et al., 2009a). Annual transect data suggests that the population is still increasing and has not yet reached carrying capacity. As this population is beyond the natural range of the species immigration is very unlikely and there has been little evidence of emigration from the site (Willis et al., 2009a). As a result, this population provides an ideal situation for comparing the two methods as the effects of migration can be assumed to be negligible.

4.2.2 Mark Release Recapture

A MRR experiment was carried out over the whole study site during the 2013 flight season. 1-2 people covered the whole site every 2-3 days over the entire flight period of *M.galathea* (05/07/2013 to 16/08/2013), depending on suitable weather conditions for butterfly activity (Pollard and Yates, 1993). No individuals were encountered on the first or last visits. A butterfly net was used to capture encountered individuals. The location of each capture was recorded on a map of the study site. The sex of the individual was also recorded and they were marked with an individually distinct pattern using a waterproof felt tip pen; marking individuals using this method does not appear to affect survival in *M.galathea* (Morton, 1982). Each individual was released immediately following marking, at its site of capture. The location and time of capture were recorded for all recaptured individuals. Nearby suitable habitats outside of the nature reserve were surveyed periodically to search for longer distance dispersers but none were recorded.

Statistical Analyses of MRR Data

The MRR data were analysed using a POPAN model (Schwarz and Arnason, 1996) in MARK to estimate (i) the probability an individual entered the population between two capture dates (*pent*), (ii) the catchability (*p*) of individuals, (iii) the probability an individual remains in the population between two capture dates (*phi*) and (iv) the overall population size (*N*). Whilst individuals can enter the population by eclosion or immigration and leave by death or emigration I assume that the effects of migration are minimal given the evidence cited above. *Pent* was calculated between all pairs of consecutive capture dates; the probability of an individual entering the population before the first capture date is then calculated as one minus the sum of the other *pent* values.

As effort was not constant between survey days *p* was constrained to vary linearly with effort (number of person hours). *Pent* and *phi* were either kept constant for all individuals or allowed to vary with sex, capture date or both. *N* was either kept constant or allowed to vary between the sexes. Where a parameter was allowed to vary with capture date (or effort) and sex, the model was tested both with and without an interaction between capture date and sex. All possible parameter combinations were tested and the most parsimonious models were selected as those with a ΔAIC ≤6 where there was no simpler model with a lower AIC value (Burnham and Anderson, 2002, Richards, 2008). As the most parsimonious model (lowest AIC value) allowed the parameters to differ between the sexes I compare this model to one which does not allow the sexes to differ and compare these two sets of parameter estimates to those estimated from transect data, the latter not accounting for sex differences.

4.2.3 Transect data

M.galathea abundance was surveyed using a 1,550m by 5m transect, following the standard UKBMS methodology (Pollard and Yates, 1993). The transect was walked every 2-3 days, depending on suitable weather conditions for butterfly activity (Pollard and Yates, 1993), from 30/06/2013 until 19/08/2013.

Statistical Analyses of Transect Data

I used the solver add-in in Microsoft Excel to estimate four parameters from the transect data involves: the transect population (*N**), mean life span (*T*), start date of eclosion (t_0) and the length of eclosion (T_E) (Soulsby and Thomas, 2012). The population curve was defined as follows:

$$n(t) = 0, \text{for } t'$$

$$n(t) = \left(\frac{3N^*}{4(a^2+9)}\right)\left(a\sin^3 X - 3\sin^2 X.\cos X + \frac{6}{a^2+1}(a\sin X - \cos X + e^{-aX})\right), \text{for } 0 \le t' \le T_E$$

$$n(t) = \frac{9N^* e^{-aX}(1+e^{a\pi})}{2(a^2+9)(a^2+1)}, \text{for } t' > T_E, \qquad \text{Equation 4.1}$$

where $a = T_E/(\pi T)$ and $X = \pi\, t'/T_E$ (Soulsby and Thomas, 2012). I assumed that the variation around the counts can be described by a negative binomial distribution, as ecological count data are often overdispersed (Richards, 2008). The parameter values were selected to maximise the log likelihood of *n* butterflies being observed on day *t*, which is given as

$$LL(\boldsymbol{\theta}|n) = ln\Gamma(n+a) - ln\Gamma(n+1) - ln\Gamma(a) + aln\left(\frac{b}{1+b}\right) - nln(1+b), \qquad \text{Equation 4.2}$$

where $a = n(t)/\varphi$, $b = 1/\varphi$ and φ is a positive parameter describing the level of variation in the data.

The normalised eclosion rate (Soulsby and Thomas, 2012) is given by

$$E(t'|T_E) = \frac{3\pi}{4} sin^3\left(\frac{\pi t'}{T_E}\right), \text{for } 0 \le t' \le T_E, \qquad \text{Equation 4.3}$$

$$E(t'|T_E) = 0 \text{ for } t' < 0 \text{ and } t' > T_E.$$

As with the MRR data above, the effect of immigration was assumed to be negligible. It is possible to estimate the site population (N) from the transect population (N*) assuming that $N^* = c.N$, where c is calculated as

$$c = \varepsilon WL/A. \qquad \text{Equation 4.4}$$

ε is the search efficiency, W is the transect width, L the transect length and A is the site area. The search efficiency refers to the probability of individuals being detected on a transect. As detectability differs between species the search efficiency is species specific (Soulsby and Thomas, 2012). It has been estimated for a range of species, by comparing estimates from standard Pollard transects to distance sampling methods; for *M.galathea* the search efficiency is estimated at 0.8 (Isaac et al., 2011).

The area of the Wingate site was calculated using Google Earth. Small areas of dense woodland thicket occur on the site, but these are not included in the transect and *M.galathea* individuals never use this habitat. As a result, the site population was estimated using the area of grassland only. This is the same area over which the MRR study was conducted.

4.3 Results

The most parsimonious POPAN model allowed survival (*phi*) and emergence (*pent*) to differ between the sexes and with capture date, and capture rate (*p*) to differ with effort and sex. Allowing the overall population size (N) to differ between the sexes, which would imply that the sex ratio differs from 1:1, did not improve the model fit (Table 4.1). Not allowing the remaining parameters to differ between the sexes results in much higher AIC values (and hence worse model fit), suggesting that there are important differences between males and females (Table 4.1). According to the most parsimonious model males emerged before females (Figure 4.2) and had lower survival rates, with a mean daily survival of 0.73 for females and 0.65 for males.

The methods of Soulsby and Thomas (2012) of estimating population emergence and size from transect data do not allow the parameters to vary between the sexes, or to change over the course of the season. The number of adults in flight differs only slightly across the season between the two methods (Figure 4.1). However, the transect data model estimates a lower population size at the beginning and end of the season, with a higher peak abundance (Figure 4.1).

Table 4.1: Number of parameters (K) and delta AIC values for parsimonious MRR models (^{p}) compared to a model (bottom) that does not allow parameters to vary between sexes. The estimated parameters are survival (*phi*), capture rate (*p*), probability of emergence (*pent*) and population size (*N*). Parameters can remain constant (.) or vary with sex (s), time of season (t) or, in the case of *p*, effort (e) or both sex and time. Where parameters vary with capture date (or effort) and sex, there may (*) or may not (+) be an interaction between these two variables.

Model	K	ΔAIC
Phi(s+t)*p*(s*e)*pent*(s*t)*N*.	48	0.00 $^{(p)}$
Phi(s+t)*p*(e)*pent*(s*t)*N*.	46	1.20 $^{(p)}$
Phi(s+t)*p*(s+e)*pent*(s*t)*N*(s)	48	1.55 $^{(p)}$
Phi(t)*p*(e)*pent*(t)*N*.	31	150.96

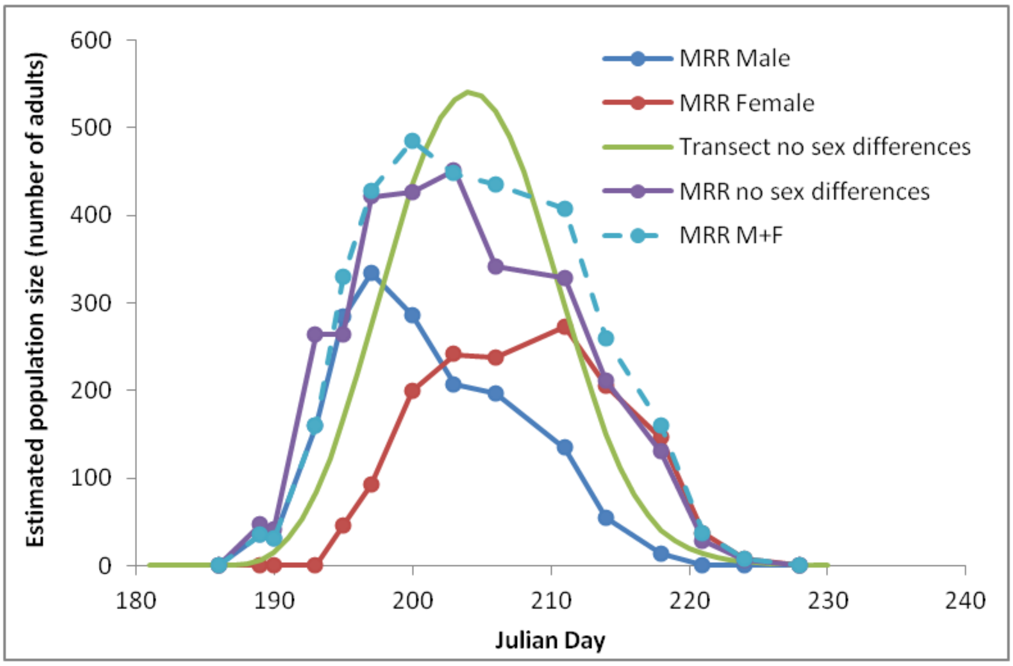


Figure 4.1: Estimated number of adults over the flight season, using transect data and mark release recapture data. The most parsimonious POPAN model estimates population size at each capture date for both sexes separately (blue and red lines); the dotted line shows the total adult population for this model as the sum of both sexes. The purple line shows the total population estimate for the MRR model with no sex differences. For the transect data the population size is estimated using Equation 4.1 (green line).

In the most parsimonious MRR model the capture probability differed between the sexes (Table 4.1), with a mean capture probability of 0.24 for males and 0.16 for females. However, despite the probability of capture being higher in males, the eclosion rate estimated from the transect data appears to be more similar to that of the females than males (Figure 4.2).

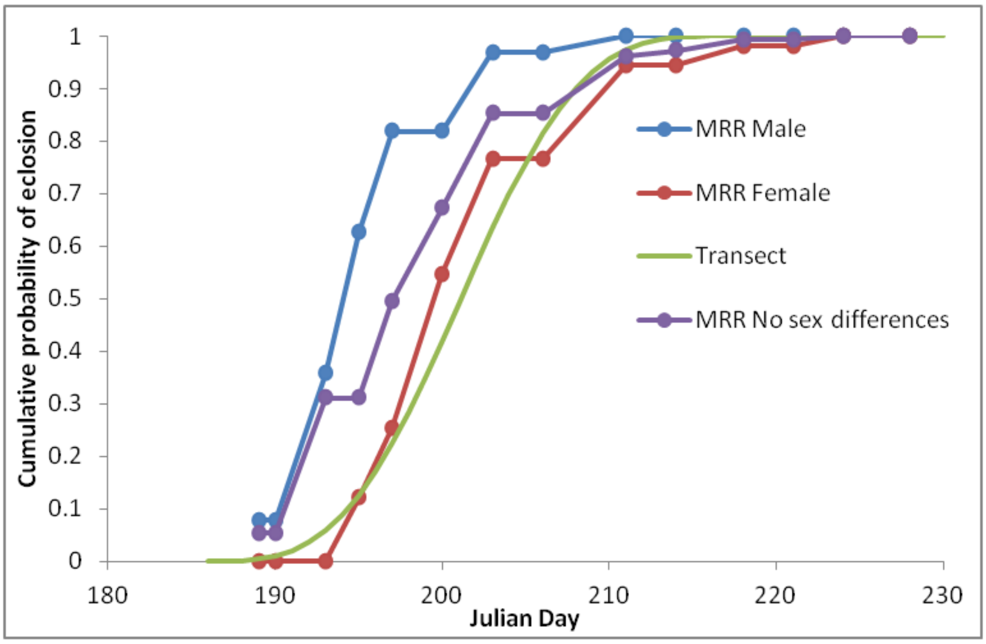


Figure 4.2: Cumulative probability of eclosion for males (blue line) and females (red line) for the MRR data using the most parsimonious model. The green line show the same for the transect data, using all individuals and the purple line is calculated from the MRR model assuming there are no differences between the sexes. For MRR data this is the cumulative *pent* parameter. For the transect data the normalised eclosion rate is calculated using Equation 4.4.

4.4 Discussion

The MRR model with no sex differences produces an emergence curve approximately mid-way between those estimated for the separate sexes using the most parsimonious model. The emergence curve from the transect data does not appear to follow that estimated from the MRR model that did not allow parameters to differ between the sexes; instead it more closely follows that of the female MRR data. Whilst this suggests that the method of estimating emergence using the method of Soulsby and Thomas (2012) on transect data produces emergence estimates biased towards one of the sexes, this is unexpected given that the capture probabilities (and therefore presumably sighting likelihood on transects) estimated from the MRR data are higher for males then females. It is possible that the interaction between sex and detectability differs between transects and MRR and that females are therefore more likely to be spotted during transects, despite males having higher MRR capture probabilities. However, it was not possible to test this during this study. Females appear to have higher survivorship so whilst the overall number of individuals did not differ between the sexes the sex ratio is female biased for a longer period of time than it is male biased (Figure 4.1). Despite a potentially lower detectability females may therefore be more likely to be seen overall.

The most parsimonious MRR model suggests that survival will vary over the course of the season, whilst the transect model assumes that survival is a constant. Compared to the sex-specific MRR model the peak population size appears to be overestimated from using the transect data, yet slightly underestimated by the MRR model which does not allow the parameters to differ between the sexes. There are other potential sources of bias in the transect data which must not be forgotten, including diurnal and daily variation in detectability and spatial distribution (Wikstroem et al., 2009). Despite transects only being carried out at certain times of day and when the weather is appropriate for butterfly activity, variation in behaviour and distribution may affect the counts (Harker and Shreeve, 2008).

In this chapter I show that the timing of emergence appears to differ between the sexes and that Soulsby and Thomas' (2012) method of analysing transect data may sometimes be biased towards estimating the emergence of one sex only, in this case the females. Population estimates may also differ between this method of analysing transect data and the more intensive MRR methods. There has been contrasting evidence previously as to whether transect data can provide accurate estimates of population sizes and emergence timings (Bergman, 2001, Collier et al., 2008, Harker and Shreeve, 2008, Shuey and Szymanski, 2012) for conservation purposes. It has been accepted previously that the accuracy of parameters estimated from transect data may differ between species, depending for example on the detectability of the species. Here I suggest that differences between sexes may also be important, including whether detectability differs between the sexes and whether protandry occurs in a population. Addtionally sex ratios may differ between populations or temporally, with a previous study on *M.galathea* reporting a 1.5: 1 male: female sex ratio (Munguira and Thomas, 1992), whilst here I found a 1:1 sex ratio. A further test of these potential biases would be to collect transect data on species where the sexes are easily identified during a transect, to see how being able to model the sexes separately affects the parameter estimates. Here, I conclude that estimates of population sizes and emergence using transect data may on some occasions lack accuracy due to a failure to account for differences between the sexes.

This does not mean that transect data do not have a use in conservation. However, they should be used with caution in some cases. Transect data has been used widely to study the phenology of butterflies (Brakefield, 1987, Diamond et al., 2011, Hodgson et al., 2011), monitor populations for conservation (Brereton et al., 2008, Pollard and Yates, 1993), assess the success of conservation strategies (Pollard, 1982) and more widely as indicators of trends in biodiversity (Brereton et al., 2011). It would be beneficial to validate population estimates and emergence estimates from transect data using more intensive surveying methods such as mark recapture (Shuey and Szymanski, 2012) for a wider range of species. For species without protandry or differing detectability and survivorship between the sexes, transect data may provide a rapid and easy approach to estimate populations and emergence accurately. By contrast, transects approaches may providing misleading estimates if differences occur between the sexes. Assuming that the sex ratio remains constant, differences between the demography of the sexes will not affect the use of transects for estimating how relative abundance changes among years. Whilst mark recapture methods are generally accepted to provide more accurate estimates of population size and demographic parameters there is a trade off with the intensity and cost of such data collection (Haddad et al., 2008). The low levels of expertise and effort needed to collect transect data mean that it provides a useful way to collect large volumes of data on the relative abundance and distribution of multiple species. In addition it is useful for extremely rare species as it does not risk damaging individuals which mark recapture methods may.

Chapter 5

The importance of heterogeneous habitats for conserving species under climate change

Abstract

Background: Heterogeneous habitats have long been recognised to increase biodiversity. Here I consider whether topographically heterogeneous habitats may aid the survival of species under climate change by decreasing phenological asynchrony and providing a range of microclimates and microhabitats for use under differing conditions or for different behaviours.

Methods: Log likelihood modelling was used to determine whether the emergence of two key nectar sources was affected by topographical diversity. A generalised linear model (GLM) was used on point count data to determine whether butterfly abundance varied with aspect, time of day or time of season. A chi square test of association was used on scan sample data to determine whether behaviour differed between aspects. The distances between multiple captures from mark-release-recapture data were analysed using multiple regression to determine whether mobility was affected by sex.

Results and Conclusions: The timing of both nectar species' flowering periods differed between aspects, resulting in extensions of the flowering period of 14 (*C.scabiosa*) and 3 (*C.nigra*) days. There was no significant difference between the sexes in the distance moved between captures (Multiple regression; R^2=0.03, $F_{3,160}$, p=0.14). *M.galathea* behaviour and abundance differed between microhabitats with mean five minute point count of 0.18 butterflies in flat sheltered areas compared with 1.32 in flat exposed areas. Topographical diversity may act as a buffer against the impacts of climate change for *M.galathea* and other insects, by increasing the length of time nectar sources are available for and by providing a range of microclimatic conditions. Topographically diverse sites may therefore be a key tool in the conservation of species and communities under future climate change.

5.1 Introduction

Heterogeneous habitats have long been recognised as important for increasing species richness, providing a range of habitats for a variety of species. Microclimate is particularly important for poikilothermic taxa such as insects; temperature can affect physiology, behaviour, survival and fecundity in butterflies (Weiss et al., 1988, Geister et al., 2008, Gibbs et al., 2010, Slamova et al., 2011, Berger et al., 2012, Koda and Nakamura, 2012). Microclimate will be affected by habitat type and local topography as well as regional climate (Bennie et al., 2008, Suggitt et al., 2011). The environment is stochastic;

heterogeneous environments may therefore also increase population stability (Kindvall, 1996, McLaughlin et al., 2002b, Oliver et al., 2010) by providing a wide range of microclimates that can be used under different macroclimatic conditions.

As the planet undergoes unprecedented rates of climate change (IPCC, 2007) heterogeneous habitats may be important in increasing the chances of populations persisting in areas that might otherwise become climatically unsuitable (Hopkins, 2007). Many species have been unable to track recent climate change (Devictor et al., 2012); prioritising the conservation of heterogeneous environments may help to increase persistence of populations within a species' current range. In addition the variability of the climate is expected to increase (Easterling et al., 2000), with increases in the frequency of heatwaves (Schar et al., 2004) and extreme precipitation events (Christensen and Christensen, 2003) predicted in the UK (Murphy et al., 2009). The effect of extreme climatic events on populations may be larger than changes in the mean climate (Bauerfeind and Fischer, 2014). An increase in precipitation variability has already been shown to be an important cause of population extinction in some butterfly species (McLaughlin et al., 2002a), whilst drought can also cause population crashes (Oliver et al., 2013). Heterogeneous environments may be able to buffer the effects of climatic variation on a population (Weiss et al., 1988, McLaughlin et al., 2002b), for example by providing refuges in order to escape high temperatures during hot summers (van Halder et al., 2011).

Studying microhabitat use and variation in behaviour between microhabitats can be useful for determining which microhabitats are most highly used for conservation purposes (Dover, 1996, Turner et al., 2009). Species may require different microhabitats for different behaviours, for example for collecting food and ovipositing (Maes et al., 2006), sexes (Zhou et al., 2012, Slamova et al., 2013) or lifestages (Freese et al., 2006). Species that require a wide range of microclimates may be more vulnerable to the effects of climate change.

The ability of a population to persist in or colonise an area will also be dependent on the presence of other species. For taxa such as Lepidoptera whose biotic interactions differ throughout the year depending on their life stage, they must be aligned both spatially and temporally with other species. As species phenologies may change at different rates under climate change there is the potential for phenological mismatches to occur (Parmesan, 2007, Thackeray et al., 2010). As plant phenology can also be affected by topography (Pellerin et al., 2012) topographically diverse sites may have longer flowering periods than homogeneous sites. This may help to prevent a phenological mismatch from occurring between butterflies and their nectar sources.

In this chapter I consider whether topographically diverse environments may be important in preventing extinctions under climate change, using the generalist butterfly *M. galathea*. Firstly I consider whether the presence of topographical diversity within a site can lengthen the flowering period of two *of M.galathea*'s key nectar sources *Centaurea scabiosa* and *Centaurea nigra*. Then I look at whether there are temporal variations in microhabitat use, both over a day and over the season, and whether behaviours differed between aspects. Finally I look for evidence that mobility differs between males and females as this may suggest differences in microhabitat use.

5.2 Methods

5.2.1 Study site and species

The study was conducted at Wingate Quarry Local Nature Reserve, county Durham (OS grid reference NZ3737). This 26.5 hectare site is beyond *M.galathea*'s natural northern range limit in the UK, the study population having been introduced in 2000 as part of an assisted colonisation experiment (Willis et al., 2009a). *C.scabiosa* is the main nectar source for *M.galathea*, although *C.nigra* and other purple flowers such as *Scabiosa* species are also used (Asher et al., 2001). Both knapweed species are perennials and are common across the study site and across the natural range of the butterfly in the UK, where they flower between June and September.

5.2.2 Flowering phenology of *C.scabiosa* and *C.nigra*

Data were collected on the flowering phenology of two knapweed species, *C.scabiosa* and *C.nigra*, (see Chapter 3 methods). Every 3-4 days throughout *M. galathea's* flight season between 30 and 40 individuals of each species were selected randomly on each aspect. The aspects studied were north east (NE), south east (SE), south west (SW) and south (S), as well as two types of flat area; flat sheltered (FS) was at the bottom of the quarry and was sheltered on all four sides, whereas, flat exposed (FE) was on the edge of the quarry, though still within the nature reserve, and was not sheltered on any side.

Statistical Analyses

The sum of flowering and past flowers is herein referred to as the cumulative number of flowers. As in Chapter 3 (Equation 3.1), the expected cumulative proportion of flowers by day x is approximated by

$$p(x) = \frac{e^{\beta(x-\bar{x})}}{1+e^{\beta(x-\bar{x})}}, \qquad \text{Equation 5.1}$$

where $\bar{x}$ is the day by which 50% of the flowers are open and β is a parameter negatively related to the length of the flowering period. I assumed that the variation in open flowers about the expected proportion is described by a beta-distribution such that when the mean is $p(x)$ the variance is $p(x)\big(1-p(x)\big)\phi/(1+\phi)$. This assumption implies that the number of open flowers among plants is described by a beta-binomial distribution. The log-likelihood of observing *n* flowers being open by day x when *N* flowers were present on a plant is given by

$$L(\boldsymbol{\theta}|N,n)=\frac{\Gamma(N+1)\Gamma(a+b)\Gamma(n+a)\Gamma(N-n+b)}{\Gamma(n+1)\Gamma(N-n+1)\Gamma(a)\Gamma(b)\Gamma(N+a+b)}, \quad \text{Equation 5.2}$$

where $a=p(x)/\phi$ and $b=(1-p(x))/\phi$. The base-line model is defined by the set of three parameters $\boldsymbol{\theta}=(\bar{x},\beta,\phi)$.

Five models were developed for each of the two *Centaurea* species, to test whether the timing of the flowering period, length of the flowering period and the amount of variation between plants, differed between aspects (Table 5.1). The Microsoft Excel add-in Solver was used to find the parameter estimates which maximised the log-likelihood for each model. All models with a ΔAIC <6, and where there was no simpler model with a lower AIC value, were considered as being supported by the data (Richards, 2008). The most parsimonious model (lowest AIC) was used to predict the length of the flowering period, which was defined as the period during which between 5 and 95% of the flowers had opened.

Table 5.1: Parameterisations of the models (Equation 5.1) to explore timing, length of flowering period and variation in phenology among plants for two knapweed species. Parameters refer to those which were allowed to vary between aspects in each model. *K* is the number of parameters estimated. The two species are modelled separately.

Model	*K*	Parameters affected by aspect	Description
M(-)	3	None	Timing and length of flowering period (FP) and variation between plants constant between aspects
M($\bar{x}$)	8	$\bar{x}$	Timing of FP varied between aspects
M($\bar{x}$ +β)	13	$\bar{x}, \beta$	Timing and length of FP varied between aspects
M($\bar{x}$+ ϕ)	13	$\bar{x}$, ϕ	Timing of FP and variation between plants varied between aspects
M($\bar{x}$+β+ ϕ)	18	$\bar{x}$, β, ϕ	Timing and length of FP and variation between plants varied between aspects

5.2.3 Microhabitat usage by *M.galathea*

I monitored replicated 5x5m randomly placed quadrats, each for a five-minute duration, recording all butterflies entering the quadrat. Scan samples at 20 second intervals were also undertaken during each five minute period, recording the behaviour of any individual within the quadrat during the scan. The following four aspects were studied; north-east, south-east, south-west and south, as well as flat areas; the latter being divided into sheltered and exposed sites. A total of 28 five minute-counts were taken on each aspect, and on each of the two types of flat ground, between 11th July and 4th August 2013. Samples were undertaken between 09:00 and 18:00, when the weather conditions were suitable for butterfly activity (Pollard and Yates, 1993).

Statistical Analyses

A generalised linear model (GLM) was used to determine whether the number of butterflies recorded during a point count varied between aspects, or with time of day or time of season. Sex was not included in the model as it was usually not possible to distinguish between the sexes. As the data were count data and there was evidence of overdispersion (i.e. the variance was higher than the mean), variation in the data about the mean was assumed to have a negative binomial distribution (Richards, 2008). Models were fitted with all combinations of the three independent parameters and their interactions. Parsimonious models were selected using AIC values (Burnham and Anderson, 2002); models with a ΔAIC ≤6, where there was no simpler model with a lower AIC value, were retained (Richards, 2008).

A chi-square test of association was used to test whether *M.galathea* behaviour differed amongst aspects. The behaviours were grouped into flying, nectaring and ‘other’ whilst the microhabitats were grouped into southerly (S, SE, SW) and ‘northerly or flat’ (FE, FS, NE), to remove combinations with expected values of less than five that would have invalidated the assumptions of the chi-square test.

5.2.4 Within-site movement

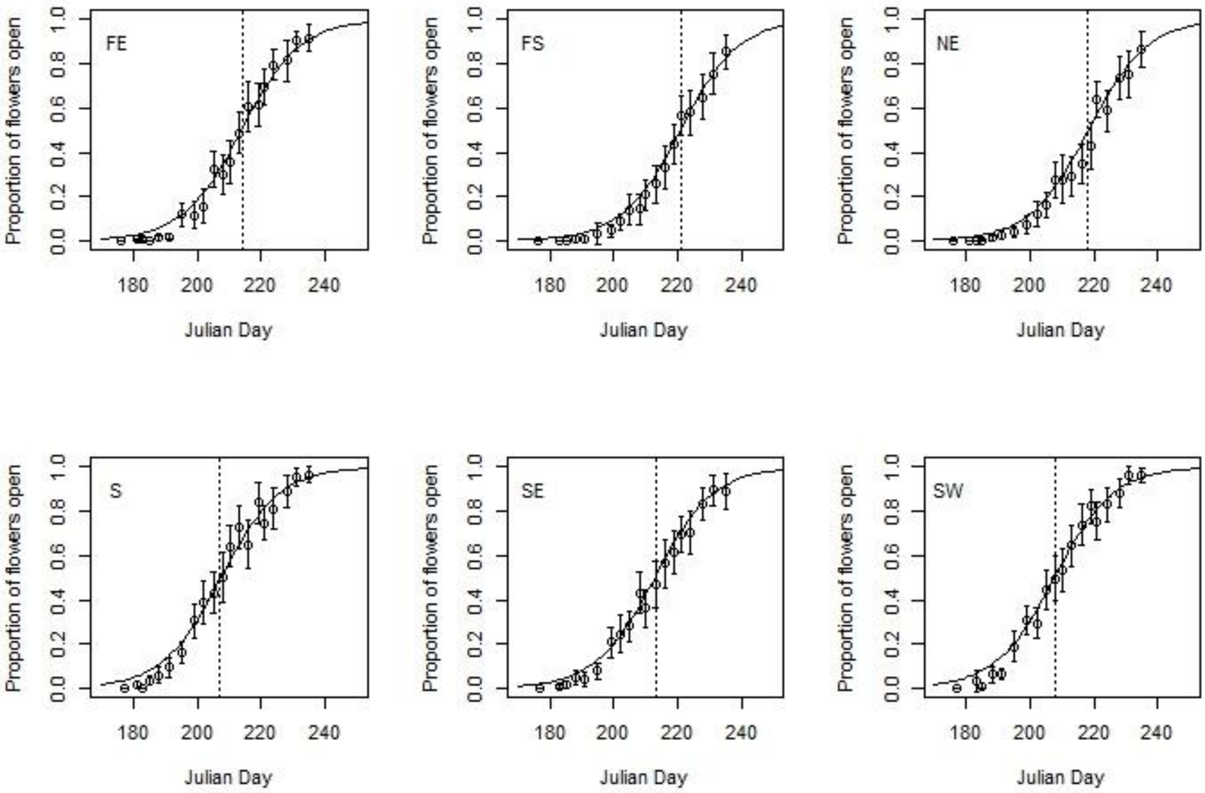
A mark release recapture experiment was carried out between 05/07/2013 and 16/08/2013, with a total of 15 capture days (see Chapter 3 methods). The location of each capture was marked on a map and the distance between captures was estimated using Google Earth. To avoid pseudoreplication the distance between the first two captures only for each individual was included (Skorka et al., 2013). The distance data was transformed by taking the natural logarithm. A multiple regression was used to determine whether the distance moved between captures was dependent on: sex, days between captures, and the time of season, which was represented by the midpoint between the two captures.

5.3 Results

5.3.1 Flowering phenology of *C.scabiosa* and *C.nigra*

For both species the most parsimonious model, $\mathrm{M}(\bar{x})$, allowed the timing of the flowering period (represented by $\bar{x}$, the day at which 50% of the flowers had opened), but not the length of the flowering period, to vary among aspects. In addition, the most parsimonious model did not demand differing variation between plants (φ) among aspects (Table 5.2; Figure 5.1). *C. scabiosa* was predicted to flower earliest on south facing slopes, 14 days before the flat sheltered areas (Table 5.3). *C. nigra* was predicted to flower first on south and south-east slopes, 3 days before it flowered on flat sheltered areas and north east slopes (Table 5.3). The flowering period on each aspect was estimated to be 54 days for *C.scabiosa* and 39 days for *C.nigra*, giving a total flowering period for the site of 68 days for *C.scabiosa* and 42 days for *C.nigra* over the four aspects and two flat areas.

C.scabiosa



C.nigra

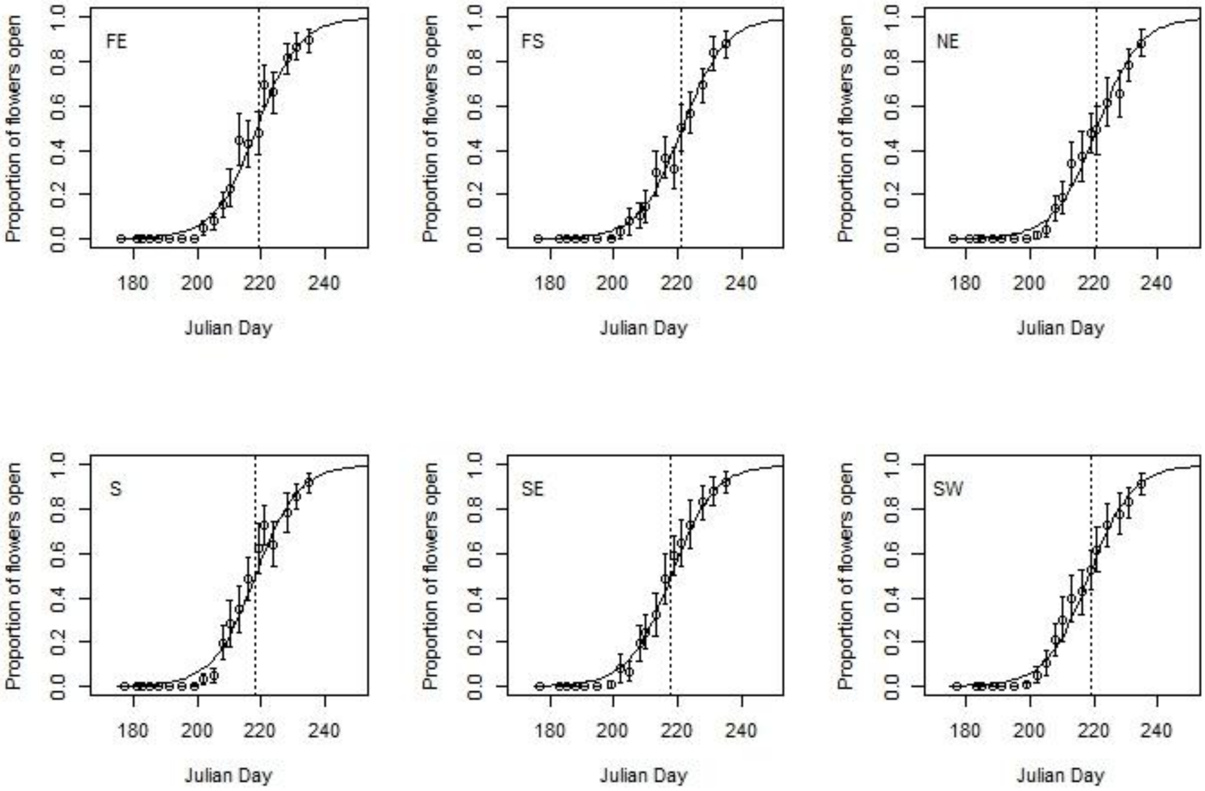


Figure 5.1: Mean proportion of flowers on each plant open on each day, for *C.scabiosa* and *C.nigra*. 30-40 plants were studied every 3-4 days during *M. galathea*'s flight period. The error bars show 95% confidence intervals. The solid lines show the predicted number of open flowers according to the best model fit (M2; Table 5.2). The dotted lines show the estimated day on which 50% of the flowers are open on each aspect.

Table 5.2: Model selection results for the estimation of the flowering phenology of *C.scabiosa* and *C.nigra* (see Table 5.1). The model with the lowest AIC was selected for both species as the only other models with ΔAIC ≤6 were nested versions of the best model (Richards, 2008). No values are reported for M4 for *C.scabiosa* as this model did not converge.

Species	Model	K	LL	ΔAIC
C. scabiosa	M(-)	3	-5826.69	416.57
	M($\bar{x}$)	8	-5613.40	0.00*
	M($\bar{x}$+β)	13	-5610.82	4.83
	M($\bar{x}$+ϕ)	13	-	-
	M($\bar{x}$+β+ϕ)	18	-5610.71	4.60
C. nigra	M(-)	3	-3692.76	33.73
	M($\bar{x}$)	8	-3670.89	0.00*
	M($\bar{x}$+β)	13	-3669.91	8.04
	M($\bar{x}$+ϕ)	13	-3670.67	9.55
	M($\bar{x}$+β+ϕ)	18	-3669.78	17.77

Table 5.3 Julian day by which 5% and 50% of the flowers opened on each aspect for *C.scabiosa* and *C.nigra* according to the best fitting model, M($\bar{x}$); Table 5.2).

Aspect	*C.scabiosa*		*C.nigra*	
	5% open	50% open	5% open	50% open
FE	187	214	200	219
FS	194	221	202	221
NE	192	218	202	221
S	181	207	199	218
SE	186	213	199	218
SW	181	208	199	219

5.3.2 Microhabitat usage by *M.galathea*

The most parsimonious model suggested that the number of adult butterflies varied with aspect but not time of day or season (Table 5.4). Flat sheltered areas had the lowest counts, with a mean of 0.18 butterflies per five minute point count. Post-hoc comparisons on the most parsimonious model suggested that this was significantly fewer butterflies than any of the other aspects (Figure 5.2; 0.0002<*p*<0.046). Flat exposed areas had the highest average count (mean of 1.32 butterflies per five minute point count), but this was not significantly higher than for south west (1.21), south east (0.82) or north east (0.64) slopes.

Table 5.4 Models for differences in abundance between aspect, time of day and Julian day. All models with a ΔAIC ≤6 are shown, with parsimonious models shown with a *.

Model	ΔAIC
Aspect	0.00*
Aspect + Time of day	0.49
Aspect * Time of day	1.25
Aspect + Julian day	1.25
Aspect + Julian day + Time of day	1.36
Aspect + Julian day * Time of day	1.81
Aspect * Time of day + Julian day	2.23
Aspect * Julian day * Time of day	4.41
Aspect * Julian day + Time of day	4.88
Aspect * Julian day	5.36

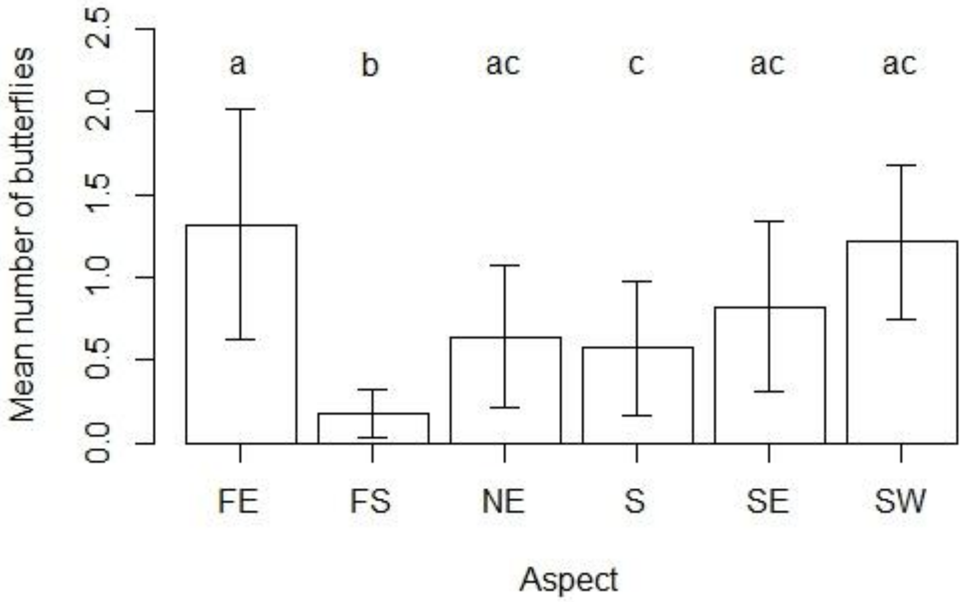


Figure 5.2: Mean number of butterflies seen during each five minute point count on each of the six aspects. Error bars show 95% confidence intervals and the labels show which aspects differed significantly. A total of 28 point counts were performed on each aspect.

The proportion of time spent in each behaviour differed between southerly and non-southerly aspects (χ^2_2=11.21, p<0.01). The majority of observations on non-south facing areas were of flying individuals, whilst a higher proportion of time was spent collecting nectar and in other behaviours, such as basking, on south facing slopes (Figure 5.3). However, the only recorded sightings of ovipositing and mating were in flat exposed areas, although these observations only accounted for three out of a total of 111 behavioural observations. When flying observations were excluded there was no significant difference between the proportion of time spent collecting nectar and in other behaviours between southerly and non-southerly aspects (Fisher's Exact Test; *p*=0.35).

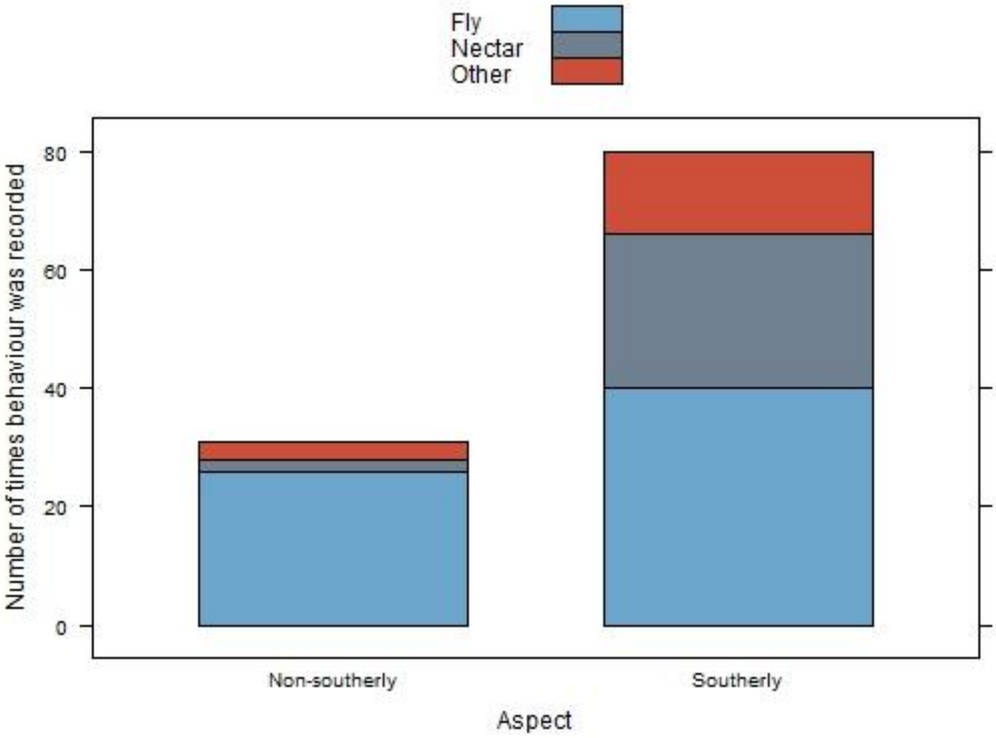


Figure 5.3 Number of times each type of behaviour was recorded on southerly and non-southerly aspects. The behaviour of any individuals within the plot was recorded every 20 seconds during a total of 168 five minute scan samples.

5.3.3 Within-site movement

Of 467 individual butterflies caught, 164 individuals were caught at least twice, 102 of which were male. 44 individuals were caught more than twice with only 12 individuals being caught more than three times. The mean distance moved between captures was 113m and the maximum was 487m. The mean number of days between captures was 6. The multiple regression was performed without interactions between any of the variables as none of the interactions were significant. The distance moved between captures was not significantly affected by sex, time between captures or time of season (Figure 5.3; Multiple regression; R^2=0.03, *p*=0.14).

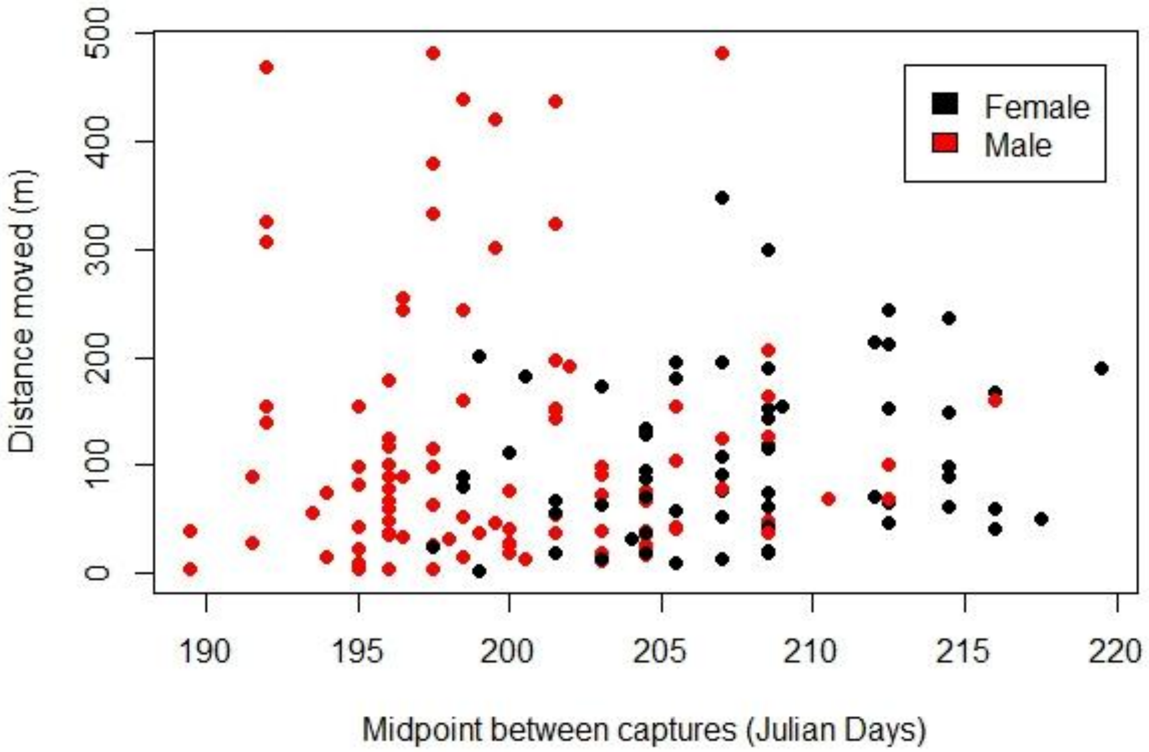


Figure 5.4: Distance between first and second captures for individuals caught multiple times during the mark release recapture experiment against the midpoint between capture days. Each point represents an individual.

5.4 Discussion

The heterogeneous topography of this site increased the overall flowering period for both species of knapweed, although the effect was considerably larger in *C.scabiosa*. This increase in flowering period may help to decrease the chance of a phenological mismatch occurring between *M.galathea* and its nectar sources as their phenologies change under climate change (see Chapter 3). In addition different microhabitats may provide suitable conditions for different behaviours, times of day or time of season. The heterogeneity of the site and an average movement between captures of 113m, suggests that individuals do travel across a topographically diverse area. Longer distance movement was seen in *M.galathea* in this study than at other sites (Munguira and Thomas, 1992), although the sites in this previous study were roadside verges and the road appeared to act as a barrier in at least one of these populations. Whilst the majority of time spent on non-south facing slopes was spent in flight, which could suggest that individuals only passed through such areas, mating and ovipositing were only ever recorded on these aspects. As the behaviours may also have been affected by factors such as temperature, time of day and time of flight season further research is needed into the spatial and temporal variation of behaviours. It seems surprising that time of day and season had no affect on abundance; it is possible that other differences between the aspects may have hidden the effects of these variables.

These preliminary results suggest that flat exposed areas were important in supporting this population as they had the highest abundances and were the only areas in which mating was seen, although this was rarely recorded. These areas are likely to receive sunlight for large portions of the day. As this study was conducted solely at one site in one year it cannot be assumed that this is the preferred microhabitat of this species over its entire range. A previous study in Switzerland found that this species mainly used southerly aspects (Erhardt, 1985). Additionally, it should be noted that mating was rarely recorded even on these areas; further studies are needed to determine whether mating also occurs on other aspects. As a previous study had found that increased shelter increased the abundance of three other species of Nymphalidae on farmland margins (Dover, 1996), the significantly lower abundances of *M.galathea* in flat sheltered areas is unexpected. However, microhabitat usage may be affected by the weather conditions (Dennis and Sparks, 2006), with an increase in the use of sheltered areas seen with increasing wind speeds in many species (Dover et al., 1997). In order to minimise the effects of variables such as weather, it would be preferable to redo the study with a recorder on each aspect at the same time.

Future studies could look at how microhabitat usage differs between sites at the core and edge of the range, as local adaptation may have occurred (e.g. Friberg et al., 2008). As temperatures differ along latitudinal gradients comparing microhabitat usage between sites may help to predict how microhabitat usage will be altered as the climate changes. Topographically diverse environments may be more important for the survival of populations at the edge of their ranges, where the climate may not be as suitable as in the core of their range. Additionally whilst there was no evidence of differences in movement between the sexes it would be interesting to see whether there are behavioural differences, or differences in habitat preferences (e.g. Zhou et al., 2012, Slamova et al., 2013). If habitat associations differ between the sexes then heterogeneous environments may be necessary to support that species (Slamova et al., 2013).

As the predominant nectar sources used by *M.galathea* (Asher et al., 2001) were widely spread across the site, and found on all of the aspects this was not taken into account in this study. However, the microdistribution of *M.galathea* has previously been shown to be affected by flower abundance (Steffan-Dewenter and Tscharntke, 1997) and the availability of nectar sources (Loertscher et al., 1995). Further studies could look at the relative abundance of nectar sources between aspects, and whether this affects *M.galathea* abundance.

Here I provide evidence that a topographically heterogeneous site may help to prevent future phenological mismatches from occurring between an insect species and its nectar source and provides a range of microhabitats that may be needed for different behaviours.

Heterogeneous habitats should be prioritised for conserving species under climate change, whilst non-topographically diverse areas may be managed to create different microclimatic conditions (Hopkins, 2007). In addition topography may be an important factor to include when predicting how species distributions will alter under climate change (Franklin et al., 2013, Storlie et al., 2013).

Chapter 6

Final conclusions and future work

Due to their charismatic nature, ease of identification and the willingness of amateur volunteers, butterflies are an extremely well studied taxa, particularly in the UK (Warren et al., 2007). However, given the recent declines in butterflies in Britain (Fox et al., 2007, Fox et al., 2011a, Fox et al., 2011b) and across Europe (van Swaay et al., 2006, van Swaay et al., 2011), additional research on the ecology of these species for conservation purposes is required. Additionally analysing data on the ecology of butterflies can provide insights into the conservation of this taxonomic group as a whole (Thomas, 2005). In this thesis I provide further knowledge on the habitat preferences, phenology and biotic interactions of *M.galathea,* which may be helpful for developing appropriate conservation strategies for this species, British butterflies generally, and other insect species. Specifically I make the following recommendations for the conservation of *M.galathea* and other insects:

1. Heterogeneity in abundance with habitat type at a broad scale (Chapter 2) and topography at a fine scale (Chapter 5) should be taken into account in the management of habitats for conservation and when predicting future species distributions (Bennie et al., 2008, Wilson et al., 2010, Bennie et al., 2013).
2. Estimates of demographic rates such as intrinsic growth rates should also be included in models predicting future species distributions, as these differ between species and may affect the ability of species to track climate change (Chapter 2).
3. Topographically diverse sites should be prioritised for conservation as these may be key to providing a range of microclimates for insects and in reducing the likelihood of phenology asynchrony between insects and their host plants (Chapter 5). For the same reason homogeneous sites should be managed in such a way as to increase the diversity in available microclimates (Hopkins, 2007).
4. Population monitoring methods should take into account the life history of the species, including whether protandry may occur as this may affect estimates of population size and demographic parameters (Chapter 4). Transect data should be used with caution when it is not possible to sex individuals.
5. The design of conservation strategies should take into account the possibility of phenological asynchrony between insects and their hostplants (Chapter 3). This may be of particular importance in planning assisted colonisations as local adaptations may increase the chance of phenological asynchrony. Measures to counteract such problems could include the translocation of other hostplants with different flowering periods as well choosing topographically diverse sites for translocations.

Throughout this thesis I have focused on the requirements of adults only. Adult butterflies are more often studied than other life stages, probably in part due to their charismatic appearance, and ease of identification. Like many insects, butterflies go through numerous discrete life stages which may have different habitat requirements (Freese et al., 2006). The larval stages of many butterfly species may be highly affected by microclimate and food plant availability, with the potential to cause major changes in population dynamics (Turlure et al., 2010, Thomas et al., 2011, Eilers et al., 2013). To truly understand the effects of climate change on Lepidoptera species such as *M.galathea,* it will be necessary to study the requirements of all of their life stages (Kingsolver et al., 2011, Radchuk et al., 2013). Future work should focus on the habitat requirements of larvae and the possible effects of climate change on egg, larval and pupae survival, development and growth. However, many of the conclusions drawn in this thesis are expected to hold true for larvae as well as adults. For example, an increase in topographical diversity is also expected to be beneficial for larval stages (Pennekamp et al., 2013). Additionally larval food plants and adult nectar plants may occur in different microhabitats (Wilson, 1985, Stace, 1991, Asher et al., 2001), in which case the importance of heterogeneous sites may be even more important than realised when studying adults alone.

Additional future work could concentrate on the climatic factors and physiological mechanisms that are driving changes in phenology; understanding these factors may help to predict whether phenological mismatches will occur between interacting species under future climate change. Furthermore testing whether there is a consistent relationship between climate and the timing of *M.galathea*'s flight period across sites and years could show whether local adaptation in emergence has occurred. This may have consequences for the ability of species to adapt to changes in the climate (Roy and Asher, 2003). A failure to take local adaptations into account could affect the success of conservation measures such as assisted colonisations (Turlure et al., 2013), if populations cannot alter their emergence to account for changes in temperatures between sites (Roy and Asher, 2003). In *M.galathea* the flight period was later at sites further north (Chapter 3), suggesting that local adaptation in flight period may not have occurred, which may have been key in the successful translocation of this species (Willis et al., 2009a). However, this study only looked at three study sites and a limited number of years. The lack of difference in phenology across temperature gradients seen in some species (Pollard, 1991, Roy and Asher, 2003), suggests that local adaptations may have occurred.

Throughout this thesis I provide knowledge to aid the conservation of insects under changing environmental conditions. Whilst anthropogenic climate change is thought to provide the largest threat to biodiversity, the ability of both species and conservation managers to cope with this climate change will be constrained by other factors such as competing land uses (Sala et al., 2000, Thomas et al., 2004a). The global human population has grown rapidly to 7.2 billion in 2013 and is still rising, with predictions that it could reach 10.9 billion by 2100 (United Nations, 2013). Within the UK the population size is expected to increase from 62.3 million in 2010 to 73.2 million in 2035 (Office for National Statistics, 2012). There are therefore conflicts between biodiversity conservation and anthropogenic land uses, with estimates that humans have appropriated around 20% of the Earth’s terrestrial net primary production (Imhoff et al., 2004). Whilst the rate at which natural land is converted to agricultural land has decreased in recent years, and may even be reversing within the UK (Firbank et al., 2008), agricultural intensification has led to increased habitat fragmentation and degradation. This intensification has been necessary to allow food production to keep pace with the increasing human population, however it has had negative impacts on biodiversity (Matson et al., 1997, Krausmann et al., 2013). In Britain an estimated 70% of semi-natural habitats have been lost since 1940 due to agricultural intensification (Asher et al., 2001). In addition the increasing homogeneity of agricultural land caused by multiple factors including the simplification of crop rotations, the presence of fewer larger fields and the use of agrochemicals, has been shown to negatively affect biodiversity (Benton et al., 2003).

Dynamic conservation strategies are necessary to conserve species, communities and ecosystems under changing environmental conditions. Many species are expected to shift their distributions as the climate changes (Parmesan and Yohe, 2003). However, a lack of connectivity between habitat patches may prevent species from reaching newly suitable areas. Habitat fragmentation and degradation are thought to have been key in restricting the ability of many species to track climate change (Warren et al., 2001, Wilson et al., 2010). This has led to an increase in landscape-scale approaches to butterfly conservation, targeting networks of sites and aiming to increase connectivity to allow movement between sites (Fox et al., 2011a, Dennis et al., 2013). Government backed agri-environment schemes may also increase heterogeneity within farmlands and allow species to disperse across otherwise hostile landscapes (Delattre et al., 2013b), whilst assisted colonisations may provide a last resort for conserving species that are unable to track climate (Willis et al., 2009a). However, knowledge on species habitat preferences, biotic interations and resource requirements are vital for the success of all of these schemes (Pywell et al., 2004, Pywell et al., 2011). Research can therefore play a key role in determining the most effective ways to protect species, communities and ecosystems under a changing climate. For example it has been shown that active management of protected areas can increase the likelihood of them being colonised by *Hesperia comma* (silver spotted skipper) (Lawson et al., 2014). The importance of research on the effectiveness of management strategies may be exacerbated by the financial constraints on conservation. Many organisations involved in managing sites for conservation are charities and are severely limited by funds. The severe limits on the amount of land and money available for conservation necessitate efficient conservation measures.

There are huge challenges facing the conservation of British butterflies and other insects including the effects of climate change and habitat loss and degradation. The rapid rates of decline seen in British butterflies coupled with the restricted resources available for conservation necessitates efficient and effective evidence based conservation strategies (Thomas et al., 2011, Fox et al., 2011a). Throughout this thesis I highlight the importance of considering the spatial and temporal effects of environmental change at multiple scales when planning strategies for the conservation of species under future climate change. Whilst I focus mainly on *M.galathea* I draw several conclusions that may aid the conservation of insects more widely. Insects are hugely important ecologically, providing a food source for taxa in higher trophic levels and providing ecosystem services such as pollination. There may therefore be wider community effects if environmental changes, cause decreases in their abundances or restrict their distributions (Pearce-Higgins et al., 2010, Nakazawa and Doi, 2012).

References

ALARCON, R., WASER, N. M. & OLLERTON, J. 2008. Year-to-year variation in the topology of a plant-pollinator interaction network. *Oikos,* 117**,** 1796-1807.

ALTERMATT, F. 2010. Climatic warming increases voltinism in European butterflies and moths. *Proceedings of the Royal Society B: Biological Sciences,* 277**,** 1281-1287.

ALTWEGG, R., COLLINGHAM, Y. C., ERNI, B. & HUNTLEY, B. 2013. Density-dependent dispersal and the speed of range expansions. *Diversity and Distributions,* 19**,** 60-68.

ANDRELLO, M., BIZOUX, J.-P., BARBET-MASSIN, M., GAUDEUL, M., NICOLE, F. & TILL-BOTTRAUD, I. 2012. Effects of management regimes and extreme climatic events on plant population viability in Eryngium alpinum. *Biological Conservation,* 147**,** 99-106.

ARAUJO, M. B., ALAGADOR, D., CABEZA, M., NOGUES-BRAVO, D. & THUILLER, W. 2011. Climate change threatens European conservation areas. *Ecology Letters,* 14**,** 484-492.

ARAUJO, M. B. & LUOTO, M. 2007. The importance of biotic interactions for modelling species distributions under climate change. *Global Ecology and Biogeography,* 16**,** 743-753.

ASHER, J., WARREN, M., FOX, R., HARDING, P., JEFFCOATE, G. & JEFFCOATE, S. 2001. *Millenium atlas of butterflies in Britain and Ireland.*, Oxford University Press, Oxford.

ASHTON, S., GUTIERREZ, D. & WILSON, R. J. 2009. Effects of temperature and elevation on habitat use by a rare mountain butterfly: implications for species responses to climate change. *Ecological Entomology,* 34**,** 437-446.

ASSESSMENT, M. E. 2005. Ecosystems and Human Well-being: Biodiversity Synthesis. World Resources Institute, Washington, DC.

BARNOSKY, A. D., MATZKE, N., TOMIYA, S., WOGAN, G. O. U., SWARTZ, B., QUENTAL, T. B., MARSHALL, C., MCGUIRE, J. L., LINDSEY, E. L., MAGUIRE, K. C., MERSEY, B. & FERRER, E. A. 2011. Has the Earth's sixth mass extinction already arrived? *Nature,* 471**,** 51-57.

BARTOMEUS, I., ASCHER, J. S., WAGNER, D., DANFORTH, B. N., COLLA, S., KORNBLUTH, S. & WINFREE, R. 2011. Climate-associated phenological advances in bee pollinators and bee-pollinated plants. *Proceedings of the National Academy of Sciences of the United States of America,* 108**,** 20645-20649.

BARTOMEUS, I., PARK, M. G., GIBBS, J., DANFORTH, B. N., LAKSO, A. N. & WINFREE, R. 2013. Biodiversity ensures plant-pollinator phenological synchrony against climate change. *Ecology Letters,* 16**,** 1331-1338.

BAUERFEIND, S. S. & FISCHER, K. 2014. Simulating climate change: temperature extremes but not means diminish performance in a widespread butterfly. *Population Ecology,* 56**,** 239-250.

BENNIE, J., HODGSON, J. A., LAWSON, C. R., HOLLOWAY, C. T. R., ROY, D. B., BRERETON, T., THOMAS, C. D. & WILSON, R. J. 2013. Range expansion through fragmented landscapes under a variable climate. *Ecology Letters,* 16**,** 921-9.

BENNIE, J., HUNTLEY, B., WILTSHIRE, A., HILL, M. O. & BAXTER, R. 2008. Slope, aspect and climate: Spatially explicit and implicit models of topographic microclimate in chalk grassland. *Ecological Modelling,* 216**,** 47-59.

BENTON, T. G., VICKERY, J. A. & WILSON, J. D. 2003. Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology & Evolution,* 18**,** 182-188.

BERGER, D., OLOFSSON, M., GOTTHARD, K., WIKLUND, C. & FRIBERG, M. 2012. Ecological Constraints on Female Fitness in a Phytophagous Insect. *American Naturalist,* 180**,** 464-480.

BERGMAN, K.-O. 2001. Population dynamics and the importance of habitat management for conservation of the butterfly Lopinga achine. *Journal of Applied Ecology,* 38**,** 1303-1313.

BRAKEFIELD, P. M. 1987. GEOGRAPHICAL VARIABILITY IN, AND TEMPERATURE EFFECTS ON, THE PHENOLOGY OF MANIOLA-JURTINA AND PYRONIA-TITHONUS (LEPIDOPTERA, SATYRINAE) IN ENGLAND AND WALES. *Ecological Entomology,* 12**,** 139-148.

BRERETON, T., ROY, D. B., MIDDLEBROOK, I., BOTHAM, M. & WARREN, M. 2011. The development of butterfly indicators in the United Kingdom and assessments in 2010. *Journal of Insect Conservation,* 15**,** 139-151.

BRERETON, T. M., WARREN, M. S., ROY, D. B. & STEWART, K. 2008. The changing status of the Chalkhill Blue butterfly Polyommatus coridon in the UK: the impacts of conservation policies and environmental factors. *Journal of Insect Conservation,* 12**,** 629-638.

BRISCOE, N. J., PORTER, W. P., SUNNUCKS, P. & KEARNEY, M. R. 2012. Stage-dependent physiological responses in a butterfly cause non-additive effects on phenology. *Oikos,* 121**,** 1464-1472.

BROHAN, P., KENNEDY, J. J., HARRIS, I., TETT, S. F. B. & JONES, P. D. 2006. Uncertainty estimates in regional and global observed temperature changes: A new data set from 1850. *Journal of Geophysical Research-Atmospheres,* 111.

BROWN, K. S. & FREITAS, A. V. L. 2000. Atlantic forest butterflies: Indicators for landscape conservation. *Biotropica,* 32**,** 934-956.

BULL, J. W., SUTTLE, K. B., SINGH, N. J. & MILNER-GULLAND, E. J. 2013. Conservation when nothing stands still: moving targets and biodiversity offsets. *Frontiers in Ecology and the Environment,* 11**,** 203-210.

BURNHAM, K. P. & ANDERSON, D. R. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*, Springer, New York.

CALABRESE, J. M. 2012. How emergence and death assumptions affect count-based estimates of butterfly abundance and lifespan. *Population Ecology,* 54**,** 431-442.

CALINGER, K. M., QUEENBOROUGH, S. & CURTIS, P. S. 2013. Herbarium specimens reveal the footprint of climate change on flowering trends across north-central North America. *Ecology Letters,* 16**,** 1037-1044.

CARROLL, M. J., ANDERSON, B. J., BRERETON, T. M., KNIGHT, S. J., KUDRNA, O. & THOMAS, C. D. 2009. Climate change and translocations: The potential to re-establish two regionally-extinct butterfly species in Britain. *Biological Conservation,* 142**,** 2114-2121.

CHERRY, S. G., DEROCHER, A. E., THIEMANN, G. W. & LUNN, N. J. 2013. Migration phenology and seasonal fidelity of an Arctic marine predator in relation to sea ice dynamics. *Journal of Animal Ecology,* 82**,** 912-921.

CHRISTENSEN, J. H. & CHRISTENSEN, O. B. 2003. Climate modelling: Severe summertime flooding in Europe. *Nature,* 421**,** 805-806.

COLLIER, N., MACKAY, D. A. & BENKENDORFF, K. 2008. Is relative abundance a good indicator of population size? Evidence from fragmented populations of a specialist butterfly (Lepidoptera : Lycaenidae). *Population Ecology,* 50**,** 17-23.

CORMONT, A., MALINOWSKA, A. H., KOSTENKO, O., RADCHUK, V., HEMERIK, L., WALLISDEVRIES, M. F. & VERBOOM, J. 2011. Effect of local weather on butterfly flight behaviour, movement, and colonization: significance for dispersal under climate change. *Biodiversity and Conservation,* 20**,** 483-503.

CORMONT, A., WAMELINK, G. W. W., JOCHEM, R., WALLISDEVRIES, M. F. & WEGMAN, R. M. A. 2013. Host plant-mediated effects of climate change on the occurrence of the Alcon blue butterfly (Phengaris alcon). *Ecological Modelling,* 250**,** 329-337.

CRICK, H. Q. P., DUDLEY, C., GLUE, D. E. & THOMSON, D. L. 1997. UK birds are laying eggs earlier. *Nature,* 388**,** 526-526.

CRICK, H. Q. P. & SPARKS, T. H. 1999. Climate change related to egg-laying trends. *Nature,* 399**,** 423-424.

DAVIES, Z. G., WILSON, R. J., COLES, S. & THOMAS, C. D. 2006. Changing habitat associations of a thermally constrained species, the silver-spotted skipper butterfly, in response to climate warming. *Journal of Animal Ecology,* 75**,** 247-256.

DELATTRE, T., BAGUETTE, M., BUREL, F., STEVENS, V. M., QUENOL, H. & VERNON, P. 2013a. Interactive effects of landscape and weather on dispersal. *Oikos,* 122**,** 1576-1585.

DELATTRE, T., VERNON, P. & BUREL, F. 2013b. An agri-environmental scheme enhances butterfly dispersal in European agricultural landscapes. *Agriculture Ecosystems & Environment,* 166**,** 102-109.

DENNIS, R. L. H., DAPPORTO, L., DOVER, J. W. & SHREEVE, T. G. 2013. Corridors and barriers in biodiversity conservation: a novel resource-based habitat perspective for butterflies. *Biodiversity and Conservation,* 22**,** 2709-2734.

DENNIS, R. L. H. & SHREEVE, T. G. 1991. CLIMATIC-CHANGE AND THE BRITISH BUTTERFLY FAUNA - OPPORTUNITIES AND CONSTRAINTS. *Biological Conservation,* 55**,** 1-16.

DENNIS, R. L. H., SHREEVE, T. G., ISAAC, N. J. B., ROY, D. B., HARDY, P. B., FOX, R. & ASHER, J. 2006. The effects of visual apparency on bias in butterfly recording and monitoring. *Biological Conservation,* 128**,** 486-492.

DENNIS, R. L. H. & SPARKS, T. H. 2006. When is a habitat not a habitat? Dramatic resource use changes under differing weather conditions for the butterfly Plebejus argus. *Biological Conservation,* 129**,** 291-301.

DENNIS, R. L. H. & SPARKS, T. H. 2007. Climate signals are reflected in an 89 year series of British Lepidoptera records. *European Journal of Entomology,* 104**,** 763-767.

DEVICTOR, V., VAN SWAAY, C., BRERETON, T., BROTONS, L., CHAMBERLAIN, D., HELIOLA, J., HERRANDO, S., JULLIARD, R., KUUSSAARI, M., LINDSTROM, A., REIF, J., ROY, D. B., SCHWEIGER, O., SETTELE, J., STEFANESCU, C., VAN STRIEN, A., VAN TURNHOUT, C., VERMOUZEK, Z., WALLISDEVRIES, M., WYNHOFF, I. & JIGUET, F. 2012. Differences in the climatic debts of birds and butterflies at a continental scale. *Nature Climate Change,* 2**,** 121-124.

DIAMOND, S. E., FRAME, A. M., MARTIN, R. A. & BUCKLEY, L. B. 2011. Species' traits predict phenological responses to climate change in butterflies. *Ecology,* 92**,** 1005-1012.

DOI, H., GORDO, O. & KATANO, I. 2008. Heterogeneous intra-annual climatic changes drive different phenological responses at two trophic levels. *Climate Research,* 36**,** 181-190.

DOVER, J. W. 1996. Factors affecting the distribution of satyrid butterflies on arable farmland. *Journal of Applied Ecology,* 33**,** 723-734.

DOVER, J. W., SPARKS, T. H. & GREATOREX-DAVIES, J. N. 1997. The importance of shelter for butterflies in open landscapes. *Journal of Insect Conservation,* 1**,** 89-97.

EASTERLING, D. R., MEEHL, G. A., PARMESAN, C., CHANGNON, S. A., KARL, T. R. & MEARNS, L. O. 2000. Climate extremes: Observations, modeling, and impacts. *Science,* 289**,** 2068-2074.

EILERS, S., PETTERSSON, L. B. & OCKINGER, E. 2013. Micro-climate determines oviposition site selection and abundance in the butterfly Pyrgus armoricanus at its northern range margin. *Ecological Entomology,* 38**,** 183-192.

ERHARDT, A. 1985. DIURNAL LEPIDOPTERA - SENSITIVE INDICATORS OF CULTIVATED AND ABANDONED GRASSLAND. *Journal of Applied Ecology,* 22**,** 849-861.

FABINA, N. S., ABBOTT, K. C. & GILMAN, R. T. 2010. Sensitivity of plant-pollinator-herbivore communities to changes in phenology. *Ecological Modelling,* 221**,** 453-458.

FIRBANK, L. G., PETIT, S., SMART, S., BLAIN, A. & FULLER, R. J. 2008. Assessing the impacts of agricultural intensification on biodiversity: a British perspective. *Philosophical Transactions of the Royal Society B-Biological Sciences,* 363**,** 777-787.

FITTER, A. H. & FITTER, R. S. R. 2002. Rapid Changes in Flowering Time in British Plants. *Science,* 296**,** 1689-1691.

FLEISHMAN, E. & MURPHY, D. D. 2009. A Realistic Assessment of the Indicator Potential of Butterflies and Other Charismatic Taxonomic Groups. *Conservation Biology,* 23**,** 1109-1116.

FORISTER, M. L. & SHAPIRO, A. M. 2003. Climatic trends and advancing spring flight of butterflies in lowland California. *Global Change Biology,* 9**,** 1130-1135.

FOX, R., BRERETON, T. M., ASHER, J., BOTHAM, M. S., MIDDLEBROOK, I., ROY, D. B. & WARREN, M. S. 2011a. The State of the UK's Butterflies 2011. Butterfly Conservation and the Centre for Ecology & Hydrology, Wareham, Dorset.

FOX, R., WARREN, M. & BRERETON, T. 2007. A new Red List of British butterflies. *Butterfly Conservation Report,* S07-13**,** 1-19.

FOX, R., WARREN, M. S., BRERETON, T. M., ROY, D. B. & ROBINSON, A. 2011b. A new Red List of British butterflies. *Insect Conservation and Diversity,* 4**,** 159-172.

FRANCO, A. M. A., HILL, J. K., KITSCHKE, C., COLLINGHAM, Y. C., ROY, D. B., FOX, R., HUNTLEY, B. & THOMAS, C. D. 2006. Impacts of climate warming and habitat loss on extinctions at species' low-latitude range boundaries. *Global Change Biology,* 12**,** 1545-1553.

FRANKLIN, J., DAVIS, F. W., IKEGAMI, M., SYPHARD, A. D., FLINT, L. E., FLINT, A. L. & HANNAH, L. 2013. Modeling plant species distributions under future climates: how fine scale do climate projections need to be? *Global Change Biology,* 19**,** 473-483.

FREESE, A., BENES, J., BOLZ, R., CIZEK, O., DOLEK, M., GEYER, A., GROS, P., KONVICKA, M., LIEGL, A. & STETTMER, C. 2006. Habitat use of the endangered butterfly Euphydryas maturna and forestry in Central Europe. *Animal Conservation,* 9**,** 388-397.

FRIBERG, M., OLOFSSON, M., BERGER, D., KARLSSON, B. & WIKLUND, C. 2008. Habitat choice precedes host plant choice - niche separation in a species pair of a generalist and a specialist butterfly. *Oikos,* 117**,** 1337-1344.

GARCIA-BARROS, E. 2000. Body size, egg size, and their interspecific relationships with ecological and life history traits in butterflies (Lepidoptera : Papilionoidea, Hesperioidea). *Biological Journal of the Linnean Society,* 70**,** 251-284.

GEISTER, T. L., LORENZ, M. W., MEYERING-VOS, M., HOFFMANN, K. H. & FISCHER, K. 2008. Effects of temperature on reproductive output, egg provisioning, juvenile hormone and vitellogenin titres in the butterfly Bicyclus anynana. *Journal of Insect Physiology,* 54**,** 1253-1260.

GIBBS, M., VAN DYCK, H. & KARLSSON, B. 2010. Reproductive plasticity, ovarian dynamics and maternal effects in response to temperature and flight in Pararge aegeria. *Journal of Insect Physiology,* 56**,** 1275-1283.

GILMAN, R. T., FABINA, N. S., ABBOTT, K. C. & RAFFERTY, N. E. 2012. Evolution of plant-pollinator mutualisms in response to climate change. *Evolutionary Applications,* 5**,** 2-16.

GORDO, O. & SANZ, J. J. 2005. Phenology and climate change: a long-term study in a Mediterranean locality. *Oecologia,* 146**,** 484-495.

GUTIERREZ, D. & MENENDEZ, R. 1998. Phenology of butterflies along an altitudinal gradient in northern Spain. *Journal of Zoology,* 244**,** 249-264.

GUTIERREZ ILLAN, J., GUTIERREZ, D., DIEZ, S. B. & WILSON, R. J. 2012. Elevational trends in butterfly phenology: implications for species responses to climate change. *Ecological Entomology,* 37**,** 134-144.

HADDAD, N. M., HUDGENS, B., DAMIANI, C., GROSS, K., KUEFLER, D. & POLLOCK, K. 2008. Determining optimal population monitoring for rare butterflies. *Conservation Biology,* 22**,** 929-940.

HAMBLER, C. & SPEIGHT, M. R. 2004. Extinction rates and butterflies. *Science,* 305**,** 1563-1563.

HANNAH, L., MIDGLEY, G. F. & MILLAR, D. 2002. Climate change-integrated conservation strategies. *Global Ecology and Biogeography,* 11**,** 485-495.

HANSEN, J., RUEDY, R., SATO, M., IMHOFF, M., LAWRENCE, W., EASTERLING, D., PETERSON, T. & KARL, T. 2001. A closer look at United States and global surface temperature change. *Journal of Geophysical Research-Atmospheres,* 106**,** 23947-23963.

HANSPACH, J., SCHWEIGER, O., KUHN, I., PLATTNER, M., PEARMAN, P. B., ZIMMERMANN, N. E. & SETTELE, J. 2014. Host plant availability potentially limits butterfly distributions under cold environmental conditions. *Ecography,* 37**,** 301-308.

HARKER, R. J. & SHREEVE, T. G. 2008. How accurate are single site transect data for monitoring butterfly trends? Spatial and temporal issues identified in monitoring Lasiommata megera. *Journal of Insect Conservation,* 12**,** 125-133.

HICKLING, R., ROY, D. B., HILL, J. K., FOX, R. & THOMAS, C. D. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology,* 12**,** 450-455.

HILL, J. K., COLLINGHAM, Y. C., THOMAS, C. D., BLAKELEY, D. S., FOX, R., MOSS, D. & HUNTLEY, B. 2001. Impacts of landscape structure on butterfly range expansion. *Ecology Letters,* 4**,** 313-321.

HILL, J. K., THOMAS, C. D., FOX, R., TELFER, M. G., WILLIS, S. G., ASHER, J. & HUNTLEY, B. 2002. Responses of butterflies to twentieth century climate warming: implications for future ranges. *Proceedings of the Royal Society B-Biological Sciences,* 269**,** 2163-2171.

HILL, J. K., THOMAS, C. D. & HUNTLEY, B. 1999. Climate and habitat availability determine 20th century changes in a butterfly's range margin. *Proceedings of the Royal Society B-Biological Sciences,* 266**,** 1197-1206.

HODGSON, J. A., THOMAS, C. D., OLIVER, T. H., ANDERSON, B. J., BRERETON, T. M. & CRONE, E. E. 2011. Predicting insect phenology across space and time. *Global Change Biology,* 17**,** 1289-1300.

HOPKINS, J. J., ALLISON, H.M., WALMSLEY, C.A., GAYWOOD, M. & THURGATE, G 2007. *Conserving Biodiversity in a Changing Climate: Guidance on Building Capacity to Adapt*. London: Defra.

IMHOFF, M. L., BOUNOUA, L., RICKETTS, T., LOUCKS, C., HARRISS, R. & LAWRENCE, W. T. 2004. Global patterns in human consumption of net primary production. *Nature,* 429**,** 870-873.

IPCC 2007. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. *Cambridge University Press, Cambridge.*

ISAAC, N. J. B., CRUICKSHANKS, K. L., WEDDLE, A. M., ROWCLIFFE, J. M., BRERETON, T. M., DENNIS, R. L. H., SHUKER, D. M. & THOMAS, C. D. 2011. Distance sampling and the challenge of monitoring butterfly populations. *Methods in Ecology and Evolution,* 2**,** 585-594.

KERR, C. L. 2013. *Range changes in British Butterflies: the Roles of Climate, Habitat and Dispersal in Patterns of Spread.* Masters thesis, Durham University.

KERR, J. T., SUGAR, A. & PACKER, L. 2000. Indicator taxa, rapid biodiversity assessment, and nestedness in an endangered ecosystem. *Conservation Biology,* 14**,** 1726-1734.

KINDVALL, O. 1996. Habitat heterogeneity and survival in a bush cricket metapopulation. *Ecology,* 77**,** 207-214.

KINGSOLVER, J. G., WOODS, H. A., BUCKLEY, L. B., POTTER, K. A., MACLEAN, H. J. & HIGGINS, J. K. 2011. Complex Life Cycles and the Responses of Insects to Climate Change. *Integrative and Comparative Biology,* 51**,** 719-732.

KODA, K. & NAKAMURA, H. 2012. Effects of temperature on the development and survival of an endangered butterfly, Lycaeides argyrognomon (Lepidoptera: Lycaenidae) with estimation of optimal and threshold temperatures using linear and nonlinear models. *Entomological Science,* 15**,** 162-170.

KONVICKA, M., MARADOVA, M., BENES, J., FRIC, Z. & KEPKA, P. 2003. Uphill shifts in distribution of butterflies in the Czech Republic: effects of changing climate detected on a regional scale. *Global Ecology and Biogeography,* 12**,** 403-410.

KRAUSMANN, F., ERB, K. H., GINGRICH, S., HABERL, H., BONDEAU, A., GAUBE, V., LAUK, C., PLUTZAR, C. & SEARCHINGER, T. D. 2013. Global human appropriation of net primary production doubled in the 20th century. *Proceedings of the National Academy of Sciences of the United States of America,* 110**,** 10324-10329.

KRAUSS, J., STEFFAN-DEWENTER, I. & TSCHARNTKE, T. 2004. Landscape occupancy and local population size depends on host plant distribution in the butterfly Cupido minimus. *Biological Conservation,* 120**,** 355-361.

KUDO, G. & IDA, T. Y. 2013. Early onset of spring increases the phenological mismatch between plants and pollinators. *Ecology,* 94**,** 2311-2320.

LAWSON, C. R., BENNIE, J. J., THOMAS, C. D., HODGSON, J. A. & WILSON, R. J. 2014. Active Management of Protected Areas Enhances Metapopulation Expansion Under Climate Change. *Conservation Letters,* 7**,** 111-118.

LOERTSCHER, M., ERHARDT, A. & ZETTEL, J. 1995. MICRODISTRIBUTION OF BUTTERFLIES IN A MOSAIC-LIKE HABITAT - THE ROLE OF NECTAR SOURCES. *Ecography,* 18**,** 15-26.

MACLEAN, I. M. D. & WILSON, R. J. 2011. Recent ecological responses to climate change support predictions of high extinction risk. *Proceedings of the National Academy of Sciences of the United States of America,* 108**,** 12337-12342.

MAES, D., GHESQUIERE, A., LOGIE, M. & BONTE, D. 2006. Habitat use and mobility of two threatened coastal dune insects: implications for conservation. *Journal of Insect Conservation,* 10**,** 105-115.

MARRA, P. P., FRANCIS, C. M., MULVIHILL, R. S. & MOORE, F. R. 2005. The influence of climate on the timing and rate of spring bird migration. *Oecologia,* 142**,** 307-315.

MATSON, P. A., PARTON, W. J., POWER, A. G. & SWIFT, M. J. 1997. Agricultural intensification and ecosystem properties. *Science,* 277**,** 504-509.

MCKINNEY, M. L. 1999. High rates of extinction and threat in poorly studied taxa. *Conservation Biology,* 13**,** 1273-1281.

MCLAUGHLIN, J. F., HELLMANN, J. J., BOGGS, C. L. & EHRLICH, P. R. 2002a. Climate change hastens population extinctions. *Proceedings of the National Academy of Sciences of the United States of America,* 99**,** 6070-6074.

MCLAUGHLIN, J. F., HELLMANN, J. J., BOGGS, C. L. & EHRLICH, P. R. 2002b. The route to extinction: population dynamics of a threatened butterfly. *Oecologia,* 132**,** 538-548.

MEMMOTT, J., CRAZE, P. G., WASER, N. M. & PRICE, M. V. 2007. Global warming and the disruption of plant-pollinator interactions. *Ecology Letters,* 10**,** 710-717.

MENENDEZ, R., GONZALEZ-MEGIAS, A., COLLINGHAM, Y., FOX, R., ROY, D. B., OHLEMULLER, R. & THOMAS, C. D. 2007. Direct and indirect effects of climate and habitat factors on butterfly diversity. *Ecology,* 88**,** 605-611.

MENENDEZ, R., GONZALEZ-MEGIAS, A., LEWIS, O. T., SHAW, M. R. & THOMAS, C. D. 2008. Escape from natural enemies during climate-driven range expansion: a case study. *Ecological Entomology,* 33**,** 413-421.

MENENDEZ, R., MEGIAS, A. G., HILL, J. K., BRASCHLER, B., WILLIS, S. G., COLLINGHAM, Y., FOX, R., ROY, D. B. & THOMAS, C. D. 2006. Species richness changes lag behind climate change. *Proceedings of the Royal Society B-Biological Sciences,* 273**,** 1465-1470.

MENZEL, A. & FABIAN, P. 1999. Growing season extended in Europe. *Nature,* 397**,** 659-659.

MERRILL, R. M., GUTIERREZ, D., LEWIS, O. T., GUTIERREZ, J., DIEZ, S. B. & WILSON, R. J. 2008. Combined effects of climate and biotic interactions on the elevational range of a phytophagous insect. *Journal of Animal Ecology,* 77**,** 145-155.

MILLER-RUSHING, A. J., HOYE, T. T., INOUYE, D. W. & POST, E. 2010. The effects of phenological mismatches on demography. *Philosophical Transactions of the Royal Society B-Biological Sciences,* 365**,** 3177-3186.

MITIKKA, V., HEIKKINEN, R. K., LUOTO, M., ARAUJO, M. B., SAARINEN, K., POYRY, J. & FRONZEK, S. 2008. Predicting range expansion of the map butterfly in Northern Europe using bioclimatic models. *Biodiversity and Conservation,* 17**,** 623-641.

MORA, C., TITTENSOR, D. P., ADL, S., SIMPSON, A. G. B. & WORM, B. 2011. How Many Species Are There on Earth and in the Ocean? *Plos Biology,* 9.

MORTON, A. C. 1982. THE EFFECTS OF MARKING AND CAPTURE ON RECAPTURE FREQUENCIES OF BUTTERFLIES. *Oecologia,* 53**,** 105-110.

MUNGUIRA, M. L. & THOMAS, J. A. 1992. USE OF ROAD VERGES BY BUTTERFLY AND BURNET POPULATIONS, AND THE EFFECT OF ROADS ON ADULT DISPERSAL AND MORTALITY. *Journal of Applied Ecology,* 29**,** 316-329.

MURPHY, J. M., SEXTON, D. M. H., JENKINS, G. J., BOORMAN, P. M., BOOTH, B. B. B., BROWN, C. C., CLARK, R. T., COLLINS, M., HARRIS, G. R., KENDON, E. J., BETTS, R. A., BROWN, S. J., HOWARD, T. P., HUMPHREY, K. A., MCCARTHY, M. P., MCDONALD, R. E., STEPHENS, A., WALLACE, C., WARREN, R., WILBY, R. & WOOD, R. A. 2009. UK Climate Projections Science Report: Climate change projections.: Met Office Hadley Centre, Exeter

NAKAZAWA, T. & DOI, H. 2012. A perspective on match/mismatch of phenology in community contexts. *Oikos,* 121**,** 489-495.

NATIONS, U. 2013. World Population Prospects: The 2012 Revision, Volume I: Comprehensive Tables United Nations, Department of Economic and Social Affairs, Population Division.

NEW, T. R., PYLE, R. M., THOMAS, J. A., THOMAS, C. D. & HAMMOND, P. C. 1995. BUTTERFLY CONSERVATION MANAGEMENT. *Annual Review of Entomology,* 40**,** 57-83.

NOWICKI, P. & VRABEC, V. 2011. Evidence for positive density-dependent emigration in butterfly metapopulations. *Oecologia,* 167**,** 657-665.

ODEGAARD, F. 2000. How many species of arthropods? Erwin's estimate revised. *Biological Journal of the Linnean Society,* 71**,** 583-597.

OLIVER, T., HILL, J. K., THOMAS, C. D., BRERETON, T. & ROY, D. B. 2009. Changes in habitat specificity of species at their climatic range boundaries. *Ecology Letters,* 12**,** 1091-1102.

OLIVER, T., ROY, D. B., HILL, J. K., BRERETON, T. & THOMAS, C. D. 2010. Heterogeneous landscapes promote population stability. *Ecology Letters,* 13**,** 473-484.

OLIVER, T. H., BRERETON, T. & ROY, D. B. 2013. Population resilience to an extreme drought is influenced by habitat area and fragmentation in the local landscape. *Ecography,* 36**,** 579-586.

OLIVER, T. H., THOMAS, C. D., HILL, J. K., BRERETON, T. & ROY, D. B. 2012. Habitat associations of thermophilous butterflies are reduced despite climatic warming. *Global Change Biology,* 18**,** 2720-2729.

PARMESAN, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics.*

PARMESAN, C. 2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology,* 13**,** 1860-1872.

PARMESAN, C., ROOT, T. L. & WILLIG, M. R. 2000. Impacts of extreme weather and climate on terrestrial biota. *Bulletin of the American Meteorological Society,* 81**,** 443-450.

PARMESAN, C., RYRHOLM, N., STEFANESCU, C., HILL, J. K., THOMAS, C. D., DESCIMON, H., HUNTLEY, B., KAILA, L., KULLBERG, J., TAMMARU, T., TENNENT, W. J., THOMAS, J. A. & WARREN, M. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature,* 399**,** 579-583.

PARMESAN, C. & YOHE, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature,* 421**,** 37-42.

PATEMAN, R. M., HILL, J. K., ROY, D. B., FOX, R. & THOMAS, C. D. 2012. Temperature-Dependent Alterations in Host Use Drive Rapid Range Expansion in a Butterfly. *Science,* 336**,** 1028-1030.

PEARCE-HIGGINS, J. W., DENNIS, P., WHITTINGHAM, M. J. & YALDEN, D. W. 2010. Impacts of climate on prey abundance account for fluctuations in a population of a northern wader at the southern edge of its range. *Global Change Biology,* 16**,** 12-23.

PELINI, S. L., KEPPEL, J. A., KELLEY, A. E. & HELLMANN, J. J. 2010a. Adaptation to host plants may prevent rapid insect responses to climate change. *Global Change Biology,* 16.

PELINI, S. L., KEPPEL, J. A., KELLEY, A. E. & HELLMANN, J. J. 2010b. Adaptation to host plants may prevent rapid insect responses to climate change. *Global Change Biology,* 16**,** 2923-2929.

PELLERIN, M., DELESTRADE, A., MATHIEU, G., RIGAULT, O. & YOCCOZ, N. G. 2012. Spring tree phenology in the Alps: effects of air temperature, altitude and local topography. *European Journal of Forest Research,* 131**,** 1957-1965.

PENNEKAMP, F., MONTEIRO, E. & SCHMITT, T. 2013. The larval ecology of the butterfly Euphydryas desfontainii (Lepidoptera: Nymphalidae) in SW-Portugal: food plant quantity and quality as main predictors of habitat quality. *Journal of Insect Conservation,* 17**,** 195-206.

PHILLIMORE, A. B., STALHANDSKE, S., SMITHERS, R. J. & BERNARD, R. 2012. Dissecting the Contributions of Plasticity and Local Adaptation to the Phenology of a Butterfly and Its Host Plants. *American Naturalist,* 180**,** 655-670.

PIMM, S. L., RUSSELL, G. J., GITTLEMAN, J. L. & BROOKS, T. M. 1995. THE FUTURE OF BIODIVERSITY. *Science,* 269**,** 347-350.

POCEWICZ, A., MORGAN, P. & EIGENBRODE, S. D. 2009. Local and landscape effects on butterfly density in northern Idaho grasslands and forests. *Journal of Insect Conservation,* 13**,** 593-601.

POLGAR, C. A., PRIMACK, R. B., WILLIAMS, E. H., STICHTER, S. & HITCHCOCK, C. 2013. Climate effects on the flight period of Lycaenid butterflies in Massachusetts. *Biological Conservation,* 160**,** 25-31.

POLLARD, E. 1982. MONITORING BUTTERFLY ABUNDANCE IN RELATION TO THE MANAGEMENT OF A NATURE RESERVE. *Biological Conservation,* 24**,** 317-328.

POLLARD, E. 1988. TEMPERATURE, RAINFALL AND BUTTERFLY NUMBERS. *Journal of Applied Ecology,* 25**,** 819-828.

POLLARD, E. 1991. CHANGES IN THE FLIGHT PERIOD OF THE HEDGE BROWN BUTTERFLY PYRONIA-TITHONUS DURING RANGE EXPANSION. *Journal of Animal Ecology,* 60**,** 737-748.

POLLARD, E., ROTHERY, P. & YATES, T. J. 1996. Annual growth rates in newly established populations of the butterfly Pararge aegeria. *Ecological Entomology,* 21**,** 365-369.

POLLARD, E. & YATES, T. J. 1993. *Monitoring Butterflies for Ecology and Conservation*, Chapman & Hall, London.

PRESSEY, R. L., CABEZA, M., WATTS, M. E., COWLING, R. M. & WILSON, K. A. 2007. Conservation planning in a changing world. *Trends in Ecology & Evolution,* 22**,** 583-592.

PRIMACK, D., IMBRES, C., PRIMACK, R. B., MILLER-RUSHING, A. J. & DEL TREDICI, P. 2004. Herbarium specimens demonstrate earlier flowering times in response to warming in Boston. *American Journal of Botany,* 91**,** 1260-1264.

PYWELL, R. F., MEEK, W. R., HULMES, L., HULMES, S., JAMES, K. L., NOWAKOWSKI, M. & CARVELL, C. 2011. Management to enhance pollen and nectar resources for bumblebees and butterflies within intensively farmed landscapes. *Journal of Insect Conservation,* 15**,** 853-864.

PYWELL, R. F., WARMAN, E. A., SPARKS, T. H., GREATOREX-DAVIES, J. N., WALKER, K. J., MEEK, W. R., CARVELL, C., PETIT, S. & FIRBANK, L. G. 2004. Assessing habitat quality for butterflies on intensively managed arable farmland. *Biological Conservation,* 118**,** 313-325.

RADCHUK, V., TURLURE, C. & SCHTICKZELLE, N. 2013. Each life stage matters: the importance of assessing the response to climate change over the complete life cycle in butterflies. *Journal of Animal Ecology,* 82**,** 275-285.

RAFFERTY, N. E. & IVES, A. R. 2011. Effects of experimental shifts in flowering phenology on plant-pollinator interactions. *Ecology Letters,* 14**,** 69-74.

RANDS, M. R. W., ADAMS, W. M., BENNUN, L., BUTCHART, S. H. M., CLEMENTS, A., COOMES, D., ENTWISTLE, A., HODGE, I., KAPOS, V., SCHARLEMANN, J. P. W., SUTHERLAND, W. J. & VIRA, B. 2010. Biodiversity Conservation: Challenges Beyond 2010. *Science,* 329**,** 1298-1303.

RICHARDS, S. A. 2008. Dealing with overdispersed count data in applied ecology. *Journal of Applied Ecology,* 45**,** 218-227.

ROOT, T. L., PRICE, J. T., HALL, K. R., SCHNEIDER, S. H., ROSENZWEIG, C. & POUNDS, J. A. 2003. Fingerprints of global warming on wild animals and plants. *Nature,* 421**,** 57-60.

ROY, D. B. & ASHER, J. 2003. Spatial trends in the sighting dates of British butterflies. *International Journal of Biometeorology,* 47**,** 188-192.

ROY, D. B., ROTHERY, P., MOSS, D., POLLARD, E. & THOMAS, J. A. 2001. Butterfly numbers and weather: predicting historical trends in abundance and the future effects of climate change. *Journal of Animal Ecology,* 70**,** 201-217.

ROY, D. B. & SPARKS, T. H. 2000. Phenology of British butterflies and climate change. *Global Change Biology,* 6**,** 407-416.

ROY, D. B. & THOMAS, J. A. 2003. Seasonal variation in the niche, habitat availability and population fluctuations of a bivoltine thermophilous insect near its range margin. *Oecologia,* 134**,** 439-444.

SALA, O. E., CHAPIN, F. S., ARMESTO, J. J., BERLOW, E., BLOOMFIELD, J., DIRZO, R., HUBER-SANWALD, E., HUENNEKE, L. F., JACKSON, R. B., KINZIG, A., LEEMANS, R., LODGE, D. M., MOONEY, H. A., OESTERHELD, M., POFF, N. L., SYKES, M. T., WALKER, B. H., WALKER, M. & WALL, D. H. 2000. Biodiversity - Global biodiversity scenarios for the year 2100. *Science,* 287**,** 1770-1774.

SCHAR, C., VIDALE, P. L., LUTHI, D., FREI, C., HABERLI, C., LINIGER, M. A. & APPENZELLER, C. 2004. The role of increasing temperature variability in European summer heatwaves. *Nature,* 427**,** 332-336.

SCHTICKZELLE, N., LE BOULENGE, E. & BAGUETTE, M. 2002. Metapopulation dynamics of the bog fritillary butterfly: demographic processes in a patchy population. *Oikos,* 97**,** 349-360.

SCHWARZ, C. J. & ARNASON, A. N. 1996. A general methodology for the analysis of capture-recapture experiments in open populations. *Biometrics,* 52**,** 860-873.

SHREEVE, T. G. 1984. HABITAT SELECTION, MATE LOCATION, AND MICROCLIMATIC CONSTRAINTS ON THE ACTIVITY OF THE SPECKLED WOOD BUTTERFLY PARARGE-AEGERIA. *Oikos,* 42**,** 371-377.

SHUEY, J. & SZYMANSKI, J. 2012. MODIFIED POLLARD TRANSECTS DO NOT PREDICT ESTIMATED DAILY POPULATION SIZE FOR THE SECRETIVE BUTTERFLY, NEONYMPHA MITCHELLII MITCHELLII FRENCH. *Journal of the Lepidopterists Society,* 66**,** 221-224.

SINGER, M. C. & PARMESAN, C. 2010. Phenological asynchrony between herbivorous insects and their hosts: signal of climate change or pre-existing adaptive strategy? *Philosophical Transactions of the Royal Society B-Biological Sciences,* 365**,** 3161-3176.

SKORKA, P., NOWICKI, P., KUDLEK, J., PEPKOWSKA, A., SLIWINSKA, E. B., WITEK, M., SETTELE, J. & WOYCIECHOWSKI, M. 2013. Movements and flight morphology in the endangered Large Blue butterflies. *Central European Journal of Biology,* 8**,** 662-669.

SLAMOVA, I., KLECKA, J. & KONVICKA, M. 2011. Diurnal Behavior and Habitat Preferences of Erebia aethiops, an Aberrant Lowland Species of a Mountain Butterfly Clade. *Journal of Insect Behavior,* 24**,** 230-246.

SLAMOVA, I., KLECKA, J. & KONVICKA, M. 2013. Woodland and grassland mosaic from a butterfly perspective: habitat use by Erebia aethiops (Lepidoptera: Satyridae). *Insect Conservation and Diversity,* 6**,** 243-254.

SMITH, T. M. & REYNOLDS, R. W. 2005. A global merged land-air-sea surface temperature reconstruction based on historical observations (1880-1997). *Journal of Climate,* 18**,** 2021-2036.

SOULSBY, R. L. & THOMAS, J. A. 2012. Insect population curves: modelling and application to butterfly transect data. *Methods in Ecology and Evolution,* 3**,** 832-841.

SPARKS, T. H., ROY, D. B. & DENNIS, R. L. H. 2005. The influence of temperature on migration of Lepidoptera into Britain. *Global Change Biology,* 11**,** 507-514.

SPARKS, T. H. & YATES, T. J. 1997. The effect of spring temperature on the appearance dates of British butterflies 1883-1993. *Ecography,* 20**,** 368-374.

STACE, C. 1991. NEW FLORA OF THE BRITISH ISLES. *Stace, C. New Flora of the British Isles. Xxx+1226p. Cambridge University Press: Cambridge, England, Uk; New York, New York, USA. Illus. Maps***,** XXX+1226P-XXX+1226P.

STATISTICS, O. F. N. 2012. Chapter 2: Results 2010 based NPP reference volume.

STEFANESCU, C., PENUELAS, J. & FILELLA, I. 2003. Effects of climatic change on the phenology of butterflies in the northwest Mediterranean Basin. *Global Change Biology,* 9**,** 1494-1506.

STEFFAN-DEWENTER, I. & TSCHARNTKE, T. 1997. Early succession of butterfly and plant communities on set-aside fields. *Oecologia,* 109**,** 294-302.

STORK, N. E. 1988. INSECT DIVERSITY - FACTS, FICTION AND SPECULATION. *Biological Journal of the Linnean Society,* 35**,** 321-337.

STORK, N. E. 1993. HOW MANY SPECIES ARE THERE. *Biodiversity and Conservation,* 2**,** 215-232.

STORLIE, C. J., PHILLIPS, B. L., VANDERWAL, J. J. & WILLIAMS, S. E. 2013. Improved spatial estimates of climate predict patchier species distributions. *Diversity and Distributions,* 19**,** 1106-1113.

SUGGITT, A. J., GILLINGHAM, P. K., HILL, J. K., HUNTLEY, B., KUNIN, W. E., ROY, D. B. & THOMAS, C. D. 2011. Habitat microclimates drive fine-scale variation in extreme temperatures. *Oikos,* 120**,** 1-8.

SUTHERLAND, W. J., ARMSTRONG, D., BUTCHART, S. H. M., EARNHARDT, J. M., EWEN, J., JAMIESON, I., JONES, C. G., LEE, R., NEWBERY, P., NICHOLS, J. D., PARKER, K. A., SARRAZIN, F., SEDDON, P. J., SHAH, N. & TATAYAH, V. 2010. Standards for documenting and monitoring bird reintroduction projects. *Conservation Letters,* 3**,** 229-235.

SWENGEL, A. B. & SWENGEL, S. R. 1997. Co-occurrence of prairie and barrens butterflies: applications to ecosystem conservation. *Journal of Insect Conservation,* 1**,** 131-144.

THACKERAY, S. J., SPARKS, T. H., FREDERIKSEN, M., BURTHE, S., BACON, P. J., BELL, J. R., BOTHAM, M. S., BRERETON, T. M., BRIGHT, P. W., CARVALHO, L., CLUTTON-BROCK, T., DAWSON, A., EDWARDS, M., ELLIOTT, J. M., HARRINGTON, R., JOHNS, D., JONES, I. D., JONES, J. T., LEECH, D. I., ROY, D. B., SCOTT, W. A., SMITH, M., SMITHERS, R. J., WINFIELD, I. J. & WANLESS, S. 2010. Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biology,* 16**,** 3304-3313.

THOMAS, C. D., BODSWORTH, E. J., WILSON, R. J., SIMMONS, A. D., DAVIES, Z. G., MUSCHE, M. & CONRADT, L. 2001. Ecological and evolutionary processes at expanding range margins. *Nature,* 411**,** 577-581.

THOMAS, C. D., CAMERON, A., GREEN, R. E., BAKKENES, M., BEAUMONT, L. J., COLLINGHAM, Y. C., ERASMUS, B. F. N., DE SIQUEIRA, M. F., GRAINGER, A., HANNAH, L., HUGHES, L., HUNTLEY, B., VAN JAARSVELD, A. S., MIDGLEY, G. F., MILES, L., ORTEGA-HUERTA, M. A., PETERSON, A. T., PHILLIPS, O. L. & WILLIAMS, S. E. 2004a. Extinction risk from climate change. *Nature,* 427**,** 145-148.

THOMAS, J. 1980. Why did the large blue become extinct in Britain? *Oryx,* 15**,** 243-247.

THOMAS, J. A. 2005. Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. *Philosophical Transactions of the Royal Society B-Biological Sciences,* 360**,** 339-357.

THOMAS, J. A. & CLARKE, R. T. 2004. Extinction rates and butterflies - Response. *Science,* 305**,** 1563-+.

THOMAS, J. A., MORRIS, M. G. & HAMBLER, C. 1994. PATTERNS, MECHANISMS AND RATES OF EXTINCTION AMONG INVERTEBRATES IN THE UNITED-KINGDOM. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences,* 344**,** 47-54.

THOMAS, J. A., ROSE, R. J., CLARKE, R. T., THOMAS, C. D. & WEBB, N. R. 1999. Intraspecific variation in habitat availability among ectothermic animals near their climatic limits and their centres of range. *Functional Ecology,* 13**,** 55-64.

THOMAS, J. A., SIMCOX, D. J. & CLARKE, R. T. 2009. Successful Conservation of a Threatened Maculinea Butterfly. *Science,* 325**,** 80-83.

THOMAS, J. A., SIMCOX, D. J. & HOVESTADT, T. 2011. Evidence based conservation of butterflies. *Journal of Insect Conservation,* 15**,** 241-258.

THOMAS, J. A., SIMCOX, D. J., WARDLAW, J. C., ELMES, G. W., HOCHBERG, M. E. & CLARKE, R. T. 1998. Effects of latitude, altitude and climate on the habitat and conservation of the endangered butterfly Maculinea arion and its Myrmica ant hosts. *Journal of Insect Conservation,* 2**,** 39-46.

THOMAS, J. A., TELFER, M. G., ROY, D. B., PRESTON, C. D., GREENWOOD, J. J. D., ASHER, J., FOX, R., CLARKE, R. T. & LAWTON, J. H. 2004b. Comparative losses of British butterflies, birds, and plants and the global extinction crisis. *Science,* 303**,** 1879-1881.

THUILLER, W., ALBERT, C., ARAUJO, M. B., BERRY, P. M., CABEZA, M., GUISAN, A., HICKLER, T., MIDGELY, G. F., PATERSON, J., SCHURR, F. M., SYKES, M. T. & ZIMMERMANN, N. E. 2008. Predicting global change impacts on plant species' distributions: Future challenges. *Perspectives in Plant Ecology Evolution and Systematics,* 9**,** 137-152.

TURLURE, C., CHOUTT, J., BAGUETTE, M. & VAN DYCK, H. 2010. Microclimatic buffering and resource-based habitat in a glacial relict butterfly: significance for conservation under climate change. *Global Change Biology,* 16**,** 1883-1893.

TURLURE, C., RADCHUK, V., BAGUETTE, M., MEIJRINK, M., VAN DEN BURG, A., WALLISDEVRIES, M. & VAN DUINEN, G. J. 2013. Plant quality and local adaptation undermine relocation in a bog specialist butterfly. *Ecology and Evolution,* 3**,** 244-254.

TURNER, E. C., GRANROTH, H. M. V., JOHNSON, H. R., LUCAS, C. B. H., THOMPSON, A. M., FROY, H., GERMAN, R. N. & HOLDGATE, R. 2009. Habitat preference and dispersal of the Duke of Burgundy butterfly (Hamearis lucina) on an abandoned chalk quarry in Bedfordshire, UK. *Journal of Insect Conservation,* 13**,** 475-486.

TURNER, J. R. G., GATEHOUSE, C. M. & COREY, C. A. 1987. DOES SOLAR-ENERGY CONTROL ORGANIC DIVERSITY - BUTTERFLIES, MOTHS AND THE BRITISH CLIMATE. *Oikos,* 48**,** 195-205.

UNDERWOOD, N. 2007. Variation in and correlation between intrinsic rate of increase and carrying capacity. *American Naturalist,* 169**,** 136-141.

VAN ASCH, M. & VISSER, M. E. 2007. Phenology of forest caterpillars and their host trees: The importance of synchrony. *Annual Review of Entomology.* Palo Alto: Annual Reviews.

VAN HALDER, I., BARBARO, L. & JACTEL, H. 2011. Conserving butterflies in fragmented plantation forests: are edge and interior habitats equally important? *Journal of Insect Conservation,* 15**,** 591-601.

VAN SWAAY, C., MAES, D., COLLINS, S., MUNGUIRA, M. L., SASIC, M., SETTELE, J., VEROVNIK, R., WARREN, M., WIEMERS, M., WYNHOFF, I. & CUTTELOD, A. 2011. Applying IUCN criteria to invertebrates: How red is the Red List of European butterflies? *Biological Conservation,* 144**,** 470-478.

VAN SWAAY, C., WARREN, M. & LOIS, G. 2006. Biotope use and trends of European butterflies. *Journal of Insect Conservation,* 10**,** 189-209.

VISSER, M. E. & BOTH, C. 2005. Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society B-Biological Sciences,* 272**,** 2561-2569.

VOS, C. C., BERRY, P., OPDAM, P., BAVECO, H., NIJHOF, B., O'HANLEY, J., BELL, C. & KUIPERS, H. 2008. Adapting landscapes to climate change: examples of climate-proof ecosystem networks and priority adaptation zones. *Journal of Applied Ecology,* 45**,** 1722-1731.

WAKE, D. B. & VREDENBURG, V. T. 2008. Are we in the midst of the sixth mass extinction? A view from the world of amphibians. *Proceedings of the National Academy of Sciences of the United States of America,* 105**,** 11466-11473.

WALTHER, G. R., POST, E., CONVEY, P., MENZEL, A., PARMESAN, C., BEEBEE, T. J. C., FROMENTIN, J. M., HOEGH-GULDBERG, O. & BAIRLEIN, F. 2002. Ecological responses to recent climate change. *Nature,* 416**,** 389-395.

WARREN, M. S. 1994. THE UK STATUS AND SUSPECTED METAPOPULATION STRUCTURE OF A THREATENED EUROPEAN BUTTERFLY, THE MARSH FRITILLARY EURODRYAS-AURINIA. *Biological Conservation,* 67**,** 239-249.

WARREN, M. S., ASHER, J., BRERETON, T. M. & ROY, D. B. 2007. The state of Britain's butterflies 2007. Butterfly Conservation and the Centre for Ecology and Hydrology, Wareham, Dorset.

WARREN, M. S., HILL, J. K., THOMAS, J. A., ASHER, J., FOX, R., HUNTLEY, B., ROY, D. B., TELFER, M. G., JEFFCOATE, S., HARDING, P., JEFFCOATE, G., WILLIS, S. G., GREATOREX-DAVIES, J. N., MOSS, D. & THOMAS, C. D. 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature,* 414**,** 65-69.

WEISS, S. B., MURPHY, D. D. & WHITE, R. R. 1988. SUN, SLOPE, AND BUTTERFLIES - TOPOGRAPHIC DETERMINANTS OF HABITAT QUALITY FOR EUPHYDRYAS-EDITHA. *Ecology,* 69**,** 1486-1496.

WESTGARTH-SMITH, A. R., ROY, D. B., SCHOLZE, M., TUCKER, A. & SUMPTER, J. P. 2012. The role of the North Atlantic Oscillation in controlling UK butterfly population size and phenology. *Ecological Entomology,* 37**,** 221-232.

WICK, A. A., PRUSS, S., SPENCE, J. & ERBILGIN, N. 2014. MICROHABITAT USE IN A NORTHERN PERIPHERAL POPULATION OF APODEMIA MORMO: FACTORS BEYOND THE HOST PLANT. *Journal of the Lepidopterists Society,* 68**,** 54-60.

WIKSTROEM, L., MILBERG, P. & BERGMAN, K.-O. 2009. Monitoring of butterflies in semi-natural grasslands: diurnal variation and weather effects. *Journal of Insect Conservation,* 13**,** 203-211.

WILLIS, S. G., HILL, J. K., THOMAS, C. D., ROY, D. B., FOX, R., BLAKELEY, D. S. & HUNTLEY, B. 2009a. Assisted colonization in a changing climate: a test-study using two U.K. butterflies. *Conservation Letters,* 2**,** 46-51.

WILLIS, S. G., THOMAS, C. D., HILL, J. K., COLLINGHAM, Y. C., TELFER, M. G., FOX, R. & HUNTLEY, B. 2009b. Dynamic distribution modelling: predicting the present from the past. *Ecography,* 32**,** 5-12.

WILSON, A. 1985. FLAVONOID PIGMENTS IN MARBLED WHITE BUTTERFLY (MELANARGIA-GALATHEA) ARE DEPENDENT ON FLAVONOID CONTENT OF LARVAL DIET. *Journal of Chemical Ecology,* 11**,** 1161-1179.

WILSON, R. J., DAVIES, Z. G. & THOMAS, C. D. 2010. Linking habitat use to range expansion rates in fragmented landscapes: a metapopulation approach. *Ecography,* 33**,** 73-82.

WILSON, R. J., GUTIERREZ, D., GUTIERREZ, J., MARTINEZ, D., AGUDO, R. & MONSERRAT, V. J. 2005. Changes to the elevational limits and extent of species ranges associated with climate change. *Ecology Letters,* 8**,** 1138-1146.

WISE, R. M., REYERS, B., GUO, C., MIDGLEY, G. F. & DE LANGE, W. 2012. Costs of Expanding the Network of Protected Areas as a Response to Climate Change in the Cape Floristic Region. *Conservation Biology,* 26**,** 397-407.

ZHOU, Y., CAO, Y., CHEN, H., LONG, Y., YAN, F., XU, C. & WANG, R. 2012. Habitat utilization of the Glanville fritillary butterfly in the Tianshan Mountains, China, and its implication for conservation. *Journal of Insect Conservation,* 16**,** 207-214.