European Nightjar and Upland Plantation Woodland Management

Thesis submitted in part fulfilment of PhD

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Conflict of Interest Statement

I certify that none of the bodies listed above had any influence on the nature of my research (site selection, data collected) or involvement in the research work undertaken to inform this thesis or on the materials discussed in the thesis chapters.

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Summary

Plantation woodland is increasing in extent globally and as a proportion of global forest cover. Plantation woodland is not only an important element of the U.K. economy, but also is an important woodland habitat in the U.K., given the pre-historic and historic loss of woodland cover. Woodland policy aspirations in the U.K. are currently heavily focused on increasing woodland extent, coupled with maximising the ecosystem services delivered by these habitats, including the provision of renewable energy developments and increasing the provision of biodiversity services. Such broad management objectives often necessitate trade-offs, where management to deliver different desired outcomes conflict. This thesis focuses on the conservation management of European nightjar *Caprimulgus europaeus* and is intended to inform the development of evidence-based conservation interventions that can support nightjar and the moth species on which they feed, in plantation coniferous woodland and in particular in the Welsh Government Woodland Estate. Specifically, I use European nightjar life history parameters (e.g. nest success) and movement data, to explore nightjar ecology in areas of changing land use and management.

In order to inform subsequent nest success analysis a comparison of the observed nesting success of tagged birds and untagged birds, whilst controlling for the potential confounding effects of weather, is used to explore and confirm the lack of observed tag effects on measures of nest success (e.g. fledging success) in nightjar breeding at Brechfa Forest Wind Farm (South Wales, UK).

Moth diversity and biomass data from open habitats within forests across a gradient of ages, is then used to confirm the importance of native vegetation primary productivity and stand management in driving moth biomass and diversity. Moth biomass is then combined with GPS tag movement data to explore nightjar foraging behaviour within the forest matrix. This analysis confirms that nightjar movement is driven by spatial and temporal variation in the availability of moth biomass.

Nest record data from sites across Wales is then used to explore the potential for wind farm construction disturbance effects on nest success (e.g. fledging success). Alongside this, I also examine the role of habitat management and foraging habitat availability.

Overall, my results show that forest management can have significant effects on both nightjar nest success, movement and food (moth) availability. I also show that forest management has an important effect on the presence or absence of moths of conservation concern. These results also confirm that modifications to the spatial and temporal patterns of forest management can be used to support the conservation of both moths and nightjar, with likely cascading benefits for other aerial insectivores.

Publications

Chapter 2: ‘Testing for effects of tail mounted radio tags on European Nightjar (*Caprimulgus europaeus*) nest survival’. Bird Study doi: https://doi.org/10.1080/00063657.2021.1927979

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Chapter 3: ‘Moth biomass and diversity in coniferous plantation woodlands’. Accepted in Forest Ecology and Management. https://authors.elsevier.com/a/1e9Sl1L%7EGwQxmz

Authors: Shewring, M., Vaughan, I. P., & Thomas, R. J. Author contributions: MS and RJT conceived of ideas; MS collected and analysed the data; MS lead the writing of the manuscript; IPV and RJT provided edits and supervision.

1.0 General Introduction

Ringing a European nightjar chick at Pen y Cymoedd in 2014

1.1 Plantation Woodland

Plantation woodland has increased in temperate regions in recent decades (Hansen et al. 2018), with significant afforestation noted in many areas (Song et al. 2019). The International Union of Forest Research Organisations (IUFRO) defines plantation woodland (synonymous with plantation forests) as woodland established through planting or seeding of one or more indigenous or introduced tree species. Global forest cover statistics (FAO 2015, Kennan et al. 2015) indicate that total forest area has declined by 3%, from 4,128 million (M) ha in 1990 to 3,999 M ha in 2015, but planted forest has increased from 168 M ha to 278 M ha. Natural forests have declined over the same period from 3961 M ha to 3721 M ha (Kennan et al. 2015). Thus planted forest area has increased both in absolute terms and as a proportion of total forest area (Kennan et al. 2015). Natural forest loss is largely driven by permanent land use change for the production of commodities, including beef, soy, palm oil, and wood fiber (Curtis et al. 2018).

The world's planted forests do however cover a significant land area, approximately 7% of global forest cover and this is expected to grow to 20% by 2100 (Brockerhoff et al. 2013). Most planted forests are grown primarily for efficient wood production and provide a variety of economically and socially important materials including timber, fibre and fuelwood (Penna 2010, Brockerhoff et al. 2013). Specifically plantation forests produced 2,028 M m^3 of round wood (fence posts etc), 493 M m^3 of sawn wood (timber beams etc), 408 M m^3 of wood panels (OSB etc), 409 million tonnes of paper and paperboard and 1,943 million m^3 of wood fuel in 2018 (FAO 2019). These products have been valued at over US$100 billion annually, and the associated forestry sector is estimated to employ around 10 million people (FAO 2010). Wood products are also an important part of the U.K. economy and in 2016 contributed £1.52 billion in gross value added through primary wood processing, and £0.59 billion through forestry (Forestry Commission, 2018).

Assessing the net effects of plantation forestry on biodiversity is complex (Brockerhoff et al. 2013). Plantation forests are generally inferior to native forests in terms of biodiversity, but such habitats can make an important contribution to the conservation of native biodiversity where establishment does not involve the replacement of native natural or semi-natural ecosystems (Brockerhoff et al. 2008). The noted lower biodiversity value is largely driven by the management intensity and differences in the tree species composition and forest structure from the natural forests of the region. In general, plantation forests usually have less habitat diversity and complexity with a resultant lower diversity of forest specialists than natural forests in the same region (Fuller et al., 2008; Redei et al., 2020).

On 20th September 2013 the European Commission adopted a new EU Forest Strategy. This detailed objectives of (i) a significant and measurable improvement in the conservation status of forest species and habitats, and (ii) to work towards the Aichi targets adopted in the context of the Convention on Biological Diversity (Secretariat of the Convention on Biological Diversity 2000 & Secretariat of the Convention on Biological Diversity 2010), specifically to;

- Address the underlying causes of biodiversity loss by mainstreaming biodiversity protection across government and society;
- Reduce the direct pressures on biodiversity and promote sustainable use;
- Improve the status of biodiversity by safeguarding ecosystems, species and genetic diversity;
- Enhance the benefits to all from biodiversity and ecosystem services;
- Enhance implementation through participatory planning, knowledge management and capacity building

U.K. forestry policy is devolved, however, meaning that Wales, England, Scotland and Northern Ireland are each able to set their own aims and objectives for woodland creation and management, and to fund this independently of the other U.K. nations. In Wales, forestry policy is set by the Welsh Government, and Welsh Ministers have delegated responsibility for management of the Welsh Government Woodland Estate (WGWE) to the government agency Natural Resources Wales (NRW).

Woodland area in the United Kingdom was 3.17 M ha in 2018, with 9,000 ha of new woodland created in 2017-18. Conifers (mainly non-native species) account for around one half (51%) of the U.K. woodland area, although this proportion of the total woodland area varies from around one quarter (26%) in England, to around three quarters (74%) in Scotland (Forestry Commission, 2018).

The Welsh Government Woodland Estate (WGWE) is the term used to describe the woodlands in Wales that are owned by the Welsh Government on behalf of the nation. The WGWE extends across Wales, covering an area of 126,000 hectares. It represents nearly 6% of Wales' total land area, and around 40% of the Welsh woodland resource (306,000 hectares). Originally, the WGWE was created to provide a strategic timber reserve. However, the legislative and policy framework has changed and grown in recent years, and since devolution, it has become clear that Welsh Government view the WGWE as a key asset to deliver on aspects of the Well-being of Future Generations (Wales) Act 2015 and the Environment (Wales) Act 2016 (Natural Resources Wales 2018).

Management of the WGWE is largely driven and framed by the U.K. Forestry Standard (2017) with the aim of delivering a sustainable timber supply; however Welsh Government (WG) policy is clear that the WGWE should deliver more than just timber. Indeed WG defines the role of the WGWE as; to maintain, conserve and appropriately enhance the provisioning and regulating of cultural and supporting ecosystem services, including biodiversity. As such, it is clear that WG views the WGWE as a key asset for delivering aspects of biodiversity ecosystem service provision, where compatible with other woodland management objectives, and research is needed to understand how commercial plantation forestry can deliver biodiversity services.

Land use in the WGWE is also evolving, and the last decade or so has seen the construction of a number of large scale onshore wind farms within the WGWE. This has been actively encouraged by Welsh Government, through planning guidance documents such as Technical Advice Note (TAN) 8 (2005), and has led to the development of the NRW Wind Energy Programme and the concentration of large-scale onshore wind development in Wales within the WGWE. The NRW Wind Energy Programme currently generates significant revenue for NRW/ WG (e.g. £4,195,274 in 2017) whilst also delivering on renewable energy targets. It also means that large areas previously managed solely or primarily as commercial forestry in the WGWE now also support wind farm infrastructure and the open/ non-forest habitat associated with it.

The climate emergency, as declared by Welsh Government in 2019, is also having other impacts on land use priorities within the WGWE. The Welsh Government's long term Peatland Policy (Welsh Government Ministers Decision Report 26, June 2019) identifies objectives to;

(i) ensure "*all peatlands with semi-natural vegetation are subject to favourable management/restoration (a minimum estimated area of 30,000 ha)*", and

(ii) restore "*a minimum of 25% (~c. 5,000 ha) of the most modified areas of peatland*".

This is supported by the recent Committee on Climate Change (CCC) Report on Land Use: Policies for a Net Zero U.K. (2020), which includes a requirement to restore 50% of upland peat by 2050. As a result of its oceanic climate in combination with extensive woodland clearance in the Holocene, Wales hosts significant extents of peaty soils (120,000 ha), of which approximately 11,000 ha is part of the WGWE (Vanguelova et al., 2012). The National Peatland Action Programme (NRW 2020) aims to implement a programme of restoration on priority sites across the WGWE, delivering 600-800 ha of restoration per year.

The balance of these land uses with other management objectives will inherently involve trade-offs to simultaneously manage productive forestry, nature recovery, safe access, recreation opportunities, and renewable energy projects. It will also require a good understanding of the potential effects of land use change on the species and habitats present especially those of conservation concern and heavily reliant on commercial forestry, such as European nightjar *Caprimulgus europaeus* (See Figure 1).

This thesis has its roots in this evolution of land use change in the WGWE and aims to provide evidence on the biodiversity implications of land management decisions to inform land management strategies and thereby to guide decision making at all levels, from land managers to government ministers.

Figure 1.1 European Nightjar Caprimulgus europaeus. Adult and two chicks at Brechfa Forest in 2017.

1.2 Plantation Woodland Management and Biodiversity

Plantation forest habitat can provide a refuge for species unable to survive in agricultural or urban matrices (Gardner 2012) and as such may be compatible with biodiversity conservation goals (Brockerhoff et al. 2008). Despite the widespread assumption that plantation forests are less favourable habitats than native forests (Carnus et al. 2003) there is evidence that there may be important opportunities for biodiversity conservation if plantation design and management are sensitive and appropriate (Lantschner et al. 2009). However, this is only likely to be the case where afforestation avoids semi-natural and native habitats of conservation concern (Brockerhoff et al. 2008, Brockerhoff et al. 2013).

Forest management strategies and extraction techniques vary, and have implications for plantation forest structure and complexity. Common management/ timber extraction strategies for plantation forests include;

- Clear-cutting – whole stand removal, the most common silviculture practice in temperate and boreal biomes;
- Thinning - selective removal of trees, primarily undertaken to improve the growth rate or health of the remaining trees;
- Retention forestry - individuals or groups of trees retained to increase structural diversity of the habitat; and
- Continuous cover forestry (CCF) or selection systems - uneven-aged stands created through selective removal of individual trees.

These timber extraction methods vary significantly in their intensity, with clear-felling considered the most intensive and CCF the least. Most timber extraction methods can, however, result in significant biophysical changes to the forest structure -altering the composition of tree species, their age structure and vertical stratification, thereby affecting local temperature, light, moisture, soil and litter conditions (Chaudhary et al. 2016). Plantation forestry management can also lead to the structural simplification of the landscape, e.g. by the creation of large areas of single age and species stands (Gustaffson et al. 2010). These changes in habitat complexity and microhabitat availability have been linked to an associated 29% reduction in forest species richness in plantation forestry compared to natural forests, although there is significant geographical variability in the scale of this difference, which is heavily dependent on the climatic zone, native biodiversity, food web structures and ecosystem properties (Chaudhary et al. 2016).

In the U.K., where pre-historic and historic deforestation has led to the loss of ~80% of our historic woodland, plantation forestry plays a key role in supporting woodland biodiversity (Humphrey et al. 2000; Brockerhoff et al. 2008). Timber extraction in these habitats has been shown to have mixed impacts, with clear-felling management having negative effects on some species groups (e.g. moths - Kirkpatrick et al. 2017a) but positive effects on other groups (e.g. heathland plant diversity - Eycott et al. 2006). Likewise, thinning has been associated with positive effects on species groups (e.g. bat species - Carr et al. 2020).

Management of plantation commercial woodlands in the U.K. and Wales is based primarily on patch clear-felling and replanting, in accordance with forest management principles set out by the Forestry commission (Forestry Commission 1994, 2017). This management strategy results in spatial heterogeneity at the landscape scale, but relative homogeneity at the stand[1] scale in mature crops (typically 5–50 ha), and varied levels of heterogeneity in pre-canopy closure and open habitats (Figures 1-6).

Figure 1.2 Forest inventory planting year for the Bryn and Afan forest blocks in the Afan Forest Park. Diversity in planting years shows the landscape scale structural diversity resulting from patch management.

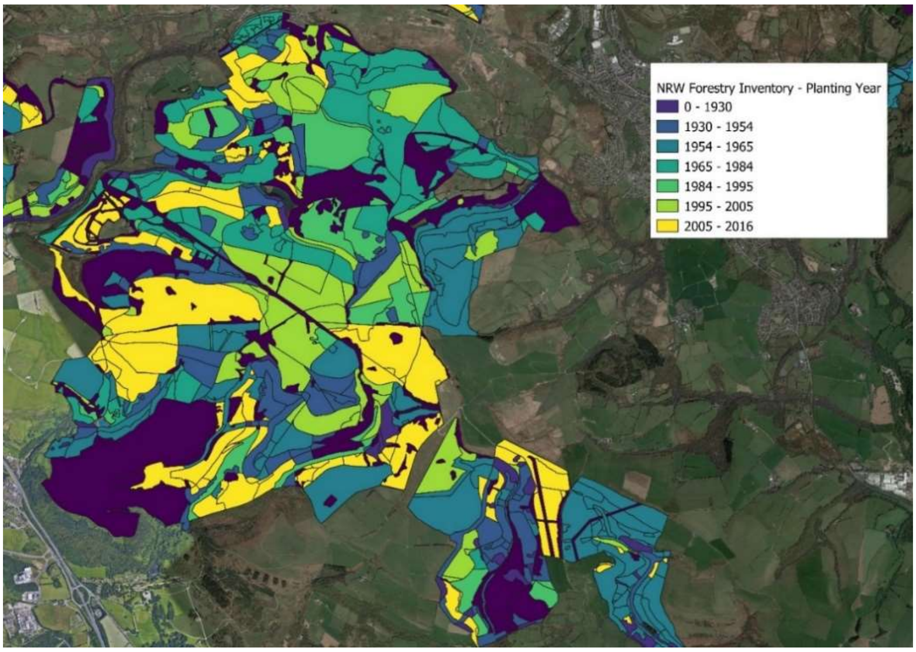
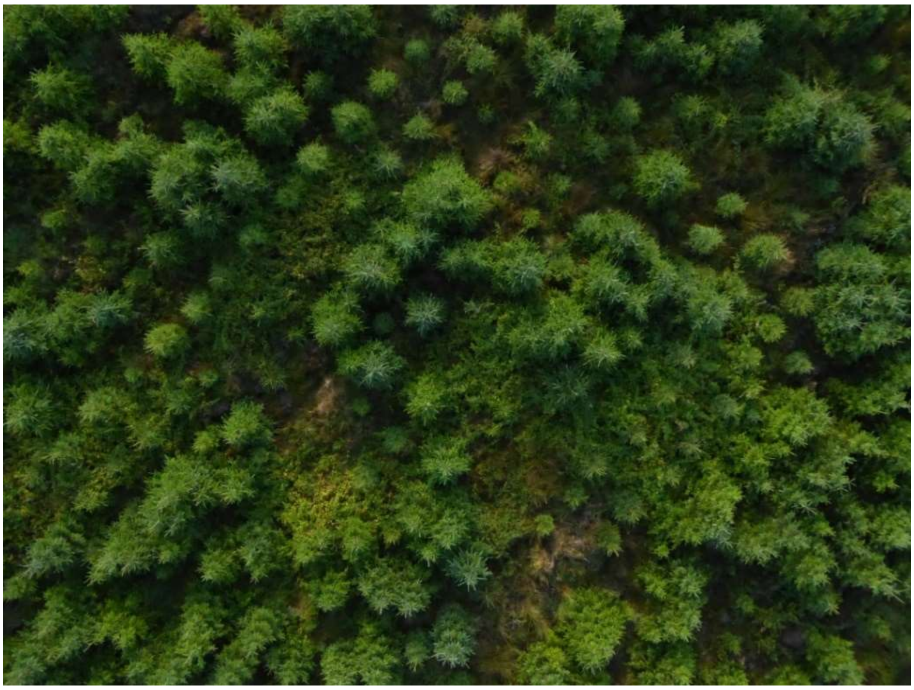


Figure 1.3 Drone-captured image (~20m agl) of pre-thicket stage restock (age 8-10 years) stand at Bryn in the Afan Forest Park



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[1] a forestry unit denoting a distinct area of tree cover that is composed of uniform group of trees in terms of species composition, age class distribution and size class distribution

Figure 1.4 Drone-captured image (20m agl) of recent clearfell (< 1 year since felling) stand at Bryn in the Afan Forest Park

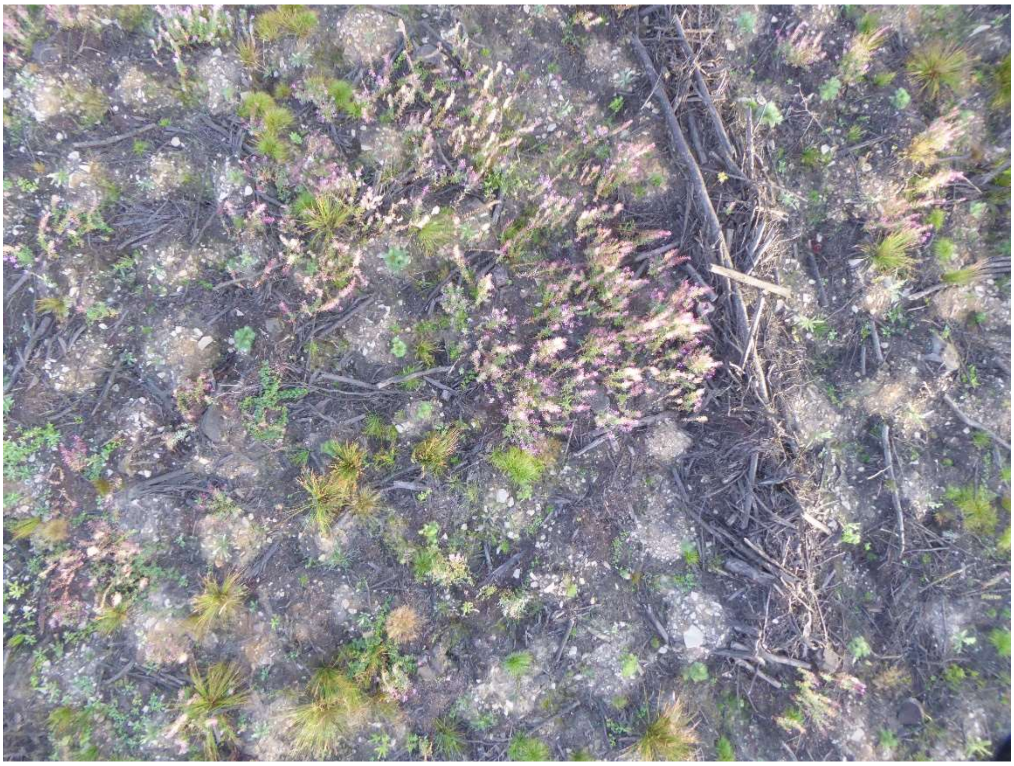


Figure 1.5 Road verge vegetation, open habitat and thicket stage Sitka spruce (age 15 years +) at Pen y Cymoedd.

Figure 1.6 Remnant open habitat (bog) with checked crop (growth inhibited by soil water levels), with a mature coupe behind, at Pen y Cymoedd.

Figure 1.7 Formerly afforested open habitat (open for >8 years) with mature coupe behind, at Pen y Cymoedd.

The mosaic of forested and non-forested habitats created by this management can support important populations of some taxa including invertebrate, lichen, fungi, bryophyte, bird and bat species (Humphrey et al. 2003, Conway et al. 2007; Quine & Humphrey 2010; Kirkpatrick et al. 2017a). The available evidence suggests that stand structure has a significant impact on both community composition and species richness for a range of taxa (e.g. Bibby et al. 1985; Fuller & Browne 2003, Paquet et al. 2006, Sullivan et al. 2009, McCarthy et al. 2021) with young growth stages of plantations in particular having been shown to support a number of conservation priority species (e.g. hen harrier *Circus cynaeus*, black grouse *Tetrao tetrix*, short-eared owl *Asio flammeus*, European nightjar *Caprimulgus europaeus*, woodlark *Lullula arborea*, tree pipit *Anthus trivialis*, whinchat *Saxicola rubetra*, grasshopper warbler *Locustella naevia* and lesser redpoll *Acanthis cabaret*) (Fuller & Browne 2003). Open areas within the forest matrix can also provide key refuge habitats for mammal species, such as water vole *Arvicola amphibious* in some areas (Hipkin 2021). These more open habitats are also important for heathland habitats/ plant species diversity where forestry has been established on previously open land (Eycott et al. 2006).

In addition, forest habitats in the plantation forest matrix can also support features of significant biodiversity value, with rich bryophyte assemblages, akin to those found in sessile oak *Quercus petraea* woodland, in mature Sitka spruce *Picea stichensis* stands, alongside diverse fungal communities (Hipkin 2021). While thicket stage stands are known to be important for a variety of woodland bird species (Fuller et al. 2007, Burgess et al. 2015), and mature stands have been shown to support key populations of wood ant *Formica lugubris (*Proctor et al. 2015) and northern goshawk *Accipiter gentilis* (Humphrey 2005).

As such, whilst plantation forests have often been viewed as green deserts (Horak et al. 2019), it is clear from the available evidence that the reality is more complex, and dependent both on where the plantation is, and the alternative viable land use it is compared with (Brockerhoff et al. 2013). However, where non-native conifer plantations are the principal forest type, it is clear they play a key role in the provision of habitat for biodiversity (Irwin et al. 2014, Horak et al. 2019, Hipikin 2021).

In Wales, pre-canopy closure habitat has become of critical importance to European nightjar, with around 80% of churring males recorded in such habitat (Conway et al. 2007), meaning approximately 9% of the U.K. population is now present in Welsh coniferous woodland (Pritchard et al. 2021). This highlights the importance of this habitat to nightjar, both within Wales and at the U.K. scale.

The selection of younger tree growth areas by nightjar is thought to reflect their preference for semi-open habitats (Sierro et al. 2001; Winiger et al. 2018). However, other studies of early stage crop cycle coupes have shown that -in general- overall bird densities increase with successional stage (Bibby et al. 1985, McCarthy et al. 2021) and these stages provide key habitats for early seral-associated species, including many insectivores, prior to canopy closure (Burgess et al. 2015, Harris et al. 2021). For example, the availability of such habitat has been implicated as a driving force in population trends for tree pipit (Burgess et al., 2015). The selection of these habitats by other insectivorous bird species and other nocturnal aerial insectivores (e.g. a variety of bat species – see Kirkpatrick et al. 2017a, Apoznanski et al. 2020, Buchholz et al. 2021) suggests that the selection of these habitats by European nightjar may not be simply due to the habitat structure. It also seems probable that these habitats provide a suitable invertebrate prey resource (largely moths (Lepidoptera) – Sierro et al. 2001).

Recent studies of spatial foraging behaviour in nightjar have identified a great deal of plasticity (Evens et al. 2017, Sharps et al. 2015), and from this work it is clear that in order to reach optimal feeding grounds birds can travel long distances, which can be physiologically costly (Evens et al., 2018). Hence, the spatial configuration of stands, and stand complexity, is likely to be of key importance in driving many life history aspects of European nightjar. To our knowledge, this has not yet been studied, and yet is potentially of critical importance to the species in Wales.

Research in other taxonomic groups at the forest scale has been limited, but studies on Lepidoptera have shown relatively low diversity compared to broadleaved/ native woodland (Luque et al. 2007, Kirkpatrick et al. 2018) and a negative effect of clear fell harvesting on species richness and abundance (Kirkpatrick et al. 2017a). Recent work has however shown that within the forest macro-moth assemblages found in edge/ open habitats are more diverse and abundant than that associated with nearby mature stands (Pinksen et al. 2021). Previous studies (Thorn et al. 2015, Sharps et al. 2015, Carr et al. 2020) have also shown that older and un-thinned stands of planted coniferous trees in general support a higher diversity and abundance of moths. There is, however, little to no published information on how moth assemblages develop through time in the open habitats of the forest habitat matrix and this may play a key role in habitat use and selection by European nightjar.

1.3 European Nightjar/ Troellwr Mawr (*Caprimulgus europaeus*)

Capimulgiformes is a globally distributed order of generally nocturnal and insectivorous bird species. The taxonomy of this order is controversial and not fully resolved (del Hoyo et al., 1999) but is thought to comprise five families including Steatornithidae (oilbird), Aegothelidae (owlet-nightjars), Podargidae (frogmouths), Nyctibiidae (potoos) and Caprimulgidae (nighthawks, nightjars and eared nightjars). The family Caprimulgidae contains approximately 120 species (del Hoyo et al., 1999) including the European nightjar *Caprimulgus europaeus* which is the only species of the order that occurs as a breeding species in the British Isles.

The majority of the 42 species in the genus *Caprimulgus* are nocturnal, aerial insect feeders (Cramp 1985; Holyoak 2001) that usually nest on the ground and tend to be inactive during the day. Peaks in activity patterns for these species (both foraging and display activity) tend to be concentrated around dusk and before dawn, and may also continue at a lower level throughout the night (Holyoak 2001;, Martin 2010). Despite their nocturnal foraging activity and insectivorous diet, individuals are thought to forage by eye (Cramp 1985, Holyoak 2001), and physiological characteristics such as the light-reflecting tapetum lucida behind their retina suggest they are well-adapted for doing so (Martin 2010).

The European nightjar, or Troellwr mawr in Welsh, has an extensive breeding range, over most of Europe except the far north and extending east across temperate Asia as far as Mongolia and northwest China; there is also a breeding population in northwest Africa. BirdLife International (2021) lists the species as Least Concern due to its large range and population size. The global population is also thought to be decreasing, and is estimated at 3,100,000-5,500,000 mature individuals, of which 1,230,000-2,200,000 are thought to breed in Europe (BirdLife International 2021). It is has become clear in recent years that the nightjar is an unusual species in the U.K. context as it is one of the few insectivorous sub-Saharan migrants with a population not in rapid decline – and may even be increasing and expanding their range (Conway et al. 2007, Balmer et al. 2013;). However due to the historical population decline in Britain and across Europe the species is currently 'amber' listed and was previously 'red' listed in the U.K.'s birds of conservation concern (Eaton et al. 2015). The nightjar is also red-listed in Wales (Johnstone and Bladwell 2016) based on the species severe historic population decline and decline in breeding range.

Female European nightjars nest on the ground in large open areas, whilst males often roost in similar habitat or on a tree perch (Martin 2010). Their cryptic plumage and tendency to 'sit tight' provides exceptional camouflage making them largely indistinguishable from their surroundings (Troscianko et al. 2016). Nightjars construct no physical nest structure beyond an occasional shallow scrape, and clutches usually consist of two eggs. Females frequently double-brood, with the second clutch laid after or shortly prior to the fledging of the first brood, and generally nearby within the same area of habitat (Lack 1957).

Nightjars feed on a variety of Lepidoptera and Coleoptera (Glutz von Blotzheim and Bauer 1994; Sierro et al. 2001) although it is clear that moths are of key importance (Winiger et al. 2018, Evens et al. 2020). Nightjars nest on bare or sparsely vegetated ground, often on free-draining soils (Cramp 1985), typically in dry, open habitats such as lowland heaths, commons and moorland, forest and woodland (especially glades, clearings and edges), recently felled woodland and young forestry plantations. Nightjars arrive back in the U.K. on their spring migration from early to mid-May with males arriving first and females arriving on average 11 days later (Cramp 1985, Holyoak 2001). Autumn migration commences anytime from June with a peak in August (Cramp 1985, Holyoak 2001).

European Nightjar in Wales

At the end of the 19th Century and in the early years of the 20th Century, nightjars were widespread and apparently common in Wales (Pritchard et al. 2021). At this time they were still breeding in sand dune systems (as they still do in Continental Europe), but were also widespread throughout coastal heathland and on bracken *Pteridium aquilinum* covered hillsides across Wales. This association with bracken-covered slopes was widespread and is reflected in their alternative English name of "fern owl".

A decline in numbers and distribution appears to have started earliest, and most severely, in the west of Britain (Pritchard et al. 2021) with significant declines across much of mid Wales noted by the 1950s and 1960s (Roderick and Davis 2010). This decline was, however, not spatially uniform, with populations seeming to hang on in the sand dunes of Anglesey well into the 1950s (Pritchard et al. 2021).

A national survey for the species undertaken by the BTO in 1981 (Gribble 1983) included the first detailed census of nightjars in Wales, and recorded only 57 singing males, of which 36 occupied sites in coniferous plantation forestry. This trend towards occupation of plantation forest habitats continued through the 1980s and 1990s (when 193 churring males were recorded at 107 sites - Morris et al. 1994), demonstrating the rising importance of such habitats for breeding nightjars (Pritchard et al. 2021). The third full U.K. census, undertaken in 2004 (Conway et al. 2007), produced a population estimate of 280 males in Wales, an increase of *c.*24% since 1992, and also confirmed the near reliance of the species on plantation forestry in Wales, with ~80% of churring males in Wales recorded in forest plantations.

Evidence for the causal drivers behind these population and distributional changes in both Wales and the U.K. as a whole are limited, although it is thought likely that habitat change and degradation are the most likely causes (Conway et al. 2007). Whilst this may explain a reduction in overall numbers, however, it does not explain the loss of birds from seemingly unchanged, little visited, habitats such as the ffridd/ bracken slope habitats in North Wales (Pritchard et al. 2021).

The current breeding estimate for Britain, of 4,600 (range 3,700-5,500) churring males (Woodward et al. 2020), is derived from the results of the 2004 survey (Conway et al. 2007) with an estimate of 280 churring males in Wales. However, the recent Birds in Wales publication (Pritchard et al. 2021) suggests a Welsh population in excess of 406 churring males for commercial forestry areas alone, and a total population in Wales in excess of 500 churring males, which equates to approximately ~1000 pairs (Conway et al. 2007). This suggests that coniferous plantation woodland in Wales hosts approximately 9% of the U.K. population and confirms the key importance of this habitat to nightjar in both Wales and the U.K.

1.4 Wind Farms and European Nightjar

Increases in wind energy development have the potential to impact on birds via collision, displacement due to disturbance, barrier effects and habitat loss (Drewitt & Langtson 2006). These effects can occur during both the construction and operational phase of any development, but it is generally accepted that construction phase disturbance is likely to be more acute ("pulse" disturbance) and greater in magnitude (Pearce-Higgins et al. 2012). Whilst operational impacts have the potential to impact bird populations through direct mortality via collision or displacement from important habitats (Drewitt & Langtson 2006, Thelander & Smallwood 2007). In general, the construction phase stage of wind farm development involves a greater density of human activity and habitat change as the wind farm infrastructure is installed. The operational phase of such schemes generally have much lower levels of human activity but support a highly modified landscape with wind turbine generators now present.

The shift in land management from standard forestry practice to the development of wind farms within the forest matrix may pose a risk to species present, especially those reliant on open habitats within the forest. Nightjars may be at risk of collision especially as they catch their insect prey in the air (Ahlén 2010) and are likely to use open habitats within the forest for nesting and foraging. However, to date there is only a single known fatality involving European nightjar from across Europe, suggesting that this risk may be small in practice (Rydell et al. 2012, Traxler 2019).

Human disturbance of wildlife is one of the principal concerns in biodiversity conservation, yet the information required to assess this threat is rarely available (Gill 2007). Human disturbance can be analogous to predation risk (Frid and Dill 2002, Le Corre et al. 2009, Kociolek et al. 2011, Ibanez-Alamo et al. 2015) and can influence population processes, such as nest success (Halfwerk et al. 2011, Francis et al. 2011, Almasi et al. 2015, Remacha et al. 2016, Gladalski et al. 2016), yet some studies show little effect (Hatchett et al. 2013, Hale et al. 2014).

Previous studies on nightjar have identified negative impacts of disturbance on nesting nightjar (Murison 2002, Liley & Clarke 2003, Langston et al. 2007). In general, these have identified a negative relationship between nest success or density and public recreational access and residential development in the areas surrounding breeding sites. The mechanism(s) of this impact are unclear, although have been hypothesised to be via trampling of nests, dog predation of chicks and/or eggs, or increased natural egg predation due to flushing of adults (Langston et al. 2007, Murison 2002).

No empirical studies of the effects of construction disturbance or industrial operation disturbance impacts on European nightjar are currently available and studies from the grey literature show inconsistent results. For example, studies in Germany identified a > 50% displacement of churring males (at wind farm area +150m) whilst studies in Sweden found no effect (Traxler 2019). The species' known sensitivity to disturbance during the nesting period would, however, suggest that nightjars are at risks from construction and/or operational phase disturbance associated with wind farm development, and as such this warrants further investigation. This has been noted and addressed during wind farm developments in the U.K. with precautionary avoidance and mitigation measures being adopted at many sites to minimise any impact (Shewring & Carrington 2015, Shewring & Vafidis 2017).

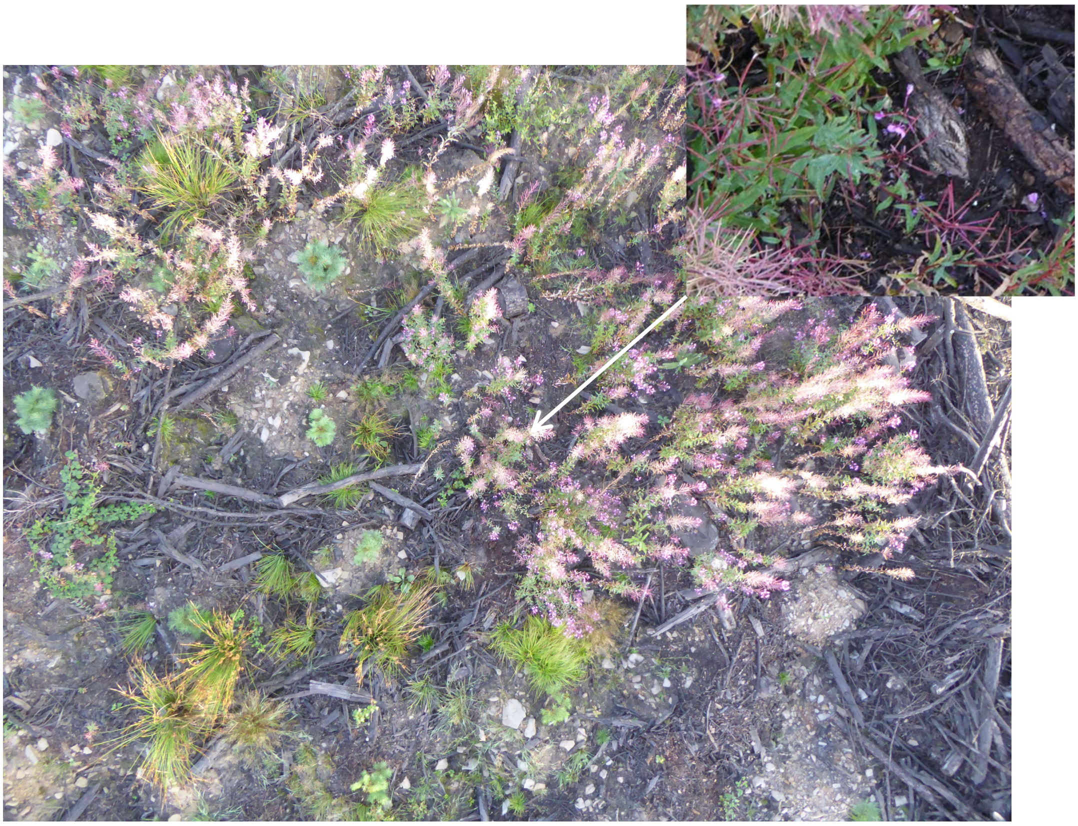
Studies of construction/operational disturbance are also rare in other bird species, but those that have been completed show a varied picture, with negative effects in some species (sagebrush songbirds and grouse (Hethcoat & Chalfoun 2015, LeBeau et al. 2014)) but not in others (golden-cheeked warbler *Setophaga chrysoparia* (Lackey et al. 2011, Long et al. 2017), Killdeer *Charadrius vociferus* (Baxter 2015), dickcissel *Spiza americana* (Hatchett et al. 2013)). Positive effects have also been noted through disruption of predator-prey interactions in some communities (Francis et al. 2009, Francis et al. 2011, Rubenstahl et al. 2012) whilst mixed effects have been noted in others (Ludlow et al. 2015, Ludlow et al. 2018). These results suggest responses to industrial construction and operation disturbance stimuli are likely to be largely species-specific and activity-specific. It is certain however, that nests are a critical element of the avian life cycle, and are particularly vulnerable to disturbance impacts as chick/ egg survival depends on intensive parental care (Fowler & Williams 2017, Clutton-Brock 2019).

Disturbance associated with wind farm construction activity, though temporary, often exceeds background levels of daily traffic/ recreational disturbance. This increased intensity of disturbance could induce threshold-based responses, where a negative effect is initiated when a threshold level of disturbance is reached, e.g. human proximity causing flight initiation (Weston et al., 2012), or amplify gradient-based negative responses (e.g. less time foraging with increased disturbance levels – Burger, 1991) for some species. Negative effects may therefore reasonably be expected during the turbine construction phase, and mitigation measures to prevent such impacts are often recommended and implemented through works buffers (Blumstein et al. 2003, Blumstein et al. 2005, Fernández-Juricic 2005, Baxter 2015). The lack of empirical species-specific evidence for appropriate mitigation or disturbance buffers (Whitfield et al. 2008, Hunter et al. 2021) can, however, result in over-precautionary approaches and poorly evidenced decisions during consent and construction, and have significant cost implications for developers. As such, there is a critical need for evidence-based mitigation measures to inform disturbance buffers and works methods.

1.5 European Nightjar Tag Effects

The nocturnal and crepuscular activity of nightjars, in combination with their cryptic plumage and behaviour, poses a significant challenge to observational research (Figure 1.8), as in other nocturnal species (Kunz & Fenton 2005). These challenges have inhibited study, as well as restricted the current understanding of conservation status (see: Conway et al. 2007, Sharps 2015). This in turn led to the relatively early adoption of radio tracking technology in nightjar research by Alexander ansd Cresswell (1990), and the widespread use of tags for conservation research (Cross et al. 2005) and nest finding associated with the monitoring of wind farm developments (Grundy 2015, Shewring et al. 2020, Jenks 2021). A similar pattern is seen in academic research, with radio tracking frequently used in the study of nightjar ecology (Sierro et al. 2001, Sharps et al. 2015, Evens et al. 2017), and this trend has continued as tracking technology has changed and GPS tags have become small enough for deployment on nightjar (Evens et al. 2017, Evens et al. 2018, Mitchell et al. 2019; Mitchell et al. 2020). These studies have delivered fascinating insights into both the ecology of the species and its migratory strategies (Evens et al. 2018), and have helped to inform conservation strategies in both the U.K. (Sharps et al. 2015, Mitchell et al. 2020) and continental Europe (Sierro et al. 2001, Evens et al. 2017).

Figure 1.8 Female European nightjar sat on two eggs at a nest site in the Afan Forest Park.



Given this long history of tag use in European nightjar studies, it is surprising there here has been no detailed investigation of the potential for tag effects upon nest success or foraging success, especially given the strong evidence for such effects in other species (Barron et al. 2010, Bodey et al. 2018, Geen et al. 2019) and particularly in aerial foragers (Costantini & Møller 2013). Most studies of nightjar to date have suggested device effects are unimportant or absent, as the device equates to a small percentage of the birds' mass (generally <3%). However, it has recently become clear that tag effects may not simply be a function of body mass, but also a product of their location on the animal, attachment method and tag design (Vandenbeele et al. 2012, 2014, Kay et al. 2019). Most tags deployed on nightjars during the breeding season use tail mounted tags (as per Alexander & Cresswell 1990) that are lost during moult (likely in the winter range). As such, there is a clear need for research into the effects of tags on nightjar behaviour and reproductive success.

1.6 Studying European Nightjar Movement to Inform Conservation

To stem global declines of biodiversity, appropriate and effective species conservation measures must be identified (Runge et al. 2015, Sergio et al. 2019) and such interventions can have beneficial cascading effects for other species of conservation concern (Runge et al. 2019), although this is not always the case (Carlisle et al. 2018, Wang et al. 2021). To improve conservation strategies so that planned outcomes (e.g. targeted population increase) are actually achieved, we need to not only document and predict where species are in the landscape (Cooke 2008, Guisan et al. 2013), but observe how species are behaving (Sutherland 1998).

In this respect, the use of tags/ tracking devices has proven a valuable tool, allowing researchers to collect detailed information on spatial and temporal patterns of landscape use, and also infer associated behaviour. This has allowed the identification of focal areas for migratory bird conservation (Knight et al. 2021), key foraging areas/ habitats in breeding/non-breeding ranges, as well as on migration (Elgin et al. 2020, Bolton 2021), and confirms the importance of landscape/ habitat configuration in influencing foraging behaviour (Evens et al. 2018). The conservation of migratory species is, however, challenging as such species are potentially exposed to different threats across their annual range, and conservation interventions must be cognisant of this (Runge et al. 2014, Runge et al. 2015, Marra et al. 2015). For many species there is insufficient evidence on stressors associated with other parts of the annual cycle (e.g. wintering period) to make informed decisions. As such, where there is reasonable evidence of the potential for positive impacts through low cost conservation interventions in the breeding range then these should be adopted, as it is likely these will be beneficial and it is crucial that such actions are taken where there is still an opportunity to act, rather than delay action until we have perfect information (Martin et al. 2012, Runge et al. 2014, Runge et al. 2015). Nevertheless, it is clear that the magnitude of this benefit will be dependent on the effects of other stressors across the annual cycle and geographical range.

As such, there is clear potential for nightjar tracking data from the breeding grounds to help identify key breeding and foraging areas within the WGWE for this species, and the key drivers behind this use of the landscape. This in turn could inform land management within the WGWE and help deliver the wider biodiversity ecosystem benefits that the Welsh Government is aiming to achieve. Similar successful examples of the use of habitat selection behaviour to inform management are available from Greater sage-grouse *Centrocercus urophasianus* populations in Wyoming, USA, where this information has been used to respond to proposed development and design restoration plans (Copeland et al. 2013).

1.7 Thesis structure and hypotheses

This thesis focuses on European nightjar as an indicator species of conservation concern, and the invertebrate prey of nightjars (specifically, nocturnal Lepidoptera) -providing new insights into conifer woodland plantation ecology in the context of changing land use/management recommendations relating to the Welsh Government Woodland Estate and plantation woodlands across the European nightjar's breeding range. This will inform the long term sustainable management of plantation coniferous woodland to deliver timber, renewable energy and biodiversity ecosystem services.

The thesis comprises of four data chapters:

- Chapter 2 uses nightjar nest record data from Brechfa Forest (South Wales, U.K.) to investigate the potential effects of tag deployment on nest success (e.g. fledging success), through a comparison of the observed nesting success of tagged birds and untagged birds. My primary hypothesis is that tags will have a negative effect on nest success.
- Chapter 3 tests the hypothesis that moth biomass and/ or diversity is dependent on seasonal native vegetation primary productivity, and plantation stand management, using extensive moth trapping data collected from open habitats within forest plantations, across a gradient of stand ages.
- Chapter 4 combines GPS tag data and predictions of moth biomass (Chapter 3) to test whether the foraging behaviour of nightjars in the forest matrix is driven by the availability of moth biomass and its seasonal variation. My primary hypothesis is that the occurrence of nightjar foraging behaviour will be more likely in higher moth biomass areas.
- Chapter 5 uses nightjar nest record data from sites across Wales to investigate the potential effects of habitat management and wind farm construction/ operation on nightjar nest success (e.g. fledging success). My primary hypothesis is that disturbance will have a negative effect on nest success.

My over-arching aims in this thesis are to (i) assess the suitability of tail mounted radio tags for nightjar nesting studies, (ii) to investigate the impacts of land management on moth biomass and diversity, (iii) to investigate the importance of land management/ moth biomass and biomass variation in determining foraging habitat selection in nightjar, and (iv) to determine the effects of wind farm construction and operation on nightjar nesting success. It is intended that this will allow the development of suite of evidence-based conservation interventions that can support nightjar and moth species in the plantation coniferous woodland and in particular, the Welsh Government

Woodland Estate, and I set out these specific management recommendations in the General Discussion (Chapter 6).

2.0 Testing for effects of tail mounted radio tags on European Nightjar (*Caprimulgus europaeus*) nest survival

2.1 Abstract

Monitoring of European Nightjar *Caprimulgus europaeus* nest sites over multiple years (2013-2019) was undertaken at the Brechfa West Wind Farm, Carmarthenshire, Wales, from 2013 to 2019. This data was collected as part of wind farm post monitoring commitments. Due to the nature of the data collection at this site (a combination of radio tracking and visual search), I have been able to use this dataset to test whether nest success of European Nightjar is affected by radio tag deployment.

A total of 85 nests were located through a combination of capture and radio tracking of breeding individuals, and direct observation combined with focused searching. All located nests were subsequently monitored through a combination of visual checks and trail camera deployment until their natural conclusion.

No evidence was identified to support a negative effect of tail mounted radio tag deployment on the nest success of European Nightjar. However, nesting success (1 or more chicks fledged) was positively associated with mean temperature during the nesting period, although the strength of this effect varied through time. I conclude that the use of tail mounted radio tags on European Nightjar has no negative effect on nest survival.

2.2 Introduction

The marking and tagging of birds are widespread and important methods that have informed studies of many aspects of animal ecology, including migration, foraging behaviour and physiological ecology (Bodey et al. 2017). The techniques used for such marking are continuously evolving, and have been used in some form for many decades. The extra mass that these devices impose, the tag configuration and attachment method used has, however, been a cause for concern, especially for relatively heavy devices such as radio tags, GPS devices and geolocators (e.g. Bowlin et al. 2014). The deployment of such devices has been shown in some cases to reduce survival, inhibit parental care (Bodey et al. 2017), induce potentially costly behavioural modifications (Vandenabeele et al. 2014), or reduce the probability of nesting (Barron et al. 2010). Several mechanisms for such effects have been identified including; increased energetic costs of flight through drag (Bowlin et al. 2010), reduced foraging success (Wanless et al. 1988), impacts on young through reduced provisioning (Robert et al. 2006) and increased thermoregulatory costs due to feather loss and skin damage (Hines and Zwickle 1985). It is likely that such effects are in many cases species specific with other studies identifying few, if any effects (e.g. Bell et al. 2017, Brlik et al. 2020).

In an attempt to overcome such device effects, the research community has adopted rules of thumb for the design of tagging studies, such as the ‘5% rule’. This dictates a maximum tag mass limit of 5% of a bird’s body mass (Brander & Cochran 1969). The figure of 5% has been considered too high by some authors or for some taxa; for example Kenward (2001) suggested a limit of no more than 3%, supported by studies of nest abandonment in albatross and petrel species (Phillips et al. 2003, Casper 2009).

In recent years, further research has shown a simple percentage mass rule of thumb is likely to be over-simplified. For example, various studies have shown that factors such as device-induced drag (Vandenabeele et al. 2013), tag shape and attachment location (Kay et al. 2019) are also critical considerations. These considerations, coupled with the apparently species-specific nature of tag effects, highlight the importance of testing for tagging impacts on individual species.

European Nightjar *Caprimulgus europaeus* (henceforth “nightjar”) breeding in Welsh upland coniferous forest, are difficult to monitor using conventional survey techniques due to their crepuscular nature, cryptic camouflage, and low density population (Cross et al. 2005, Gilbert et al. 1998). Therefore, a combination of radio tracking and observational nest finding methods have generally been utilised together for such studies at upland sites in Wales.

Radio transmitters and GPS devices suitable for deployment on nightjar have been available for some time, and have been widely used in breeding studies, most often as tail mounted devices (e.g. Alexander et al. 1990, Cross et al. 2005, Evens et al. 2018). Despite their widespread use in studies of breeding nightjars (e.g. Sharps et al. 2015, Evens et al. 2017) there is to my knowledge no published study of the effects of such tag deployment on breeding success. It is, however, critical that such effects should be investigated so that risks can be evaluated and minimised (Wilson et al. 2006, Casas et al. 2015).

An additional challenge in evaluating tag effects is to distinguish them from environmental impacts on survival or breeding success due to factors such as habitat quality or weather. Previous studies on nest survival in nightjars have identified probable effects of weather on nest survival (English et al. 2018) and similar effects are widely documented from studies in other species (e.g. Miller et al. 2017, Martin et al. 2017). As such, it is critical in studies of tag effects to account for such variables to accurately gauge any evidence of effects. In the present study, I therefore considered tag effects together with a set of environmental variables that I hypothesised may influence nightjar breeding success.

The present study directly compares observed nesting success of tagged birds and untagged birds, in order to investigate the potential effects of tag deployment and environmental variables on nesting nightjars. These data have been collected as part of on-going ecological impact monitoring requirements associated with the Brechfa West Wind Farm development. The data set includes nest record data from the study site during the pre-development, construction and operational phases of the wind farm.

2.3 Methods

2.3.1 Study Species

Nightjars are ground nesting birds that typically lay two eggs (occasionally one egg) and usually produce two broods per breeding season (Holyoak et al. 2001). The nightjar is usually thought of as a heathland species, but in Wales they mainly breed in clear-fell forestry (i.e. recently felled forestry, before substantial re-planting / re-growth), check coupes (i.e. stands of stunted tree growth) and recently restocked conifer plantations (Conway et al. 2007). Male nightjars establish breeding territories within the study area in May; females arrive in mid-May and subsequently become paired with established territorial males.

Nightjars are of conservation concern due to historic population declines and range contraction (Balmer et al. 2013, Hagemeijer & Blair 1997). The nightjar is an Annex 1 species in the EU (Council Directive 2009/147/EC), has Amber status in the U.K. (Bird of Conservation Concern; Eaton et al. 2015) and is listed under Section 7 of the Environment (Wales) Act 2016. The nightjar population in Wales has been increasing since at least 1981 (Morris et al. 1994), possibly due to increased habitat availability following the maturation and felling of plantations that were planted in the 1950's.

2.3.2 Study Site

This study utilises nest data from Brechfa Forest (South Wales, U.K. – Latitude 51.967432, Longitude -4.1964175), a commercial plantation forestry managed by Natural Resources Wales on behalf of Welsh Government. The forest is dominated by dense Sitka Spruce *Picea stitchensis* forest blocks (coupes), interspersed with recently felled areas around wind turbines, and with semi-natural woodland along watercourses.

Topography and forest age at this site has enabled observational nest finding to be relatively successful during recent commercial ecological monitoring work.

2.3.3 Nest data collection

The inclusion of nightjar in species protection legislation ensures that nightjar nest locations are protected from damage/ destruction under the Wildlife and Countryside Act (1981). Suitably licensed and experienced individuals undertook all tagging and nest monitoring visits completed in this study.

2.3.4 Territory identification

Active territories were located by systematic searches in areas of suitable habitat, and were confirmed by observation of pairs or of displaying males, which produce a distinctive "churring" call (Ferguson-Lees et al. 2011).

2.3.5 Observational nest location

Nest searching commenced annually in late May, and continued until August. Active territories were systematically watched on multiple occasions by multiple observers at dusk, and visual cues were used to guide follow up nest searches (Langston et al. 2009). Subsequent nest searches consisted of detailed visual inspection in areas of observed nightjar activity during dusk watches, with searchers aiming to pass within 3-4 metres of any point within the search area.

2.3.6 Radio tracking nest location

Where observation of active nightjar territories yielded little information, or nest searches were unsuccessful, or where pairs were considered likely to attempt a 2nd brood, then these territories/ pairs were targeted for radio tagging effort. Mist nets were set up in the vicinity of identified territories, and male nightjars were then tape lured into the mist nets by playing the species' typical territorial song (Squire and Alexander 1981). Tape luring proved less effective at attracting incubating females. Females were caught by mist-netting at favoured feeding sites, or by trapping at known 1st brood nests (found by field observation) to allow radio tracking to 2nd brood nests.

Captured birds were fitted (under licence) with PIP-3 radio-transmitters (from Lotek Ltd – as per Alexander and Cresswell (1990)), attached to the base of one of the central tail feathers. Attaching the radio-transmitters in this way ensures that they are shed during post-breeding moult in the wintering grounds, and thus does not affect the birds during their spring migration. The tags used in this study each weighed 1.2g, male nightjars weighed between 60.2–87.0 g (n=34), and females weighed between 69.0–100.8 (n=23) - so tags weighed 1.38–1.99% of male body weight, and 1.19–1.72% of female body weight.

Tags were deployed across the breeding season, with tagging dates ranging between the 3rd of June and 24th of July. The median tagging date was the 25th of June; the mean tagging date was the 25th of June for females and 27th of June for males. Tags were deployed both prior to and after nests were located; 19 of the 39 tagged females were tagged after their nest was located, as were 11 of the 25 tagged males.

Following the identification of active nests through either observation or radio tracking, all nests were monitored to their natural completion (fledging or nest failure) by an experienced nightjar fieldworker, using regular (~weekly) nest site visits. Nests were classified as either successful or failed, based on a combination of the timing of nest visit records and available evidence at the nest site and within the territory (i.e. flying young present).

2.3.7 Weather data

In order to account for the influence of weather on nesting success, data from the closest available weather station (Pembrey; 51.7144117°N, -4.366197°E, approximately 30km south of the study site) was obtained using the GSODR package (Sparks, Hengl, and Nelson 2017) using R software version 3.6.1 (R Core Team 2019), implemented via R Studio (RStudio team 2018). The GSODR package provides automated downloading, parsing and cleaning of Global Surface Summary of the Day

(GSOD) (United States National Oceanic and Atmospheric Administration National Climatic Data Center) weather data. This provided daily rainfall (mm) and mean temperature (Tm, °C). Data manipulation and visualisation was undertaken using the R libraries tidyverse (Wickham et al. 2019), lubridate (Groelmund & Wickham 2011) and ggplot2 (Wickham, 2016). Mean temperature and mean precipitation were calculated for the active period of each nest (laying date to last known presence) and utilised in subsequent analysis.

2.3.8 Statistical analysis

I performed all statistical analyses in R 3.6.0 (R Core Team 2019). In order to account for the inherent bias in nest studies arising from the lower detection probability of failed nests (due to their shorter time available for potential observation), I estimated daily nest survival rates - DSR (Mayfield 1975, Dinsmore et al. 2002) using RMark version 2.2.7 and MARK (Laake 2013, White and Burnham 1999).

Daily nest survival rates were estimated and modelled with selected covariates using the R package RMark version 2.2.7 (Laake 2013). I undertook model selection of nest survival models using an information theoretical approach based on the second-order Akaike information criterion for small sample sizes (AICc; Burnham and Anderson 2002).

A set of 193 biologically plausible models was derived, including additive effects of Julian day, nest age (as estimated based on hatch date, if available, or if not then using estimates based on egg floatation (Westerskov 1950) or observational information), brood (1st, 2nd, 3rd), year, mean rainfall within the relevant active nest period, mean temperature (Tm) within the relevant active nest period, the presence of windfarm construction activity (binary yes/no – nest active in year of construction activity), adult male tag status (tag status of the male associated with nest - binary yes/ no), adult female tag (tag status of the female associated with nest - binary yes/ no) and combined adult tag status (tag status of both adults associated with nest - binary yes/ no - i.e. both birds tagged or not). The candidate models also included the interaction between mean temperature and date, to help distinguish the effect of temperature from seasonality. The combined adult tag status variable was included to account for potential synergistic effects of tagging both parents. All covariates were scaled prior to analysis, to have a mean of zero and a standard deviation of one. The set of candidate models also included a global model (containing all candidate independent variables) and a null model (containing no independent variables). Co-linearity between variables was determined using Pearson's correlation coefficient, and this identified low levels of correlation between candidate model variables. No candidate model variables exceeded the threshold correlation of 0.7 (Dorman et al. 2013) and all candidate variables were thus included in the analysis.

Models were ranked using AICc, and the ΔAICc values and Akaike weights (wi) were used to infer support for each of the candidate models (Appendix A). In the model selection analysis, no single model was clearly better than all others, and to account for model selection uncertainty, models within two AICc units of the top model, were selected for model averaging, as this can provide a robust means of obtaining parameter estimates in such scenarios (Burnham & Anderson 2002, Grueber et al. 2011, Harrison et al. 2018). A weighted average of the parameter estimates (and 95% confidence limits) was calculated for all of the variables contained in the top models, using the package MuMIn (Grueber et al. 2011, Barton 2018, Mwangi et al. 2018) (Table 2.2). Parameters were considered statistically significant where their model-averaged 95% confidence limits did not span zero.

Overall nest survival was calculated from predictions daily of nest survival rate (DSR) made by the final, averaged model. These were converted to the overall nest success by assuming a 36 day standard nesting period (DSR^36) from the median nest initiation date. Variance in the nest survival estimates were obtained using the delta method (Powell 2007).

The same suite of models was also re-run using a subset of the data representing the egg stage and chick stage respectively. Whilst this reduced the sample size for these models, it was considered to potentially provide greater insights into potential tag effects during the two different breeding stages, given the likely different energetic demands and behaviours associated with each stage. Due to convergence problems, because of small sample sizes, the chick stage models were run without the year parameter.

2.4 Results

2.4.1 Nest finding and monitoring

Eighty-five nightjar nests were located over the course of the study (2013-2019); sixty-one of these were located through direct observation of adult behaviour, and twenty-four were located using radio tracking. Median nest initiation date was 16th June (range = 27th May – 27th July). In total, 59 nests were confirmed first brood nests and 13 confirmed second brood nests. Two nest attempts were also recorded as ‘third brood’ nests, although these were a result of early failure of previous nesting attempts (1st or 2nd brood) and thus are replacement clutches; they have nevertheless been referred to as third brood nests for the ease of reference. Brood number could not be confirmed at 11 of the located nests.

I found nests at different stages of development: 52 (61.1%) during incubation and 33 (38.8%) were found during the nestling period. From all of the nests, 52 fledged at least one chick, whilst the remainder (33) failed, with 15 at the egg stage and 18 failing at the chick stage. A summary of nest success and the number of nests with attending tagged adults is provided in Table 2.1, whilst Table 2.2 details the breakdown of nests attended by tagged adults, by adult sex, and brood number.

Table 2.1 Summary of nest monitoring results (total no. of nests fledging one chick or more, and percentage success rates) with a breakdown by tag status of the attending adults and brood status (e.g. known 1st, 2nd or 3rd brood or unknown brood status).

	TOTAL NO. NESTS	NO. SUCCESSFUL	% SUCCESS	% SUCCESS 1ST BROOD	% SUCCESS 2ND BROOD	% SUCCESS 3RD BROOD	% SUCCESS UNKNOWN BROOD
ALL NESTS	85	52	61.2	69.5	46.2	50	36.4
UNTAGGED NESTS	34	21	61.8	70.4	33.3	100.0	0
NESTS ATTENDED BY AT LEAST 1 TAGGED ADULT	51	31	60.8	68.8	50.0	0.0	50.0
NESTS ATTENDED BY TAGGED ADULT MALE	25	16	64.0	66.7	60.0	NA	60.0
NESTS ATTENDED BY TAGGED ADULT FEMALE	39	26	66.7	75.0	55.6	0.0	60.0
NESTS ATTENDED BY TAGGED ADULT MALE AND FEMALE	13	11	84.6	85.7	75.0	NA	100.0

Table 2.2 Summary of number of nests attended by tagged parents, broken down by brood status(e.g. known 1st, 2nd or 3rd brood or unknown brood status).

	TOTAL	1ST BROOD	2ND BROOD	3RD BROOD	UNKNOWN BROOD
NO. OF NESTS	85	59	13	2	11
NO. ATTENDED BY TAGGED ADULT	51	32	10	1	8
NO. ATTENDED BY TAGGED ADULT MALE	25	15	5	0	5
NO. ATTENDED BY TAGGED ADULT FEMALE	39	24	9	1	5
NO. ATTENDED BY 2 TAGGED ADULTS	13	7	4	0	2
% ATTENDED BY TAGGED ADULT	60.0	54.2	76.9	50.0	72.7
% ATTENDED BY TAGGED ADULT MALE	29.4	25.4	38.5	0.0	45.5
% ATTENDED BY TAGGED ADULT FEMALE	45.9	40.7	69.2	50.0	45.5
% ATTENDED BY 2 TAGGED ADULTS	15.3	11.9	30.8	0.0	18.2

2.4.2 Nest survival

In the model selection analysis, there were three models within 2 AIC units and they contained the following variables – nest age, female tag status, adult tag status, temperature, precipitation and Julian day (Table 2.3). In order to account for model selection uncertainty, a conditional weighted average (averaged over only the models containing those parameters) and a full weighted average (all models using zero value for parameters not present) of the parameter estimates and 95%

confidence limits was calculated for all of the variables contained in the top three models (conditional weighted averages in Table 2.4, and full weighted averages in Table 2.5). Full weighted model average parameter estimates are reported below, along with the standard error (SE).

Estimated average daily nest survival (± SE), across all years and tag treatments, was 0.986 (± 0.008). This extrapolates over the 36-d nesting cycle to an average annual nest success rate of 0.63 (± 0.18).

The same suite of models run on subsets of the full data set for the egg stage of the nesting cycle failed to identify any parameters as having an important effect on DSR and identified no detectable difference between DSR for tagged nests vs. untagged nests at either stage. Top selected models and model averaged coefficients for the identified top models are presented in supplementary materials Appendix B – Table B1 to Table B3. The same suite of models for the chick stage of the nesting cycle failed to converge due to low sample sizes.

Table 2.3. Top models (i.e. models within 2 AICc units of the top model) of nightjar daily nest survival rates, for a set of models including mean rainfall mm (m_prcp2), average temperature °C (m_temp), nest age days (NestAge), time (Julian day), adult female tag status (f_tag), year (2013 to 2019) and adult tag status (fm_tag).NPAR – Number of parameters. AICc – Akaike information criterion with a correction for small sample sizes, Delta AICc – the relative difference in AICc between the best performing model and other candidate models. Weight – Model weight based on relative performance.

MODEL	NPAR	AIC$_C$	DELTA AIC$_C$	WEIGHT	DEVIANCE
S(~NESTAGE + F_TAG + M_TEMP * TIME + M_PRCP2)	7	170.12	0	0.1227	156.02
S(~NESTAGE + FM_TAG + M_TEMP * TIME + M_PRCP2)	7	171.27	1.15	0.072	157.17
S(~NESTAGE + M_TEMP * TIME + M_PRCP2)	6	171.86	1.75	0.05	159.79

Table 2.4 Conditional model averaged estimates (± SE) of the effects of mean rainfall, mean temperature, nest age, time (days from 28th of May), construction year, adult female tag status and adult male or female tag status, on daily nest survival rates (DSR) of nightjars at Brechfa Forest. Model averaged parameter estimates were derived by weighted averaging across all models within 2 AICc units of the top model (Table 2.3). Parameters in bold are considered to have an important effect based on 95% CL.

	ESTIMATE	**SE**	**95% CONFIDENCE LIMITS**
INTERCEPT	5.7157	0.99284	3.770 to 7.662
NEST AGE	**0.07146**	**0.02756**	**0.017 to 0.125**
FEMALE ADULT TAG STATUS (TAGGED)	0.76275	0.43062	-0.081 to 1.607
MEAN TEMPERATURE	**2.50182**	**1.08336**	**0.378 to 4.625**
MEAN PRECIPITATION	0.61952	0.33058	-0.028 to 1.268
TIME	**-0.07332**	**0.0233**	**-0.119 to -0.028**
ADULT TAG STATUS (TAGGED)	0.80302	0.6496	-0.470 to 2.077
MEAN TEMPERATURE: TIME	-0.03543	0.01924	-0.073 to 0.002

Table 2.5 Full model averaged estimates (± SE) of the effects of total rainfall, mean temperature, nest age, time (days from 28th of May), construction year, adult female tag status and adult male or female tag status, on daily nest survival rates (DSR) of nightjars at Brechfa Forest. Model averaged parameter estimates were derived by weighted averaging across all models within 2 AICc units of the top model (Table 2.3). Parameters in bold are considered to have an important effect based on 95% CL.

	ESTIMATE	**SE**	**95% CONFIDENCE LIMITS**
INTERCEPT	5.7157	0.99284	3.770 to 7.661
NEST AGE	**0.07146**	**0.02756**	**0.017 to 0.126**
FEMALE ADULT TAG STATUS (TAGGED)	0.44476	0.49955	-0.534 to 1.424
MEAN TEMPERATURE	**2.50182**	**1.08336**	**0.378 to 4.625**
MEAN PRECIPITATION	0.50877	0.38222	-0.240 to 1.258
TIME	**-0.07332**	**0.0233**	**-0.119 to -0.028**
ADULT TAG STATUS (TAGGED)	0.15784	0.42985	-0.685 to 1.000
MEAN TEMPERATURE: TIME	-0.03543	0.01924	-0.073 to 0.002

2.4.3 Radio tag effects

There was no evidence for tags reducing nesting success. Although two of the three top models of daily nest survival rate included either female tag status or adult tag status variables, these all indicated a positive relationship that was not significant: a result confirmed by the averaged model (β fm_tag (male and/or female tagged) = +0.158 ± 0.429; β f_tag (female only tagged) = +0.445 ± 0.499).

Overall DSR rates for untagged female attended nests and tagged female attended nests were 0.984 (± 0.010 [SE]) and 0.990 (± 0.006 [SE]) respectively (Figure 2.1). Estimated DSR for untagged and tagged adult attended nests (male or female) were very similar, at 0.986 (± 0.010) and 0.991 (± 0.006) respectively (Figure 2.2).

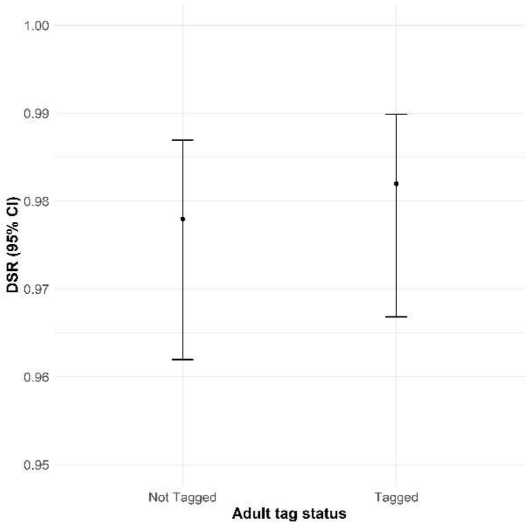


Figure 2.1 - Relationship between daily survival rate (DSR) and radio tag deployment status of parental adult nightjar at Brechfa Forest, Carmarthenshire, Wales, 2013–2019. Daily survival results are based on 85 nests pooled across 2013–2019. The points represent the estimated mean DSR values, and the bars represent the 95% confidence intervals.

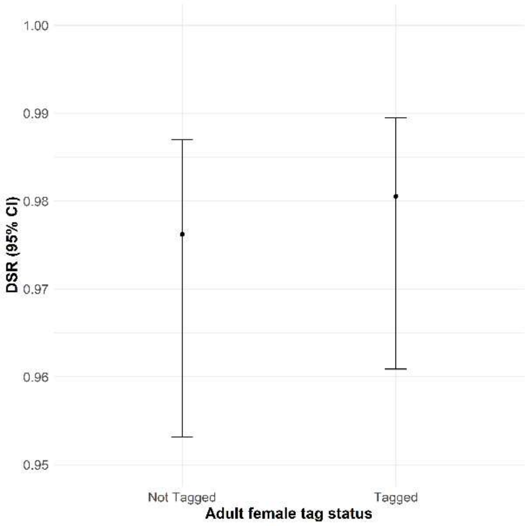


Figure 2.2 - Relationship between daily survival rate (DSR) and radio tag deployment status of parental female adult nightjar at Brechfa Forest, Carmarthenshire, Wales, 2013–2019. Daily survival results are based on 85 nests pooled across 2013–2019. The points represent the estimated mean DSR values, and the bars represent the 95% confidence intervals.

2.4.4 Nest age and Julian day

The top model of daily survival rate included significant effects of Julian day and nest age (initiation date; Table 2.3). Nest survival rate of nightjar decreased as the season progressed (model-averaged parameter ± SE; β Julian day = -0.07 ± 0.023) but increased with the age of the nest (β nest initiation date = +0.072 ± 0.028). Over the nesting season, model averaged DSR ranged from 0.988 (± 0.012) on day 1 of the nesting season (28th May), to 0.986 (± 0.013) on day 81 (17th August).

2.4.5 Weather effects

Initial data exploration of weather data for the active period of each nest (laying date to last known presence) identified a weak positive correlation between relative humidity (surrogate for cloud cover) and minimum temperature (tau = 0.177), with a similar positive correlation noted between relative humidity (surrogate for cloud cover) and minimum temperature (tau = 0.219). As such, weather effects should be interpreted in this context.

The top models together provide good evidence that temperature has an important effect on nest success, as temperature was consistently selected in top models. Alternative models without this variable did not receive strong statistical support and were at least 2.7 AICc units from the top model.

Average temperatures during active nest periods over the study years ranged from 12.8 to 19.5 °C, and model predictions showed a positive relationship with temperature (β m_temp = +2.501 ±1.083; Table 2.5). As confidence intervals did not include zero, this is considered a statistically significant effect. The top models also consistently incorporated an interactive effect between temperature and Julian day on DSR, and this interaction term appeared in all top models.

Model estimates show a negative parameter for the temperature x Julian day interaction term (β m_temp: Time = -0.035 ±0.019; Table 2.5). As confidence intervals include zero this is however not considered to be a statistically significant interaction. Despite this, the important effects of temperature on DSR must be viewed in the context of its relationship with time, as its inclusion in top models suggests that the magnitude of the positive effect temperature is potentially conditioned on Julian day. This interaction term describes how the effect of temperature varies through time, and indicates that the positive effect of temperature on DSR depends on the Julian day and decreases through the breeding season. This may be due to threshold effects of temperature, as temperature exhibits a non-linear relationship with time through the season, or could be due to further interactions with the stage of nest development – i.e. nests are more likely to have chicks later in the season.

Predicted DSR increased from 0.36 (95% CI 0.03 to 0.920) to 0.999 (95% CI 0.994 to 0.999) over the recorded temperature range (12.8 to 19.5 °C), for a nest initiated on the 16th June (median date of nest initiation) assuming average values for the other covariates (Figure 2.3).

Mean daily rainfall during the active nest periods ranged from 0 mm to 10.55 mm, with a mean of 2.10 mm. No significant effect of precipitation on DSR was detected (β m_prcp 0.509 ± 0.382, Table 2.5); confidence intervals for this estimate spanned zero, suggesting a lack of any statistically significant effect.

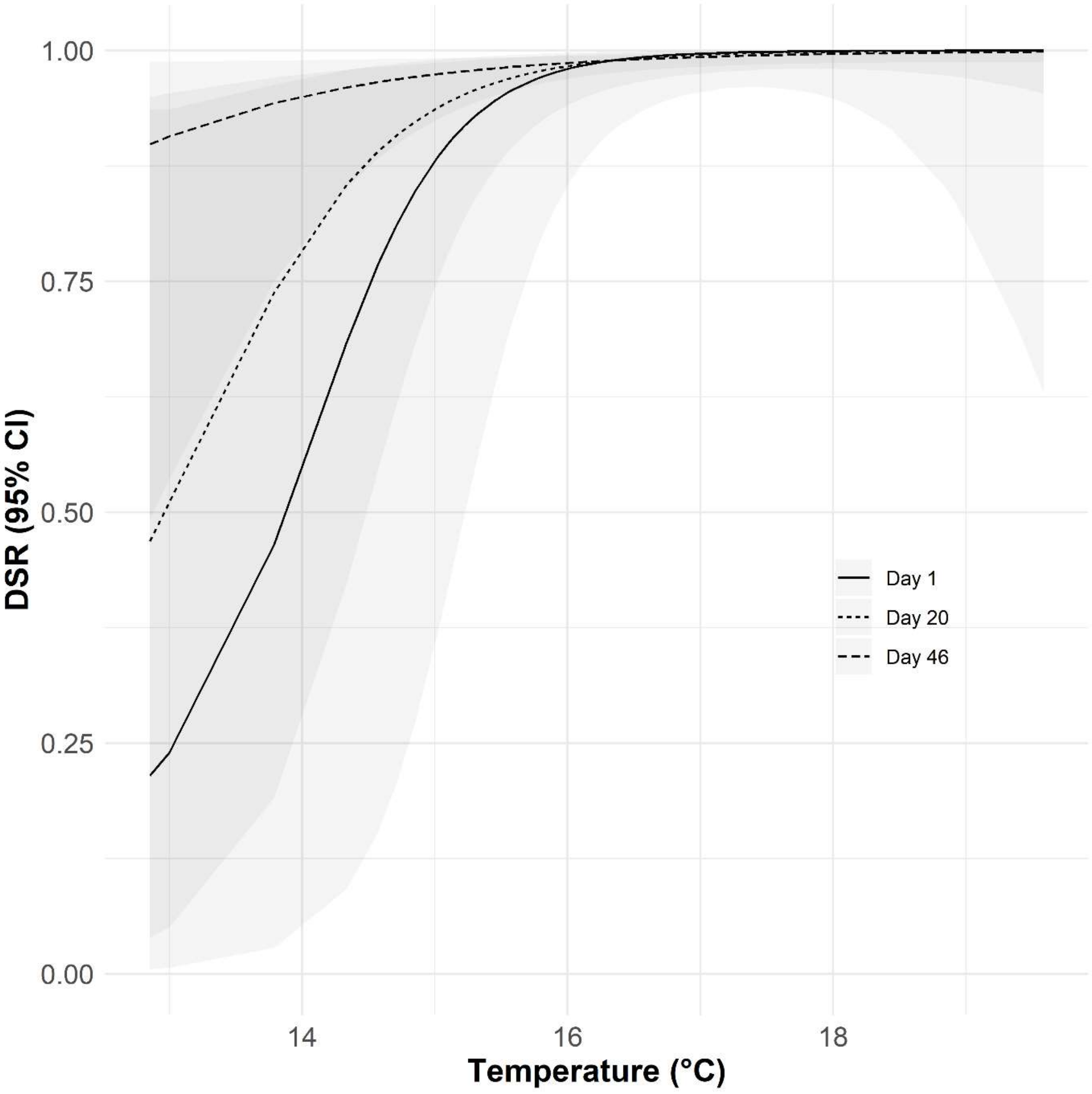


Figure 2.3 -Model averaged predicted daily survival rate in relation to mean temperature during the nightjar nesting period in Brechfa Forest, Carmarthenshire, Wales, 2013-2019. Estimates (lines) and 95% confidence bands (shaded) are shown for day 1 of the season (28th May), day 20 (16th June – median nest initiation date), and day 46 (12th July – median hatch date), with other covariates fixed at mean values.

2.5 Discussion

Mean temperature and nest age were identified as important factors associated with annual reproductive success of nightjars at the study site (see Table 2.4 and Table 2.5). No evidence for a negative effect of tagging was identified by the models of nest survival, and this is consistent with the raw data, where mean nest success across the seven years of the study was 61% for nests attended by one or two tagged parents, and 62% for nests attended by untagged parents. This provides good evidence that the continued use of tail mounted radio tag's to facilitate nest finding is unlikely to impact nest survival. There was also no evidence of survivorship bias, with the majority of tagged individuals (>96%) relocated following tagging, giving additional confidence to this conclusion.

Models identified no evidence that any of the other candidate variables affected nesting success, with no statistically significant effect noted for Julian day, precipitation, brood or year of construction. Previous studies of nightjar nest success have focused on the effects of recreational disturbance (e.g. Langston et al. 2007; Lowe et al. 2014) and in general have identified a negative effect of such disturbance, but have not investigated relationships with tagging, time or weather. Langston et al. (2007) estimated overall nesting success to be 39% in the Dorset heathlands, whereas Lowe et al. (2014) estimated success at 53% in Nottinghamshire plantation forestry sites. Overall nest success estimates of 61-62% from the upland forestry habitats of the Brechfa Forest study site thus compare favourably with reported nest success rates from other studies.

A significant effect of nest age on daily survival rate was identified, with DSR increasing with nest age within individual breeding attempts. Similar variation in chick/ nest survival with age has been observed in other species (e.g. Grant et al. 2005, McDonald et al. 2016, English et al. 2018, Maziarz et al. 2019, Zhao et al. 2020). The positive pattern noted here could be due to older chicks having greater resilience to poor weather and being more able to overcome the nutritional and thermoregulatory burden of poor weather, as has been suggested for Northern Bobwhite chicks (*Colinus virginianus* – Terhune et al. 2019).

The identified positive association between temperature and nest survival is unsurprising, as during periods of low temperature nests can fail due to chick starvation (pers. Obs.) and similar positive effects of temperature have been made in North American nightjar species - whip-poor-will (*Antrostomus vociferous* - English et al. 2018). In general, young, downy chicks are likely to be less able to thermally regulate effectively (Du Rant et al. 2001, Newberry et al. 2018), and thus may be particularly vulnerable to adverse weather and predation. Young chicks will repeatedly call when chilled; this advertisement is likely to increase predation risk as has been observed in other bird species (e.g. Deardon 1999, Briskie et al. 1999, Ibanez-Alamo et al. 2012, Husby 2019, Gonchorova et al. 2019), and may form part of the mechanism by which low temperature leads to nest failure. In addition, moth activity is generally positively correlated with temperature (Holyoak et al. 1997), so a direct negative effect of cold weather on nest success through reduced food availability, would be expected though direct impacts on provisioning at the chick stage, or indirectly through reduced incubation intensity at the egg stage. Similar effects of temperature on chick survival have also been noted in a North American nightjar species (the Whip-Poor-Will - *Antrostomus vociferus*, English et al. 2018) with higher chick survival recorded on warmer nights.

It is surprising, however, that rainfall did not show a negative effect on nest survival, as nest failure due to hypothermia/starvation has previously been recorded following protracted heavy rain (pers. obs), and moth activity is generally negatively correlated with rainfall (Holyoak et al. 1997). One explanation may be the presence of a positive correlation between the minimum daily temperature (likely at night) and rainfall (tau = 0.177), as during cloudy conditions night-time temperatures are usually higher than under clear skies. This may be particularly relevant for the dawn foraging period for nightjars, when at 300m elevation (as at the study site), the temperature is often below 10°C following a night of clear skies during the main breeding season. Hence it may be that extreme rainfall events have a negative effect by causing direct chick mortality, as has been shown in White Stork (*Ciconia ciconia* - Tobolka et al. 2015) and Northern Wheatear (*Oenanthe oenanthe* - Oberg et al. 2015), but food availability is perhaps increased both when evenings are warm following sunny weather, and during cloudy, drizzly conditions, when both dusk and dawn foraging periods are relatively mild. This increase in food availability may lead to improved nest survival, as has been noted in other species (White Ibis *Eudocimus albus* - Herring et al. 2011, and Eurasian reed warbler *Acrocephalus scirpaceus* - Vafidis et al. 2016). However, more work is needed in this area, including collecting insect abundance data, to try to unpick the relationships between weather, insect abundance and nest survival (Shewring et al. in prep.).

Wind farm construction had no observable effect on the daily nest survival rate, and the year of construction variable was not selected in any of the top models. It is, however, worth noting that any effects of construction disturbance are likely to be influenced by the proximity of individual nests to construction activity. Such detailed data were not available to inform the current study, but would certainly be recommended in future studies focused on the effects of construction disturbance. In addition, there were deliberate attempts to limit construction effects on nightjar at the Brechfa windfarm (e.g. by using disturbance exclusion buffers around located nests) and as such, this conclusion is only relevant to construction where such mitigation procedures are implemented. In light of this, it is advised that this aspect of the analysis be treated with the appropriate caution when interpreting the sensitivity of nightjar to construction disturbance.

It should however be noted that nest survival is a single metric for impact identification of tagging, and other effects of tag deployment on nightjar cannot be discounted based on the current study. It is certainly possible that tagging has affected foraging success and ranging behaviour, as has been noted in other species (e.g. Taylor et al 2001, Phillips et al. 2003), but any such effects have not fed through to detectable effects on nest survival. As such, further study of tag effects in nightjar, especially where tagging is proposed for longer durations or where heavier tags are proposed, is recommended.

In conclusion, the current study confirms the importance of weather effects on nightjar nest survival, particularly the positive effect of temperature. It also confirms the lack of observable tagging effects on nest survival when using tail mounted radio tags, and indicates that their continued use in nest finding studies is unlikely to have a negative impact on nest survival. Integrating these two conclusions leads us to recommend that future tagging studies adequately consider potentially confounding weather effects.

3.0 Moth biomass and diversity in coniferous plantation woodlands

Emperor moth Saturnia pavonia and Brown silver-line Petrophora chlorosata at Pen y Cymoedd forest block, South Wales

3.1 Abstract

Moths are a vital ecosystem component and key food source for many species, but have shown widespread and often severe declines across large parts of the Northern hemisphere over the past ~100 years. Multiple factors have been implicated in these declines, although the most important large-scale factors in the temperate zone are considered to be land use change and climate change. The majority of forest cover in the U.K. and elsewhere in Europe is dominated by intensively managed plantation woodlands, and studies have shown reduced broadleaved woodland cover can negatively affect moth diversity and biomass. However, few studies have examined how open habitats within the plantation forest matrix, are utilised by moth species. Open habitats in the context of this these specifically refers to non-forest habitats within the forest matrix this includes both those habitats that form part of the forest cycle (i.e. recently felled areas and young crops) as well as areas of managed/ maintained open habitat (i.e. failed crops and rides, glades etc). Here, I aimed to determine: (1) how moth biomass in open habitats within plantation forests (i.e. recently felled areas, failed crops and permanently open habitats (e.g. rides, glades etc)) varies seasonally and in response to management; and (2) how species diversity and Welsh conservation priority ("Section 7") species respond to management at multiple spatial scales. I sampled moth communities in open habitats within five coniferous plantation forests across Wales, using light traps deployed in areas that ranged from <1 to >20 years post-felling. I found a significant non-linear relationship between space, time and moth biomass, with a significant peak in biomass in the summer months (~ 29th June) suggesting important phenological effects with associated implications for dependent species. Biomass was also strongly affected by time since felling, with older habitats in general supporting a higher moth biomass, although this was dependent on the seasonal variation in habitat 'greenness' and productivity, as measured by NDVI. I also found that the abundances of Welsh priority species responded positively to increased extents of open habitats of ages 1–10 years post felling, but the amount of recent clear felling (0 years post felling) in the surrounding landscape had a negative correlation with both abundance and diversity. I conclude that habitat, seasonality/ productivity and short-term weather variations play a key role in determining moth biomass, species diversity and the presence of Welsh priority moth species within managed coniferous plantation woodland. This means there is an opportunity for forest management practices to adopt measures that can not only enhance moth biomass productivity, in turn supporting insectivorous species such as European nightjar *Caprimulgus europaeus*, but also deliver wider ecosystem services through the provision of habitat matrices that support invertebrate species of conservation concern.

3.2 Introduction

Woodland habitat in temperate regions is dynamic in its extent (Hansen et al. 2013) and in recent years has increased its extent globally (Song et al. 2018). This dynamic nature is largely driven by commercial woodland planting and harvesting. The demand for wood-based products is growing (Carnus et al. 2006) and this increasing demand, combined with the value of woodland creation for carbon capture, is driving a rising interest in -and implementation of- woodland creation, largely of commercial plantation forests dominated by non-native species (Paquette et al. 2010, Forster et al. 2021). In the U.K., wood products are an important part of the economy, contributing £0.59 billion through forestry, and £1.52 billion through primary wood processing in 2016 (Forestry Commission, 2018).

Plantation forests are in general considered poor for biodiversity, as they are primarily monocultures of non-native tree species (Brockerhoff et al. 2008). It has, however, been suggested that plantations can support native biodiversity in productive landscapes (Brockerhoff et al. 2008), through buffering remnant native habitat, enhancing connectivity between landscape patches, and through the provision of a matrix of forested and non-forested habitats (e.g. Caryl et al. 2012, Hipkin 2021).

Stands in plantation woodlands are typically of an even-aged structure, with an even spacing of trees, especially in the first planting-to-harvest rotation. The main objective is often the production of timber or fuel, but some plantations are established to reduce erosion, to capture carbon, to shelter livestock or to provide other environmental, economic, or social benefits. Thinning, and clear-cut harvesting, often occurs with short rotations (typically <30 years between planting and harvesting), resulting in a dynamic woodland environment with active successional processes, often creating a mosaic of differently aged stands within a relatively small geographical area.

This mosaic of forested and non-forested habitats can support important populations of some taxa including invertebrate, lichen, fungi, bryophyte, bird and bat species (Humphrey et al. 2003, Quine & Humphrey 2010; Conway et al. 2007, Kirkpatrick et al. 2017a). A striking example is European Nightjar *Caprimulgus europaeus* (Glutz von Blotzheim and Bauer 1994, Sierro et al. 2001, Winiger et al. 2018, Evens et al. 2020), for which coniferous plantations in Wales have become key habitats, hosting densities equivalent to its traditional lowland dry heath habitat, such as those found in the Dorset Heaths and Thames Basin Heaths Special Protection Area (Conway et al. 2007, Langston et al. 2007). The reason for this change in habitat preference is likely to be multi-faceted, and research to date has identified no clear biological drivers for this trend (See Conway et al. 2007). However, given the known importance of the proximity to foraging habitat for this species (Evens et al. 2020) food availability may be a key factor. It is possible that the relatively low intensity land use of upland plantation coniferous forestry (e.g. low levels of pesticide input - see Willoughby et al. 2004) and their remote nature (lack of artificial light pollution – known to negatively impact moths (Conrad et al, 2006, Van Langevelde et al. 2017)) may provide higher productivity foraging habitat with greater moth biomass than observed in lowland intensive agricultural habitats.

In recent years, alarming declines in insect abundance and diversity have been identified in many studies from around the world (Thomas et al. 2004, Conrad et al. 2006, Hallman et al. 2017, Lister & Garcia 2018, Von Klink et al. 2020), with suggested causative factors including agricultural intensification, habitat loss, pesticides, decreased resource diversity, extreme weather events, warming climate and artificial light at night (Potts et al. 2010, Ewald et al. 2015, Wilson et al. 2018, Sánchez-Bayo & Wyckhuys 2019, Boyes et al. 2021). Such declines in insect abundance are likely to have cascading effects along food chains, and affect a wide variety of insectivorous species, especially those dietary specialists (such as nightjars) which have little capacity to diversify their diet (Bowler et al. 2019).

The primary focus of studies examining such effects has been on diurnal invertebrates (e.g. beetles, butterflies) but more recent studies have identified declines amongst primarily nocturnal groups such as moths, linked to factors such as light pollution and agricultural intensification/ land use change (MacGregor et al. 2019; 2021). Few studies have examined plantation forestry insect assemblages and the influence of management practices on moth communities and abundance within plantations. Previous studies (Thorn et al. 2015, Sharps et al. 2015, Carr et al. 2020) have shown that older and un-thinned stands of planted coniferous trees in general support a higher diversity and abundance of moths, whilst increasing clearfell extents have a negative effect on moth abundance and diversity (Kirkpatrick et al. 2017b). High tree species diversity and an increased proportion of native tree species is reported to result in a higher moth abundance and species richness (Fuentes-Montemayor et al. 2012) and primary productivity has also been implicated in observed richness patterns for some moth species (Bärtschi et al. 2019). Primary productivity, as measured by satellite imagery proxies (NDVI) has also been shown to be a key predictor of species biomass in other groups (Fernández-Tizón et al. 2020).

There is, however, scant information on how moth assemblages develop through time in the open habitats of the upland forestry habitat matrix, such as clearfell stands and re-stocked plantation stands, and the potential biodiversity value of these habitats to moth species. Such habitats can form a significant proportion of the total forest area, for example in the forest inventory data for Wales (Forestry Commission 2017), areas of pre-canopy closure or open area covered 764km^2, or 25% of the total woodland area. Natural disturbances are important habitat drivers in natural forest ecosystems (Angelstam 1998; Kuuluvainen 2009) as they create “pioneer” habitats and support distinct faunal and floral communities (Angelstam 1998). It is likely that felling in commercial forests can mimic this process and the resultant habitats to some extent, and thus support distinct communities of invertebrates that would be associated with such habitats.

In this chapter, I investigate how moth diversity and abundance in non-forest habitats within the forest matrix vary as a result of time since management, coupled with the seasonal productivity of open habitats. Moth data were collected in several commercial forests across Wales growing non-native conifers, sampling across an age gradient of open habitats within the forest matrix, from recent clearfell, through young restock (pre-canopy closure) to permanently open habitats e.g. remnant pre-afforestation habitats. I also explore the value of such habitats to moth species of conservation concern, focusing on those moth species listed under Section 7 of the Environment Act (Wales) 2016. This is a list of species in Wales that are considered '*to be of key significance to sustain and improve biodiversity*' (see https://www.biodiversitywales.org.uk/Environment-Wales-Act), for which conservation action is a legal requirement of the Act. I also aim to identify practical forest management strategies that can help support moth species of conservation concern as well as wider species reliant on moths as a food source.

3.3 Methods

3.3.1 STUDY SITES

Moth trapping was completed, using portable light traps, at five study sites across Wales in the summers of 2017–2019. Study sites were located at the forestry plantation sites of Bryn (Lat. 51.593546, Lon. -3.7059232), Afan (Lat. 51.628561, Lon. -3.6998060), Pen y Cymoedd (Lat. 51.695158, Lon. -3.5838970), Brechfa (Lat. 51.971539, Lon. -4.2053404) and Clocaenog (Lat. 53.069281, Lon. -3.4728997), which ranged from 814 to 4,900 ha (Table 3.1; Figure 3.1). These sites are all part of the Welsh Government Woodland Estate and are managed by Natural Resources Wales following standard practice as set out in the U.K. Forestry Standard. In general, this means following felling, where restocking is planned, planting will occur within 2-3 years and crops generally reach canopy closure around 15 years post-planting. This cycle in Wales has however been impacted in recent years through the impacts of *Phytophthora ramorum* (*Phytophthora ramorum* Strategy for Wales, 2019) and around 11,000 ha has been subject to control (Punalekar et al. 2021) – often felling, leaving many areas open for longer than would be usual in standard forest cycle management.

Prior to the period of extensive afforestation following World War Two (1946-1980), the five sites would have largely consisted of upland moorland. Anthropogenic deforestation during the Holocene in these areas created extensive areas of open moorland, predominantly used for sheep grazing (Rackham 2020). Remnant areas of such habitat remain within the forests where initial afforestation or harvest was deemed too difficult (i.e. very wet bog habitat) or where crops failed due to poor ground conditions. These are present as permanently open habitats within the forest maintained through either their soil conditions or grazing pressure (Brown Hare *Lepus europaeus*, Sheep *Ovis aries* and Fallow deer *Dama dama*). Areas of younger open habitats are also present, having been felled either to facilitate wind farm development (focused through policy into these areas– see Welsh Assembly Government 2005), or to meet U.K. Forestry Standard guidance (Forestry Commission, 2017) on habitat buffers.

In combination, these factors mean that these forests now support large stands of plantation coniferous woodland of various ages, dominated by Sitka spruce *Picea sitchensis*, the most commonly planted coniferous tree species in the U.K. (Houston Durrant et al. 2016), interspersed with significant areas of non-forest habitats. Those open habitats, created post afforestation, vary greatly in their time since felling (e.g. habitat buffer felling often initiated >20 twenty years ago) and as such vary greatly in their structure and ecology. The oldest created open habitats have however generally reached a stable habitat state, maintained through light grazing pressure from a combination of Brown Hare, Sheep and Fallow deer*,* soil conditions or in some cases fire. These habitats in many ways are analogous to pre-afforestation habitats. Younger open habitats do however vary significantly in their habitat cover dependent on grazing pressure and soil properties with many supporting a level of Sitka regeneration along side developing semi-natural habitats.

3.3.2 MOTH TRAP LOCATIONS

Weekly moth samples from multiple light traps (up to four running concurrently) were collected from each of the five different study sites between July and August 2017, and between May and September in the subsequent years (2018 and 2019). Moth trap locations were determined prior to deployment using a random sampling study design within areas of non-forest habitat within the forest matrix. This habitat was mapped in QGIS (Version 3.12, QGIS 2019) from aerial imagery and a random point generator was used to generate the total number of required deployment locations for each field season (~50 sample points in 2017 and ~100 in 2018 and 2019). The generator was constrained to ensure no points were located within 30m of each other, as the attraction radii of Heath light traps do not exceed 30 m (Beck & Linsenmair 2006, Truxa & Fiedler 2012). Traps were selectively positioned to ensure that individual trap locations were not visible from each other. Traps were deployed on a rotational basis with each study site visited approximately once per week during the survey season. A minimum of two traps were deployed at each site during each survey visit, and a total of 266 trapping nights were completed across the five study sites over the three years, with the following breakdown of samples per site: Afan = 47, Bryn = 53,Brechfa = 52, Clocaenog = 56, PyC = 58. Traps were deployed prior to dusk and were collected at or around dawn the following day.

Moth traps consisted of a mixture of 6 watt plastic bucket portable Heath moth traps (available from https://www.watdon.co.uk/acatalog/E7588C-Combo-6W-Rigid-portable-trap.html) and metal portable traps (available from https://www.watdon.co.uk/acatalog/E7585C-Combo-6W-Heath-trap.html), both using a Phillips Actinic BL TL 6W/10 1FM/10X25CC bulb. Traps were powered using 12-volt rechargeable batteries.

Moths were identified to species where possible in the field using the Waring and Townsend (2017) and Parsons and Sterling (2012) field guides to U.K. moths. Where identification to species could not be completed (~4.3% of individuals) then the lowest identifiable taxonomic unit was noted (i.e. genus, family, order etc). Following identification, all moths were released into surrounding vegetation. Species data were shared with local moth recorders and added to the National Moth Monitoring Scheme (Fox et al. 2010).

3.3.3 MOTH BIOMASS

Moth biomass was calculated using the dry weights of museum specimens from The National Museum of Wales, Cardiff, Wales, U.K. (n=103 species), supplemented by weights collected by Kinsella et al. (2020) and available in the supplementary information (n = 135 species). Where museum specimens were utilised, approximately 10 specimens of each species were weighed using a digital scale (smart weight Digital Jewellery Scale GEM20) with a reported accuracy of 0.001g.

The data were then summarised by trap to give moth biomass per trap per night using the count of each species present in a trap and the biomass for the relevant species. The moth weights used in this analysis are provided in Appendix D.

3.3.4 METEOROLOGICAL DATA

In order to account for the influence of weather on moth capture, data from weather stations within 40km of each moth trap location (mean 30.4 km, range = 16.5 to 39.8 km) (Figure 3.1) were obtained using the GSODR package (Sparks, Hengl, and Nelson 2017) using R software version 3.6.1 (R Core Team 2019), implemented via R Studio (RStudio team 2018). The GSODR package provides automated downloading, parsing and cleaning of Global Surface Summary of the Day (GSOD; United

States National Oceanic and Atmospheric Administration National Climatic Data Center) weather data. This data set provided daily rainfall (mm), and mean temperature, minimum temperature and dewpoint (all °C). Where more than one station was present within 40 km of a trapping point then the data were averaged. Data manipulation and visualisation was undertaken using the R packages tidyverse (Wickham et al. 2019), lubridate (Groelmund & Wickham 2011) and ggplot2 (Wickham, 2016). Daily temperature, precipitation, minimum temperature, wind speed and dewpoint were collated for the date of moth trap retrieval for each individual moth trap deployment. Retrieval date was selected, as minimum temperature is usually the lowest in the hours prior to awn (Gough et al. 2020) and this was to be more representative of the temperature conditions overnight than those associated with the date of deployment i.e. the dawn prior to the night of deployment. It should be noted that a number of the nearest weather stations were located at lower elevations than trapping sites (~300-400m lower) and as such, absolute temperature measurements may not be specifically correct for the sample sites. However, the relative magnitudes of temperature changes are likely to be correct and it is this variation I will be accounting for within the models.

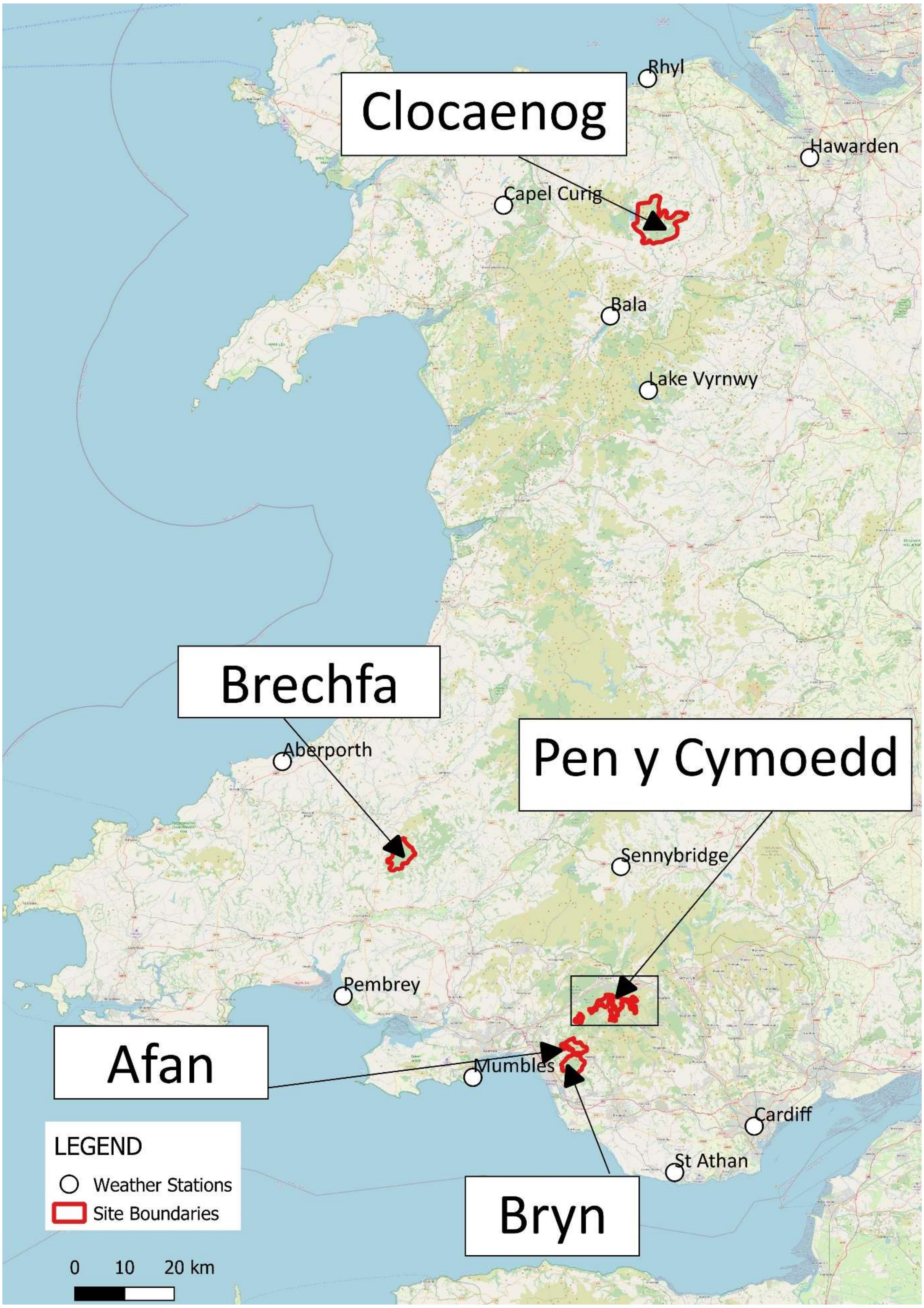


Figure 3.1 Study sites and weather station locations.

3.3.5 BIOPHYSICAL DATA

Two habitat variables were recorded at each moth trap location: (i) time since felling (= clearfell age) and (ii) seasonality of the vegetation. Time since felling was determined to the nearest year for all open areas within the study sites, *via* review of historic aerial imagery (Google Earth, 2020) and satellite imagery, using Google Earth Engine (Gorelick et al. 2017) to identify the year of harvest. These data were mapped in QGIS (QGIS 3.12, 2019) to produce a shapefile of clearfell age polygons for each site. The extent of open habitat within each site varied considerably between sites (Table 3.1).

Table 3.1 Total Commercial Forestry Area and Open Habitat within the Forest

SITE	**TOTAL AREA (HA)**	**OPEN HABITAT AREA (HA)**	**% OPEN**
AFAN	814	400	49%
BRYN	1241	514	41%
BRECHFA	1825	260	14%
CLOCAENOG	5035	721	14%
PEN Y CYMOEDD	4900	1450	30%

The relative seasonal productivity of vegetation was determined through the subtraction of the winter (Dec-Feb) mean Normalized Difference Vegetation Index (NDVI) from the summer (May- July) mean NDVI, for each moth trap point in the relevant year of trapping. NDVI is often used to quantify photosynthetically active vegetation and consists of a simple band ratio between the near infrared (which vegetation strongly reflects) and red light (which vegetation absorbs) received at the sensor. Similar band ratio approaches have been used previously to identify coniferous trees (See Yang et al. 2019) and NDVI is a frequently used proxy for primary productivity (Fernández-Tizón et al. 2020). As such, calculated values for seasonality or seasonal productivity are considered likely to represent the primary productivity of non-coniferous plant species at my sample sites. Index values were calculated using the 30m x 30m pixel size Landsat 7 Collection Tier 1 32-Day NDVI Composite dataset (https://developers.google.com/earth-engine/datasets/catalog/LANDSAT_LE07_C01_T1_32DAY_NDVI) available in Google Earth Engine (Gorelick et al. 2017).

The aspect of each sampling location was also measured (in degrees) from the OS Terrain 50 digital terrain model (https://www.ordnancesurvey.co.uk/business-government/products/terrain-50) using the Raster package (Hijmans 2020). This was then susquently encoded to the nearest cardinal direction of the compass (i.e. North, South, East and West) as a categorical variable.

3.3.6 DATA ANALYSIS

All analysis and spatial data manipulation detailed below was undertaken using Rstudio (RStudio Team 2020) and the R statistical software, version 3.6.2 (R Development Core Team 2019).

3.3.6.1 Biomass

To estimate the sampling completeness of the moth assemblage, I estimated the rate at which the richness of moth species accumulated as sampling effort increased, firstly pooling the data for all sites and then repeating this for each site in turn. To do this, I computed the species accumulation curve and the Hill number estimator of asymptotic species richness using the iNEXT package (Hsieh et al*.* 2016).

Initial data exploration identified a probable non-linear seasonal variation in biomass and therefore the effects of clearfell age, vegetation seasonality and weather variation on moth biomass were investigated using Generalised Additive Models (GAMs), fitted using the R package 'mgcv' (Wood 2011). GAMs of moth biomass (response variable) were fitted with a smoothed interaction of space (longitude and latitude) and date (Julian day), to account for spatial and temporal autocorrelation structures within the data, as well as to capture any seasonal pattern. To ensure that the fitted values were continuous and positive, a gamma distribution, with a log link function was used. Basis dimension choice for smoothers was k=5 for spatial smoothers, and k=12 for temporal smoothers. The aim with the temporal smoother was to capture the potentially substantial non-linear variation in moth biomass across the study period; hence a relatively high k-value was chosen. The aim with the spatial smoother was to capture the broad scale spatial variation at the national scale and not capture the spatial variation in habitat data to be explored with specific clearfell age and seasonality parameters; hence a lower k-value was used.

Minimum temperature, precipitation and wind speed – which have been shown to influence moth activity (e.g. Holyoak et al. 1997) – were included as linear terms in all models. Year was also included as a categorical term in models where it was not already included as an interaction term in spatial or spatio-temporal smooths. Vegetation seasonality was included as a linear term.

Alongside these linear terms, I included two smoothed interaction terms; one between wind speed and the cardinal direction of slope aspect, and another between clearfell age and the smoothed effect of the seasonality of the vegetation index (NDVI). These terms were included as it was hypothesised that the effect of wind speed on moth abundance may be conditional on aspect, given the prevailing westerly nature of winds at my study sites. It was also considered likely that the effect of clearfell age and habitat development post-felling would depend on the level of Sitka Spruce regeneration/ planting post felling, and thus on the seasonality of the vegetative greenness in sample locations. It was also hypothesised that the higher the seasonal productivity of the habitat the more productive this would be for moth species with phytophagous larval stages.

Two spatio-temporal and two spatial models were developed, based on a conceptual model of the system and the methods of data collection, these are summarised in Table 3.2. These included the same explanatory parameters as detailed above, but differed in their treatment of the spatio-temporal smoothing. This approach was adopted to help identify potential biological drivers of the observed spatial and temporal variation in moth biomass, and to account for potential spatial differences in phenology due to the spread of study sites across Wales. Model structures utilising additional spatial and temporal smoothers alongside spatio-temporal smoothers were also explored during model development, but subsequently discounted due to lack of biological interpretability and possible overfitting (summarised in Appendix C).

Collinearity between variables was assessed using pairwise plots and variance inflation factors (VIFs), with a threshold of VIF < 3 / correlation of < 0.7 considered to represent sufficiently low levels of collinearity (Zuur et al. 2010). Post model fitting, the degree of concurvity (i.e. the non-linear form of collinearity, Buja et al. 1989), was assessed using the concurvity function within the mgcv package (Wood 2011). A significant positive correlation between year, treated here as a numeric rather than categorical variable, and vegetation seasonality was identified, however VIF/concurvity values for seasonality did not identify any issue with the inclusion of this term in models 1, 2 or 3. As such, vegetation seasonality was retained in these models but removed from model 4 as a linear term due to high a VIF value (> 3). A summary of model structure is provided in Table 3.2 below.

Table 3.2 Model Structure Comparison. Each model is represented by a row. Linear and non spatio-temporal smoothed parameters - linear and non-spatial or temporal smoothed parameters used in the model. Smoothed space and time pararmeters – spatial and temporal parameters used and the relevant approach to smoothing. Reason for spatio-temporal smooth approach – narrative justification for approach.

MODEL	LINEAR AND NON SPATIO-TEMPORAL SMOOTHED PARAMETERS	SMOOTHED SPACE AND TIME PARAMETERS	REASON FOR SPATIO-TEMPORAL SMOOTH APPROACH
MODEL 1	• Minimum Temperature • Wind Speed, • Precipitation • Aspect • Vegetation Seasonality • Year (as a categorical variable) • Smoothed interaction of clearfell age and seasonality, • Smoothed interaction of wind speed and aspect.	• Smooth of longitude x latitude; • Smooth of julian day;	Simplest model for comparison with other models.
MODEL 2	• Minimum Temperature • Wind Speed, • Precipitation • Aspect • Vegetation Seasonality • Smoothed interaction of clearfell age and seasonality, • Smoothed interaction of wind speed and aspect.	• Smooth of longitude x latitude; • Smooth of julian day by year.	Test between year variations in moth biomass phenology.
MODEL 3	• Minimum Temperature • Wind Speed, • Precipitation • Aspect	• Tensor smooth of longitude x latitude x Julian day;	Test for interactive effects between space and time on the phenology of moth abundance.

	• Vegetation Seasonality • Year (as a categorical variable) • Smoothed interaction of clearfell age and seasonality, • Smoothed interaction of wind speed and aspect.		
MODEL 4	• Minimum Temperature, • Wind Speed, • Precipitation • Aspect. • Smoothed interaction of clearfell age and seasonality, • Smoothed interaction of wind speed and aspect.	• Tensor smooth of longitude x latitude x Julian day by year	Test for interactive effects between space and time on the phenology of moth abundance in different years.

Continuous variables were scaled (i.e. standardised and centred around a mean of zero and a standard deviation of 1), to allow direct comparisons of coefficient estimates and ease numerical estimation.

Semi-automatic variable selection was completed using the “double penalty” approach as described by Marra & Wood (2011). The double penalty uses a penalty that restricts the ‘wiggliness’ of any basis functions in the range space but also introduces a penalty for basis functions in the null space, where such functions are flat and/ or linear in nature and as such unaffected by the standard penalization approach. This means that both null and range space functions are treated in the same way in terms of shrinkage; under heavy penalization they are penalized to zero, and thereby ‘selected out’ of the model.

Whether biomass per trap differed among the five sites was tested using a GLM with a gamma error-family, to statistically control for other variables that may influence capture rates or biomass: temperature, wind speed, clearfell age, vegetation seasonality and the slope aspect of each trap location. A separate gamma GLM was used for this analysis, as the site as a categorical variable was not included in the biomass models – See Table 3.2 and Appendix E.

Models were compared using (i) Akaike’s Information Criterion (AIC) adjusted for small sample sizes (AICc; Burnham & Anderson, 2002), (ii) the root mean square prediction error, using leave-one-out cross-validation (Webb et al., 2011), and (iii) the percentage deviance explained by the model (analogous to variance in a linear regression; Murase et al., 2009).

3.3.6.2 “Section 7” Priority Species

In addition to the overall moth biomass per trap analysis outlined above, I also modelled the influence of local and landscape habitat characteristics on the occurrence of Section 7 priority species. Twenty-two Section 7 species were encountered during trapping (See Appendix D), although only 12 of these species were encountered on more than one occasion. The abundance of each of these twelve Section 7 priority species per trap (the count of each S7 species) was modelled using a single Poisson mixed effects model with a log link function, and species identity (ID) and site as random terms.

Local habitat covariates utilised within the analysis consisted of the extent of open habitat (pre-canopy closure restock, non-forest habitats or clearfell) around each trap location, sub-divided into the following broad age classes post felling: <1 year, 1-5 years, 6-10 years, 11-15 years, 16-20 years, and >20 years. For the purposes of this analysis, permanently open habitats (i.e. habitats that were never planted) were classified as >20 years post felling as both these and >20 year old clearfell habitats were considered likely to have reached a stable habitat state at this point i.e. open habitats maintained through grazing pressure or soil properties.

Three generalised linear mixed effect models were fitted, representing habitat variables recorded within three different radii around the trapping location – 250m, 500m, and 1km – as it is known that habitat effects can be scale-dependent (Botham et al. 2015, Stoll et al. 2016). These scales were chosen as they were considered to be most appropriate to help identify local habitat management effects, and similar scales have been used previously to investigate the effects of agri-environment scheme management on moths (see Fuentes-Montemayor et al. 2011). Each model thus included the following fixed effects: extent of open/clearfell habitat in each age class, minimum temperature and wind speed. Models were checked for over- and under- dispersion using the relevant overdispersion statistic for each model.

Continuous variables were scaled to a mean of zero and a standard deviation of one, to allow direct comparisons of coefficient estimates, and model fit was assessed by comparing the change in Akaike Information Criterion (AIC), retaining the best model (change in AIC greater than 2). In the event that model differences were <2 AIC units, then both models were retained and discussed.

3.3.6.3 Species Diversity

The same suite of covariates used in the Section 7 priority species analysis was utilised to investigate the effects of local scale habitat configuration on moth species diversity. The influence of local and landscape habitat variables on moth species richness was also investigated, using Margalef diversity (Margalef, 1958) per trap as the unit of measurement of diversity. I used generalised linear models with a gamma error structure to allow for the zero bounded continuous nature of the diversity data, and included an interaction between latitude and longitude, allowing for north-south, east-west or diagonal linear gradients to be modelled, as a fixed effect in all models. A small constant (0.1) was added to the Margalef diversity values to remove zero values and allow the use of the gamma error distribution. Continuous variables were standardised and centred around a mean of zero and a standard deviation of 1, to allow direct comparisons of estimates and aid computation. Pseudo R^2 (Zhang 2017) was used to assess the amount of variation explained by each model.

3.3.6.4 Model validation

Model assumptions for each of the analysis approaches described above were verified by plotting residuals versus fitted values, residuals versus each covariate in the model, and residuals versus each covariate excluded from the model. I also assessed the residuals for temporal and spatial dependency (Zuur et al. 2007).

3.4 Results

A total of 7,345 moths of 238 species (Appendix D) were collected over 266 trap nights. On average each trap contained a mean (± SE) of 30 (± 2.1) individual moths, comprising 10 (± 0.4) species. My sampling detected 88.5% of the estimated asymptotic moth species richness (269 species (± 11.7); Figure 3.2). Estimated sampling completeness was high across all individual sites: Afan 82.5%, Bryn 80%, Brechfa 63%, Clocaenog 82%, Pen y Cymoedd 78%. Of the 238 species recorded, 22 species were Welsh priority moth species listed on Section 7 of the Environment (Wales) Act 2016.

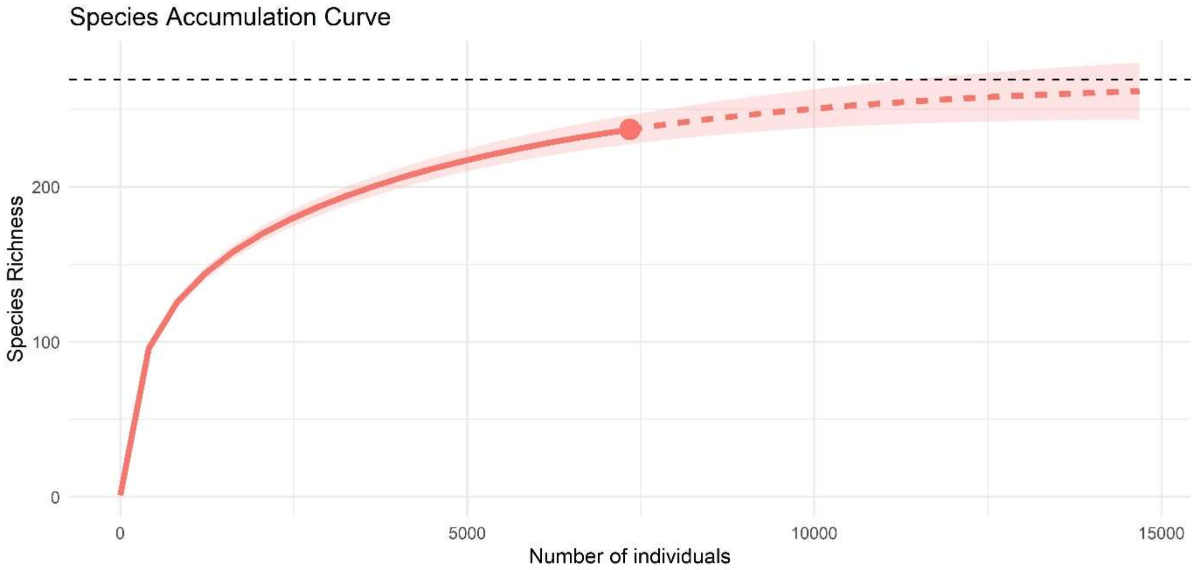


Figure 3.2 Sample-size-based rarefaction (solid red line segment) and extrapolation (dotted red line segments) sampling curves for species richness across all study sites (iNEXT (Hsieh et al., 2016) setting q=0) with 95% confidence intervals (shaded areas), using individual-based abundance data. The dotted black line shows the estimated asymptotic estimated species richness.

Moth community composition varied, but a few highly abundant species dominated the catches. For example, two species – the true lovers knot *Lycophotia porphyria* (1,162 individuals recorded) and large yellow underwing *Noctua pronuba* (307 individuals recorded) – accounted for ~ 20% of all individual moths collected.

3.4.1 Biomass

Moth biomass over the 266 trapping nights varied between 0 mg and 13,655 mg per trap per night, with a mean biomass of 1,653 mg (SE ± 124). Biomass per trap differed significantly between sites, with Clocaenog on average having around 50% higher average biomass per trap than both Pen y Cymoedd and Bryn (Figure 3.3).

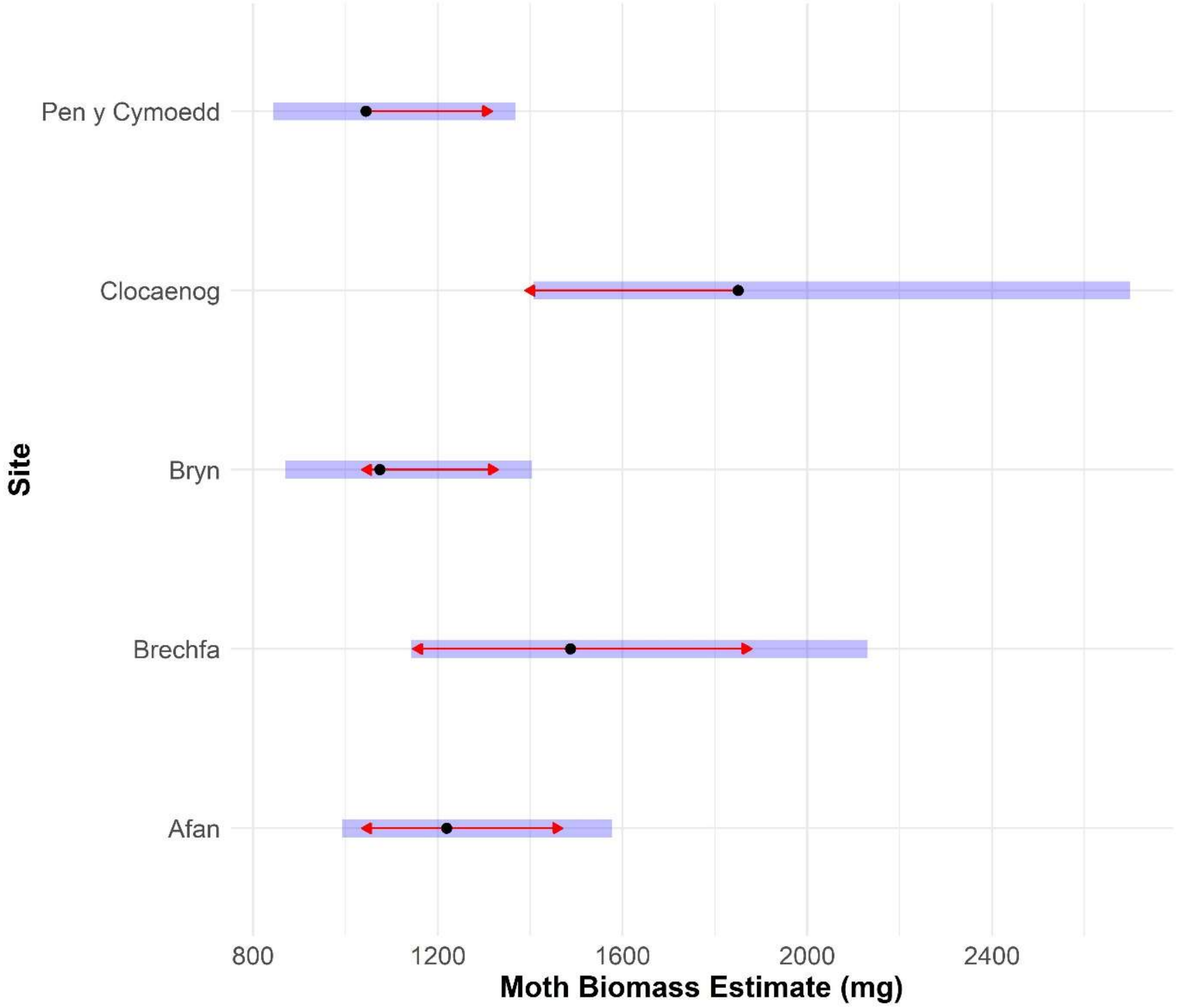


Figure 3.3 Comparison of average predicted biomass per trap by site. Blue bars are confidence intervals for the estimated means, and the red arrows are for the comparisons among them. Comparison arrows are based on the statistical properties of the differences between estimated marginal means solved by weighted regression and not confidence intervals alone. If an arrow from one mean overlaps an arrow from another group, the difference is not significant at p = 0.05.

3.4.2 Model evaluation/ selection

Table 3.3 Model selection metrics -the best-performing models according to each criterion are highlighted in bold. DF – Degrees of Freedom, AICc – Akaike information criterion with a correction for small sample sizes, Delta AICc – the relative difference in AICc between the best performing model and other candidate models, RMSE – Root mean square error. See Table 3.2 for details of model structure and parameters.

MODEL	MODEL DF	RESIDUAL DF	DEVIANCE EXPLAINED	AICc	DELTA AICc	RMSE
MODEL 1	17.53	248.47	44.7%	4344.31	24.31	1694.04
MODEL 2	23.44	242.56	50.8%	4329.03	9.03	1686.58
MODEL 3	34.25	231.75	57.6%	**4320.00**	**0**	**1650.26**
MODEL 4	34.82	231.18	**58.6%**	4320.37	0.37	1657.82

Model 3 was identified as the most parsimonious and best performing model based on AICc and RMSE, whilst Model 4 explained only 1% more of the deviance (Table 3.3). As such, model 3 was considered to be the best performing model and I thus discuss the results of model 3 in detail below. The model selection process indicates there is strong evidence for interactive effects of space and time due to the poor support of Models 1 and 2. The modelled results for each linear parameter and smoothed terms are presented in Appendix E.

There was a significant non-linear spatio-temporal pattern in moth biomass in all models where a spatio-temporal smoother was included (see Appendix C). Model 3 also identified a significant non-linear seasonal pattern in moth biomass (Figure 3.4). Linear parameters showed a positive relationship between biomass and minimum temperature, and a negative relationship with wind speed (Appendix E, Appendix F). The overall positive effect of minimum temperature was approximately twice that of the negative effect of wind speed (See Appendix E). Models were also consistent in identifying minimum temperature as having a greater effect than wind speed (See Appendix E). However, the negative overall effect of increased wind speed on moth biomass was modulated by the aspect of the light trapping location. This smoothed interaction effect was significant and indicated that the overall negative effect was reversed for northerly aspect areas, where increased wind speed had a positive effect on moth biomass (Appendix E, Appendix F, Appendix G). No significant linear effect on biomass of precipitation, year, aspect, clearfell age or seasonality of vegetation was identified.

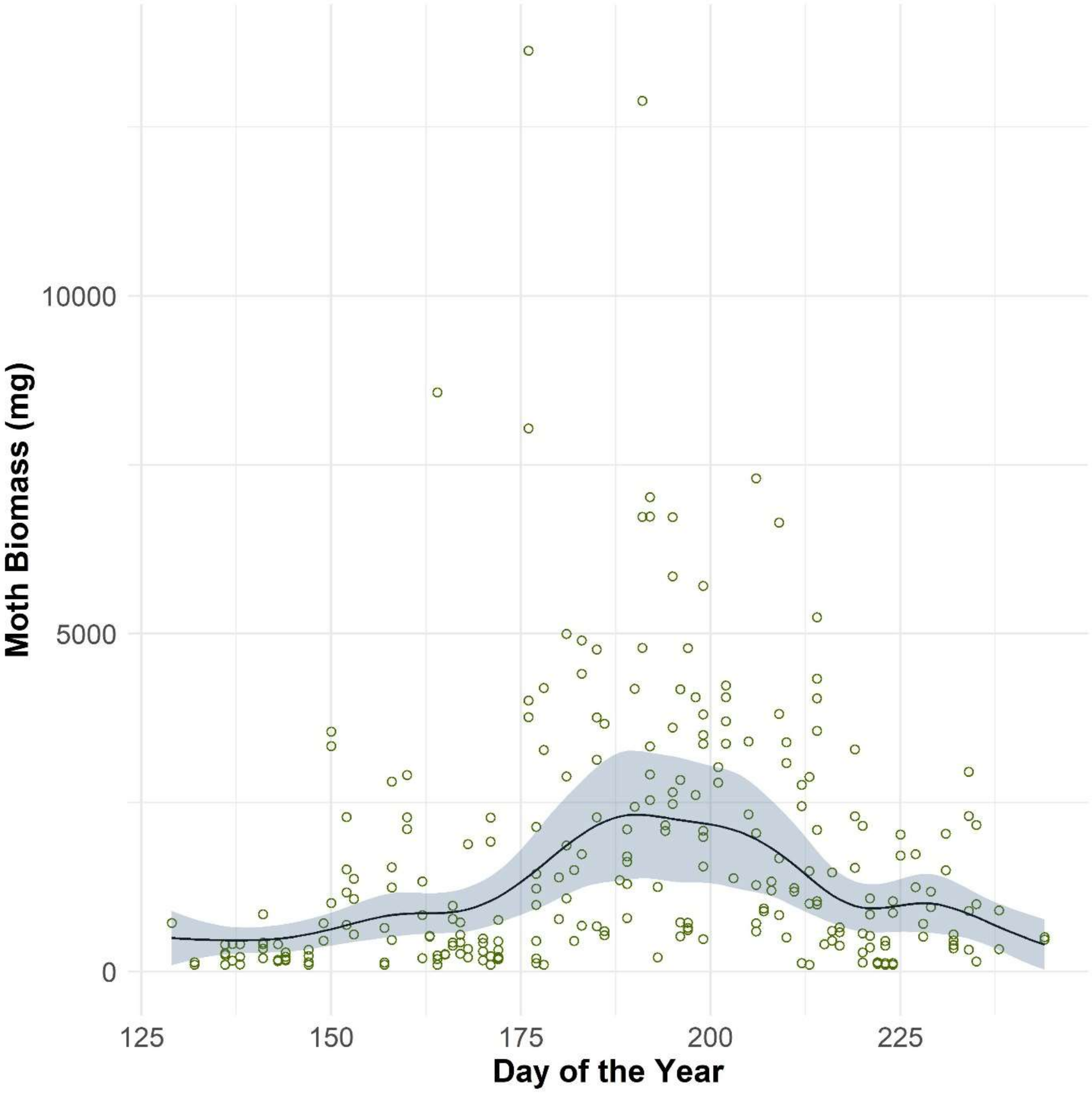


Figure 3.4 Seasonal variation in moth biomass–The fitted line shows Model 3 predicted moth biomass and 95% CI limits for each day between Julian day 125 (5th of May) and 240 (28th of August) at a sample location with a Southerly aspect in 2018 with all other variables held at their mean value.

A significant non-linear relationship between moth biomass and clearfell age dependent on the seasonality of vegetation was identified (Appendix E, Figure 3.5). This indicated that moth biomass in general increased as clearfell age increased, with a noted peak at 10 years post felling and in more permanently open habitats (~20 year post felling/ unplanted). However, this effect was dependent on the seasonal productivity of the vegetation present, with a larger positive effect of clearfell age on biomass noted where vegetation 'greeness' or productivity was higher.

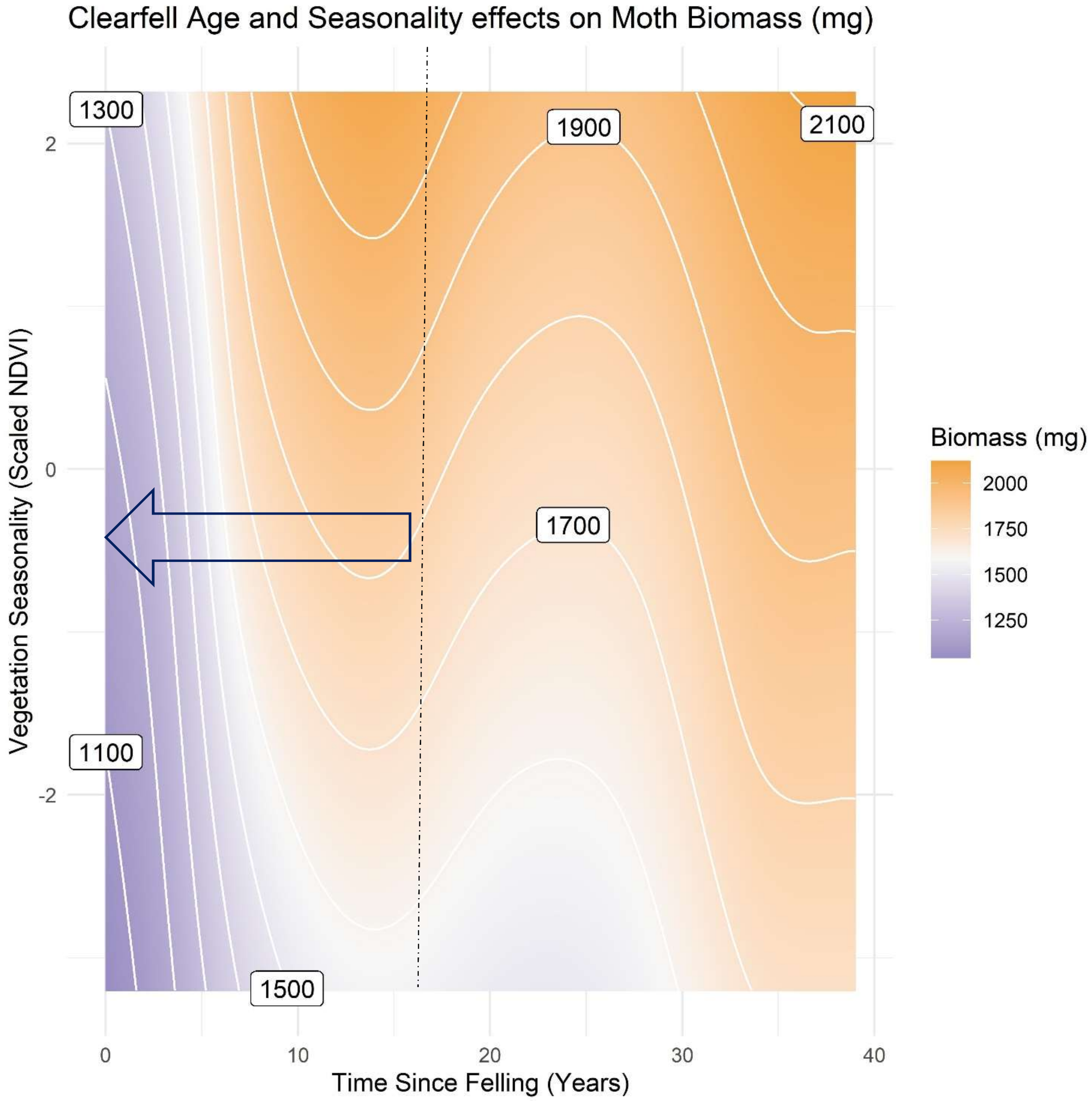


Figure 3.5 Model 3 Contour plot of predicted moth biomass dependent on vegetation seasonality and the time since felling (Orange = higher moth biomass, Blue = lower moth biomass) across all habitats contained within the open areas of plantation forestry including those that form part of the productive forest cycle (e.g. clearfell and pre-canopy closure woodland) those that form more longer term open areas (e.g. failed crops, forest rides/ glades).. Broadly the productive forest stage is represented in the areas shown to the left of the dashed vertical line as illustrated by the arrow.

3.4.3 Section 7 Priority Species occurrence and Species Diversity

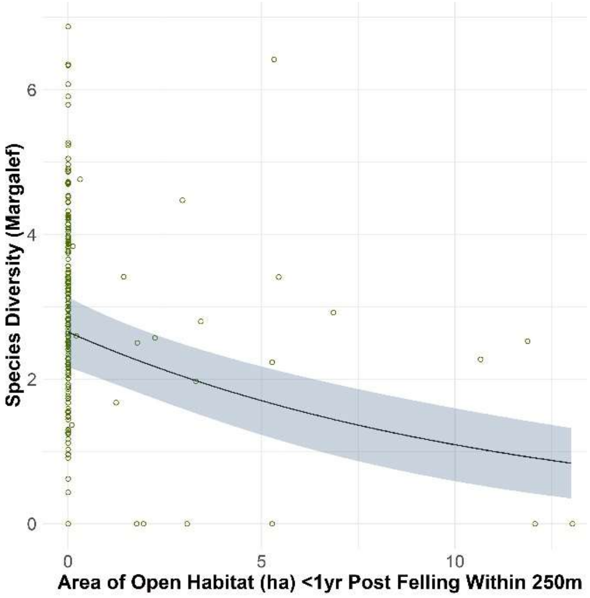
Twelve Section 7 moth species were recorded over the 266 trapping nights completed. These species were a mix of generalist and upland/ heathland specialists (See Appendix D), and included the following – autumnal rustic *Eugnorisma glareosa*, buff ermine *Spilosoma luteum*, dusky brocade *Apamea remissa*, shaded broad bar *Scotopteryx chenopodiata*, heath rustic *Xestia agathina*, knot grass *Acronicta rumicis*, garden tiger *Arctia caja*, neglected rustic *Xestia castanea*, blood-vein *Timandra comae*, broom moth *Ceramica pisi*, small phoenix *Ecliptopera silaceata* and white ermine *Spilosoma lubricipeda*. The most frequently encountered Section 7 species was white ermine, which was recorded on 31 separate occasions.

Hierarchical mixed modelling results identified a significant impact of habitat on the number of Section 7 moth priority species recorded, although the nature of these habitat differences varied by species and landscape scale (Appendix G). In general, however, Section 7 moth abundance increased as the area of older open habitat areas increased, up to a threshold of 10 years post-felling (Appendix G – Mixed models). Suprisingly, where the area of new open habitat (clearfell < 1 year old) increased around sample points, no significant effect was noted on Section 7 moth abundance, with the exception of a positive effect at the 250m scale. A similar consistent pattern was also noted (increased Section 7 moth abundance) across all spatial scales where moth abundance increased with the area of open habitat age classes <10 years old, with the greatest effect noted at the 500m spatial scale for habitats 6-10yr post felling.

3.4.4 Species Diversity Results

Species diversity, as represented by the Margalef diversity indices, varied significantly over the 266 trapping nights completed, with a maximum diversity value of 6.9 and mean of 2.8 (± 0.08). The highest diversity index was recorded at the Afan forestry site in August 2018, within an area of open habitat clearfelled in 2012 (6 years old at the time of sampling).

The results of modelling species diversity were consistent across habitat scales, with newly cleared areas (open areas < 1 year old) having a consistently negative effect on surrounding species diversity at the 250 m, 500 m and 1 km scale (Appendix G, Figures 3.6 - 3.8). Species diversity also increased at all scales as minimum temperature and time of year increased, but species diversity decreased with increased wind speed. Spatial location also had a significant effect on species diversity, with lower diversity at higher latitudes and longitudes.



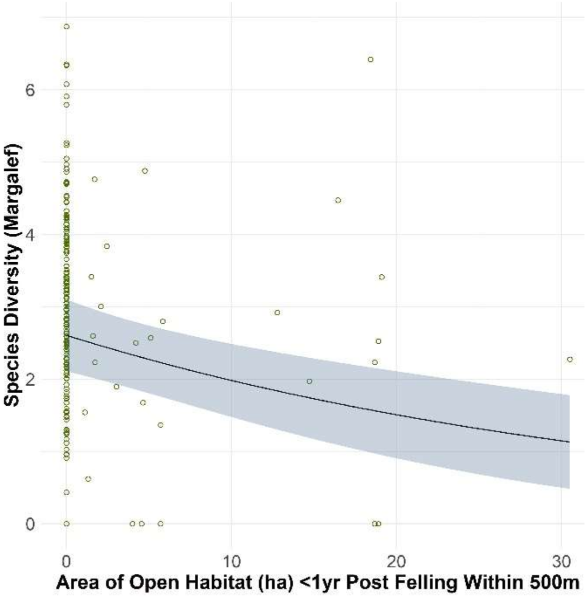


Figure 3.6 Predicted July trap Species Diversity as the extent of open habitat <1yr post felling within 250m radius of the trap location increases. All other variables held at their mean value for the month of July.

Figure 3.7 Predicted July trap Species Diversity as the extent of open habitat <1yr post felling within 500m radius of the trap location increases. All other variables held at their mean value for the month of July.

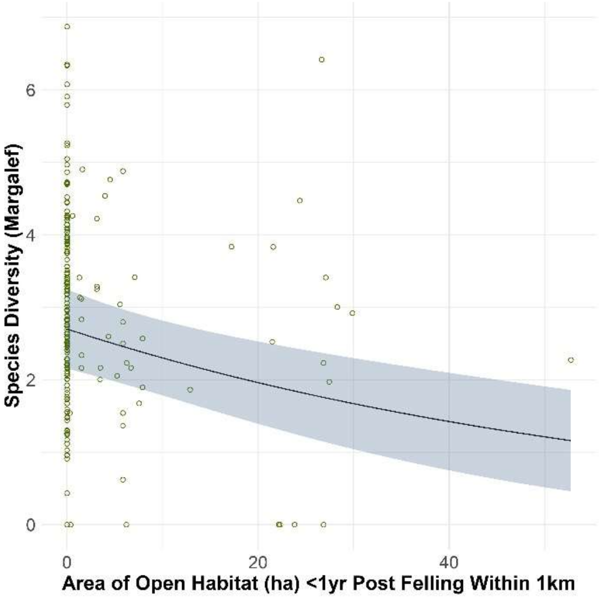


Figure 3.8 Predicted trap Species Diversity as the extent of open habitat <1yr post felling within 1km of the trap location increases. All other variables held at their mean value.

3.5 Discussion

Lepidoptera is one of the most abundant and diverse insect orders, but is currently undergoing widespread declines across Europe (Fox et al*.* 2013). Previous studies at a national scale have demonstrated that managed coniferous plantation woodland / forestry plantations can support diverse invertebrate communities, and that the structure of the plantation is important for some groups (Humphrey et al*.* 2003). From my study, it seems that forestry management actions and resource planning may have the potential to enhance moth habitat suitability through modifying felling and open area habitat management to support moth communities. This is expected to in turn have cascading beneficial effects for insectivorous species, such as European nightjar, bats and various diurnal bird species that utilise these habitats.

The modelling results identified a significant non-linear effect of time since tree felling on moth biomass, conditioned on the seasonal productivity of the vegetation. This identified that moth biomass increased with time since felling, but this increase levelled off at around 10-12 years post felling. The relationship was stronger where the vegetation was more seasonally variable in its ‘greenness’. This higher level of seasonal ‘greenness’ is likely to reflect an overall increase in primary productivity (e.g. more photosyntehitically active plants) through a combination of a higher abundance of ruderal annual species and deciduous scrub/ woodland species (e.g. Willow *Salix sp.*) and also a lower cover of coniferous tree species. This result is consistent with the results for conservation priority species, showing that on average the abundance of Section 7 listed moth species had a similar relationship with clearfell age (i.e. increasing abundance up to a threshold around 10 years post felling), although this was not accompanied by a similar increase in diversity (See Appendix G). This suggests that the forest open habitat moth community develops through time, and that open habitats are in general capable of supporting a greater abundance of moths - and thus biomass- up to this point. This is likely due to the dominance of a few species adapted to these early sucessional habitats, rather than a corresponding increase in the number of moth and plant species supported. For example, clear felling is generally followed by rapid colonisation by ruderal plant species (e.g. fireweed - *Chamaenerion angustifolium*) that provide an abundant food source for generalist macro-moths such as small phoenix *Ecliptopera silaceata* and elephant hawk moth *Deilephila porcellus*.

This result also suggests that forest structure at the regional/ national scale may be of key importance for supporting moth species of conservation concern (i.e. Section 7 species) and also have cascading effects for moth-eating aerial insectivores such as the European nightjar (Evens et al.

2020), especially where such insectivore populations are highly reliant on coniferous plantation woodland - as is the case in Wales (Conway et al. 2007).

In general, my results demonstrate that plantations can support diverse moth communities, including several Section 7 priority species, and this diversity may be partially dependent on the habitat dynamics affected by the forest management regime. The change in biodiversity or conservation value of the plantation forest moth assemblage, relative to that of the pre-afforestation community, is dependent on the habitats present prior to afforestation. Many habitats have a higher moth species diversity than plantation woodland (Kirkpatrick et al. 2017, da Silva et al. 2019) and woodland creation planning should be cognisant of this. For example, afforestation of a species rich grassland with an associated diverse moth assemblage is unlikely to increase the diversity of the moth assemblage and provide a biodiversity benefit, but this may not be the case for afforestation of improved grassland, where the original moth diversity was lower.

Woodland creation is a future land use priority in Wales (Welsh Government, 2018), for both timber production and climate mitigation, and therefore, identifying ways to increase woodland cover whilst supporting biodiversity will be essential to tackle both the ecological and climate emergencies. In terms of forest management, this study supports a strategy of creating a wide range of open habitats at various ages post-felling, and maintaining a substantial area of open habitat between 5-10 years post felling in each actively managed commercial woodland, as a valuable conservation intervention.

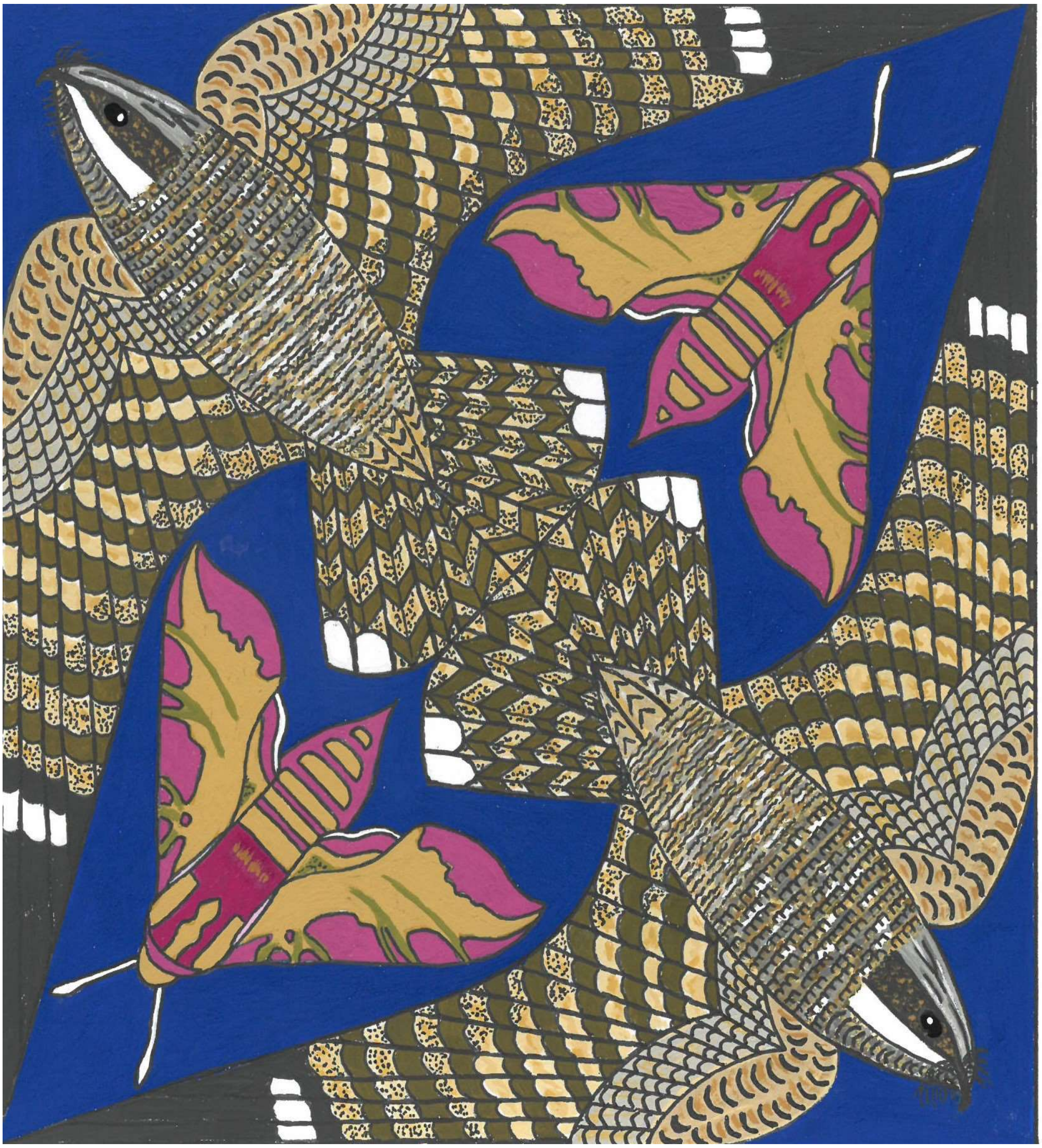
The biomass models also identified significant non-linear spatial and temporal variations in moth biomass. In general, biomass peaked around Julian day 180 (29th June), although the timing of this peak varied between locations. Seasonal variation in moth biomass is to be expected, given the seasonal nature of vegetation growth in the temperate zone and the herbivorous nature of the larvae of many moth species. However, this pattern will also have significant implications for insectivorous species that rely on moths as a food source in such habitats, in particular the European nightjar, which is known to nest in the area and favour plantation forests for breeding in Wales (Conway et al. 2007). Nightjars rely heavily on moths (Evens et al. 2020) and have a short time-window available for completion of their breeding cycle due to their migratory behaviour. The availability of an abundant food source in close proximity to nesting habitat is likely to increase nesting success through reduced energy expenditure, increased food supply to chicks and greater capacity for nest defence (Martin 1992, Vafidis et al. 2018). These positive effects do however depend on the timing of peak moth biomass/ abundance coinciding with peaks in energy demand for nightjar during the nesting season. Specifically, the significant seasonal variation in biomass may have important implications for many insectivorous species as there is also the potential for trophic mismatch, where a lack of synchrony between the phenology of consumers and that of their resources can impact food supply, as has been documented in other systems (Durant et al. 2007, Burgess et al. 2018). This could occur, for example, should increases in spring/summer temperatures lead to moth biomass peaking prior to nightjar chick-hatching. Modelling results also confirm that weather conditions in these habitats are likely to be key drivers of foraging success and habitat selection for moth-reliant insectivore species (e.g. nightjar and a variety of bat species such as the Barbastelle bat *Barbastella barbastellus*), which in turn may have knock on effects on reproductive success.

I have shown that weather, and in particular minimum temperature and wind speed, are key factors influencing variation in available moth biomass within open habitats in coniferous plantation woodland, around the overall seasonal pattern. Moth biomass increased with minimum temperature, and decreased with wind speed, as has been noted from previous studies (Holyoak et al. 1997, Jonason et al. 2014). See Appendix F- Figures F1 and F2.

In conclusion, habitat, seasonality and shorter-term weather variations all play a key role in determining both moth biomass availability, species diversity and the presence of Section 7 priority moth species within managed coniferous plantation woodland. The effects of habitat on these metrics means that there is an opportunity for forest management practices to adopt measures that can not only enhance moth biomass productivity to support nocturnal insectivorous species such as European nightjar, but also to deliver wider ecosystem services through the provision of habitats that support invertebrate species of conservation concern.

The key practical measures suggested by my work to support both moth species of conservation concern, and species that rely on moths as a food source, revolve around the landscape-scale and regional-scale management of forest habitats. Specifically, forest managers should aim to retain consistent extents of open habitats of various age classes post felling, with key age brackets within the forest cycle being 2-10 years post harvest, and avoid forest wide transitions to continuous cover forestry systems. These recommendations could be incorporated into the standard forest cycle management approach and would support Section 7 moth species of conservation concern, as well as insectivorous species such as nightjar.

4.0 Movement and foraging habitat selection of European Nightjar during the breeding season



4.1 Abstract

The use of high-resolution GPS tag data to investigate habitat selection is widespread and such approaches in European nightjar have been used to determine habitats of value to the species in the U.K. (Mitchell et al. 2020) and Europe (Evens et al. 2017, 2018). It is however likely that foraging habitat selection, may in part, be driven by food availability, and in an aerial insectivore system such as the European nightjar, food availability will vary spatially and temporally driven by factors other than simply habitat type. How animals respond to this spatial and temporal variation in food availability is unclear especially in European nightjar, where studies have simply concentrated on identifying habitats of importance. In this study, I use high-resolution GPS tag data from 25 individuals tracked for between 4 and 16 nights per individual in a single year, to explore how food availability, as represented by predicted moth biomass, affects resource selection by breeding nightjar. Predicted moth biomass and its variation are shown to be important drivers of foraging behaviour in male and female nightjar and home range size in male nightjar. This suggests that open habitats within the forest matrix provide a key foraging resource for this species. The probability of nightjar foraging increased in response to both moth biomass and the predictability of this biomass, and males who settle in areas of higher average moth biomass have a smaller home range size. This confirms the importance of spatio-temporal variation in determining movement patterns and has important implications for conservation management where moth biomass varies spatiotemporally dependent on the forest management cycle.

4.2 Introduction

Understanding how animals use a landscape in response to its biophysical attributes is a critical question in pure and applied ecology, and has been studied across many taxa using resource selection functions (RSF) (Manly et al. 2002, Strickland et al. 2006). Resource selection, defined as the strength of use of a habitat or resource compared with its availability (Johnson, 1980; Thomas, Manly, & McDonald, 1992), may reflect the quality of the resource and may remain consistent or vary through time and space in response to spatio-temporal changes in the resource or other factors e.g. breeding status, age, sex, competition, or weather (Godvik et al. 2009, Duquette et al. 2017; Zurrell et al. 2018, Ruffler et al. 2018, Sinnott et al. 2021).

Optimal foraging theory (OFT) is a widely used conceptual framework for explaining and predicting the foraging behaviours of animals but is rarely linked to patterns of space use (although see Foo et al. 2016, Peaz et al. 2018). OFT attempts to predict how an animal makes foraging decisions to maximize the net rate of energy intake by minimizing energy costs while maximizing energy gain (Pyke et al. 1977, Stephens and Krebs, 1986). As such, OFT is well placed to provide testable predictions of how animals make foraging decisions in heterogeneous environments where food availability fluctuates spatially and temporally.

Studies testing OFT predictions often focus on fine-scale foraging behaviour in experimental settings with direct observational data collected over relatively short periods (e.g. Brunner et al 1992). However, foraging behaviour of free ranging, highly mobile animals is likely to follow a hierarchy of spatial and temporal scales, representing decision-making at a variety of biologically relevant scales. This decision-making is also likely to be influenced by the previous experiences of the individual and their preference for the predictability of resource availability, as has been noted in a number of seabird species – see Phillips et al. (2017). As such, where resources vary spatially and temporally it is likely that movement patterns will vary in response to these patterns (e.g. van Overveld et al. 2018) to maximize the net rate of energy intake, this will be further affected by a combination of the temporal variability and an individual's past experience i.e. factors that influence predictability. For example, an individual's decisions are constrained by information availability (e.g. Egert-Berg et al 2018). However, as feedback on the accuracy of a foraging decisions is received promptly due to rapid changes in foraging rates and satiation, it is likely that birds can adjust behaviour promptly (e.g. leave a patch with low resource levels).

Responses to spatiotemporal variation in resource availability may be observable as second order (home range selection by an individual) or third order (areas within the home range used for foraging) selection (Johnson, 1980). For instance, home ranges may be located in areas of higher productivity or may change size in response to food availability (Mcloughlin & Ferguson, 2000; Rolando, 2002; Schoepf et al. 2015) and this may be evidence of a second order habitat selection. Movement behaviour within the home range, or third order habitat selection, may also respond to spatial and temporal variation in resource availability with greater use of areas rich in food resources. Such behaviour may be detectable using an RSF analysis framework, where not obscured by other ecological trade-offs such as conspecific interaction and competition (Buskirk & Millspaugh, 2006; Tarugara et al. 2021) or avoidance of predators (Walther & Gosler, 2001; Viejou et al, 2018).

The European nightjar (henceforth nightjar) is an obligate aerial insectivore whose diet is largely dominated by moths (Glutz von Blotzheim and Bauer 1994, Sierro et al. 2001, Winiger et al. 2018, Evens et al. 2020, Mitchell et al. 2021). Moth abundance is therefore likely key for determining foraging success and may drive local habitat selection, as well as being implicated in larger-scale changes such as nightjar population declines and failures to recolonise previously occupied regions in both the U.K. (Langston et al. 2007) and mainland Europe (Winiger et al. 2018).

Previous studies exploring foraging behaviour in lowland dry heaths revealed that nightjar activity extends into surrounding meadows and grasslands, oak *Quercus* sp. scrubland and grazed grass heath (Alexander and Cresswell 1990, Sierro et al. 2001, Sharps et al. 2015, Feather 2015, Rayner 2016, Evens et al. 2017). Moreover, nightjars show a degree of plasticity in spatial foraging behaviour (Evens et al. 2017, Sharps et al. 2015) and can travel long distances to reach high quality feeding grounds, despite the energetic costs (Evens et al. 2018). It has been suggested that this behaviour reflects the greater food availability in these habitats (Evens et al. 2017), but the link between habitat selection and spatio-temporal changes in food availability has not previously been tested.

In this study, I use high-resolution GPS tag data to explore how food availability, as represented by predicted moth biomass (using predictions from Chapter 3), affects resource selection by breeding nightjar. I hypothesise that due to the low levels of competition at our study sites (few nocturnal insectivores and low density nightjar populations) and low predation risk, individuals will attempt to forage optimally (i.e. maximise their net energy gain) through foraging more often in high moth biomass productivity areas.

4.3 Methods

I collected information on the spatial habitat use of nightjars and spatial variation in food availability, at five forestry plantation sites across Wales (Figure 4.1). Data collection was undertaken in the summers of 2017, 2018 and 2019. Study sites were located at Bryn (Lat. 51.593546, Lon. -3.7059232), Afan (Lat. 51.628561, Lon. -3.6998060), Pen y Cymoedd (Lat. 51.695158, Lon. -3.5838970), Brechfa (Lat. 51.971539, Lon. -4.2053404) and Clocaenog (Lat. 53.069281, Lon. -3.4728997). These sites are all part of the Welsh Government Woodland Estate and are managed on behalf of the Welsh Government by Natural Resources Wales (See Chapter 2 for further details on each study site).

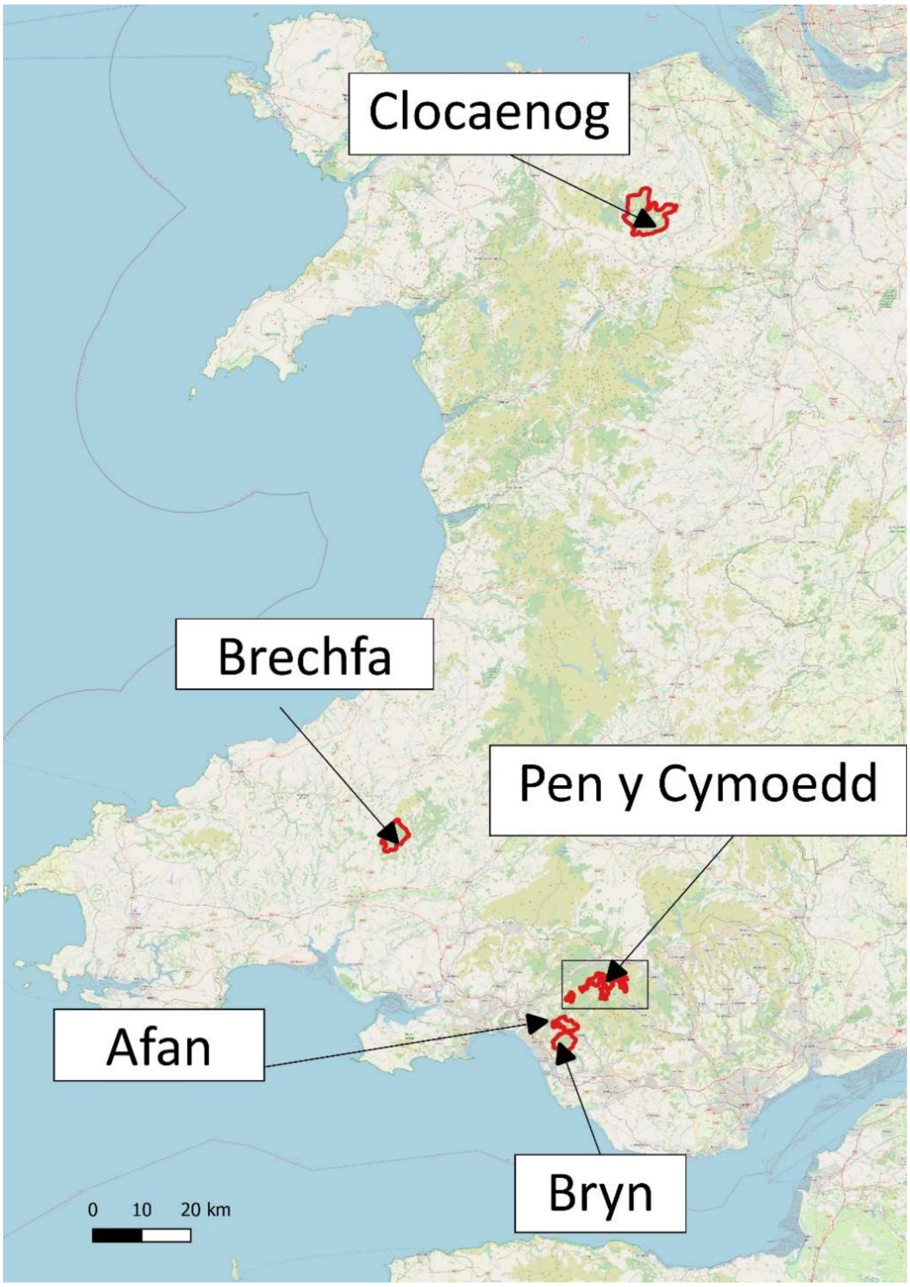


Figure 4.1 Overview map of study sites.

4.3.1 GPS tracking

In order to deploy GPS tags, nightjars were captured using 12 and 18m long, 20-40mm hole mist nets (Ecotone), accompanied by a tape lure playing the song of male nightjars when targeting birds away from known nests. Mist netting, ringing, tagging, and use of a tape lure during the breeding season were all completed under licence from the British Trust for Ornithology (BTO). Birds, once captured, were ringed, measured, and weighed, to ensure they were of sufficient weight to carry a GPS tag (maximum 3% of the bird's body weight).

Thirty five GPS archival tags (Pathtrack Nanofix - https://www.pathtrack.co.uk/products/nanofix-geo-mini.html) were deployed across the five study sites between 2015 and 2019. Paired birds, or those from known nest sites, were targeted for tag deployment to aid in the recapture and retrieval of tags: the final number in each year depended on the number of nests located, and on the presence of paired birds at each site. Over the course of the study we deployed two tags at Afan, four at Brechfa, six at Bryn, sixteen at Clocaenog and seven at Pen y Cymoedd.

Tags were set up to collect GPS fixes every 3 min from 21:00 to 05:00 (BST) and have been shown to be accurate to ±30 m (Mitchell et al. 2020). Tags were targeted for deployment durations of ~7-10 days/nights based on expected battery life. Tags were deployed across the breeding season in each year with a mean duration of 10 (+0.5 s.d.) nights. The within-year tag deployment periods for each bird are shown in Figure 4.2 below.

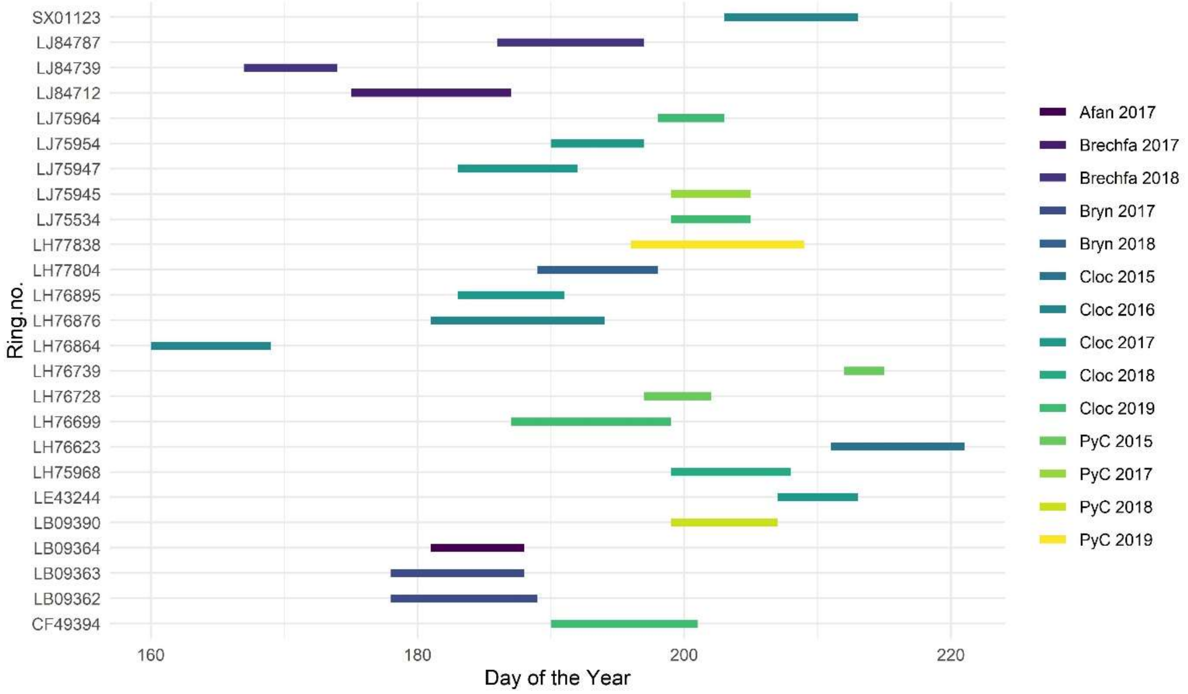


Figure 4.2 Gantt chart of tag deployment periods within the year of deployment (Day of year). Individual birds represented by rows with the duration of deployment illustrated through a solid colour bar covering the duration of active tracking. Colours represent the site and year of deployment as shown in the legend.

4.3.2 Movement analysis

Maximum foraging distances for each bird were calculated from known nest sites and/or regular roost sites using the sf package (Pebesma 2018) in R version 4.0.2 (R Core Team 2021) via the RStudio (RStudio Team, 2020) integrated development environment. Prior to analysis, tracks were visually reviewed to identify and remove erroneous points (i.e. points recorded at incorrect locations due to weak GPS signal) and the data were also filtered to exclude points collected prior to 21:30 (BST) and after 05:30 (BST) – average sunset was 21:30 (BST) and sunrise 05:11 (BST). The main period of European nightjar activity commences at or just after sunset in the majority of birds (Cramp and Simmons 1985, Holyoak 2001), so the GPS data were filtered to exclude these points as they were considered likely to be associated with birds at the nest site or roost site.

Behavioural classification of tracks was completed using expectation–maximization binary clustering -EMbC (Garriga & Bartumeus, 2016). EMbC is an unsupervised, multivariate, state-space modelling framework that can be used for behavioural annotation of movement trajectories. It has the additional benefit of having no underlying assumptions with regards to temporal dependence, meaning it can handle time series data with large gaps or heterogeneous sampling scheduling. EMbC is a simple method of analysing movement data based on its geometry, and the associated step lengths and tortuosity of the path described. Analysis was undertaken using the EMbC package in R

(Garriga & Bartumeus, 2016), using calculated velocities and turning angles to classify behaviour at each fix location into one of the following two classes: Foraging (movements with lower velocity and low or high turn angles) and Commuting (movements with high velocity and low turn angle). No resting state behaviour classification was used as it was considered that this might exclude fly-catching behaviour, a known foraging strategy for nightjar (Cramp & Simmons 1985, Holyoak 2001) and resting periods could be better excluded through temporal filters as described above.

4.3.3 Food availability – predicted moth biomass

Given the high reliance of nightjar on moths as a food source, moth biomass was identified as a likely accurate proxy for prey mass availability as has been used in other systems for aerial insectivores (e.g. Tree Swallow *Tachycineta bicolor* – Twining et al. 2018). In this study, moth biomass represents the mass of flying/ active moths captured at light traps and thus is a proxy for the mass of active/ flying moth species that are phototactic. Moth biomass and standard error predictions for all sites were produced for each of the dates of GPS tracking using the best performing predictive model identified in Chapter 3 (model 3). Models utilised the same parameters as used in Chapter 3 with the only amendment being the removal of the year term in years outside of the range used to train the model (i.e. for years 2015 and 2016 model 3 was modified to remove the year term). Moth biomass predictions and standard errors were produced as geotiff raster files at 50m pixel resolution using model 3 for each night of tracking data. The coefficient of variation in predicted biomass was also calculated for each 50m pixel in every year of tracking data to estimate the predictability of food resources within the tracking period as this may influence foraging decisions (Bastille-Rousseauet et al. 2015). Data manipulation was completed using the sf (Pebesma 2018) and raster (Hijmans 2021) packages in R (R Core Team 2021) implemented in RStudio (RStudio Team, 2020).

Predicted moth biomass (±S.E.) was extracted at the points classified as nightjar foraging for the relevant date and location using the sf package.

4.3.4 Home range analysis

I used the ctmm package (Calabrese et al. 2016, Fleming & Calabrese 2021) in R to calculate variograms, fit movement models, and estimate home ranges for each tracked individual. Autocorrelated kernel density estimation (AKDE) is a method that accounts for the inherent spatial autocorrelation in GPS data with frequent fixes. In order to implement the AKDE method an appropriate autocorrelation structure, or tau value, is required. For the purpose of this analysis, I generated tau using the ctmm package function ctmm.guess. The ctmm.guess function returns an ordered array of autocorrelation timescales (tau) and dependent on the length of this either a bi-variate Gaussian model, Ornstein-Uhlenbeck (OU) model (Brownian motion restricted to a finite home range), Brownian motion (BM) or OUF model (continuous-velocity motion restricted to a finite home range) is fit to the data (See Appendix H). Models were fit via maximum likelihood and ranked based on AICc. From the top model for each bird, I estimated home range conditional on the fitted, selected model for each individual using the akde function. This allowed me to estimate the 95% utilisation distribution, its associated 95% confidence intervals and home range area for each individual.

During initial data exploration, one male individual, (Ring no. - LH76623) was noted as having a seemingly much larger home range than other individuals, with an estimated size of 7,592.01 ha (other birds 119 ha (±SE 28)). Despite capture near an active nest site, it appears from the data that this individual was not associated with a nesting attempt or defending a defined territory during the tracking period, and is considered likely to be a ‘floating’ or ‘prospecting’ individual. As such, it was considered unlikely that the behaviour and resultant home range of this bird would be subject to the same energetic constraints as breeding birds, and on this basis, I excluded this individual from the home range analysis.

Food availability within each home range was estimated by averaging/summing the predicted moth biomass within the 95% utilisation distribution polygon for each of the nights that each bird was tracked. All data manipulation was completed using the sf (Pebesma 2018) and raster (Hijmans 2021) packages in R (R Core Team 2021) using RStudio (RStudio Team, 2020). Linear models were used to investigate how home range size varied with availability of moth biomass and variation in moth biomass. Home range size (ha) was log transformed in all analyses where it was the dependent variable, to reduce heteroscedasticity (following Ofstad et al. 2019 and Mitchell et al. 2020). Initial data exploration and modelling included sex as a term in the models but as this caused issues with model convergence, separate models with the same terms were fitted for each sex. Linear models were fit with log home range size (ha) as the dependent variable and mean moth biomass, moth biomass coefficient of variation and an interaction between these parameters alongside sex and duration of tracking period (in days) as independent fixed effects.

Collinearity between variables was assessed using variance inflation factors (VIFs), with a threshold of VIF < 3 considered to represent sufficiently low levels of collinearity (Zuur et al. 2009; Zuur et al. 2010). Continuous variables were scaled (i.e. standardised and centred around a mean of zero and a standard deviation of 1), to allow direct comparisons of coefficient estimates and ease numerical estimation. Model assumptions were verified by plotting residuals versus fitted values, versus each covariate in the model and other potential covariates of interest. I also assessed the residuals for temporal and spatial dependency (Zuur et al. 2009).

Inferences about the statistical importance of fixed effects have been interpreted with regards to their direction (positive/negative), effect size (magnitude), and uncertainty (95% confidence intervals), but avoided interpreting the “significance” of estimates using arbitrary *p*-value thresholds when possible (Amrhein et al. 2019). *Post hoc* pairwise comparisons and 95% CIs were made using the ‘emmeans’ R library and estimating the marginal means (Lenth, 2020).

4.3.5 Resource selection analysis

Data analysis adopted a use-availability conceptual framework, contrasting those areas used for foraging with the available space (the availability sample: Manly et al. 2002). Predicted moth biomass at the locations where foraging activity was identified are contrasted with moth biomass at locations taken from an area deemed to be available for selection. The availability space was defined as the 95% utilisation distribution for each individual.

The data were analysed using mixed-effects resource selection functions utilising a logistic regression approach with intercepts and slopes that varied by individual and day of the year (Duchesne et al. 2010; Muff et al. 2020), with the day of the year random effect nested within individual as biomass predictions were available at the tracking day temporal scale. Including coefficients that vary by individual enables modelling of functional responses (Mysterud and Ims 1998; Jones et al 2020) and reduces bias in estimated population-level (fixed) effects (Duchesne et al. 2010). Available points were assigned weight (W = 1000) to facilitate approximate convergence to the inhomogeneous Poisson process likelihood, and I fixed the variance term for individual-specific intercepts to a large value ($\sigma^2 = 1000$) to avoid shrinkage toward zero, following Muff et al (2020).

A series of nested models was fitted with moth biomass and moth biomass variation (coefficient of variation for each year) as singular terms, additive terms and as additive terms including an interaction term. Both parameters were included as it was hypothesised that the variation in moth biomass, in addition to its magnitude, and the interaction between the two could influence foraging habitat selection, as has been shown with prey availability in some seabird species (Phillips et al. 2017). Where moth biomass and moth biomass variation were included as an interaction term the nested random structure was also modified to include both of these parameters and random slopes for each at the relevant temporal scale e.g. individual level (biomass variation) and sample night level (moth biomass). This resulted in the fitting of five distinct models with a different fixed parameters and random structure. Models were evaluated compared using Akaike's information criterion adjusted for small sample sizes (Burnham, & Anderson, 2002).

Collinearity between variables was assessed using variance inflation factors (VIFs), with a threshold of VIF < 3 considered to represent sufficiently low levels of collinearity (Zuur et al. 2009). Continuous variables were scaled (i.e. standardised and centred around a mean of zero and a standard deviation of 1), to allow direct comparisons of coefficient estimates and ease numerical estimation.

We made inferences about the statistical importance of fixed effects from their direction (positive/negative), effect size (magnitude), and uncertainty (95% confidence intervals), but avoided interpreting the "significance" of estimates using arbitrary *p*-value thresholds when possible (Amrhein et al. 2019). We rescaled all continuous covariates to range from 0 to 1. We used the R packages glmmTMB v. 0.2.3 to fit models. All analyses were conducted in program R version 4.0.2 (R Core Team 2021).

4.4 Results

4.4.1 GPS tracking

We recaptured 25 of the 35 nightjars carrying GPS-loggers. The 25 tracking devices retrieved provided a total of 22,029 points, with an average of 881 (± 60) points per individual. This equates to 4–16 nights of data per individual, with a mean of 10 (± 0.5) nights. Retrieved tags were deployed in 2015 (3), 2016 (3), 2017 (9), 2018 (5) and 2019 (5). The majority of tags were deployed during July and early August in any given year, with a median deployment date of Julian day 190 (9th/10th July).

We retrieved the following number of tags at each site - 1 at Afan (50% of those deployed), 3 at Brechfa (75%), 3 at Bryn (50%), 13 at Clocaenog (81%) and 5 at Pen y Cymoedd (71%). Tags were retrieved from a mix of males (n=16) and females (n=9), with 8,896 data points collected from female birds and 13,133 points from male birds.

Across all tagged birds associated with a known roost or nest site (n=24), the mean maximum foraging distance was 3266m (± 521), with males tending to forage up to greater distances than females (female mean upper foraging distance = 2621m (± 99); male = 3653m (± 653)). Maps of tracking data are shown for four birds in Figures 4.3-4.6.

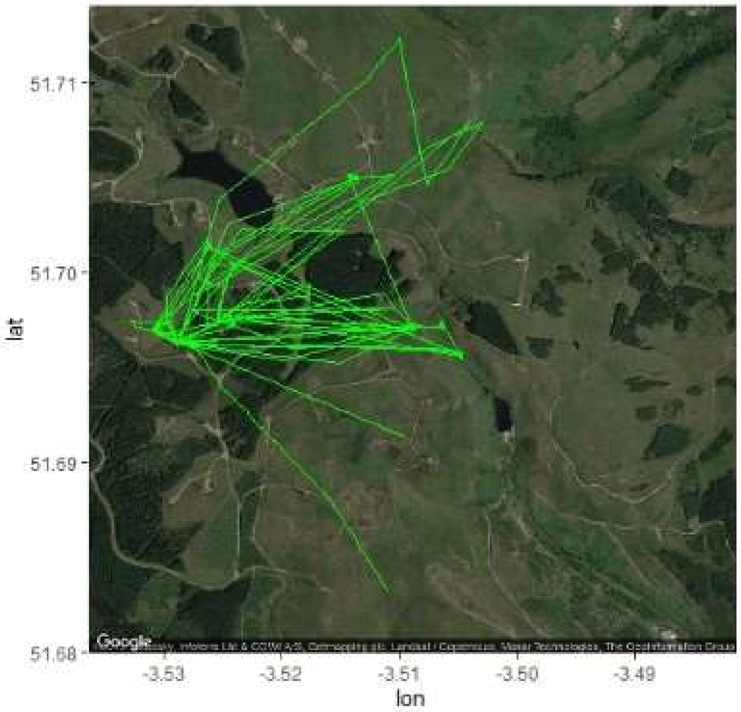


Figure 4.3 GPS Track (sequence of points connected by timestamp) for LH76739. A male bird tracked at PyC in 2015.

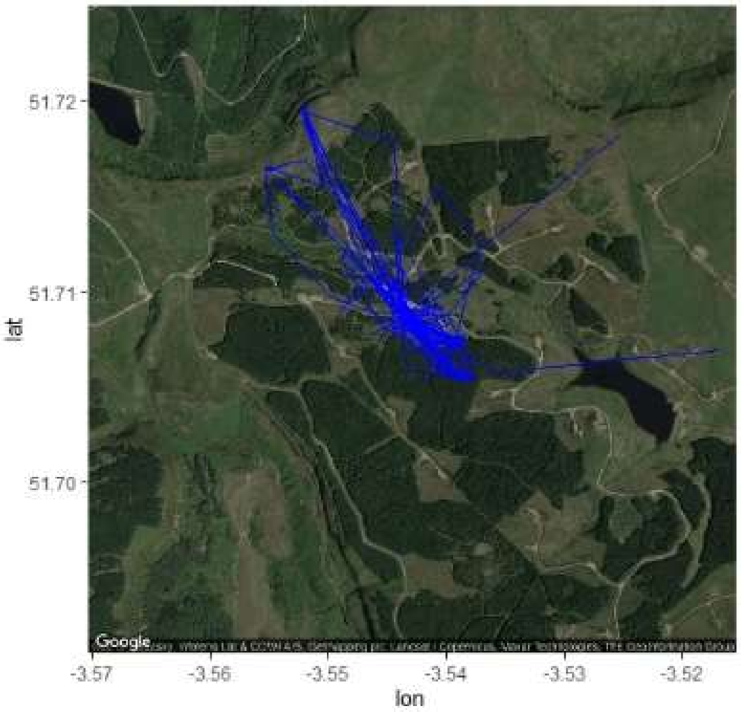


Figure 4.4 GPS Track (sequence of points connected by timestamp) for LH77838. A female bird tracked at PyC in 2019.

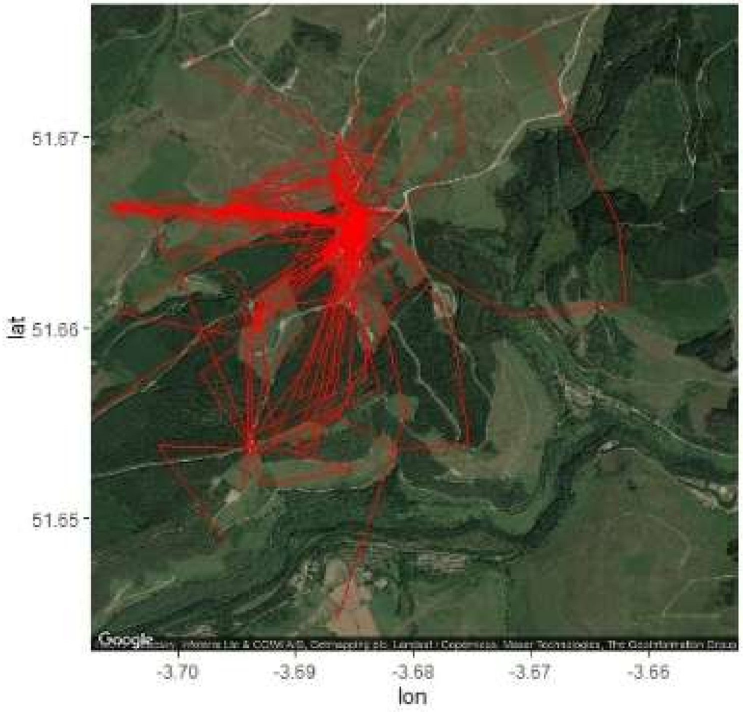


Figure 4.5 GPS Track (sequence of points connected by timestamp) for LB09390. A female bird tracked at PyC in 2018

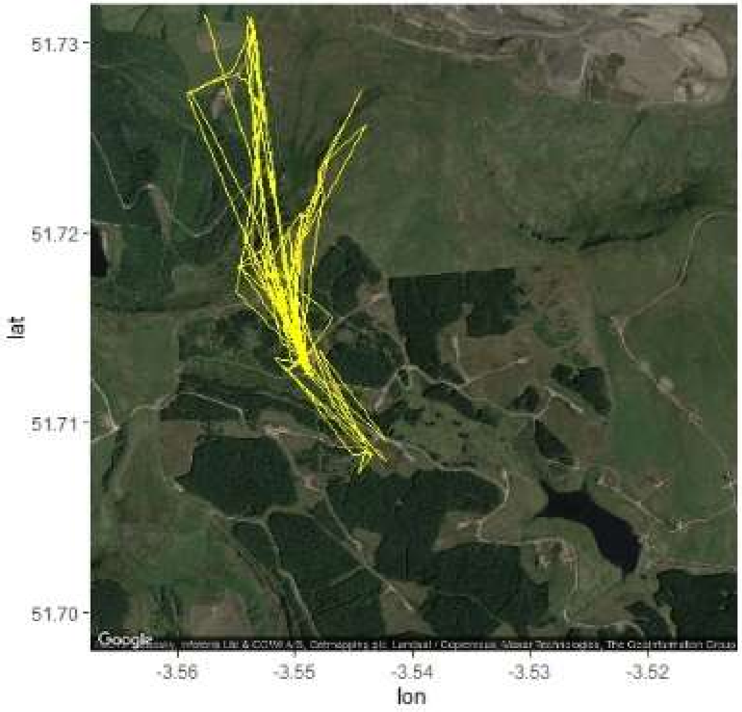


Figure 4.6 GPS Track (sequence of points connected by timestamp) for LJ75945. A female bird tracked at PyC in 2017.

4.4.2 Home range

Mean home range size was estimated as 119 ha (±SE 28), however the large standard error indicates that there was strong individual and/or sex variation around this. Separate models for each sex estimated male average home range size as 217 ha (±SE 55), whilst estimated female home range size was 64 ha (±SE 16).

The model run using data for both sexes, and sex as a fixed factorial term, identified a significant sex difference in home range size; (β_{male} = 0.98, CI 0.13 to 1.84). This suggests that on average male home ranges were 167% larger than female home ranges (CI 13% to 528%). This model and the female only model did not identify any other parameters of importance (See Table 4.1 and 4.3).

The male only model did however identify a significant negative effect of moth biomass on home range size (β -0.66, CI -1.24 to -0.09). This suggests that male home ranges decrease in area, by approximately 48% (CI 8.4% to 70.99%), for each one standard deviation increase (~ 620 mg) in average moth biomass within the home range area (See Figure 4.7, Table 4.2).

Table 4.1 Home range size model coefficient estimates for model run using both male and female data. Important parameters are highlighted in bold for ease of interpretation.

ALL SEXES MODEL	ESTIMATE	STD. ERROR	LCI	UCI
(INTERCEPT)	**4.30**	**0.36**	**3.58**	**5.01**
MOTH BIOMASS	-0.02	0.26	-0.52	0.49
MOTH BIOMASS VARIATION	0.30	0.26	-0.21	0.80
NO. OF TRACKING DAYS	-0.09	0.23	-0.54	0.35
SEX (MALE)	**0.98**	**0.44**	**0.13**	**1.84**
MOTH BIOMASS : MOTH BIOMASS VARIATION INTERACTION	0.21	0.32	-0.42	1.48

Table 4.2 Home range size model coefficient estimates for model run using only male data. Important parameters are highlighted in bold for ease of interpretation. Estimate – model estimated mean, STD. Error – model estimated standard error around the mean. LCL – 95% lower confidence limit. UCL – 95% upper confidence limit.

MALE ONLY MODEL	ESTIMATE	STD. ERROR	LCI	UCI
(INTERCEPT)	**5.35**	**0.24**	**4.89**	**5.81**
MOTH BIOMASS	**-0.66**	**0.29**	**-1.24**	**-0.09**
MOTH BIOMASS VARIATION	0.23	0.27	-0.29	0.76
NO. OF TRACKING DAYS	0.14	0.23	-0.32	0.59
MOTH BIOMASS : MOTH BIOMASS VARIATION INTERACTION	0.39	0.43	-0.46	1.24

Table 4.3 Home range size model coefficient estimates for model run using only female data. Important parameters are highlighted in bold for ease of interpretation Estimate – model estimated mean, STD. Error – model estimated standard error around the mean. LCL – 95% lower confidence limit. UCL – 95% upper confidence limit.

FEMALE ONLY MODEL	ESTIMATE	STD. ERROR	LCI	UCI
(INTERCEPT)	4.16	0.27	3.64	4.68
MOTH BIOMASS	0.55	0.28	-0.01	1.09
MOTH BIOMASS VARIATION	0.18	0.38	-0.56	0.92
NO. OF TRACKING DAYS	-0.72	0.35	-1.40	-0.04
MOTH BIOMASS : MOTH BIOMASS VARIATION INTERACTION	-0.01	0.40	-0.79	0.77

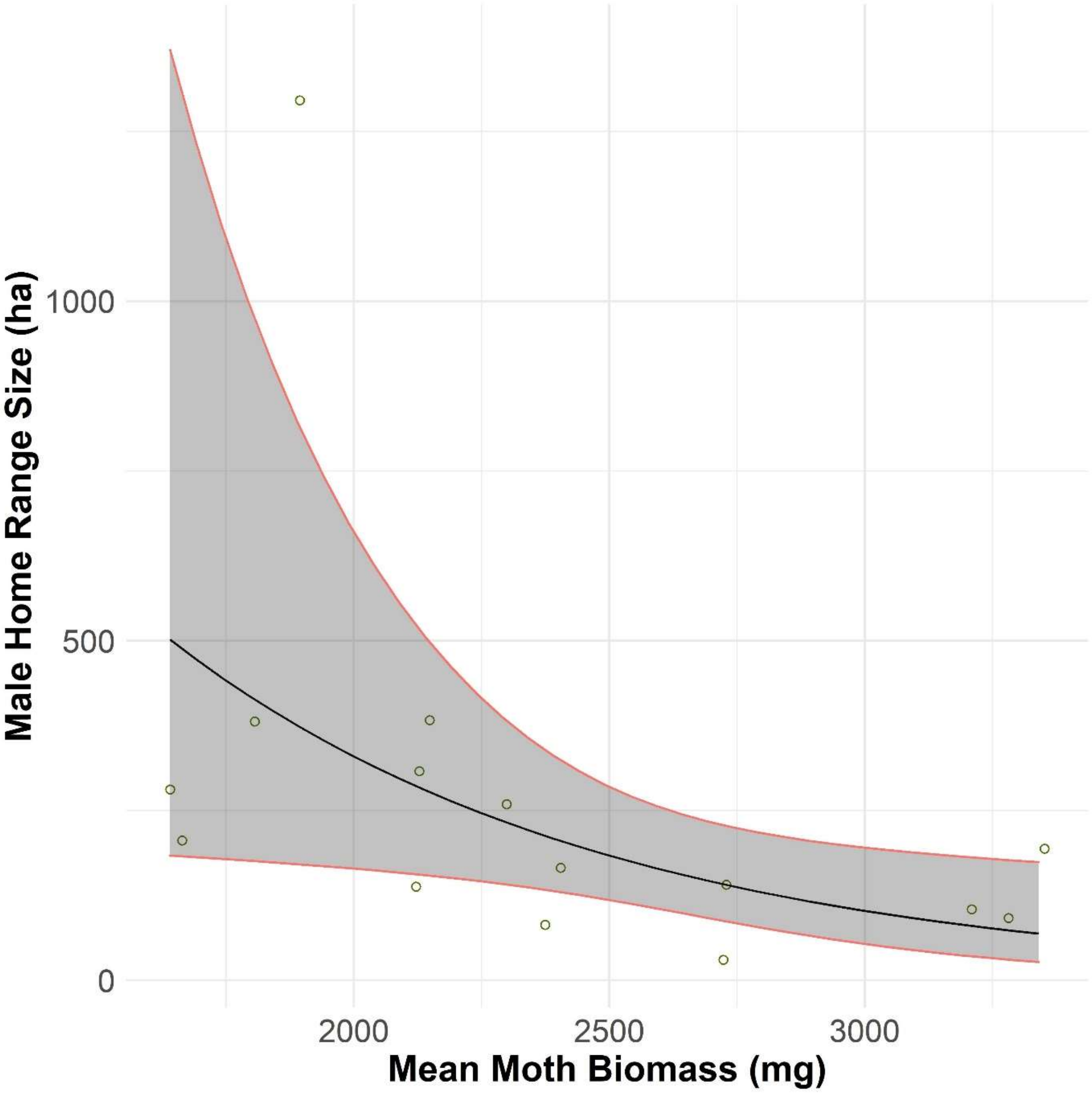


Figure 4.7 Predicted male home range size vs mean moth biomass (mg) with other variables held at their mean value. It is also worth noting that the negative relationship shown remains, even if the outlier at ~ 1300 ha is removed.

4.4.3 Movement analysis

Tracks were clustered into four behavioural categories using EMbC: high velocity/low turning angle (HL), high velocity/high turning angle (HH), low velocity/low turning angle (LL) and low velocity/high turning angle (LH). These were further sub-divided into low precision (L) and high precision (H) classifications based on the uncertainty associated with the temporal irregularity of the sampling. HL and HH behaviours correspond to rapid movements, which we consider to be commuting phases (i.e. high flight speed and varied directionality) as has been suggested in other studies (e.g. de

Grissac et al. 2017). LL and LH behaviours correspond to slow movements and likely represent foraging behaviours typically exhibited by nightjar such as hawking and fly catching (Cramp & Simmons 1985, Holyoak 2001). These points were further divided into low precision and high precision categories e.g. HHH high velocity/high turning angle/high precision, HHL - high velocity/high turning angle/low precision etc.

This analysis indicated a broad split of points between foraging-like movements (75% of points) and commuting-like movements (25%), suggesting nightjar spend 75% of their nocturnal activity either foraging, or in movement patterns that are indistinguishable from foraging movements using this classification method. Table 4.4 provides a detailed breakdown of this point classification and an example of the point classification is shown in Figure 4.8.

Table 4.4 EMbC Clustered movement points and parameter values associated with the clustered categories and the interpreteted behaviour. Velocity – speed in m/s, Turning angle – angle between succesive points, No. of Satellites – number of satellies used to define GPS position (proxy for accuracy). No. of points – number of points identified in this cluster/ category. % of points – percentage of total points assigned to this cluster. Interpreted behaviour – semantic interpretation of cluster.

CLUSTERED BEHAVIOUR CATEGORIES	VELOCITY		TURNING ANGLE		NO. OF SATELLITES		NO. OF POINTS	% OF TOTAL	INTERPRETED BEHAVIOUR
	Mean	SD	Mean	SD	Mean	SD			
LLL	0.33	0.21	0.08	0.06	1.44	0.85	3045	14.93	Foraging
LLH	0.15	0.36	0.09	0.15	3.05	0.08	787	3.86	Foraging
LHH	0.48	0.19	0.65	0.39	1.68	0.95	3248	15.93	Commuting
HLL	0.61	0.15	0.03	0.02	1.19	0.73	4991	24.48	Foraging
HLH	0.51	0.17	0.05	0.03	2.75	0.28	6515	31.95	Foraging
HHL	0.55	0.17	3.29	2.08	0.68	0.55	1237	6.07	Commuting
HHH	0.72	0.23	2.08	1.56	2.75	0.32	532	2.61	Commuting

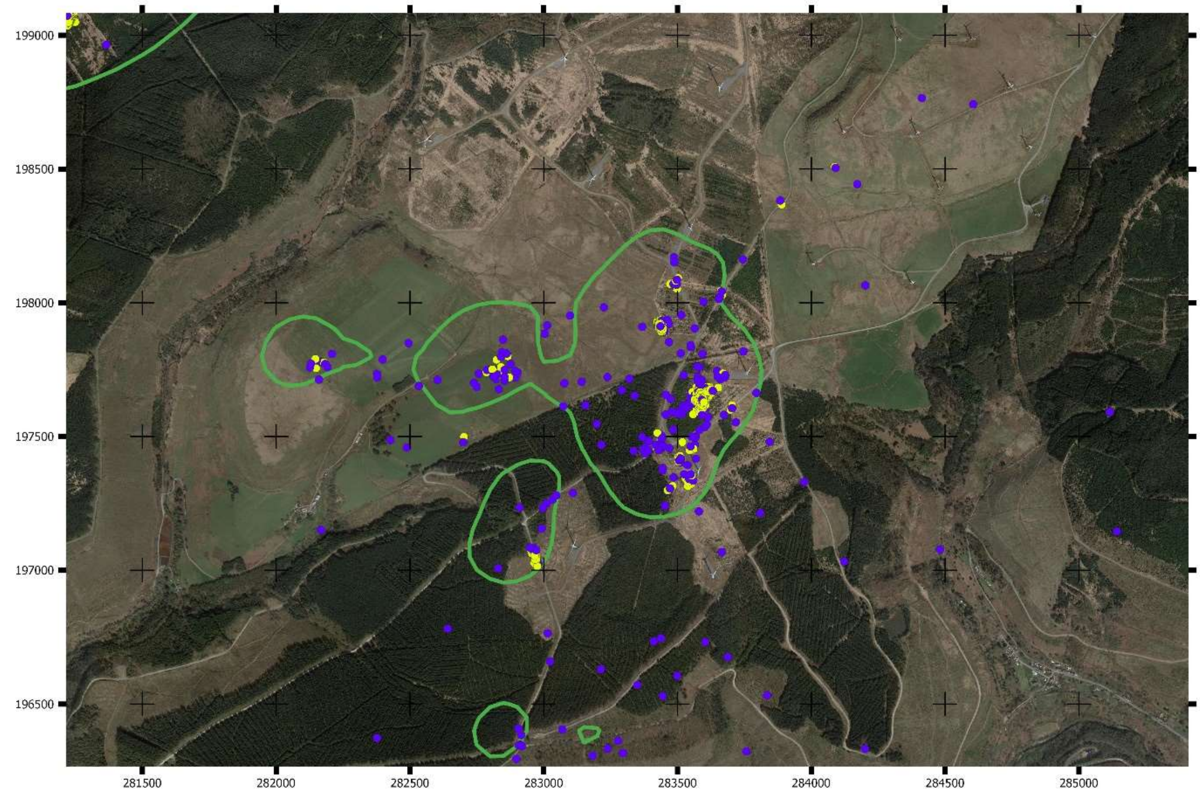


Figure 4.8 Estimated home range (95% UD – shown in green) for LB09390, a female nightjar tracked at PyC in 2018. Tracking points have been clustered into interpreted behaviour categories using EMbC with blue showing commuting points and yellow foraging points.

4.4.5 Resource selection

Model evaluation of resource selection models identified model 5, where the probability of foraging behaviour was modelled as a function of predicted moth biomass, biomass variation and their interaction, whilst also incorporating individual variation though a nested hierarchical structure, as the most parsimonious model based on AICc- See Table 4.5.

Table 4.5 Resource Selection Function model comparison. Model parameters are as follows – Pres = presence/ absence of foraging, Ring.no. = individual bird identifier, biomass = predicted moth biomass, biomassVAR = coefficient of moth biomass variation, sample = individual identifier of grouping variable for day of year nested with Ring.no.

MODEL NO.	MODEL FORMULA	DF	AICc	DELTA AICc
1	Pres ~ (1|Ring.no.) + (0+biomass|sample)	2	247899	10799.2
2	pres ~ biomass + (1|Ring.no.) + (0+biomass| sample)	3	245611.5	8511.67
3	Pres ~ biomass + biomassVAR + (1|Ring.no.) + (0+biomass| sample)	4	245612.3	8512.47
4	pres ~ biomass * biomassVAR + (1|Ring.no.) + (0+biomass| sample)	5	245585.3	8485.5
5	pres ~ biomass * biomassVAR + (1|Ring.no.) + (0+biomass| sample) + (0+biomassVAR|Ring.no.)	6	237099.8	0

Population-level (fixed) effects for variables describing the availability of moth biomass and its variation on the foraging behaviour of European Nightjar indicated an important negative interaction effect of moth biomass and moth biomass variation on foraging habitat selection (β= -0.54, CI -0.69 to -0.39) from the best supported model (model 5). The model also identified an important positive effect of moth biomass on foraging habitat selection (β= 0.77, CI 0.28 to 1.25) although in light of the significant interaction effect this must be considered in the context of the moth biomass variation. This means, the magnitude of the effect of increased moth biomass on the probability of observing foraging type behaviour is dependent on the within year variation of moth biomass and in general, as biomass variation increases the threshold predicted moth biomass value required to initiate a transition to foraging decreases (See Table 4.6 and Figures 4.8 – 4.11).

Table 4.6 Resource Selection Function model estimates.

PARAMETER	ESTIMATE	STD. ERROR	LCL	UCL
(INTERCEPT)	0.06	200.02	-391.97	392.09
BIOMASS	**0.77**	**0.25**	**0.28**	**1.25**
BIOMASS VARIATION	-20.71	18.44	-56.86	15.43
BIOMASS :BIOMASS VARIATION INTERACTION	**-0.54**	**0.08**	**-0.69**	**-0.39**

A series of plots below show the predicted probability of foraging dependent on the predicted moth biomass for the 25%, mean and 75% quantile of the predicted moth biomass coefficient of variation and an interaction plot across the recorded levels of predicted biomass variation and moth biomass (Figures 4.9 – 4.12) for a single individual (ring number CF49394). Plotting by individual is required due to the structure of the models used (individual level random effect) and the overall response is considered to be well summarised by CF49394, despite a significant amount of among individual variation, this individuals response is also consistent with the population level estimates shown in Table 4.6.

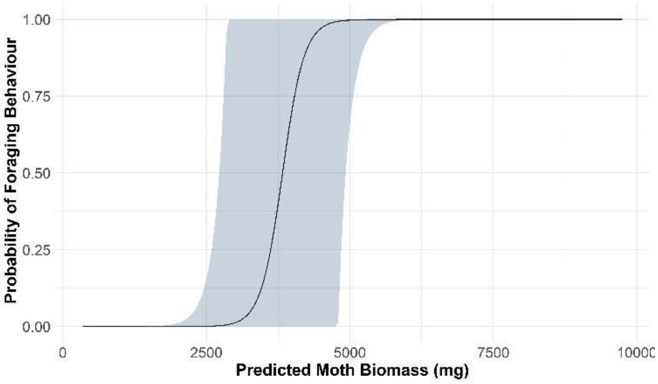


Figure 4.9 Predicted probability of foraging vs predicted moth biomass at the 25% quantile of biomass variation for CF49394 on the 13th July 2019.

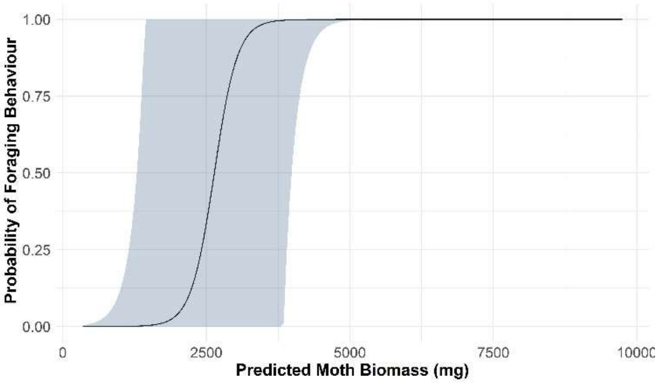


Figure 4.10 Predicted probability of foraging vs predicted moth biomass at mean biomass variation for CF49394 on the 13th July 2019.

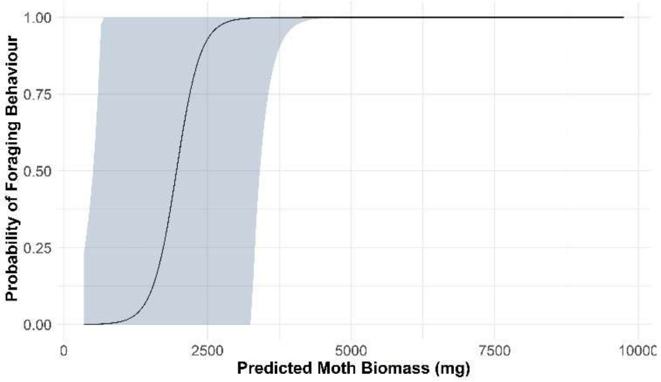


Figure 4.11 Predicted probability of foraging vs predicted moth biomass at the 75% quantile of biomass variation for CF49394 on the 13th July 2019.

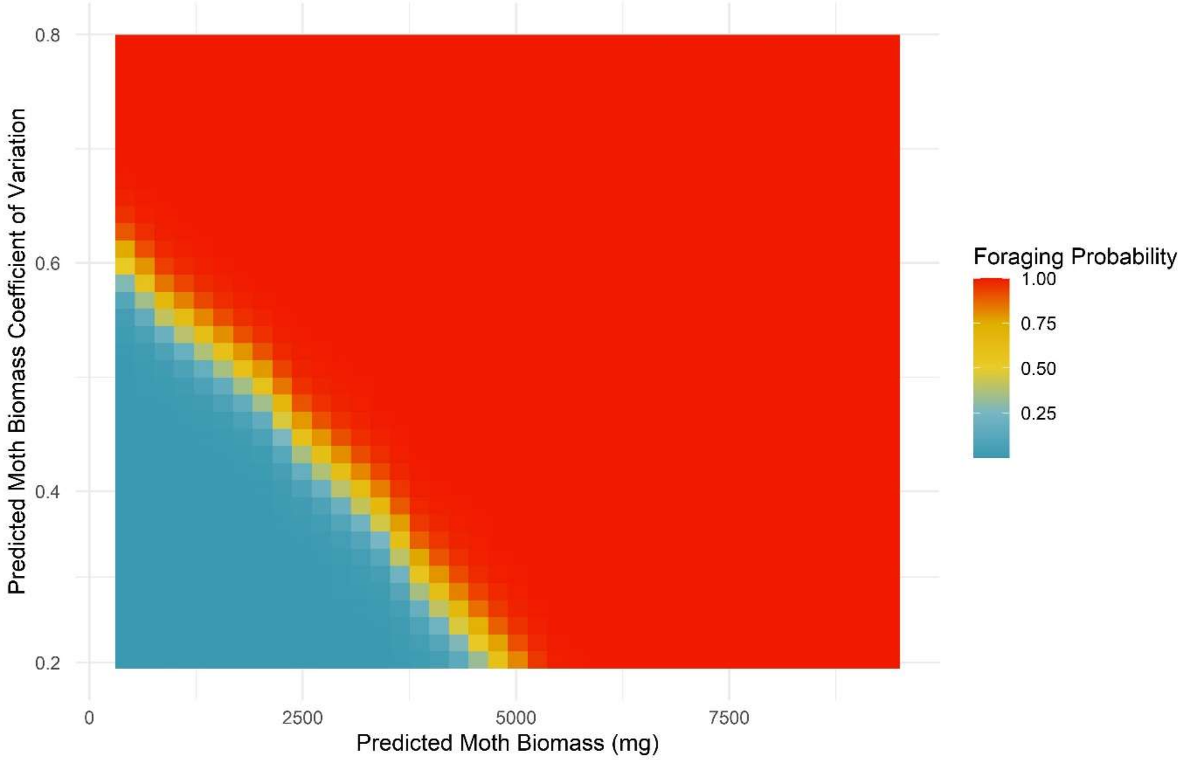


Figure 4.12 Predicted probability of foraging at predicted moth biomass and biomass variation values for CF49394 on the 13th July 2019.

4.5 Discussion

In this study I have identified behaviour consistent with optimal foraging theory in a natural system, confirming the importance of food availability, as represented by predicted moth biomass (or flight density of phototactic species), to animal behaviour patterns. I have shown that predicted moth biomass is an effective predictor of both home range size in male nightjars and of the spatial location of foraging behaviour in both male and female nightjar at the scale of individual nights during the breeding season. This is consistent with studies describing the importance of moths in the diet of European Nightjars (Glutz von Blotzheim and Bauer 1994, Sierro et al. 2001, Sharps et al. 2013, Winiger et al. 2018, Evens et al. 2020) and the regular commuting of Belgian nightjars to habitats with higher invertebrate productivity than around their nest sites (Evens et al. 2017). The importance of the spatio-temporal availability of food in driving movement behaviour has also been demonstrated in other animal species (e.g. Bastille-Rousseauet et al. (2015) Caribou *Rangifer tarandus*) but not, to our knowledge, in an aerial insectivore. It is also clear from our modelling results that individual identification accounts for a large amount of the observed variation, confirming the importance of individual responses, as suggested in general by Muff et al. (2020) and specifically for nightjar by Mitchell et al. (2020).

The positive effect of predicted moth biomass on the probability of foraging was dependent on the spatiotemporal variation in predicted moth biomass: higher moth biomass was associated with an increased likelihood of foraging, but this relationship weakened as biomass variation increased i.e. the importance of high average biomass decreased as resources became less consistent through time. This means that lower biomass areas with higher variation were more likely to be used as foraging habitat than low biomass areas with low variation. This is suggestive of the active selection of predictable areas of high biomass and avoidance of low biomass area, but also some plasticity to spatial and temporal variation, with individuals less selective where and when variation is higher. Or alternatively, they are simply able to compensate for lower biomass through greater foraging effort in higher biomass variation areas but as variation decreases there is threshold of biomass below which this becomes unprofitable and these low biomass and low variation habitats are avoided. A similar pattern for the preferential selection of spatiotemporally predictable resources has also been recorded in other species e.g. Griffon vulture *Gyps fulvus* (Monsarrat et al. 2013) and has been suggested as a potential driver of movement patterns (Riotte-Lambert & Matthiopoulos, 2020). Considerable plasticity in foraging behaviour due to food availability is also evident in other species (e.g. Monaghan et al. 1994 – Guillemot *Uria aalge*) consistent with the idea that foraging habitat selection is driven, at least in part, by the spatiotemporal variation in food availability. These results suggest a great deal of flexibility in foraging habitat selection and the use of prospecting behaviours to locate profitable foraging habitat across wide areas. As individuals exploit spatio-temporally variable food patches the efficient location of such patches is likely to be critically important for survival and reproduction. This suggests a strong selective driver for efficient patch location perhaps through mechanisms such as the use of conspecific cues to identify profitable food patches. Intra-specific competition is also likely to be more intense and evident whilst exploiting such patches, and as food availability decreases intra-specific competition is likely to become more intense perhaps having knock on effects on ranging/prospecting behaviour with likely associated impacts on resources for display and nest defence.

The results of the home range size analysis identified a significant effect of sex on home range size with on average males having a much larger home range than female nightjars at our study sites (male = 217 ha (±SE 55.0), female = 64.3 ha (±SE 15.8)). This strongly contrasts with the findings of Mitchell et al. (2020) where the converse was observed, with males having an average 95% UD of 74.36 ha (±SD 87.78) and females 131.11 ha (±SD 119.96), whilst similar results to Mitchell et al (2020) were also obtained by Sharps et al. (2015). Interestingly, previous nightjar studies by Evens et al. (2017) in Belgium found no sex differences in home range size, with an average 95% UD of 189.76 ha (SE = 124.61 ha). Evens et al. (2017) did, however confirm that area of key foraging habitat was negatively correlated with home range size, suggesting a food resource effect on home range size in both males and females. This is consistent with our results for male nightjars where predicted moth biomass was noted to have a significant negative effect on home range size (95% UD) and has been noted previously in other species (e.g. Village 1982 – Common Kestrel *Falco tinnunculus)*. It is also clear that across these studies significant variation in home range size exists, suggestive of strong individual variation in home range size as has been noted in other species (Börger et al. 2006; Patrick & Weimerskirch, 2017).

It is also interesting to contrast this variation in home range size with mean maximum foraging distances from other studies. The mean maximum foraging distance in this study was 3,266m (± 521), with females averaging 2,621m (± 99) and males 3,653m (± 653). This again contrasts markedly with Sharps et al. 2015, who recorded a mean nightly maximum distance of 747 m (±SD 513), and this could be due to either a greater moth biomass in the habitats in this study (Thetford Forest – lowland dry heath and coniferous plantation woodland) or perhaps simply the tracking methods used (radio tracking). The results of this study do, however, correspond well with the results of Evens et al. 2017, where average maximum foraging distance was 2,603 m (±SE 1,094 m). It is perhaps unsurprising that where average maximal foraging distances are similar (between this study and Evens et al 2017) home range sizes are also of comparable scale. It is, however, notable that the Belgian birds were utilising a very different movement behaviour strategy by commuting large distances to favoured foraging areas, in which foraging activity was concentrated. In contrast, activity in our study was largely confined to within the forest matrix, with diffuse foraging behaviour noted across open areas within the forest and -in part- driven by spatiotemporal variation in biomass productivity. This suggests that individuals are utilising different behavioural strategies of movement, dependent on the site-specific landscape habitat configuration and food resource availability, and suggests considerable phenotypic plasticity in foraging behaviour.

In conclusion, it is clear from our results that the probability of nightjar foraging increases in response to both moth biomass and the predictability of this biomass, and that males who settle in areas of higher average moth biomass productivity have a smaller home range size. This confirms the importance of spatio-temporal variation in determining movement patterns, and provides evidence as to how individuals manage trade-offs between food abundance and predictability. This has important implications for conservation management of this species in coniferous plantation woodland where moth biomass varies spatiotemporally dependent on the forest management cycle.

5.0 The effects of wind farm construction and operation on nest success of European Nightjar

Wind turbine at the Pen y Cymoedd wind farm, South Wales.

5.1 Abstract

Disturbance can disrupt ecosystem, community, or population dynamics and change resource availability because of natural events and/or human-induced disturbance. Disturbance has also been shown to have a significant effect on nesting success in various bird species and previous studies have identified significant impacts of disturbance on nesting European nightjar *Caprimulgus europeaus* due to urban development and human recreational disturbance. Given the proximity of nightjar nesting habitat in Wales to wind farm developments and proposed developments, it is possible that significant impacts through disturbance could occur.

In this study, I use nest-monitoring data from five upland forestry sites across Wales (of which 3 support wind farms) in a logistic exposure modelling framework to investigate the effects of wind farm construction phase and operational phase disturbance in the presence of professional judgement based mitigation measures on nesting nightjar. This data is used in combination with weather and habitat availability to investigate nest success/ survival. A total of 193 nightjar nests were located between 2013 and 2019 at the study sites. Nightjar nest survival at my study sites was relatively high (69%) and favourably compares to those reported elsewhere in the U.K. - 39% in the Dorset heathlands, 53% in Nottinghamshire.

The models of nest success developed identified no evidence of negative effects on nest survival due to construction phase disturbance where mitigation measures are adopted. Weather was identified as a key predictor of nest success with an important interactive effect noted between temperature and precipitation and the combination of low temperatures and high precipitation having the greatest negative effect on nest survival. Habitat was also identified as key factor, of equivalent magnitude to weather effects, for nightjar nesting success in plantation habitats. In particular, the extent of long-term open habitat (i.e. those habitats that are not part of the productive forest cycle) in the forest matrix was key, meaning that factoring this into forest management plans could be used to support nightjar populations in commercial forest plantations.

5.2 Introduction

Disturbance is defined within ecological literature as any event or phenomenon that can disrupt ecosystem, community, or population dynamics and change resource availability, or the physical environment (White & Pickett 1985, Krebs 2001, Marzano & Dandy 2012). Disturbance can be divided into natural events and human-induced disturbance. Disturbance can be sub-divided further by the temporal pattern of impact intensity and duration, giving pulse and press disturbances (Lake, 2000). Pulses are short term and sharply delineated interruptions (e.g. Construction phase activity), whilst press disturbances may arise sharply and then reach a constant level that is maintained over long timeframes (e.g. Operational phase activity). Disturbance can produce long-term effects on individuals, populations and communities and has been shown to have a significant effect on nesting success in various bird species (Hockin et al. 1992, Gladalski et al. 2016)

Animals are expected to maximize fitness by overestimating rather than underestimating risks (Gladalski et al. 2016) as overestimation will result in smaller fitness consequences than underestimating potential lethal events (Bouskila & Blumstein 1992). The effects of disturbance on breeding success and behaviour are known to be analogous to predation risk in many systems (Frid & Dill, 2002, Beale et al. 2004a, Le Corre et al. 2009, Kociolek et al. 2011, Marzano & Dandy, 2012). Thus, individuals may react to disturbance with a variety of behavioural and physiological responses, including a reduction in offspring provisioning, changes in territory settlement patterns or habitat use, or increased levels of stress hormones (Holberton et al. 1996, Platteeuw & Henkens, 1997, Fowler, 1999, Romero & Remage-Healey 2000, Verhulst et al. 2001, Cockrem & Silverin 2002, Clinchy et al. 2004, Botsch et al. 2017, Fernández-Bellon et al. 2019, Fielding et al. 2021).

Human disturbance of wildlife is one of the principal issues of concern in biodiversity conservation, yet the information required to assess the extent of this threat is rarely available (Gill 2007). In particular, we often lack detailed information on species-specific responses to disturbance and -crucially- the demographic implications of such disturbance (Gill, 2007; Tablado & Jenni, 2017). This is particularly relevant in development control (the U.K.'s system of town and country planning via which local government, regulates land use and new building) and environmental impact assessment as the current lack of evidence can result in over precautionary approaches and poorly evidenced decisions (Hunter et al. 2021). Evidenced based construction and operational phase mitigation measures for European Nightjar are currently lacking and this means, as with many other species, mitigation measures for this species are based on professional judgement alone.

Bird eggs, and hatchlings in the nest, are particularly vulnerable to disturbance because their survival depends on a substantial level of care from their parents. There are two principal causes for bird nest failure: nest desertion and predation (Götmark 1992). These two causes are linked to the stage of incubation; in general the likelihood of desertion decreases and nest defence increases with time spent incubating (Dawkins & Carlisle 1976, Montgomerie & Weatherhead 1988, Strnadová et al. 2018). Accordingly, the impact of human disturbance on rates of egg predation and nest desertion has been related to the timing of the disturbance (Livezey, 1980; Major, 1990; Gloutney et al. 1993; Bolduc et al. 2003) and the frequency of disturbance (Robert & Ralph, 1975; Bolduc & Guillemette, 2003; Border et al. 2018). The impact of disturbance is also dependent on both environmental and social/community factors such as nest concealment, density of egg predators, whether birds nest colonially or solitary, and parental defence behaviour (Götmark 1992).

Previous studies on the impact of disturbance on nesting European nightjar *Caprimulgus europaeus* have largely focused on urban development and human recreational disturbance (i.e. Lowe et al. 2014, Murison et al. 2002), on the lowland heaths of southern and the south eastern England, and the potential of these factors to have a long term detrimental impact on the population. Liley et al. (2003) demonstrated that the numbers of nightjars present on Dorset heathland sites were negatively affected by the level of urban development around the periphery of the sites. Langston et al. (2007) also showed that failed nests were significantly closer to footpaths and were surrounded by a greater length of footpath per unit area, than successful nests were. These studies suggested potential mechanisms of disturbance such as egg predation following flushing, and trampling or predation by dogs.

A more recent study by Lowe et al. (2014) in Sherwood Pines Forest Park, Nottinghamshire (north-central England) examined potential effects of differences in recreational access pressure on nest success over a ten year period. The study identified significantly more nests in the less disturbed (south) section part of the forest park than in the (north) section of the study area. However, they also found no significant difference in individual reproductive success between nightjars nesting in the north section compared with the south section, suggesting that those birds tolerant of disturbance could be as successful as birds in low disturbance areas.

In this study, I use nest-monitoring data from five upland wind farm sites across Wales to investigate the effects of on nightjar nest success of construction phase and operational phase disturbance, in the presence of professional judgement based disturbance mitigation measures. In particular, I aimed to answer three questions for both the construction and operational phases;

1. Is the probability of nest success (fledging one or more chicks) negatively affected by the proximity of construction/operational activity and/or vehicle access tracks during the nesting period?

2. Is the probability of hatching success (hatching of one or more eggs) negatively affected by the proximity of construction/ operational activity and/or vehicle access tracks during the nesting period?
3. Is the probability of fledging success (fledging a chick from a successfully hatched egg) negatively affected by the proximity of construction/ operational activity and/or vehicle access tracks during the nesting period?

5.3 Methods

5.3.1 Study site

This study utilised nest data from five study sites across Wales in the summers of 2013–2019. Study sites were located at the forestry plantation sites of Bryn (Lat. 51.593546, Lon. -3.7059232), Afan (Lat. 51.628561, Lon. -3.6998060), Pen y Cymoedd (Lat. 51.695158, Lon. -3.5838970), Brechfa (Lat. 51.971539, Lon. -4.2053404) and Clocaenog (Lat. 53.069281, Lon. -3.4728997), which ranged in extent from 814 to 4,900 ha (Table 3.1; Figure 3.1). These sites are all part of the Welsh Government Woodland Estate and are managed by Natural Resources Wales (See Chapter 3 for further details on each study site).

Of these study sites, Pen y Cymoedd, Brechfa and Clocaenog, host operational wind farm sites that were constructed and operated during this study, whilst the remaining two sites are considered undeveloped control sites in this study. These wind farm sites were developed as part of the Natural Resources Wales Wind Energy Programme that aims to integrate wind farm development into the sustainable management of the Welsh Government Woodland Estate. Clocaenog Forest Wind Farm supports 27 turbines and generates up to 96MW, whilst Brechfa has 28 turbines (57MW) and Pen y Cymoedd has 72 turbines (227MW).

5.3.2 Nest data collection

The inclusion of nightjar in species protection legislation ensures that nightjar nest locations are protected from damage/ destruction under the Wildlife and Countryside Act (1981). Suitably licensed and experienced individuals undertook all nest monitoring visits completed in this study. I led data collection at Pen y Cymoedd, Bryn and Afan, whilst Paddy Jenks and Tony Cross completed nest data collection across 2013-2019 at Brechfa and Clocaenog respectively.

5.3.3 Nest location

Nest searching commenced annually in late May, and continued until August. Active territories were systematically watched on multiple occasions by multiple observers at dusk, and visual cues were used to guide follow-up nest searches (Langston et al. 2007). Subsequent nest searches consisted of detailed visual inspection in areas of observed nightjar activity during dusk watches, with searchers aiming to pass within 3-4 metres of any point within the search area.

Where observation of active nightjar territories yielded little information, or nest searches were unsuccessful, or where pairs were considered likely to attempt a 2nd brood, then these territories/ pairs were targeted for radio tagging effort using methods as set out in Chapter 2.

Following the identification of active nests through either observation or radio tracking, all nests were monitored to their natural completion (fledging or nest failure) by an experienced nightjar fieldworker, using regular (~weekly) nest site visits. Nests were classified as either successful or failed, based on a combination of the timing of nest visit records and available evidence at the nest site and within the territory (e.g. flying young present).

5.3.4 Habitat

In order to evaluate the effect of habitat on nest success, a number of habitat variables were determined for each nest location and the surrounding area within a 3km buffer. This radius was chosen because it equates to the mean maximum nightly foraging distance of nightjars (See Chapter 4 and Evens et al. 2018). This included the time since felling (= clearfell age), determined to the nearest year, via review of aerial imagery (Google Earth 2020) and satellite imagery, using Google Earth Engine (Gorelick et al. 2017) and land cover mapping data from LCM 2017, 2018 and 2019 with a 20m by 20m classified pixel resolution (Morton et al. 2020). Land cover map (LCM) data were manipulated to provide summary variables using the R statistical software (R Core Team, 2018) and raster package (Hijmans et al. 2019). Land cover habitat classes were filtered and re-ordered from the initial 22 twenty-two habitat classes, to provide aggregated broad habitat classes for habitats of likely relevance.

- Semi-Natural Grassland - inclusive of LCM habitats “Neutral Grassland”, “Calcareous Grassland” and “Acid Grassland”.
- Upland Habitats – inclusive of LCM habitats “Heather”, “Heather grassland”, “Bog”, “montane habitats” and “inland Rock”.
- Urban - inclusive of LCM habitats “urban” and “sub-urban”.

5.3.5 Wind farm infrastructure

In lieu of detailed site level activity data such as traffic movement data (volume and type) or detailed sound/ground vibration data, distance from each nest to the nearest vehicle access track in metres was used as a measure of potential disturbance. This variable was considered likely to be proportionate to the exposure of nest sites to disturbance during construction and operation. It should also be noted that measures to limit construction effects on nightjar (e.g. by using disturbance exclusion buffers around located nests) were adopted during construction at each wind farm site and as such construction effects should be viewed in this context. Distance to nearest track was calculated using the R Studio (R Studio Team 2020) interface to R 4.0.5 (R Core Team 2020) and the nngeo (Dorman 2021) and sf (Pebesma 2018) packages.

For the purpose of this analysis, construction and operation years were defined relative to the period of nest activity, e.g. activity restricted to outside of the nesting period (May-Aug) was not considered relevant. For example, a nest was only defined as being active in a construction year if construction activity on site overlapped with that nesting period. The relative dates of construction and operational phases for each wind farm site are shown in Figure 5.1 below.

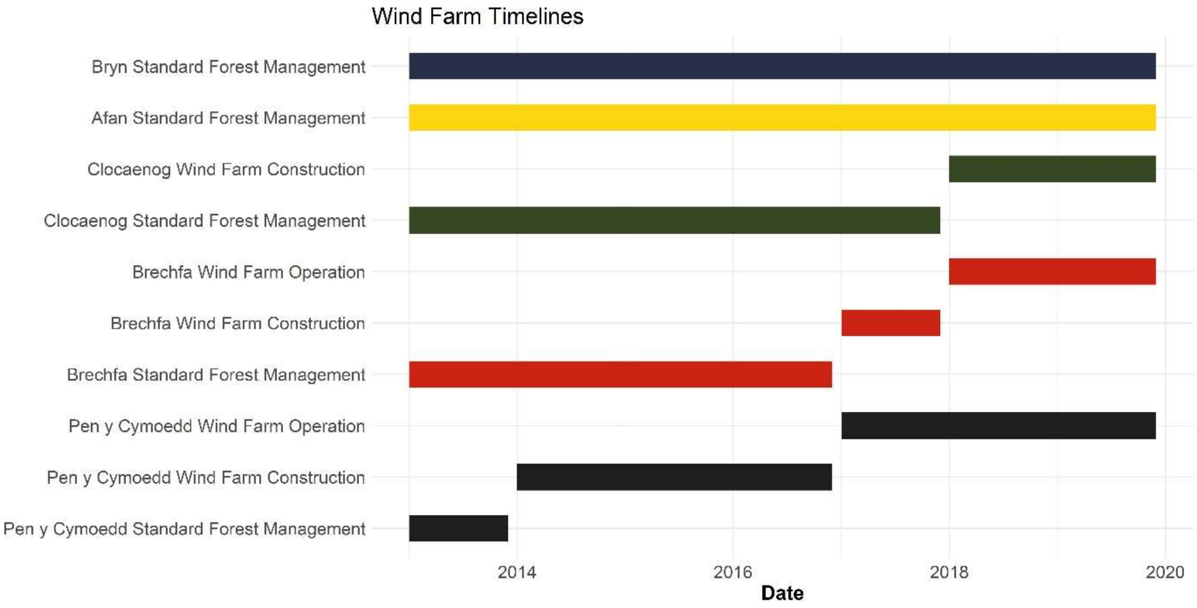


Figure 5.1 Gantt chart of site management and wind farm construction and operation timelines. Solid coloured bars indicate the time period of the relevant activity/ land management approach listed in the first column.

5.3.6 Meteorological data

In order to account for the influence of weather as an important predictor of nest survival in nightjar (Shewring et al. 2020), data from weather stations within 40km of each nest location (mean 29.7km, range = 16.5 to 39.9km; See Chapter 3 - Figure 3.1) were obtained using the GSODR package (Sparks, Hengl & Nelson 2017) using R software version 3.6.1 (R Core Team 2019), implemented via R Studio (RStudio Team 2018). The GSODR package provides automated downloading, parsing and cleaning of Global Surface Summary of the Day (GSOD; United States National Oceanic and Atmospheric Administration National Climatic Data Center) weather data. This data set provided daily rainfall (mm), and mean temperature, minimum temperature and dewpoint (all °C). Where more than one station was present within 40 km of a trapping point, then the data were averaged. Data manipulation was undertaken using the R packages tidyverse (Wickham et al. 2019) and lubridate (Groelmund & Wickham 2011). Daily temperature, precipitation and minimum temperature, were collated for the period of nest presence (laying date to last known presence) and summarised to produce mean values for the relative period of nest activity (e.g. laying to completion/ failure).

5.3.7 Statistical analysis

In order to investigate the effects of environment and disturbance on nest survival, I modelled daily nest survival (DSR) using generalized linear models (GLMs) with a binomial error distribution and the logistic exposure link function (Shaffer 2004). Models were developed for the entire nesting period (egg stage and chick stage combined) and for the egg and chick stage separately. DSR for each was modelled as a function of known important predictors of nest survival in nightjar (Shewring et al. 2020): temperature (as minimum temperature), date of nest initiation and nest age. Mean precipitation was also included, as this is known to reduce moth activity (Holyoak et al. 1997) and has been hypothesised to increase chick mortality (Shewring et al. 2020 – see also Chapter 2), along with an interaction between mean precipitation and mean minimum temperature, as it was hypothesised that these parameters may have multiplicative effects.

In addition to these parameters I also included the extent of: i) nightjar foraging habitat within 3km of the nest site, and ii) urban habitats, as this is a proxy for recreational disturbance pressure, a factor known to affect nest success (Langston et al. 2007). Nightjar foraging habitat was sub-divided into (i) coniferous plantation woodland open habitat less than 15 years old, (ii) open habitat greater than 15 years old, (iii) upland habitats, (iv) grassland habitat and (v) urban habitat extents.

Prior to modelling, multi-collinearity between variables was checked using the vif function from the car package to calculate the variance inflation factor (VIF) (Fox & Weisberg, 2019). High collinearity (high VIF) can be problematic and result in biased parameter estimates and variables with VIF values > 5 were removed (Zuur et al. 2010, Cobos et al. 2019). This resulted in the removal of mean temperature from the combined model and chick stage model, and minimum temperature from the egg stage model.

To assess the relative importance of wind farm construction and operation in predicting daily nest survival probability, I evaluated the additive combination of disturbance proxy parameters for construction (construction year as a binary factor – yes/no, and distance to nearest track in metres) and operation (operation year (binary factor), distance to nearest wind turbine and distance to nearest track) to the environmental model detailed above. Models were ranked based on AICc scores (Burnham & Anderson 2002) and under the principle of parsimony, I selected the simplest model within 2 AICc units of the top-ranked model. Unfortunately, the combined and chick stage models incorporating operational stage disturbance proxies did not converge and these are considered no further. A summary of the models fitted can be seen in Table 5.1.

Continuous variables were scaled (i.e. standardised and centred around a mean of zero and a standard deviation of 1), to allow direct comparisons of coefficient estimates and ease numerical estimation. I then made inferences about the statistical importance of fixed effects from their influence (positive/negative), magnitude, and uncertainty (95% confidence intervals) and avoided interpreting using *p*-value thresholds alone (Amrhein et al. 2019).

5.3.8 Model validation

To assess model fit and test for under- and overdispersion, zero-inflation and spatial autocorrelation, I used the DHARMa package (Hartig, 2018) in R. Model assumptions were also verified by plotting standardised residuals versus fitted values, standardised residuals versus each covariate in the model, and standardised residuals versus each covariate excluded from the model using the DHARMa package.

Initial review of the combined and chick stage model residuals identified a potential non-linear relationship with nest age in residual plots, but no similar pattern in the egg stage model. As such, the combined and chick models were refit separately with a cubic polynomial and quadratic polynomial nest age terms, and backward stepwise deletion, using AICc (Burnham & Anderson 2002), was used to select the most appropriate term and residual plots were rechecked. Model validation identified no further significant issues of concern.

Table 5.1 Model Summary. Stage – the relevant stage of nesting cycle being modelled e.g. egg, chick or both combined. Model – model number. Model parameters – pseudo mathematical representation of model formula illustrating the parameters included in each model.

STAGE	MODEL	MODEL PARAMETERS
COMBINED ENVIRONMENTAL	1	DSR = α + β_1(Mean minimum temperature (^{o}C)) + β_2(Precipitation (mm)) + β_3(Lay date (day of the year)) + β_4(Open habitat <15 years old extent (ha))+ β_5(Open habitat >15 years old (ha))+ β_6(Semi- natural Grassland (ha)) + β_7(Upland vegetation (ha)) + β_8(Urban (ha)) + β_9(Mean minimum temperature (^{o}C) x precipitation (mm)) + β_{10}(Nest Age) + β_{11}(Nest Age^3) + ε
COMBINED WIND FARM CONSTRUCTION DISTURBANCE	2	DSR = model 1 parameters + β_{12}(Construction Year) + β_{13}(Distance to nearest track (m)) + β_{14}(Distance to nearest track (m) x Construction Year)
EGG STAGE	3	DSR = α + β_1(Mean minimum temperature (^{o}C)) + β_2(Precipitation (mm)) + β_3(Lay date (day of the year)) + β_4(Open habitat <15 years old extent (ha))+ β_5(Open habitat >15 years old (ha))+ β_6(Semi- natural Grassland (ha)) + β_7(Upland vegetation (ha)) + β_8(Urban (ha)) + β_9(Mean temperature (^{o}C) x precipitation (mm)) + β_{10}(Nest Age) + ε
EGG STAGE WIND FARM CONSTRUCTION DISTURBANCE	4	DSR = model 3 parameters + β_{11}(Construction Year) + β_{12}(Distance to nearest track (m)) + β_{13}(Distance to nearest track (m) x Construction Year)
EGG STAGE WIND FARM OPERATION DISTURBANCE	5	DSR = model 3 parameters + β_{11}(Operation Year) + β_{12}(Distance to nearest track (m)) + β_{13}(Distance to nearest track (m) x Operation Year) + β_{14}(Distance to nearest turbine (m)) + β_{15}(Distance to nearest turbine (m) x Operation Year)
CHICK STAGE ENVIRONMENTAL MODEL	6	DSR = α + β_1(Mean minimum temperature (^{o}C)) + β_2(Precipitation (mm)) + β_3(Lay date (day of the year)) + β_4(Open habitat <15 years old extent (ha))+ β_5(Open habitat >15 years old (ha))+ β_6(Semi- natural Grassland (ha)) + β_7(Upland

		vegetation (ha)) + β_8(Urban (ha)) + β_9(Mean minimum temperature (^{o}C) x precipitation (mm)) + β_{10}(Nest Age) + β_{11}(Nest Age^3) + ε
CHICK STAGE WIND FARM CONSTRUCTION DISTURBANCE	7	DSR = model 6 parameters + β_{11}(Construction Year) + β_{12}(Distance to nearest track (m)) + β_{13}(Distance to nearest track (m) x Construction Year)

5.4 Results

5.4.1 Nest finding

One hundred and ninety-three nightjar nests were located over the course of the study (2013-2019). Median nest initiation date was 21st June (range = 21st May – 27th July). In total, 109 nests were located during incubation (56.5%) and 72 nests (37.3%) were found during the nestling period, whilst twelve nests were located post fledging. Nests located post fledging were excluded from further analysis and thus one hundred and eighty one nests were available for subsequent analysis (n=181). Of these 181 nests, 130 nests fledged at least one chick, whilst the remainder (51) failed, with 21 failing at the egg stage and 30 at the chick stage.

5.4.2 Nest survival model comparison

The model comparison results indicate that construction disturbance was not important in determining nest success either over the whole nesting cycle or during the chick rearing period. The environmental model was more than 2 AICc units from models that included any construction phase disturbance variables (See Table 5.1). Estimated average daily nest survival (± SE) for the combined nest and egg stages, with all variables (e.g. laying date) held at their mean or median value as appropriate, was 0.989 (± 0.003). This extrapolates over the 36-d nesting cycle to an average nest success rate of 0.694 (± 0.070). Estimated average daily chick stage nest survival (± SE) was 0.985 (± 0.006), which extrapolates over the 18-d chick stage nesting cycle to an average fledging success rate of 0.762 (± 0.081). This means that on average 69% of nests were successful and that 76% of hatched chicks survived to fledging.

Meanwhile model comparison of operational stage disturbance identified a probable effect of operational activities at the egg stage, with the operational disturbance model selected as the top model. Whilst both the environmental and construction phase models were separated from this by greater than 2 AICc units. This suggests that operational activities are important in determining nest success at the egg stage of the nesting cycle. Estimated average daily egg stage nest survival (± SE) was 0.994 (± 0.004) at operational sites and 0.992 ((± 0.004) at other sites. This extrapolates over the 18-d egg stage nesting cycle to an average hatching success rate of 0.898 (± 0.064) at operational wind farm sites and 0.874 (± 0.062) at non-operational wind farm sites, meaning that on average ~1.5% more of egg stage nests were successful at wind farm sites. Tables presenting parameter estimates for each of the top models can be seen in Tables 5.2 - 5.5 below.

Table 5.2 Model Comparison Table. Most parsimonious/ efficient models as rated by AICc and the lowest number of parameters where models are within 2 AICc units are highlighted in bold. Stage – nesting cycle stage e.g. egg, chick or both combined. Model comparison – model parameter structure, AICC – Akaike information criterion adjusted for small sample sizes. ΔAICc – Difference in AICc. No. Pararmeters – the number of parameters in the model.

STAGE	MODEL COMPARISON	AICC	ΔAICC	NO. PARAMETERS
COMBINED	**Environmental Model**	**236.23**	**0.00**	**11**
	Wind Farm Construction Disturbance	**239.90**	**3.67**	**14**
EGG	Environmental Model	145.05	5.96	10
	Wind Farm Construction Disturbance	**149.64**	**5.70**	14
	Wind Farm Operation Disturbance	**139.09**	**0.00**	**15**
CHICK	**Environmental Model**	**169.46**	**0.00**	**11**
	Wind Farm Construction Disturbance	**172.50**	**3.04**	**14**

Table 5.3 Combined (egg and chick stage) model parameter estimates (Estimate), standard error (STD. Error) and confidence intervals (CI 2.50% and CI 97.5%). Parameters where estimated 95% confidence intervals do not overlap with zero are highlighted in bold.

PARAMETER	ESTIMATE	STD. ERROR	CI 2.50%	CI 97.50%
(INTERCEPT)	12.68	2.45	**7.88**	**17.47**
MINIMUM TEMPERATURE	0.12	0.25	-0.37	0.62
PRECIPITATION	-0.07	0.20	-0.46	0.31
LAY DATE	**-0.04**	**0.01**	**-0.07**	**-0.02**
PRECANOPY CLOSURE OPEN HABITAT WITHIN 3KM (HA)	-0.17	0.20	-0.56	0.22
PERMANENTLY OPEN HABITAT WITHIN 3KM (HA)	**0.81**	**0.24**	**0.34**	**1.29**
SEMI-NATURAL GRASSLAND WITHIN 3KM (HA)	-0.29	0.18	-0.65	0.07
UPLAND VEGETATION WITHIN 3KM (HA)	**0.62**	**0.26**	**0.11**	**1.12**
URBAN WITHIN 3KM (HA)	0.44	0.45	-0.45	1.32
NEST AGE	-0.07	0.04	-0.14	0.01
NEST AGE ^3	0.00	0.00	0.00	0.00
MINIMUM TEMPERATIRE X PRECIPITATION	**0.79**	**0.20**	**0.39**	**1.18**

Table 5.4 Egg stage model parameter estimates (Estimate), standard error (STD. Error) and confidence intervals (CI 2.50% and CI 97.5%). Parameters where estimated 95% confidence intervals do not overlap with zero are highlighted in bold.

PARAMETER	ESTIMATE	STD. ERROR	2.50%	97.50%
(INTERCEPT)	**8.84**	**3.55**	**1.87**	**15.80**
MINIMUM TEMPERATURE	0.29	0.32	-0.34	0.93
PRECIPITATION	0.37	0.31	-0.24	0.97
LAY DATE	-0.02	0.02	-0.06	0.01
PRECANOPY CLOSURE OPEN HABITAT WITHIN 3KM (HA)	-0.18	0.27	-0.72	0.36
PERMANENTLY OPEN HABITAT WITHIN 3KM (HA)	0.26	0.27	-0.26	0.79
SEMI-NATURAL GRASSLAND WITHIN 3KM (HA)	0.31	0.32	-0.31	0.93
UPLAND VEGETATION WITHN 3KM (HA)	0.73	0.50	-0.25	1.70
URBAN WITHIN 3KM (HA)	1.94	1.55	-1.09	4.97
NEST AGE	0.04	0.05	-0.06	0.14
DISTANCE TO NEAREST TRACK	-0.15	0.18	-0.49	0.20
OPERATION YEAR	0.23	0.56	-0.88	1.33
MINIMUM TEMPERATURE X PRECIPITATION	**0.79**	**0.23**	**0.34**	**1.23**
DISTANCE TO NEAREST TRACK X OPERATION YEAR	**-2.04**	**0.74**	**-3.49**	**-0.60**

Table 5.5 Chick stage model parameter estimates (Estimate), standard error (STD. Error) and confidence intervals (CI 2.50% and CI 97.5%)intervals. Parameters where estimated 95% confidence intervals do not overlap with zero are highlighted in bold.

PARAMETERS	ESTIMATE	STD. ERROR	2.50%	97.50%
(INTERCEPT)	**17.51**	**3.39**	**10.86**	**24.15**
MINIMUM TEMPERATURE	**0.64**	**0.31**	**0.04**	**1.25**
PRECIPITATION	**0.68**	**0.31**	**0.07**	**1.29**
LAY DATE	**-0.07**	**0.02**	**-0.10**	**-0.03**
PRECANOPY CLOSURE OPEN HABITAT WITHIN 3KM (HA)	-0.31	0.30	-0.90	0.27
PERMANENTLY OPEN HABITAT WITHIN 3KM (HA)	**1.49**	**0.48**	**0.54**	**2.44**
SEMI-NATURAL GRASSLAND WITHIN 3KM (HA)	**-0.67**	**0.24**	**-1.15**	**-0.19**
UPLAND VEGETATION WITHIN 3KM (HA)	**0.90**	**0.37**	**0.16**	**1.63**
URBAN WITHIN 3KM (HA)	0.03	0.33	-0.63	0.68
NEST AGE	**-0.20**	**0.06**	**-0.32**	**-0.07**
NEST AGE ^3	0.00	0.00	0.00	0.00
MINIMUM TEMPERATIRE X PRECIPITATION	**0.69**	**0.24**	**0.22**	**1.16**

5.4.3 Disturbance effects on daily survival rate (DSR)

Of the models investigating potential construction and operational disturbance impacts on the success of the egg, chick and combined nesting periods, only the egg stage operational disturbance model was ranked as performing better than its equivalent environment-only parameter model. The egg stage operational model was separated by greater than 2 AICc units from both the construction disturbance and environment only models. This model identified an important large interaction effect between distance to nearest track and if a nest was in an operational wind farm year (β= -

2.04, (± 0.74 SE), see Tables 5.2-5.5 and Figure 5.2). This means that as the distance between nest sites and tracks increased at operational sites, nests were less likely to be successful.

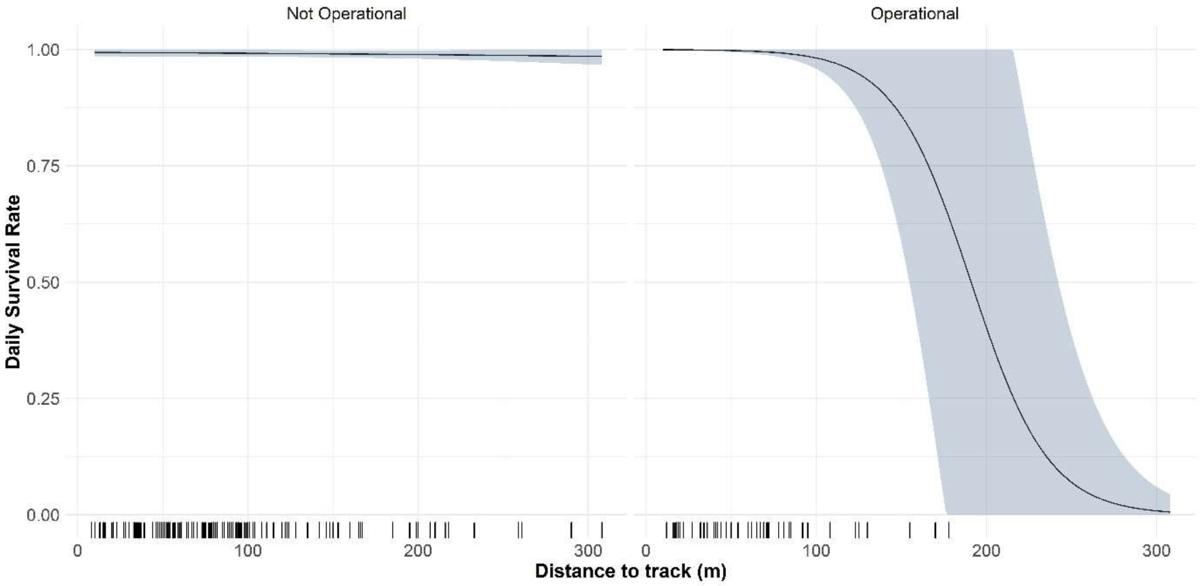


Figure 5.2 Egg stage model predicted DSR vs distance to track at operational and non-operational wind farm sites. Predictions were generated with all other variables held at their mean/ median values.

5.4.4 Environmental effects on daily survival rate (DSR)

The best performing combined (egg and chick stage) nest survival model and chick stage model identified effects of both weather and habitat on daily nest survival (DSR), whereas the best performing egg stage model only identified an effect of weather. This suggests that weather, as represented by mean minimum temperature and mean precipitation, is important across the nesting cycle but that habitat extent is of greater importance during the chick rearing period (See Tables 5.2-5.4).

The interactive effects of minimum temperature and precipitation had an important effect on nest survival in all models (β = 0.79 ± 0.20 SE) with a magnitude similar to that of the most important habitat parameters (see Figure 5.2 – 5.4). The magnitude of this effect, whilst still important, decreased in the chick stage only model (β = 0.69 ± 0.24 SE). This interaction identified a predominantly positive effect of minimum temperature on nest survival except at low levels of rainfall (See Figure 5.2-5.4) and a negative effect of increased precipitation when coupled with lower minimum temperatures in all models (See Figure 5.3 for example from the combined stage model).

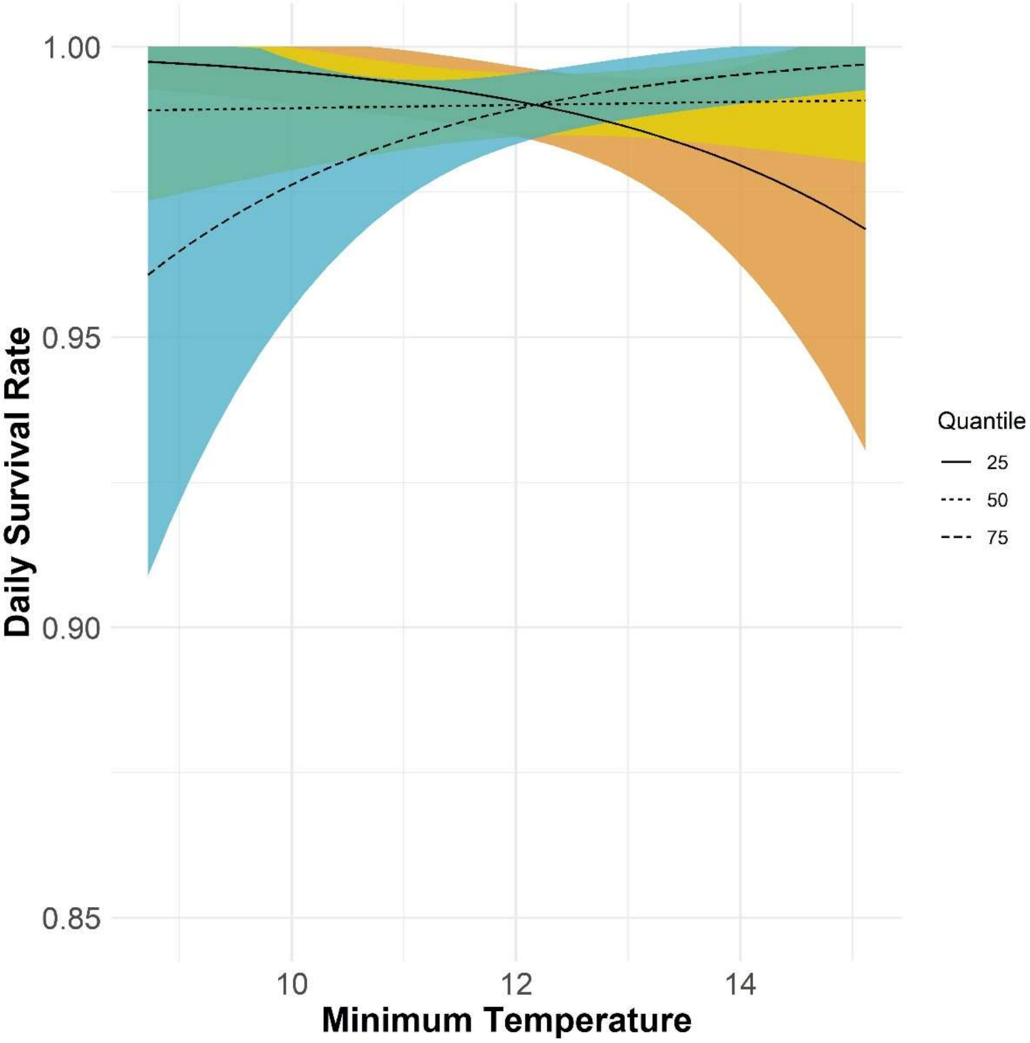


Figure 5.3 Combined model predicted DSR and its standard error vs mean minimum temperature (°C) at 25% (Red), 50% (Yellow) and 75% (Blue) quantile precipitation. Predictions were generated with all other variables held at their mean/ median values.

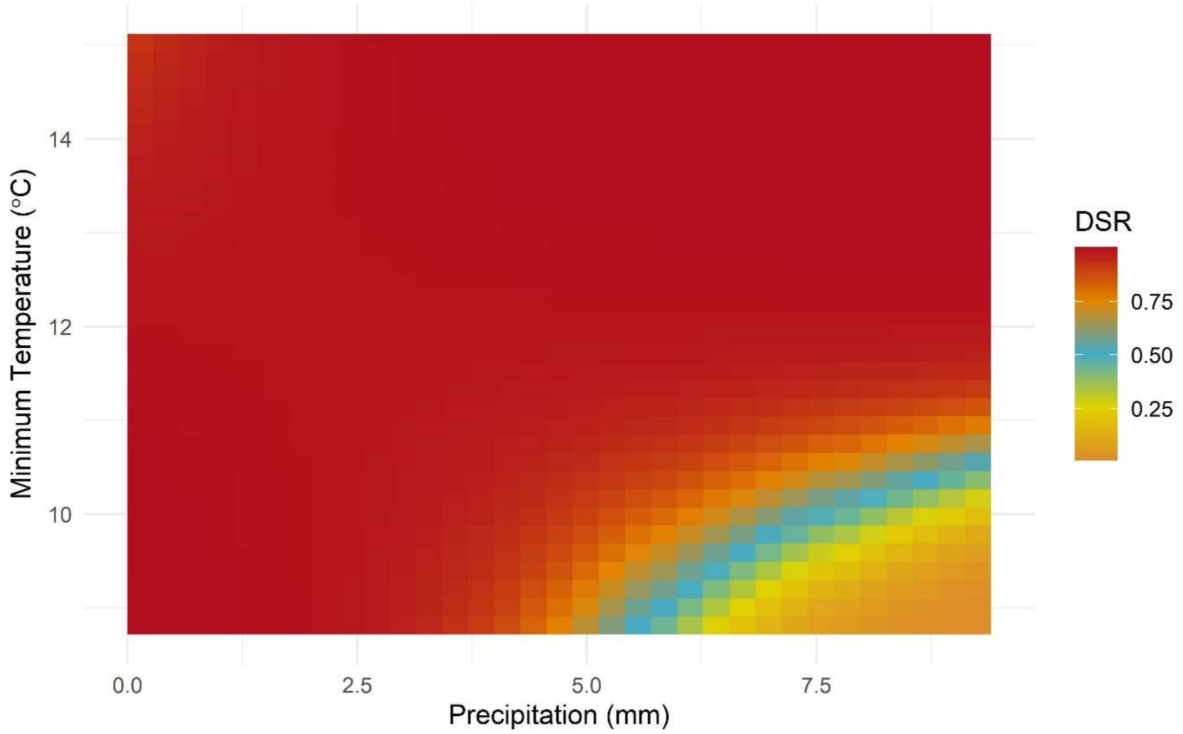


Figure 5.4 Combined model predicted Daily Survival Rate (DSR) across the range of mean minimum temperature and mean precipitation, with all other variables held at their mean/ median value.

Habitat also had a significant effect on DSR in both combined and chick stage models, but not in the egg stage model. DSR increased with the extent of permanently open habitat within 3km of the nest site for both the combined and chick stage models, with a larger magnitude effect noted in the chick stage model (Combined β = 0.81 ± 0.24 SE, Chick β = 1.49 ± 0.48 SE; Figures 5.5 and 5.6). DSR also increased with the extent of upland vegetation within 3km of the nest site (Combined β = 0.62 ± 0.26 SE, Chick β = 0.90 ± 0.37 SE). The chick stage model identified an important but smaller magnitude negative effect of semi-natural grassland extents on daily survival rate (chick β = -0.67 ± 0.24 SE).

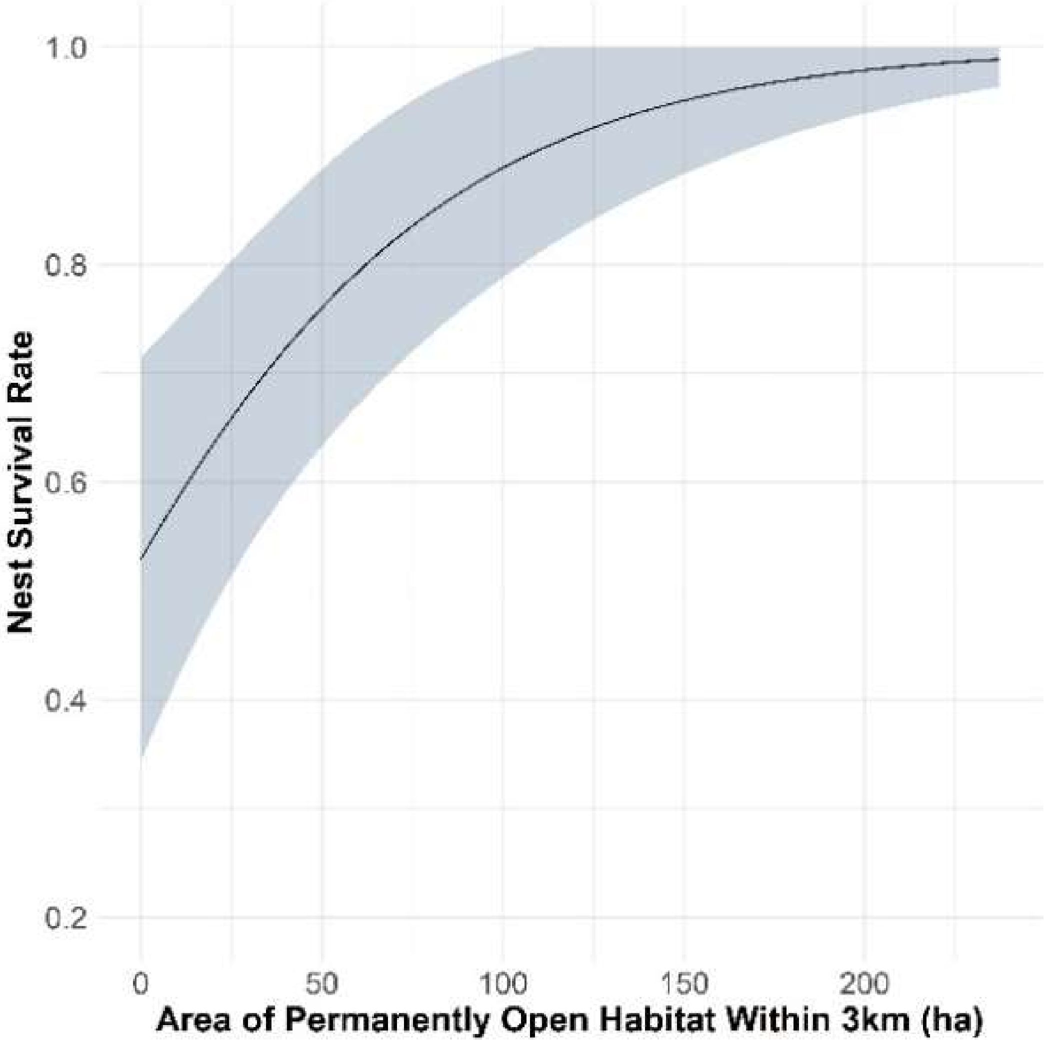


Figure 5.5 Combined stage model predicted nest survival rate (DSR^36) vs area of permanently open habitat (ha) with all other variables at their mean/ median value.

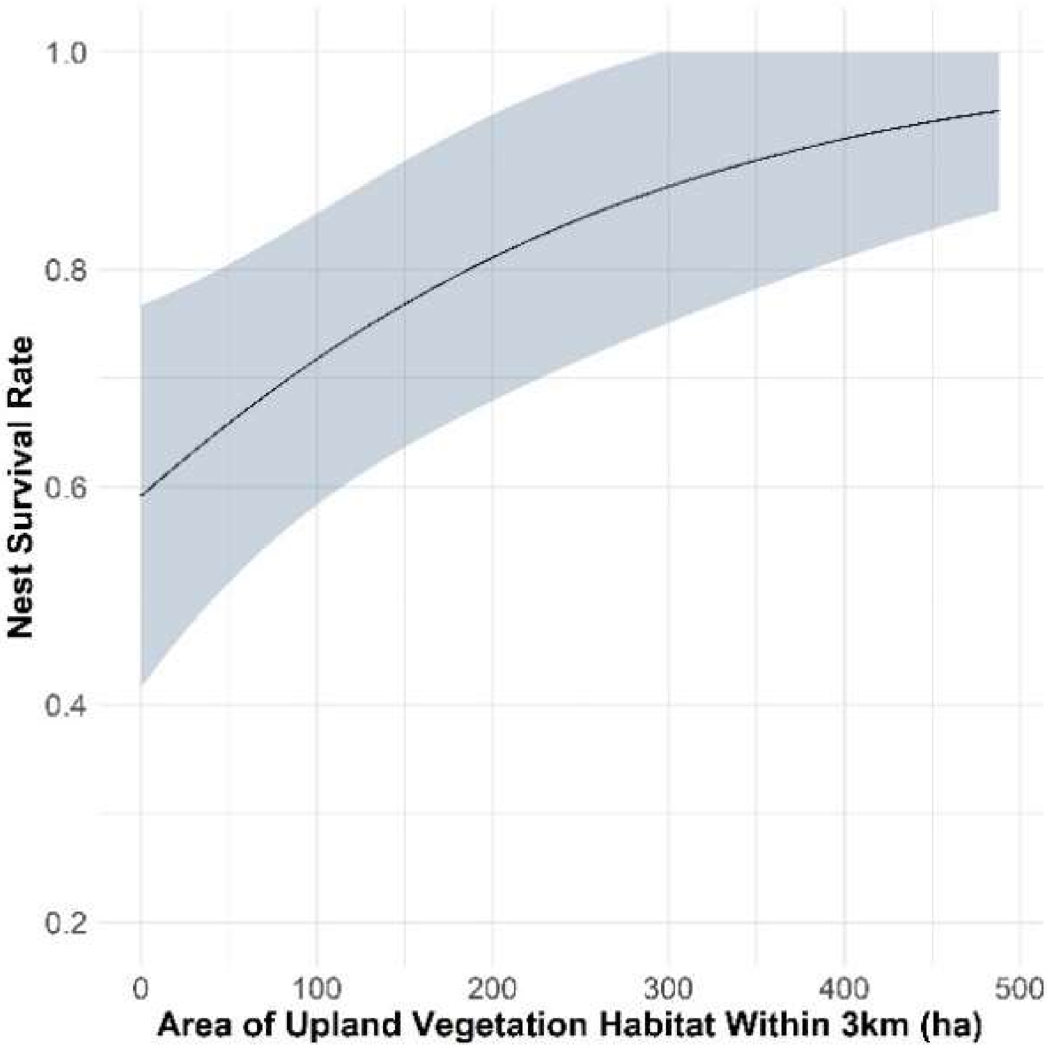


Figure 5.6 Combined stage model predicted nest survival rate (DSR^36) vs area of upland habitat (ha) with all other variables at their mean/ median value

5.4.5 Time effects on daily nest survival

The best performing combined (egg and chick stage) nest survival model and chick stage model identified important effects of laying date on daily nest survival (DSR), with the best performing chick stage model also identifying an effect of nest age. The best performing egg stage model identified no effect of laying date or nest age on DSR (See Tables 5.3).

Laying date had a relatively small, negative relationship with DSR in both chick and combined models (Combined $\beta = -0.04 \pm 0.01$, Chick $\beta = -0.07 \pm 0.02$; Figures 5.7 and 5.8; Tables 5.2-5.5). The effect of nest age was again negative (Chick $\beta = -0.20 \pm 0.06$) and of a greater magnitude than laying date (see Tables 5.2-5.5 and Figure 5.9).

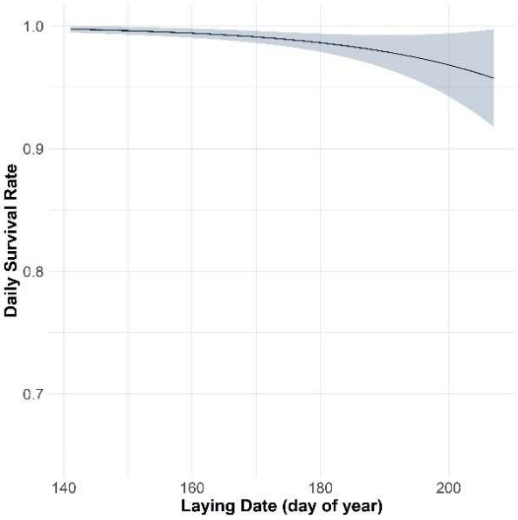


Figure 5.7 Combined stage environmental model predicted DSR vs laying date with all other variables held at their mean/ median value.

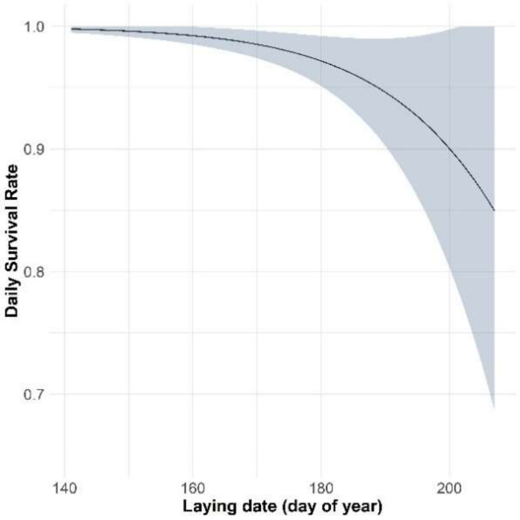


Figure 5.8 Chick stage environmental model predicted DSR vs laying date with all other variables held at their mean/ median value.

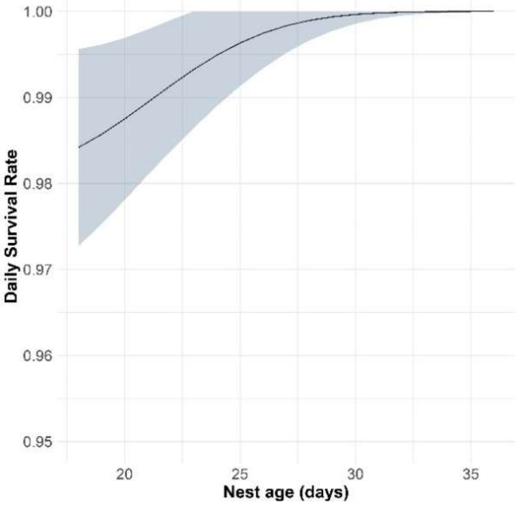


Figure 5.9 Chick stage environmental model predicted DSR vs nest age post hatching (>18 days) with all other variables held at their mean/ median value

5.5 Discussion

I investigated survival of nightjar nests, eggs and chicks, representing critical periods of the life cycle, and specifically how survival rates are affected by environmental factors coupled with potential disturbance due to construction and wind farm operation. Nightjar nest survival at my study sites was relatively high (69%) and compares favourably with those reported by other studies e.g. Langston et al. (2007) estimated overall nesting success to be 39% in the Dorset heathlands, whereas Lowe et al. (2014) estimated success at 53% in Nottinghamshire plantation forestry sites. This relatively high nest survival compared to other study sites is intriguing, and shows that Welsh conifer plantations should be viewed as a productive part of the nightjar range in the U.K., crucial to maintaining the national population in the long term.

A key aim of my study was the investigation of wind farm construction and operation disturbance on nest success. I identified no evidence of construction phase disturbance effects on nest success at any stage of the nesting cycle. No previous studies have looked at this in European nightjar, however studies in other species have shown that construction can have significantly greater effects than operation on populations of some species (Pearce-Higgins et al. 2012) and negative effects on nest success have also been noted (Sutter et al. 2016). These results are, however, only relevant in the context of the mitigation measures implemented at my study sites, which included no works disturbance buffer zones of between 50 and 150m around nests. Where such buffers are not implemented, such as in general U.K. forestry practice where European nightjar nests are not routinely located (Personal communication Iolo Loyd at Natural Resources Wales), then disturbance may result in a negative impact on nest success. Further research into the potential impacts of forestry management on nightjar nest success would be helpful to accurately quantify the impact of such disturbance.

Unfortunately, it was not possible to fully explore the potential effects of operational disturbance due to a lack of model convergence for both combined and chick stage models. These models were intended to tease apart the relative effects of habitat, weather and the potential 'press' disturbance impact of operational wind farm activity. The failure to converge was possibly due to relatively low sample sizes at operational wind farm sites (n=46) and as such future research in this area would be warranted. Indeed, studies in other species of nest survival at operational wind farm sites, have shown mixed results, with no negative effects noted in some species (e.g. Hatchett et al. 2013; Hale et al. 2014) but negative effects on nest survival and fledging success noted in others (e.g. LeBeau et al. 2014; Kolar et al. 2016). This suggests that responses to such disturbances are species specific, and thus require species-specific research to inform impact assessment.

The operational disturbance egg stage model was, however, selected as the best performing egg stage model. Interestingly, this showed evidence of enhanced survival of nests closer to tracks at operational wind farm sites. This result is surprising, given the potential for disturbance associated with tracks and their other potential negative effects e.g. increased predator density (Gómez-Catasús et al. 2021). Similar positive effects of proximity to tracks have been noted in other systems where reduced brood parasitism has been noted as the mechanism (Bennett et al. 2014). It is possible that in this study operational activity is having a positive effect through reducing predation pressure by egg predators (e.g. perhaps by a reduction in Jay *Garrulus garrulous* density, due to felling). It should however be noted that in our study there were very few nest sites at operational wind farms >200m from tracks and as such the extrapolation of the model beyond this point should be viewed with some caution.

Weather was shown to be important in determining nightjar nest success, with both minimum temperature and precipitation interacting to affect nest survival. A similar relationship between nest survival and minimum temperature has been noted previously for a number of nightjar species(whip-poor-will *Antrostomus vociferous*- English et al. 2018; European nightjar Shewring et al. 2021) but no previous negative relationship with precipitation has been identified, although negative impacts of precipitation are known from other species such as Lark Bunting *Calamospiza melanocorys* and a variety of grassland bird species (Skagen & Adams, 2012; Zuckerberg et al. 2018). This effect is not surprising given the noted negative impacts of rainfall on moth activity especially when in combination with low temperatures (Holyoak et al. 1997; Chapter 2) and given the potential for these conditions to also impact chick survival (English et al. 2018).

My results also suggest that the availability of habitat is a key driver of nest success in nightjar at upland coniferous plantation sites in Wales, and of particular importance at the chick stage. The extent of permanent, or long-term, open habitats within the forest matrix and located within foraging distance of the nest site (~3km, see Chapter 3 and Evens et al. 2018) was the most important habitat variable (by magnitude) in predicting daily survival, and survival increased as the extent of this habitat increased. A similar pattern was also associated with upland vegetation types. This is consistent with results from Chapter 2, where I found peaks in biomass associated with habitats in forest open habitats >20 years old, although the present analysis does not reflect the similarly identified peak in moth biomass associated with habitats ~10 years post felling, described in Chapter 2. This suggests that the actual mechanism behind this increased nest survival is due to a greater foraging resource and foraging success, and it is likely this is similar for upland vegetation types where semi-natural habitats such as bog and heath are likely to support greater moth biomass than alternative more intensively managed habitats (See Chapter 3, Henderson et al. 2013).

It is also evident from the modelling results that time (day of year) and nest age have an important effect on nest survival with nests initiated later in the season generally being less successful. The best performing chick stage model also identified an important effect of nest age, with daily survival increasing significantly as nest age increased. This result shows that as chicks grow older their probability of survival increases, suggesting that they become more resilient with age. Similar patterns of nest age effects on survival were noted in my analysis detailed in Chapter 2 (Shewring et al. 2020) and have also been noted in other species (e.g. Dove species; Saad et al. (2020) and Northern Bobwhite *Colinus virginianus*; Terhune et al. (2019), suggesting that this maybe a general effect across many species.

5.5.1 Conclusions

In summary, this chapter builds upon the results of Chapter 1 (Shewring et al. 2020) to confirm that nightjar nest survival is as high, if not higher, in upland coniferous plantation habitats than in traditional nesting habitats (e.g. lowland dry heath). It also indicates that there is no evidence of negative effects on nest survival due to construction phase disturbance, where mitigation measures are adopted. Weather and habitat appear to be key drivers of nightjar nesting success in these plantation habitats. The role of habitat (with similar magnitude to the effect of weather), and in particular the extent of long-term open habitat in the forest matrix, means that factoring this into forest management plans could be highly effective in supporting nightjar populations in commercial forest plantations.

6.0 General Discussion

European Nightjar female incubating two eggs at the Bryn forest block of the Afan Forest Park, South Wales in June 2018.

6.1 Overview of the Chapter

Despite their large size, and predominance in the upland landscapes of Wales, commercial coniferous plantations are probably one of the least studied habitats in the U.K. Whilst they are generally viewed as being of low biodiversity value (Carnus et al., 2003, Plantlife 2012), conifer plantations are key to maintaining European nightjar populations in Wales and the U.K., supporting ~10% of the U.K. nightjar population. There is, however, scant information on the effects of land management choices on the provision of foraging and nesting habitat for this species. It is also apparent that both European and Welsh Government policy is seeking to adapt future management of these plantations to deliver wider societal benefits, alongside timber production, with policy drivers for renewable energy development (Welsh Government 2005) and enhanced ecosystem service provision, including biodiversity conservation (Welsh Government 2018, European Commission 2021). This, alongside the push for increasing the rate and scale of afforestation for carbon sequestration and other purposes (Welsh Government 2018), means there is an urgent need for research into how biodiversity enhancement in coniferous plantation woodland can be delivered, alongside competing (or sometimes complementary) demands for carbon capture, timber production and renewable energy developments.

In this thesis, five large, intensively managed coniferous woodland plantations in Wales, three of which supported operational wind farms, were surveyed for European nightjar and night-active Lepidoptera (moths - a key food source for nightjar). Key nightjar life history metrics were recorded, including nest success and movement patterns through GPS tagging. Alongside this, moth species composition and abundance / biomass were recorded using light trapping. The results and recommendations from this thesis, brought together in this General Discussion chapter, are relevant for forest management, wind farms in plantation woodland, and nightjar conservation. They confirm that with sympathetic management, commercial coniferous forestry plantations may be an important habitat for many moth species, and a key habitat for European nightjar in Wales and the U.K.

6.2 Chapter 2 – Tag effects on nest survival

In this chapter, I use nest success data from the Brechfa West wind farm site to investigate tag effects and confirm the lack of observable effects on nest survival when using tail mounted radio tags. This confirms that the continued use of low weight (<3 % bodyweight) tail mounted tracking tags in nightjar studies is unlikely to have a negative impact on nest survival. It should be noted that as my study utilised relatively small tail mounted radio tags (< 1.5g) it is not suitable to extrapolate the findings of this study to other mounting methods (e.g. backpack harness mounted tags, or leg loop harness mounted tags) which orientate/distribute the load differently in relation to the centre of gravity, or to tags with significantly greater mass - as these are known to change the effects on an individual's flight characteristics (Vandenabeele et al. 2012, 2014). This also means that where such tags are proposed for deployment on nightjars, that further studies of potential tag impacts would be warranted.

It should also be understood that the lack of impact on nest survival may not mean a lack of impact overall, and further study is required to investigate the potential effects of tags on individual behaviour and overwinter survival. This is required as nightjars moult in their winter range and thus must carry any plumage-mounted (or harness- mounted) tag on their southward post breeding migration. It is, already, likely that given the sustained ringing and radio tagging effort on nightjar in Wales over the last decade that a suitable dataset exists to explore any such tag effects on overwinter survival, and this should be a key priority for future work. Recent advances in "drop-off" tag technology (e.g. Evens et al. 2018) do however provide a potential alternative to tags that remain attached for the migration period, and where no migration data is being gathered then this approach should be adopted to minimise risk.

It is also possible that tag impacts occur through impaired flight performance, resulting in decreased foraging success or increased predation risk, but these costs may be compensated for through greater energy expenditure by the individual. This could result in a lack of observable effects on nest survival but lower individual fitness and long-term survival. Again it should be possible to explore such effects using existing datasets, and this should be a key priority for future work on nightjar.

This chapter also confirms the importance of temperature in determining nest success in this species, suggesting that pole-wards range expansion is a likely outcome of climate change across the European nightjar's range, as average temperatures increase.

6.3 Chapter 3 – Moth diversity and biomass within plantations

In this chapter, I use moth abundance data (based on moth trapping) to demonstrate that forest management can influence not only the abundance of moth species of conservation concern, but also the availability of moth biomass as a foraging resource for European nightjars and other insectivorous species. My results confirm the importance of forest management on moth biomass and abundance of “Section 7” (Section 7 of the Environment (Wales) Act (2016)) listed species of conservation concern. I show that moth biomass increases with the age of open habitat both within the productive forest cycle (i.e. clear fell through to pre-thicket stage crop) and within more long term open habitats as they are converted from crop to open habitat (i.e. rides, glades etc), and that this relationship is stronger where the vegetation is more seasonally productive, i.e. supporting a higher abundance of ruderal annual species and deciduous scrub / woodland species (e.g. Willow *Salix* sp.) and a lower cover of coniferous tree species. My results also confirm the importance of forest open habitats for conservation priority moth species, with the abundance of Section 7 listed moth species also increasing with time since felling in open habitats.

These results also suggest that forest structure at the regional and national scale can be beneficial to moth species of conservation concern (i.e. Section 7 species) and also have cascading effects for moth-eating aerial insectivores such as the European nightjar (Evens et al., 2018). Taken together, this means that with sympathetic management at the landscape, regional and national scales, forest plantations may help support aerial insectivore species conservation through a bottom up, foraging habitat enhancement approach, as suggested by Nebel et al. (2020). Achieved through both management of the productive forest cycle elements of a forest alongside the creation of non-forest permanently open habitats within the forest matrix.

6.4 Chapter 4 – Nightjar movement in response to biomass

In this chapter, I use GPS tag data from 25 individual nightjar at five sites across Wales, to investigate the effects of moth biomass and biomass variation in determining foraging habitat selection. To do this, I use a resource source selection function (use vs. availability) analysis approach (Manly et al., 2007, Muff et al., 2020). The results of this analysis clearly identify the importance to nightjar of moth biomass within open habitats in the forest matrix, with the probability of presence of foraging nightjars increasing as moth biomass increases. They also identify the importance of the variation in this moth biomass determining foraging probability, with birds selecting either consistently low variation habitats, or high variation with low productivity habitats, and generally avoiding low productivity with low variation habitats. To my knowledge this is also one of the first studies for any terrestrial bird species where movement data have been explicitly linked to food availability.

In summary, it is likely that moth biomass in open habitats within the forest matrix, as driven by habitat age and vegetation productivity (as investigated in Chapter 3), is of critical importance in determining where nightjar forage. Food availability has cascading impacts on other life history metrics for nightjar (e.g. fledging probability), so this finding confirms that sympathetic forest management to increase available moth biomass will provide important benefits for nightjar, and will likely have additional cascading benefits for other aerial insectivores in plantation forest habitats (e.g. bat species - Kirkpatrick et al., 2017b). This also suggests that conservation strategies for nightjar in more “traditional” habitats (i.e. habitats in which they were previously most abundant), such as lowland heath, would benefit from a focus on providing high moth biomass productivity, in nightjar foraging habitat in close proximity to nesting habitat. This could be achieved through the adoption of measures to support moths, such as reducing crop pesticide application and reduction / removal of artificial light at night (Fox 2013; Boyes et al., 2021).

6.5 Chapter 5 – Nightjar nest success

In this chapter, I use nightjar nest monitoring data from five sites across Wales to investigate the potential impacts of habitat availability on nesting nightjar nest success, alongside potential disturbance effects as a result of wind farm construction.

I confirm that construction phase disturbance had no detectable effect on nest success at any of the study sites where mitigation measures consisting of a 150-200m disturbance buffer are utilised, although unfortunately I was unable to resolve the potential for operational disturbance impacts due to analytical constraints (model convergence issues).

This work also identified the critical importance of weather in determining nightjar nest success, with both minimum temperature and precipitation interacting to affect nest survival (as has been noted previously; English et al., 2018, Chapter 2 / Shewring et al., 2020). It is also clear from these results that the availability of foraging habitat is a key driver of nest success in nightjar at upland coniferous plantation sites in Wales and of particular importance at the chick stage. In particular, the extent of long-term open habitats within the forest matrix, and upland vegetation types in the vicinity (< ~3km), were key drivers of nightjar daily nest survival.

6.6 Key management recommendations

6.6.1 Chapter 3 – Key recommendations to support biodiversity within plantations

The results of my analysis in Chapter 3 confirm the importance of forest management in determining moth biomass and abundance of “Section 7” listed moth species of conservation concern. These results identify the importance of open habitat age, and the seasonal productivity of vegetation in influencing moth abundance and diversity. These findings suggest management strategies which may better support moths and other invertebrate species, and provides potential opportunities for forest managers and the commercial timber industry in general to improve the biodiversity provisioning through relatively minor changes to their forest management regimes. Specific management actions/ interventions that could be adopted are detailed in the following paragraphs and summarised in Box 1 below.

Given the importance of open habitat age to both moth biomass and species diversity with the productive forest part of the forest cycle, and the noted peaks in both of these moth indicators in the forest age brackets of 2-10 years post-harvest, as well as in areas of permanently open habitat, then the spatial and temporal patterns of felling is of key importance. The manipulation of both the spatial pattern and temporal pattern would allow forest managers to design forest structures to support moth populations and species conservation as part of the long term forest design process. Specifically, forest managers should aim to retain consistent extents of open habitats of various age classes post felling, particularly including the key age bracket of 2-10 years post-harvest, as well extents of permanently open habitat.

The importance of vegetation seasonality to biomass productivity also suggests that open areas with a greater cover of broadleaved tree species (native species in the Welsh context) are likely to also support greater moth biomass and thus be relatively more important for aerial insectivores that prey on them. As such, measures to increase broadleaved tree cover in open habitats would likely be beneficial. This could include the planting and / or natural regeneration of native broadleaved species, coupled with the removal of commercial conifer crop species from open habitats.

The combination of these factors confirms the value of forest open areas to moth biomass and diversity, with a specific importance for a suite of early successional habitat specialist moth species of conservation importance. The dynamic nature of this habitat and the fact that it develops through time also suggests that forest management should avoid forest-wide transitions to stable habitat systems such as continuous cover forestry, where the frequency of early successional habitat creation will be greatly reduced, especially where the supporting of moth species and aerial insectivores is a desired management objective.

Box 1. - Key recommendations to support biodiversity within plantations

1. Forest managers should aim to retain consistent extents of open habitats of various age classes post felling, with key age brackets being 2-10 years post-harvest;
2. Remove conifer regeneration / seed throw in open habitats and / or plant or encourage regeneration of native broadleaved species;
3. Avoid forest-wide transitions to continuous cover forestry systems.

6.6.2 Chapter 4 - Key recommendations to support aerial insectivores

The results of this analysis clearly identify the importance to nightjar of moth biomass within open habitats in the forest matrix, alongside the importance of the variation in this moth biomass in determining foraging habitat selection by nightjar. In general, foraging birds avoided low productivity, low variation moth biomass habitats and foraged more often in higher biomass productivity areas. Specific management actions / interventions that could be adopted are detailed in the subsequent paragraphs and summarised in Box 2 below.

It is likely that forest management to increase available moth biomass will provide important benefits for nightjar, as well as other aerial insectivores, providing opportunities for forest managers to adopt sympathetic management measures (such as detailed in section 6.61 above) that benefit moth species, nightjar, and aerial insectivores in general. This general response of foraging behaviour to available moth biomass does, however, also provide additional opportunities to support nightjar specifically, with likely cascading benefits for other aerial insectivores. Specific management actions / interventions that could be adopted are detailed in the subsequent paragraphs and summarised in Box 2 below.

For example, the spatial and temporal manipulation of planned felling to drive the spatial distribution of habitats producing high moth biomass could be used to provide attractive foraging habitat in close proximity to suitable nesting habitat or known favoured nesting locations. This would minimise energy expenditure during foraging for individuals and thus help support nightjar breeding populations. This could be achieved through the retention of consistent extents of open habitat of various age classes post felling (key age brackets being 2-10 years post-harvest) within 2 km of areas of nightjar nesting habitat. Creating such spatial arrangements may be achieved through the spatial clustering of stand harvest (within a 1-2 km area) and temporal separation of harvesting in the same spatial cluster (5-10 years separation) to create structural diversity.

Additionally, this element of spatial and temporal design of forest habitats may also provide an opportunity to 'guide' or attract aerial insectivores away from areas of risk (e.g. the rotor swept areas of wind turbines or busy roads). This strategy may be of key interest where conflicts occur such as in the case of bat mortality at wind turbines (Rydell et al. 2010).

Box 2. - Key recommendations to support aerial insectivores

4. Remove conifer regeneration/ seed throw in open habitats;
5. Retain consistent extents of open habitats of various age classes post felling (key age brackets 2-10 years) within 2 km of areas nightjar nesting habitat.

6.6.3 Chapter 5 - Key recommendations to support European nightjar nest success

The results of this analysis identified no significant effects of construction phase disturbance on nest survival, in the presence of standard no works mitigation buffers of 150-200m. It also identified the critical importance of weather (minimum temperature and precipitation) in determining nightjar nest success. These factors, alongside the availability of foraging habitat (long-term open habitats and upland vegetation) are identified as key drivers of nest success in nightjar at upland coniferous plantation sites in Wales, particularly at the chick stage. How these results can be fed into specific management actions / interventions for adoption are detailed in the subsequent paragraphs and summarised in Box 2 below.

Perhaps the simplest measures to feed from the thesis results into management strategies are those around construction phase disturbance. My results suggest that where wind farm developments are located in suitable European nightjar nesting habitat, then in order to minimise disturbance active nests should be located and a disturbance buffer of a minimum of 150 m be implemented for the duration of the nesting cycle.

In addition to the lack of a disturbance of effect, I also identified the key importance of weather on nest survival. Whilst there are few practical management interventions that can be implemented to mitigate weather effects on nest success, it is recommended that future species monitoring and development in nightjar habitats acknowledges the potential for interaction and amplification of nest disturbance with 'poor' (e.g. cold and / or wet) weather, and adopts strategies that minimise such risks. This could include avoiding nest monitoring visits, nest finding surveys or other potential disturbing operations during cool and wet weather.

The identified importance of foraging habitat availability to nest success is, however, something that can feed through into forest management recommendations alongside those detailed above, to support moth priority species / biomass, and aerial insectivores. My results suggest that forest managers should aim to retain consistent extents of open habitats of various age classes post felling, including permanently open habitats within 3 km of known nesting habitat, in order to support nightjar breeding success.

Box 3. - Key recommendations to support nightjar nest success

6. Wind farm developments in European nightjar nesting habitat should use a disturbance buffer of a minimum of 150-200 m from active nest sites, to minimise construction phase disturbance impacts;
7. Nest disturbance during cool and wet weather should be avoided due to the potential for combined negative effects of weather and disturbance on nest survival;
8. Forest managers should aim to retain consistent extents of open habitats of various age classes post felling, including permanently open habitats within 3 km of known nesting habitat.

6.6.4 Management risks

Few species solely rely on large extensive stands of mature coniferous woodland. However, in the U.K., and Wales in particular, red squirrel *Sciurus vulgaris* are increasingly restricted to large conifer woodlands and plantations, due to competition from encroaching grey squirrels *Sciurus carolinensis*. The red squirrel is protected under Schedule 5 of the U.K. Wildlife & Countryside Act (1981) and is listed as a priority species in Section 7 of the Environment Act (Wales) 2016. In general, it is recommended that the extent of conifer cover is maintained in regions containing red squirrel, to maintain current populations (Shuttleworth et al., 2012) and as such, the key management recommendations for nightjar and moths detailed above may not be suitable in key areas for red squirrel.

The spatial distribution of red squirrel in Wales is, however, restricted -with Anglesey, Clocaenog Forest and the Tywi Forest complex in mid-Wales identified as focal sites for red squirrel conservation action (Wales Squirrel Forum, 2018), and as such, outside of these areas my recommendations could be implemented with minimal risk to red squirrels.

6.7 The European Nightjar - moth - plantation forestry system as a monitoring tool

Cost effective monitoring is required, as in all conservation management works (Sutherland et al., 2004), to appraise the outcomes of management interventions to support the conservation of aerial insectivores. The relative simplicity of the nightjar-moth-forest open habitat system and its wider relevance to aerial insectivores make this a potentially good candidate model system for monitoring forestry biodiversity ecosystem services. This is especially so given the relevance of remotely sensed data to the productivity of the system (e.g. NDVI is proportional to moth biomass - Chapter 3), suggesting that such monitoring could be completed, at least in part, through remotely sensed data analysis and interpretation, thereby reducing monitoring costs. This - perhaps coupled with lower frequency surveys for moth biomass and nightjar presence - could be combined in a formal framework (i.e. “data fusion” (Wald, 1999)), as has been suggested for biodiversity monitoring elsewhere (Luque et al., 2018), providing overall higher quality data than singular monitoring approaches. This could allow open habitats within the forest matrix to be monitored at a national scale, perhaps using an occupancy modelling approach (Mackenzie et al., 2002) and benefits to aerial insectivore populations to be inferred, and would contribute to the evidence base for biodiversity ecosystem service delivery from plantation forest habitats.

Currently, coniferous plantation biodiversity monitoring is undertaken at a national level by Forest Research as part of the national forest inventory (Forest Research 2020a), using methods as set out in Forest Research (2020b) NFI woodland ecological condition in Great Britain: Methodology. This approach contains an element of monitoring open space according to the proportional cover of open space within the forest, adjusted according to the quality of the open space present, based on habitat and land use type. As such, the “data fusion” approach described above could be integrated into the NFI monitoring methodology, potentially allowing a reduction of field time and thus reducing the costs of such monitoring.

6.8 Future directions

As discussed above, the simplicity of the study system, its relevance to a wider suite of aerial insectivores and other insectivorous species, coupled with the direction of woodland policy seeking to increase the provision of biodiversity ecosystem services (Welsh Government 2018), together make further research in this area likely to be highly relevant to land management and policy development. This includes not only the development of forestry land management strategies to support insects and aerial insectivores, but also wider research into how these can be combined with other land uses (renewable energy, recreational access) to deliver biodiversity and wider ecosystem service benefits. It is also clear, however, that large areas of the nightjar lifecycle and the species behaviour and ecology remain unknown and would warrant further research.

In addition, some issues addressed by the research presented in this thesis remain unresolved. For example, I was unable to test the potential effects of operational wind farm disturbance on nest success in European nightjar due to the lack of convergence in chick stage models and combined (chick and egg stage) models. Further work in this area would be warranted (requiring even larger datasets) and would help to inform the long-term risks to nightjar of wind farm development in upland plantation habitats. The coupling of this line of research with studies of recreational access activity levels and type (e.g. walking, mountain biking, horse riding) would also be a productive area of study, and would help inform the delivery of biodiversity-sensitive cultural ecosystem services, within timber and energy-productive landscapes. It is also apparent that where wind farms are “key-holed” into productive forest habitats, the habitats that develop in the open spaces around turbines (in the absence of management) will support invertebrate biomass that may be attractive to a suite of aerial insectivores (See Chapters 3 & 4). This may have the unwanted effect of attracting aerial insectivores towards turbines in plantation forest habitats and act as an ecological trap (Gates & Gysel 1978) for aerial insectivores that are susceptible to collision risk (Drewitt & Langston, 2006).

It should also be acknowledged that the approaches used to study nest and chick survival in my study are focused on the egg and pre-fledging chick periods, and that the factors driving chick survival post fledging may be different. Thus, this stage of chick development would certainly warrant more focused research, although it does pose significant logistical challenges given the mobile nature of nightjar chicks at this stage. Alongside this breeding season predation rates of adults are also largely unknown, as well as how this influences nest success, with only anecdotal reports from field workers of Tawny owl (*Strix aluco)*, Long-eared owl (*Asio otus)* and Goshawk (*Accipiter gentilis)* being attracted to tape lures suggesting predation by these species in upland plantation landscapes. Thus interaction of nightjar populations, nests and individuals with the distribution and abundance of these predator species would also warrant further study.

We also know little of the actual mechanisms behind nest failure; the correlation with poor weather may suggest a linkage with thermoregulation, but it is currently impossible to rule out food availability as an alternative explanation, and as such further research into the mechanisms is certainly warranted. There is also little known of nest predators and nest predation rates in these upland clear fell habitats although anecdotal and field evidence suggests nest predation largely by Red fox (*Vulpes vulpes),* although flushing/ predation by sheep (*Ovis aries)* and deer (*Cervidae*) is also suspected. Additional work in this area would be warranted and interesting to pursue, perhaps through the use of nest cameras. This would however require a significant number of cameras and nests given the relatively high nest survival rate at my sites and thus would be a non-trivial undertaking.

The present study also identifies a clear need for more fundamental research on the ecology of European nightjar. Information on the role of migratory pathways, and wintering habitat landscape change, in influencing population trends is lacking, and this is likely to be important for the future conservation of this species - given the great changes to climate and land use envisioned in Africa in the coming decades (Biggs et al., 2008). Also, despite a recent number of tracking studies focused on migration (Evens et al., 2017, Norevik et al., 2017, Norevik et al., 2021), additional fundamental research on migratory strategies is needed to explore phenotypic variation in migratory behaviour of European nightjar, how this varies across populations, and how this variation may interact with conservation objectives.

In addition, despite the widespread research on this species in its breeding grounds there is still little known on the fundamental demographic metrics of the species, for example it is known that European nightjar can live up to 12 years, and that average survival is ~4 years (Holyoak 2001, Robinson 2005). However, there is nothing known on the spatial and temporal variation in adult survival and the factors that may be key drivers in this; for example is this driven mainly by factors on the wintering grounds, factors during the migration stage, or breeding season energetic costs.

Potential future research directions are, however, not limited to the fundamental biology of the species. The identification of a clear seasonal trend in moth biomass productivity in forest open habitats raises the possibility of phenological mismatch (Renner & Zohner, 2018) between moth availability and the timing of breeding in European nightjar, especially if the seasonal trend in moth biomass is largely driven by temperature-induced primary productivity. Further long-term monitoring of vegetation growth and moth biomass in plantation forest open habitats is recommended, to investigate the causal factors driving the observed seasonal patterns. The linking of this with future temperature predictions made from General Circulation Models (Flato et al., 2013) under scenarios of increasing atmospheric CO_2, would be a valuable addition to our understanding of the potential impacts of climate change on aerial insectivores in plantation forest habitats. Additional work on the dietary preferences of European nightjar utilising molecular methods (e.g. Evens et al., 2020) would clarify the links between species-level variation in moth availability / biomass and nightjar food availability, foraging behaviour and energetics. This would potentially allow the development of a mechanistic model of the system, which would be the first such model for an aerial insectivore.

It is clear from the literature that vegetation characteristics such as biomass / productivity (Haddad et al., 2001; Ober & Hayes, 2008) may influence patterns of abundance of both diurnal and nocturnal insects, and as such it is reasonable to expect that management to increase nocturnal invertebrate biomass (through increasing vegetation diversity and seasonal productivity – see Chapter 3) would have knock on beneficial effects for the abundance / biomass of diurnal insects as well. As such, it would also be an interesting avenue of research to examine the potential conservation benefits to other aerial insectivores of targeted conservation efforts within the forest matrix. This could include the creation of nesting opportunities (e.g. artificial nestboxes) for species such as Barn Swallow (*Hirundo rustica*) and Swift (*Apus apus*) or bat roost habitat.

6.9 Overall conclusions

In conclusion, it is clear from the evidence in the available literature, and from my work in this thesis, that open habitats within plantation forestry can support important populations of invertebrates and associated aerial insectivores such as European nightjar. In particular, it is clear that appropriately managed coniferous plantation habitat in Wales is key for moth species of conservation concern as well as European nightjar, providing nightjars with high quality nesting habitat in close proximity to foraging habitat, and supporting around 10% of the U.K. nightjar population. I have also been able to identify practical conservation measures that could be implemented by forest managers to support both aerial insectivores and the invertebrates on which they depend. The adoption of these measures would help to deliver Welsh Government ambitions for the Welsh Government Woodland Estate to provide important biodiversity ecosystem services. The continuation of research into the importance of forest open habitats, and their management to support aerial insectivores, would build on this work, and allow the development of further practical conservation interventions to support aerial insectivores.

Appendices

Pen y Cymoedd Wind Farm and forest block with the village of Blaencwm in the foreground

Appendix A - Candidate Model Details

Table A1 - All candidate models of nightjar daily nest survival rates, for a set of independent variables comprising: total rainfall (s_prcp), average temperature (m_temp), nest age (NestAge), time, construction year (ycons), adult female tag status (f_tag), adult male tag status (m_tag), both adult tag status (fm_tag), adult male or female tag status (f_m_tag) and year (2013 to 2019).

MODEL	NPAR	AICC	DELTAAICC	WEIGHT	DEVIANCE
S(~NESTAGE + F_TAG + M_TEMP * TIME + M_PRCP2)	7	170.11	0.00	0.12	156.02
S(~NESTAGE + FM_TAG + M_TEMP * TIME + M_PRCP2)	7	171.27	1.15	0.07	157.17
S(~NESTAGE + M_TEMP * TIME + M_PRCP2)	6	171.86	1.75	0.05	159.79
S(~NESTAGE + F_TAG + M_TEMP * TIME)	6	172.46	2.35	0.04	160.39
S(~NESTAGE + F_TAG + TIME * M_TEMP + M_PRCP2 + BROOD1 + BROOD2 + BROOD3)	10	172.96	2.84	0.03	152.77
S(~NESTAGE + FM_TAG + Y13 + Y14 + Y15 + Y16 + Y17 + Y18	14	173.35	3.23	0.02	144.99

+ Y19 + M_TEMP * TIME + M_PRCP2)					
S(~NESTAGE + FM_TAG + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 + M_PRCP2 + TIME * M_TEMP)	14	173.35	3.23	0.02	144.99
S(~NESTAGE + FM_TAG + M_TEMP * TIME)	6	173.40	3.29	0.02	161.33
S(~NESTAGE + F_TAG + BROOD1 + BROOD2 + BROOD3 + TIME * M_TEMP)	9	173.53	3.42	0.02	155.38
S(~NESTAGE + F_TAG + M_TEMP + M_PRCP2 + TIME)	6	173.58	3.47	0.02	161.51
S(~NESTAGE + F_TAG + TIME)	4	173.60	3.49	0.02	165.57
S(~NESTAGE + M_TEMP * TIME)	5	173.66	3.55	0.02	163.61
S(~F_TAG + TIME)	3	173.80	3.69	0.02	167.78

S(~NESTAGE + F_TAG + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 + M_TEMP * TIME + M_PRCP2)	14	173.80	3.69	0.02	145.45
S(~NESTAGE + F_TAG + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 + M_PRCP2 + TIME * M_TEMP)	14	173.80	3.69	0.02	145.45
S(~NESTAGE + M_TAG + M_TEMP * TIME + M_PRCP2)	7	173.88	3.76	0.02	159.78
S(~NESTAGE + FM_TAG + TIME)	4	173.94	3.82	0.02	165.90
S(~FM_TAG + TIME)	3	173.96	3.85	0.02	167.94
S(~NESTAGE + FM_TAG + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 + M_TEMP * TIME)	13	174.19	4.08	0.02	147.88
S(~NESTAGE + FM_TAG + M_TEMP + M_PRCP2 + TIME)	6	174.20	4.09	0.02	162.13

S(~NESTAGE + M_TEMP + M_PRCP2 + TIME)	5	174.34	4.23	0.01	164.29
S(~F_TAG + M_TEMP * TIME)	5	174.41	4.29	0.01	164.35
S(~NESTAGE + F_TAG + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 + M_TEMP * TIME)	13	174.49	4.38	0.01	148.18
S(~NESTAGE + FM_TAG + TIME * M_TEMP + M_PRCP2 + BROOD1 + BROOD2 + BROOD3)	10	174.50	4.38	0.01	154.31
S(~NESTAGE + FM_TAG + BROOD1 + BROOD2 + BROOD3 + TIME * M_TEMP)	9	174.82	4.70	0.01	156.66
S(~FM_TAG)	2	175.00	4.89	0.01	170.99
S(~F_TAG + NESTAGE * M_TEMP * TIME)	9	175.01	4.90	0.01	156.86
S(~FM_TAG + M_TEMP * TIME)	5	175.09	4.97	0.01	165.04

S(~NESTAGE + TIME * M_TEMP + M_PRCP2 + BROOD1 + BROOD2 + BROOD3)	9	175.29	5.17	0.01	157.13
S(~F_TAG + M_PRCP2 + M_TEMP * TIME)	6	175.37	5.26	0.01	163.30
S(~NESTAGE * M_TEMP * TIME)	8	175.45	5.34	0.01	159.33
S(~F_TAG)	2	175.48	5.36	0.01	171.47
S(~NESTAGE * TIME + M_TEMP + M_PRCP2)	6	175.50	5.39	0.01	163.43
S(~NESTAGE + BROOD1 + BROOD2 + BROOD3 + TIME * M_TEMP)	8	175.55	5.43	0.01	159.42
S(~NESTAGE + M_TAG + M_TEMP * TIME)	6	175.68	5.57	0.01	163.61
S(~NESTAGE + TIME)	3	175.70	5.58	0.01	169.68
S(~FM_TAG + NESTAGE * M_TEMP * TIME)	9	175.72	5.61	0.01	157.57

S(~NESTAGE * M_TEMP * TIME + FM_TAG)	9	175.72	5.61	0.01	157.57
S(~NESTAGE + F_TAG + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 + M_TEMP + M_PRCP2 + TIME)	13	175.87	5.75	0.01	149.55
S(~TIME)	2	175.89	5.77	0.01	171.88
S(~NESTAGE + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 + M_TEMP * TIME + M_PRCP2)	13	175.92	5.80	0.01	149.61
S(~NESTAGE + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 + M_PRCP2 + TIME * M_TEMP)	13	175.92	5.80	0.01	149.61
S(~M_TEMP * TIME)	4	176.09	5.98	0.01	168.06
S(~FM_TAG + M_PRCP2 + M_TEMP * TIME)	6	176.15	6.04	0.01	164.08

S(~NESTAGE + FM_TAG)	3	176.32	6.21	0.01	170.30
S(~NESTAGE + M_TAG + M_TEMP + M_PRCP2 + TIME)	6	176.36	6.25	0.01	164.29
S(~NESTAGE * TIME + M_TEMP + BROOD1 + BROOD2 + BROOD3)	8	176.48	6.37	0.01	160.36
S(~F_TAG + M_TEMP + M_PRCP2 + TIME)	5	176.54	6.42	0.00	166.49
S(~NESTAGE + F_TAG + M_TEMP + M_PRCP2 + TIME + BROOD1 + BROOD2 + BROOD3)	9	176.55	6.44	0.00	158.40
S(~NESTAGE + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 + M_TEMP * TIME)	12	176.62	6.50	0.00	152.35
S(~1)	1	176.65	6.54	0.00	174.65
S(~FM_TAG + M_TEMP + M_PRCP2 + TIME)	5	176.91	6.80	0.00	166.86

S(~NESTAGE + F_TAG)	3	176.91	6.80	0.00	170.89
S(~NESTAGE + F_TAG + TIME + BROOD1 + BROOD2 + BROOD3)	7	177.04	6.93	0.00	162.95
S(~NESTAGE * TIME)	4	177.12	7.01	0.00	169.09
S(~NESTAGE + FM_TAG + M_TEMP + M_PRCP2 + TIME + BROOD1 + BROOD2 + BROOD3)	9	177.14	7.03	0.00	158.99
S(~NESTAGE + M_TAG + TIME * M_TEMP + M_PRCP2 + BROOD1 + BROOD2 + BROOD3)	10	177.25	7.14	0.00	157.07
S(~M_PRCP2 + M_TEMP * TIME)	5	177.31	7.19	0.00	167.25
S(~NESTAGE + M_TEMP + M_PRCP2 + TIME + BROOD1 + BROOD2 + BROOD3)	8	177.37	7.25	0.00	161.24
S(~F_TAG + M_TEMP * TIME + M_PRCP2 + YCONS)	7	177.38	7.26	0.00	163.28

S(~F_TAG + M_PRCP2 + YCONS + TIME * M_TEMP)	7	177.38	7.26	0.00	163.28
S(~NESTAGE + M_TAG + BROOD1 + BROOD2 + BROOD3 + TIME * M_TEMP)	9	177.39	7.27	0.00	159.24
S(~NESTAGE + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 + M_TEMP + M_PRCP2 + TIME)	12	177.39	7.28	0.00	153.13
S(~M_TAG + NESTAGE * M_TEMP * TIME)	9	177.48	7.36	0.00	159.33
S(~NESTAGE * M_TEMP * TIME + M_TAG)	9	177.48	7.36	0.00	159.33
S(~YCONS + NESTAGE * M_TEMP * TIME)	9	177.48	7.37	0.00	159.33
S(~NESTAGE + FM_TAG + TIME + BROOD1 + BROOD2 + BROOD3)	7	177.53	7.42	0.00	163.44

S(~FM_TAG + M_TEMP * TIME + M_PRCP2 + YCONS)	7	177.62	7.50	0.00	163.52
S(~FM_TAG + M_PRCP2 + YCONS + TIME * M_TEMP)	7	177.62	7.50	0.00	163.52
S(~YCONS + TIME)	3	177.66	7.54	0.00	171.64
S(~NESTAGE + M_TAG + TIME)	4	177.67	7.56	0.00	169.64
S(~NESTAGE + M_TAG + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 + M_TEMP * TIME + M_PRCP2)	14	177.74	7.62	0.00	149.38
S(~NESTAGE + M_TAG + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 + M_PRCP2 + TIME * M_TEMP)	14	177.74	7.62	0.00	149.38
S(~M_TAG + TIME)	3	177.88	7.77	0.00	171.86
S(~F_TAG + BROOD1 + BROOD2 + BROOD3 + TIME * M_TEMP)	8	177.95	7.84	0.00	161.83

S(~NESTAGE)	2	177.97	7.85	0.00	173.96
S(~NESTAGE + F_TAG + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 + TIME * M_TEMP + M_PRCP2 + BROOD1 + BROOD2 + BROOD3)	17	178.09	7.97	0.00	143.56
S(~YCONS + M_TEMP * TIME)	5	178.10	7.98	0.00	168.05
S(~M_TAG + M_TEMP * TIME)	5	178.11	7.99	0.00	168.06
S(~NESTAGE + M_TAG + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 + M_TEMP * TIME)	13	178.24	8.12	0.00	151.93
S(~F_TAG + M_TEMP + M_PRCP2 + YCONS + TIME)	6	178.37	8.25	0.00	166.29
S(~F_TAG + TIME + BROOD1 + BROOD2 + BROOD3)	6	178.44	8.32	0.00	166.36
S(~FM_TAG + M_TEMP + M_PRCP2)	4	178.53	8.42	0.00	170.50

S(~NESTAGE + FM_TAG + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 + TIME * M_TEMP + M_PRCP2 + BROOD1 + BROOD2 + BROOD3)	17	178.55	8.43	0.00	144.02
S(~FM_TAG + TIME + BROOD1 + BROOD2 + BROOD3)	6	178.58	8.46	0.00	166.51
S(~M_TAG)	2	178.66	8.54	0.00	174.65
S(~YCONS)	2	178.66	8.54	0.00	174.65
S(~FM_TAG + M_TEMP + M_PRCP2 + YCONS + TIME)	6	178.91	8.79	0.00	166.83
S(~F_TAG + M_TEMP + M_PRCP2)	4	178.95	8.84	0.00	170.92
S(~M_TEMP * TIME + M_PRCP2 + YCONS)	6	179.10	8.98	0.00	167.02
S(~M_TEMP + M_PRCP2 + YCONS + TIME * M_TEMP)	6	179.10	8.98	0.00	167.02

S(~NESTAGE + M_TAG + M_TEMP + M_PRCP2 + TIME + BROOD1 + BROOD2 + BROOD3)	9	179.31	9.19	0.00	161.15
S(~M_TAG + M_PRCP2 + M_TEMP * TIME)	6	179.32	9.21	0.00	167.25
S(~NESTAGE + FM_TAG + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 + M_TEMP + M_PRCP2 + TIME + BROOD1 + BROOD2 + BROOD3)	16	179.35	9.24	0.00	146.89
S(~NESTAGE * TIME + FM_TAG + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19)	12	179.37	9.25	0.00	155.10
S(~F_TAG + TIME * M_TEMP + M_PRCP2 + BROOD1 + BROOD2 + BROOD3)	9	179.51	9.39	0.00	161.36
S(~NESTAGE + F_TAG + Y13 + Y14 + Y15 +	16	179.75	9.64	0.00	147.29

Y16 + Y17 + Y18 + Y19 + M_TEMP + M_PRCP2 + TIME + BROOD1 + BROOD2 + BROOD3)					
S(~+M_TEMP + M_PRCP2 + YCONS + TIME)	5	179.77	9.65	0.00	169.72
S(~M_TAG + M_TEMP + M_PRCP2 + TIME)	5	179.77	9.66	0.00	169.72
S(~F_TAG + BROOD1 + BROOD2 + BROOD3)	5	179.81	9.70	0.00	169.76
S(~NESTAGE + TIME + BROOD1 + BROOD2 + BROOD3)	6	179.81	9.70	0.00	167.74
S(~NESTAGE + M_TAG)	3	179.98	9.86	0.00	173.96
S(~NESTAGE + FM_TAG + M_TEMP + M_PRCP2)	5	180.08	9.96	0.00	170.03
S(~NESTAGE + FM_TAG + Y13 + Y14 +	11	180.09	9.98	0.00	157.87

Y15 + Y16 + Y17 + Y18 + Y19 + TIME)					
S(~M_TEMP + M_PRCP2)	3	180.10	9.99	0.00	174.08
S(~FM_TAG + TIME * M_TEMP + M_PRCP2 + BROOD1 + BROOD2 + BROOD3)	9	180.47	10.35	0.00	162.31
S(~FM_TAG + M_TEMP + M_PRCP2 + YCONS)	5	180.55	10.44	0.00	170.50
S(~NESTAGE + FM_TAG + BROOD1 + BROOD2 + BROOD3)	6	180.58	10.46	0.00	168.50
S(~NESTAGE + F_TAG + M_TEMP + M_PRCP2)	5	180.58	10.47	0.00	170.53
S(~F_TAG + M_TEMP + M_PRCP2 + YCONS)	5	180.58	10.47	0.00	170.53
S(~BROOD1 + BROOD2 + BROOD3 + M_TEMP * TIME)	7	180.84	10.73	0.00	166.75

S(~TIME * M_TEMP + BROOD1 + BROOD2 + BROOD3)	7	180.84	10.73	0.00	166.75
S(~NESTAGE + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 + BROOD1 + BROOD2 + BROOD3 + TIME * M_TEMP)	15	180.86	10.74	0.00	150.45
S(~F_TAG + M_TEMP + M_PRCP2 + TIME + BROOD1 + BROOD2 + BROOD3)	8	181.01	10.90	0.00	164.89
S(~M_TAG + M_TEMP * TIME + M_PRCP2 + YCONS)	7	181.12	11.00	0.00	167.02
S(~M_TAG + M_PRCP2 + YCONS + TIME * M_TEMP)	7	181.12	11.00	0.00	167.02
S(~TIME + BROOD1 + BROOD2 + BROOD3)	5	181.15	11.03	0.00	171.09
S(~NESTAGE + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 + TIME *	16	181.17	11.06	0.00	148.71

M_TEMP + M_PRCP2 + BROOD1 + BROOD2 + BROOD3)					
S(~FM_TAG + M_TEMP + M_PRCP2 + TIME + BROOD1 + BROOD2 + BROOD3)	8	181.27	11.15	0.00	165.14
S(~NESTAGE + F_TAG + BROOD1 + BROOD2 + BROOD3)	6	181.41	11.30	0.00	169.34
S(~BROOD1 + BROOD2 + BROOD3)	4	181.42	11.30	0.00	173.38
S(~F_TAG + TIME * M_TEMP + M_PRCP2 + YCONS + BROOD1 + BROOD2 + BROOD3)	10	181.50	11.38	0.00	161.31
S(~NESTAGE + M_TEMP + M_PRCP2)	4	181.55	11.43	0.00	173.52
S(~NESTAGE + M_TAG + TIME + BROOD1 + BROOD2 + BROOD3)	7	181.61	11.50	0.00	167.52

S(~M_TAG + M_TEMP + M_PRCP2 + YCONS + TIME)	6	181.78	11.66	0.00	169.71
S(~NESTAGE + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 + BROOD1 + BROOD2 + BROOD3 + NESTAGE * TIME * M_TEMP)	18	181.81	11.69	0.00	145.22
S(~NESTAGE + F_TAG + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 + TIME)	11	181.92	11.81	0.00	159.70
S(~NESTAGE * TIME + F_TAG + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19)	12	181.99	11.87	0.00	157.72
S(~M_TEMP + M_PRCP2 + YCONS)	4	182.07	11.95	0.00	174.03
S(~M_TAG + M_TEMP + M_PRCP2)	4	182.11	12.00	0.00	174.08
S(~FM_TAG + TIME * M_TEMP + M_PRCP2	10	182.26	12.14	0.00	162.07

+ YCONS + BROOD1 + BROOD2 + BROOD3)					
S(~NESTAGE + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 + M_TEMP + M_PRCP2 + TIME + BROOD1 + BROOD2 + BROOD3)	15	182.32	12.21	0.00	151.91
S(~TIME * M_TEMP + M_PRCP2 + BROOD1 + BROOD2 + BROOD3)	8	182.35	12.23	0.00	166.22
S(~F_TAG + M_TEMP + M_PRCP2 + YCONS + TIME + BROOD1 + BROOD2 + BROOD3)	9	182.37	12.26	0.00	164.22
S(~NESTAGE + M_TAG + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 + BROOD1 + BROOD2 + BROOD3 + TIME * M_TEMP)	16	182.57	12.45	0.00	150.10
S(~M_TAG + BROOD1 + BROOD2 + BROOD3 + TIME * M_TEMP)	8	182.79	12.68	0.00	166.67

S(~NESTAGE + BROOD1 + BROOD2 + BROOD3)	5	182.82	12.70	0.00	172.76
S(~FM_TAG + M_TEMP + M_PRCP2 + BROOD1 + BROOD2 + BROOD3)	7	182.82	12.70	0.00	168.72
S(~M_TEMP + M_PRCP2 + TIME + BROOD1 + BROOD2 + BROOD3)	7	182.82	12.71	0.00	168.73
S(~YCONS + BROOD1 + BROOD2 + BROOD3 + TIME * M_TEMP)	8	182.87	12.75	0.00	166.75
S(~YCONS + TIME + BROOD1 + BROOD2 + BROOD3)	6	182.99	12.88	0.00	170.92
S(~NESTAGE + M_TAG + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 + TIME * M_TEMP + M_PRCP2 + BROOD1 + BROOD2 + BROOD3)	17	183.01	12.90	0.00	148.49

S(~M_TAG + TIME + BROOD1 + BROOD2 + BROOD3)	6	183.03	12.91	0.00	170.96
S(~NESTAGE + FM_TAG + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19)	10	183.18	13.06	0.00	162.99
S(~FM_TAG + M_TEMP + M_PRCP2 + YCONS + TIME + BROOD1 + BROOD2 + BROOD3)	9	183.28	13.16	0.00	165.12
S(~M_TAG + BROOD1 + BROOD2 + BROOD3)	5	183.35	13.24	0.00	173.30
S(~F_TAG + M_TEMP + M_PRCP2 + BROOD1 + BROOD2 + BROOD3)	7	183.43	13.31	0.00	169.33
S(~YCONS + BROOD1 + BROOD2 + BROOD3)	5	183.43	13.32	0.00	173.38
S(~NESTAGE + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 + TIME)	10	183.48	13.37	0.00	163.29

S(~NESTAGE + M_TAG + M_TEMP + M_PRCP2)	5	183.57	13.45	0.00	173.52
S(~NESTAGE * TIME + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19)	11	183.65	13.53	0.00	161.42
S(~NESTAGE + M_TAG + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 + M_TEMP + M_PRCP2 + TIME + BROOD1 + BROOD2 + BROOD3)	16	183.72	13.61	0.00	151.26
S(~M_TAG + M_TEMP + M_PRCP2 + YCONS)	5	184.08	13.97	0.00	174.03
S(~TIME * M_TEMP + M_PRCP2 + YCONS + BROOD1 + BROOD2 + BROOD3)	9	184.29	14.17	0.00	166.13
S(~M_TAG + TIME * M_TEMP + M_PRCP2 + BROOD1 + BROOD2 + BROOD3)	9	184.32	14.21	0.00	166.17

S(~NESTAGE + FM_TAG + M_TEMP + M_PRCP2 + BROOD1 + BROOD2 + BROOD3)	8	184.37	14.26	0.00	168.25
S(~F_TAG + M_TEMP + M_PRCP2 + YCONS + BROOD1 + BROOD2 + BROOD3)	8	184.70	14.59	0.00	168.58
S(~NESTAGE + FM_TAG + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 + TIME + BROOD1 + BROOD2 + BROOD3)	14	184.73	14.61	0.00	156.37
S(~NESTAGE + M_TAG + BROOD1 + BROOD2 + BROOD3)	6	184.73	14.62	0.00	172.66
S(~M_TEMP + M_PRCP2 + YCONS + TIME + BROOD1 + BROOD2 + BROOD3)	8	184.77	14.65	0.00	168.64
S(~M_TAG + M_TEMP + M_PRCP2 + TIME + BROOD1 + BROOD2 + BROOD3)	8	184.80	14.69	0.00	168.68

S(~FM_TAG + M_TEMP + M_PRCP2 + YCONS + BROOD1 + BROOD2 + BROOD3)	8	184.81	14.70	0.00	168.69
S(~M_TEMP + M_PRCP2 + BROOD1 + BROOD2 + BROOD3)	6	184.96	14.85	0.00	172.89
S(~NESTAGE + F_TAG + M_TEMP + M_PRCP2 + BROOD1 + BROOD2 + BROOD3)	8	185.13	15.02	0.00	169.01
S(~NESTAGE + M_TAG + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 + TIME)	11	185.16	15.04	0.00	162.93
S(~NESTAGE * TIME + M_TAG + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19)	12	185.19	15.07	0.00	160.92
S(~NESTAGE + F_TAG + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 + TIME + BROOD1 + BROOD2 + BROOD3)	14	185.57	15.45	0.00	157.21

S(~NESTAGE + FM_TAG + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 + M_TEMP + M_PRCP2)	12	185.99	15.88	0.00	161.72
S(~M_TAG + TIME * M_TEMP + M_PRCP2 + YCONS + BROOD1 + BROOD2 + BROOD3)	10	186.24	16.13	0.00	166.06
S(~NESTAGE + F_TAG + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19)	10	186.26	16.15	0.00	166.07
S(~NESTAGE + M_TEMP + M_PRCP2 + BROOD1 + BROOD2 + BROOD3)	7	186.37	16.26	0.00	172.28
S(~NESTAGE + FM_TAG + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 + BROOD1 + BROOD2 + BROOD3)	13	186.37	16.26	0.00	160.06
S(~M_TAG + M_TEMP + M_PRCP2 + YCONS	9	186.77	16.65	0.00	168.61

+ TIME + BROOD1 + BROOD2 + BROOD3)					
S(~M_TEMP + M_PRCP2 + YCONS + BROOD1 + BROOD2 + BROOD3)	7	186.86	16.75	0.00	172.77
S(~M_TAG + M_TEMP + M_PRCP2 + BROOD1 + BROOD2 + BROOD3)	7	186.93	16.82	0.00	172.84
S(~NESTAGE + FM_TAG + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 + M_TEMP + M_PRCP2 + BROOD1 + BROOD2 + BROOD3)	15	187.39	17.28	0.00	156.98
S(~NESTAGE + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 + BROOD1 + BROOD2 + BROOD3 + NESTAGE * TIME)	14	187.95	17.83	0.00	159.59
S(~NESTAGE + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19)	9	187.99	17.88	0.00	169.84

S(~NESTAGE + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 + TIME + BROOD1 + BROOD2 + BROOD3)	13	188.26	18.14	0.00	161.95
S(~NESTAGE + M_TAG + M_TEMP + M_PRCP2 + BROOD1 + BROOD2 + BROOD3)	8	188.33	18.22	0.00	172.21
S(~NESTAGE + F_TAG + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 + M_TEMP + M_PRCP2)	12	188.61	18.50	0.00	164.35
S(~M_TAG + M_TEMP + M_PRCP2 + YCONS + BROOD1 + BROOD2 + BROOD3)	8	188.86	18.75	0.00	172.74
S(~NESTAGE + M_TAG + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19)	10	189.57	19.46	0.00	169.38
S(~NESTAGE + M_TAG + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19	14	190.06	19.95	0.00	161.70

+ TIME + BROOD1 + BROOD2 + BROOD3)					
S(~NESTAGE + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 + M_TEMP + M_PRCP2)	11	190.60	20.49	0.00	168.38
S(~NESTAGE + F_TAG + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 + BROOD1 + BROOD2 + BROOD3)	13	190.71	20.59	0.00	164.40
S(~NESTAGE + F_TAG + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 + M_TEMP + M_PRCP2 + BROOD1 + BROOD2 + BROOD3)	15	191.95	21.84	0.00	161.54
S(~NESTAGE + M_TAG + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 + M_TEMP + M_PRCP2)	12	192.13	22.01	0.00	167.86
S(~NESTAGE + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 +	12	192.78	22.66	0.00	168.51

BROOD1 + BROOD2 + BROOD3)					
S(~NESTAGE + M_TAG + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 + BROOD1 + BROOD2 + BROOD3)	13	194.09	23.98	0.00	167.78
S(~NESTAGE + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 + M_TEMP + M_PRCP2 + BROOD1 + BROOD2 + BROOD3)	14	194.49	24.37	0.00	166.13
S(~NESTAGE + M_TAG + Y13 + Y14 + Y15 + Y16 + Y17 + Y18 + Y19 + M_TEMP + M_PRCP2 + BROOD1 + BROOD2 + BROOD3)	15	195.38	25.26	0.00	164.96

Appendix B – Egg and Chick Stage Model Parameter Estimates

__Table__ B1. Top models (i.e. models within 2 AICc units of the top model) of nightjar daily nest survival rates during the __egg stage__, for a set of models including mean rainfall (m_prcp2), average temperature (m_temp), time (Julian day) and adult female tag status (f_tag).

MODEL	NPAR	AICC	DELTAAICC	WEIGHT	DEVIANCE
S(~F_TAG + M_PRCP2 + M_TEMP * TIME)	6	66.22	0	0.07	53.99
S(~F_TAG + TIME)	3	66.75	0.53	0.06	60.689
S(~F_TAG)	2	66.94	0.72	0.05	62.909
S(~F_TAG + M_TEMP * TIME)	5	67.18	0.95	0.04	57.01
S(~F_TAG + M_TEMP + M_PRCP2 + TIME)	5	67.54	1.32	0.04	57.37

Table B2. Full model averaged estimates (± SE) of the effects of mean rainfall, mean temperature, Julian day (Time) and adult female tag status, on daily nest survival rates (DSR) of ***egg stage*** *nightjar nests at Brechfa Forest. Model averaged parameter estimates were derived by weighted averaging across all models within 2 AICc units of the top model (Table B1).*

PARAMETER	ESTIMATE	SE	95% CONFIDENCE LIMITS
S((INTERCEPT))	4.48	2.08	0.41 to 8.55
S(F_TAG1)	1.56	0.84	-0.08 to 3.19
S(M_PRCP2)	0.24	0.46	-0.66 to 1.14
S(M_TEMP)	0.78	2.37	-3.87 to 5.43
S(TIME)	-0.04	0.05	-0.13 to 0.06
S(M_TEMP:TIME)	-0.01	0.05	-0.1 to 0.09
S(NESTAGE)	0.07	0.22	-0.36 to 0.51
S(M_TEMP:NESTAGE)	0.09	0.27	-0.45 to 0.62
S(NESTAGE:TIME)	0	0	-0.01 to 0.01
S(M_TEMP:NESTAGE:TIME)	0	0.01	-0.01 to 0.01

Table B3. Nest survival rate (DSR^18) estimates for ***egg stage*** *nests at Brechfa Forest using predicted DSR from model averaged top models for nests initiated on day 20 (16th June – median nest initiation date).*

TAG STATUS	SAMPLE SIZE	NSR ESTIMATE	95% CONFIDENCE LIMITS
FEMALE TAGGED	27	0.82	0.56 to 1.00
FEMALE UNTAGGED	23	0.55	0.37 to 0.72
ADULT TAGGED	33	0.91	0.82 to 0.99
ADULT UNTAGGED	17	0.87	0.77 to 0.98

Appendix C – Spatio-temporal and spatial and temporal smoother models

Table C-1- Spatio-temporal and spatial and temporal smoother models..

MODEL	LINEAR AND NON SPATIOTEMPORAL SMOOTHED PARAMETERS	SPATIOTEMPORAL SMOOTHERS
STMSS MODEL 1	Minimum Temperature Wind Speed, Precipitation Aspect Vegetation Seasonality Year Smoothed interaction of clearfell age and seasonality, Smoothed interaction of wind speed and aspect.	Smooth of longitude and latitude; Tensor smooth longitude and latitude and Julian day
STMSS MODEL 2	Minimum Temperature Wind Speed, Precipitation Aspect Smoothed interaction of clearfell age and seasonality, Smoothed interaction of wind speed and aspect.	Smooth of julian day in an interaction with year; tensor smooth of longitude and latitude and Julian day in an interaction with year

STMSS Model 1

Table C-2 – STMMS Model 1 parameter estimates for linear parameters.

Parametric coefficients:				
	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	7.39221	0.19102	38.699	< 2e-16
Minimum Temperature	0.71055	0.06523	10.893	< 2e-16
Wind Speed	-0.24194	0.08651	-2.797	0.00559
Precipitation	-0.10343	0.06577	-1.573	0.11711
Vegetation Seasonality	0.08883	0.09479	0.937	0.34967
Northerly Aspect	0.09486	0.17284	0.549	0.58365
Southerly Aspect	-0.05288	0.16693	-0.317	0.75169
Westerly Aspect	-0.02839	0.17644	-0.161	0.87232
Year 2018	-0.34282	0.18001	-1.904	0.05806
Year 2019	-0.17354	0.16774	-1.035	0.30191

Table C-3 – STMSS Model 1 smoothed parameter estimates

Smooth terms:				
	edf	Ref.df	F	p-value
s(xkm,ykm)	1.86E+00	4	3.965	0.000177
ti(xkm,ykm,jday)	1.19E+01	44	0.775	0.000278

s(cfell.age,seas1)	7.89E-01	28	0.045	0.183515
s(wind1):aspect1E	1.85E+00	9	0.79	0.013118
s(wind1):aspect1N	1.84E+00	9	1.308	0.000922
s(wind1):aspect1S	6.47E-04	9	0	0.687113
s(wind1):aspect1W	5.81E-04	9	0	0.881182

STMSS Model 2

Table C-4 - STMSS2 model linear parameter estimates.

Parametric coefficients:				
	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	6.91392	0.11145	62.039	< 2e-16
Minimum Temperature	0.39913	0.0592	6.742	1.24E-10
Wind Speed	-0.21071	0.06376	-3.305	0.0011
Precipitation	0.02936	0.05267	0.557	0.5777
Northerly Aspect	0.21075	0.1417	1.487	0.1383
Southerly Aspect	0.05663	0.13569	0.417	0.6768
Westerly Aspect	0.18396	0.151	1.218	0.2244

Table C-5 – STMSS2 model smoother parameter estimates.

Smooth terms:				
	edf	Ref.df	F	p-value
s(xkm,ykm)	1.86E+00	4	3.965	0.000177
ti(xkm,ykm,jday)	1.19E+01	44	0.775	0.000278
s(cfell.age,seas1)	7.89E-01	28	0.045	0.183515
s(wind1):aspect1E	1.85E+00	9	0.79	0.013118
s(wind1):aspect1N	1.84E+00	9	1.308	0.000922

s(wind1):aspect1S	6.47E-04	9	0	0.687113
s(wind1):aspect1W	5.81E-04	9	0	0.881182

Appendix D – Moth data

Table D-1 – Moth Species List

COMMON SPECIES NAME	BINOMIAL SPECIES NAME	SITES
MAGPIE MOTH	*Abraxas grossulariata*	Afan
MILLER	*Acronicta leporina*	Bryn
LIGHT KNOT GRASS	*Acronicta menyanthidis*	Clocaenog
KNOT GRASS	*Acronicta rumicis*	Brechfa, Afan, Bryn, Clocaenog
NA	*Aethes cnicana*	Afan, Bryn
NA	*Agapeta hamana*	Bryn
NA	*Agriphila geniculea*	Brechfa
NA	*Agriphila straminella*	Pen y Cymoedd, Bryn
NA	*Agriphila tristella*	Clocaenog
HEART AND DART	*Agrotis exclamationis*	Bryn, Afan, Brechfa, Clocaenog
DARK SWORD GRASS	*Agrotis ipsilon*	Pen y Cymoedd, Bryn
SHUTTLE SHAPED DART	*Agrotis puta*	Bryn, Afan
MOTTLED BEAUTY	*Alcis repandata*	Afan, Pen y Cymoedd, Brechfa, Clocaenog
EAR MOTH	*Amphipoea oculea*	Brechfa, Afan, Bryn, Pen y Cymoedd, Clocaenog
LARGE EAR	*Amphipoea lucens*	Clocaenog
GREEN ARCHES	*Anaplectoides prasina*	Afan
GREY CHI	*Antitype chi*	Bryn
CLOUDED BORDERED BRINDLE	*Apamea crenata*	Pen y Cymoedd, Brechfa, Afan
CLOUDED BRINDLE	*Apamea epomidion*	Pen y Cymoedd, Clocaenog, Brechfa, Bryn
THE CONFUSED	*Apamea furva*	Brechfa
DARK ARCHES	*Apamea monoglypha*	Brechfa, Pen y Cymoedd, Clocaenog, Bryn, Afan
DUSKY BROCADE	*Apamea remissa*	Pen y Cymoedd, Brechfa, Bryn
SLENDER BRINDLE	*Apamea scolopacina*	Brechfa, Afan
TREBLE BAR	*Aplocera plagiata*	Clocaenog
BLACK RUSTIC	*Aporophyla nigra*	Clocaenog, Afan

DINGY SHEARS	*Apterogenum ypsillon*	Brechfa
ORANGE UNDERWING	*Archiearis parthenias*	Clocaenog
GARDEN TIGER	*Arctia caja*	Afan, Pen y Cymoedd, Clocaenog, Bryn, Brechfa
STRAW BELLE	*Aspitates gilvaria*	Afan
YELLOW BELLE	*Aspitates ochrearia*	Brechfa, Pen y Cymoedd
RED NECKED FOOTMAN	*Atolmis rubricollis*	Afan, Bryn
SILVER Y	*Autographa gamma*	Pen y Cymoedd, Clocaenog, Afan, Bryn, Brechfa
PLAIN GOLDEN Y	*Autographa jota*	Pen y Cymoedd, Bryn
BEAUTIFUL GOLDEN Y	*Autographa pulchrina*	Brechfa, Pen y Cymoedd, Clocaenog, Afan
FLAME	*Axylia putris*	Bryn, Afan
SCARCE SILVER LINES	*Bena bicolorana*	Clocaenog
PEPPERED MOTH	*Biston betularia*	Pen y Cymoedd, Afan, Brechfa, Bryn, Clocaenog
MINOR SHOULDER KNOT	*Brachylomia viminalis*	Brechfa, Pen y Cymoedd
BORDERED WHITE	*Bupalus piniaria*	Clocaenog
COMMON WAVE	*Cabera exanthemata*	Bryn, Brechfa, Afan, Pen y Cymoedd, Clocaenog
COMMON WHITE WAVE	*Cabera pusaria*	Brechfa, Afan, Clocaenog, Pen y Cymoedd, Bryn
NA	*Calamotropha sp.*	Bryn, Afan, Brechfa, Pen y Cymoedd, Clocaenog
PALE TUSSOCK	*Calliteara pudibunda*	Pen y Cymoedd, Afan, Brechfa, Bryn, Clocaenog
LIGHT EMERALD	*Campaea margaritata*	Clocaenog, Afan, Bryn
RED UNDERWING	*Catocala nupta*	Afan
HAWORTH MINOR	*Celaena haworthii*	Clocaenog, Brechfa
BROOM MOTH	*Ceramica pisi*	Pen y Cymoedd, Afan, Bryn, Brechfa, Clocaenog
ANTLER MOTH	*Cerapteryx graminis*	Bryn, Afan, Pen y Cymoedd, Brechfa, Clocaenog
RED CHESTNUT	*Cerastis rubricosa*	Pen y Cymoedd
PUSS MOTH	*Cerura vinula*	Pen y Cymoedd, Brechfa, Clocaenog
TREBLE LINES	*Charanyca trigrammica*	Brechfa, Afan
ANNULET	*Charissa obscurata*	Pen y Cymoedd, Bryn, Afan

RED GREEN CARPET	*Chloroclysta siterata*	Brechfa, Afan, Pen y Cymoedd
SALLOW	*Cirrhia icteritia*	Clocaenog
CHOCOLATE TIP	*Clostera curtula*	Afan, Bryn, Brechfa
SMALL RUFOUS	*Coenobia rufa*	Clocaenog, Bryn
STRIPED TWIN SPOT CARPET	*Coenotephria salicata*	Pen y Cymoedd
NUT TREE TUSSOCK	*Colocasia coryli*	Bryn, Brechfa, Clocaenog
MOTTLED GRAY	*Colostygia multistrigaria*	Brechfa
GREEN CARPET	*Colostygia pectinataria*	Afan, Pen y Cymoedd, Brechfa, Clocaenog, Bryn
CHESTNUT	*Conistra vaccinii*	Clocaenog
PURPLE BAR	*Cosmorhoe ocellata*	Brechfa, Afan, Clocaenog, Bryn
CRAMBUS PASCUELLA	*Crambus pascuella*	Brechfa
CRAMBUS SP.	*Crambus sp.*	Bryn, Pen y Cymoedd, Afan, Brechfa
CORONET	*Craniophora ligustri*	Brechfa
SCALLOPED OAK	*Crocallis elinguaria*	Brechfa, Clocaenog, Afan
FOUR DOTTED FOOTMAN	*Cybosia mesomella*	Brechfa
ELEPHANT HAWK-MOTH	*Deilephila elpenor*	Afan, Bryn, Clocaenog, Pen y Cymoedd
SMALL ELEPHANT HAWK-MOTH	*Deilephila porcellus*	Bryn
MARBLED WHITE SPOT	*Deltote pygarga*	Afan, Brechfa, Bryn, Pen y Cymoedd
SMALL WAINSCOT	*Denticucullus pygmina*	Bryn, Afan, Clocaenog, Brechfa, Pen y Cymoedd
BURNISHED BRASS	*Diachrysia chrysitis*	Pen y Cymoedd, Clocaenog, Afan
MUSLIN	*Diaphora mendica*	Brechfa
PURPLE CLAY	*Diarsia brunnea*	Brechfa, Bryn, Pen y Cymoedd, Clocaenog, Afan
INGRAILED CLAY	*Diarsia mendica*	Pen y Cymoedd, Afan, Brechfa, Clocaenog, Bryn
DARK TUSSOCK	*Dicallomera fascelina*	Brechfa, Clocaenog
PEBBLE HOOKTIP	*Drepana falcataria*	Clocaenog
DARK MARBLED CARPET	*Dysstroma citrata*	Clocaenog
COMMON MARBLED CARPET	*Dysstroma truncata*	Clocaenog, Bryn
SMALL PHOENIX	*Ecliptopera silaceata*	Pen y Cymoedd, Brechfa, Bryn, Afan, Clocaenog

ENGRAILED	*Ectropis crepuscularia*	Brechfa, Bryn
HOARY FOOTMAN	*Eilema caniola*	Afan, Clocaenog, Bryn
BUFF FOOTMAN	*Eilema depressa*	Bryn, Afan, Brechfa
COMMON FOOTMAN	*Eilema lurideola*	Bryn, Afan, Brechfa, Clocaenog, Pen y Cymoedd
BROKEN BAR CARPET	*Electrophaes corylata*	Bryn, Brechfa
AUGUST THORN	*Ennomos quercinaria*	Afan
GREY MOUNTAIN CARPET	*Entephria caesiata*	Brechfa, Pen y Cymoedd
EPINOTIA RAMELLA	*Epinotia ramella*	Afan
BORDERED BEAUTY	*Epione repandaria*	Bryn, Brechfa
COMMON CARPET	*Epirrhoe alternata*	Pen y Cymoedd
GALLIUM CARPET	*Epirrhoe galiata*	Afan
EUDONIA PALLIDA	*Eudonia pallida*	Bryn, Afan
EUDONIA SP.	*Eudonia sp.*	Bryn, Afan, Pen y Cymoedd, Brechfa, Clocaenog
EUDONIA TRUNCONOLA	*Eudonia trunconola*	Afan
AUTUMNAL RUSTIC	*Eugnorisma glareosa*	Clocaenog
NORTHERN SPINACH	*Eulithis populata*	Afan, Bryn, Pen y Cymoedd, Clocaenog, Brechfa
PHOENIX	*Eulithis prunata*	Clocaenog, Afan, Bryn, Pen y Cymoedd, Brechfa
CHEVRON	*Eulithis testata*	Clocaenog, Afan
SHARP ANGLED CARPET	*Euphyia unangulata*	Brechfa
TAWNY PUG	*Eupithecia icterata*	Afan, Bryn
NARROW WINGED PUG	*Eupithecia nanata*	Pen y Cymoedd, Brechfa, Clocaenog, Bryn
FOXGLOVE PUG	*Eupithecia pulchellata*	Brechfa, Bryn, Afan, Pen y Cymoedd
GREY PUG	*Eupithecia subfuscata*	Brechfa, Afan
WHITE SPOTTED PUG	*Eupithecia tripunctaria*	Afan, Clocaenog, Bryn
COMMON PUG	*Eupithecia vulgata*	Bryn, Afan, Brechfa, Clocaenog, Pen y Cymoedd
SMALL ANGLE SHADES	*Euplexia lucipara*	Bryn, Pen y Cymoedd, Afan, Clocaenog
DRINKER	*Euthrix potatoria*	Afan, Bryn, Brechfa, Pen y Cymoedd, Clocaenog
SPECKLED BEAUTY	*Fagivorina arenaria*	Afan, Brechfa

SCALLOPED HOOK TIP	*Falcaria lacertinaria*	Bryn, Brechfa
SALLOW KITTEN	*Furcula furcula*	Bryn, Brechfa, Afan
BARRED STRAW	*Gandaritis pyraliata*	Pen y Cymoedd, Clocaenog, Afan, Brechfa
LARGE EMERALD	*Geometra papilionaria*	Afan, Clocaenog, Bryn, Brechfa
BUFF ARCHES	*Habrosyne pyritoides*	Afan, Brechfa, Pen y Cymoedd, Bryn, Clocaenog
BORDERED STRAW	*Heliothis peltigera*	Pen y Cymoedd
GHOST MOTH	*Hepialus humuli*	Bryn, Pen y Cymoedd
SMALL FAN FOOT	*Herminia grisealis*	Afan
THE FANFOOT	*Herminia tarsipennalis*	Afan, Brechfa, Clocaenog
UNCERTAIN/RUSTIC	*Hoplodrina sp.*	Bryn, Afan, Brechfa, Clocaenog, Pen y Cymoedd
FERN	*Horisme tersata*	Brechfa, Clocaenog, Afan
ROSY RUSTIC	*Hydraecia micacea*	Brechfa
SMALL YELLOW WAVE	*Hydrelia flammeolaria*	Afan
JULY HIGH FLYER	*Hydriomena furcata*	Bryn, Brechfa, Afan, Pen y Cymoedd, Clocaenog
MAY HIGH FLYER	*Hydriomena impluviata*	Clocaenog
SNOUT	*Hypena proboscidalis*	Afan, Bryn
RIBAND WAVE	*Idaea aversata*	Bryn, Brechfa
SMALL SCALLOP	*Idaea emarginata*	Afan
SATIN WAVE	*Idaea subsericeata*	Afan
MAP WINGED SWIFT	*Korscheltellus fusconebulosa*	Pen y Cymoedd, Bryn, Afan, Brechfa, Clocaenog
COMMON SWIFT	*Korscheltellus lupulina*	Pen y Cymoedd, Afan, Bryn, Brechfa
BRIGHT LINE BROWN EYE	*Lacanobia oleracea*	Bryn, Pen y Cymoedd, Clocaenog, Brechfa, Afan
PALE SHOULDERED BROCADE	*Lacanobia thalassina*	Pen y Cymoedd, Afan, Clocaenog, Brechfa, Bryn
POPLAR HAWK-MOTH	*Laothoe populi*	Afan, Pen y Cymoedd, Clocaenog, Brechfa, Bryn
OAK EGGAR	*Lasiocampa quercus*	Clocaenog, Brechfa, Bryn
CLOUDED BORDER	*Lomaspilis marginata*	Clocaenog, Brechfa, Afan, Bryn
FLOUNCED RUSTIC	*Luperina testacea*	Bryn, Brechfa, Clocaenog, Pen y Cymoedd
BRINDLED BEAUTY	*Lycia hirtaria*	Brechfa

TRUE LOVER'S KNOT	*Lycophotia porphyrea*	Afan, Bryn, Pen y Cymoedd, Brechfa, Clocaenog
BLACK ARCHES	*Lymantria monacha*	Afan, Pen y Cymoedd
SHARP ANGLED PEACOCK	*Macaria alternata*	Afan
TAWNY BARRED ANGLE	*Macaria liturata*	Afan, Pen y Cymoedd, Clocaenog
FOX MOTH	*Macrothylacia rubi*	Pen y Cymoedd, Afan, Brechfa, Bryn, Clocaenog
CABBAGE MOTH	*Mamestra brassicae*	Brechfa
BARRED CARPET	*Martania taeniata*	Afan
PYLA FUSCA	*Matilella fusca*	Clocaenog
COMMON RUSTIC	*Mesapamea sp.*	Bryn, Afan, Pen y Cymoedd, Clocaenog, Brechfa
BEAUTIFUL CARPET	*Mesoleuca albicillata*	Bryn, Afan, Clocaenog, Brechfa
CLOAKED MINOR	*Mesoligia furuncula*	Pen y Cymoedd, Bryn
TWIN-SPOT CARPET	*Mesotype didymata*	Pen y Cymoedd
ROSY FOOTMAN	*Miltochrista miniata*	Afan
CLAY	*Mythimna ferrago*	Bryn, Afan, Pen y Cymoedd
SMOKY WAINSCOT	*Mythimna impura*	Bryn, Brechfa, Pen y Cymoedd, Clocaenog, Afan
COMMON WAINSCOT	*Mythimna pallens*	Afan, Bryn, Brechfa, Pen y Cymoedd, Clocaenog
STRIPED WAINSCOT	*Mythimna pudorina*	Pen y Cymoedd, Bryn
DOUBLE LINE	*Mythimna turca*	Pen y Cymoedd, Bryn, Afan
LESSER YELLOW UNDERWING	*Noctua comes*	Bryn, Brechfa, Pen y Cymoedd, Clocaenog, Afan
LEAST YELLOW UNDERWING	*Noctua interjecta*	Pen y Cymoedd, Afan, Clocaenog, Brechfa, Bryn
LESSER BROAD BORDERED YELLOW UNDERWING	*Noctua janthe*	Clocaenog
LARGE YELLOW UNDERWING	*Noctua pronuba*	Afan, Bryn, Brechfa, Pen y Cymoedd, Clocaenog
BRAMBLE SHOOT MOTH	*Notocelia uddmanniana*	Bryn
IRON PROMINENT	*Notodonta dromedarius*	Brechfa, Bryn, Afan
PEBBLE PROMINENT	*Notodonta ziczac*	Brechfa, Afan, Pen y Cymoedd, Clocaenog, Bryn
FLAME SHOULDER	*Ochropleura plecta*	Afan, Bryn, Brechfa, Pen y Cymoedd, Clocaenog

SCALLOPED HAZEL	*Odontopera bidentata*	Bryn, Pen y Cymoedd, Clocaenog, Brechfa, Afan
MIDDLE BARRED MINOR	*Oligia fasciuncula*	Pen y Cymoedd, Clocaenog
TAWNY MARBLED MINOR	*Oligia latruncula*	Bryn
MARBLED MINOR	*Oligia strigilis*	Bryn, Pen y Cymoedd, Clocaenog, Afan
RUFOUS MINOR	*Oligia versicolor*	Bryn
BRIMSTONE	*Opisthograptis luteolata*	Afan
COMMON QUAKER	*Orthosia cerasi*	Pen y Cymoedd
HEBREW CHARACTER	*Orthosia gothica*	Clocaenog, Bryn, Afan, Brechfa, Pen y Cymoedd
POWDERED QUAKER	*Orthosia gracilis*	Afan, Brechfa
CLOUDED DRAB	*Orthosia incerta*	Clocaenog
ORTHOTAENIA UNDULANA	*Orthotaenia undulana*	Bryn
GLAUCOUS SHEARS	*Papestra biren*	Pen y Cymoedd
GREEN PUG	*Pasiphila rectangulata*	Bryn, Afan
COMMON FANFOOT	*Pechipogo strigilata*	Clocaenog
GRASS WAVE	*Perconia strigillaria*	Bryn, Pen y Cymoedd
WILLOW BEAUTY	*Peribatodes rhomboidaria*	Brechfa, Bryn, Afan, Pen y Cymoedd, Clocaenog
GRASS RIVULET	*Perizoma albulata*	Bryn
BROWN SILVER LINE	*Petrophora chlorosata*	Pen y Cymoedd, Afan, Clocaenog, Brechfa, Bryn
BUFF TIP	*Phalera bucephala*	Afan, Bryn, Brechfa, Clocaenog
LESSER SWALLOW PROMINENT	*Pheosia gnoma*	Bryn
SWALLOW PROMINENT	*Pheosia tremula*	Afan, Clocaenog
ANGLE SHADES	*Phlogophora meticulosa*	Pen y Cymoedd, Bryn, Brechfa, Clocaenog, Afan
SMALL DOTTED BUFF	*Photedes minima*	Bryn
RUBY TIGER	*Phragmatobia fuliginosa*	Bryn, Afan, Brechfa, Pen y Cymoedd
BARRED UMBER	*Plagodis pulveraria*	Clocaenog
MOTHER OF PEARL	*Pleuroptya ruralis*	Afan
GOLD SPOT	*Plusia festucae*	Pen y Cymoedd, Afan, Brechfa
GREY ARCHES	*Polia nebulosa*	Afan, Pen y Cymoedd

GREEN SILVERLINES	*Pseudoips prasinana*	Afan
PALE PROMINENT	*Pterostoma palpina*	Afan, Brechfa, Bryn, Clocaenog
COXCOMB PROMINENT	*Ptilodon capucina*	Pen y Cymoedd, Afan, Bryn, Brechfa, Clocaenog
PUG SP.	*Eupithecia sp.*	Bryn, Afan, Clocaenog
PYRAUSTA PURPURALIS	*Pyrausta purpuralis*	Pen y Cymoedd, Afan
VESTAL	*Rhodometra sacraria*	Clocaenog
STRAW DOT	*Rivula sericealis*	Pen y Cymoedd, Bryn, Clocaenog, Afan, Brechfa
BROWN RUSTIC	*Rusina ferruginea*	Pen y Cymoedd, Afan, Brechfa, Clocaenog, Bryn
EMPEROR	*Saturnia pavonia*	Afan
PINION STREAKED SNOUT	*Schrankia costaestrigalis*	Afan, Bryn, Pen y Cymoedd, Brechfa, Clocaenog
HERALD MOTH	*Scoliopteryx libatrix*	Clocaenog
SCOPARIA AMBIGUALIS	*Scoparia ambigualis*	Brechfa
NA	*Scoparia sp.*	Brechfa, Afan, Clocaenog
CREAM WAVE	*Scopula floslactata*	Brechfa
SHADED BROAD BAR	*Scotopteryx chenopodiata*	Clocaenog, Afan
EARLY THORN	*Selenia dentaria*	Afan, Bryn, Brechfa, Clocaenog
EYED HAWK-MOTH	*Smerinthus ocellata*	Pen y Cymoedd, Bryn
WHITE ERMINE	*Spilosoma lubricipeda*	Bryn, Pen y Cymoedd, Afan, Brechfa, Clocaenog
BUFF ERMINE	*Spilosoma lutea*	Afan, Brechfa, Bryn, Clocaenog
NORTHERN RUSTIC	*Standfussiana lucernea*	Clocaenog, Pen y Cymoedd
LOBSTER MOTH	*Stauropus fagi*	Brechfa
ANOMALOUS	*Stilbia anomala*	Clocaenog
POPLAR GREY	*Subacronicta megacephala*	Afan, Bryn
SCARCE SILVER Y	*Syngrapha interrogationis*	Pen y Cymoedd, Clocaenog
SPRUCE CARPET	*Thera britannica*	Pen y Cymoedd, Bryn, Clocaenog, Brechfa, Afan
GREY PINE CARPET	*Thera obeliscata*	Afan
HEDGE RUSTIC	*Tholera cespitis*	Bryn
ROUND-WINGED MUSLIN	*Thumatha senex*	Afan

PEACH BLOSSOM	*Thyatira batis*	Afan, Bryn, Clocaenog
BLOOD VEIN	*Timandra comae*	Clocaenog, Bryn, Afan
ORANGE SWIFT	*Triodia sylvina*	Bryn, Clocaenog
UDEA PRUNALIS	*Udea prunalis*	Clocaenog
WELSH WAVE	*Venusia cambrica*	Bryn
PINK-BARRED SALLOW	*Xanthia togata*	Clocaenog
RED CARPET	*Xanthorhoe decoloraria*	Clocaenog
FLAME CARPET	*Xanthorhoe designata*	Pen y Cymoedd
SILVER GROUND CARPET	*Xanthorhoe montanata*	Clocaenog, Pen y Cymoedd, Brechfa, Afan, Bryn
RED TWIN SPOT CARPET	*Xanthorhoe spadicearia*	Afan, Bryn, Brechfa
HEATH RUSTIC	*Xestia agathina*	Clocaenog
DOTTED CLAY	*Xestia baja*	Afan, Pen y Cymoedd, Brechfa, Bryn, Clocaenog
SETACIOUS HEBREW CHARACTER	*Xestia c-nigrum*	Afan
NEGLECTED RUSTIC	*Xestia castanea*	Clocaenog, Brechfa, Bryn, Pen y Cymoedd
TRIPLE SPOTTED CLAY	*Xestia ditrapezium*	Pen y Cymoedd, Brechfa, Clocaenog, Bryn, Afan
SIX-STRIPED RUSTIC	*Xestia sexstrigata*	Brechfa
DOUBLE SQUARE SPOT	*Xestia triangulum*	Bryn, Pen y Cymoedd, Brechfa, Clocaenog, Afan
SQUARE SPOT RUSTIC	*Xestia xanthographa*	Bryn, Pen y Cymoedd, Brechfa, Clocaenog, Afan
GOLDEN ROD BRINDLE	*Xylena solidaginis*	Clocaenog
5 SPOT BURNET	*Zygaena trifolii*	Bryn

Table D2 – Moth dry mass data.

SPECIES	BINOMIAL.SP.	DRY MASS IN MG	SOURCE
TRUE LOVER'S KNOT	*Lycophotia porphyrea*	23.5	Museum
TAWNEY BARRED ANGLE	*Macaria liturata*	9.9	Museum
NORTHERN SPINACH	*Eulithis populata*	39.1	Museum
MARBLED WHITE SPOT	*Deltote pygarga*	9.6	Museum
DRINKER	*Euthrix potatoria*	182.9	Museum
COMMON WAINSCOT	*Mythimna pallens*	34.3	Museum
FLAME SHOULDER	*Ochropleura plecta*	19.4	Museum
EARLY THORN	*Selenia dentaria*	41.6	Museum
RED NECKED FOOTMAN	*Atolmis rubricollis*	31.4	Museum
PINION STREAKED SNOUT	*Schrankia costaestrigalis*	8.0	Museum
LARGE YELLOW UNDERWING	*Noctua pronuba*	177.3	Museum
GREEN CARPET	*Colostygia pectinataria*	18.2	Museum
GARDEN TIGER	*Arctia caja*	288.3	Museum
JULY HIGH FLYER	*Hydriomena furcata*	35.4	Museum
COMMON WAVE	*Cabera exanthemata*	15.3	Museum
COMMON RUSTIC	*Mesapamea sp.*	35.6	Museum
SQUARE SPOT RUSTIC	*Xestia xanthographa*	60.1	Museum
SMALL ANGLE SHADES	*Euplexia lucipara*	51.1	Museum

(2020)

LESSER YELLOW UNDERWING	*Noctua comes*	95.3	Museum
GREEN PUG	*Pasiphila rectangulata*	4.5	Museum
COMMON PUG	*Eupithecia vulgata*	5.6	Museum
COMMON FOOTMAN	*Eilema lurideola*	10.7	Museum
CLAY	*Mythimna ferrago*	88.0	Museum
BROKEN BAR CARPET	*Electrophaes corylata*	16.9	Museum
BRIGHT LINE BROWN EYE	*Lacanobia oleracea*	73.0	Museum
PURPLE CLAY	*Diarsia brunnea*	79.5	Museum
AGRIPHILA GENICULEA	*Agriphila geniculea*	5.0	Kinsella et al. (2020)
COMMON WHITE WAVE	*Cabera pusaria*	27.4	Museum
RUSTIC/ UNCERTAIN	*Hoplodrina sp.*	33.3	Kinsella et al. (2020)
MINOR SHOULDER KNOT	*Brachylomia viminalis*	28.1	Museum
BEAUTIFUL GOLDEN Y	*Autographa pulchrina*	76.1	Museum
SPRUCE CARPET	*Thera britannica*	33.1	Museum
NARROW WINGED PUG	*Eupithecia nanata*	7.9	Museum
INGRAILED CLAY	*Diarsia mendica*	71.0	Museum
GOLD SPOT	*Plusia festucae*	60.8	Museum
COXCOMB PROMINENT	*Ptilodon capucina*	58.1	Kinsella et al. (2020)

BROOM MOTH	*Ceramica pisi*	47.3	Kinsella et al. (2020)
PYRAUSTA PURPURALIS	*Pyrausta purpuralis*	77.7	Museum
DOUBLE LINE	*Mythimna turca*	108.8	Museum
CALAMOTROPHA SP.	*Calamotropha sp.*	7.0	Kinsella et al. (2020)
BUFF FOOTMAN	*Eilema depressa*	6.0	Museum
ANTLER MOTH	*Cerapteryx graminis*	76.3	Museum
GRASS RIVULET	*Perizoma albulata*	7.5	Museum
EUDONIA PALLIDA	*Eudonia pallida*	69.2	Museum
DOTTED CLAY	*Xestia baja*	98.3	Museum
POPLAR HAWKMOTH	*Laothoe populi*	483.1	Museum
BUFF ARCHES	*Habrosyne pyritoides*	77.3	Museum
BARRED CARPET	*Martania taeniata*	1.2	Museum
BARRED STRAW	*Gandaritis pyraliata*	12.6	Museum
STRAW DOT	*Rivula sericealis*	7.3	Museum
SMALL PHOENIX	*Ecliptopera silaceata*	12.8	Museum
PLAIN GOLDEN Y	*Autographa jota*	52.0	Kinsella et al. (2020)
MAP WINGED SWIFT	*Korscheltellus fusconebulosa*	103.4	Museum
COMMON CARPET	*Epirrhoe alternata*	22.9	Museum

BURNISHED BRASS	*Diachrysia chrysitis*	71.1	Museum
AGRIPHILA STRAMINELLA	*Agriphila straminella*	22.1	Museum
WILLOW BEAUTY	*Peribatodes rhomboidaria*	51.3	Museum
SCOPARIA AMBIGUALIS	*Scoparia ambigualis*	3.3	Kinsella et al. (2020)
PURPLE BAR	*Cosmorhoe ocellata*	8.9	Museum
PEBBLE PROMINENT	*Notodonta ziczac*	67.7	Kinsella et al. (2020)
SLENDER BRINDLE	*Apamea scolopacina*	32.7	Museum
	Scoparia sp.	3.8	Kinsella et al. (2020)
TREBLE LINES	*Charanyca trigrammica*	60.8	Museum
DARK ARCHES	*Apamea monoglypha*	137.6	Museum
WELSH WAVE	*Venusia cambrica*	18.1	Museum
BEAUTIFUL CARPET	*Mesoleuca albicillata*	18.3	Museum
ROUND-WINGED MUSLIN	*Thumatha senex*	4.5	Museum
GREY ARCHES	*Polia nebulosa*	114.0	Museum
LARGE EMERALD	*Geometra papilionaria*	71.3	Museum
BLACK ARCHES	*Lymantria monacha*	133.4	Museum
SNOUT	*Hypena proboscidalis*	31.4	Museum
MOTHER OF PEARL	*Pleuroptya ruralis*	76.2	Museum

BORDERED STRAW	*Heliothis peltigera*	77.5	Museum
BROWN RUSTIC	*Rusina ferruginea*	61.9	Museum
DARK SWORD GRASS	*Agrotis ipsilon*	102.9	Museum
LEAST YELLOW UNDERWING	*Noctua interjecta*	61.6	Museum
YELLOW BELLE	*Aspitates ochrearia*	14.1	Museum
CRAMBUS PASCUELLA	*Crambus pascuella*	10.6	Museum
OAK EGGAR	*Lasiocampa quercus*	273.2	Museum
SATIN WAVE	*Idaea subsericeata*	8.5	Museum
EUDONIA TRUNCONOLA	*eudonia trunconola*	3.7	Kinsella et al. (2020)
EPINOTIA RAMELLA	*Epinotia ramella*	2.7	Museum
GREY CHI	*Antitype chi*	42.7	Kinsella et al. (2020)
STRIPED WAINSCOT	*Mythimna pudorina*	65.0	Museum
SCALLOPED OAK	*Crocallis elinguaria*	48.3	Museum
SHADED BROAD BAR	*Scotopteryx chenopodiata*	23.8	Museum
SILVER GROUND CARPET	*Xanthorhoe montanata*	12.4	Museum
NORTHERN RUSTIC	*Standfussiana lucernea*	91.7	Museum
AGRIPHILA TRISTELLA	*Agriphila tristella*	6.5	Kinsella et al. (2020)
SMALL WAINSCOT	*Denticucullus pygmina*	16.5	Museum

SMALL DOTTED BUFF	*Photedes minima*	13.0	Museum
GREY PINE CARPET	*Thera obeliscata*	13.3	Museum
TAWNEY PUG	*Eupithecia icterata*	10.2	Museum
STRIPED TWIN SPOT CARPET	*Coenotephria salicata*	6.6	Museum
TWIN-SPOT CARPET	*Mesotype didymata*	1.3	Museum
HEATH RUSTIC	*Xestia agathina*	43.4	Museum
NEGLECTED RUSTIC	*Xestia castanea*	60.3	Museum
HAWORTH MINOR	*Celaena haworthii*	35.0	Museum
CHEVRON	*Eulithis testata*	21.5	Museum
GREY MOUNTAIN CARPET	*Entephria caesiata*	31.8	Museum
THE CONFUSED	*Apamea furva*	65.4	Museum
EAR MOTH	*Amphipoea sp.*	32.0	Museum
SHARP ANGLED CARPET	*Euphyia unangulata*	7.1	Museum
DARK TUSSOCK	*Dicallomera fascelina*	142.1	Museum
IRON PROMINENT	*Notodonta dromedarius*	78.4	Kinsella et al. (2020)
EUDONIA SP.	*Eudonia sp.*	83.2	Museum
BORDERED BEAUTY	*Epione repandaria*	3.9	Museum
ORANGE SWIFT	*Triodia sylvina*	51.2	Museum
SCALLOPED HOOK TIP	*Falcaria lacertinaria*	17.5	Museum

LESSER SWALLOW PROMINENT	*Pheosia gnoma*	92.4	Museum
SALLOW KITTEN	*Furcula furcula*	71.1	Museum
FLOUNCED RUSTIC	*Luperina testacea*	55.2	Museum
HEBREW CHARACTER	*Orthosia gothica*	38.4	Kinsella et al. (2020)
CLOUDED DRAB	*Orthosia incerta*	47.3	Kinsella et al. (2020)
PHOENIX	*Eulithis prunata*	15.5	Kinsella et al. (2020)
STRAW BELLE	*Aspitates gilvaria*	12.4	Kinsella et al. (2020)
POWDERED QUAKER	*Orthosia gracilis*	42.7	Kinsella et al. (2020)
MOTTLED GRAY	*Colostygia multistrigaria*	9.7	Kinsella et al. (2020)
BRINDLED BEAUTY	*Lycia hirtaria*	23.0	Kinsella et al. (2020)
PUSS MOTH	*Cerura vinula*	303.6	Kinsella et al. (2020)
RED CHESTNUT	*Cerastis rubricosa*	36.3	Kinsella et al. (2020)
PALE SHOULDERED BROCADE	*Lacanobia thalassina*	47.6	Kinsella et al. (2020)

BROWN SILVER LINE	*Petrophora chlorosata*	12.4	Kinsella et al. (2020)
GLAUCOUS SHEARS	*Papestra biren*	40.6	Kinsella et al. (2020)
LIGHT KNOT GRASS	*Acronicta menyanthidis*	47.3	Kinsella et al. (2020)
MAY HIGH FLYER	*Hydriomena impluviata*	8.9	Kinsella et al. (2020)
WHITE ERMINE	*Spilosoma lubricipeda*	40.3	Kinsella et al. (2020)
MARBLED MINOR	*Oligia strigilis*	20.4	Kinsella et al. (2020)
SCALLOPED HAZEL	*Odontopera bidentata*	25.9	Kinsella et al. (2020)
FLAME CARPET	*Xanthorhoe designata*	6.1	Kinsella et al. (2020)
ANGLE SHADES	*Phlogophora meticulosa*	72.7	Kinsella et al. (2020)
PEPPERED MOTH	*Biston betularia*	36.0	Kinsella et al. (2020)
SILVER Y	*Autographa gamma*	42.7	Kinsella et al. (2020)
CLOUDED BORDERED BRINDLE	*Apamea crenata*	56.9	Kinsella et al. (2020)

FOX MOTH	*Macrothylacia rubi*	148.3	Kinsella et al. (2020)
PALE TUSSOCK	*Calliteara pudibunda*	72.1	Kinsella et al. (2020)
CLOUDED BRINDLE	*Apamea epomidion*	49.6	Kinsella et al. (2020)
PEACH BLOSSOM	*Thyatira batis*	41.7	Kinsella et al. (2020)
BUFF ERMINE	*Spilosoma lutea*	35.6	Kinsella et al. (2020)
ELEPHANT HAWKMOTH	*Deilephila elpenor*	227.9	Kinsella et al. (2020)
BLACK RUSTIC	*Aporophyla nigra*	52.0	Kinsella et al. (2020)
FOXGLOVE PUG	*Eupithecia pulchellata*	4.4	Kinsella et al. (2020)
CREAM WAVE	*Scopula floslactata*	8.9	Kinsella et al. (2020)
CORONET	*Craniophora ligustri*	47.3	Kinsella et al. (2020)
RED GREEN CARPET	*Chloroclysta siterata*	10.6	Kinsella et al. (2020)
LOBSTER MOTH	*Stauropus fagi*	185.3	Kinsella et al. (2020)

GREY PUG	*Eupithecia subfuscata*	4.4	Kinsella et al. (2020)
KNOT GRASS	*Acronicta rumicis*	47.3	Kinsella et al. (2020)
DUSKY BROCADE	*Apamea remissa*	47.3	Kinsella et al. (2020)
LIGHT EMERALD	*Campaea margaritata*	25.9	Kinsella et al. (2020)
CLOUDED BORDER	*Lomaspilis marginata*	6.1	Kinsella et al. (2020)
BUFF TIP	*Phalera bucephala*	175.5	Kinsella et al. (2020)
FERN	*Horisme tersata*	11.5	Kinsella et al. (2020)
DOUBLE SQUARE SPOT	*Xestia triangulum*	47.3	Kinsella et al. (2020)
HEART AND DART	*Agrotis exclamationis*	42.7	Kinsella et al. (2020)
MIDDLE BARRED MINOR	*Oligia fasciuncula*	19.9	Kinsella et al. (2020)
CLOAKED MINOR	*Mesoligia furuncula*	19.9	Kinsella et al. (2020)
BARRED UMBER	*Plagodis pulveraria*	15.5	Kinsella et al. (2020)

BLOOD VEIN	*Timandra comae*	12.4	Kinsella et al. (2020)
SMOKY WAINSCOT	*Mythimna impura*	38.4	Kinsella et al. (2020)
CRAMBUS SP.	*Crambus sp.*	4.9	Kinsella et al. (2020)
PUG SP.	*Pug sp.*	6.0	Museum
VESTAL	*Rhodometra sacraria*	6.7	Kinsella et al. (2020)
CHOCOLATE TIP	*Clostera curtula*	28.8	Kinsella et al. (2020)
AUGUST THORN	*Ennomos quercinaria*	20.3	Kinsella et al. (2020)
HOARY FOOTMAN	*Eilema caniola*	21.9	Kinsella et al. (2020)
CHESTNUT	*Conistra vaccinii*	32.3	Kinsella et al. (2020)
SMALL RUFOUS	*Coenobia rufa*	19.9	Kinsella et al. (2020)
RUBY TIGER	*Phragmatobia fuliginosa*	23.6	Kinsella et al. (2020)
TAWNY MARBLED MINOR	*Oligia latruncula*	23.2	Kinsella et al. (2020)

GALLIUM CARPET	*Epirrhoe galiata*	8.1	Kinsella et al. (2020)
RED TWIN SPOT CARPET	*Xanthorhoe spadicearia*	6.1	Kinsella et al. (2020)
SIX STRIPPED RUSTIC	*Xestia sexstrigata*	38.4	Kinsella et al. (2020)
RUFOUS MINOR	*Oligia versicolor*	21.5	Kinsella et al. (2020)
SHUTTLE SHAPED DART	*Agrotis puta*	30.4	Kinsella et al. (2020)
PALE PROMINENT	*Pterostoma palpina*	78.3	Kinsella et al. (2020)
SHARP ANGLED PEACOCK	*Macaria alternata*	8.1	Kinsella et al. (2020)
SMALL SCALLOP	*Idaea emarginata*	5.5	Kinsella et al. (2020)
RED UNDERWING	*Catocala nupta*	165.9	Kinsella et al. (2020)
SPECKLED BEAUTY	*Fagivorina arenaria*	11.4	Kinsella et al. (2020)
ANOMALOUS	*Stilbia anomala*	34.3	Kinsella et al. (2020)
ORANGE UNDERWING	*Archiearis parthenias*	14.4	Kinsella et al. (2020)

AUTUMNAL RUSTIC	*Eugnorisma glareosa*	36.3	Kinsella et al. (2020)
HERALD MOTH	*Scoliopteryx libatrix*	42.7	Kinsella et al. (2020)
DARK MARBLED CARPET	*Dysstroma citrata*	12.4	Kinsella et al. (2020)
HEDGE RUSTIC	*Tholera cespitis*	42.7	Kinsella et al. (2020)
RED CARPET	*Xanthorhoe decoloraria*	7.4	Kinsella et al. (2020)
LARGE EAR	*Amphipoea sp.*	36.3	Kinsella et al. (2020)
TREBLE BAR	*Aplocera plagiata*	21.6	Kinsella et al. (2020)
GOLDEN ROD BRINDLE	*Xylena solidaginis*	54.4	Kinsella et al. (2020)
PINK-BARRED SALLOW	*Xanthia togata*	32.3	Kinsella et al. (2020)
UDEA PRUNALIS	*Udea prunalis*	5.5	Kinsella et al. (2020)
PYLA FUSCA	*Matilella fusca*	13.2	Kinsella et al. (2020)
COMMON MARBLED CARPET	*Dysstroma truncata*	12.4	Kinsella et al. (2020)

NUT TREE TUSSOCK	*Colocasia coryli*	36.3	Kinsella et al. (2020)
POPLAR GREY	*Subacronicta megacephala*	49.6	Kinsella et al. (2020)
AETHES CNICANA	*Aethes cnicana*	8.7	Museum
SMALL FAN FOOT	*Herminia grisealis*	10.8	Kinsella et al. (2020)
MOTTLED BEAUTY	*Alcis repandata*	27.5	Kinsella et al. (2020)
GREEN ARCHES	*Anaplectoides prasina*	70.0	Kinsella et al. (2020)
GREEN SILVERLINES	*Pseudoips prasinana*	41.7	Kinsella et al. (2020)
SMALL YELLOW WAVE	*Hydrelia flammeolaria*	3.4	Kinsella et al. (2020)
MAGPIE MOTH	*Abraxas grossulariata*	24.4	Kinsella et al. (2020)
SETACIOUS HEBREW CHARACTER	*Xestia c-nigrum*	40.6	Kinsella et al. (2020)
ORTHOTAENIA UNDULANA	*Orthotaenia undulana*	7.9	Museum
BRAMBLE SHOOT MOTH	*Notocelia uddmanniana*	7.8	Museum
SWALLOW PROMINENT	*Pheosia tremula*	124.1	Kinsella et al. (2020)

EMPEROR	*Saturnia pavonia*	317.7	Kinsella et al. (2020)
BRIMSTONE	*Opisthograptis luteolata*	14.4	Kinsella et al. (2020)
COMMON QUAKER	*Orthosia cerasi*	34.3	Kinsella et al. (2020)
CABBAGE MOTH	*Mamestra brassicae*	47.3	Kinsella et al. (2020)
MUSLIN	*Diaphora mendica*	23.6	Kinsella et al. (2020)
WHITESPOT PUG	*Eupithecia tripunctaria*	4.4	Kinsella et al. (2020)
5 SPOT BURNET	*Zygaena trifolii*	34.9	Kinsella et al. (2020)
UNCERTAIN/RUSTIC	*Hoplodrina sp.*	33.3	Kinsella et al. (2020)
SWIFT	*Korscheltellus lupulina*	28.8	Kinsella et al. (2020)
ANNULET	*Charissa obscurata*	12.4	Kinsella et al. (2020)
EYED HAWKMOTH	*Smerinthus ocellata*	522.0	Kinsella et al. (2020)
GRASS WAVE	*Perconia strigillaria*	14.4	Kinsella et al. (2020)

FLAME	*Axylia putris*	34.3	Kinsella et al. (2020)
MILLER	*Acronicta leporina*	49.6	Kinsella et al. (2020)
GHOST MOTH	*Hepialus humuli*	175.5	Kinsella et al. (2020)
RIBAND WAVE	*Idaea aversata*	9.7	Kinsella et al. (2020)
SMALL ELEPHANT HAWKMOTH	*Deilephila porcellus*	96.2	Kinsella et al. (2020)
TRIPLE SPOTTED CLAY	*Xestia ditrapezium*	47.3	Kinsella et al. (2020)
FOUR DOTTED FOOTMAN	*Cybosia mesomella*	17.2	Kinsella et al. (2020)
PEBBLE HOOKTIP	*Drepana falcataria*	53.7	Kinsella et al. (2020)
ROSY FOOTMAN	*Miltochrista miniata*	14.4	Kinsella et al. (2020)
ENGRAILED	*Ectropis crepuscularia*	16.6	Kinsella et al. (2020)
SCARCE SILVER Y	*Syngrapha interrogationis*	40.6	Kinsella et al. (2020)
ROSY RUSTIC	*Hydraecia micacea*	45.0	Kinsella et al. (2020)

DINGY SHEARS	*Apterogenum ypsillon*	42.7	Kinsella et al. (2020)
LESSER BROAD BORDERED YELLOW UNDERWING	*Noctua janthe*	47.3	Kinsella et al. (2020)
SALLOW	*Cirrhia icteritia*	36.3	Kinsella et al. (2020)
BORDERED WHITE	*Bupalus piniaria*	15.5	Kinsella et al. (2020)
COMMON FANFOOT	*Pechipogo strigilata*	18.7	Kinsella et al. (2020)
SCARCE SILVER LINES	*Bena bicolorana*	72.9	Kinsella et al. (2020)
FANFOOT	*Herminia tarsipennalis*	17.2	Kinsella et al. (2020)

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Appendix E – Biomass Model Parameter Estimates

Table E-1 Moth Biomass Model Parameter Estimates and Standard Error (in parentheses). Bold text indicates a significant effect – p=<0.05

PARAMETRIC COEFFICIENTS	MODEL 1		MODEL 2		MODEL 3		MODEL 4	
	Estimate (SE)	**T statistic**	**Estimate (SE)**	**T statistic**	**Estimate (SE)**	**T statistic**	**Estimate (SE)**	**T statistic**
INTERCEPT	**7.29 (0.2)**	**36.23**	**7.02 (0.13)**	**55.4**	**7.06 (0.18))**	**38.60**	**6.95 (0.11)**	**61.94**
MIN. TEMP	**0.57 (0.07)**	**8.30**	**0.59 (0.07)**	**8.65**	**0.37 (0.07)**	**5.11**	**0.41 (0.07)**	**6.27**
WIND	**-0.30 (0.08)**	**-3.88**	**-0.27 (0.07)**	**-3.64**	**-0.2 (0.07))**	**-2.99**	**-0.19 (0.07)**	**-2.96**
PRECIPITATION	-0.04 (0.06)	-0.60	-0.05 (0.06)	-0.74	-0.06 (0.06)	0.34	-0.02 (0.06)	-0.935
2018	-0.29 (0.19)	-1.50	NA	NA	-0.04 (0.17)	-0.25	NA	NA
2019	-0.22 (0.18)	-1.23	NA	NA	-0.17 (0.16)	-1.05	NA	NA
SEASONALITY	0.03 (0.12)	0.27	0.03 (0.12)	0.28	0.04 (0.16)	0.26	NA	NA
NORTHLY ASPECT	0.23 (0.17)	1.34	0.14 (0.17)	0.87	0.26 (0.15)	1.74	0.17 (0.15)	1.16

SOUTHERLY ASPECT	-0.06 (0.17)	-0.36	0.01 (0.16)	0.08	-0.06 (0.15)	-0.40	0.09 (0.14)	0.62
WESTERLY ASPECT	0.05 (0.18)	0.25	0.02 (0.17)	0.12	0.12 (0.16)	0.74	0.04 (0.16)	0.29

Table E2 Moth Biomass Model Smoothed Parameter Estimates and Standard Error (in parentheses). Bold text indicates a significant effect – p=<0.05

	MODEL 1		**MODEL 2**		**MODEL 3**		**MODEL 4**	
SMOOTH TERMS	**edf (ref.df)**	**F statistic**	**edf (ref.df)**	**F statistic**	**edf (ref.df)**	**F statistic**	**edf (ref.df)**	**F statistic**
S(X,Y)	**1.78 (4)**	**2.52**	**1.73 (4)**	**1.73**	NA	NA	NA	NA
S(JDAY)	**3.49 (11)**	**2.94**	NA	NA	NA	NA	NA	NA
S(JDAY):2017	NA	NA	3.39 (9)	0.80	NA	NA	NA	NA
S(JDAY):2018	NA	NA	**2.59 (11)**	**1.49**	NA	NA	NA	NA
S(JDAY):2019	NA	NA	**5.05 (11)**	**3.70**	NA	NA	NA	NA
TE(XKM,YKM,JDAY):2017	NA	NA	NA	NA	NA	NA	**2.41 (40)**	**0.14**
TE(XKM,YKM,JDAY):2018	NA	NA	NA	NA	NA	NA	**8.24 (59)**	**0.77**
TE(XKM,YKM,JDAY):2019	NA	NA	NA	NA	NA	NA	**15.3 (59)**	**1.78**

TE(XKM,YKM,JDAY)	NA	NA	NA	NA	**19.3 (59)**	**2.12**	NA	NA
S(CLEARFELL AGE, SEASONALITY)	0.72 (28)	0.07	0.77 (28)	0.09	**3.09 (28)**	**0.29**	0 (29)	0
S(WIND):EAST	0 (9)	0	0 (9)	0	0 (9)	0	0 (9)	0
S(WIND):NORTH	**1.54 (9)**	**1.2**	**1.91 (9)**	**1.21**	**1.83 (9)**	**1.48**	**1.86 (9)**	**1.29**
S(WIND):SOUTH	0 (9)	0	0 (9)	0	0 (9)	0	0 (9)	0
S(WIND):WEST	0 (9)	0	0 (9)	0	0 (9)	0	0 (9)	0

Appendix F – Moth Biomass Weather Effects

Figure F1 - Predicted Moth Biomass vs Temperature - This graph shows Model 3 predicted moth biomass over the range of recorded temperatures (oC) for Julian day 180 (29th June) at a sample location with a Southerly aspect in 2018 with all other variables held at their mean value.

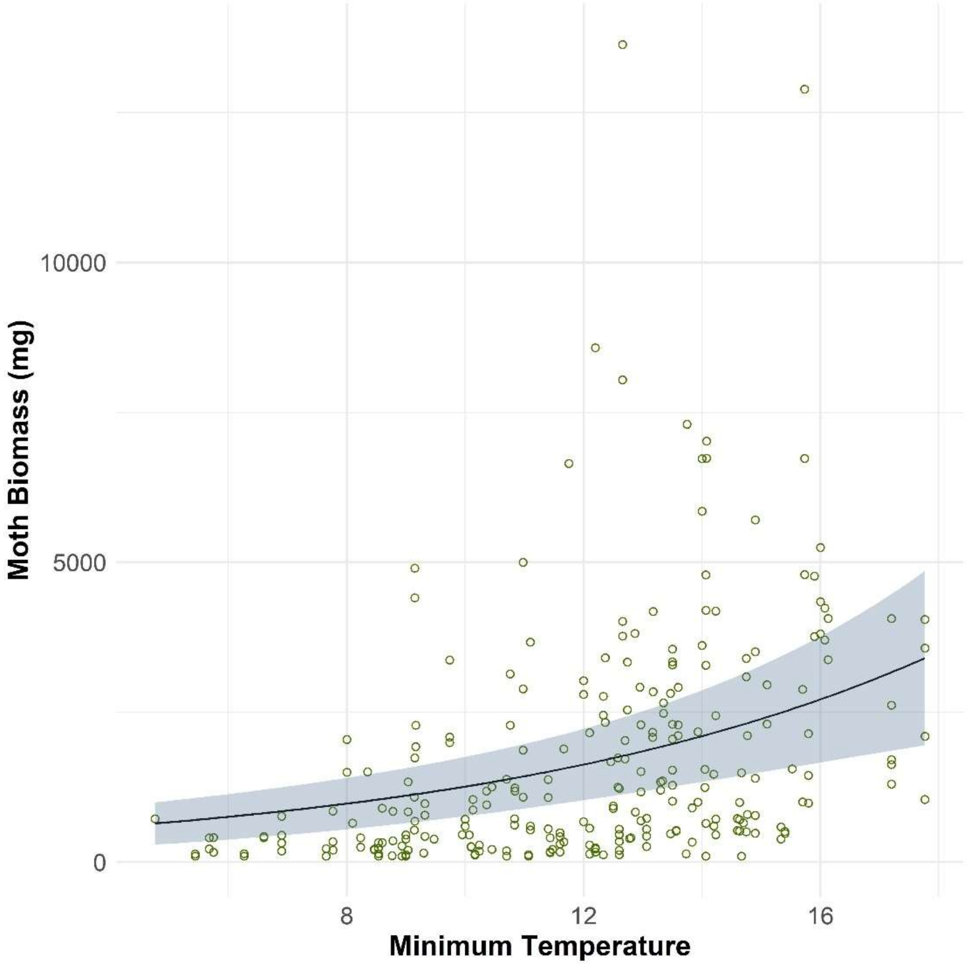
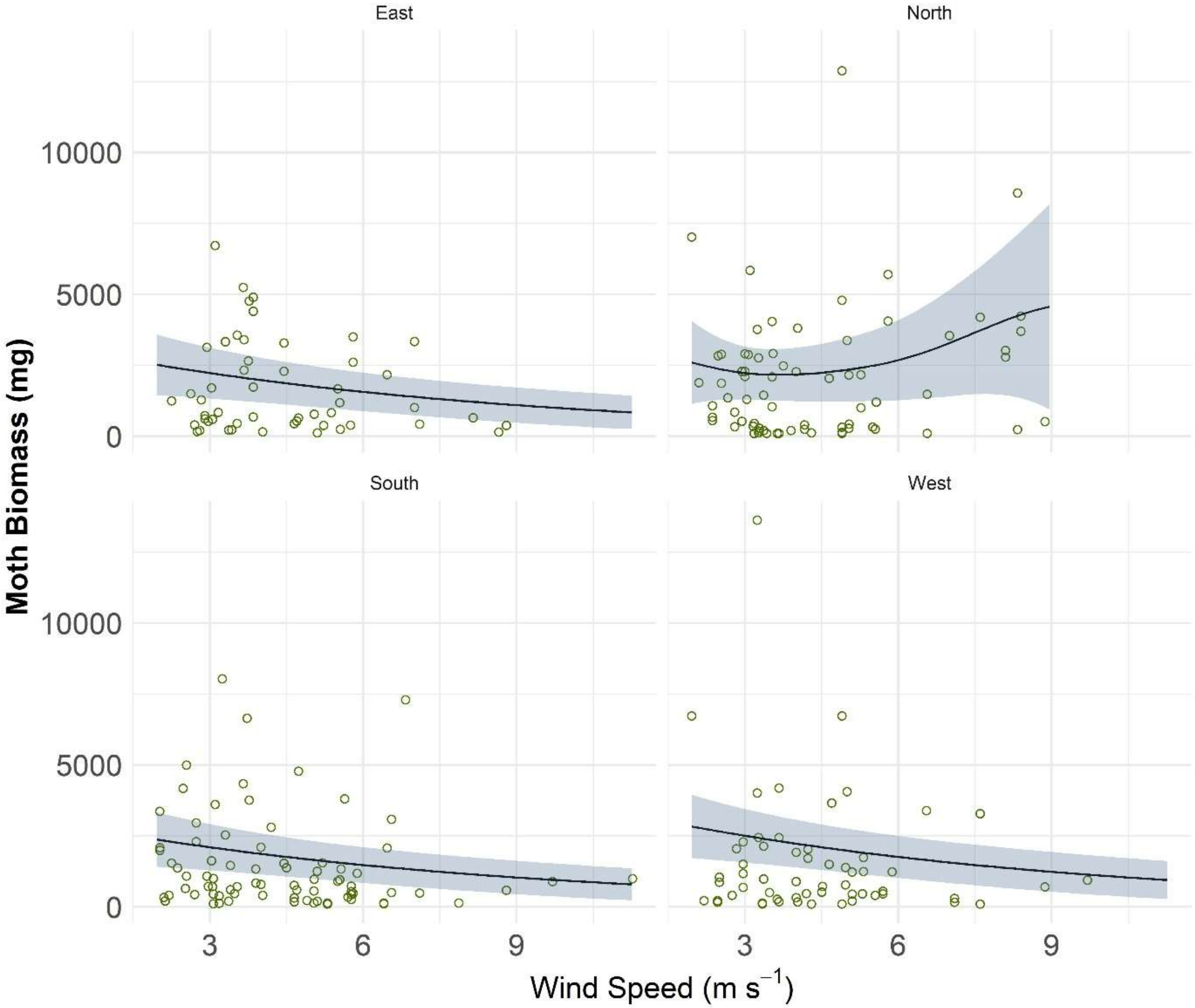


Figure F2 - Predicted Moth Biomass vs Wind Speed (m/s) for different aspect sampling locations - This graph shows Model 3 predicted moth biomass over the range of recorded wind speeds for Julian day 180 (29th June) across the cardinal direction aspects at a sample location in 2018 with all other variables held at their mean value.



Appendix G – Section 7 and Species Diversity Model Parameter Estimates

Table G1 Section 7 Species Model Parameter Estimates and Standard Error (in parentheses). Bold text indicates a significant effect – p=<0.05

MODEL	PARAMETER															EVALUATION CRITERIA	
	Time felling <1yr	Time felling 1-5yr	Time felling 6-10yr	Time felling 11-15yr	Time felling 15-20yr	Time felling 20yr+	Month (6)	Month (7)	Month (8)	Month (9)	X	Y	Min Temp	Wind	X:Y	R squared	AICc
MOTH MIXED MODEL (250M)	**0.31 (0.11)**	**0.15 (0.06)**	**0.3 (0.09)**	-0.05 (0.1)	-0.01 (0.05)	-0.02 (0.05)	NA	NA	NA	NA	NA	NA	**0.12 (0.05)**	**0.31 (0.11)**	NA	NA	597.6
MOTH MIXED MODEL (500M)	0.1 (0.07)	**0.19 (0.05)**	**0.42 (0.07)**	-0.04 (0.09)	-0.02 (0.06)	0.02 (0.04)	NA	NA	NA	NA	NA	NA	**-0.02 (0.06)**	0.1 (0.07)	NA	NA	627.3
MOTH MIXED	-0.02 (0.07)	**0.21 (0.06)**	**0.4 (0.08)**	-0.06 (0.06)	0.05 (0.09)	0.11 (0.08)	NA	NA	NA	NA	NA	NA	**0.03 (0.06)**	-0.02 (0.07)	NA	NA	608.8

MODEL (1KM)																
SPECIES DIVERSITY (250M)	**-0.15 (0.04)**	-0.02 (0.05)	-0.03 (0.05)	0.04 (0.04)	-0.03 (0.04)	0.04 (0.04)	**0.29 (0.12)**	**0.51 (0.13)**	0.23 (0.13)	-0.54 (0.43)	**-0.17 (0.04)**	**-0.2 (0.05)**	**0.39 (0.04)**	**-0.13 (0.04)**	**0 (0)**	**0.23**	**NA**
SPECIES DIVERSITY (500M)	**-0.11 (0.04)**	0.01 (0.04)	0.03 (0.05)	0.02 (0.04)	-0.04 (0.04)	0.06 (0.04)	**0.32 (0.12)**	**0.52 (0.13)**	0.26 (0.13)	-0.51 (0.43)	**-0.17 (0.04)**	**-0.2 (0.05)**	**0.4 (0.04)**	**-0.14 (0.04)**	**0 (0)**	**0.22**	
SPECIES DIVERSITY (1KM)	**-0.1 (0.04)**	0 (0.04)	0.01 (0.05)	0.01 (0.04)	-0.04 (0.04)	0.02 (0.05)	**0.32 (0.12)**	**0.54 (0.13)**	0.25 (0.13)	-0.53 (0.43)	**-0.16 (0.05)**	**-0.19 (0.06)**	**0.39 (0.04)**	**-0.13 (0.04)**	**0 (0)**	**0.23**	

Appendix H – CTMM Movement Models

Table H1 – CTMM Movement Model Details

RING NUMBER	MODEL TYPE
CF49394	OU anisotropic
LB09362	OUF anisotropic
LB09363	OUF anisotropic
LB09364	OU anisotropic
LB09390	OUF anisotropic
LE43244	OUF anisotropic
LH75968	OUF anisotropic
LH76623	OUF anisotropic
LH76699	OUF anisotropic
LH76728	OUF anisotropic
LH76739	OUF anisotropic
LH76864	OUF anisotropic
LH76876	OUF anisotropic
LH76895	OUF anisotropic
LH77804	OUF anisotropic
LH77838	OUF anisotropic
LJ75534	OUF anisotropic
LJ75945	OUF anisotropic

LJ75947	OUf anisotropic
LJ75954	OUF anisotropic
LJ75964	OUF anisotropic
LJ84712	OUF anisotropic
LJ84739	OUF anisotropic
LJ84787	OUF anisotropic
SX01123	OUF anisotropic