

The Effects of Rotational Coppicing on a *Thecla Betulae* (Brown Hairstreak Butterfly) Population at the West Williamston Nature Reserve in Pembrokeshire

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Abstract

The effects of increased rotational coppicing on *Thecla betulae* were investigated by analysing annual egg counts dating back to 1995 from the West Williamston Nature Reserve (Pembrokeshire, Wales). This was done by studying the trends in the dataset and comparing them to those of another important *T. betulae* stronghold in Grafton Wood (Worcestershire, England). Furthermore, possible relationships between the egg count data and climate were also investigated. The eggs were counted along a 500m transect set up along the foreshore of the West Williamston reserve, where *Prunus Spinosa* bushes are systematically searched annually. Where rotational coppicing has increased into other areas of the reserve in 2009, the trends along the 500m transect characterising the period before and after this point have been investigated to determine effects of management on the West Williamston population. An overall increasing trend was observed at West Williamston since 1995, but unlike Grafton Wood, there were no significant correlations with any of the nearby climate data, indicating that other factors are more influential for this site. The 500m transect mean egg counts before 2009 and from 2009 onwards were found to differ significantly, with the latter being characterised by increased counts, supporting the view that rotational coppicing has a positive impact on the egg numbers. However, variability in the egg counts of each section making up the 500m transect were also found, suggesting that other factors in addition to management are influencing the numbers. This is because the sections with higher counts had a larger amount of good quality *P. spinosa* habitat and had increased shelter from adjacent woodland. Furthermore, the surrounding land-use is not generally characterised by sympathetic hedgerow management for *T. betulae* and it is likely that the population is unable to spread into adjacent habitat patches. Therefore, the findings support rotational coppicing as an effective way of encouraging the population growth of *T. betulae*, but it needs to be utilised on a larger number of sites so that this butterfly can increase its range into other areas, reducing the risk of extinction events and encouraging its recovery.

Abbreviations

°	Degrees
ANOVA	Analysis of Variance
H ₀	Null hypothesis
H ₁	Hypothesis
m	Metres
mm	Millimetres
NERC	Natural Environment Research Council
<i>P. spinosa</i>	Prunus Spinosa
<i>T. betulae</i>	Thecla Betulae
UK BAP	United Kingdom Biodiversity Action Plan
UK BMS	United Kingdom Butterfly Monitoring Scheme

1. Introduction

As increasing amounts of natural habitat have become converted into urban and agricultural environments to meet anthropogenic demands, many species have declined. Over the last 100 years European agriculture has undergone substantial changes to a more mechanized nature, mainly resulting from the increased pressure for higher yields and the rising cost of labour (Tscharntke *et al.*, 2005; Dahlström *et al.*, 2008; Nilsson *et al.*, 2013). Therefore, large quantities of land that were once characterised by traditional management including late summer mowing, low impact grazing, and coppicing, have become intensively used or abandoned (Eriksson *et al.*, 2002; Dahlström *et al.*, 2008; van Swaay *et al.*, 2013; Nilsson *et al.*, 2013). These activities lead to habitat fragmentation, where either the surrounding landscape becomes more homogenised in structure, or abandonment of previously managed land succumbs to natural succession (Haddad, 2000; van Swaay and Warren, 2003; Skorka *et al.*, 2007; Concepcion *et al.*, 2008; and Kalarus and Norwicky, 2015). Based on the concepts of island biogeography and metapopulation ecology, smaller and more isolated fragments will be characterised by lower species richness and are more prone to extinctions than larger connected habitats (MacArthur and Wilson, 1967; Hanski, 1999; and Halder *et al.*, 2015). This is because many habitats will not contain all the required resources or do not cover enough area to support a metapopulation, and so a metapopulation's persistence is affected by its ability to disperse, which is in turn affected by its mobility and the quality and connectivity of the surrounding landscape (Thomas *et al.*, 1992; Hanski, 1999; Baguette *et al.*, 2000; Dennis, 2010; Thomas *et al.*, 2012, Kalarus and Norwicky, 2015).

Butterflies are one group that is particularly affected by habitat fragmentation [KN1] (Öckinger and Smith 2006; Wenzel *et al.*, 2006; Kőrösi *et al.*, 2012; Bubova *et al.*, 2015). As many butterfly species are specialists that are often restricted to natural habitats, the increase in these anthropogenically created landscapes means that many of them now only persist as metapopulations in small and discrete patches (Petit *et al.*, 2001; Baguette *et al.*, 2003). For *Thecla betulae* [KN2] (Brown Hairstreak), the increasing amounts of agricultural land characterised by widespread mechanical management such as hedgerow flailing has proven to be particularly detrimental (Thomas, 1974; Bourn and Warren, 1998; van Swaay and Warren, 1999; Merckx and Berwaerts, 2011). This is primarily because this species lays its eggs on young *Prunus spinosa* [KN3] (Blackthorn), which whilst being a particularly abundant host plant, is subjected to a high level of annual flailing. This has meant that many *P. spinosa* hedgerows now act as population sinks, where unsympathetic management is a big contributor to the mortality of *T. betulae* populations (Thomas, 1974; Merckx and Berwaerts, 2011). Over time this has led to significant contractions in the range of *T. betulae* throughout the UK, and

therefore it is vitally important that effective sympathetic management strategies are put in place both locally and on a wider scale to ensure their conservation and potential recovery. *T. betulae* is now restricted to a small number of strongholds in England and Wales including the West Williamston Nature Reserve in Pembrokeshire.

This study will seek to identify how specific management can influence the breeding cycle and ultimately the number of eggs produced by *T. betulae*. A 500m transect was selected at West Williamston in order to investigate this research. Rotational coppicing has occurred along this transect since the creation of the habitat management plan in 1998, which has involved dividing the transect out into five blocks and alternating the cutting of each block annually. That way each block is cut once every five years. However, in 2009 this method of management was introduced on the hedgerows of two of the meadows on the site with the aim of increasing the amount of viable habitat for oviposition. The purpose of the present paper is to investigate the effectiveness of this management strategy for *T. betulae* conservation where it is hypothesised that the years following the implementation of rotational cutting into the meadows in 2009 will be characterised by increased egg counts compared to those in the years prior. Furthermore, the West Williamston data will be compared to egg counts for Grafton Wood; another important *T. betulae* stronghold in Worcestershire. The aim of this is to further support the effectiveness of rotational coppicing in increasing egg counts as this site also implements this strategy on many of its hedgerows. It is therefore hypothesised that the Grafton Wood egg count data will show similar trends to those of West Williamston. Finally, as well as management influences, it is important to consider other factors that cause fluctuations in butterfly populations. As butterfly activity is often governed by climate, this will also be considered by comparing the West Williamston and Grafton Wood datasets to historic climate data for Aberporth and Ross-on-Wye respectively. Furthermore, previous butterfly literature will be reviewed in the following chapter to help provide possible explanations for any patterns observed in the data set.

2. Literature Review

The following chapter will begin with an overview of the distribution and ecology of *Thecla betulae*. Then the various factors that cause fluctuations in butterfly populations at both the local and landscape-scale will be discussed. This is because it is important to consider the other possible drivers of butterfly abundance in addition to management, so that the findings of other previous research can help explain any patterns observed in the West Williamston egg count dataset. Furthermore, because the habitat management plan has not been updated since 1998, most literature included in this review has been published since that time. This will provide a picture of how research has progressed since 1998 and will help inform any recommendations of how management of the site should continue moving forward.

2.1. *T. betulae* species information

2.1.1. Distribution

T. betulae occurs throughout the palearctic between the latitudes 40° to 60°N (Thomas, 1974; Thomas and Emmett, 1990; Karsholt and Razowski, 1996; Bourn and Warren, 1998). It reaches its northern range limit in southern Scandinavia, its southerly range limit the northern Mediterranean region and westerly range limit southern England, Wales and Ireland (Thomas, 1974; Ebert and Rennwald, 1991; Asher *et al.*, 2001; Kudrna, 2002; and Fartmann and Timmermann, 2006). Its distribution in the UK has been widely recorded over the last century, its three main strongholds being: west Weald in West Sussex and Surrey; Holsworthy east to Sedgemoor and Polden Hills in north Devon and south-west Somerset; and Carmarthenshire, Ceredigion and Pembrokeshire in south-west Wales (Bourne and Warren, 1998; Walton, 2009). These records have revealed that *T. betulae*'s numbers have declined drastically by an estimated 22.9% between 1990 and 2010 and of 53.1% between 2000 and 2010 (Botham *et al.*, 2011; Wood, 2012). These losses are mainly attributable to the reduction in the number of hedges from the increasing use of mechanical cutting techniques.^[KN4] Its decline in abundance have led this butterfly to receive a multitude conservation statuses, which are:

- It is a UK BAP Priority Species;
- It is protected under Schedule 5 of the 1981 Wildlife and Countryside Act; and,
- It is listed as a Section 41 and Section 42 species of principal importance as part of the NERC Act in England and Wales respectively (JNCC, 2016; JNCC, 2015).

2.1.2. Habitat Preferences

Perhaps the most important habitat requirement for *T. betulae* is the presence of its preferred host plant, *P. spinosa*. Therefore, this species of butterfly is generally found on sites with heavy clay-based soils where blackthorn is dominant, usually around a woodland (Thomas, 1974;

Bourn and Warren, 1998). Fartmann and Timmermann (2006) state that *T. betulae* is also known to breed over a wider selection of other habitats including parks and gardens, provided they have *Prunus* species within them. Another habitat preference of *T. betulae*^[KN5] is that the area needs to be both exposed to the sunshine, but also sheltered from harsh winds. It is particularly important that hedgerows are also characterised by younger *P. spinosa* growth, either in the form of suckering growth or shoots growing out of the hedge, as this newer growth is where the butterflies prefer to lay their eggs (Worcestershire Biodiversity Partnership, 2008). It is equally important that their habitat contains large, mature trees such as ash, elm or oaks, as these are used by adults to congregate and mate. These trees are often referred to as 'master trees' and in addition to providing shelter and a meeting point for the butterfly, they also provide a source of food in the form of aphid honey dew, especially on ash trees (Thomas, 1974; Green, 1990; and Bourn and Warren, 1998). Additional nectar sources at ground level such as hemp agrimony, ragwort and bramble are also required, particularly for females searching for sites to oviposit. Finally, as this is a highly mobile species of butterfly that lays its eggs over a wide area, it does best in structurally heterogeneous landscapes with extensive networks of *prunus* hedgerows, scrub and woodland edges, as these provide superior micro-habitat resources for feeding, mating, shelter and oviposition (Bourn and Warren, 1998; Wood, 2012).

2.1.3. Life cycle

The eggs of *T. betulae* take a rough hemispherical appearance and are white in colouration due to the thick wax layer that encases the chorion, making them stand out against the darker bark of *P. spinosa* (Thomas, 1974). The ova are laid throughout late August and September where they enter diapause during the winter period. They then hatch after about 8 months in the following May, which coincides with the leaf break of *P. spinosa* (Thomas, 1974; Fartmann^[KN6] and Timmermann, 2006; de Vries *et al.*, 2011). However, as a result of this overwintering behaviour, the ova are extremely susceptible to destruction from annual flailing of hedgerows (Williams, 2007; Thomas and Lewington, 2010). According to Thomas (1974) losses by mechanised cutting regimes in Surrey equated to around 80% mortality of eggs (Bourn and Warren, 1998).

The larva of *T. betulae* hatch from around late April to early May, where they develop through four instars in total. When first hatching out, the larvae have a translucent pale white appearance with long hairs covering their body (Thomas, 1974). The hatching of *T. betulae* is always at the same time as the leaf break for *P. spinosa* so that the larvae can immediately crawl inside the bud of these leaves (Fartmann and Timmermann, 2006; Wood, 2012). The bud not only provides a source of food for the caterpillar at this early stage, but also enables it to

hide from predators. De Vries *et al.* (2011) found that even with temperature shifts from year to year, synchrony between the two was not affected.

For the remaining instars, the caterpillar attaches itself to silk pads under leaves where it rests throughout the day, leaving them at dusk to feed (Thomas, 1974; Newland *et al.*, 2010; Thomas and Lewington, 2010; Wood, 2012). The appearance of the larvae for these instars is very similar with their green colouration. However, they can be recognised by differences in size. According to Thomas (1974) after the final instar is fully fed it makes its way to the ground where it develops a slightly purple colouration, ready for pupation to occur in late June. However, throughout this period of development, it has been estimated that around 80% of caterpillars are predated by spiders, harvestmen, and insectivorous birds (Thomas and Lewington, 2010; Wood, 2012).

Those larvae that make it to the pupation stage do so by burying themselves in the leaf litter layer or in cracks in the ground where the pupa takes around a day to develop (Thomas, 1974). These micro-habitats will provide the pupa with some form of protection, especially as its brown colouration enables it to be inconspicuous within its surroundings (Wood, 2012). Even with crypsis, it has been estimated that pupa mortality is up to 80%, primarily due to predation by small mammals (Thomas, 1974; Bourn and Warren, 1998). According to Wood (2012), the pupa is tended to by ants who bury it loosely in earth cells, a relationship that characterises many species of butterfly larva that emit chemical signals and sugary secretions (Asher *et al.*, 2001; Thomas and Lewington, 2010). In total this stage in the *T. betulae* lifecycle takes around four weeks to complete.

T. betulae then enters imago where butterflies generally begin to emerge between late July and early August, flying up until early September and occasionally into early October (Thomas, 1974; Bourn and Warren, 1998; Botham *et al.*, 2011; Wood, 2012). In terms of appearance, both males and females have dark brown upper wings with an orange spot on each of their forewings, whilst their undersides are characterised by a dark orange colouration (Wood, 2012; Davies, 2014). Females are larger with wingspans up to 45mm compared to 41mm for males (Wood, 2012).

Despite emerging first, males are rarely seen in the field as they spend almost all their life at the top of the master trees in order to mate with females. After a period of around six to ten days, the females descend from the master trees in order to lay their eggs (Bourn and Warren, 1998). The female butterflies will spend the rest of their adult lives doing this over a wide area, where a large amount of time and energy is spent carefully selecting appropriate host plants (Merckx and Berwaerts, 2010; Wood, 2012). This usually occurs between 11am and 4:30pm on

warm and sunny days (>20 °C) with little wind (Green, 1990, Merckx and Berwaerts, 2010). Based on observations at Cranleigh in Surrey, Thomas (1974) found that upon finding a suitable host plant the female would crawl down the stem and probe the twig with their abdomen curled beneath the thorax. After about five minutes the female would lay an egg if it deemed the site to be suitable. Usually only a single egg is laid although occasionally up to three more may be laid on the same plant. Generally, eggs are laid on the fork of a stem on *prunus* plants under six years old, usually close to ground level (Thomas, 1974). At times when sunlight is weak, female butterflies may be observed basking with their wings spread open in order to thermoregulate (Butterfly Conservation, 2004; Merckx and Berwaerts, 2010).



Fig. 1: Photograph of an adult female *T. betulae*, taken at West Williamston by David Moore (Redhead pers comms, 2018).

2.2. Local-scale Factors Affecting Butterflies

Local-scale factors will influence the quality of a habitat and thus its suitability for a given butterfly population. Many previous studies have stressed the importance of habitat quality on

the occurrence and persistence of butterflies. For instance, Thomas *et al.* (2001) conducted one of the first studies to show that habitat quality was a better predictor of site occupancy across landscapes than patch area and isolation for the butterflies *Melitaea cinxia* (Glanville fritillary), *Polyommatus bellargus* (Adonis blue), and *Thymelicus action* (Lulworth skipper), throughout central and southern England. Kramer *et al.* (2012) support this where they concluded that habitat quality was at least as important as landscape factors, having the most significant impacts on both species' richness and density in pre-alpine calcareous grasslands in the German Alps. They found that habitat specialists were mainly influenced by the presence of larval food sources, whereas the more mobile habitat generalists were more influenced by the amount of adult food sources (Warren *et al.*, 2001; Kramer *et al.*, 2012). Furthermore, Kalarus and Norwicki (2015) also found habitat patch quality to be the more influential parameter for the persistence of *Minois dryas* (The Dryad) in the Vistula River Valley, finding that more fragmented patches of smaller size had increased abundance reflecting their higher quality and the positive effect of patch edges.

2.2.1. Plant Abundance, Diversity and Characteristics

Perhaps one of the most influential habitat quality parameters is the vegetation structure and composition of a site. This is because various plant species will provide food sources for adults and larvae as well as providing sites for oviposition to occur. Many studies have stressed the importance of larval host plants on the presence of butterflies (Clarke *et al.*, 1998; Bergman, 2001; Saarinen, 2002; Pywell *et al.*, 2004; Krauss *et al.*, 2004; Kramer *et al.*, 2012; Halder *et al.*, 2015). In general, a higher abundance of host plants means that there are more potential sites for egg laying and larval development (Salz and Fartmann, 2017). Grundel *et al.* (1998) investigated *Lycaeides melissa samuelis* (Karner blue) and its use of its host plant, *Lupinus*, in the Indiana Dunes National Lakeshore, USA. They found that the conditions under which the plant grew and their phenological stage had significant effects on the duration of the larval period, with those fed leaves from flowering plants having the shortest duration. Additionally, those feeding on shade-grown *Lupinus* completed their larval stage 22% more rapidly than those on sun-grown ones. The authors state that this faster rate of development results in higher levels of survivorship where the butterflies remain in their most vulnerable form for less time. Bergman (1998) also found that host plants growing in partially shaded conditions proved to be vitally important for *Lopinga achine* (Woodland brown) in Ostergotland, Sweden, where adult females showed preference for such plants as a means of limiting desiccation and predation. It was determined that eggs in sun-exposed conditions were subject to higher chances of desiccation due to the dryer conditions, whereas predation seemed to be the main cause of mortality within the woods. Similarly, *Thecla betulae*, have been found to be very

selective in where they oviposit. Thomas (1974) states that *T. betulae* only lays its eggs on *Prunus* species, where *Prunus spinosa* is clearly preferred. In his study based in Cranleigh, England, he found that plants under six years old were usually selected and that 97% of eggs were laid near to ground level, peaking at around 50cm. In contrast to this, Fartmann and Timmermann (2006) observed egg heights generally higher, stating that 94% of clutches were laid between 50 and 170cm above the ground. However, these differences in height could be due to geographical differences, where their study was conducted in Munster, North Rhine-Westphalia. Furthermore, their study supports that of Thomas (1974) and Merckx and Berwaerts (2010) where there was clear preference for young growth and suckers. Fartmann and Timmermann (2006) suggest that this selectivity could be to avoid inter-specific competition with other species that are able to defoliate *Prunus* bushes during the *T. betulae* larval period, whilst also taking advantage of the new leaf growth provided by the younger plants that can aid in faster development. Bergstrom (2005) in his study based near Stockholm, also found a high level of selectivity in oviposition site for *Parnassius mnemosyne* (Clouded Apollo), where it was determined that successful sites had lower ground temperatures with a tendency to be closer to host plants and shrubs. Therefore, from the findings of these studies it can be deduced that, in addition to their abundance, the conditions under which the host plants are growing in as well as their perceived quality are equally as important in influencing butterfly populations.

The presence of a range of nectar-providing plants is also crucial for butterfly diversity and abundance, particularly for adult specimens (Schneider and Fry, 2001; Saarinen, 2002; Pywell *et al.*, 2004; Rosin *et al.*, 2011; Kramer *et al.*, 2012; and Rusman *et al.*, 2016). Schneider and Fry (2001) found that as the abundance of flowering plants increased in two grasslands in Sweden, so too did the butterfly species richness. In contrast, in locations with higher nutrient levels there were less individuals as this led to a reduction in plant species diversity. Pywell *et al.* (2004) support this as they were able to determine that field margins diverse in flowers were highly important in explaining the abundance of numerous butterfly species. Additionally, they determined that legume species proved to be highly important in explaining the abundance of less mobile butterfly species, whilst larval host plants in the crucifer family attracted more mobile species in arable farms throughout England. With that being said, the presence of nectar plants alone is not the only factor, and the plant structure and physical characteristics of individual species also need to be considered. Rusman *et al.* (2016) discovered this in their study in Mount Sago, West Sumatra, where they found that *Lycaenid* butterflies visited herbs with flag shapes most frequently such as those in the *Papilionaceae* and *Fabaceae* families, whereas *Papilionid* butterflies usually visited shrub flowers with a crown shaped tube such as

Ixora javanica. Furthermore, Skorka *et al.* (2007) found that vegetation height had a significant negative effect on species richness and abundance in southern Poland. They suggest that this is because taller vegetation blocks access to flowers whilst also restricting movement between them. Therefore, later successional vegetation stages usually have a negative impact on butterfly populations, although this can also vary among species depending on their habitat preference. Salz and Fartmann (2017) support this, identifying that the key factors determining whether a heavy metal grassland supports *Argynnis niobe* (Niobe fritillary) were open vegetation with a warm microclimate and sufficient cover of its host plant, *Viola calaminaria*. Later successional stages characterised by tall shrubs and trees will often lead to reductions in various host plants and flowers and thus will lead to a reduction in overall habitat quality.

2.2.2. Habitat Type

The availability of resources for, and the influence that various environmental factors have on butterfly populations will largely depend on the type of habitat. For instance, Sanford *et al.* (2011) found that the importance of different environmental factors such as patch area, isolation, topography and habitat structure varied in their ability in influencing the presence of *Speyeria callippe callippe* (Callippe silverspot butterfly) depending on the habitat type of a patch. They found that in agricultural sites patch occupancy was mainly explained by vegetation height, whereas in spring sites numerous parameters of habitat structure were its primary determinants. Kalarus *et al.* (2013) support this where they determined that the resource use of *Minois dryas* in wet grasslands were mainly limited by the availability of nectar plants and thermal conditions, whereas in xerothermic meadows it was the amount of grass cover that influenced them more. This led the authors to conclude that the wet grasslands were superior in terms of larval host plant availability, whereas the xerothermic meadows were better habitats for adult butterflies. By using multivariate analysis on two habitats, Berg *et al.* (2011) also found similar contrasts in species composition between power-line corridors and semi-natural pastures. In contrast to many previous studies which focus on their negative effects, they determined that power-line corridors had the most species, the highest abundances and the most individuals of red-listed species within south-central Sweden (Brown, 1995; Clarke and White, 2008; Berg *et al.*, 2011).

Similar to the findings of Berg *et al.* (2011), there have been a number of studies which have investigated the value of anthropogenically created habitats such as hedgerows, green-lanes, glades and road verges as alternative habitats (Dover, 1996; Sutcliffe and Thomas, 1996; Dover *et al.*, 2000; Dover and Sparks, 2000; Haddad and Tewksbury, 2005; Valtonen *et al.*, 2005; Soderstrom and Hedblom, 2007; Berg *et al.*, 2011). Dover *et al.* (2000) stressed the importance of green-lanes as additional habitats for butterflies, finding that they were superior in

abundance and species richness to other farmland biotopes except woodland. They state that this may be because green-lanes contain an interior section characterised by lower wind speeds and more bramble nectar sources than those of hedgerows and grass banks, whilst also providing additional resources on their exterior. Dover *et al.* (2000) also found that hedgerows and grass banks were similar in butterfly abundance, but both habitats were significantly poorer than the inside of green-lanes (Dover and Sparks, 2000). Other studies have investigated the degree of utilisation of different quality man-made habitats by butterflies. Soderstrom and Hedblom (2007) investigated the use of road verges as corridors in fragmented grassland landscapes in Sweden, finding that individuals did not use strips of lower quality. This led them to determine that corridors of intermediate quality are the most effective at promoting dispersal. However, Haddad and Tewksbury (2005) demonstrate that even corridors of lower quality can be important for butterflies. In their study based in South California, they found that for *Junonia coenia* (Common buckeye) and *Euptoieta Claudia* (Variegated fritillary), as long as the corridor was higher in quality than the other possible routes, corridors of lower quality were enough to increase dispersal. They stated that the reduction in key features in corridors such as host and nectar plants meant that butterflies were more likely to fly through them without stopping, provided they aren't too long. However, Haddad and Tewksbury (2005) don't define in detail the thresholds that they used to differentiate a high-quality habitat to a low-quality one (e.g. percentage cover of host plants, number of habitat specialists, the number of butterflies within a certain distance to edges, etc). This information would be useful for other studies investigating similar relationships. It should be noted that the use of such features as either corridors or habitats varies amongst species according to their requirements. For instance, Soderstrom and Hedblom (2007) found that only specialist butterflies used their experimental strips, with the sheltered grassland strip being utilised by *Polyommatus semiargus* (Mazarine Blue), whilst *Coenonympha arcania* (Pearly heath) used the nectar strip.

2.2.3. Management

The level and type of management that a site receives also has its own influence (Wood and Gillman, 1998; Wettstein and Schmid, 1999; Ellis, 2003; Filz *et al.* 2013; and Stuhldreher and Fartmann, 2014). Depending on what a site is used for, management can be intensive or non-existent, where usually it favours butterfly populations when it falls somewhere in between the two. Although it should once again be noted that this varies amongst butterfly species and locations. Schneider and Fry (2001) found that sites richest in butterfly diversity in southern Sweden were those with a low intensity of management, whereas Saarinen (2002) found that in south east Finland, intensively managed monocultures were actually preferred by eurytopic

species such as *Aphantopus hyperantus* (Ringlet) as these butterflies have a high tolerance for disturbance, often use weeds as larval host plants and also have little competition for resources. Management effects on oviposition were observed by Ellis (2003), where *Aricia artaxerxes* (Northern brown argus) laid fewer eggs in managed plots characterised by shorter vegetation. They state that as the sward height increases due to lack of grazing, so too does the host plant growth, leaf size and leaf nitrogen, all of which will have a positive effect on larval development. Management effects can also vary according to habitat type, as identified by Lunja *et al.* (2017). In their study based in Lower Saxony, Germany, farmland butterflies were positively affected by regular mowing and grazing of calcareous grasslands as this leads to a higher cover of flowering plants. Alternatively, farmland butterfly abundance in orchard meadows seemed to be positively affected by abandonment as the lack of invasive management would initially enable the growth of herbs and flowers whilst flowering shrubs would provide an extra source of nectar. Overall however, the later successional stages would inevitably cause negative impacts on these butterflies.

Depending on the type of management, the important environmental influences will be altered in various ways. This was investigated by Wettstein and Schmid (1999) on fen sites in central and north-eastern Switzerland, where butterfly diversity was higher on mown sites as it encourages a higher abundance of nectar plants. However, grazed sites were characterised by higher abundances of *Clossiana selene* (Small pearl-bordered fritillary) and *Boloria aquilonaris* (Cranberry fritillary) as mowing removed many of their larval food plants. Aschehoug *et al.* (2015) further support this, finding that habitat manipulation can lead to indirect increases in the mortality of eggs and juveniles due to predation. Tree removal was found to cause the highest rates of predation whilst dam creation decreased it. Many previous studies have also found that the use of pesticides, commonly implemented throughout the agricultural landscape, can often have profound effects on butterfly populations (Rands and Sotherton, 1986; Davis *et al.*, 1991; Cilgi and Jepson, 1995; Kjær *et al.*, 2014; Brittain *et al.*, 2010; Goulson, 2013; Wood and Goulson, 2017; Braak *et al.*, 2018). Rands and Southerton (1986) compared a sprayed plot of arable land to one that had its field edges left unsprayed, discovering that the second plot had a significantly higher abundance of butterflies than the first. However, Braak *et al.* (2018) state that the effect of pesticides will be dependent on the species of butterfly and its life stage as these can affect the resistance of any given individual. Furthermore, the magnitude of impacts will also depend on the method of application as factors such as spray drift can affect large areas. Overall it can be determined that no one form of management is applicable to all species at the same time and consideration must be given to what butterflies are using any given site before an option is selected.

2.3. Landscape-scale Factors Affecting Butterflies

In addition to local habitat quality, much research has also been conducted on factors affecting butterfly populations at broader scales (e.g. Schweiger *et al.*, 2006; Cozzi *et al.*, 2007; Binzenhofer *et al.*, 2008; Heer *et al.*, 2013; Stuhldreher and Fartmann, 2014; Kalarus and Nowicki, 2015). The main factors at the landscape-scale include habitat fragmentation, habitat area and the types of habitats which surround a patch. It is generally the process of habitat loss and resulting fragmentation that can have the most profound effects on butterflies (Sih *et al.*, 2000). When considering the landscape-scale, metapopulation theory acts as the main model for investigating the effects. It dictates that spatially structured populations are made up of smaller sub-populations, each separated by dispersal barriers and connected by movements of individuals (Opdam, 1991; Hanski and Ovaskainen, 2003; Hanski, 2004). According to Sih *et al.* (2000), the persistence of a metapopulation relies on the balance between occupied patches going extinct and empty patches being recolonised. The size of a given fragment and any degradation in its quality will influence the rate of extinction, whilst the level of isolation will influence the rate of recolonization (Opdam, 1991; Sih *et al.*, 2000). The importance of any of the landscape-scale influences will again, vary with location and species, in turn affecting their metapopulations in various ways.

2.3.1. Fragmentation/Isolation

According to Didham (2010), fragmentation describes the process in which habitat loss leads to the separation of large, continuous habitats into smaller patches of lower total area, separated from each other by numerous dissimilar habitats. This can lead to butterfly populations becoming 'trapped' in isolated patches. There have been many studies that have investigated this phenomenon, many of which suggest that it has negative impacts on butterflies (Wettstein and Schmid, 1999; Filz *et al.*, 2013; Orvosy *et al.*, 2013). Filz *et al.* (2013) found that where the level of isolation was higher for calcareous grasslands compared to vineyard fallows in south-west Germany, migration would be increasingly unable to compensate for the loss of species in that habitat. This could eventually result in the degradation of gene flow for that population and could lead to its eventual disappearance. Binzenhofer *et al.* (2008) support this where the extinction risk of *Cupido minimus*_[KN7] (Small Blue) in the Hohe Wann nature reserve in Germany strongly increased with the isolation of small habitat patches. This along with the positive effect that *Anthyllis*_[KN8] has on *C. minimus* populations, lead them to conclude that lower habitat quality can be somewhat mitigated by higher connectivity between host plant patches in fragmented landscapes. Species specific responses to isolation have also been demonstrated by Bauerfeind *et al.* (2009), who partially attributed the negative impacts of fragmentation on *Lycaena helle* (Violet Copper) in western

Germany to their low dispersal ability. This meant that their populations would be easily isolated even with small interpatch distances. Orvosy *et al.* (2013) support this and suggest that gender also has an influence where a low dispersal capacity for *Coenonympha oedippus* (False ringlet), particularly for females, was observed. However, Kalarus and Nowicki (2015) observed a positive effect of isolation where smaller and more fragmented habitat patches in Poland resulted in an increase in the abundance of *M. dryas*. They suggest that these patches are of higher quality and the butterflies within them benefit from the presence of their patch edges. Their results suggest that local habitat quality takes precedence over fragmentation for this species. Additionally, the presence of corridors may also mitigate the negative impacts of fragmentation (Dover and Sparks, 2000; Haddad and Tewksbury, 2005; Soderstrom and Hedblom, 2007; Berg *et al.*, 2011).

2.3.2. Surrounding Habitats

Linked to the degree of fragmentation is the variety of habitats that surround a patch. The suitability of the surrounding habitats for utilisation by a given butterfly population will help determine whether a patch is isolated. This has been demonstrated by Cozzi *et al.* (2007), where they determined that colonisation depends on dispersal ability as well. They found that *Boloria selene* [KN9] (Small Pearl-bordered Fritillary) occurrence was positively correlated to higher amounts of wetland on a larger scale, whereas the poorest disperser, *Boloria titania* (Titania's Fritillary) [KN10], had its occurrence positively correlated to a higher amount of wetland on a much smaller scale. Perhaps on a more surprising note, the presence of human settlements in the surrounding environment have also been seen to have a positive effect on certain butterfly populations. Rosin *et al.* (2011) discovered that patches adjacent to human settlements were characterised by a higher density of *Polyommatus coridon* (Chalkhill blue). They attribute this to the fact that these grasslands may have been abandoned last and so succession would not have progressed enough to have too much of an impact on this species, whilst the higher diversity in flower rich gardens may provide additional resources (Rosin *et al.*, 2011). Numerous studies have also found positive effects of wooded landscapes on butterfly populations (Bulman, 2007; Cozzi *et al.*, 2007; Kuussaari *et al.*, 2007; Merckx *et al.*, 2008; Berg *et al.*, 2011; Kramer *et al.*, 2012; Liivamagi, 2014; Halder *et al.*, 2015; Lunja *et al.*, 2017; Luppi *et al.*, 2018). Whilst this may initially seem surprising given that dense forests could act as barriers for dispersal, it has been found that for many species they are important sources of additional resources and shelter. Because of this, Berg *et al.* (2011) suggest that landscapes characterised by forests are important for the conservation of species that are more sensitive to habitat fragmentation. Furthermore, they state that with these benefits, forests can offer

dispersal opportunities for some butterflies, supporting them as they move through the landscape in search for more suitable patches.

A mix of habitats also helps to create more of a mosaic in the landscape, which in turn caters for a range of different species. Schneider and Fry (2001) found that a coarse-grained landscape made up of larger grasslands had a lower number of species than a finer grained landscape characterised by a mix of grasslands adjacent to forest areas. Liivamagi *et al.* (2014) support this where they were able to identify a positive relationship between the amount of forest habitats and the butterfly species richness in a 250m radius. The authors state that it is the presence of forest edges that help to create a more diverse microclimate and compositional structure that benefits butterflies in terms of feeding, oviposition and refuge from disturbance. Furthermore, Liivamagi *et al.* (2014) also found a negative correlation between meadow area in the landscape and butterfly species richness and abundance.^[KN11] This reflects the negative impacts that less sheltered habitats and higher wind speeds may have on populations. However, this may also be caused by the overall species composition of where the study was based in northeast Estonia which is likely characterised by woodland species. It should also be noted that whilst Schneider and Fry (2001) found fine-grained mixed landscapes had twice the number of species, they also had half the number of individuals than coarse-grained ones. This could reflect the fact that homogenous coarse-grained landscapes are more likely to be characterised by generalist species, which in turn are more common. It could also be due to the larger patch size of the habitats in the coarse-grained landscape being able to contain larger populations within them.

2.3.3. Patch Area

Studies such as those by Wettstein and Schmid (1999), Cozzi *et al.* (2007), and Rosin *et al.* (2011) have also found effects of patch size on occurrence, population size and species richness. For instance, Krauss *et al.* (2004) found that as the cover of the host plant *Anthyllis vulneraria* (common kidneyvetch) increased with patch area so too did the occurrence of *C. minimus*, with habitat isolation and quality being of subordinate importance in comparison. Bauerfeind *et al.* (2009) also found that for populations of *L. helle* in western Germany, patch occupancy was linked to habitat area and the abundance of its larval host plant, with occupied patches being significantly larger and less isolated than non-occupied ones. They also found that other parameters of habitat quality were generally less important for this low-dispersing butterfly. However, whilst these studies demonstrate the importance of patch area for various species, others have shown that it is less influential. Thomas *et al.* (2001) state that occupancy and patch area were not correlated for any of the observed species in their study. Furthermore, Merckx and Berwaerts (2010) found no effect of patch area on the number of *T.*

betulae eggs laid on hedgerows, most likely due to its high mobility enabling it to find its resources across the landscape with ease. As with most of the other environmental influences, the effects are largely dependent on the species. Habitat specialists in northern Bavaria were found to have a significantly higher abundances, species diversity and species richness in larger cities compared to smaller ones (Bruckman *et al.*, 2010). Bruckman *et al.* (2010) suggest that edge effects can help to explain this where habitat generalists benefit more from a higher proportion edges when the patch size decreases (Laurance and Yensen, 1991). Furthermore, Schultz and Crone (2005) found that for *Icaricia icarioides fender* (Fender's blue butterfly), short and long-term predictions indicated that small, connected patches can be just as valuable as large connected ones. In this case, the authors identified that if the patches were well connected then it can compensate for their area for this species. This also proves that often these variables are intertwined in their effects on butterflies, either compensating each other or mitigating their impacts.

2.3.4. Climate

Butterflies are very sensitive to weather regimes and temperature, usually only flying on days where conditions are warm and calm. Therefore, climate has a big influence on the inter-annual variance in metapopulation success. Schweiger *et al.* (2006) ran models for both humid and dry years to investigate the responses of *Pararge aegeria* (Speckled Wood) to them. They were able to conclude that climate helps determine what factors limit this species the most when extreme fluctuations occur. For instance, the dry year model predicted that only patches and landscapes of the highest quality could support butterflies, where regional factors dominated over local ones. The humid year model showed that *P. aegeria* is not very dependent on either local or regional factors, and as such is particularly abundant regardless. The results ultimately show that a landscape of high quality is vitally important, acting as the primary safeguard for these populations as extreme weather events occur increasingly into the future (Schweiger *et al.*, 2006). Warren *et al.* (2001) support this with their study based on the distribution and sizes of 46 UK butterfly species. They found that three-quarters of them were in decline, and through the combined effect of climate change and habitat alteration, specialist species are more likely to be reduced in numbers. This in turn will lead to a simplification in the species composition of the UK, being dominated more by generalist communities. These findings are surprising given that with warmer climates one would expect an increase in the range of many of the butterfly species, however when the effects of isolation and habitat degradation are also considered then the less mobile specialists will be unable to expand.

Whilst these studies highlight the negative effects of climate change on butterflies, de Vries *et al.* (2011) demonstrate that increasing temperature will not necessarily be detrimental to the

synchronisation of *T. betulae* larvae hatching and the budburst of blackthorn. From their experiments they were able to find that there was plenty of food available at all tested temperatures and that the hatching date is adapted to shifts in budburst during warmer temperatures. However, they did still observe an effect of spring temperatures on the level of synchrony where in 2006 colder temperatures from previously in the year caused egg hatch to occur 20 days later than usual whilst budburst remained unchanged. This poses a potential issue in that leaves may not retain the same nutritional value by the time the eggs hatch. Furthermore, they found that an increase in temperature of 5°C lead the period of budburst being 11 days longer whilst the hatching period was 3 days shorter. de Vries *et al.* (2011) go on to state that this could lead to a lower availability of high-quality young leaves for the first instars resulting from the lack of a sharp peak in leaf flush and thus reduced chances of a perfect match between egg hatch and budburst. Overall, as climate change continues and warmer temperatures become the norm, it will affect various butterfly species differently. Based on data from Massachusetts, Breed *et al.* (2012) found that an increase in temperature lead to increases of species near the northern limit of their range whilst those near the southern limit of their range declined. This means that conditions are becoming increasingly favourable for warm-adapted butterflies which are, to a degree, becoming invasive by moving into areas previously inhabited by cold-adapted species (Jakuboski, 2012).

2.4. Summary

Overall, the literature has shown that there are variety of anthropogenic and naturally occurring factors that lead to the fluctuations in butterfly populations over time. These factors are either specific to a local or larger scale and vary in importance depending on the butterfly species and location. This is particularly true of management, where different practices have their own influence on different species. Furthermore, geographical differences also become more evident when climate is considered, where species existing at borders of their range will be more affected by increases and decreases in temperature compared to those living closer to the centre (Breed *et al.*, 2012). For instance, with regards to *T. betulae*, as it is at the northern limit of its range in UK, one would expect to see an increase in abundance with increasing temperature.

It would be of benefit if future research investigated whether the factors at either scale amplify the effects seen at the other one and to what degree. The vast majority of research acknowledges that each set of factors influence butterfly populations in addition to one another but don't generally indicate the degree to which one factor at the regional-scale, for example, increases the magnitude of another factor at the local-scale. Additionally, it should be noted that because the West Williamston Nature Reserve will have its own specific local

and regional environmental conditions, and that *T. betulae* has its own set of characteristics and habitat preferences, the influence of any of the factors on the local population will likely differ to those from other studies. Because of this, the present study aims to assess how *T. betulae* egg counts have fluctuated over time in order to gain an insight into the health of the population specifically at West Williamston, whilst also assessing whether management has been effective in increasing the number of eggs recorded along the 500m transect. This should help to provide justification for the change in management strategy for the site in 2009, whilst also providing a basis for other sites to adopt similar management strategies where appropriate.

3. Site Description

This study is based on egg count data obtained from the West Williamston Nature Reserve (SN033058), approximately two miles from the village of Carew, within the Pembrokeshire Coast National Park (fig. 2). The reserve is situated at the confluence between the rivers Cresswell and Carew, where the surrounding environment is characterised by estuarine salt marsh and farmland (Anderson and Walton, 1998). The reserve itself contains a mixture of woodland, scrub, limestone grassland, saltmarsh and tidal mudflats (Anderson and Walton, 1998). Perhaps the most important feature of the reserve with respect to *T. betulae* is the considerable coverage of *P. spinosa* along the foreshore and scattered throughout the other parts of the site. Furthermore, large quantities of *P. spinosa* are also present in many of the patches and hedgerows surrounding the reserve. Notable sites include West Williamston Park, New Park Farm, Croft Quarry and Tything Barn (Redhead, 2018). The limestone ridges support rendzina soils, characterised by organic material from the decay of limestone plants, whilst the quarried sections are made up of calcareous soils. Furthermore, the woodland parts of the reserve lie on top of brown earth soils, whilst the tidal creeks frequently receive deposits of mud and silt from the rivers (Anderson and Walton, 1998).

The reserve is currently managed by the Wildlife Trusts of South and West Wales as part of a 42 year-lease with the National Trust. The management involves rotational coppicing on a four to five-year basis along the foreshore, the north field and the middle field. Rotational coppicing was introduced into the north and middle fields in 2009 as part of a new management strategy, whereas it occurred along the foreshore before this as part of the 1998 management plan. For the north field there are three blocks corresponding to three years of cutting and one year of no cuts at all. The middle field contains four blocks which are cut on a four-year rotational basis. Finally, the foreshore is separated in to five 100m sections, with each getting cut on a five-year rotation. The location of the foreshore 100m subsections is represented by the red dots in fig. 2, whilst the north and middle fields fall within the yellow National Trust boundary on the map. Cuts are done around June/July during the period at which *T. betulae* is buried in the ground in its pupa stage. In each location, where other species are overshadowing young *P. spinosa*, they are cut back to encourage its growth.

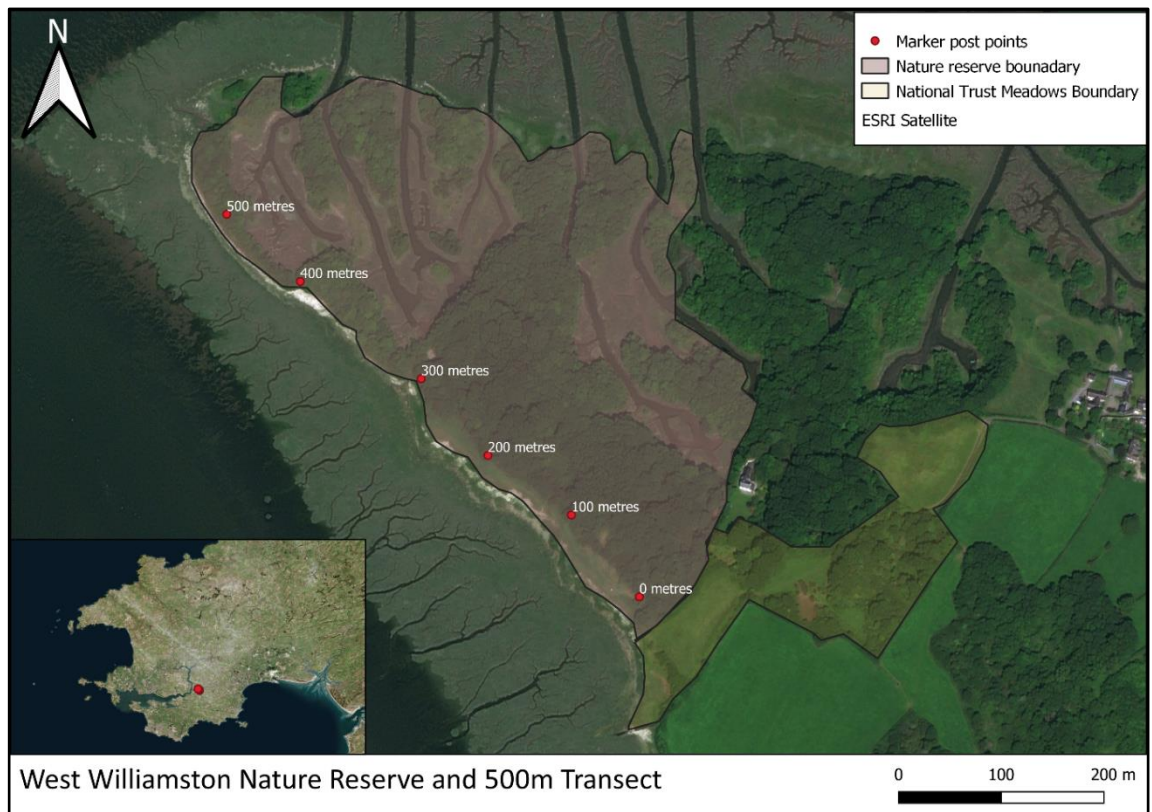


Fig. 2: 500m egg survey transect and its location in the West Williamston Nature Reserve. The yellow section contains the meadows that are also occasionally surveyed separately from the main transect and have also proven to be important sites for oviposition. Map created using QGIS and the 'ESRI Satellite' basemap.

4. Methodology

As the West Williamston and Grafton Wood *T. betulae* egg counts and the climate data used in the present paper are from secondary sources, their layouts and origins are discussed in the following chapter. Furthermore, the methods that were used to obtain and statistically analyse the *T. betulae* egg counts are also outlined. From this, justification can be provided for the inclusion of specific data and use of particular methods in order to investigate the effects of rotational coppicing on the annual *T. betulae* egg numbers at West Williamston.

4.1. Egg Count Dataset

The egg count data was provided by David Redhead who has been directly involved with the monitoring of *T. betulae* eggs since 2013. Volunteers form a big part of the egg monitoring for the site and therefore large quantities of the data were collected by them. Most of the survey work for the egg counts was overseen by Nikki Anderson up until she was unable to continue from 2016 onwards, therefore the 2016 and 2017 counts were overseen by David Redhead as a result. Whilst much of the data used in this study has been previously collected by Nikki Anderson, David Redhead and numerous volunteers, I had active participation in the collection of the 2017 and 2018 egg counts, where the methodology has remained the same throughout the monitoring period.

The survey data dates from 1995, taken from a 500m transect along the foreshore of the reserve. In addition to the 500m transect, data was also collected for some non-linear sections along the route including two glades, a bracken patch and a shallow pool, as well as in other parts of the reserve such as the limestone ridges and the meadows. However, the recording of these sections has been very inconsistent from year to year, with many gaps throughout the dataset. For this reason, these counts have been omitted from this study and a revised count based solely on the 500m transect data will be used. The transect is further split into five 100m sections, each of which has a total count for most years. The 100m sections are also further divided into 25m sub-sections, each with their own totals. However, it should be noted that since the monitoring project has had two different people overseeing it in the past, and the fact that it covers a time period of 20 years, some of the data for the 100m sections could not be recovered. This includes the entirety of 2005 and the 300 to 400m section of 2007. Furthermore, for the years 1995, 2003, 2017 and the 400 to 500m section of 1996, the individual counts for the 25m sub-sections are not present and instead only include the total counts for the 100m sections. Therefore, the totals for each 100m section will be focused on for all years.

4.2. Egg Count Data Collection

As adult *T. betulae* are scarce and rarely seen, the monitoring of populations is too difficult to do using traditional adult counting techniques^[KN12]. Therefore, it has been determined that the best way to investigate *T. betulae* population trends is via egg count surveys. Egg monitoring is always conducted once per year in the winter time, usually from mid-November to mid-December. The egg counts at West Williamston rely heavily on the help of volunteers, where the 500m transect is covered relatively quickly by separating out into groups that cover each 100m section. In conjunction with the method proposed by the UK Butterfly Monitoring Scheme (UK BMS), counts do not last longer than two hours, as beyond this time the effects of eye fatigue and lapses in concentration can take effect and increase the chances of obtaining unreliable results (Green, 1990). Overall, the count methods loosely follow those outlined by the UK BMS whereby eggs are counted in 100m sections annually. However, the search time and the amount of suitable habitat are not recorded. According to Walton (2018) the reasoning behind this is that the habitat for the reserve is considered to be good overall, with blackthorn being the focus during all counts.

The 500m^[KN13] transect egg counts start in the morning, from around 10:00 and finish at around 12:00. Each 100m section is covered by a group of volunteers, usually in groups of three to four, where the suckering shoots and the twigs of young blackthorn are searched, and any identified eggs are counted. All *T. betulae* eggs are counted, including those that appear damaged, predated and parasitized. At the end of the search the totals for each section are added together in order to receive an overall count for the transect.

It should be noted that the UK BMS guidance suggests that each survey route is monitored by one trained observer as opposed to multiple volunteers. Therefore, this will need to be taken into consideration when analysing the results of this study as inexperience could affect the reliability of some of the results. Furthermore, as many people are involved in the monitoring there may be inconsistencies in the pace at which searching is conducted and so some volunteers may spend longer searching than others which could also skew results. Even so, many of the volunteers have helped with *T. betulae* monitoring for many years and there is a good amount of experience from them to ensure that egg counts are as representative as possible.



Fig. 3: *T. betulae* eggs found on black thorn at West Williamston (left) and the foreshore in which the transect is located (right).

4.3. Grafton Wood Data

In addition to the data collected from West Williamston, previous egg count data was also acquired from Grafton Wood in Worcestershire, courtesy of Simon Primrose, one of the country recorders for the West Midlands. The data set extends back to 1970 and is based on the 'core hedgerows' that mainly inhabit an orchard area as well as along the southern border of the wood. It should be noted that over this period *T. betulae* has expanded rapidly throughout the area where by the end of 2016-17 winter the butterfly's range was up to 215 one-kilometre grid squares (Primrose, 2018). The data also follows the methodology proposed by the UK BMS, and unlike the West Williamston counts, includes the heights at which the eggs were laid. The additional information that the recorded heights provide could be valuable in building a picture of regional trends in *T. betulae* behaviour and potentially help guide future management. The egg height data also includes data taken from five additional hedgerows not included within the core hedgerow counts. However, an immediate issue with the dataset is that the heights have been recorded in unequal categories (e.g. 0-1 foot, 2-4 foot, and 4.5-6 foot). This may have been a useful way of recording in the field and may provide a general idea of the preferences in height for oviposition, but in terms of statistical analysis it is not useful which meant that the data needed to be standardised into equal categories. Categories were standardised into 'one foot' intervals where the category for 2-4 foot was divided by 2, 4-4.5 foot was multiplied by 2 and 4.5-6 foot was divided by 1.5. The category for 6 foot and above was not used as no upper margin is specified and at this height it is unlikely that people would be able to observe all the eggs making it an unrepresentative count. Also included within the data are the groupings of the eggs (e.g. single, doubles, trebles, etc), and the allotted search times for each hedgerow.

4.4. Temperature and Rainfall Data

Historical mean temperature and rainfall data was sourced from the MetOffice. The Aberporth dataset (Altitude: Approx. 67m) was used to analyse weather effects on the West Williamston (Altitude: Approx. 13m) egg counts, whilst the Ross-on-Wye (Altitude: Approx. 60m) dataset was used for Grafton Wood (Altitude: Approx. 40m) (Ordnance Survey, 2017; ElevationMap.net, 2018). The selection of these sites was based on their distance from the respective egg count locations where both Aberporth and Ross-on-Wye were approximately 30 miles away from their respective *T. betulae* sites. However, it should be noted that the relatively significant distance between the weather stations and the reserves, along with the differences in altitude particularly for Aberporth and West Williamston, means that the climate data may not always reflect the actual values experienced at the reserves. Regardless of this, the weather stations were chosen because they were the closest available ones to the reserves and this data was only used to investigate any general trends and correlations between the datasets.

4.5. Statistical Tests

Minitab was used for all statistical testing. Prior to analysis, the results from the Anderson-Darling test showed that both the 500m egg counts and the Aberporth mean temperature were not normally distributed whilst the mean rainfall data was found to follow a normal distribution. Because of this, the egg count and mean temperature data were square root transformed in excel with the SQRT function. Whilst the egg counts achieved a normal distribution this way, the mean temperature did not. Therefore, it was decided that Spearman's Rank would be used to infer whether there was a relationship between mean temperature and the observed egg counts (H_0 : there is no relationship between temperature and the number of eggs; H_1 : there are more eggs at higher temperatures). It was also investigated whether there was a relationship between the egg counts and average rainfall which was done using Pearson's Product Moment Correlation (H_0 : there is no relationship between average rainfall and the number of eggs; H_1 : there are more eggs as average rainfall increases). Regarding the Grafton Wood data, it was found to be non-normal in distribution so also had to be square root transformed. Once this was complete, Pearson's Product Moment Correlation was also used to determine whether there was a relationship between the transformed Grafton Wood egg counts and the Ross-on-Wye mean temperature and rainfall for the entire period of recording since 1970. Furthermore, the West Williamston and Grafton Wood egg counts were checked to see if they were significantly different from each other by running a Student's T-test (H_0 : there is no significant difference between the two datasets; H_1 : the datasets are significantly different from each other). This helped to determine whether the

two sites have similar counts to enable inferences as to whether the use of rotational coppicing at both locations has been equally effective.

Next, the total square-root transformed 500m transect egg counts before 2009 and from 2009 onwards were analysed using a Student's T-test in order to determine whether there was a significant difference between the two sets of data before and after increased rotational coppicing (H_0 : there is no significant difference before 2009 and from 2009 onwards; H_1 : there is a significant difference before 2009 and from 2009 onwards). Furthermore, the difference between each of the sections that make up the 500m transect was investigated using two separate ANOVA tests (H_0 : there are no significant differences between each section; H_1 : there are significant differences between the sections). One ANOVA test was used to analyse the difference between each section before management changed in 2009 and the other was used to check for this difference from 2009 onwards. By checking for significant differences before and after further rotational coppicing in 2009 it can help deduce whether increased management has been effective on all sections equally. In addition to the ANOVAs, post hoc testing in the form of Fisher's individual error rate was conducted in order to determine exactly which sections were significantly different from the others. Since not all the possible variables influencing the egg counts were measured in this project, a 99% confidence level was used to test for significance in both tests.

5. Results

With the methods for the current research explained and justified, the results from the analysis of the datasets are discussed below. Initially the trends in the West Williamston and Grafton Wood egg counts are outlined, whilst the results from the T-test are given to check for the degree of similarity between the two datasets. Next, climate relationships are also explored to find out the level of influence these variables have on the egg counts. Finally, the influence of increased rotational coppicing on the 500m transect egg counts at West Williamston is investigated by displaying the results from the T-tests and ANOVA tests before 2009 and from 2009 onwards. In addition to this, the height data for Grafton Wood is also outlined to check for its usefulness explaining *T. betulae* oviposition preferences.

5.1. West Williamston and Grafton Wood Egg Counts

As expected, the 500m transect egg counts for West Williamston fluctuate highly from year to year. This can be seen in fig. 4 where during the first thirteen years the counts stay below 200, with the lowest count being 16 eggs in 2002. However, as time progresses beyond this period they seem to increase to significantly higher numbers, the most pronounced of which is in 2013 at 632 eggs. The trend line demonstrates this steady increase over time^[KN14], although the R-value is still low and there is still substantial variability in the counts. The Grafton Wood egg counts (fig. 3) extend over a much longer period of time than the West Williamston ones, but still seem to follow a similar trend characterised by low egg counts including some years with nothing (1974, 1976, 1977, 1984 and 1985) during the first 22 years, until a sharp increase in counts can be observed in 1993, reaching 365. From this point the counts stay above 100 except for the years 1996, 1998, 1999, 2000 and 2001, where it peaks in 2005 at 408 eggs. However, during this period characterised by higher egg counts, significant fluctuations do still frequently occur. Regarding the similarity between the West Williamston 500m transect and the Grafton Wood core hedgerow counts since 1995, the Student's T-test presented a T-value of 1.23 and a P-value of 0.224. Because of this H_0 ^[KN15] had to be accepted as little confidence could be given to them being significantly different from each other.

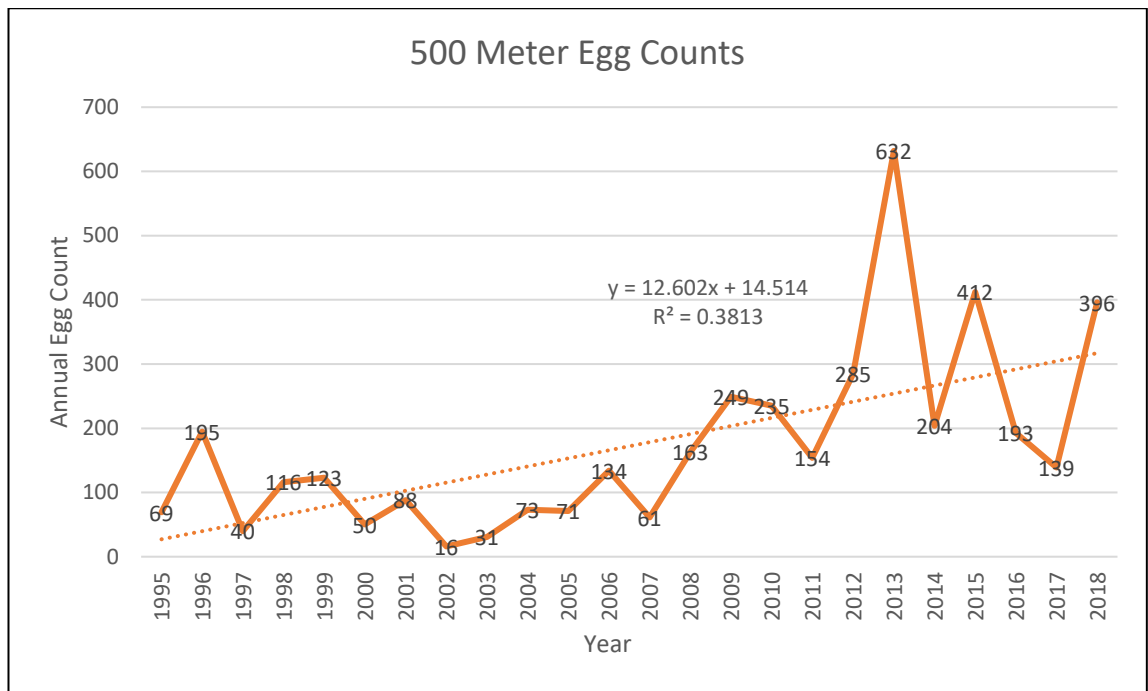


Fig. 4: Line graph showing the total observed egg counts along the 500m foreshore transect (not including non-linear sections) for each the annual surveys since 1995.

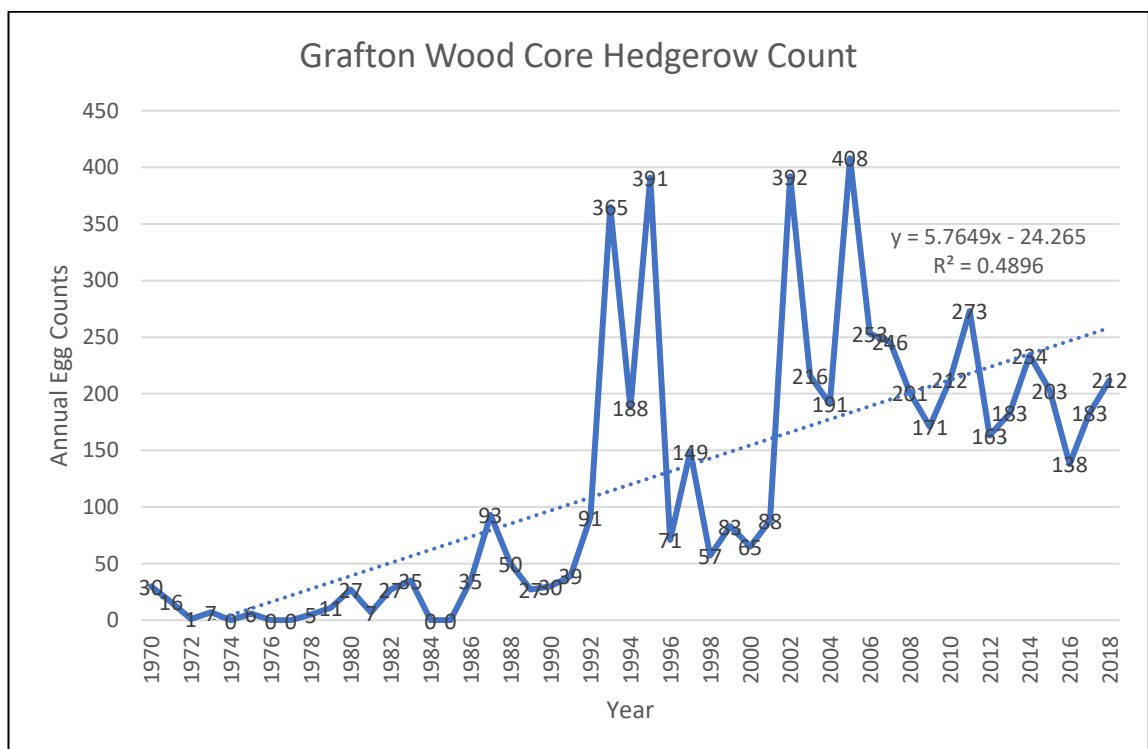


Fig. 5: Line graph showing the total observed egg counts along the core hedgerows at Grafton Wood for each of the annual surveys since 1970.

5.2. Relationship with Climate

With regards to climate relationships, upon conducting Spearman's rank on the mean temperature and 500m egg count data, a r_s value of -0.350 was obtained, indicating a weak

negative relationship. Furthermore, it was determined from the P-value of 0.102 that this is not significant at the 95% confidence level and therefore there is unlikely to be a relationship between the two datasets. This weak relationship can also be seen in fig. 6 where an R^2 value of 0.1194 was obtained. Furthermore, upon conducting Pearson's correlation coefficient on the mean rainfall and square root transformed egg count data, an r-value of 0.075 was obtained. From this and the P-value of 0.735 it can be concluded that there is no significant relationship between these either. Once again, a scatter graph was also created for the two variables which obtained an R^2 value of 0.0056 supporting this conclusion (fig. 6).

In contrast to the West Williamston counts, a significant and relatively strong relationship was found between the Ross-on-Wye average temperature data and the transformed Grafton Wood counts, where an r-value of 0.6 and P-value <0.001 was obtained from the Pearson's correlation test. This seems to indicate an increase in eggs with increasing temperature. However, the Grafton Wood egg counts did not significantly correlate with the mean rainfall data, achieving a low r-value of 0.181 and a P-value of 0.219. Scatter graphs for the Grafton Wood data are included in fig. 7 and help support the egg-climate relationships found from the statistical tests where an R^2 value of 0.3102 was obtained for the mean temperature, whilst an R^2 value of 0.0228 was obtained for mean rainfall.

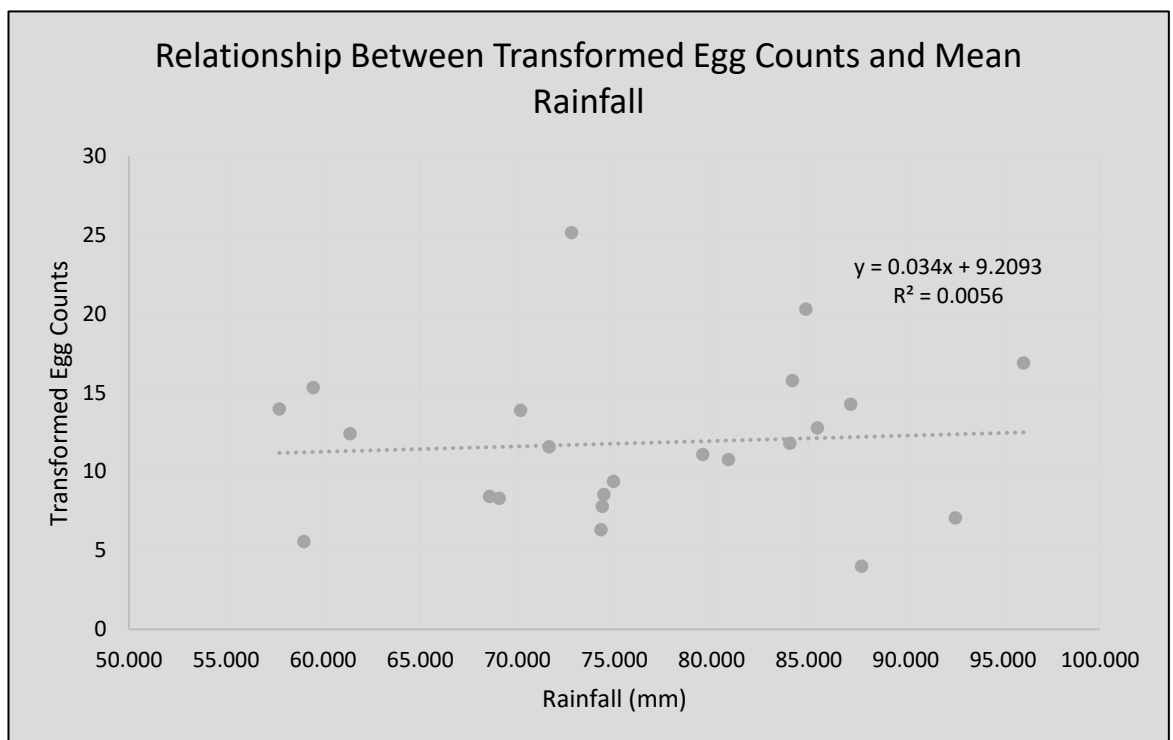
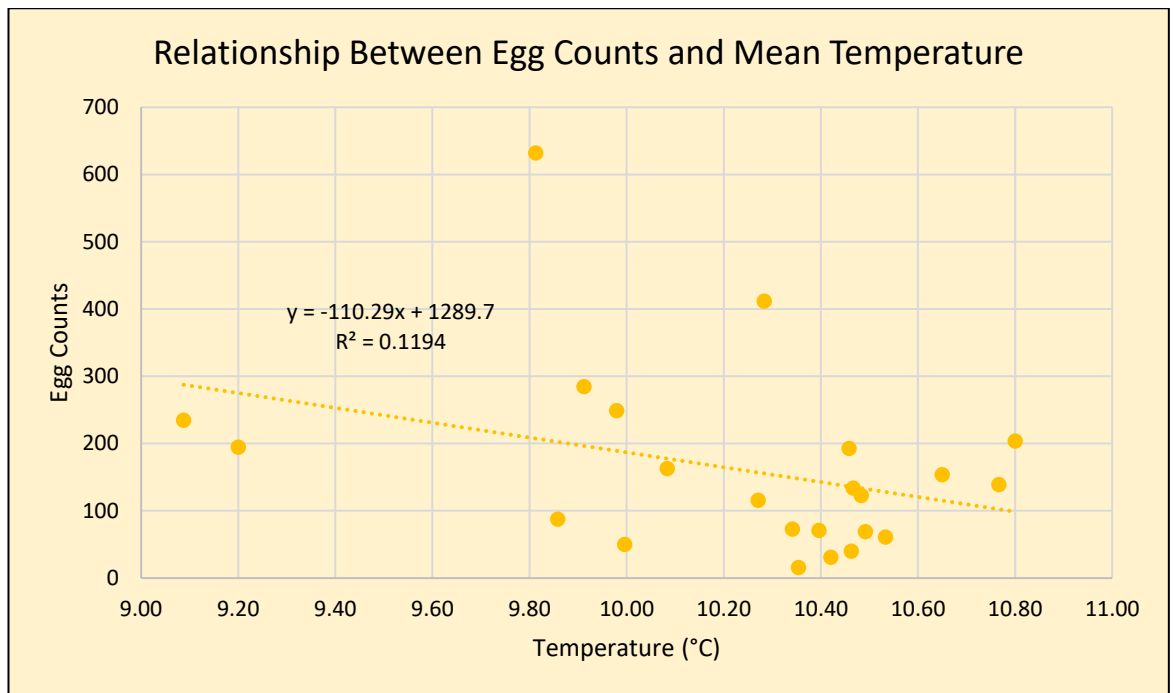


Fig. 6: Scatter graphs to show the relationship between the 500m West Williamston transect egg counts and the MetOffice Aberporth mean temperature and rainfall data respectively.

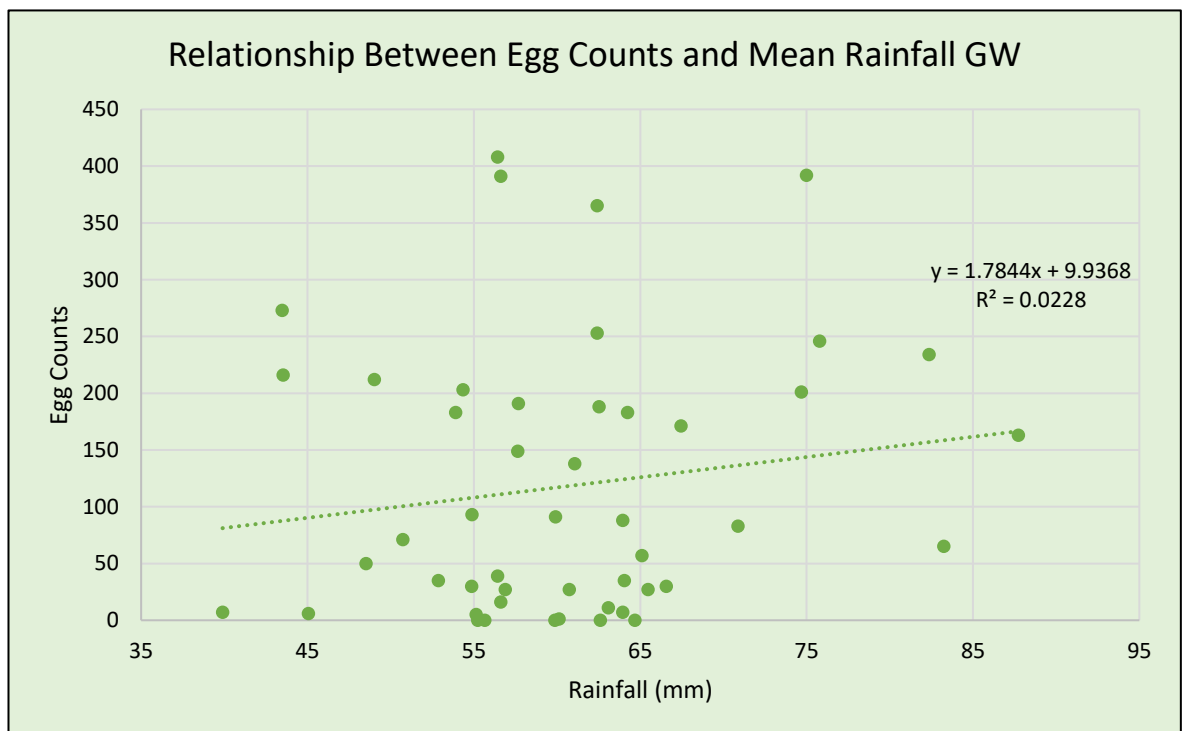
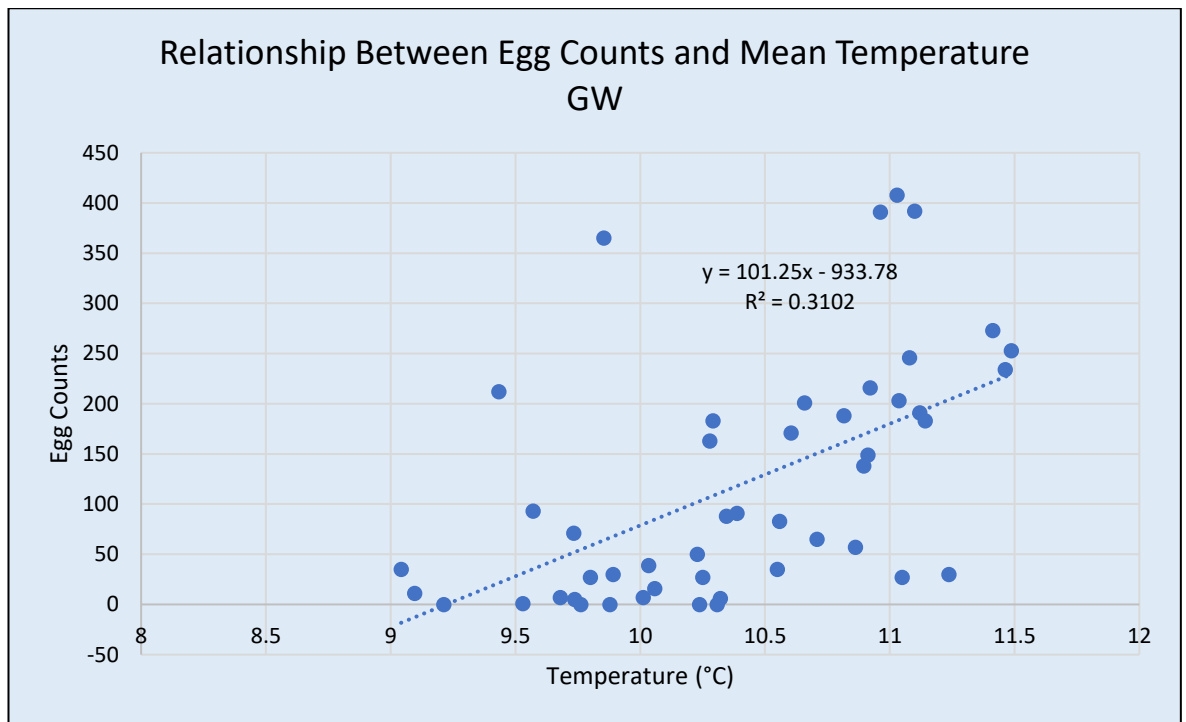


Fig. 7: Scatter graphs to show the relationship between the Grafton Wood core hedgerow egg counts and the MetOffice Ross-on-Wye mean temperature and rainfall data respectively.

5.3. Influence of Management

When investigating the effect of increased rotational coppicing, the Student's two sample T-test conducted on the egg count data before 2009 and from 2009 onwards demonstrated that their means were significantly different at the 99% confidence level, with a P-value of <0.001 . Additionally, upon running ANOVA tests to determine whether there are any differences between each 100m section along the transect, it was determined that before 2009 and from 2009 onwards not all the means are equal. This is because for both tests a P-value of 0.000 was obtained indicating that it is highly significant at the 99% confidence level. The graphs showing the results from the post-hoc Fisher's test show which sections are significantly different from the others (fig. 8). For the period before 2009, section one is significantly higher than all the others whilst section three is also significantly higher than section four. The period from 2009 onwards shows slightly different results where section one is only significantly higher than sections two, four and five. Furthermore, section three is now significantly higher than sections four and five but not section one or two. Overall these reflect how section one has the highest average counts along the transect. However, they may also suggest that section three has increased in egg counts very significantly since the introduction of rotational coppicing into other parts of the reserve, where the counts for section one are no longer significantly higher than it.

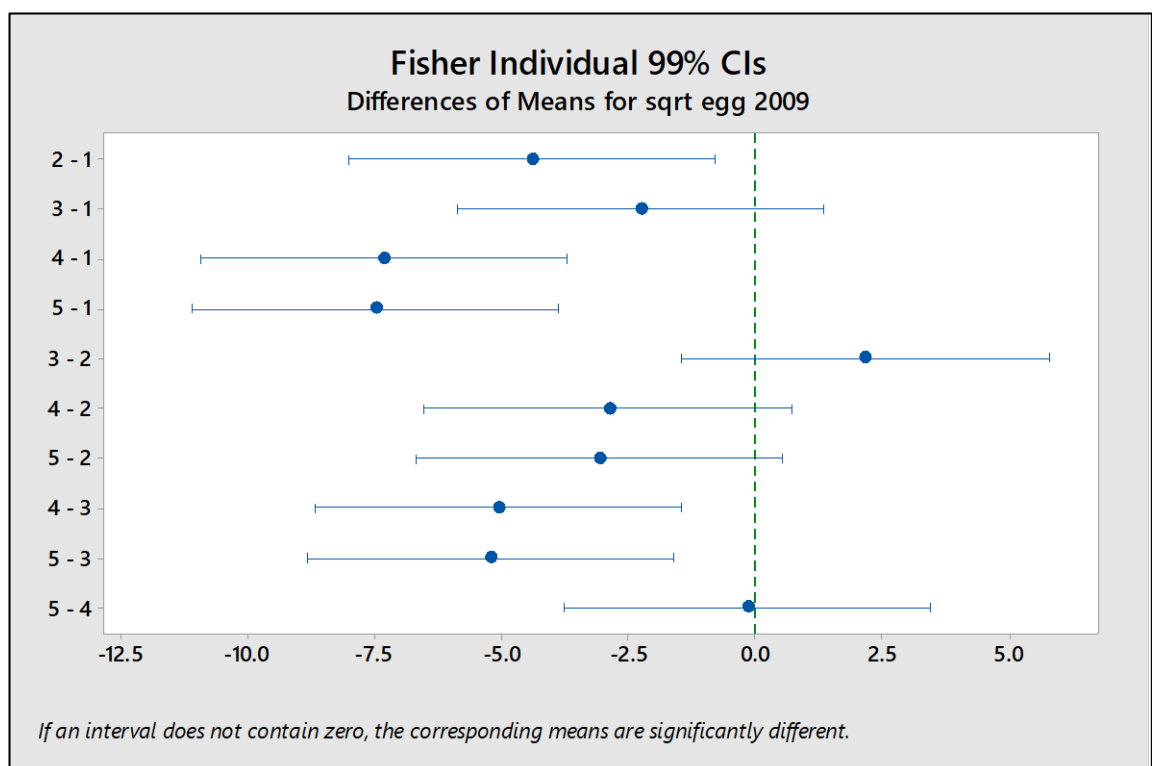
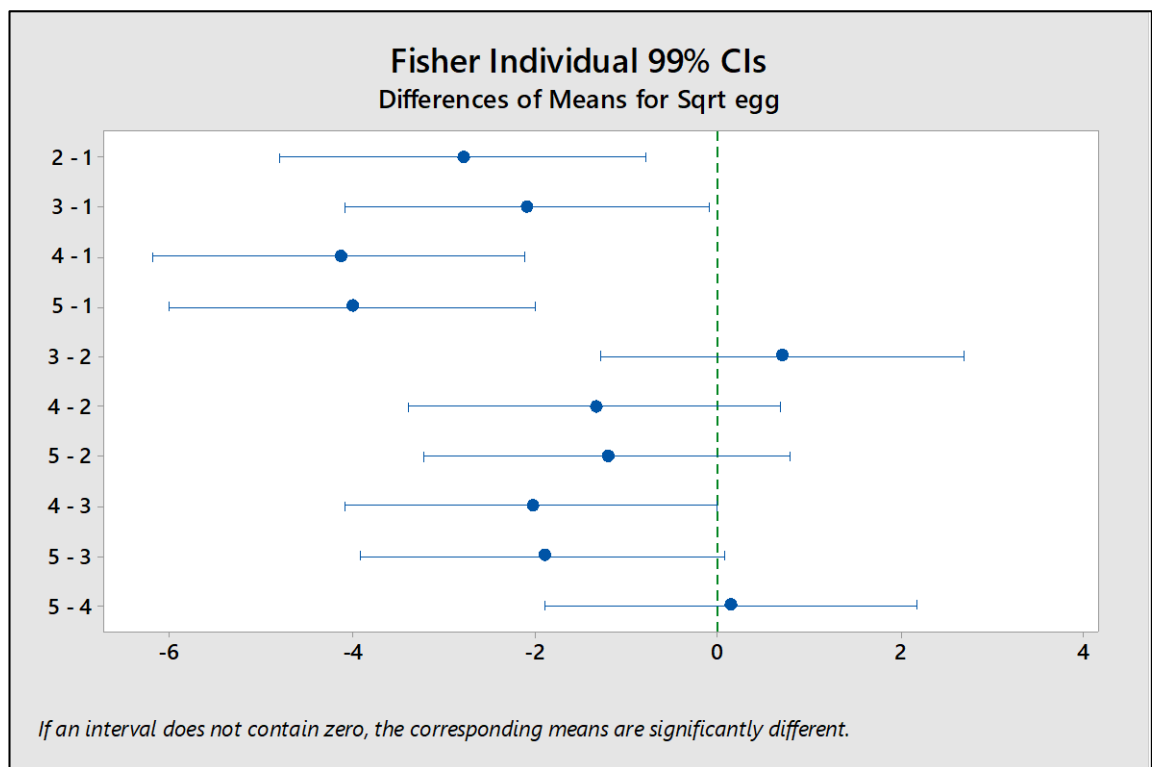


Fig. 8: Graphs showing the results from the Fisher's test, which include the results for the data before 2009 (above) and the results for the data from 2009 onwards (below). In instances where pairs of sections (represented along the y-axis) intercept 0 along the x-axis, then their means are not significantly different.

The observations in fig. 8 are supported in fig. 9 where the averages for each section are displayed visually. Increases in the number of eggs are observed for all sections. The most pronounced of these occurs in the first 100m section, where an increase of 84.29 occurs. The second and third 100m sections also show substantial increases in average eggs at 31.3 and 59.12 respectively. It is likely that these trends are the result of the continued rotational coppicing along the 500m transect as well as these practices moving into other parts of the reserve. Williams (2007) reports on the successes of Grafton Wood, stating that as a result of the four-year rotational coppicing, the egg counts seem to peak two to three years afterwards, where in subsequent years they drop again until cutting resumes. This can be seen to some degree in fig. 10 where section 3 experiences continuous increases in its egg counts in the years following cutting in 2010. Section two also experiences substantial increases in egg counts in 2013. However, despite still having a high egg count in 2015, section one had higher egg counts the year after its cutting in 2012. Furthermore, section three had higher egg counts in the year it was cut in 2015 than either of the subsequent years, whilst a substantial drop in eggs occurs in 2014 for section two. Because of the lack of an obvious trend in the West Williamston counts, it is therefore concluded that whilst increases are evident after further management in 2009, the data for this reserve does not follow the same patterns found by Williams (2007).

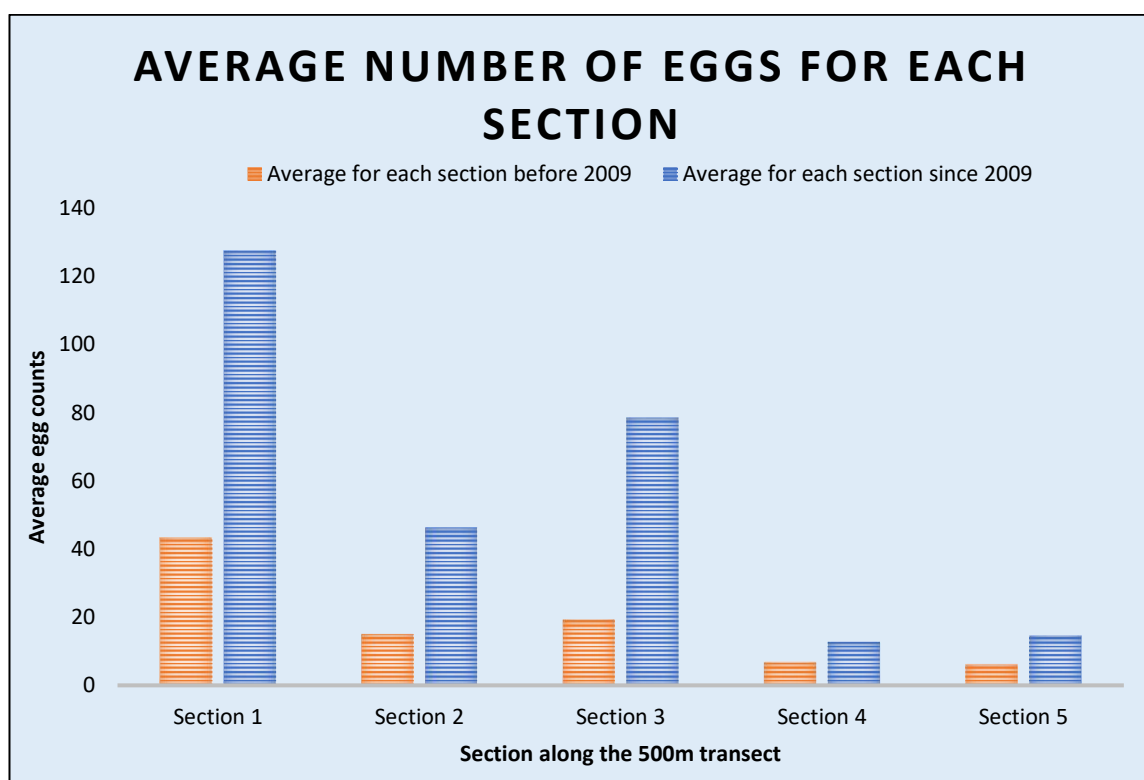


Fig. 9: Graph showing average number of observed eggs for each section along the 500m transect both before 2009 and from 2009 onwards.

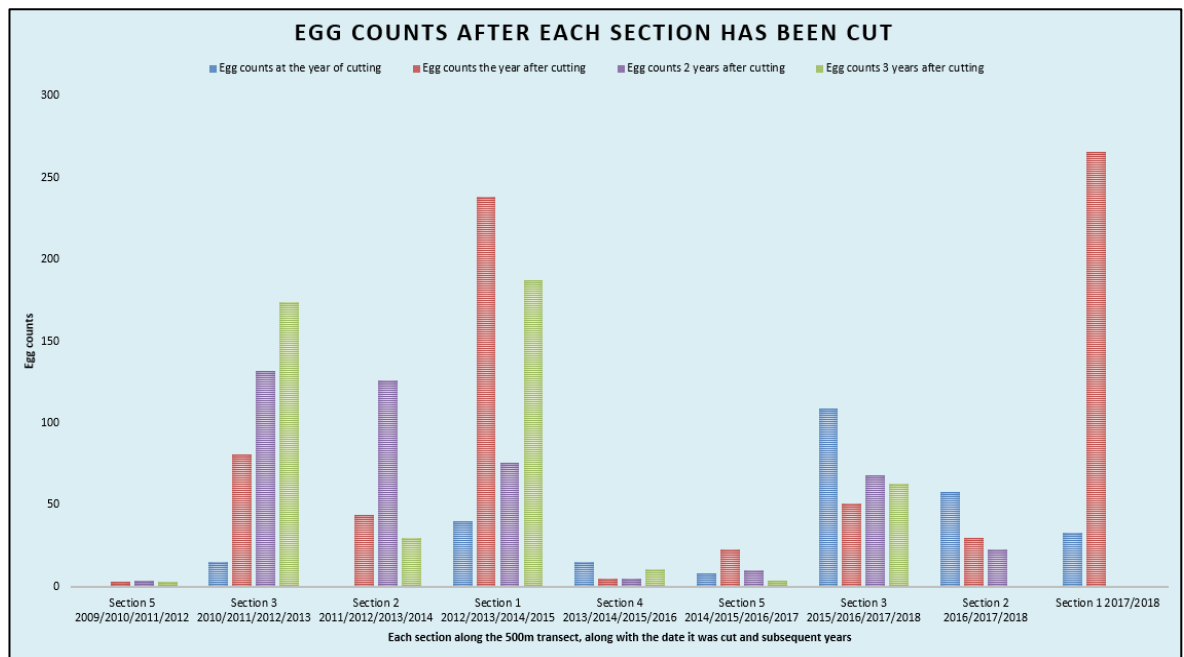


Fig. 10: Graph showing the egg counts for each section along the 500m transect on the year it was cut and for the following three years after cutting.

The average counts for each section before and after increased rotational cutting are visualised in a spatial context in fig. 11 by representing the values for each section as points of various sizes. This confirms what fig. 9 displays where section one is consistently the highest with 48% and 46% of the observed eggs for both time periods respectively, whilst section four and five remain the lowest. Furthermore, section three remains the second highest showing an approximate 59% increase in average observed eggs after the introduction of rotational cutting in the middle and north fields.

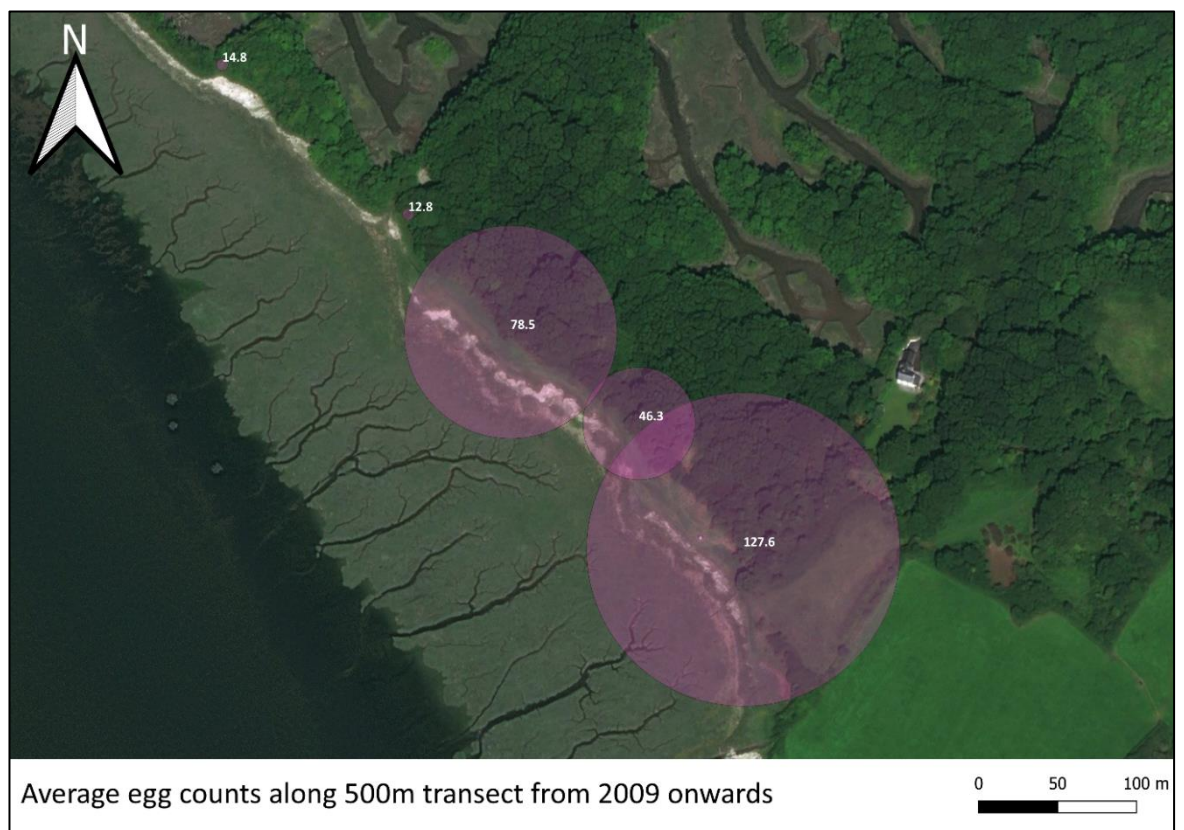


Fig. 11: Maps displaying the average observed egg numbers for each section along the 500m transect both before 2009 and from 2009 onwards.

Finally, fig. 12 displays the average numbers of eggs laid at various heights in all the surveyed hedgerows at Grafton Wood. The first graph was created from the raw data which was

recorded in categories of unequal sizes. From this, most of the observed eggs were laid between two and four-foot with an average of 151.42. The lowest number of eggs were found above six-foot at an average of 3.92. However, because the categories are not of equal measurements in size, this data is not very useful for analysis and so an additional graph was created to display the data standardised into categories of one-foot increments. From this, the category with the largest number of average eggs was between one and two-foot with an average of 100.74. Because the six-foot plus category was removed to avoid potential biases from recorders not being able to see eggs at this height, the lowest category in this graph was between 5 and 6-foot at an average of 19.82 eggs. However, little can be deduced from this graph as it is unlikely that the standardised values accurately represent the actual heights in which the eggs were laid.

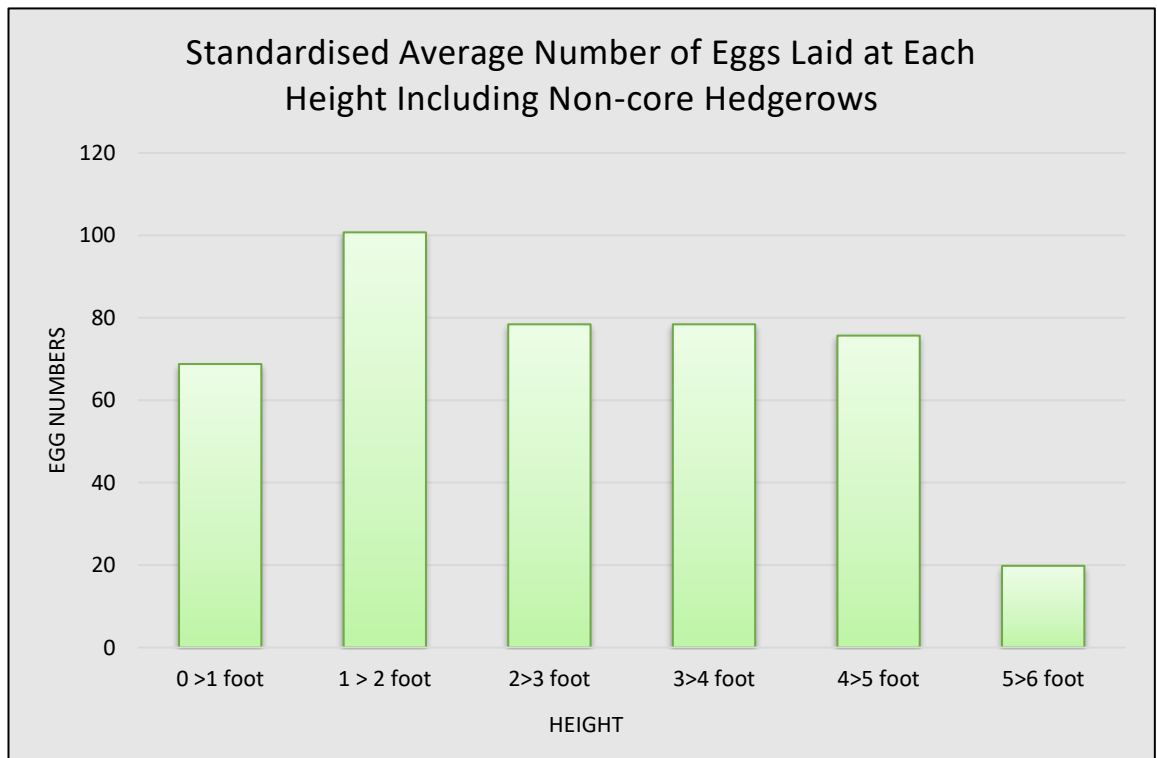
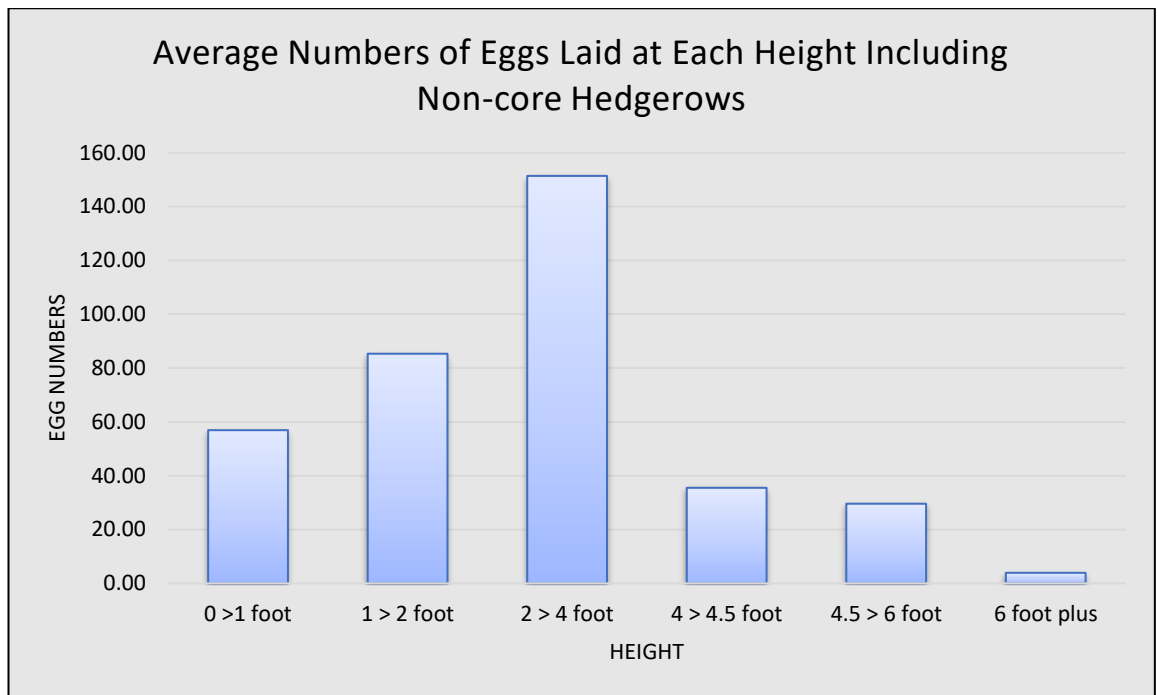


Fig. 12: Graphs to show the average numbers of observed eggs laid within various height categories of unequal sizes and the average number of eggs laid within height categories of equal sizes respectively. This data includes both core hedgerows and other hedgerows throughout Grafton Wood.

6. Discussion

The following sections will discuss the findings obtained from the data analysis and any trends evident in the figures. This will begin with the climatic analysis, with emphasis on the possible reasons for differences in climate relationships between those of West Williamston and Grafton Wood. Next the variability within the 500m transect is discussed based on the findings of the post-hoc Fisher's tests and the average counts for each section. This will help to identify any factors that are influencing the counts within particular locations along the transect, placing the results within a spatial context. This will also enable the consideration of other factors in addition to management that may be influencing the 500m transect egg counts at West Williamston. Finally, the findings which highlight the effects of management at West Williamston are discussed, where consideration is also given to the Grafton Wood dataset and its site-specific characteristics, as well as the land surrounding West Williamston and the management that occurs there. By discussing these various factors, inferences can be made regarding the degree to which additional rotational coppicing is influencing the egg counts at West Williamston.

6.1. Relationship with Climate

Overall it was found that there was no significant relationship between the Aberporth mean temperature and rainfall data and the observations at West Williamston. This is surprising given that butterfly activity is frequently governed by climate. For instance, Thomas (1974) found that most *T. betulae* eggs were laid at above 21°C, where his observations of caged females showed strong correlations between daily maximum temperatures and egg numbers. However, Aberporth is located approximately 30 miles away from West Williamston and may not reflect the actual temperatures and rainfall amounts that have occurred at the reserve. This may be weakening the relationship between these variables and the egg count data. It should be noted that there was a significant relationship between the Ross-on-Wye temperature data and the observed egg counts at Grafton Wood, where the distance between the weather station and the reserve is also around 30 miles. This implies that this distance from the reserve may not be a primary factor in limiting the relationship between the two variables. It may be possible that the altitude of each location could be influencing the strength of these relationships instead, where Aberporth is located at approximately 67m compared to 13m for West Williamston, whilst Ross-on-Wye is located at approximately 60m compared to 40m for Grafton Wood (Ordnance Survey, 2017; ElevationMap.net, 2018). Aberporth is more than five times higher than West Williamston, and as such it is likely that the reserve will be experiencing different temperatures. This strong relationship between

temperature and egg counts at Ross-on-Wye and Grafton Wood could be a direct result of their more comparable altitudes.

These observations may also reflect the special differences in climate across the UK. Such differences were identified by Fartmann and Timmermann (2006) who found that regional climates alter the way *T. betulae* behaves. For instance, whilst primarily ovipositing on *P. spinosa* in the UK, the researchers found that further south this butterfly utilises a range of *prunus* species including *P. domestica* and *P. insitia* (Heddergott, 1962; Koschuh *et al.*, 2005; Fartmann and Timmermann, 2006). For West Williamston, it is more likely that habitat quality and site management are the more important factors in determining egg numbers than climate because of *T. betulae*'s strict oviposition preferences. For instance, there are years where egg counts increase substantially whilst a drop in temperature occurs, such as in 2013. In years such as these, it can be inferred that the quality of the habitat at West Williamston is high, although other factors including the quality of adjacent habitats and their management will also be contributing to these trends.

6.2. Variability Along the 500m Transect

The view that habitat quality is one of the key factors in influencing egg counts at West Williamston is further supported by investigating where *T. betulae* lays its eggs within the reserve. For example, Thomas (1974) found that *T. betulae* eggs were only laid in specific areas of his study site on all years of surveying. This is a trend that has also been observed in West Williamston, particularly along the 500m transect, where the 0-100m section has the highest average egg counts, whilst the 300-400m and 400-500m sections consistently have the lowest. A possible reason for these findings could be that the level of woodland cover decreases towards the edge of the reserve, which can be seen clearly in fig. 2 and in appendices 1 to 5. Sections four and five are located within this area of the transect and this may explain their significantly lower egg counts. Many studies have found that woodland cover can have a positive effect on butterfly populations. For example, Liivamagi *et al.* (2014) found a positive correlation between forest cover and total butterfly species richness within a 250m radius in north-eastern Estonia. This is because these habitats often have their own unique microclimate, offer shelter from high winds, and can provide complementary sources of nectar and host plants (Bulman, 2007; Berg *et al.*, 2011; Liivamagi, 2014). Furthermore, Bulman (2007) states that mature woodland habitats are preferred by canopy dwelling species such as *Apatura iris*, as adults fly high in the treetops and occur at low densities over large areas; characteristics that are shared by *T. betulae*.

The south-west facing woodland edges along the foreshore will also help to provide the sheltered conditions and warmer micro-climates that the female specimens prefer to lay their eggs in (Thomas, 1974; Bourn and Warren, 1998). This is supported by many studies which have found that more exposed areas have a higher rate of convective cooling and are avoided by various butterfly species (Kuussaari *et al.*, 2007; Merckx *et al.*, 2008; Liivamagi *et al.*, 2014). For instance, Merckx *et al.* (2008) states that convective cooling decreases with a higher degree of shelter and lower flight height, where they determined that butterflies were able to cover larger distances with higher ambient temperature and lower wind speed. Not only are sections four and five characterised by less adjacent woodland cover than the first three sections, but they are also at the more exposed edge of the reserve, close to the confluence of the Carew and Cresswell rivers. A large portion of the area beyond sections four and five is therefore characterised by unsuitable habitat. This could also influence the lack of egg laying in these sections as butterfly activity in general could be lower. Furthermore, it could be possible that the risks of predation increase towards the more exposed parts of the reserve, and this may be deterring females from laying their eggs in these sections. For instance, Thomas (1974) found that predation, mainly by small mammals, resulted in the losses of 50-70% of pupae in Cranleigh Woods. In the more sheltered locations closer to the woods where a leaf litter layer is more prevalent, there would be more opportunities for pupae to blend in with their surroundings making them less susceptible to predation. It is also more likely that adult female *T. betulae* will oviposit in locations where they are less exposed to predation themselves. However, it is unlikely that the distance from the woods and any master trees will be limiting factors as *T. betulae* disperses over a wide area, with females travelling many kilometres to oviposit. This is supported by Thomas (1974) who found that there was no significant correlation between the number of eggs found in his study and the distance of the hedge from a wood. And whilst he observed significantly more eggs within 250m of woods, the hedges within sections four and five in the present study are certainly within that distance from the more wooded sections at West Williamston.

Another reason that egg numbers in sections four and five are considerably lower than the first three sections may be due to the higher quality habitat located in the limestone ridges directly behind them. These trends can be seen in fig. 13, where in both 2010 and 2015 the egg counts across the limestone quarries can be seen to be considerably higher than those of sections four and five. Because the ridges cover a larger area and are contained within a mosaic of limestone grassland, scrub and woodland, they may be a preferable habitat by *T. betulae* to lay its eggs in (Appendix 6) (Walton, 2009). Furthermore, by being surrounded by fragments of woodland on all sides, along with the varying heights of the ridges themselves, host plants

contained within this part of the reserve are also less exposed to strong winds, adding to its attractiveness as an oviposition site for *T. betulae*. The limestone ridges are also characterised by well-drained calcareous soils that form the calcareous grasslands along them; rare habitats which are known to support a range of different wildflowers and grasses such as *Hypericum ellipticum*, *Ophrys apifera* and *Gentianella amarella* (Anderson and Walton, 1998; Butterfly Conservation, 2012; Save Our Magnificent Meadows, 2019; Walton pers comms., 2019). Van Swaay (2003) demonstrated the importance of this habitat for butterflies, stating that 274 (48%) of European butterflies occur on calcareous grasslands, 37 of which are considered threatened. The importance of disused limestone quarries for butterflies has also been highlighted by Beneš *et al.* (2003). They discovered that quarries serve as a refuge for xerophilous and sedentary species, where their habitats explained a higher proportion of variance than either latitude or the other variables related to quarrying in the Moravia region of the Czech Republic. Therefore, it is likely that this part of the reserve will be attracting a high proportion of butterfly activity, especially as female *T. betulae* specimens feed on plant nectar in between oviposition (Thomas, 1974; Bourn and Warren, 1998; Fartmann and Timmermann, 2006).

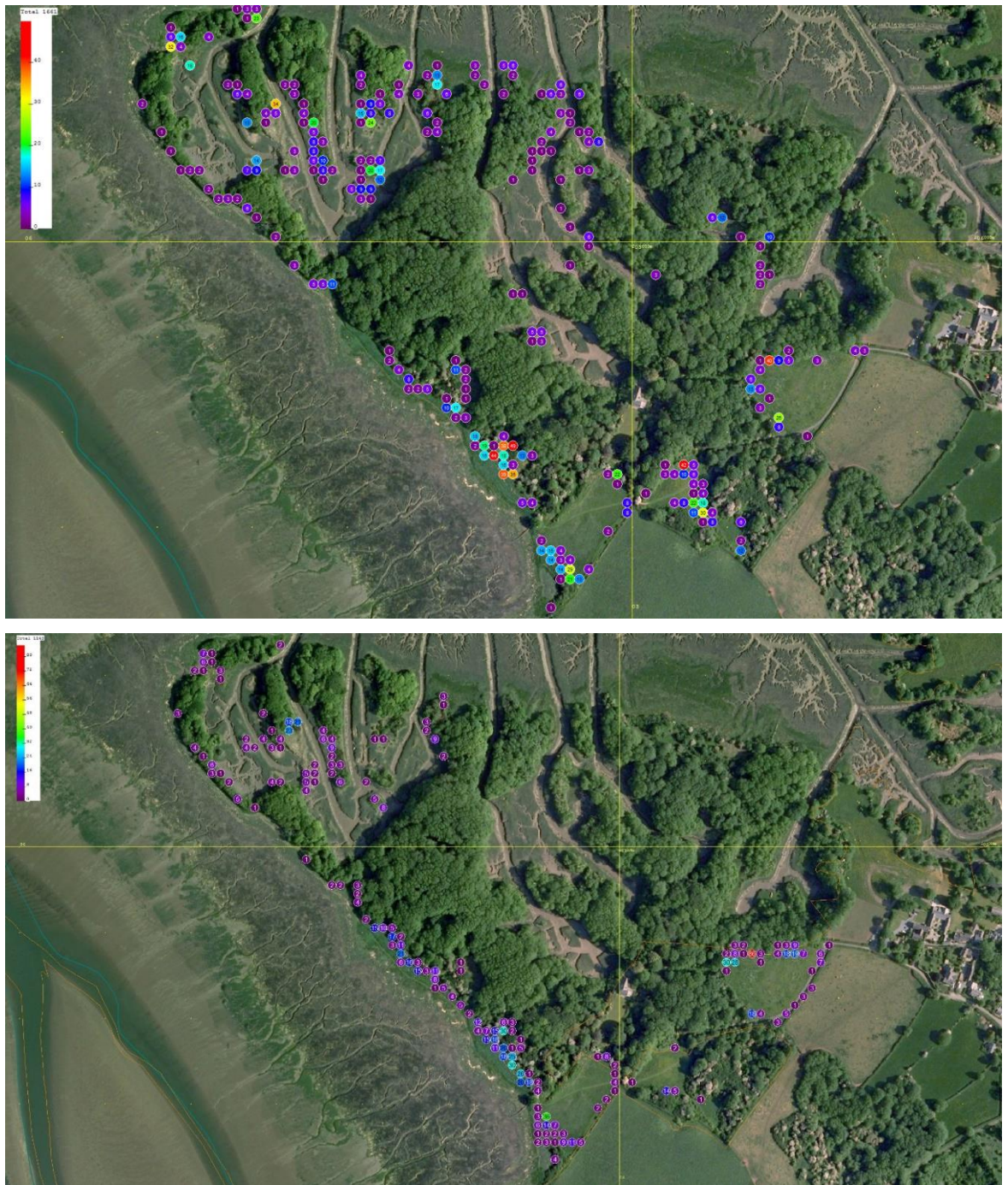


Fig. 13: Full site survey egg counts for 2010 (top) and 2015 (bottom). Egg count locations were recorded via GPS and then plotted on the maps, both of which have been provided by David Redhead (Redhead pers comms., 2018).

Whilst sections four and five are characterised by significantly lower egg counts, the factors that result in the first three sections (particularly the 0-100m section) being higher must also be considered. There are several non-linear sections along the transect route that also provide suitable habitat for oviposition. These include two glades, one located along the 0-100m section and the other along the 100-200m section (appendix 7). Bulman (2007) states that both woodland and grassland specialists will make use of glades, where the main features that

will determine their suitability are the amount of shade and the composition and structure of vegetation. As the 500m transect and the glades along it are south-west facing they will also be exposed to a large amount of daily sunshine, whilst the increased shelter within the glades will provide additional protection from wind on all sides. This will help to increase the suitability of these sites for egg laying. Furthermore, the glades are easily accessible along sections one and two creating a continuous habitat meaning that *T. betulae* is more likely to search for additional oviposition sites in the adjacent transect sections. The findings of Sutcliffe and Thomas (1996) support this, where they identified that *Aphantopus hyperantus* readily moved from glades into rides, demonstrating the importance of connectivity between habitats influencing butterfly activity. However, it should still be noted that recording of eggs in the non-linear sections has been inconsistent, resulting in the omission of this data from the present study, and therefore only inferences can be made about their importance as additional egg laying habitats.

Of all the locations along the transect, section one has by far the most egg counts both before and after additional rotational coppicing was introduced in 2009, as demonstrated by the ANOVA tests and figures 8, 9 and 11. A possible cause for this trend could be the fact that section one is located nearest to the meadows, with it being directly adjacent to the lower field. According to the 'Soilscapes soil viewer' the soil properties of West Williamston are generally free draining, slightly acid but base-rich (Cranfield University, 2004). As the reserve predominantly lies on limestone rock the soils in the meadows will likely resemble those of the ridges (Walton pers comms., 2018). Furthermore, the previous management in them has been low except for occasional grazing by horses (Walton, 2009). These factors mean they will be characterised by additional sources of nectar which will help attract females to this area of the reserve and act as a corridor to the host plants. However, based on the calcareous soil that characterises much of the reserve, it is likely that additional nectar sources are available in many locations, all of which will be attractive to *T. betulae* females in between oviposition. Therefore, it is unlikely that this will be the primary driver for section one's abnormally high average.

Instead, it is more probable that the quality and structure of the host plants within each 100m section will have the biggest influence on the observed counts. The amount of host plant cover will have an influence by offering more potential locations for oviposition, where Thomas (1974) found 100m sections that were characterised by little *P. spinosa* had significantly less eggs than those with higher host plant cover. This is supported by Salz and Fartmann (2017) who also found that high abundance of the host plant *Viola canina* was one of the main factors that determined the occurrence of *Argynnis niobe* larvae in heavy metal grasslands. However,

Fartmann and Timmermann (2006) discovered that host plants were abundant throughout Wienburg Park, in Munster, but only a few areas had high egg numbers as they were characterised by young shoots and were adjacent to woodland. Based on the differences between each section along the 500m transect, this seems to be the case for West Williamston, and would indicate that the quality of *P. spinosa* in relation to *T. betulae* oviposition preferences is more important. Easily accessible young growth was frequently found to contain many eggs during the surveys of 2017 and 2018. This can be seen in fig. 14, where young blackthorn growth separated from the bushier woodland edges contains many egg observations, each marked with string. The photograph was taken of section one during the 2018 survey, where it contained by far the highest number of observations for that year at 266 eggs.

Unfortunately, the amount and height of blackthorn has not been historically recorded, and so it can only be speculated that the high host plant quality is leading to these high counts. However, since the coppicing of this section occurred in 2017 and was followed by high egg counts in 2018, and similar findings to this can be seen in other studies, it is likely that this is the case (Thomas, 1974; Fartmann and Timmermann, 2006; Walton, 2009; Merckx and Berwaerts, 2010; Salz and fartmann, 2017). For instance, Thomas (1974) states that shoots younger than six years but older than one year are preferred, where observations at Cranleigh Woods showed that 84% of the eggs were laid on wood without flowers which is indicative of young growth. This preference is likely to ensure that the larvae have access to nutrient rich young plants in order to aid their development. Fartmann and Timmermann (2006) also state that this could be an attempt to avoid interspecific competition, where other species may utilise the bushier older growth containing more leaves. However, based on their study in Baden-Württemberg, Ebert and Rennwald (1991) found that most eggs were laid on older specimens, although this could be the result of climate and site-specific differences between these locations. Furthermore, Fartmann and Timmermann (2006) state that female specimens will only use older *P. spinosa* plants if younger suckers after coppicing are scarce. This could also explain why section two is significantly lower than section one both before and after 2009 (fig. 11) even though it is directly adjacent to it, where it is likely characterised by a lower number of young suckers.



Fig. 14: Young blackthorn growth marked with string identifying eggs along the 0-100m section.

6.3. Effect of Management

Rotational coppicing has occurred along the 500m transect since the implementation of the management plan in 1998. This has involved alternating the cutting of the blackthorn in each 100m section on a five-year rotational basis (Walton, 2009). The trends in the egg counts over time along the transect reflect the benefits of implementing this management strategy, where an overall increasing trend can be observed in fig. 4. The benefits of rotational coppicing have also been evident at Grafton Wood, where an overall increase in counts can be observed in fig. 5. This seems to reflect the gradual increase in the number of butterflies occupying the reserve as a result of more offspring hatching out from generation to generation. It can then be argued that the Grafton Wood data shows similar trends to the West Williamston data, and that this can be at least partially attributed to the fact that rotational coppicing management occurs at both sites. However, the trends observed by Williams (2007) at Grafton Wood showing peaks in egg counts two to three-years after cutting are not present in the West Williamston dataset (fig. 10). This along with their differences in response to average temperature seems to reflect site specific patterns, and that other factors are influencing the egg counts differently within either site. Complex population dynamics will be occurring with their respective *T. betulae*

communities, whilst the surrounding land use around each site may differ considerably. Additionally, as Grafton Wood covers a much larger area at 56ha compared to 20ha for West Williamston (The Wildlife Trusts of South and West Wales, 2012; Worcestershire Wildlife Trust, 2011), this will therefore equate to a larger area of protected habitat that will receive more sympathetic management than the surrounding environment. Furthermore, there are substantial differences in the habitat structure of both sites, where Grafton Wood is primarily composed of Ancient Woodland containing rides and glades, whilst West Williamston is characterised by a mix of open habitats and woodland on a smaller scale. As *T. betulae* lays its eggs over a wide area, it may be possible that egg densities are lower across the larger areas covered by suitable habitat in Grafton Wood, and thus the counts recorded on the core hedgerows may not represent the true size of the population. Finally, it must also be noted that the dataset for Grafton Wood extends back further than that of West Williamston and may help to create the more significant increase observed in fig. 5.

For West Williamston, the significant increase in counts from 2009 onwards is likely the result of the introduction of rotational coppicing into the meadows in 2009. According to Walton (2009) this has involved dividing the *T. betulae* habitat into three and four blocks in the north and middle field respectively, where the hedges are coppiced on a four-year rotational basis. In particular, the benefits can be seen along the first three sections of the 500m transect where the average counts essentially triple in size from 2009 onwards. Whilst these observations will reflect the quality of the individual sections (e.g. host plant structure, shelter, and resources), they are also indicative of the higher number of adult *T. betulae* specimens on the site year on year as a result of the increasing amounts of viable habitat for oviposition in other parts of the reserve. Positive effects of coppicing were also found by Taylor *et al.* (2013) at Gait Barrows and Witherslack in Morecambe Bay, where sites characterised by both traditional coppicing and commercial management had significantly higher butterfly species richness and abundance compared to low management woodland. This also indicates that the rotational coppicing occurring at West Williamston will benefit other species and taxa. However, Clarke *et al.* (2011) state that many woodland butterflies and moths of conservation concern often have conflicting requirements, where some will require regular clearance and other species will only thrive in closed canopies of mature trees. Whilst this is a factor that needs to be considered with future management, the woodland habitat on the site is characterised by both rotational coppicing and areas of minimal management and so generally caters to both requirements.

It seems that the results of the 500m transect egg counts and the statistical analyses conducted on them confirm that rotational coppicing is an effective management strategy in

the conservation of *T. betulae* populations. However, it must still be noted that the peaks and troughs in the data sets indicate that rotational coppicing is not the only factor influencing the *T. betulae* populations. And whilst habitat quality clearly has big influence on the West Williamston population at a local scale, the surrounding habitats will also affect its health on a wider scale and may play a significant role in the fluctuations observed in the dataset. As previously stated, *T. betulae* is a particularly mobile species and lays its eggs over wide areas. Therefore, locations outside of the reserve will also act as important sites for oviposition. However, whilst sympathetic management occurs within the reserve, this is not widely replicated in the surrounding environment. For instance, Redhead (pers comms., 2018) found considerable egg counts in multiple locations during an extended survey of the wider West Williamston peninsula in 2015. These included approximately 55 in West Williamston Park, 25 in New Park Farm, 100 in Croft Quarry, and 30 in Tything barn. Additional visits to New Park Farm over two winters lead to further counts of approximately 100 and 55 eggs, whilst a revisit to Croft Quarry the following winter resulted in counts of approximately 200. These findings have led him to estimate that around 17% of the eggs are laid outside of the reserve (Redhead pers. Comms., 2018). In terms of the management for each of these sites, Redhead (pers. Comms., 2018) goes on to state that West Williamston Park is an unmanaged site, New Park Farm has its hedgerows cut back each winter, Croft Quarry has silage cuts taken each summer, whilst Tything Barn is a camping site where the field gets heavily trimmed. It should be noted that the high counts observed in Croft Quarry are the result of the surveying occurring before the silage cuts were taken, whilst the lower counts observed in New Park Farm are probably due to the surveyors arriving after hedge cutting had occurred (Redhead pers. Comms., 2018). It is therefore likely that many of the eggs laid in the sites characterised by these management practices would have been lost. Thomas (1974) supports this where upon mapping the positions of every egg on seven hedges in Surrey in the Autumn of 1970 and then revisiting them in April 1971 after 5 had been cut, he was able to determine that losses were between 50 and 100% depending on the severity of the cut. Overall, he estimated that around 47.5% of all eggs in the area would have been lost due to unsympathetic hedge management. Therefore, the *T. betulae* population may be actively trying to expand onto other sites but is being suppressed by these management practices. This will result in lower counts along the transect for some years, reflecting instances where females may be laying high proportions of eggs outside of the reserve only for them to be lost in this way causing reductions in the size of the following generation.

7. Conclusion and Recommendations

Overall, the egg count data seems to indicate that the introduction of rotational coppicing into other parts of the reserve in 2009 has been beneficial for the West Williamston *T. betulae* population. It therefore also indicates that the implementation of this management strategy should occur on other sites where *T. betulae* inhabits in order to increase the amount of viable host plant growth available to it on a yearly basis. This is because the results from the students t-test showed that the data before 2009 and from 2009 onwards are significantly different at the 99% confidence level, whilst substantial increases can be observed between these two time periods. This therefore supports the hypothesis that the years following the implementation of rotational coppicing into the fields will be characterised by increased egg counts. However, as all the other possible variables influencing *T. betulae* egg counts were not measured in this present study, it must also be noted that a range of other factors could be at play. These have also been considered and it is feasible to conclude that local habitat quality is also a key factor in influencing the year on year variations in egg counts. This is because habitat quality seems to dictate where the butterflies are laying their eggs along the transect, with section one receiving significantly higher counts than almost all the others both before and after 2009, whilst sections four and five consistently have the lowest. This assumption is based on the fact that *T. betulae* has strict oviposition requirements. Because section one is characterised by a high degree of shelter from the adjacent woods, with a large volume of younger *P. spinosa* growth, particularly during the last count, it seems that this is likely. Furthermore, the fact that sections four and five are located towards the more exposed edge of the reserve with low quality *P. spinosa* habitat also supports this. It must also be noted that the transect egg count data failed to achieve a significant correlation with the Aberporth climate data, and whilst distance and altitudinal differences may factor into this, it does still indicate that other factors such as habitat quality and management are influencing these observations instead. As rotational coppicing helps to create this preferential egg-laying habitat, the findings of the present study therefore indicate that sympathetic management and high-quality habitat are working in conjunction to increase the average size of the West Williamston population overall.

However, it remains a fact that much of the surrounding land use does not follow similar sympathetic management strategies and it is likely that this is limiting the possible population size in the area. As the present study has only analysed data from the 500m transect on the reserve, it would be highly beneficial for future studies to investigate the effects of the land management in the surrounding sites on *T. betulae* egg counts in order to obtain a substantial dataset to support this assumption. Constraints for this research are likely to present

themselves though, with permission to access private land for frequent surveying and obtaining information on previous management being very much dependant on the cooperation of private land-owners. Perhaps a more achievable recommendation is to develop additional transects along the *P. spinosa* in the fields. Whilst the fields have been occasionally monitored in the past, this should continue on a consistent basis in order to develop annual totals for each location for comparison with the 500m transect. By doing this, a better understanding of oviposition preferences with regards to location within the site can be obtained.

Regarding the trends for both West Williamston and Grafton Wood, both show overall positive increases over time, whilst the Student's T-test conducted on both datasets indicated that they are not significantly different. However, it also seems that they each follow their own unique year on year fluctuations likely resulting from site specific variables. For instance, it was determined that the larger size of Grafton Wood, along with its predominantly woodland habitat and longer period of egg surveying will have their own significant influences on its egg counts. It is therefore concluded that whilst it is likely that rotational coppicing is having a positive influence on the egg counts of both reserves and that the average number of observations on each are increasing, the two data sets are shaped by their own site-specific differences and are therefore not directly comparable. Furthermore, the Grafton Wood dataset differs from the West Williamston one in that it includes information regarding the heights on the blackthorn at which the eggs were observed. This therefore creates an additional opportunity for the monitoring at West Williamston where future surveys should also contain this information. However, it should be noted that whilst this has been done at Grafton Wood, the data was particularly skewed with its unequal categories and little could be inferred from it. To avoid this, future monitoring at West Williamston should ensure that the categories in which the observations are grouped in are of equal sizes to enable detailed analysis to be conducted. This analysis would prove useful in identifying if there are any site-specific oviposition preferences and may help to inform future management such as ideal heights and ages for coppicing.

As with West Williamston, other sites throughout *T. betulae*'s range will be characterised by habitat management that fails to replicate the more sympathetic practices that encourage adequate host plant growth and increase the abundance of additional resources. As previously stated, this has been the primary driver for the suppression of this butterfly to only a few locations in the country. Whilst it would be unreasonable to expect landowners to completely transform the way they manage their land; sympathetic hedgerow management should be more prominent in the surrounding landscape and work needs to continue to encourage them

to adopt practices such as rotational coppicing on adjacent sites to enable this butterfly to fully increase its range. This may be in the form of grants such as the hedgerow incentive schemes as part of the countryside stewardship seen in Worcestershire (Williams, 2007). However, incentives will need to be attractive enough to convince many landowners and farmers to fully cooperate and it is therefore also acknowledged that this is a complex task and new ways need to be developed to achieve large-scale change. Another solution would be to simply work with landowners to identify hedgerows which could provide ideal habitat for oviposition and then to create a simple sympathetic management strategy such as rotational coppicing that ultimately requires a low amount of effort to implement if planned properly. Either way, they will need to ensure that a well-connected network of habitat patches can be maintained in order to reduce the risk of population extinctions and increase the amount of viable locations for oviposition; all of which will aid in the recovery of this species.

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Appendices



Appendix 1: 0-100m section of the West Williamston 500m transect.



Appendix 2: 100-200m section of the West Williamston 500m transect.



Appendix 3: 200-300m section of the West Williamston 500m transect.



Appendix 4: 300-400m sections of the West Williamston 500m transect.



Appendix 5: 400-500m sections of the West Williamston 500m transect.



Appendix 6: Limestone ridges behind the 500m transect.



Appendix 7: Glades along the 500m transect. Left: The first glade within the 0-100m section. Right: The second glade within the 100-200m section.