The influence of environmental variation on individual foraging and habitat selection behaviour of the European nightjar

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Abstract

Animals experience a variety of environmental stressors, for example climate and habitat change. These changes can alter the distribution and population dynamics of species indirectly through disruption of behavioural processes, including foraging. Collecting behavioural data, such as foraging tracks, from multiple individuals can help to identify how response to habitat change, is driven by factors such as resource distribution, intra-specific competition and intrinsic factors such as sex and age. This thesis combined behavioural and dietary information collected from individual European nightjars *Caprimulgus europaeus*, to analyse variation in behaviour amongst the population, in response to habitat change and the consequences this might have in terms of future change and for beneficial management.

This population of nightjars showed significant individual variation in home range size and habitat selection therein. Home ranges sizes increased by 1% and decreased by 9% in wetland and newly cleared habitat respectively. This indicated that although birds possess individual preferences for specific habitat types, there are foraging constraints that affect multiple individuals. Foraging behaviour changed most strongly in relation to habitat type, NDVI and more weakly in relation to the lunar cycle and temperature. Time spent foraging increased in cleared habitat (β: 0.03, R^2 0.08, p: 0.07), which became more available during the study. Males spent 33% of their time foraging compared to females which spent only 18.6% of their time foraging, representing differing breeding roles. However, strong methodological influence was clear, whereby an increase in the fix interval from 3 to 5 minutes caused a 39% increase in step length, unaccounted for by year or habitat change. Individual diet composition differed and changed between years, in response to prey availability, however common species occurred in 40-50% of samples. Overall nightjars selected for larger moths compared to local availability. Collectively, my results and demonstrated flexibility at the population level and the potential to respond positively to habitat. As a species specialising in a spatially- and temporally-varying prey resource, maintenance of complex habitat mosaics that encourage a wide diversity of moth and other flying insect species, along with the diversity of habitat types to encourage breeding and survival of all individuals.

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Declaration

I declare that this thesis is a presentation of original work and I am the sole author. This work has not previously been presented for an award at this, or any other, University. All sources are acknowledged as references.

Publications

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“The ‘capacious mouth’ of a nightjar could certainly accommodate an egg, perhaps even two, just as it could probably accommodate the teat of a goat, but there is no more evidence of it being an egg-carrier than there is of it being a goatsucker”

HD Jackson, 2007

Chapter 1: Introduction

The decisions that animals make with regard to foraging and reproduction are often strongly influenced by environmental characteristics at multiple scales. Changes in environmental characteristics, such as structural alterations through habitat manipulation, seasonal fluctuations or long-term climate change, impact the distribution, quantity and quality of resources. A change in resource availability or abundance can lead to changes in population dynamics and species distribution, through shifts in behaviour. Behavioural adaptations can vary among the individuals in a population, which can dictate overall population flexibility; thus, making it important to understand individual variation and how this shapes the population response to change.

To this end, it is important to collect behavioural information from multiple individuals within a population. In this introduction, I outline concepts developed around individual variation, specifically related to foraging and diet, including habitat selection, niche variation and foraging efficiency. I outline previous work, the limitations therein, and lastly outline the thesis structure, aims and objectives.

1.1 Species decline

Species from all taxa face multiple global threats (Dirzo *et al.*, 2014) from climate change, habitat destruction for urban and agricultural development, as well as pollution (IPBES, 2018, 2019). Of these pressures, anthropogenically-driven habitat loss is recognised as the most severe, threatening persistence of many vertebrates and invertebrates alike (Sih, Ferrari and Harris, 2011; van Baaren and Candolin, 2018). Habitat loss exacerbates and is exacerbated by the effects of other threats, such as climate change (Haddad *et al.*, 2015; Colloff *et al.*, 2017), by limiting species' movement (Lendrum *et al.*, 2013; Fraser *et al.*, 2018) and their ability to disperse (Tuomainen and Candolin, 2011; Doherty and Driscoll, 2018). Populations may be unable to disperse or migrate in response to changes in climate, because there is no suitable habitat to move to (Bellard *et al.*, 2012; Iwamura *et al.,* 2013; Dirzo *et al.*, 2014; Pringle, 2017). This inability to alter or expand their distribution disproportionately affects sedentary and habitat-specific species (Warren *et al.*, 2001), despite the protection of habitats important to declining species (Fox *et al.*, 2014). Even mobile species, such as birds that should be able to disperse more easily, may not be able to if the habitat they prefer does not exist, or if they are unable to quickly evolve new preferences or adaptations to cope with novel environments (Pereira *et al.*, 2013). For example, declines in multiple, migratory wading bird species has been accelerated by the removal of vital wetland stopover sites in the Yellow sea due to land reclamation (Iwamura *et al.,* 2013). These bottleneck sites that support individuals from different breeding and wintering populations using the East Asian-Australasian Flyway (EAAF) have reduced survival of birds (Piersma *et al.,* 2015; Zhang *et al.,* 2018) by removing productive feeding areas and causing a break in the chain of migratory sites.

Humans have altered both quality and abundance of habitats (Morris, 2003), thus directly impacting species' survival and reproduction by reducing the space available for breeding and foraging activities (Fraser *et al.*, 2012), and by reducing the distribution and abundance of prey (Nocera *et al.*, 2012; Sánchez-Bayo and Wyckhuys, 2019). Particularly impacted are species of mammal, birds and reptiles that predate on insect taxa (Nebel, Mills, McCracken, *et al.*, 2010; Fox *et al.*, 2014; Smith *et al.*, 2015). Invertebrates, in particular flying insects, have declined alarmingly over the past decades. Declines in numbers upwards of 75% of all flying insects have occurred in Germany over a 27 year period (Hallmann *et al.*, 2017), >65% decline in macro moths in the UK over 35 years (Conrad *et al.*, 2006) and >80% decline in butterflies in the Netherlands over the last 100 years (van Strien *et al.*, 2019). Sánchez-Bayo and Wyckhuys (2019) estimate that worldwide 40% of insect species are at risk of extinction, thus effects of habitat loss are present at a global scale. Human population growth and the intensification of agricultural production, means that not only are original habitats removed or damaged, but they become homogenised single species cropland (Erdős *et al.*, 2018). Such crops are often heavily treated with pesticides, which can have direct effects on mortality as well as indirect effects through changes in behaviour (Benton *et al.*, 2002; Nocera *et al.*, 2012). Reduction in suitable habitat for breeding and foraging caused by agricultural expansion, can restrict populations of birds to refuges within intensified landscapes, increasing their vulnerability (Boggie *et al.*, 2018).

The effects of landscape change and habitat loss do not target species randomly but instead are associated with particular traits. These traits might relate to restricted geographical or elevational ranges (Sekercioglu, 2006), or ecological traits such as body size and dietary specialism (Coulthard *et al.*, 2019). Movement capabilities and habitat specificity were found to be important predictors of the ability of birds to expand their range in southern Africa (Okes, Hockey and Cumming, 2008). The importance of habitat specificity of birds for coping with anthropogenic threats was also highlighted by Owens and Bennett (2000). Species most at risk from habitat loss were found to be those with a small body size, or a high degree of specialisation, and long-distance migrants (Owens and Bennett, 2000). It is widely recognised that long-distance migratory bird species are in decline worldwide (Vickery *et al.*, 2014a; Murray *et al.*, 2018). Migratory species are subject to a number of different threats across their annual range, which may include crossing oceans and continental boundaries (Murray *et al.*, 2018) and thus encountering widespread land use change, persecution and differential effects of climate change (Newton, 2004; Dhanjal-Adams, 2016). Developing priority actions for migratory species' conservation is challenging, because these species require conservation measures that can extend to multiple parts of their range (Newton, 2004; Fraser *et al.*, 2012; Runge *et al.*, 2014, 2015).

1.2 Conservation measures

To stem global declines of biodiversity, adequate species conservation measures must be identified (Runge *et al.*, 2015). Measures should be designed to manipulate one or more demographic measures (e.g. survival, productivity and/or recruitment; Green and Hirons, 1991; Newton, 2007). This can be through the provision of resources where they have been lost (e.g. nest boxes to replace lost nest sites in trees – Fattebert *et al.*, 2018) or by removing a threat, such as an invasive species or presence of human development. For example Black-tailed godwit (*Limosa l. limosa*) population decline has been strongly linked to agricultural processes that destroyed nests and chicks in intensified grassland landscapes in the Netherlands (Kleijn *et al.*, 2010). Where the causes of population decline or instability relate to the availability and quality of habitat, opportunities for habitat protection, management and restoration should be prioritised according to their proposed influence, the cost and the evidence of results (Miller and Hobbs, 2007; Wortley, Hero and Howes, 2013; Torok and Helm, 2017). Restoration infers the return of a site or habitat type to a past state (Bradshaw, 1997) and often aims to increase functioning of ecological processes on sites (Wortley, Hero and Howes, 2013). It is assumed that restorative efforts will reverse degradation or increase habitat resilience (Mitchell *et al.*, 2000) and thus increase species persistence (Failing, Gregory and Higgins, 2013). Evidence of past success is crucial to increase current progress of projects (Sutherland *et al.*, 2004), and can be fed into restoration scenarios using a Conservation Planning Tool (CPT) framework (Ricca *et al.* 2018) to produce the best results.

Monitoring of outcomes and the efficacy of restoration is central to the success of projects and should aim to improve understanding of how targeted species and habitat types are responding to management (Block *et al.*, 2001). Lack of inclusion of previous experience and differences between sites and populations, can mean that the desired outcomes of restoration are not always achieved, particularly when species-focused. For example, Smith and Beck (2018) demonstrated that small-scale restoration attempts of sage-brush habitat by fire and chemical treatment were associated with negative population trends in responses of the Greater sage-grouse (*Centrocercus urophasianus*), a keystone species. 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 (Guisan *et al.*, 2013), but observe how species are behaving (W J Sutherland, 1998). Consequently, we need to be willing to use adaptive management, whereby management actions can be discontinued following an initial phase, if they are found to be unproductive (Block *et al.*, 2001).

Restoration planning in this form requires comprehensive knowledge of a species' ecology (Morris, 2003; Sharps, 2013; Davies *et al.*, 2014). Successful examples include the use of breeding and habitat selection behaviour to predict population change in Greater sage-grouse, in response to proposed development and restoration plans in Wyoming, USA (Copeland *et al.*, 2013). Species behaviour, be it nest siting decisions, foraging habitat preferences or mating system dynamics (Kertson and Marzluff, 2011; Evens *et al.*, 2017; Dunn, Morris and Grice, 2017), need to be assessed before *and* after actions take place, to ensure measures are correctly targeted and to monitor responses to change and to better direct conservation (Fernández-Juricic and Schulte, 2016).

1.3 Individual and population-level responses to environmental change

Interpreting species' behavioural responses to environmental change, such as habitat restoration, can ensure better success of these endeavours through the implementation of ecologically-appropriate actions (Copeland *et al.*, 2013; Baxter *et al.*, 2017). The impact of restoration trade-offs can only be fully realised through monitoring and assessment of species behavioural responses to these changes (Block *et al.*, 2001; Lindell, 2008). Assessing the response of species using their immediate behavioural reactions, can act as an early warning system (Berger-Tal *et al.*, 2011; Greggor *et al.*, 2016). Significant demographic impact may not manifest itself for a longer period of time, by which time a population may be too isolated or reduced, resulting in limited conservation options (Tuomainen and Candolin, 2011). To this end, in recent decades the study of animal behaviour has started to integrate with species conservation work (Sutherland, 1996; Buchholz, 2007) and applied wildlife management (Fernández-Juricic and Schulte, 2016).

Behaviour is ‘part of the pattern that produces the ecology of the animal’ (Gordon, 2011), therefore understanding how the behavioural mechanisms affect ecology and then fitness, reproduction and survival (Goss-Custard and Sutherland, 1997; Caro, 1999) is a necessary, significant challenge. Measures of behaviour, such as habitat selection or foraging movements, are key to understanding the use of a landscape, rather than just distribution data alone, where no underlying mechanism is taken into account. Behaviour of a species may be context dependent and so may vary between populations (Garamszegi and Møller, 2017). Thus data should be collected ideally over multiple spatial scales (Sauter *et al.*, 2012; Shaffer *et al.*, 2017), to compare mean population habitat selection values that might correlate with landscape differences (Shaffer *et al.*, 2017). To understand behavioural change or development, researchers require individual longitudinal data, over multiple temporal scales that might give an indication of plasticity and ability to respond to change (Hall Sawyer *et al.*, 2006; Hall and Chalfoun, 2019). Distance of repeated individual measures to a mean annual or population habitat selection, foraging duration and direction, can provide information on within-population variation (Garamszegi and Møller, 2017; Phillips *et al.*, 2017) that may indicate how likely it is that a population can maintain its current niche. Observing the initial behavioural choices of animals in the field at a variety of spatial scales can indicate differences in resource quality across areas or time, which can therefore assess the success of restoration (Baxter *et al.*, 2017), more accurately than simple resource metrics such as vegetation density or height (Lindell, 2008; Smith and Beck, 2018). The connection between animal behaviour and conservation management still needs to be consolidated (Linklater, 2004; Caro and Sherman, 2011). Multiple frameworks for integrating behavioural responses and processes into conservation planning and monitoring have been conceptualised (Block *et al.*, 2001; Berger-Tal *et al.*, 2011; Sih, Ferrari and Harris, 2011; Sih, Ehlman and Halpin, 2015; Sih, Trimmer and Ehlman, 2016; van Baaren and Candolin, 2018) and are represented in Figure 1. These frameworks attempt to link themes relating to direct (e.g. habitat fragmentation) and indirect disturbance (reducing the strength of the cue-reponse relationship) on animal behaviour and their evolutionary outcomes (Sih, Ferrari and Harris, 2011). Proactive management techniques for practitioners include developing ‘behaviour-sensitive’ management of species following the use of indicator behaviours, which can be used to signify the current state of a population. For example, Tarjuelo *et al.*, (2015) identified a disturbance-related increase in Little bustard (*Tetrax tetrax*) vigilance behaviour with increased human activity that also induced an increase in concentration of stress hormones. In relation to habitat change, Shochat *et al.*, (2005) and Cutting *et al.*, (2019) identified negative consequences of restored habitat for ground nesting birds as a consequence of ‘decoupled’ cue-response behaviours (Sih, Ehlman and Halpin, 2015). Multiple ground-nesting grassland bird species (Shochat *et al.*, 2005) including greater sage-grouse (Cutting *et al.*, 2019) selected for managed areas based on structural cues that ought to favour nesting success, but actually resulted in lower levels of survival because novel environments changed the validity of the cues (open areas and low vegetation that would normally create positive nesting areas instead induced increased predator presene, because of the particular way the vegetation had been cleared). These unforeseen responses to altered environments show that even if animals can adjust their behaviour, they may ultimately be stifled by antropogenic disruption that induces maladaptive behaviour (Robertson and Hutto, 2006; Tuomainen and Candolin, 2011). It also reiterates the utility of behavioural information in a conservation setting, where distributional data cannot elaborate on the reasons for declines. Information on both maladaptive behaviours and positive responses need to be identified and fed back into conservation plans.

As discussed above, migratory birds are particularly under threat from multiple processes in many different areas and often possess specific requirements that cause them to migrate substantial distances to follow peaks in prey resources and acquire suitable breeding habitat. Behavioural data can help to identify specific stressors on the breeding or wintering grounds, and identify pinch points, that can be used to implement conservation decisions on the ground.

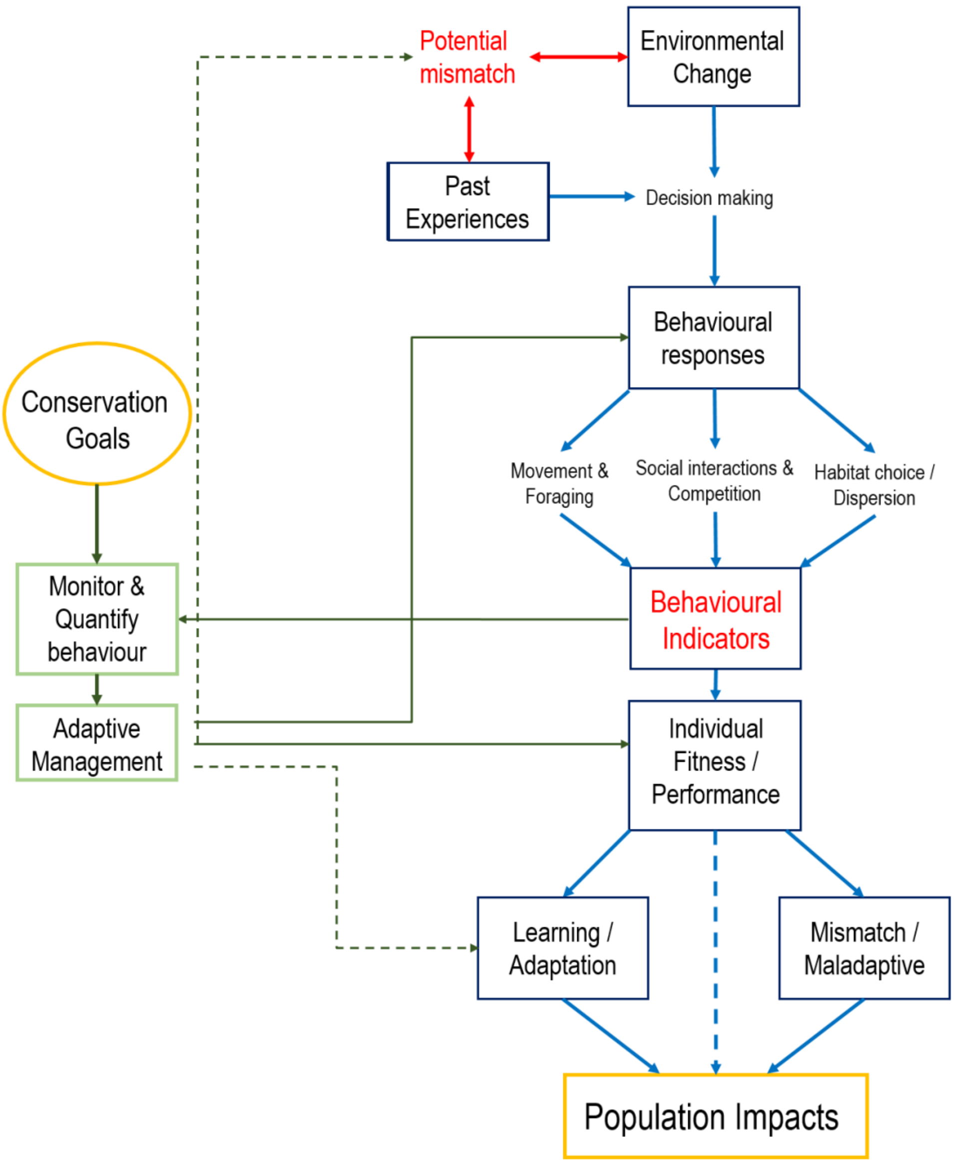


Figure 1.1: Schematic representing multiple combined frameworks for the identification of behavioural processes and the integration of behavioural responses into conservation management (based on: Block *et al.*, 2001; Berger-Tal *et al.*, 2011; Sih, Ferrari and Harris, 2011; Sih, Ehlman and Halpin, 2015; Sih, Trimmer and Ehlman, 2016; van Baaren and Candolin, 2018).

Migratory birds are often strongly site faithful (Hoover, 2003), but the behavioural responses of returning migrants to discrete, anthropogenic habitat changes at breeding areas have not been well studied (Jones and Cresswell, 2010; Cresswell, 2014, Morant *et al.,* 2018). There is a need therefore, to identify the factors that most strongly influence territory choice and site fidelity (Switzer, 1993; Hoover, 2003), such as nest site availability (Orians and Wittenberger, 1991) or a mixture environmental characteristics in the surrounding area (Morant *et al.,* 2018) and previous experience of the individual at the site (Switzer, 1993). If species are driven to return to the same site because of previous breeding success (Hoover, 2003, Morant *et al.,* 2018), then habitat change whilst birds are on their wintering grounds might remove preferred habitat features, alter familiarity (Switzer, 1993), or change social cues (Betts *et al.*, 2008) potentially leading to a negative behavioural response (Morant *et al.,* 2018). Orians and Wittenberger (1991) found that female yellow-headed blackbirds (*Xanthocephalus xanthocephalus*) settled in territories according to a combination of cues related to habitat structure, proximity to productive foraging areas and overall insect density, which might be disrupted should habitat change.

For migratory birds arriving on the breeding ground, information and cues may no longer be reliable due to habitat change (Miner *et al.*, 2005; Nussey, Wilson and Brommer, 2007). For birds unable to adjust their behaviour, which might include moving territory or changing their foraging location, studies have shown that there can be significant impacts on population dynamics. Morant *et al.* (2018) reported increased nest switching, decreased reproduction and complete abandonment by Egyptian vultures (*Neophron percnopterus*) when returning to their breeding sites after habitat management had taken place. Previous used sites consequently remained unused for more than 4 – 5 years after abandonment, suggesting an inflexibility of this species when faced with habitat manipulation. Establishing the ability of populations of birds to adjust their behaviour in response to environmental change is key to understanding the effects of habitat management and may depend not only on the species but the size of the specific population and their ecological traits, such as longevity or dietary niche.

1.4. Behavioural variation

Animals may be able to change their behaviour in response to a change in the environment, known as 'behavioural plasticity' (Stamps, 2016). This behavioural plasticity may manifest itself in the form of functional responses (Mysterud and Ims, 1998), which represent a change in habitat use in line with a change in availability of habitat types (Holbrook *et al.,* 2019). These functional responses may occur in relation to temporary environmental heterogeneity e.g. seasonal ice distribution (Mauritzen *et al.*, 2003), or due to land management or human disturbance (Dussault *et al.*, 2012; Losier *et al.*, 2015). Functional responses have been observed in multiple species (Godvik *et al.*, 2009; Bjørneraas *et al.*, 2012; Mason and Fortin, 2017; Holbrook *et al.,* 2019), although have been less studied in birds (Gillies, Cassady and Clair, 2010). Whilst population-level effects are implied, plasticity is necessarily considered at the individual level (Tuomainen and Candolin, 2011). Plasticity can result from inherited traits, termed 'developmental' or endogenous plasticity (Sol and Maspons, 2015; Stamps, 2016), implicating life-history experience and genetics in the production of specific behaviours (Snell-rood, 2013). Natal habitat type (Stamps and Swaisgood, 2007) and developmental conditions such as temperature (Glanville and Seebacher, 2006) might influence response to stimuli as adults. Conversely, 'activational' or 'contextual' plasticity can induce immediate responses and is driven more by acclimatisation to an environment in the short term than by life experiences (Stamps, 2016).

These contextual responses are especially relevant given the rapidity of recent anthropogenic disturbance to both the landscape and the climate (Chevin, Lande and Mace, 2010). Species that have evolved to exploit temporally-varying prey resources, e.g. flying insects, may naturally be more plastic and opportunistic in their behaviours (Sergio *et al.,* 2011), as unstable habitats and resources are thought to favour more reactive individuals (Hewes, Delventhal and Chaves-Campos, 2017). Higher levels of responsiveness may consequently facilitate their adaptation to change (Sergio *et al.,* 2011; Wong and Candolin, 2015). Whether phenotypic plasticity will be sufficient in every species is unknown. Black Kites (*Milvus milvus*) were found to adjust their diet in response to short-term fluctuations in prey within a season, thus increasing their ability to fledge offspring (Sergio *et al.,* 2011). Meanwhile, Both *et al.*, (2010) found that Pied flycatchers

(*Ficedula hypoleuca*), a migrant insectivore, could only make a limited adjustment to changes in peak prey availability due to the timing of migration. Equally, Charmantier *et al.*, (2019) found that a Great tit (*Parus major*) population was able to track shifts in peak prey resources over more than 40 years, but that individuals themselves were constrained in their responses. Indeed, the multiple stressors that different populations of species find themselves under pressure from (e.g. combined climate change and landscape alteration), may interact to increase the amount of stress expressed by individuals and will thus have knock-on effects on energetics and finally, survival (Noonan *et al.*, 2019).

Behaviour is not necessarily consistent within populations (Nilsson *et al.*, 2014; M. Leclerc *et al.*, 2016; R. A. Phillips *et al.*, 2017) and frequently varies substantially between individuals (Nussey, Wilson and Brommer, 2007; Bolnick *et al.*, 2003). Individuals often occupy a narrower niche compared to that of the population, which both reduces competition and provides relative benefits for that individual (Wong and Candolin, 2015; Maldonado *et al.*, 2019). The presence of individual variation can create a flexible, generalist population, which can drive occupation of a broad niche. However, within the population, individuals themselves might be fixed, i.e. specialised (Bolnick *et al.*, 2003; Araújo, Bolnick and Layman, 2011; Snell-Rood, 2013; Patrick and Weimerskirch, 2017). For example Northern gannets (*Morus bassanus*) have been shown to use foraging strategies that vary strongly and consistently between individuals (Wakefield *et al.*, 2015), within and between years, primarily related to learning and foraging efficiency. The formation of consistent and repeatable individual behaviours can be driven by intraspecific competition (Dall *et al.*, 2012), as a mechanism for increasing efficiency (Dingemanse *et al.*, 2010) or for coping with uncertainty (Mathot *et al.*, 2012). Increasing interest in individuals that maintain consistent behaviours such as risk taking or certain resource exploitation has occurred under the umbrella of animal personality, or behavioural reaction norms (Dingemanse *et al.*, 2010), whereby consistent ‘bold’ or ‘shy’ behaviours are carried across contexts (Cornwell *et al.*, 2019).

In many studies, by using the population mean to describe habitat selection or foraging behaviour, can hide individual variability in responses to change (Gillies and St. Clair, 2010; Roche, Careau and Binning, 2016). For example, brown bears (*Ursus arctos*) in North America displayed population-level selection for cut forest blocks, but at the individual-level, responses towards this habitat type were mixed (Leclerc *et al.*, 2016). Similarly, forest structural change was both positive and negative for different individuals, in terms of home range size and movement parameters within a population of black bears (*Ursus americanus*; Karelus *et al.* 2016). Individual variation has the ability to facilitate population reaction to change as a whole (Sih *et al.*, 2012), particularly where there are individuals that possess high contextual plasticity (Stamps, 2016), and can adapt their decision making processes based on short-term cues (Owen, Swaisgood and Blumstein, 2017). Individuals with certain flexible phenotypes may hold fitness advantages over inflexible conspecifics (Sih, Bell and Johnson, 2004; Miner *et al.*, 2005). These individuals can therefore support and stabilise a population when environmental change occurs (Phillips *et al.*, 2017; Shaffer *et al.*, 2017). Differential survival rates were observed between coyote (*Canis latrans*) individuals in Alberta, Canada, due to individual differences in their attraction to roads and human settlements (Murray and St. Clair, 2015). Evidence of direct fitness consequences of among-individual variation in behaviour such as this, may encourage population-level behavioural change through heritable traits from surviving individuals, depending on the mechanism behind the plasticity (Sih, Ferrari and Harris, 2011; Mathot *et al.*, 2012). Flexibility between individuals appears to be an important factor in driving evolution of behavioural traits within a population and/ or species, whether the flexibility be in avoiding human interaction as in the coyote study (surviving individuals avoided roads when busy and crossed when quiet; Murray and Cassady St Clair, 2015), or in avoiding certain habitat types due to increased predation risk (Dussault *et al.*, 2012). Behavioural plasticity also has important implications for species continued persistence as climates become less predictable and more stressful. Hall and Chalfoun (2019) highlighted that although individual American pikas (*Ochotona princeps*) possessed either flexible or inflexible foraging strategies related to the time of day they left their burrows. Both behavioural phenotypes collected a similar amount of forage material, however the former flexible strategists were able to avoid the hottest temperatures, thus exposing themselves to fewer potentially lethal situations. Differential mortality or fitness consequences can drive evolution by encouraging more flexible individuals to persist within the population (Foster, 2013; Snell-rood, 2013). For species previously exposed to higher levels of environmental variation, behavioural adaptation to change may be more rapid

(Chevin, Lande and Mace, 2010; Mathot *et al.*, 2012). Conversely, a lack of response, or a maladaptive response to change in the environment, because of prior evolutionary development, might induce negative consequences in the future (Chevin, Lande and Mace, 2010; Snell-rood, 2013). Particularly in relation to habitat restoration and management, creation of ecological traps due to mismatches in perception and an inability to distinguish between the quality of novel habitats, can create potentially disastrous population consequences as discussed in Hale, Swearer and Hayward (2017). Dussault *et al.,* (2012) highlights differential mortality of female caribou and calves in rotational cut pine forests, where site-faithful adult females gradually experienced higher predation of their calves, and thus their contribution to the population, as cleared forest blocks regenerated. This demonstrated a lack of individual plasticity and recognition of cues that should indicate negative habitat choice. However, this was not pervasive throughout the population, with differential habitat selection enabling females that chose pristine forest away from cut forest to successfully rear their offspring. Whatever the mechanism behind behavioural adaptation, it is clear that within a population, one size of habitat management does not fit all and that individual variation should be incorporated into conservation management plans.

1.5. Incorporating individual behaviour into habitat management

In the face of multiple threats to biodiversity, conservation biologists need to know where best to deploy resources to conserve animal populations (Fedy *et al.*, 2014; Greggor *et al.*, 2016; Ricca *et al.*, 2018). For example, why does dispersal behaviour of certain animals restrict colonisation of new or restored sites (Caro, 1999)? How does land use change influence connectivity between breeding and foraging areas, and does this consequently affect fitness (Evens *et al.,* 2018)? Behaviour-based research needs to link closely with managers in the field and connect questions with practical management outcomes (Greggor *et al.*, 2016). Using behavioural information to facilitate species persistence has been successful where these links have been made and a multi-faceted approach has been used (Copeland *et al.*, 2013; Ricca *et al.*, 2018). A key example is the conservation of Greater sage-grouse in the US, a wide-ranging, weak-flying, ground-nesting bird species that declined severely due to loss of appropriate sage-brush habitats (Ricca *et al.*, 2018). Behaviour at multiple spatial and temporal scales (Fedy *et al.*, 2014, Baxter *et al.*, 2017), during lekking, nesting and brooding (Rice, Apa and Wiechman, 2017), has been combined with diet analysis (Sullins *et al.*, 2018) and evidence of breeding success, to develop dynamic conservation strategies. Positive and negative sage-grouse responses to different scales and varieties of habitat manipulation have been combined (Copeland *et al.*, 2013) and have shown population benefits, through increased nest survival, in mechanically-manipulated areas (Baxter *et al.*, 2017; Sandford *et al.*, 2017, Smith and Beck, 2018). This is compared to open ground created through grazing or burning, which were heavily-selected for, but produced negative fitness outcomes for the population. It is important to recognise that such thorough studies involving multiple measures of behaviour and demography, are constrained by financial impediments that are common in conservation (Miller and Hobbs, 2007). This not only means that land managers need a good return on investment of limited funding, but that there is often the need for a quick turn around and obvious results, which means that behavioural change research is not appropriate (Sutherland, 1998).

Obtaining information on species’ behaviour has also been hindered in the past because of the difficulty in observing individuals and monitoring their behaviour over long periods of time, for example a whole breeding season or longer. This is especially true of small species and those that are absent from their breeding or wintering range for a significant period of time, due to migration. However, the past decades have seen enormous growth in technology that allows researchers to study animal behaviour, at an individual level, and to provide the necessary evidence for their conservation, through information about their movements within and between different habitat types, as well as their diet. For animals sporadically distributed in specific, sometimes inaccessible areas, methods that allow us to collect data that would be otherwise absent are vital. The following section will discuss the two main technologies used in this project, namely GPS tracking and diet metabarcoding.

1.6 New technologies for applied ecology and conservation

1.6.1. Tracking animals for behavioural studies

The desire to discover more about the behaviours expressed by wild animals and their implications on population processes, has motivated ecologists and biologists to create and develop novel ways of individually identifying and following organisms in the field (Ropert-Coudert, 2005; Wilson *et al.*, 2015). Observing and recording the movements of animals allows us to understand why individuals, and therefore populations, spend time in certain locations (Chambault *et al.*, 2016; Bracis, Bildstein and Mueller, 2018), how predators and prey interact (Eriksen *et al.*, 2011) and the influence of conspecifics and humans on residence and migration (Lendrum *et al.*, 2013; Sawyer, Kauffman and Nielson, 2009). The effect of these behaviours on recruitment, fitness and survival can now be directly measured (Cagnacci *et al.*, 2010), through the addition of miniature accelerometers, magnetometers and heart rate monitors, which can directly connect movement to measurements of animal physiology (Shepard *et al.*, 2008; Fieberg and Ditmer, 2012; Brown *et al.*, 2013; Elliott *et al.*, 2013). Information from devices has been particularly valuable for conservation in relation to quantifying the efficacy of managed and protected areas (Godley *et al.*, 2008; Augé *et al.*, 2014; Tancell *et al.*, 2013). Tancell *et al.* (2013) identified previously unknown feeding areas of the Wandering albatross (*Diomedia exulans*) and Godley *et al.* (2008) describes the wealth of information on movements between foraging and nesting grounds, collected via tracking devices, for multiple endangered turtle species. An increase in storage capacity and battery life has combined with a decrease in size, and we are now able to track small species over several seasons, collecting multiple migratory tracks from individuals, thus enabling the identification of repeatability in migration strategies (Bridge *et al.*, 2011, 2013; Åkesson *et al.*, 2012; Hallworth and Marra, 2015; Evens *et al.*, 2017a; Norevik, Akesson and Hedenstrom, 2016). A concurrent increase in the available software and methods to deal with the ever increasing amounts of data has followed (Kranstauber *et al.*, 2011; Joo *et al.*, 2013; Buchin *et al.*, 2015; Chimienti *et al.*, 2017; van Toor *et al.*, 2018). We are now able to map areas of resource use (Fleming *et al.*, 2014; Fleming *et al.*, 2015; Gurarie *et al.*, 2016; Michelot *et al.*, 2017), including the identification of areas of repeated use by individuals which can help us to understand more about foraging specialisation and the implications for population success (Wakefield *et al.,* 2015; Patrick and Weimerskirch, 2017;

Weimerskirch, 2017). This information can then be employed in species conservation plans to protect valuable foraging and breeding areas (Tancell *et al.*, 2013).

1.6.2. Device effects

Frequently, an assumption is made by researchers that data collected from attached devices is the product of 'typical' behaviour (Cooke *et al.,* 2017). However, this perceived normality may in fact represent behaviour under the influence of the device (Calvo and Furness, 1992; Casper, 2009; Barron, Brawn and Weatherhead, 2010). Many logger studies report an effect of the device on the study organism ranging from 'initial discomfort' (e.g. increased pecking rates, increased preening of feathers) through to impairment of flying ability and even mortality (Calvo and Furness, 1992; Barron, Brawn and Weatherhead, 2010). Although mortality from tag-attachment, of whatever size, is rare (Conway & Garcia, 2005), Barron, Brawn and Weatherhead (2010) reported strongly increased energy expenditure and reduced propensity to nest in tagged kittiwakes (*Rissa tridactyla*), which may ultimately have an effect on survival. Brigham (1989), Wanless, Harris and Morris (1989), Elliott *et al.*, (2012) and Heggøy *et al.* (2015) all found that tagged birds differed significantly from controls in their foraging trip frequency and duration, with higher levels of corticosterone also found in kittiwakes and common murres (*Uria algia*) carrying GPS units. Reports of altered activity levels, reduced breeding success and productivity should encourage ecologists to report the effects of devices (Calvo and Furness, 1992; Wilson and McMahon, 2006).

There is a lack of evidence supporting the load limits of up to 5% or, more recently, 3% (Vandenabeele *et al.*, 2012), particularly regarding smaller species. Decreased manoeuvrability has been recorded in bats with transmitters of 5% body weight (Aldridge and Brigham, 1988). In birds, Tomotani *et al.*, (2018) found that tags of 5 and 7% relative body mass significantly slowed down escape flight speed, potentially influencing survival. In contrast, Åkesson *et al.*, (2012) found no adverse effects of geolocators (~3% relative mass) on swift (*Apus apus*) nest provisioning rates. However, aerially insectivorous birds such as these, have a high wing aspect ratio for manoeuvrability and higher energy expenditure than other passerines (Bryant & Tatner, 1991). These factors may mean that aerial feeders, including swifts, swallows and nightjars, incur increased stress levels due to tag weight and placement, both of which might induce imbalance whilst foraging. Attachment method (Giroux *et al.*, 1990; Barron, Brawn and Weatherhead, 2010) and shape (Obrecht, Pennycuick and Fuller, 1988; Bowlin *et al.*, 2010) also determine tag effect size, with increased drag from inadequately positioned devices combined with weight to detrimentally increase the energetics of flight (Caccamise and Hedin, 1985; Gessman and Nagy, 1988).

It is clear that for cryptic species, for which traditional ecological data collection is difficult, that new technology is important for developing our knowledge of movement and the impacts on population dynamics (Hebblewhite and Haydon, 2010), but caution must be taken to ensure no adverse effects of these devices on vulnerable species. The integration of different technologies is also key, to provide information on multiple aspects of breeding and foraging behaviour (Marvin *et al.*, 2016; Shafer *et al.*, 2016). This is not limited solely to location, but what habitat types are being used, through use of fine-scale remote sensing data. It should also address what prey items animals consume when they are in their foraging habitat of choice, through the application of dietary analysis (Vesterinen *et al.*, 2016).

1.6.3. Diet metabarcoding

Identifying dietary composition of mammals and birds lends substantial weight to conservation management plans, especially the relationship between diet and the distribution and abundance of their food resources (Groom *et al.*, 2017). Diet is fundamentally linked to fitness, reproduction, recruitment and survival and may contribute to population change in response to climatic or habitat variation (Nocera *et al.*, 2012; Mallord *et al.*, 2016; Howells *et al.*, 2017). Climate change and habitat alteration can cause a shift in resource abundance that may require species to consume sub-optimal food items (Schrimpf, Parrish and Pearson, 2012; Howells *et al.*, 2017). Altered dietary components may not be as profitable and may therefore increase stress (Stanton, Clark and Morrissey, 2017) and consequently influence body condition or growth rate of chicks (Pomfret *et al.*, 2014; Franci *et al.*, 2015a; Howells *et al.*, 2017). It is often challenging to study diet and animal feeding interactions in the field, thus the need has arisen for dietary analysis that can be used without necessarily observing a feeding interaction, (Zeale *et al.*, 2011; Vesterinen *et al.*, 2013; Bussche *et al.*, 2016; Nielsen *et al.*, 2018).

The term molecular scatology (Oehm *et al.*, 2011; Jedlicka, Vo and Almeida, 2017) is used to describe the analysis of faeces to reveal the diet of animals using molecular techniques (Kohn and Wayne, 1997). It is necessary to evaluate diet and assess any changes therein as a consequence of habitat management, to understand how habitat change affects foraging (Symondson, 2002; Nocera *et al.*, 2012; Jarman *et al.*, 2013; Clare *et al.*, 2014; Pomfret *et al.*, 2014). Short genetic sequences from mitochondrial DNA (mtDNA) that are unique within a species, can be used to identify unknown individuals, potentially of any taxa (Hebert and Gregory, 2005; Savolainen *et al.*, 2005; Valentini, Pompanon and Taberlet, 2009). These DNA ‘barcodes’ have enabled the rapid development of species identification using degraded biological matter (P. D. Hebert *et al.*, 2003; Rubinoff, 2006; Meusnier *et al.*, 2008). The barcodes most commonly come from the Cytochrome c oxidase subunit I (COI) region of the mtDNA, a string of 658 base-pairs (bp) in mammals, birds and insects (Folmer *et al.*, 1994; Elbrecht and Leese, 2017), owing to its high copy and variance properties (Stoeckle, 2003). Other genes are used for amplification of plant DNA (trnL, Raye *et al.*, 2011; Ando *et al.*, 2013), fungi and reptiles (ITS, 12S, 18S, Fiser Pecnikar and Buzan, 2014). Recent results from in silico and mock community testing of multiple sets of primers have indicated that for arthropods, 16S primers can provide a higher level of taxonomic coverage (Epp *et al.*, 2012; Clarke *et al.*, 2014). Using two different mtDNA regions can also improve coverage particularly when the full breadth of the diet is not known (Freeland, 2016).

Recent developments in the field of molecular biology involve high processing-power technology, termed high throughput or Next Generation Sequencing (NGS) (Schuster, 2008; Ansorge, 2009; Littlefair and Clare, 2016). Over the last decade, commercially available NGS platforms have enabled laboratories worldwide to engage in genome studies and metabarcoding, quickly and at low cost (Lerner and Fleischer, 2010; Metzker, 2010; Coisac, Riaz and Puillandre, 2012). Metabarcoding describes the amplification and sequencing of hundreds of samples simultaneously (Kelly, 2016; Cilleros *et al.*, 2019). This has been especially beneficial for ecologists, allowing the rapid identification of mixed environmental samples (eDNA; Valentini *et al.*, 2009; Taberlet *et al.*, 2012; Bohmann *et al.*, 2014), such as river or pond water, and faeces (Creer *et al.*, 2016). Samples of soil, water or animal pellets can be amplified using PCR and sequenced en masse (Shokralla *et al.*, 2012), using Multiplex Identifier (MID) tags. These tags individually identify single samples within a larger pool (Glenn, 2011; Razgour *et al.*, 2011; De Barba *et al.*, 2014; Sint *et al.*, 2014), exponentially multiplying the amount of data collected using traditional sanger-sequencing methods of analysing DNA content (Zakharov *et al.*, 2018). Limitations of molecular barcoding of faeces include the degradation of DNA, during and after the digestive process (Oehm *et al.*, 2011; Pompanon *et al.*, 2012), issues surrounding low DNA density and a lack of comprehensive quantification (Deagle *et al.* 2018). Degradation due to gut or soil microbes means that only small fragments of DNA are available for amplification, leading to low species resolution (Regnaut, Lucas and Fumagalli, 2005; Deagle, Eveson and Jarman, 2006; Demay *et al.*, 2013). 'Miniature' barcodes of around 100 to 300 bp can be successfully amplified from degraded DNA (Hajibabei *et al.*, 2006; Meusnier *et al.*, 2008; Hajibabaei and McKenna, 2012), aiding the identification of the composition of faecal matter from mammals (Zeale *et al.*, 2011), birds (B K Trevelline *et al.*, 2016) and reptiles (Kartzinel and Pringle, 2015). Issues can also arise from the fact that DNA from prey species is significantly lower in density and more fragmented than that of the predator in question. This can cause amplification of non-target species, even with targeted primers (Vestheim and Jarman, 2008), and can also produce 'accidental' binding of primer fragments to themselves, when they are unable to bind to the template (Brownie *et al.,* 1997), a process known colloquially as 'primer dimer'.

NGS technology can unravel species' relationships, resource partitioning and reveal the dietary spectrum of species rapidly, and with relatively lower cost and sampling effort than before (Pompanon *et al.*, 2012; Krehenwinkel *et al.*, 2016; Littlefair and Clare, 2016). It is also a non-invasive technique, unlike methods such as neck collars (Tanneberger *et al.*, 2017) and stomach flushing (Zarzoso-Lacoste *et al.*, 2016; Nielsen *et al.*, 2018), therefore presenting itself as a useful tool with which to observe species and their interactions (Arrizabalaga-Escudero *et al.*, 2018), for which disturbance from collecting this data could be damaging.

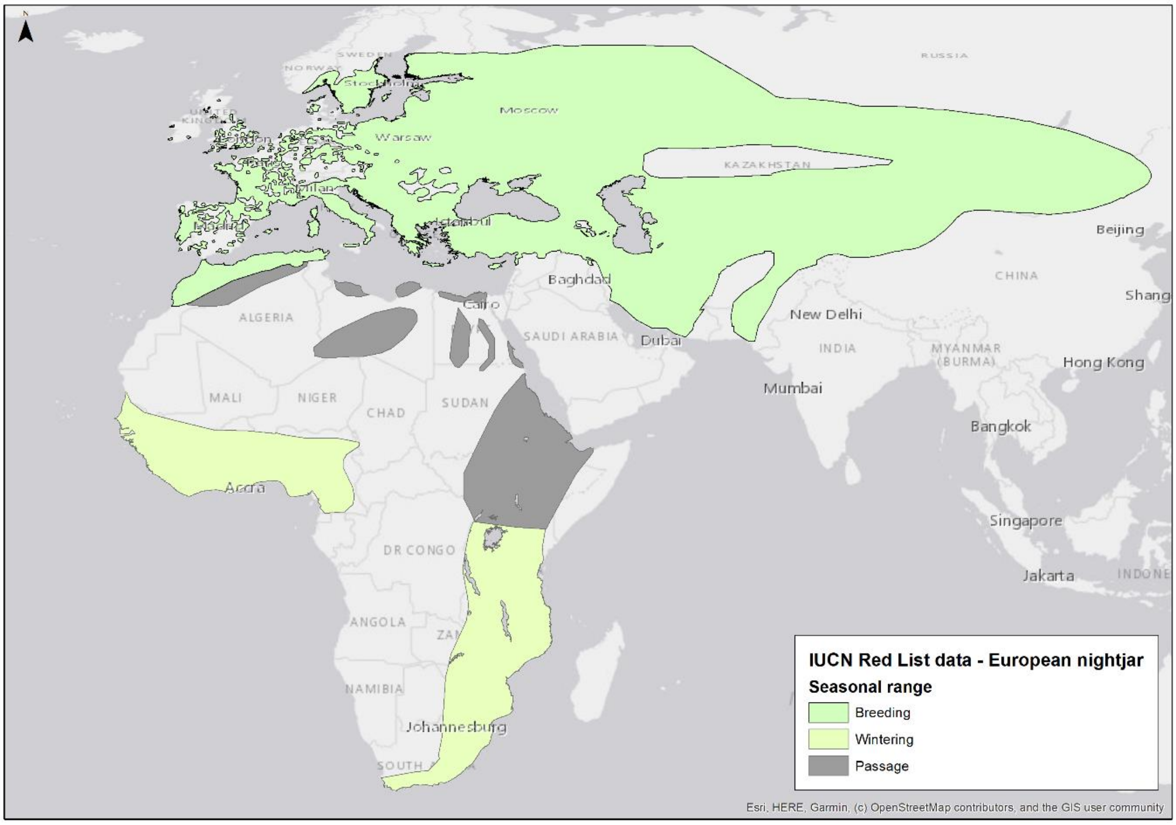
These techniques are especially useful when a study species of interest that possesses cryptic habits that hinder researchers in understanding their behaviour and needs. In this thesis I address the foraging and habitat selection behaviour of a single species, the European nightjar. The nightjar is a useful and interesting study species; it has a roughly nationwide but sporadic distribution and is a long-distance, slow-breeding migrant, which means it is site-faithful, although due to the paucity of records, it is not known exactly how strong this is. Their distribution – apparently restricted to heather- and birch-dominated habitats – coupled with their insectivorous diet, makes them vulnerable to both habitat loss and climate change, but again, a lack of data means that their true vulnerability is not known. The study site here is atypical and likely to have been added to the list of nightjars' breeding locations due to the degradation that has dried out the soil. However, how they use a peatland dominated landscape has not been studied, and as a single, discrete area of valuable habitat in an otherwise intensely agricultural landscape, the Humberhead peatlands as a site of importance for a vulnerable, nocturnal bird species presents itself as an opportunity to understand more about how variable and flexible nightjars are as foragers, and how managers can improve sites for their breeding populations.

1.7 The European nightjar

The European nightjar (*Caprimulgus europeaus*) is a nocturnal, aerially-insectivorous bird that is part of the order Caprimulgiformes, in which there are numerous species found worldwide (Cleere and Nurney, 1998). The European nightjar has a wide Eurasian distribution, breeding as far east as Mongolia (Figure 1.2); however, like many Afro-Palearctic migrants, has suffered large declines (Vickery *et al.*, 2014a). Fortunately, they still hold stable populations in several northern and western European countries including Belgium and the United Kingdom (Conway *et al.*, 2007; Evens, Beenaerts, *et al.*, 2017a) but continue to decline in Switzerland and Austria (Sierro *et al.*, 2001; Wichmann, 2004; Verstraeten, Baeten and Verheyen, 2011).

1.7.1. Population status

The UK status of the nightjar is currently 'amber' (Eaton, Aebischer, Brown, Hearn, *et al.*, 2015); an improvement on its previous 'red' designation. Multiple standardised national surveys in the UK identified a 50% decline in both population size and range from 1966 – 1981 (Gribble, 1983; Conway *et al.*, 2007; Eaton *et al.*, 2009), attributed largely to the loss and degradation of preferred habitat (Ravenscroft, 1989; Bright *et al.*, 2007; Langston, Wotton, *et al.*, 2007). A national survey conducted by the British Trust for Ornithology (BTO) in 2004 suggested an increase of 34% since 1992 (Morris *et al.*, 1994; Conway *et al.*, 2007); however, this growth in numbers has not been followed by an apparent increase in range. Although areas have been colonised in the south of England and North Yorkshire, there has also been a retraction of range in the north-west (Conway *et al.*, 2007), despite apparently suitable habitat being available and reasons for this are currently unknown. In a study in Switzerland, Sierro and Erhardt (2019) have identified light pollution as the biggest factor restricting recolonization of sites by nightjars, by disrupting both their highly sensitive vision and the behaviour of the moths they prey upon, but no examination of light levels in abandoned areas in the UK has been conducted.



Esri, HERE, Garmin, (c) OpenStreetMap contributors, and the GIS user community

Figure 1.2: Seasonal range distribution map of the European nightjar, using data from: Birdlife International and the Handbook of the birds of the world (2016). Caprimulgus europaeus. The IUCN Redlist, Version 2019-1. http://www.iucnredlist.org. Downloaded on 27/06/2019.

Expansion of sympathetic clear fell management and restocking in coniferous forest has helped to boost population growth throughout the UK, particularly in North Yorkshire (Scott *et al.*, 1998), where there has been an increase of 101% since 1992 (Morris *et al.*, 1994). Nightjar populations in Belgium and Sweden are distributed across similar coniferous and heathland habitat types (Evens, Beenaerts, *et al.*, 2017a). Related species in North America, such as the Common poorwill (*Phalaenoptilus nuttallii*), eastern whippoorwill (*Antrostomus vociferus*) and the common nighthawk (*Chordeiles minor*) are additionally found in boreal habitat at a much higher latitude than in Europe (Garlapow, 2007; English *et al.*, 2016; Knight and Bayne, 2017). Unique anatomical adaptations have allowed nightjars to exploit a nocturnal niche (Figures 1.3 – 1.5). Large eyes with very sensitive 'tapeta lucida' give them superb vision (Nicol and Arnott, 1974), which along with their rictal bristles and huge gape, enable them to catch large numbers of night-flying insects (Cramp, 1985; Cleere and Nurney, 1998; Jackson, 2000; Jackson, 2003).

Figure 1.3: Physical features of an adult (*left*) European nightjar showing large eyes and rictal bristles adapted to foraging on aerial prey at night; (*right*): a juvenile nightjar displaying wide gape, capable of swallowing whole moths.

Figure 1.4: Image of an adult male nightjar’s wing with large white spots for territorial and sexual signalling. The equivalent spots on a female nightjar wing are smaller and a light beige colour.

Figure 1.5: Image of an adult male nightjar’s tail with large white tail spots for territorial and sexual signalling. The equivalent tail spots on a female nightjar are smaller and a light beige colour.

Studies of nightjar population dynamics are scarce; two published annual survival rates range from 0.64 to 0.74 (Forero, Tella and Oro, 2001; Silvano and Boano, 2012) for adults. Rate of fledglings per breeding attempt has declined significantly from 1.4 to 0.75 (a decline of nearly 47%; Robinson *et al.*, 2015), resulting in their inclusion on the Nest Record Survey (NRS) concern list (Leech and Barrimore, 2008). Nest predation by foxes (*Vulpes vulpes*), adders (*Viperus berus*) and crows (*Corvus corone*) is relatively common in the UK *(*Berry, 1979; Berry *et al.* 1981; Cross *et al.* 2005) and in North America (English 2017). However, average first laying date has remained around mid-June (Cramp, 1985; Baillie *et al.*, 2014), which potentially suggests a restriction on migration and arrival timing on the breeding grounds. Information on nightjar population dynamics such as this is sparse and mostly comprised of small sample sizes (Table 1.1). Thus, key information that might provide a basis to conservation plans is lacking.

The European nightjar breeds in the UK from May to August, before travelling south to winter in tropical and southern Africa (Cramp, 1985; Cresswell and Edwards, 2013). Recent studies of their migration routes found a ‘loop’ type migration, with intra-continental movement west from their original wintering point before migrating back to Europe to breed (Norevik, Akesson and Hedenstrom, 2016; Evens *et al.*, 2017b, 2017c; Figure 1.6). Precise wintering locations, habitat types and indeed, key threats on the wintering grounds are still unknown, making it difficult to ascertain where population bottlenecks and constraints to growth lie. As migrants, nightjars spend a significant proportion of time outside of the UK, therefore there are multiple other threats that contribute to their population status, such as poaching, both on migration and on their wintering grounds, as well as weather and the effects of climate change on the wintering grounds, known to influence overwinter survival of many migrant birds (Cresswell *et al.,* 2014; Vickery *et al.,* 2014). Even if conservation efforts are directed towards increasing breeding success of nightjars in north-western Europe, there are elements outside of this that cannot be controlled for, although may be compensated for through an increase in recruitment of juveniles to the population.

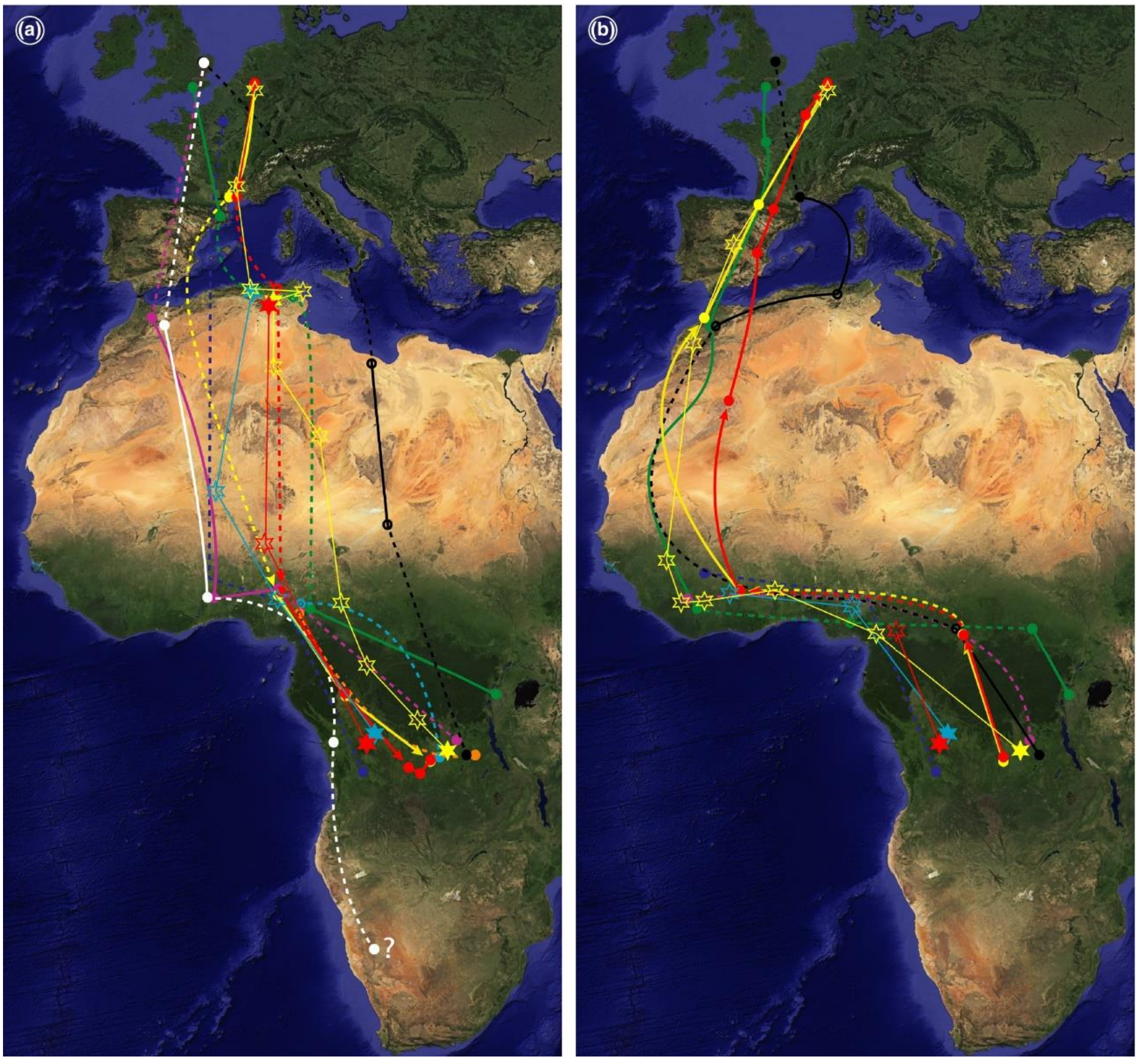


Figure 1.6a) autumn southward and b) spring northward migration of the European nightjar (n= 12 tracks, from 11 birds). Reprinted from Evens *et al.*, 2017b.

1.7.2. Previous studies of nightjar behaviour

Studies of nightjar breeding and behaviour, and those of other Caprimulgids such as the common nighthawk (Lack, 1932; Berry and Bibby, 1981; Kramer and Chalfoun, 2012), have studied habitat associations and resource factors, which influence presence and absence (Wichmann, 2004; Verstraeten, Baeten and Verheyen, 2011; Winiger *et al.*, 2018). Specific preference for areas with patches of bare ground and sparse vegetation seem to be dictated by nest placement and background complexity (Figure 1.7), to improve bird and egg camouflage (Camacho, 2014; Troscianko *et al.*, 2016).

Table 1.1: Summary of nightjar nesting studies. Nest sample size = total number of nests found. Number of nests fledged = the number of nests out of the original sample size that fledged chicks. Failure of nests: Egg stage = the number of nests that failed before hatching. Chick stage = the number of nests that failed after hatching (NB: number of fledgings/failures may refer to single chicks/eggs, which may confuse the total value). Failure reason identified from camera traps, evidence of predator disturbance or anecdotal data.

		Failure of nests				
Nest Sample size	**Number of nests fledged**	**Egg stage**	**Chick stage**	**Reason**	**Location**	**Authors**
8	5	1	3	Fox	UK	Berry 1979
28	16	8	4	Unknown	UK	Berry & Bibby 1981
13	8	1	2	Unknown	UK	Cross 2005
75	37	35	3	Fox/ Deer/ Disturbance	UK	Langston 2007
38	24	11	6	Snakes/ Porcupine/ Deer	Canada	English *et al.,* 2017
192	55.5%	47.4%	8.1%	Disturbance	UK	Lowe *et al.,* 2014

Nightjars also appear to be sensitive to human disturbance, particularly dog walkers (Langston *et al.*, 2007a). Lowe *et al.* (2014) demonstrated that increased presence of human activity was the cause of reduced nesting density but did not necessarily directly influence the survival of adults or nest productivity. Differences between the sexes during the breeding season are distinct; incubation is carried out by the female, who forages for short periods at dusk (Berry and Bibby, 1981) and shortly before dawn (Palmer and England, 2002; Jenks, Green and Cross, 2014). Active periods (based on direct observations of churring males; Cadbury, 1981; Morris *et al.*, 1994; Rebbeck, Eaglestone and Stainton, 2001) coincide with bat and moth activity (Aldridge and Brigham, 2008), however there are only a small number of studies that actually analyse nightjar behaviour in terms of movements, not solely calling activity or distribution.

Figure 1.7: Images of nightjar ‘nests’. No structure is built, eggs (usually n = 2) are laid directly onto soil, leaves or moss. Patterns on eggs are unique to females (A.Lowe, pers comm.).

Of those few studies, Camacho *et al.*, (2014) and Evens *et al.*, (2018) found regular use of spatially segregated foraging and nesting sites (Table 1.2). Segregation of habitats that provide different, essential functions has been identified in Belgium and Spain (Evens *et al.*, 2018; Red-necked nightjar (*Caprimulgus ruficollis*): Camacho *et al.*, 2014), where nightjars regularly make direct trips to specific foraging points separate in geography, habitat type and structure to their roosting and nesting sites. This indicates that nightjars are potentially capable of making trade-offs in nesting locations and foraging sites, if single sites cannot provide both at once. The impact of the separation of nesting and foraging areas on energy expenditure and population processes needs further exploration, collation and analysis of demographic data, namely survival, return rates and breeding success. Evens *et al.,* (2018) found increased amounts of stress hormones through blood sampling, demonstrating that although mobile, they are subject to extra energetic pressures by undertaking an extra ‘commute’ to foraging grounds. Of those studies that have collected data on foraging, the amount and the duration of activity of nightjars, including large variation in maximum foraging distances (Table 1.2), varies between habitat types (Alexander and Cresswell, 1989; Sierro *et al.*, 2001; Sharps *et al.*, 2015; Evens, Beenaerts, *et al.*, 2017b; Evens *et al.*, 2018). Cross *et al.* (2005) and Sharps *et al.* (2015) found that diverse, large scale, multi-aged coniferous forests can reduce foraging area size and thus appear to meet multiple requirements especially where these habitats provide a mixture of vegetation types and structures (Winiger *et al.*, 2018). However, these studies did not explicitly present nightjar foraging data in the context of a changing landscape, so we cannot directly appreciate their behavioural responses to habitat manipulation and how individual variation contributes to population response.

Three nightjar radio-tracking studies (Sierro *et al.,* 2001 (n = 3), Cross *et al.,* 2005 (n = 23) and Sharps *et al.,* 2015 (n = 31)), suggested the presence of a trade-off for the nightjars between prey abundance and accessibility of where they choose to feed. All three studies reported of higher usage of habitats containing lower prey biomass than the most productive sites, which are often densely wooded, and in the case of both Sharps and Cross, were thick coniferous forestry plantation. Sierro *et al.,* (2001) found nightjars in Switzerland spent a much higher proportion of their time in oak scrublands, despite pine forests supplying higher moth biomass. Although areas of highest moth density would maximise energy intake (Pyke, 1984), their choice of areas with lower prey density is thought to relate to foraging efficiency and ease of prey capture, i.e. the ‘foraging-efficiency hypothesis’ postulated by Imber (1975). In theory, birds should spend more time foraging in areas that make foraging easier, than they otherwise would compared with more densely resourced areas in order to provide equivalent returns (Macarthur and Pianka, 1966). However, none of the aforementioned nightjar studies presented data on time allocation of behaviours in nightjars and how time might be allocated differently if the structure or configuration of the environment changes. Using VHF radio tracking of 8 male and female nightjars on Hatfield Moors, South Yorkshire (Table 1.2), Palmer (2002) found that larger home ranges belonged to females, with males infrequently leaving their territories and moving into their wider home ranges. For improved habitat management, knowledge of relative prey resource provision of different habitats that nightjars use needs to be coupled with a measure of diet. This combined information can elucidate whether different habitats possess varying functional importance as posited by Evens *et al.* (2018), and how this may influence future population trends.

1.7.3. Nightjar diet

Diet of Caprimulgiformes has previously been explored either through the use of faecal analysis (Sierro *et al.*, 2001; Sharps *et al.*, 2015), or through the examination of stomach contents (Howes, 1978; Jackson and Oatley, 2000; Jackson T.B., 2000; Knight *et al.*, 2018). Aerial insects including Lepidoptera and Coleoptera comprise the bulk of their diet, although records of other insect families (Ephemeroptera, Neuroptera, Orthoptera, Diptera and rarely, Tricoptera) are present (Cramp, 1985; Jackson and Oatley, 2000; Sierro *et al.*, 2001). Studies using physical faecal pellet dissection have reported that Lepidoptera are the most important element of Nightjar diets, present in 99% of samples (Sierro *et al.*, 2001; Sharps, 2013). In the same studies, Coleoptera contributed to between 2 and 16% of samples. Both Sierro (2001) and Sharps (2013) related prey choice to availability through moth trapping, with seasonal changes in abundance of moths and beetles correlating with a change in dietary composition.

Table 1.2: Summary of nightjar European foraging studies including mean and maximum foraging distances (kilometres), method used (VHF radio tracking or GPS), sample size obtained (no. of birds), authors and location of the study. NB^1: Camacho *et al.* 2014 studies the red-necked nightjar (*C. ruficollis*) a related species. NB^2: Sierro *et al.,* 2001 mentioned in the text is not presented in the table as it provides none of the listed metrics.

Mean foraging dist (km)	**Maximum dist (km)**	**Sample size**	**Method**	**Authors**	**Location**
0.75 +/- 0.51	2.6	31	VHF	Sharps *et al*. 2015	Thetford forest, Norfolk
0.88 +/- 0.06 (natural area); 0.28 +/- 0.02 (managed area)	*Not given*	13	VHF	Camacho *et al.* 2014	Donana National Park, Spain
Not given	*Not given*	23	VHF	Cross *et al*. 2005	Brecon Beacons, Wales
~1	4.5	8	VHF	Palmer 2002	Hatfield Moor, South Yorkshire
Not given	*Not given*	3	VHF	Sierro *et al.* 2001	Switzerland
3.1 (+/- 1.2)	5.8	11	VHF	Alexander & Cresswell 1998	Wareham forest & Hartland Moor, Dorset
Not given	5.63	48	VHF	Evens *et al*. 2017	Bosland, Flanders, Belgium
B: 1.2 (+/- 1.06); MG: 0.59 (+/- 0.27); NHPK: 3.35 (+/- 1.92)	*Not given*	30	GPS	Evens *et al*. 2018	Bosland (B), Meeuwen-Gruitrode (MG) & National Park Hoge-Kempen (NPHK), Flanders, Belgium

Jackson and Oatley (2000) examined the diet of a number of Caprimulgiformes in Africa and found that in contrast to birds on the breeding grounds in Europe, European nightjars took more Coleoptera specimens (found in 84% of stomachs) than Lepidoptera (35%). This seasonal and geographical change in prey choice may represent opportunity, the birds becoming ‘facultative specialists’ (Gulka and Davoren, 2019), by consuming the most locally abundant prey resource. It may also highlight a difference in habitat structure, which along with warmer temperatures in Africa, encourage better accessibility of more active large Coleopterans. This enables the birds to access and catch these specimens in the air, where perhaps in colder climates they would remain unobtainable in ground vegetation (Rubolini *et al.*, 2015). However, these hypotheses have not been tested and no studies have produced comparative invertebrate trapping data to produce a measure of diet selectivity.

Due to the nature of their primary food resources, moths, little physical evidence remains of what nightjars have consumed (Jackson, 2000), so visual examination of faeces for dietary exploration is difficult and time consuming. It also means that these studies are biased towards larger specimens and specimens containing hard parts, for example beetle elytra (Sharps *et al.,* 2015). As previously discussed, this is not limited to this insectivorous species, nor their prey taxa (Murray *et al.*, 2011; Oehm *et al.*, 2011). Combined with the nightjar's nocturnal, cryptic behaviour that prohibits observation of foraging events, more detailed information on their diet is lacking that could provide further insight into their foraging strategies. For example, is the population generalist in its feeding habitats? What is the importance of particular resources, i.e. are they size selective? Additionally, and rather crucially, how might diet may change with landscape alteration, given the possibility that they are indeed, size-selecting specialists? The difficulty in obtaining a comprehensive measure of diet from faecal samples means that new molecular metabarcoding techniques offer a valuable opportunity to unravel dietary differences within a population.

1.7.4. Study site: Humberhead Peatlands National Nature Reserve

The Humberhead Peatlands National Nature Reserve (NNR) covers 2878 hectares within the wider Humberhead Levels region (Natural England, 2015), on the border of South Yorkshire and Lincolnshire (Figure 1.8). It is comprised of two distinct areas: Thorne Moor to the north (53° 38' 17, 0° 53' 50) and Hatfield Moor to the south (53° 32' 36, 0° 56' 37), separated by 10km of arable agriculture and urban development. Both sections were designated as Sites of Special Scientific Interest (SSSI) under the current Wildlife and Countryside Act 1981 in the 1980s, becoming a joint NNR in 1995 (Natural England, 2015), a joint Special Protection Area (SPA) in 2000 and separate Special Areas of Conservation (SACs) in 2002 (Thorne Moor) and 2003 (parts of Hatfield Moor) (McLeod *et al.* (2005). The SPA designation highlights the international importance of the breeding European nightjar population (>1% of the total breeding population in Great Britain; Stroud *et al.* (2001).

Both sites are classified as degraded lowland raised mire, due to a long history of peat extraction and drainage (Key, 1988), although the vegetation composition of the two sites remains different. Thorne Moors has a large amount of open water and a higher water level than Hatfield Moors, and as such is dominated by wetter, *Eriophorum* along with reeds (P*hragmites spp*.) (McLeod *et al.*, 2005). Despite a long history of peat excavation (Smart, Wheeler and Willis, 1986), there are still specialised, acidophilus plant species present among the conserved sections, including cranberry (*Vaccinium oxycoccus)*, bog myrtle (*Myrica gale)* and bog rosemary (*Andromeda polifolia)* (Smart, Wheeler and Willis, 1986). These plants, along with 4000 species of invertebrate (Natural England, 2015), designate Thorne and Hatfield Moors as some of the richest lowland peatlands in the country (Key, 1988) and Thorne Moor alone remains the largest surviving raised bog in England (Smart, Wheeler and Willis, 1989).

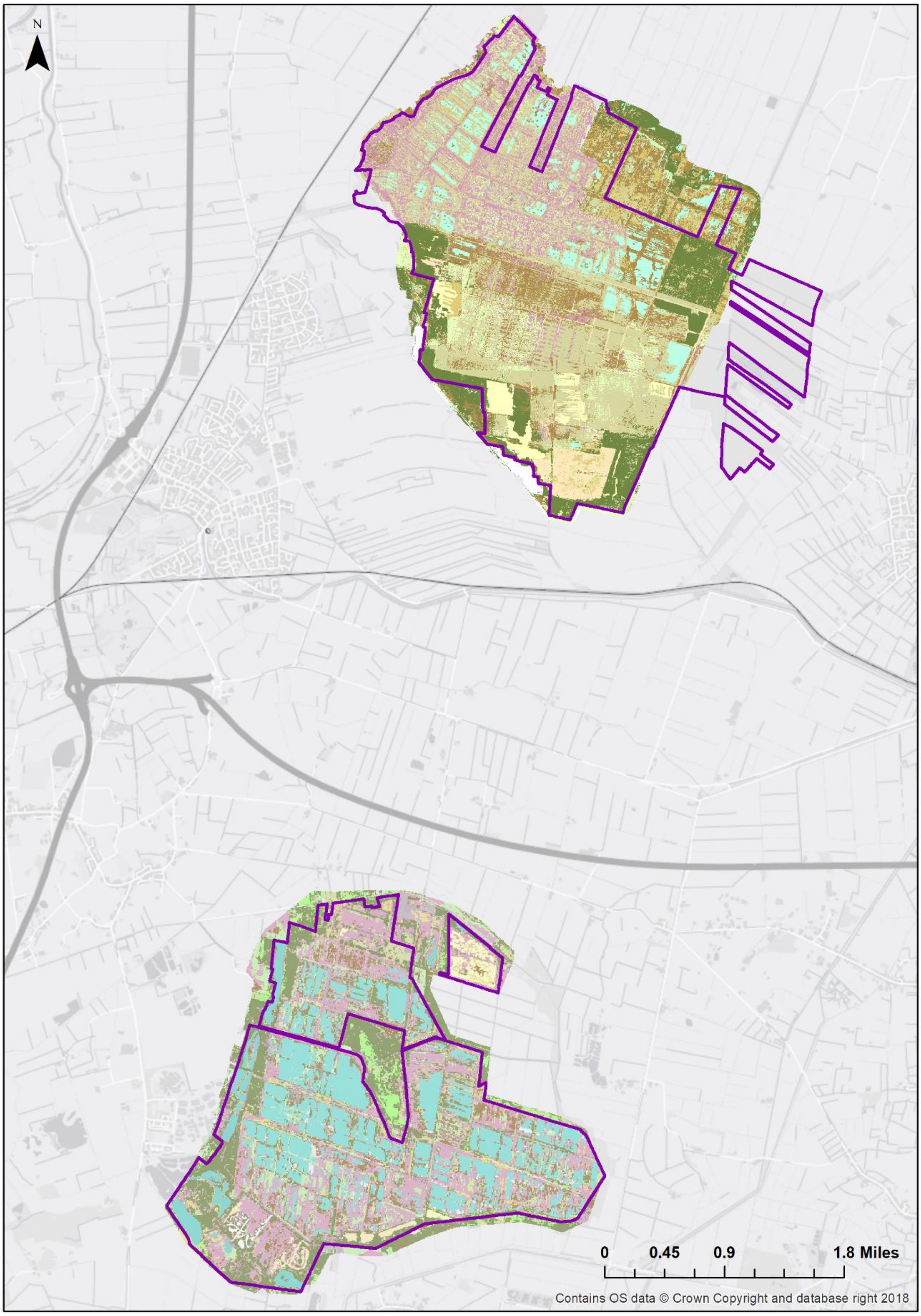


Figure 1.8: Site location map of Thorne Moor (north) and Hatfield Moor (south), part of the Humberhead Peatlands NNR (NNR outline in purple), South Yorkshire. Habitat of NNR highlighted within boundary using categorical map created (see chapters 2 and 3 for details).

1.7.5. LIFE+ Restoration Project

In 2014, Natural England received £2.3 million from the European Commission as part of the LIFE+ environment programme (Silva *et al.*, 2012; Ryan, White and Arnold, 2018). The LIFE+ scheme is dedicated to the 'protection and improvement of the quality of the environment and to halting and reversing biodiversity loss' and to support projects making a contribution to the development of policy and legislation in Europe, particularly relating to the birds and habitats directives (Silva *et al.*, 2010). The LIFE+ grant for the Humberhead Peatlands NNR had the specific objectives of increasing the area of peatland under active restoration. Two primary methods of practical habitat restoration took place, firstly through improving water control measures to stabilise the hydrology of the sites; and secondly, scrub clearance and post-management monitoring (Natural England, 2015). Both of these measures aimed to improve the rare habitats onsite that support 'focal' species, such as the nightjar, crane (*Grus grus*) and hobby (*Falco Subbuteo*), as well as peatland-specialist plant species such as *Eriophorum spp*., *Sphagnum spp*., cranberry (*Vaccinium oxycoccus)* and Bog rosemary (*Andromeda polifolia)*. The project began at the end of 2014 and ended in early 2019 and restoration has covered 28km^2 of degraded peat, including clearing a total of 572 hectares of birch (*Betula spp.*), willow (*Salix spp.*) and *Rhododendron* scrub (European Union, 2014; Figure 1.9).

Whilst the project aims to increase the availability of nightjar breeding areas, through management of scrub, concurrent rewetting of the site through implementation of dams and tilting weirs, could lead to a rise in the overall water table and could potentially create conditions that are too wet to support breeding nightjar (Conway *et al.*, 2007). The use of practical water management tools in this fashion may also increase the chance of flash flooding after heavy rain due to its degraded status (Holden *et al.*, 2006; Grayson, Holden and Rose, 2010). Therefore, it is critical that monitoring of vegetation and hydrological changes is immediate and thorough in order to identify further management changes that might be needed to support the nightjar population.

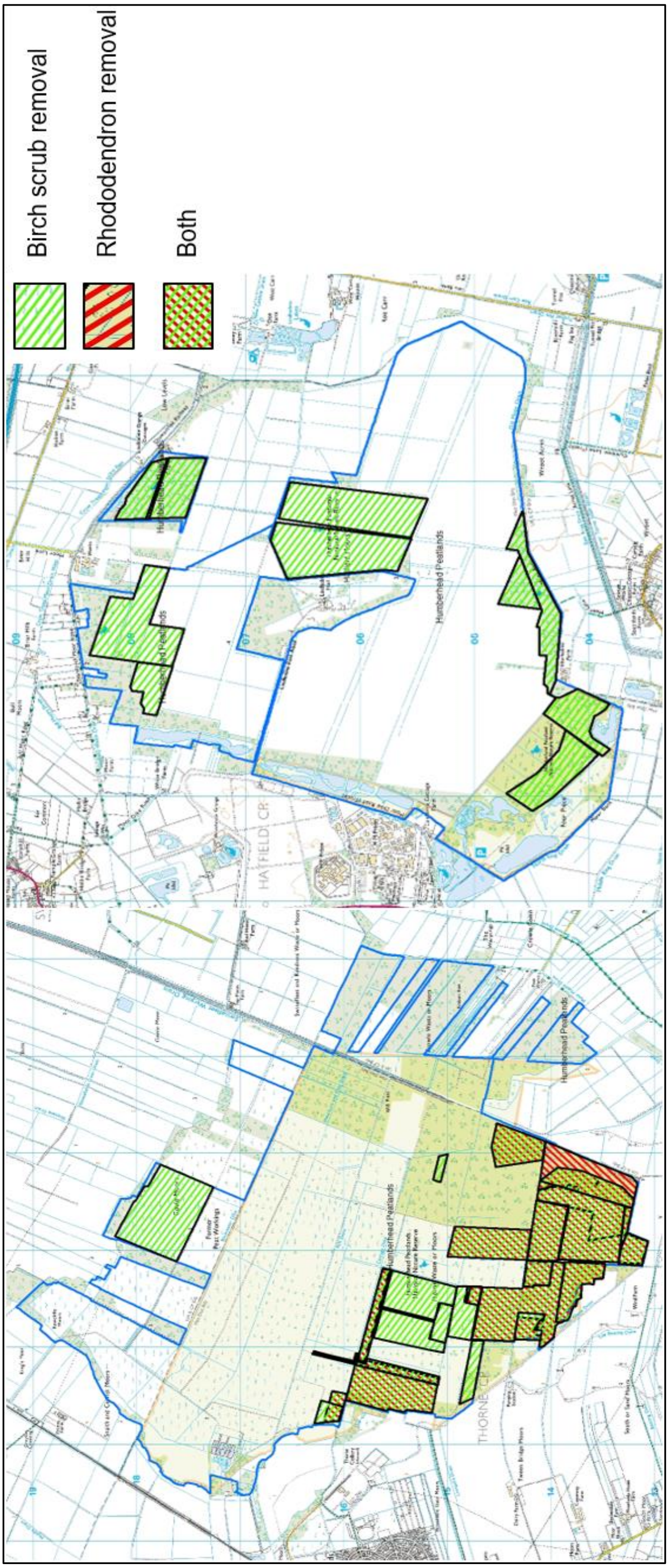


Figure 1.9: Map of scrub clearance works completed as part of the LIFE+ restoration project on Hatfield and Thorne Moors from 2015 to 2019.

Nightjars have been surveyed continuously for more than ten years on Thorne and Hatfield Moors (Middleton, 2017) using survey methodology based on that presented by Cadbury (1981). Numbers peaked in 2018 (n = 93 churring males in total on Thorne, Hatfield and Crowle Moors; Figure 1.10), having undergone a steady rise in numbers over the past eight years. These surveys provide a useful year-to-year comparison at the Humberhead Peatlands and with other sites in the UK. Numbers counted churring cannot be equated entirely to numbers of breeding birds, as unpaired males churr for longer and range more widely, potentially confounding results (Lowe, Rogers and Durrant, 2014; Jenks, Green and Cross, 2014; Sharps *et al.*, 2015). However, it still allows a rough estimation of population size of returning and new males, and of their distribution across the NNR. A previous tracking study on Hatfield Moors only (Palmer, 2002), used VHF devices to follow 8 male and female nightjars for a full night each, during a ten-day period. The study found that the birds rarely left the moors and when they did, it was to forage briefly within the local area. 98% of all non-NNR movements were within 2 km of the site, closer than other studies of foraging distance in nightjars (Table 1.2; Alexander and Cresswell, 1989; Cross *et al.*, 2005; Sharps *et al.*, 2015; Evens, Beenaerts, *et al.*, 2017a; Evens *et al.*, 2018). Individuals foraging onsite almost always avoided the open peat areas, whilst most activity was located over and around birch woodland.

1.7.6. Aims and objectives

Despite some population recovery in the UK following years of decline, the lack of range expansion of the nightjar is concerning. Potential habitat appears to be available, which suggests that there are key factors influencing nightjar habitat preferences and breeding requirements that have not been identified, including the strength of natal philopatry. The lack of large sample sizes in many studies demonstrates the difficulty in locating and tracking this species, but the research highlighted in this introduction suggests that as mobile aerial foragers, nightjars are able to cross substantial distances rapidly, a trait which may allow them to adjust to a new landscape configuration.

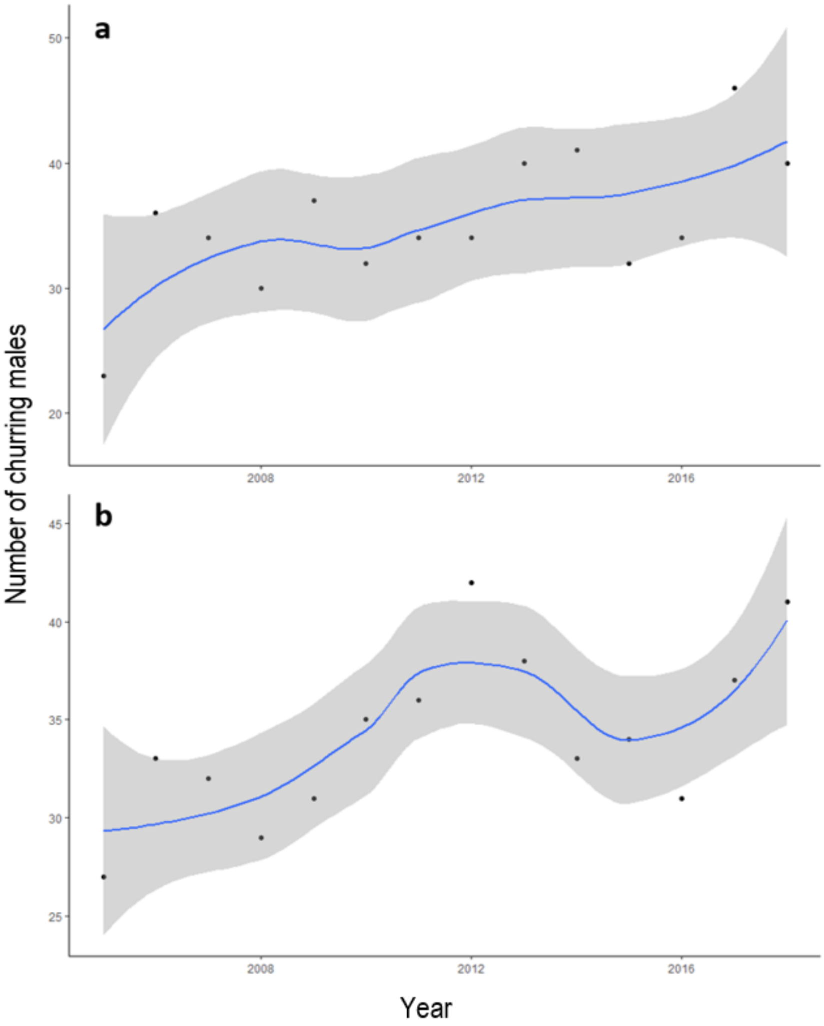


Figure 1.10: Numbers of churring male nightjars recorded on a) Thorne and b) Hatfield Moors from 2005 to 2018 with mean smoothed regression line calculated from Middleton (2018).

This thesis investigates the behavioural responses of the European nightjar to habitat restoration. The practical restoration works have taken place during the winter period, whilst the nightjars are on their wintering grounds in Africa (Cresswell and Edwards, 2013; Evens, Conway, *et al.*, 2017b, 2017c). Thus, nightjars returning to the breeding ground will experience novel habitat composition and structure (Morant *et al.,* 2018). Habitat restoration such as this is a form of discrete landscape change, which may affect distribution of resources and satisfactory nesting sites. Increased fragmentation and heterogeneity of the landscape may alter their optimal foraging strategy; for example the reduction in vegetation through scrub clearance might cause a decrease in prey resources in the vicinity of the territory centre, driving the birds to feed further away (Jackson, 2003), for longer periods of time (Macarthur and Pianka, 1966; Krebs, 1980). Information on behavioural responses through movement and diet, to habitat change, can help to explore the mechanisms regulating behaviour. By obtaining information from different individuals over time, we can explore individual variation and its contribution to population-level trends. High within-population variation should demonstrate flexibility in foraging behaviour and habitat preferences (Owen-Smith and Cain, 2007; Charmantier *et al.*, 2019). Individuals can successfully demonstrate different phenotypes within a population, which should allow exploitation of a broader niche, enabling the population to adapt to change (Chevin, Lande and Mace, 2010; Stamps, 2016).

Table 1.3: Summary of the number of adult birds of each sex caught in each year, and subsequently retrapped in one or more following years.

			Birds retrapped in →		
Birds caught in ↓			**2016**	**2017**	**2018**
2015	♀	9	2 (22%)	1 (11%)	1 (11%)
	♂	8	3 (38%)	2 (25%)	1 (13%)
2016	♀	11		2 (18%)	1 (9%)
	♂	26		8 (31%)	4 (15%)
2017	♀	13			5 (38%)
	♂	29			7 (24%)
2018	♀	9			
	♂	18			

Although this project is restricted to behavioural changes, these changes may ultimately affect the fitness of individuals and thus the population as a whole. Limited breeding data were collected as part of the project, but unfortunately consistent breeding information about tagged birds could not be obtained due to logistical issues. As a result, robust phenological information is not included in the modelling but is referenced throughout and is summarised in Figures 1.11 and 1.12. Figure 1.11 in particular displays ringing data (number of birds caught per week and the number of those GPS tagged), alongside breeding data (the number of nests found each week containing eggs and chicks), to understand where in the breeding cycle most birds were caught and tagged. Number of nests containing eggs appears to peak around week 3 to 4 (21st June – 5th July), whilst

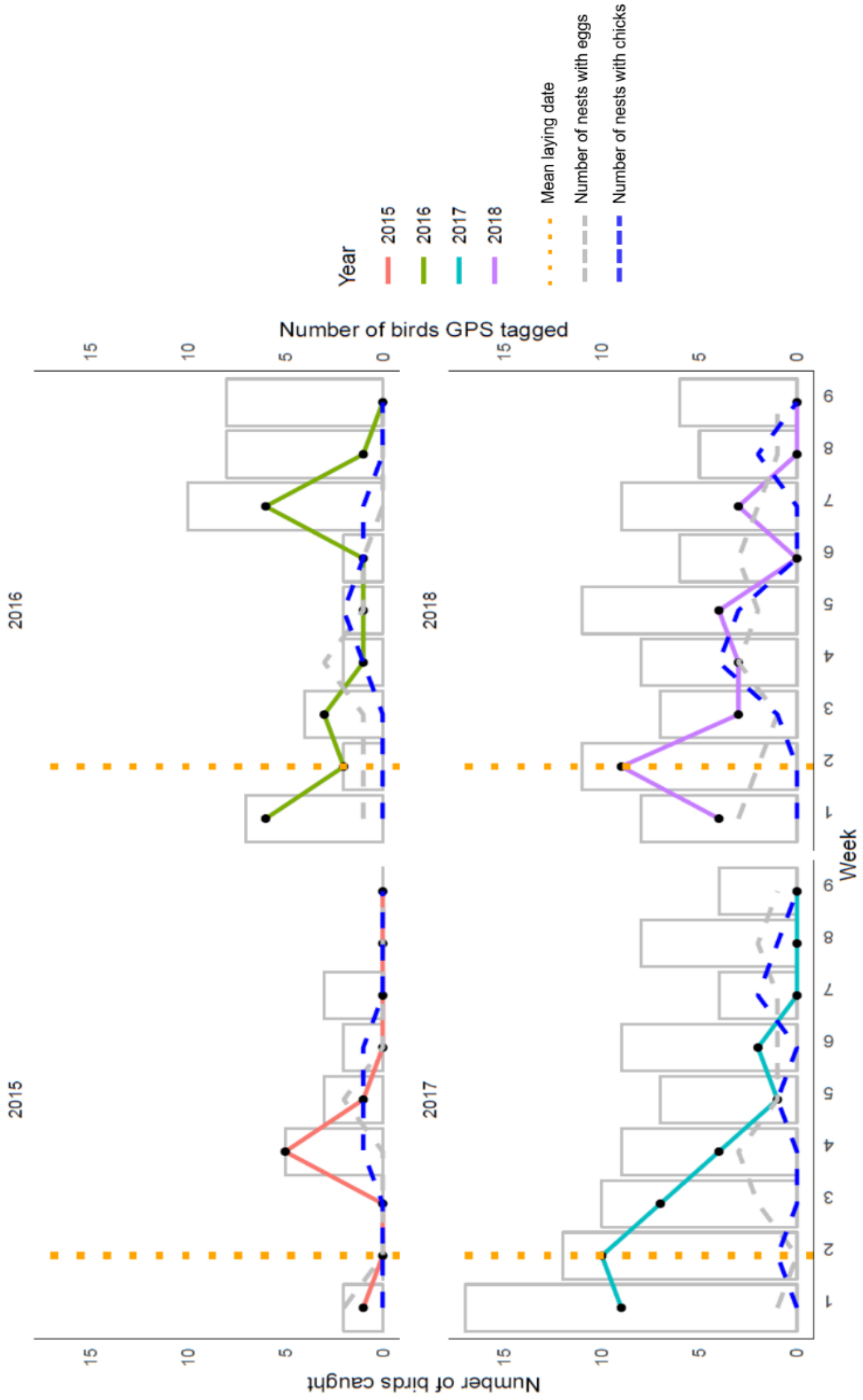


Figure 1.11: Raw nightjar data collected in this study, ordered by week of the breeding season to examine phenology. Histogram shows number of birds caught each week; coloured lines per year are number of individuals GPS tagged; grey and blue dashed lines represent number of nests found containing eggs and chicks respectively; orange vertical line = mean laying date (from BTO using ringing and nest recording data).

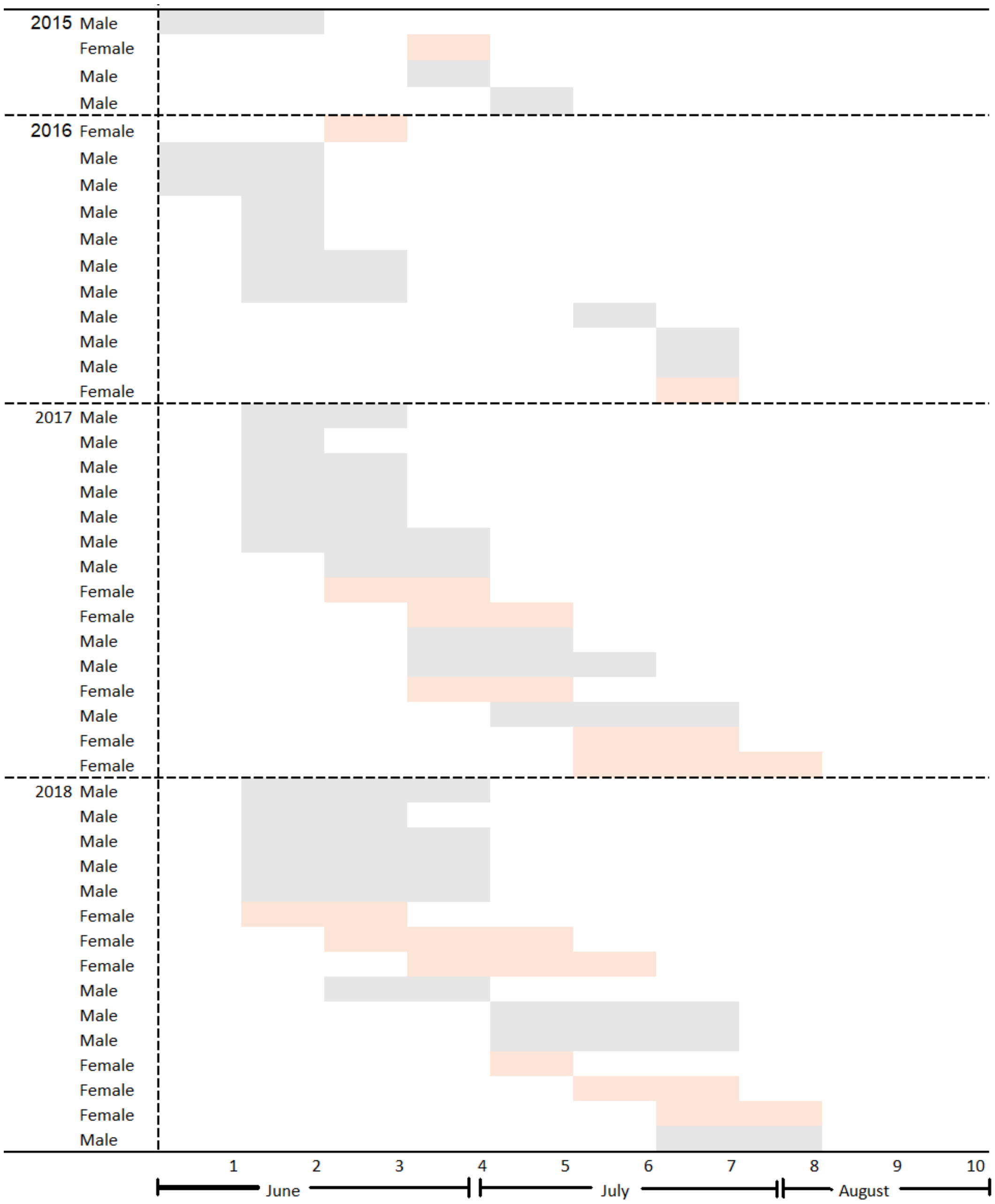


Figure 1.12: Summary of the weeks of the breeding season during which all male and female adult birds were GPS-tracked, during all four years.

number of nests with chicks peaks around weeks 4 to 5 (28th June to 12th July). Birds were not synchronised, as can be seen from the mistmatches in peaks and in 2017 and 2018, the peaks of the first and second broods can be seen more clearly, whereby second nests appear to be laid around week 7 (19th – 26th July). Therefore, I suggest that the majority of the birds in this study were GPS tracked during incubation, with a similar but slightly lower number tracked during chick provisioning, towards to middle/end of July.

This study is novel in its location, its use of GPS trackers in combination with diet metabarcoding, and its application of statistical methods to data from nightjars. Studies have previously been limited to lowland dry heathland and coniferous plantations with no detailed studies completed on habitat similar to the Humberhead Peatlands, notably an atypical habitat type for this species due to peatland often maintaining a high water level. One GPS tracking study of European nightjars does exist (Evens *et al.* 2018), but this is the first time to my knowledge that the information has been used to explicitly study foraging patterns over a period of landscape change and where knowledge of resource use has been linked with diet data gathered from metabarcoding.

1.8. Thesis Outline

Following on from this introduction, chapters 2 to 5 are data analysis chapters, bounded at the end by a general discussion.

In Chapter 2, I explore the use of GPS tag technology for understanding home ranges and habitat use of nightjars. Specifically, I take data from multiple years, acquired at different fix rates, to explore how variation of tracking parameters can influence the size of the home range. This chapter sets out to test the methods used in chapter 3 and highlights the importance of obtaining comparable data, particularly when trying to compare home range sizes and habitat use over time. I discuss the benefits of high frequency tracking data for creating movement-based kernel home ranges, which for an aerial feeder such as the nightjar are valuable for identifying corridors and links between patches, rather than discrete patches used for foraging.

In Chapter 3, I investigate the habitat selection behaviour of individual nightjars over four breeding seasons to understand what this might mean for the population as a whole in terms of their flexibility. I also investigated functional responses of nightjars, i.e. how home range size and habitat selection changed with availability of habitats, to identify common constraints as well as individual differences. This chapter highlights the importance of including multiple measures of habitat selection behaviour, to provide a more comprehensive understanding of individual habitat selection, and how variation within the population might impact on factors responsible for whole population maintenance.

In Chapter 4, I explore nightjar foraging behaviour more closely to understand the impact of external factors that might influence the allocation of time to foraging and will affect their efficiency and rate of energy intake. Nightjars exploit a spatially- and temporally-patchy invertebrate prey that may change in composition and abundance on different scales. I used Hidden Markov Models (HMMs) to identify specific movement behaviours within high frequency tracking data and was able to identify flexible foraging behaviour in relation to changes in visibility, habitat and weather, all of which may affect prey distribution and density as well as nightjar foraging ability.

In Chapter 5, I analyse nightjar diet obtained from faecal samples from multiple birds over all four years of study, to investigate change in dietary richness and variation within and between years. I couple diet data with moth trapping data, to estimate availability of moth species in different habitats across the NNR to identify any selection based on ecological traits. Nightjar diet has not previously been explored using metabarcoding methods and the benefits of including molecular techniques are clear when visual identification of samples is difficult.

Lastly, Chapter 6 presents the general discussion. Here, I sum up the main conclusions from this body of work and emphasise the importance of combining multiple methods to interpret animal behaviour as well as using measures of individual variation to explore population flexibility. Future research should be directed towards connecting the outputs of tracking and diet work to measures of fitness and other demographic parameters to fully integrate measures of population health into conservation plans.

Chapter 2: The trade-off between fix rate and tracking duration on estimates of home range size and habitat selection for small vertebrates

2.1 Abstract

Despite advances in technology, there are still constraints on the use of some tracking devices for small species when gathering high temporal and spatial resolution data on movement and resource use. For small species, weight limits imposed on GPS loggers and the consequent impacts on battery life, restrict the volume of data that can be collected. I applied two commonly-used methods of home range estimation, Movement-based Kernel Density Estimation (MKDE) and Kernel Density Estimation (KDE) to investigate the influence of fix rate, tracking duration and method on home range size and habitat selection, using GPS tracking data collected at two different fix rates from a small, aerially-insectivorous bird, the European nightjar (*Caprimulgus europaeus)*.

Effects of tracking parameters varied with home range estimation method; overall the MKDE method produced more variability in home range size than the KDE, particularly at the lowest fix rate of 32 per day (343 ha +/- 328 (MKDE) v. 119ha +/- 133 (KDE)). Tracking duration drove a 4% and 3.5% increase in MKDE and KDE home range size respectively. Fix rate was only important for the MKDE, and a 1-unit increase in rate caused a -0.59% change in home range size. Total number of fixes had the strongest impact on habitat selection, increasing it by 0.1% in both methods. High between- and within-individual variation strongly influenced outcomes and was most evident when exploring the effects of varying tracking duration, potentially related to phenology and/or habitat. To reduce skew and bias in home range size estimation and especially habitat selection caused by individual variation and estimation method, I recommend tracking animals for the longest period possible even if this results in a reduced fix rate. If accurate movement properties, (e.g. trajectory length and turning angle) and biologically-representative movement occurrence ranges are more important, then a higher fix rate should be used, but priority habitats can still be identified with an infrequent sampling strategy.

2.2. Introduction

Effective species conservation management requires detailed knowledge of a species' ecology (Baxter *et al.*, 2017), including but not limited to, an understanding of movement and resource use to make appropriate management decisions that will help conserve populations (Fedy *et al.*, 2014; Rice, Apa and Wiechman, 2017). For certain groups of species, such as small, nocturnal or range-limited species, gathering this information can be logistically challenging. As such, researchers are mostly reliant on indirect observation methods, such as animal-attached devices, including Very High Frequency (VHF) tags, geolocators and Global Positioning System (GPS) units (Cagnacci *et al.*, 2010) to make an assessment of what habitats are being used (Land *et al.*, 2008; Hinton, van Manen and Chamberlain, 2015; Boggie *et al.*, 2018).

The rapid advancement of tracking technology has allowed us to remotely gather information on a wide variety of species (Wilson and Vandenabeele, 2012; Wilson *et al.*, 2015). This information can be used to answer questions about how the animal interacts with the landscape, how it moves in relation to habitat type and structure (Karelus *et al.*, 2016; Boggie *et al.*, 2018), its territoriality and interactions with conspecifics (Wakefield *et al.*, 2013), and its foraging strategy (Guilford *et al.*, 2008). GPS units in particular are associated with the ability to collect data from more locations, including previously inaccessible areas, at a higher level of accuracy than before (Hebblewhite and Haydon, 2010; Tomkiewicz *et al.*, 2010). Researchers attaching GPS devices are reliant on the assumption that the data are producing accurate, consistent representations of the animal's spatial and temporal activities (Recio *et al.*, 2011; Dujon *et al.*, 2014; Latham *et al.*, 2015). However, studies have shown that movements and habitat use may be represented differently at different temporal and spatial scales (Börger *et al.*, 2006; Frair *et al.*, 2010), by using different methods of home range and habitat selection estimation (Huck, Davison and Roper, 2008; Calabrese, Fleming and Gurarie, 2016; Fleming and Calabrese, 2017; Stark *et al.*, 2017). This may be dependent on whether the methods take into account the autocorrelation structure of the data or not (Noonan *et al.*, 2019). Previous studies addressing these issues recommend obtaining data from multiple temporal and spatial scales for comparison (Börger *et al.*, 2006; Börger *et al.*, 2006), and have focused on large mammals (Girard *et al.*, 2002; Luca Borger *et al.*, 2006) that are able to be followed year-round. For small mammal and bird species however, it is often only viable to collect data for a limited, fixed, single-season period as a small battery size is necessary to avoid exceeding maximum percentage bodyweight threshold (Tomotani *et al.*, 2018b).

Trade-offs resulting from the incompatibility of low weight and long battery life may affect which individuals can be tracked (Recio *et al.*, 2011; Tomotani *et al.*, 2018b) and may limit how much data can be collected . Movement patterns recorded may therefore be influenced by the parameters used when collecting tracking data (Huck, Davison and Roper, 2008), fix-acquisition bias (D'Eon, 2003; Frair *et al.*, 2010), or method of analysis. The impact of variation in fix rate or duration of tracking period on resulting home ranges and habitat selection estimates is seldom explicitly considered or taken into account (but see Girard *et al.*, (2002); Borger *et al.*, (2006)). However, it is important to ensure that data are collected at the most appropriate temporal scale in order to acquire data of a certain quality or quantity necessary to answer the questions posed.

Studies that report the implications of varying fix rate and duration of tracking period, often address these issues with simulated, rather than empirical data (Blundell, Maier and Debevec, 2001; Huck, Davison and Roper, 2008). They also do so largely in the context of GPS fix failure (Frair *et al.*, 2010), movement distance (Cain *et al.*, 2005; Rowcliffe *et al.*, 2012) or home range estimation, rather than effects on estimates of habitat selection (Girard *et al.*, 2002; Luca Borger *et al.*, 2006; Börger *et al.*, 2006; Frair *et al.*, 2010). Studies often use VHF tags, rather than GPS tags (Blundell, Maier and Debevec, 2001; Luca Borger *et al.*, 2006), often due to limited sample size. A small number of in-depth studies regarding estimation of home range using conventional estimators, such as the Minimum Convex Polygon (MCP), conclude that changing fix rate and duration of tracking can alter estimates of home range and consequently inferences about movement and behaviour (D'Eon, 2003; Luca Borger *et al.*, 2006; Mills, Patterson and Murray, 2006). This is in part due to the effect these parameter changes have on the autocorrelation within the data (Fleming and Calabrese, 2017). Borger *et al.*, (2006) identified tracking duration (number of days) as the key parameter influencing home range estimation, whilst Huck, Davison and Roper, (2008), Walter, Onorato and Fischer, (2015) and Byer, Smith and Seigel, (2017) identified method of estimation as the most important factor for both home range size and proportion of habitats available. Stark *et al.*, (2017) found that movement-based home range estimation methods, such as the biased random bridge, handled missing GPS points of up to 75% of the total dataset better than conventional kernel density estimates and similarly Walter *et al.* (Walter *et al.*, 2018) found that incorporating the temporal aspect of the data produced more reliable estimates.

Tracking data are inherently autocorrelated (Kie *et al.*, 2010; Fleming *et al.*, 2015; Noonan *et al.*, 2019), although if fixes are taken infrequently enough so as to be longer than the autocorrelation timescale of the data, data can be considered independent (Fleming and Calabrese, 2017; Noonan *et al.*, 2019). The autocorrelation timescale is often interpreted as the time it takes for an animal to cross its home range (Fleming and Calabrese, 2017; Noonan *et al.*, 2019); the number of points that satisfy this assumption, equating to the number of home range crossings, are referred to as 'effective sample size' (Fleming and Calabrese, 2017). Not accounting for autocorrelation in the data can lead to bias and variation using traditional estimators, such as the KDE (Fleming *et al.*, 2015; Noonan *et al.*, 2019). Movement-based estimations such as the MKDE (Benhamou and Cornélis, 2010) and BBMM (Horne *et al.*, 2007) do account for autocorrelation, but do not estimate 'true' home range, but rather the animal's occurrence range (Fleming *et al.*, 2015; Fleming and Calabrese, 2017), i.e. a picture of where it has been, rather than what it does or needs long term. The recently introduced AKDE ('Autocorrelated Kernel Density Estimator') attempts to combine both the autocorrelation structure of the data and estimation of a traditional home range, estimating area used on the effective sample size which better represents the longer-term distribution of points (Noonan *et al.*, 2019).

The use and incorporation of autocorrelated data also relates to how the smoothing parameter of kernel home range analyses functions (Kie *et al.*, 2010). The smoothing parameter, or bandwidth, (commonly: '*h*') influences the weight of each data point within the probability distribution function that creates the home range (Hemson *et al.*, 2005; Gitzen, Millspaugh and Kernohan, 2006; Horne Garton E.O., 2006). There is no consensus as to which bandwidth parameter to use, however it should minimize variation in the home range estimate between sampling frequencies and individuals (Hemson *et al.*, 2005; Gitzen, Millspaugh and Kernohan, 2006). It should strike a balance between assigning an overly high influence to outer points, resulting in disjointed home ranges where this may not make sense (under-smoothing) and averaging over outer points, thus disguising details of the foraging range (over-smoothing) (Gitzen, Millspaugh and Kernohan, 2006; Schuler *et al.*, 2014).

Home ranges are also linked to the estimation of habitat selection by providing an individual measure of habitat availability (Borger, Dalziel and Fryxell, 2008; Huck, Davison and Roper, 2008). As the shape and size of the home range may depend on the configuration of the tracking schedule (Mills, Patterson and Murray, 2006), as well as estimation method and bandwidth parameter (Gitzen, Millspaugh and Kernohan, 2006), it can then influence the strength of habitat selection estimates (Girard *et al.*, 2006; Huck, Davison and Roper, 2008). However, the extent to which a decrease in fix rate and number of days tracked can directly affect these estimates, is largely unstudied. Few studies discuss the effects of tracking parameters on habitat selection and those that do mostly discuss habitat-related biases in fix collection (D'Eon, 2003; Frair *et al.*, 2010), rather than decisions made regarding the fix rate and how this might influence duration and therefore the results obtained. Girard *et al.*, (2006) simulated fix rate changes using empirical GPS data from moose (*Alces alces*) and found that decreasing fix rate did not significantly alter habitat selection conclusions and that preferences for specific habitat types were clear even at low fix rates (e.g. 1 fix every 7 days). It should be noted however, that this research was conducted on a large, slow-moving mammal, with the ability to conduct a tracking study for multiple months, which is not the case for many small species such as bats and birds, which present a very different system to larger mammals (Wikelski *et al.*, 2007). The scale and timing of movement undertaken by large herbivores (e.g. deer, bison) (Owen-Smith, Fryxell and Merrill, 2010) or carnivores could be orders of magnitude higher (Pépin *et al.*, 2004; Dickson, Jenness and Beier, 2005), causing positional autocorrelation to last for a number of days (Godvik *et al.*, 2009). Not only that but small insectivores have higher energy requirements (Kelly *et al.*, 2013) and are exploiting a more spatially- and temporally-variable resource which will influence the time they spend moving and the configuration of their movements (Aldridge and Brigham, 2008).

Given the increasingly widespread use of relatively cheap, miniature GPS units, it is pertinent that the influence of tracking parameters and data analysis methods are studied in the context of habitat use by species (Kochanny, Delgiudice and Fieberg, 2009; Hofman *et al.*, 2019). As such, this study is framed particularly in the context of the increased use of high-temporal resolution GPS units as opposed to VHF tags, on a small mobile central place forager.

I concentrate particularly on how decisions made by researchers before deployment can influence analysis and results, as well as the use of a movement-based method of estimating home range, which has not been studied in the context of manipulation of these parameters.

2.2.1 Study scenario

My study focused on a migratory, insectivorous bird of conservation concern (Conway *et al.*, 2007; Eaton, Aebischer, Brown, Hearn, *et al.*, 2015), the European nightjar *Caprimulgus europaeus* (hereafter referred to solely as 'nightjar'). Numbers fell significantly throughout Great Britain in the early part of the 20th century due to afforestation, and loss of habitat (Morris *et al.*, 1994). Nationally, the population size has now stabilised (Eaton, Aebischer, Brown, Hearn, *et al.*, 2015), but threats such as climate change, urban development and agricultural intensification that remove both nesting and foraging resources, still continue (Vickery *et al.*, 2014b; English *et al.*, 2016). Although nightjars are mobile and thought to be adaptable to land use change (Camacho, Sebastian Palacios, *et al.*, 2014), they are also site-faithful (Lowe, Rogers and Durrant, 2014) and there is little evidence in the literature to demonstrate their resilience to significant habitat transformation, particularly with smaller populations on atypical sites. Summer residency in northern Europe, including Great Britain, is short, lasting from May until September, with some females only arriving in mid-June (Berry and Bibby, 1981). This provides a limited window in which to track this species.

I have tracked a number of individuals from a relatively stable breeding population of nightjars (Palmer, 2002; Middleton, 2017) on one of the more northerly breeding sites in Great Britain (Balmer *et al.*, 2013). I aimed to determine the effect of fix rate and tracking duration from GPS data, on estimates of home range size and habitat selection and to assess the trade-off between fix rate and tracking duration in terms of the information gained about an animal's area of use.

I had the following research questions:

1. How sensitive are estimates of home range size and shape to changes in fix rate and tracking duration?
2. How sensitive are estimates of habitat selection to any changes in tracking parameters and method of home range estimation and are the conclusions equivalent across all rates, durations and methods?

2.3. Materials and methods

This work was carried out on the Humberhead Peatlands National Nature Reserve, South Yorkshire, which consists of Thorne Moors (53.636, -0.89682) and Hatfield Moors (53.545, -0.93493). The project was developed as part of an EU-funded LIFE+ project to monitor behavioural responses of European nightjars to habitat restoration. All fieldwork was subject to ethical approval through the University of York and was conducted with appropriate licences to capture and deploy tags onto birds through the British Trust for Ornithology. The data consist of GPS fixes collected from 32 adult birds from 2015 – 2018, tracked over 6 or more days at two different rates. Birds were tracked from 21:00 to 05:00 hrs, but points spent at the roost in the first and last 30-minute periods (i.e. 21:00 – 21:30 and 04:30 – 05:00) were removed to avoid bias (Lair, 1987; Schaming, 2016). Data were collected using miniature nanofix GPS tags (Pathtrack, Otley, UK; Figure 2.1), at rates of 20 fixes per hour (n = 15), totalling 160 per 8-hour tracking session in 2015 and 2016, and 12 per hour (n = 17), totalling 96 per 8 hour tracking session in 2017 and 2018. This was equivalent to setting a 3-minute and 5-minute fix interval respectively, in the pre-programmed tag parameters.

Figure 2.1: Nightjar with GPS tag attached to the two central retrices. Tags attached with a small amount of double sided sticky padding, dental floss and superglue.

The tags weighed approximately 1.75g (equivalent to 3% or less of the bird's bodyweight). In order to achieve such a small size, the battery and memory chip inside the GPS tags were necessarily small and their use requires a decision on the trade-off made between fix rate and tracking duration. In 2017, the interval between fixes was increased from three to five minutes, thus decreasing the fix rate from 160 to 96 per session, in order to obtain an increased number of days of data, rather than collecting more frequent fixes over fewer days.

2.3.1. Habitat Mapping

Habitat types across the study site were primarily mapped using supervised classification of Unmanned Aerial Vehicle (UAV) photographs within ArcMap (v. 10.5). I created a five-metre resolution habitat map, which was then updated in subsequent breeding seasons using hand-held GPS units on site, to incorporate annual habitat management activities. I classified 13 habitats, relating to both vegetation type and structure, both thought to be important to nightjars.

2.3.2. GPS data processing

The data were processed and analysed in R (v.3.5.1). In order to explore the effect of fix rate on estimates of home range and habitat selection, the original data were subsampled. Firstly, fix rate was halved according to the initial rate (i.e. 6 or 10 fixes per hour, totalling 48 or 80 fixes per 8 hour session, equivalent to a 6- or 10-minute fix interval); secondly the data were subsampled to give a rate of four fixes per hour (i.e. 32 per session or a fix interval of 15 minutes). To investigate the effect of tracking duration on home range and habitat selection, the full datasets for each bird were subsampled into the first 3- and 6-day periods.

These data were then used to estimate individual home ranges using the Biased Random Bridge method for movement-based kernel density estimation (MKDE) (Calenge, Dray and Royer-Carenzi, 2009; Benhamou, 2011) and the static kernel density estimation (KDE), using package 'adehabitatHR' (Calenge, 2006). These represent one of the most commonly used methods of range estimation and a more recently developed occurrence estimator, or movement-based home range, that explicitly uses the connections between tracking data fixes to identify heavily-used areas and corridors (Benhamou and Cornélis, 2010). For the MKDE, specific movement information gathered from the tracking data was used to parameterise a more descriptive, movement-based home range (Benhamou and Riotte-Lambert, 2012), compared with the KDE method. Each GPS fix is associated with a timestamp (date and time combined), meaning the exact time between fixes is calculated. Specific calculations include: a diffusion parameter comprised of the maximum time permitted between fixes ('*Tmax*'; here, I have used 3 x fix frequency, i.e. either 9 or 15 minutes; Benhamou and Cornélis, 2010) and the minimum distance that represents movement (10 metres) (Benhamou and Cornélis, 2010). The inclusion of the 'Tmax' value therefore excludes the 16-hour gap present in the schedule that occurs while the units are switched off during the day. As a central place forager, the nightjar is constrained to its nest or roost during the day, when it is unable to feed. Thus, the inclusion of this area would likely bias the home range unfairly downwards, as with seabirds constrained to nesting on land (Briscoe *et al.*, 2018).

Constructing home ranges for such constrained foragers is difficult, but this decision likens the nightjar MKDE to an 'active' home range, as in Barraquand and Benhamou (2008). These parameter values are used in conjunction with a variable smoothing parameter applied to different parts of the track, which is calculated from values chosen by the user. These values are: '*hmin*'; a value in the units of the GPS locations, chosen to balance the GPS-related error and the mean distance moved between points (here, 60 metres); '*hmax'* at the interpolated point furthest from two known locations (Benhamou and Cornélis, 2010; Benhamou, 2011; Papworth *et al.*, 2012). Finally, '*Tmax'* (as above) and the grid size (here, this was the underlying 5 x 5 metre habitat map). The smoothing parameter used within the KDE analysis was '*href*', also referred to as the reference bandwidth (Gitzen, Millspaugh and Kernohan, 2006; Kie, 2013), which is estimated using the standard deviation of the x and y coordinates (Kie, 2013). This was used in preference to the 'LSCV' method, which tends to under-smooth (Horne and Garton, 2006) and may less accurately account for the possible distance travelled between points, especially by such a mobile bird that can cross its home range very quickly (Noonan *et al.*, 2019). I used the variable smoothing parameter and '*href'* throughout the analysis for all full- and subdivided samples, to avoid adding variance and bias into the study related to this parameter. I anticipated that as the MKDE has been found to cope better with missing points, it should also maintain an accurate representation of animal space use even with a decreased fix rate (Stark *et al.*, 2017). Home range sizes using both MKDE and KDE were calculated only for the 95% level as this is the most commonly used level in the literature.

Habitat availability within individual 95% home range estimates was identified using the 'over' function in package sp (Pebesma and Bivand, 2005). Home range habitat availability was combined with used points, identified using the 'join' function in adehabitatMA (Calenge, 2006), excluding points outside of the home range boundary, to estimate Manly Selection Ratios (Manly *et al.*, 2002). These were estimated using the 'widesIII' function in adehabitatHS (Calenge, 2006), where use and availability differ between individual animals and as such, a selection ratio is produced for each habitat type along with an overall selectivity measure of an individual bird across all habitats (Manly *et al.*, 2002; Calenge, 2006). Here I use the latter, termed within the adehabitatHS package as Khi2Lj, that incorporates all single-habitat selection ratios within each individual, into a combined measure of habitat selection (from here-on I will refer to this as the selection statistic). These selection values are a special case of the more-commonly used Resource Selection Function (RSF; Manly *et al.*, (2002); Rice, Apa and Wiechman, (2017). Estimating habitat selection in this way provides a simple, easily-interpreted statistic that makes better use of a single variable containing multiple categories, such as the habitat type variable in thisstudy (Manly *et al.*, 2002; Beyer *et al.*, 2010).

2.3.3. Autocorrelation assessment

To further understand the results from the MKDE and KDE home range estimation, it is important that the underlying structure of the data is assessed (Fleming *et al.*, 2015). I visualised data from all individuals, using variograms and correlograms in package ‘ctmm’ (Calabrese, Fleming and Gurarie, 2016), to gather information relevant to home range estimation such as positional- and temporal-time-to-independence. I then ran AKDE home range estimation analyses, which incorporate an underlying movement model into the estimation of a ‘true’ home range (Noonan *et al.*, 2019), using Ornstein-Uhlenbeck foraging (OUF) model-estimated variance and bandwidth parameters model (Calabrese, Fleming and Gurarie, 2016; Fleming *et al.*, 2017) that brings in both positional and velocity autocorrelation. The values produced for these were compared to those produced from the KDE and MKDE to observe any differences cause explicitly by the autocorrelation structure of the data.

Variograms displayed immediately strong autocorrelation, followed by a rapid but individually varying asymptote (Appendix I, Figure 2.3, 2.4). The data possessed strong positional and velocity autocorrelation within the first 30 minutes of tracking, which equates to 10 -12 or 6 -8 fixes at the two sample rates (160 or 96 per day). This demonstrates that to achieve true independence the data would need to be subsampled to a 30-minute fix interval (approximately 16 fixes per day), far less frequently than currently taken. However, the relationship between the size of the area traversed by the individuals, meant that effective sample size was still high. This highlights that although there is autocorrelation in such frequently acquired data, for a central place forager holding a small home range relative to the tracking duration, this is not as significant as it would be for an animal traversing a larger area, relative to the fix rate (Fleming and Calabrese, 2017; Noonan *et al.*, 2019). This resulted in no significant difference between KDE and AKDE home range sizes (One-way Anova, $F_{2,536}$: 19.93, $p < 0.0001$; Tukey post-hoc tests: MKDE :: KDE $p < 0.0001$; MKDE :: AKDE $p < 0.0001$; KDE :: AKDE $p = 0.57$; Appendix I).

Consequently, I have analysed the data for habitat selection with the KDE and MKDE, to demonstrate the use of both a range and an occurrence estimator with data that is initially strongly autocorrelated but asymptotes quickly, relative to the total length of tracking.

2.3.4. Modelling

Estimates of home range size and habitat selection, for all home range estimation methods were used linear mixed effects models (‘lmer’ function in lme4; Douglas Bates *et al.*, (2015). Mixed effects models were able to identify the influence of both spatial and temporal variables using fixed effects, as well as identifying individual variation in these variables, using random effects. Methods such as this to deal with individual variance, i.e. mixed-effects models, are being used more widely (Gillies *et al.*, 2006; Leclerc *et al.*, 2016) and prior exploratory analysis in this study showed clear influence of the individual bird on the strength of the response to change in the tracking duration and fix rate. Both response variables, home range size and selection statistic, for both methods were log transformed for normality (Luca Borger *et al.*, 2006; Kochanny, Delgiudice and Fieberg, 2009). Four separate models were created (Table 2.1). Variables were subject to prior exploratory analysis related to *a priori* hypotheses. Sex of the bird did not have an influence on the result and was thus not included. Two models were run for the two different home range estimation methods, in order to test the sensitivity of the home range estimates to variation in tracking parameters, followed by two habitat selection models, to test the sensitivity of the habitat selection estimates to variation to the same tracking parameters.

Table 2.1: Outline of the four linear mixed models used in analysis. Response variable is modelled against the corresponding fixed and random effects listed in each row.

Response variable	Fixed effects	Random effects
1. MKDE/KDE/AKDE Home Range size (hectares)	Number of days + Fix rate + Number of fixes + Year + Site + Dominant habitat	1. Individual (intercept) / Days (slope) 2. Week number
2. Habitat selection statistic (derived from MKDE Home Range)	Number of days + Fix rate + Number of fixes+ Year + Site	1. Individual (intercept) / Days (slope) 2. Week number

Fixed effects in all starting models were:

1. Tracking Duration: number of days, ranging from 3 to 17.
2. Fix Rate: expressed as the number of fixes per session; one of 32, 48, 80, 96 or 160 (corresponding to 4, 6, 10, 12 or 16 fixes per hour).
3. Number of fixes; the total number of fixes in a bird's full, or subset dataset.
4. Year; either 2015, 2016, 2017, 2018.
5. Site; Hatfield or Thorne.

Dominant habitat, representing the habitat type within a bird's home range (derived from the MKDE or KDE polygon and overlaid on a five-metre resolution habitat raster) with the highest number of pixels (i.e. largest availability) was included as a fixed-effect only in the home range models. Random effects to account for variation in the coefficient values were the same for all models and included Individual and tracking duration as the random intercept and slope respectively (Table 2.1). Including tracking duration as both a fixed effect and a random slope (Harrison *et al.*, 2018) aimed to improve the fit of the model by recognising individual variation in response to changing tracking duration, something that was uncovered during the prior exploratory analysis. Week of the breeding season in which the bird was tracked was also included as a random effect. To compare the impact of the parameters on the data originally collected at two different fix rates, I subsampled all data to a 15-minute interval. I again ran four models with the same starting dependent variables of home range size and habitat selection statistics, which did not include fix rate as a fixed effect, but did include tracking duration, temperature, year, habitat and site, to attempt to unpick underlying variation.

For all models, AICc (AIC corrected for small sample size) was used to judge the most appropriate model for all analyses. I followed a stepwise selection procedure, whereby dropping single terms from the model resulted either in a decrease or increase in AICc value. The final model was determined when no further decrease could be achieved by removing single terms. Single terms were added back into the final model, in a random order and a secondary model selection procedure was employed using MuMin (v. 1.42.1; Barton, 2011) in R, to check the validity of the reduced model. Fit of the final models was assessed through normality of the residuals using the plot function in package 'lme4' (v. 1.1-17) and by simulating residuals and testing for uniformity in package 'DHARMa' (v. 0.2.0; Hartig, 2016). Where model selection did not achieve delta AIC > 2, i.e. there was no 'best' model, I used the 'model.avg' function in MuMin and produced model-averaged parameters. Final model coefficients for both fixed and random effects are presented in the results. As response variables were log-transformed, the values are presented as percentage increase in y, with a 1-unit increase in x.

2.4. Results

2.4.1. Home range information

Across the whole dataset of 32 birds, the mean (+/- SD) home range sizes were 204.04 ha (+/- 229.42) and 115.1 ha (+/- 153.62) for the MKDE and KDE respectively (Table 2.2). All estimators varied between and within fix rate and day subsets; MKDE range sizes were at their highest at the lowest fix rate of 32 fixes per day (342.88 ha +/- 327.61), whereas KDE range sizes were largest in the 5-minute fix interval category (125.25 ha +/- 182.61). Mean values for the shortest tracking duration subset of 3 days were 138.57 ha (+/- 167.11) for MKDE; 109.84 ha (+/- 184.89) for KDE (Table 2.2). Large standard deviations represent high individual variation, addressed in much more detail in the following sections.

Table 2.2: Mean values (+/- S.D.) for MKDE and KDE estimated home range sizes (hectares) for each fix rate (fixes per hour) subset and two shorter duration subsets within the dataset (mean value across all subsets per year). Sample sizes vary between subsets; 16 and 10 fixes per hour, n = 9; 12 and 6 fixes per hour, n = 23; 4 fixes per hour, n = 32; 3 days, n = 64; 6 days, n = 32.

	At a fix rate of:						*At a subset of:*	
	16/ hour	**12/ hour**	**10/ hour**	**6/ hour**	**4/ hour**	**All**	**3 days**	**6 days**
Mean *MKDE* (ha)	94.74	179.87	158.04	260.89	342.88	204.04	138.57	163.42
(+/- S.D.)	92.13	187.94	195.18	235.4	327.61	229.42	167.11	162.98
Mean *KDE* (ha)	80.81	125.36	104.5	118.96	119.17	115.1	109.84	91.53
(+/- S.D.)	91.49	182.61	140.76	117.54	133.08	153.62	184.89	118.92

2.4.2. Modelling results

To test the influence of multiple tracking parameters on estimates of home range size, I ran three models with MKDE and KDE sizes as the dependent variable. For both estimators, tracking parameters were influential (Table 2.3). MKDE home range size was most strongly influenced by fix rate and tracking duration (Appendix II: Table 2.7). Dominant habitat type within the individual’s area was also influential, whilst number of fixes, site and temperature had a negligible influence and were removed. The final model indicates that every one-unit decrease in the fix rate results in a -0.59% change in home range size, i.e. the lower the fix rate, the fewer fixes collected per day and the larger the home range (Table 2.3; Figure 2.1). A one-day increase in tracking duration equated to a 4% increase in home range (Table 2.4, Fig 2.3a). This final model containing just Fix rate, tracking duration and habitat held most of the model weight (0.63; Appendix II: Table 2.7). Individual as a random effect accounted for the majority of the variation in MKDE home range size (Table 2.3). Number of days (included as a random slope) explained only a small amount of extra variation (0.004; Fig 2.3 a).

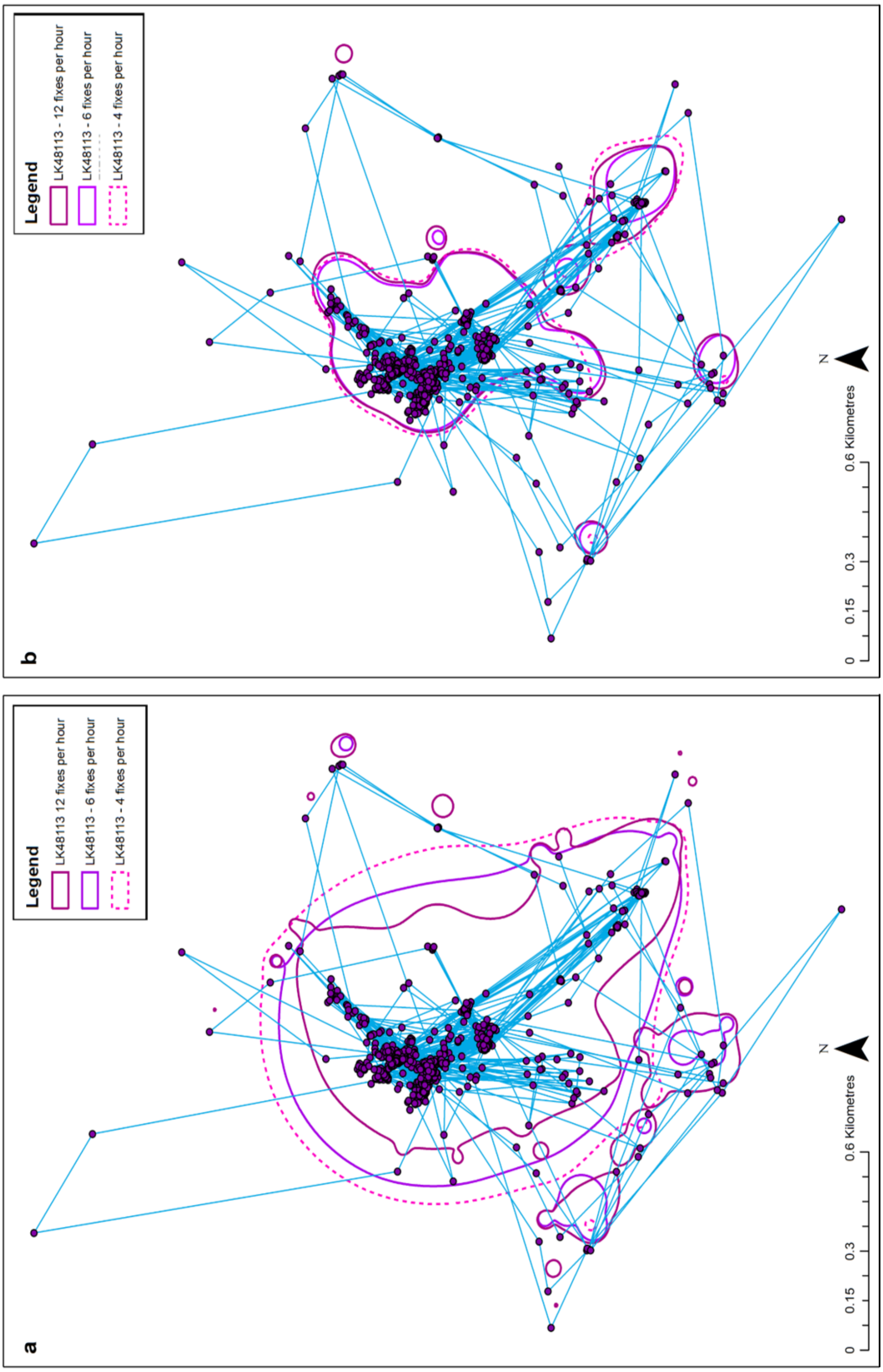


Figure 2.2: Example of a) MKDE and b) KDE home ranges calculated at three different fix rates for one bird tracked in June 2018. Estimates were calculated at 12 fixes per hour (96 per 8-hour tracking session, equivalent to a 5 minute fix interval), 6 fixes per hour (48 per session, equivalent to a 10 minute fix interval) and 4 per hour (32 fixes per session, equivalent to a 15-minute fix interval), as identified in the key. GPS fixes outside of the home range polygons were removed when calculating habitat selection.

Table 2.3: Final model coefficient estimates and random effect variance parameters for each of the four models run to explore factors affecting home range and habitat selection. 95% confidence intervals are presented in brackets, following fixed effect coefficients. Standard deviation is presented in brackets following random effect coefficients.

	Coefficient estimates			
Predictors	**MKDE Home Range**	**KDE Home Range**	**MKDE Habitat Selection**	**KDE Habitat Selection**
Intercept	7.049	4.234	4.65	4.179
	(5.871- 8.228)	*(2.56- 5.909)*	*(4.187 - 5.113)*	*(3.763 - 4.594)*
Fix Rate	-0.006		0.001	
	(-0.007 - -0.004)		*(-0.001 - 0.006)*	
Tracking Duration	0.039	0.034	0.048	0.03
	(0.007 - 0.071)	*(0.002 - 0.066)*	*(0.009 - 0.087)*	*(0.012 - 0.049)*
Number of fixes			0.001	0.001
			(0.0006 - 0.002)	*(0.001 - 0.002)*
Site		0.184	-0.408	-0.245
		(-0.256 - 1.165)	*(-0.814 - -0.002)*	*(-0.941 - 0.036)*
Dominant habitat	**+**	**+**		
Random effects				
Intercept/Individual	0.343	1.234 - 1.244	0.261 - 0.269	0.62 - 0.752
(+/- SD)	*(+/- 0.585)*	*(+/- 1.111 – 1.115)*	*(+/- 0.511 – 0.518)*	*(+/- 0.788 – 0.862)*
Days/Individual	0.004	0.005	0.0004 – 0.0005	0.001
(+/- SD)	*(+/- 0.062)*	*(+/- 0.072)*	*(+/- 0.019 - 0.022)*	*(+/- 0.028 – 0.031)*
Intercept/Date	0	0.00 - 0.098	0.013 - 0.03	0.04 - 0.089
(+/- SD)	*(+/- 0.000)*	*(+/- 0.314)*	*(+/- 0.112 – 0.174)*	*(+/- 0.20 – 0.299)*
Sigma (Resid. var.)	0.091	0.101	0.118 - 0.121	0.09
(+/- SD)	*(+/- 0.302)*	*(+/- 0.318)*	*(+/- 0.343 – 0.348)*	*(+/- 0.30)*

Tracking duration and dominant habitat were the most influential parameters when estimating KDE home range size (Appendix II: Table 2.8). In contrast to the estimates from the MKDE, fix rate had minimal impact (Fig 2.2). An increase of one day resulted in a 3.46% increase in the KDE home range size (Table 2.4, Fig 2.4a). However, several of the reduced models held similar AICc values, resulting in model-averaged parameters from the best two models (Table 2.3), the second of which also included site. These two models combined held an Akaike weight of 0.7 (Appendix II: Table 2.8). Variance attributed to individuals was higher than for MKDE home range (Table 2.3). Further to individual random variation, tracking duration also provided some explanation of the variance along with residual variation.

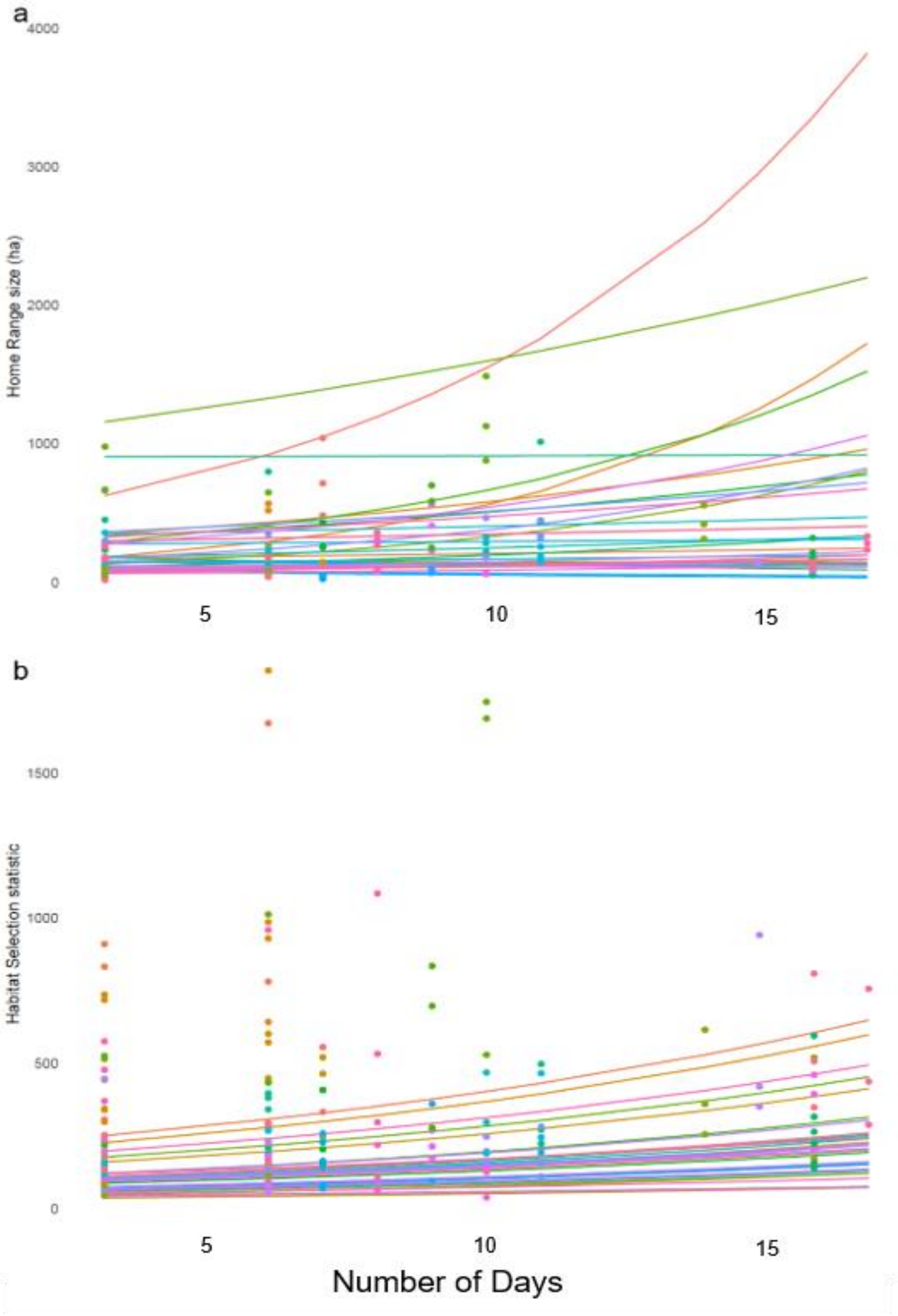


Figure 2.3: Outputs from the linear mixed models showing variation in individual response to altered tracking duration in a) MKDE home range size and b) MKDE-derived habitat selection, for both home range estimation methods. Predictive regression lines are displayed for each individual (n = 33). NB: different y-axis scales on each plot.

2.4.3. Habitat Selection

To assess the sensitivity of habitat selection estimates to changes in tracking parameters, variation in the estimated habitat selection statistic (Manly *et al.*, 2002), derived from both home range estimators was modelled against tracking parameters, and weather and temporal covariates. For the MKDE-derived habitat selection, fix rate, the number of fixes, tracking duration and site (Table 2.3, Appendix II: Table 2.9) were significant, but the top model was within ΔAIC 2 of the second ranked model, therefore these have been averaged. The removal of the total number of fixes resulted in an increase in AICc of >20 and its inclusion provided the most weight to the final model selection table (Appendix II: Table 12.9). An increase of one fix resulted in a 0.1% increase in selection strength (Table 2.4), which although small was significant. An increase in fix rate by one unit resulted in an increase of 0.3% in the selection estimate, whilst an increase in tracking duration caused an increase in the selection estimate of 4.9% per day (Figure 2.3b). Unlike the home range models, site on which the birds were tracked was heavily influential, with a 98% decrease in selectivity from Hatfield Moor to Thorne Moor (Table 5). Individual differences accounted for a considerable amount of the random variation, along with tracking duration; date-related variation was negligible, but higher residual variation was present (Table 2.3).

For the KDE-derived selection statistic the number of fixes had the most weight, and increased AICc by >100 if dropped from the model (Appendix II: Table 2.10). Tracking duration was also important, with site less important but still relevant to the model. As with MKDE-derived habitat selection, the top model was within ΔAIC 2 of the second best, so these were model averaged. An increase of one fix resulted in a 0.1% increase in KDE-derived selection (Table 2.4).

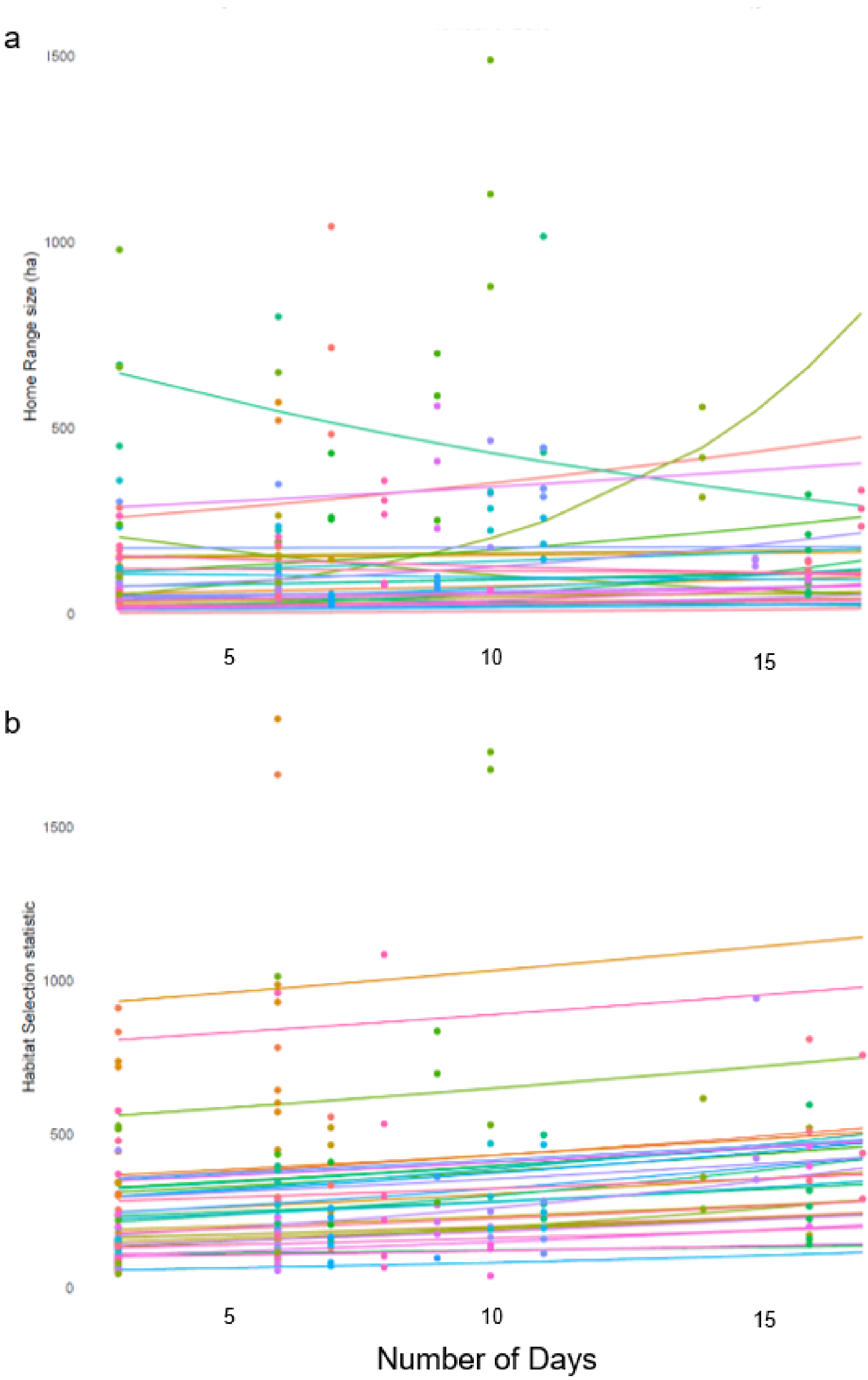


Figure 2.4: Outputs from the linear mixed models showing variation in individual response to altered tracking duration in a) KDE home range size and b) KDE-derived habitat selection, for both home range estimation methods. Predictive regression lines are displayed for each individual (n = 33). NB: different y-axis scales on each plot.

Table 2.4: Influence of tracking parameters on MKDE and KDE home range and habitat selection. For every one-unit increase in the variables in the left-hand column, there was a change in the corresponding home range or habitat selection estimate, given in percentage increase or decrease.

Increase ***per unit*** *in:*	**MKDE Home Range**	**Selection statistic**	**KDE Home Range**	**Selection statistic**
Fix Rate (Fixes per session)	↑ 0.59%	↑ 0.3%	[1]NA	NA
Tracking Duration (Days)	↑ 4%	↑ 4.92%	↑ 3.46%	↑ 3.01%
Number of fixes	NA	↑ 0.1%	NA	↑ 0.1%

[1]NA where variable did not appear in final model.

Likewise, an increase in tracking duration of one day caused a 3% increase in SR (Table 2.4; Figure 2.4b). A progression of two weeks through the breeding season – the maximum any bird was tracked for – would give an increase of 42% increase in home range size and would potentially represent the change from incubation to hatched chicks. Site influence was clear, although varied between individuals, with a decrease in selectivity when moving from Hatfield Moor to Thorne Moor (Table 2.3). The magnitude of the individual variation was stronger than when estimating MKDE selection (Table 2.3). Both the intercept and slope of the home range and habitat selection models vary between individuals (Fig 2.4b). Home range both increases and decreases with an increased tracking duration, depending on the individual. The relationship is clearer for habitat selection, where an increased tracking duration leads to an increased habitat selection statistic, indicating higher selection strength (Fig 2.3b & 2.4b).

2.4.4. Direct data comparison

I carried out additional analysis of the tracking data at a 15-minute fix interval where direct comparison among years was possible, in an attempt to understand if changes in fix rate over the course of the study might have masked other changes. For each dependent variable, a different set of parameters were most influential (Appendix III). Only within the MKDE home range analysis was there a clear effect of year, with home range size increasing from 2015 linearly through to 2018 but decreasing with temperature (Table 2.5). In comparison, KDE home range size was influenced most strongly by the tracking duration and number of fixes. Neither habitat selection model displayed an effect of year; habitat selection derived from the MKDE home range was influenced by tracking duration, but also temperature, whereas that derived from KDE home range was only influenced by site (Table 2.5, Appendix III).

Table 2.5: Model coefficients from four models testing the effects of tracking-parameter-related, temporal and weather covariates. Data were subsampled to a 15 minute fix interval (32 fixes per day, n = 32). Models tested the influence of parameters on MKDE and KDE home range and habitat selection estimates. 95% Confidence intervals in brackets.

	Coefficient estimates from models testing effects on:			
Predictors	**MKDE HR**	**KDE HR**	**MKDE HS**	**KDE HS**
Intercept	7.499	3.75	6.443	4.887
	(4.36 - 11.363)	(2.688 - 4.865)	(4.666 - 8.211)	(4.581 - 5.192)
Tracking Duration		0.249	0.068	
		(-0.077 - 0.586)	(-0.005 - 0.141)	
Number of fixes		-0.007		
		(-0.019 - 0.004)		
Site				-0.385
				(-0.864 - 0.095)
Year	+			
Temperature	-0.183		-0.112	
	(-0.346 - 0.01)		(-0.219 - -0.004)	
Random effects				
Week number	0.033	0.059	0.089	0
(+/- S.D.)	(+/- 0.182)	(+/- 0.526)	(+/- 0.299)	(+/- 0.000)
Residual variation	0.642	0.99	0.315	0.435
(+/- S.D.)	(+/- 0.801)	(+/- 0.995)	(+/- 0.562)	(+/- 0.66)

2.5. Discussion

Manipulation of tracking parameters influenced all aspects of this study results in some form. All the factors presented here have relevance for researchers looking to plan their own tracking study and should at least be considered when planning and analysing, as they may mask other elements. All parameter values should be reported to allow for full understanding of the results. I have provided information on the magnitude of the change in home range and habitat selection where possible, to aid understanding of the strength of the relationships between variables should researchers need to make this trade-off when studying a small species for which 'unlimited' tracking is not possible. Below I discuss these factors in the context of my original research questions and in the context of movement research overall.

2.5.1. How sensitive are estimates of home range size and shape to changes in fix rate and tracking duration?

Both methods of home range estimation were sensitive to tracking duration, but only the MKDE was sensitive to fix rate. The influence of fix rate on MKDE, is a reflection of the autocorrelation assumptions within the method and the underlying structure of the data (Benhamou, 2011; Fleming *et al.*, 2015; Fleming and Calabrese, 2017). For the MKDE, the density of, and the space between, consecutive points is weighted, which means that if fix rate were decreased in order to extend tracking duration, this would increase the area in which there is a probability of finding the animal (creating more uncertainty), producing a larger MKDE.

Sensitivity to tracking duration of both methods identifies this parameter as a key variable. A longer tracking duration means that extra information is gained, producing a larger sample size (Fleming and Calabrese, 2017) and – referring back to Figure 1.12 in Chapter 1 – may cover different aspects of the breeding season. For species that have previously only been tracked for short periods, the information gained from extra days of tracking could be very valuable, because what animals do for a few days is not necessarily representative of what they do longer term, perhaps because of prey depletion in the area around the nest (Kouba *et al.*, 2017), or because of phenological changes such as the development of their brood (Borger *et al.*, 2006; Van Beest *et al.*, 2011). Many species have been found to forage more widely when provisioning their chicks, as opposed to self-feeding only (REF) Where the relationship between home range crossing time and frequency of fixes gives rise to strongly autocorrelated data (i.e. crossing time exceeds the interval between fixes), longer tracking enables the effective sample size to increase, making the results more interpretable. I identified strong bias in the estimation of home range size if data are only collected for a few days for both estimators, due to a substantial amount of both between- and within-individual variation in foraging locations. Within- individual variation in movement behaviours is also identified by Fleming and Calabrese (Fleming and Calabrese, 2017) as a constraint to standardisation across different tracking durations. Therefore I recommend that researchers acquire tracking data over a longer duration not only to provide a more balanced understanding of where the animal is going in the presence of strong individual variation, but to increase effective sample size (Noonan *et al.*, 2019). This contrasts with recent information from a study of the large mammal literature by Hofman *et al.* (Hofman *et al.*, 2019), who recommend more regular tracking than is thought necessary in order to counteract issues with retained ephemeris data and fix acquisition (see also McGregor *et al.*, (2016).

In this study, the MKDE provided an accurate representation of used areas and is therefore suitable for habitat selection and resource use analyses, particularly when observing year to year changes, due to its position as an occurrence rather than a range estimator (Fleming *et al.*, 2015). However, the influence of tracking parameters on this method means this might not be true for larger, slower moving animals, such as deer (Fischer, Walter and Avery, 2013; Walter *et al.*, 2018), compared with small, mobile species such as the nightjar. The spatial and temporal scales over which species of different sizes and traits operate, will influence appropriate data collection schedule (and thus autocorrelation). Large herbivores such as deer or moose (Van Beest *et al.*, 2011) track resources that may only vary over a weekly- or monthly timescale, and therefore may only necessitate daily fixes. Nightjars and other small, insectivorous aerial foragers (Arrizabalaga-Escudero *et al.*, 2015), track mobile resources that may vary on shorter timescales related to daily weather conditions and small-scale spatial changes in temperature (Boiteau, Bousquet and Osborn, 2009; Rainho, Augusto and Palmeirim, 2010; English *et al.*, 2016). The effects of stochastic resource distribution may be amplified by habitat type and structure in their home range, differing by metres rather than kilometres (Merckx *et al.*, 2010, 2012). Nightjars are visual predators that feed on-the-wing, making the connections between points and not just stationary locations, more important. Therefore, to quantify changes on this scale requires shorter tracking intervals. The increase in MKDE home range size with a longer tracking duration, along with strong individual variation signals the need for tracking data to be analysed with a method appropriate for its structure. Consequently, I suggest that researchers undertaking any movement-based kernel analysis, to do so at a standardised rate across individuals, or to use analysis methods that incorporate varying autocorrelation structures, such as the AKDE.

2.5.2. How sensitive are estimates of habitat selection to any changes in the tracking parameters and method of home range estimation and are the conclusions equivalent across all rates, durations and methods?

The strong influence of number of fixes for both MKDE and KDE-derived habitat selection is partly explained by Manly selection statistic calculation methods. This method considers how many points are selected in each different habitat and compares this to the respective relative availabilities, and collates this information over all habitat types used and available per individual (Manly *et al.*, 2002). Each extra fix collected adds weight to the use of each habitat, compared to its availability, and the relationship becomes stronger if availability does not change. Whilst there are limitations of the selection ratio method, it is an intuitive method with which to observe habitat selection and preferences of animals when faced with a simple habitat-type metric, that would struggle to be modelled in a linear format (Manly *et al.*, 2002; Rice, Apa and Wiechman, 2017).

Fix rate and tracking duration influenced habitat selection estimates derived from the MKDE and KDE home ranges respectively. Decreasing fix rate could decrease the level of habitat selection as calculated with the MKDE home range. Firstly because there are simply fewer fixes in total, but also due to the longer interval between fixes, the autocorrelation has reduced and the animal is potentially less likely to be in the same place, particularly for a very mobile aerial feeder such as the nightjar, which can cross its home range in less than the time between consecutive fixes. If the decrease in fix rate results in an increased tracking duration due to battery life and/or memory space, a similar level of selectivity may be reached during the extra tracking time, particularly if individuals are consistent in their foraging. I achieved the same number of fixes over a 10-day tracking period at a lower fix rate, as I did over only 6 days at the original, higher rate, providing us with an almost 50% increase in the number of days of data, with a reduction of only 8 fixes per hour, or 64 per tracking session.

It is also important to note that habitat selection estimates from both the MKDE and KDE were sensitive to the site studied, which concurs with Börger *et al.*, (2006) and Byer, Smith and Seigel, (2017). This suggests that selection estimates could be sensitive to habitat configuration as well as method. Bearing in mind that home range size dictates the individual availability of habitat to calculate the habitat selection, change in the home range size with method could result in inclusion of different habitat types, ultimately influencing the resulting habitat selection ratios. Animals could appear to be much more selective if they use habitats that are sparsely distributed, meaning they have to ‘commute’ across large areas of unsuitable habitat. If modelled with the MKDE, rather than the KDE, this may (depending on the frequency of these commutes) lead to much larger, contiguous areas of available, but unused, habitat being included.

Strong individual variation in the habitat selection estimates were particularly related to tracking duration. Week number only explained some of the variation in habitat selection estimates, not those of home range, which is likely to reflect changes in food availability and weather conditions. Ultimately in this study, although the selection estimate changed with number of fixes, the primary conclusions (i.e. the most selected habitat) did not change, (in accordance with Girard *et al.*, (2006), although occasionally the precise order in which habitats were selected did.

Models run with subsampled data, therefore making the results directly comparable across the individuals in the population, show that external factors that are not dictated by the tracking parameters (temperature, site, year) are also influential. This clarifies the need to track individuals at the same rate and for the same duration, to allow the effects of these parameters to be more evident. In particular, variation in home range estimates and habitat selection due to site and year, could reflect differences in vegetation type and structure and may indicate the potential for there to be underlying differences in fitness, survival or breeding success (Dussault *et al.*, 2005). These models also highlight the difference between the range and occurrence estimators; the latter (MKDE) uses movement parameters within the data and here has highlighted a decrease in home range with temperature and year, external influences not picked up by the range estimator (KDE).

2.6. Conclusions

Fix rate and tracking duration acquired from miniature GPS units influenced the results of thistracking and habitat selection study, where the size of the species restricted the type of tag, required a trade-off between fix rate and tracking duration. I concur with recent literature on autocorrelation; changing fix rate alters data structure. I recommend that data are analysed in accordance with autocorrelation structure and the ecology of the species; an understanding of scale in temporal and spatial movement is necessary to achieve a high effective sample size. For a small, mobile, central place forager such as the nightjar, which can travel rapidly across its home range and is exploiting localised, temporary resources, it is important to maintain the data collection at a sufficient schedule so to balance small-spatial scale movements with longer-term changes in prey distribution that can provide information about their needs for productivity and survival. Overall, I recommend tracking animals for as long as possible, to reduce the skew and bias that can arise from individual variation in movement patterns, so as not to make conservation recommendations based on potentially unusual behaviour. The overall conclusions from the habitat selection analyses however, did not change, despite the estimate of habitat selection strength changing by some magnitude. Therefore, for species where the main concern is to identify priority habitat type for conservation, more infrequent fixes over a longer time will suffice.

Chapter 3: Multi-year tracking reveals high individual variability in habitat selection and functional habitat relationships in European nightjars

3.1. Abstract

An animal's choice of breeding and foraging habitat represents an individual's needs but this choice may vary within the population. Understanding how individual variation in habitat selection contributes to the population mean is important for the development of conservation management strategies. I collected GPS tracking data from European nightjars (*Caprimulgus europaeus*) at a UK breeding site where restoration measures have altered large areas of habitat. For each bird I calculated home range size and habitat selection ratios to observe the level of individual variation within the population. For the population as a whole, I analysed differences in mean home range size and habitat selection between years, to test for functional responses to habitat change.

Individual variation in habitat selection was high and explained more of the variation than the year. Specialist and generalist individuals were present and differed in their strength of selection for different habitat types. Across the population, home range size decreased by 1% as availability of cleared habitat within the home range increased (by 1%), but increased as the amount of open water expanded (by 9%), indicating the presence of functional responses to habitat availability. Use of cleared habitat increased significantly within the breeding site (by >400% over the course of the study) and was significantly more selected for when more available. Contrary to predictions, selection for woodland, which also decreased in availability (by 17-21%), did not strengthen, These results demonstrate the use of measures of resource selection at the individual level , in conjunction with population-level responses to change, to better understand the needs of a population. The variation in habitat selection within this population represents flexibility and has positive implications for their ability to adapt to further change, particularly the divergent responses to different habitats. Providing a mosaic of habitats is therefore key in order to maintain the variation necessary for persistence.

3.2. Introduction

An animal’s decision-making process should drive it to choose habitat that improves its chance of survival and reproductive success (Dussault *et al.*. 2005; Beyer *et al.*, 2010; Roever *et al.*. 2014; Leclerc *et al.,* 2016, Owen *et al.,* 2017). This choice (variation in use of a habitat compared to its availability; Johnson 1980; Thomas *et al.,* 1992) may reflect habitat quality or configuration, may remain consistent over time (Augé *et al.*, 2014) or may be responsive to a number of intrinsic and extrinsic factors, such as age, sex, competition or climate (Mauritzen *et al.*, 2003; Godvik *et al.*, 2009; Treinys *et al.*, 2016). Functional responses refer to alteration of movement behaviour or habitat use in response to a change in habitat availability and may occur in response to varying needs (Holbrook *et al.,* 2019), for example, foraging and predator protection (Godvik *et al.,* 2009). Analysing functional responses is important in terms of understanding behavioural plasticity (Godvik *et al.,* 2009; Leclerc *et al.,* 2016; Lesmerises *et al.,* 2018a), costs and benefits of different habitats (Godvik *et al.,* 2009) and the ability of a species to respond to spatial and temporal landscape change (Mauritzen *et al.*, 2003; Boggie *et al.*, 2018; Lesmerises *et al.*, 2018b).

Functional responses represent ecological trade-offs related to habitat type (Mabille *et al.*, 2012), conspecific interaction and competition (Jones 2001; Buskirk and Millspaugh 2006; Lesmerises *et al.,* 2018b), avoidance of predators (Mao *et al.,* 2005), or human influence (Sawyer *et al.,* 2006; Karelus *et al.,* 2016). For example, black bears (*Ursus americanus floridansus*) displayed a functional response by increasing average home range size in fragmented habitats, compared to conspecifics in continuous undisturbed habitat (Karelus *et al.,* 2016). Baxter *et al.,* (2017) found that Greater Sage-Grouse (*Centrocercus urophasianus)*, indicated a positive functional response to landscape change through strong selection of new, mechanically cleared habitats as they were created, compared to other land-use types. Moose (*Alces alces*) habitat selection changed with both habitat availability and home range size, indicating a direct response to the absolute amount of particular habitat types (Oftsad *et al.,* 2019).

Habitat preferences and responses to change may not be consistent within populations; the direction and magnitude of behavioural responses may vary among- and be repeated within-individuals (i.e. individual specialisation), and this variation has been reported in many mammal and bird species (Bolnick *et al.*, 2003; Nussey *et al.*, 2007; Forsman and Wennersten 2016). Populations can contain individuals that display both generalist and specialist tendencies (Patrick *et al.,* 2017), where generalists possess a broader niche and exploit a wider range of resources than specialists, whose diet or habitat choice is narrower and more rigid (Roughgarden, 1974; Wilson and Yohimura, 1994). A high degree of specialisation encourages higher efficiency in the foraging individual (Garrick *et al.,* 2006), however this can also mean these individuals are less able to switch to a different set of resources and are therefore more sensitive to change (Wilson and Yoshimura, 1994; Polito, 2015). The benefits of specialising are more numerous when resources are abundant and individuals are able to segregate their resource use from conspecifics (Maldonado *et al.,* 2017). However, where animals are utilising ephemeral prey and stochastic resources in a heterogeneous environment (Patrick *et al.,* 2017), generalist individuals that can use multiple resource types and may be more opportunistic, have a better chance of maintaining individual condition and passing on their traits to their offspring (Wilson and Yoshimura, 1994).

Quantifying individual variability, potential mechanisms of it and how it drives population responses (Nussey *et al.,* 2007), can identify sub-populations in need of extra protection, or those individuals that may ‘buffer’ a population when faced with large scale resource change (Forsman and Wennersten 2016; Phillips *et al.*, 2017). However, the population-level implications of changing habitat selection in response to altered availability, such as reduced fitness (Evens *et al.,* 2018), reproductive success (Phillips *et al.,* 2017) or survival of adults and young (Dussault *et al.,* 2012; Benson *et al.*, 2015; Losier *et al.*, 2015), are not well understood (Mason and Fortin, 2017b). Linking behavioural responses in resource selection to demographic consequences is needed in order to create appropriate management or protection interventions, to ensure species continued survival (Germain and Arcese 2014; Roever *et al.*, 2014). Individual variation can be incorporated into habitat selection studies through comparison of habitat use and availability within each individual’s home range (i.e. 'third-order' selection; Johnson *et al.*, 2006). Quantifying habitat selection at this level can reveal responses to change that may be hidden by pooling individuals (Leclerc *et al.*, 2016; Lesmerises and St-Laurent 2017). This can provide an insight into population variation, including consistency in foraging decisions among and between individuals; (Leclerc *et al.*, 2016) and differences driven by bioloigcal variation between sexes (Ofstad *et al.,* 2019), as well as population dynamics (Losier *et al.*, 2015; Baxter *et al.*, 2017) that can aid future management (Allen and Singh 2016; Tanner *et al.*, 2016).

3.2.1. Study species

The European nightjar is a breeding migrant to the UK and is a bird typically of dry heathland and woodland sites (Berry 1979; Cramp 1985; Bright *et al.*, 2007). Their cryptic camouflage and nocturnal foraging, along with their sporadic distribution, means that there is only limited information on their foraging behaviour and their habitat preferences (Wichmann 2004; Verstraeten *et al.*, 2011; Sharps *et al.*, 2015; Evens *et al.,* 2018). Nightjars display variable foraging behaviour but apparently specific habitat preferences. Birds will fly between 1km (Palmer, 2002) and 7km (Evens *et al.*, 2017a) from their nest sites to locate favourable or less competitive habitat. Recent radio- and GPS-tracking studies of nightjars in the UK, Belgium and Spain show that use of coniferous plantation including clearfell, as well as grazed grassland, heathland and birch woodland is common (Alexander and Cresswell 1989; Morris *et al.*, 1994; Camacho *et al.*, 2014; Sharps *et al.*, 2015; Evens *et al.*, 2017). Work by Camacho *et al.* (2014) and Evens *et al.* (2017, 2018) showed that nightjars used complementary ‘functional’ habitats for segregated breeding and foraging, and highlighted the importance of maintaining a mosaic of habitats in an appropriate configuration, in order to reduce the distance between these areas (Camacho *et al.*, 2014; Evens *et al.*, 2018). As the nightjar is a relatively range-limited species, detailed information on individual habitat selection and foraging movements are needed, to measure behavioural, and potentially functional, responses to planned habitat change.

3.2.2. Study aims

To identify variation within the population in habitat selection or movement patterns, particularly in relation to the cleared habitat that has been specifically created to encourage use by breeding nightjars, I analysed space use and habitat selection by individual nightjars over a four-year-period of landscape change. A substantial contribution of European Union LIFE+ funding was acquired in 2014 for the restoration of the Humberhead Peatlands NNR. The project aimed to increase wet bog habitat to improve peatland stablitiy and improve the diversity of peatland species. Concurrently, the funding aimed to increase the population of nightjar by 15%, by improving the open habitat available to them in which they could breed (Natural England, 2015). This was managed through mechanical and hand removal of birch woodland (Figure 3.1). The substantial compositional and structural change presented a potential conflict to the breeding nightjar population that should be investigated thoroughly through analysis of nightjar behaviour. I anticipated clear trends towards selection of “typical” nightjar habitats such as heather and woodland, across all years, by all birds within the population. I also predicted that a change in the availability of various habitat types with habitat management, would lead to a change in home range size and strength of habitat selection between years. Specifically, I hypothesised that a) home range size and b) habitat selection ratios, would increase over the four years of the study with a decrease in birch woodland and scrub, due to a decrease in invertebrate-rich foraging resources surrounding their nesting sites. I also hypothesised that regardless of year there would be a significant difference in c) home range size and d) distance travelled, but not habitat selection, between males and females, because of their different parental roles.

Figure 3.1: Example of mechanical birch scrub clearance work on Hatfield Moor that took place overwinter 2017 to 2018.

3.3. Materials and methods

3.3.1. GPS data collection

Data were collected at the Humberhead Peatlands NNR, South Yorkshire (see Chapter 1 for more details) during nightjar breeding seasons (June to August) in 2015 - 2018 (Hatfield Moor) and 2016 - 2018 (Thorne Moor). I attempted to collect data from both males and females over all stages of the breeding season (i.e. incubation, chick provisioning), during the four years (see Figure 1.12 in Chapter 1). GPS data were used to estimate home range size, movement and habitat selection. These data were collected via miniature, archival GPS tags (PathTrack, Otley, UK), = deployed on adult birds of both sexes and programmed to collect fixes every 3 minutes (2015 - 2016) or 5 minutes (2017 - 2018) from 21:00 – 05:00 and were accurate to +/- 30 metres (Pathtrack company information and my own stationary tests). In total, 45 tracking devices provided between 2 and 16 nights of data from 41 individual birds. One tracking device failed after two nights and one device was accidentally retrieved after three nights, so these were excluded from the analyses. Thus, data from 43 tags (n = 40 birds) were subsequently processed and analysed. The data were cleaned and transformed into trajectory format using packages adehabitatHR (Calenge, 2006) and maptools (Bivand and Lewin-Koh, 2013) to allow production of home range contour shapefiles and habitat selection metrics in R (v. 3.5.1.).

3.3.2. Habitat mapping

To estimate habitat availability and use within each bird's home range and how this changes between years, high-resolution Unmanned Aerial Vehicle (UAV) photography of both Thorne and Hatfield Moors was acquired in April 2016. This was translated into a high-resolution (5 x 5 metre) habitat map, which was sufficient for the purposes of identifying nightjar habitat selection, given the resolution of the GPS data. Classification of the habitat map combined unsupervised image classification in ArcMap (v. 10.4.1) and manual mapping of areas using a hand-held GPS unit. This allowed us to update the map annually before the breeding season, once new areas of scrub clearance had been completed. Thus, I could observe use and any change in use, in specific ages of cleared habitat from year to year (i.e. brand-new clearance, plus one year or plus two years of vegetation regrowth). Fourteen habitat categories were selected (Appendix IV) and an arbitrary value was attributed to all values outside of the

NNR boundary to represent ‘off site’ areas. These were comprised of a mixture of arable farming, industry and residential areas, including allotments and gardens.

3.3.3. Home range models

Movement-based Kernel Density Estimation (MKDE; Benhamou 2011) home ranges were created as spatial polygons in R (using package adehabitatHS, Calenge 2006) to estimate individual home ranges and therefore habitat availability and consequent use. The MKDE contrasts with other commonly-used methods (e.g., Minimum Convex Polygons (MCPs) and Kernel Density Estimators (KDE); Boyce *et al.,* 2002), by modelling occurrence data (Fleming *et al.,* 2017), and accounting for non-independence between points. The difficulty in defining the true habitat available to individuals, highlights the importance of the choice of estimator (Stark *et al.,* 2017; and see Chapter 2) and the importance of including movement behaviour (Martin *et al.,* 2008; Benhamou and Cornélis 2010; Van Moorter *et al.*, 2013). This better characterises the pattern of a ‘goal-oriented’ animal searching a landscape and produces a more representative picture of an animal’s movements, which can be viewed across the trajectory (Calenge *et al.,* 2009). As MKDEs place weight on the area between points rather than the points themselves, this allows distinct areas to be connected by regular use of common corridors, particularly relevant for birds that frequently commute to a feeding area, as nightjars have been shown to do (Camacho *et al.*, 2014; Evens *et al.*, 2017, 2018). Using the MKDE, tracking duration is influential in both home range and habitat selection calculation. Therefore, birds were compared and collectively analysed over a six-day period, in line with the minimum achieved by all tags in the dataset. This allowed the data to be standardised for reasonable comparison (see Chapter 2). MKDEs were created for each individual at both the 50% and 95% home range level, to try to address differences in the birds’ requirements. The core (50%) home range should more strongly reflect needs associated with nesting and the wider (95%) home range should more strongly reflect foraging needs.

3.3.4. Habitat selection

Home range-level habitat selection, also known as third-order selection (Johnson *et al.*, 2006) compares habitat availability with habitat used (designated by the GPS fix locations) within the boundaries of an individual’s home range. Habitat selection ratios (Manly *et al.* 2002) were created using adehabitatHS

(Calenge, 2011). These ratios provide a value that is proportional to the probability of use of an area or habitat type and represent a type of Resource Selection Function (RSF; Manly *et al.* 2002) more commonly used when there is only one dependent variable (here, it is one variable of habitat type, summarised in 14 categories). Manly's Selection Ratios consider several hypotheses; 1) that each resource is used in equal proportions; 2) they are used in proportion to availability and 3) that all animals use the habitat equally. A selection ratio with a value > 1 denotes use of a habitat away from random (i.e. the habitat is being selected for), whereas a value < 1 represents habitat avoidance. Larger values suggest higher selection strength and significant selection for or against across the population of tracked individuals can be identified when 95% confidence intervals do not overlap one.

3.3.5. Changes in home range size and habitat selection ratios

To test for differences in habitat selection ratios among years and to identify if there was significant individual variation, I ran a set of linear mixed models for each of the 10 most commonly used habitats for which I had a robust selection ratio value. Selection ratio acted as the dependent variable, with year (a factor) and also home range size as fixed effects. Individual ID was included as random effects.

To understand the functional relationships between nightjars, habitat types and resulting movement distances, habitats were pooled into 'higher-level' categories comprising woodland, open & dry (heather and bracken), cleared (previously temporally-defined clearance categories pooled into one; see *Habitat mapping* subsection), wetland (cottongrass and wetland) and water (open water, lakes).The effect of availability of different habitat types, year and week of the breeding season on home range size at both the 50 and 95% levels, were tested for using linear mixed models in R (similarly to Ofstad, 2019). All mixed models were run using single term deletions and AIC comparison in package lme4 (Bates *et al.*, 2015) and MuMin (Barton, 2015), with residual analysis for goodness-of-fit in DHARMa (Hartig, 2016). Due to the extremely large home ranges of some of the birds, the data for the 95% home ranges was strongly right-skewed. As a result, the data were log transformed, which reduced the skew to a level that was interpretable, but still heteroskedastic, which must be taken into account. Lastly to understand the relationship between home range size and overall habitat heterogeneity, I calculated patch richness density using package ‘landscapemetrics’ in R (McGarigal, Cushman and Ene, 2012). Patch richness density is a relative diversity measure that assesses the number of different habitat classes and their size compared to the total area of land within the home range of individual birds (McGarigal, Cushman and Ene, 2012). I anticipated that home ranges would increase in areas with less patch richness density, i.e. larger home ranges in areas with swathes of continous single-class habitat.

3.4. Results

3.4.1. Habitat Selection

Median selection ratios for the nightjar population across four years of study varied widely and indicated strong individual differences within the population (Figure 3.2), with no single habitat type used by the whole population. Multiple birds used heather, bracken and woodland, as well as newly cleared habitat (see Appendix IV for home ranges of all birds in years 2016- 2018). Median habitat selection values for these four habitat types were close to 1 in more than one breeding season, although the range of values was still wide (Figure 3.2). In particular there were consistent strong selection behaviours by several individuals for wet, cottongrass-dominated habitat, which directly contrasted strong avoidance by others. There was more consistency in the habitat types avoided; grass- and cottongrass-dominated areas were significantly avoided within the 50% home range and open water was significantly avoided at both home range levels. Selection strength differed between core (50%) and wider (95%) home range; habitats were used in line with availability within the core home range, whereas there was stronger selection (ratio values far away from 1) within the wider home range. Heather and all cleared habitat regardless of year cleared, had significantly higher selection ratios in the 95% home range, compared to the 50% home range (Figure 3.2, Table 3.1).

Change in selection ratios over time was only significant in all years for scrub, which decreased between 62 - 67% from 2015 in a non-linear manner (Table 3.1). Selection ratios for new and two-year old clearance were significantly higher in 2017 compared to 2015. For all other habitat types, no significant change in selection was detected. Related to this, birch woodland removal produced substantial changes in landscape composition and configuration, influencing the availability of woodland and cleared habitat within nightjar home ranges over time. Woodland became significantly less available within nightjar home ranges (regardless of home range level) in 2017 by 21% (95% CI: 8.4 – 33.5%) and in 2018 by 17% (95% CI: 4.6 – 29.6%) compared to 2015. In contrast, cleared habitat became significantly more available, by between 400 and 900%, from 2015 all other years (Appendix IV).

Table 4.1: Coefficients and 95% profile-computed confidence intervals from mixed linear models exploring individual variation in and change in selection ratio by year and according to home range level, within nightjar home ranges. Significant results (where 95% confidence intervals do not overlap 1) are in bold.

	Scrub		**Woodland**		**Heather**		**Bare peat**		**Clearance +1**	
Parameter	***β***	**(95% CI)**	***β***	**(95% CI)**	***β***	**(95% CI)**	***β***	**(95% CI)**	***β***	**(95% CI)**
Intercept	1.41	(0.86 - 1.96)	0.68	(0.41 - 0.94)	0.46	(0.10 - 0.82)	0.59	(-0.01 - 1.19)	-0.07	(-0.64 - 0.5)
Year 2016	**-1.12**	**(-1.75 - -0.50)**	-0.16	(-0.46 - 0.16)	0.14	(-0.25 - 0.61)	-0.31	(-0.97 - 0.36)	-0.07	(-0.72 - 0.56)
2017	**-0.97**	**(-1.67 - -0.26)**	-0.29	(-0.63 - 0.05)	0.27	(-0.19 - 0.73)	0.44	(-0.33 - 1.21)	0.12	(-0.61 - 0.85)
2018	**-1.01**	**(-1.62 - -0.39)**	-0.18	(-0.5 - 0.11)	-0.01	(-0.45 - 0.38)	-0.17	(-0.83 - 0.49)	0.48	(-0.15 - 1.11)
Home range level 95	0.13	(-0.02 - 0.29)	0.02	(-0.07 - 0.12)	**0.13**	**(0.04 - 0.23)**	0.01	(-0.09 - 0.12)	**0.13**	**(0.00 - 0.27)**
Individual variation	0.25	(0.37 - 0.67)	0.05	(0.14 - 0.32)	0.1	(0.21 - 0.47)	0.33	(0.45 - 0.76)	0.28	(0.41 - 0.7)
Residual variation	0.09	(0.24 - 0.39)	0.04	(0.15 - 0.25)	0.04	(0.14 - 0.26)	0.04	(0.16 - 0.26)	0.07	(0.21 - 0.34)

	Wetland		**Bracken**		**Cottongrass**		**Clearance**		**Clearance + 2**	
Parameter	***β***	**(95% CI)**	***β***	**(95% CI)**	***β***	**(95% CI)**	***β***	**(95% CI)**	***β***	**(95% CI)**
Intercept	0.4	(-0.02 - 0.82)	0.54	(0.05 - 1.02)	-0.05	(-0.34 - 0.24)	-0.08	(-0.52 - 0.36)	-0.09	(-0.54 - 0.36)
Year 2016	-0.11	(-0.59 - 0.36)	0.23	(-0.32 - 0.78)	0.1	(-0.23 - 0.43)	0.4	(-0.11 - 0.9)	0.4	(-0.11 - 0.91)
2017	-0.22	(-0.76 - 0.32)	-0.3	(-0.92 - 0.32)	-4.40E-17	(-0.37 - 0.37)	**0.75**	**(0.18 -1.31)**	**0.59**	**(0.08 - 1.08)**
2018	0.03	(-0.43 - 0.5)	-0.19	(-0.73 - 0.35)	0.37	(-0.02 - 0.74)	0.14	(-0.35 - 0.64)	0.24	(-0.25 - 0.74)
Home range level 95	0.03	(-0.07 - 0.12)	0.15	(-0.01 - 0.31)	0.1	(-0.01 - 0.22)	**0.19**	**(0.05 - 0.33)**	**0.21**	**(0.1 - 0.32)**
Individual variation	0.15	(0.29 - 0.53)	0.18	(0.3 - 0.58)	0.06	(0.18 - 0.36)	0.15	(0.27 - 0.53)	0.16	(0.3 - 0.54)
Residual variation	0.04	(0.15 - 0.25)	0.1	(0.25 - 0.41)	0.03	(0.15 - 0.25)	0.08	(0.22 - 0.37)	0.06	(0.21 - 0.32)

Although among-individual variation was high, three birds tracked during two separate breeding seasons displayed remarkably consistent habitat selection between years. Individuals' home ranges overlapped between 61 – 78%, showing very high site-fidelity (Figure 3.3). There was no significant difference seen between the selection ratios of two of the three birds (Linear regression, nj1; $F_{1,46}$: 0.008, p = 0.93; nj2; $F_{1,46}$: 0.15, p = 0.70). This demonstrates that use of habitats was similar, even when availability changed, which for nj1 it did, significantly from 2016 to 2017, resulting in 13% more cleared habitat within the bird's home range. For nj3, a significant change in selection between years was identified ($F_{1,46}$: 5.44, p = 0.02), despite the fact that in the second recorded year, the overlapped the previous year by 100% (Figure 3.3). Specifically, an increase in the use of woodland of 10% and a decrease in use of bracken-dominated habitat by 1% was enough to produce a significant change in selection ratio, given the availability of these habitat types.

3.4.2. Functional responses to habitat availability

Across the population, nightjars showed functional responses to habitat availability at both home range levels (Table 3.2). In contrast to the habitat selection ratios, there was no significant influence of individual in the functional responses (Individual variation values did not deviate from zero). Core home range size decreased by <1% when available cleared habitat increased by 1% and by 1% when dry, open habitat increased by 1%. Wider home range size increased by 9% with an increase of 1% open water (Figure 3.4, Table 3.2). Home range size was not significantly influenced by year nor week of the breeding season, but they were retained in the model to control for variation amongst these groups and greatly improved the fit of the residuals. Mean distance travelled per night was also impacted by habitat type, but less so than home range size; none of the multiple model-averaged terms were significant (95% confidence intervals always overlapped 1). Water was the most important factor, contributing to all four of the averaged models; nightjars flew longer distances per night when the availability of open water was higher in the 95% home range (Table 3.3).

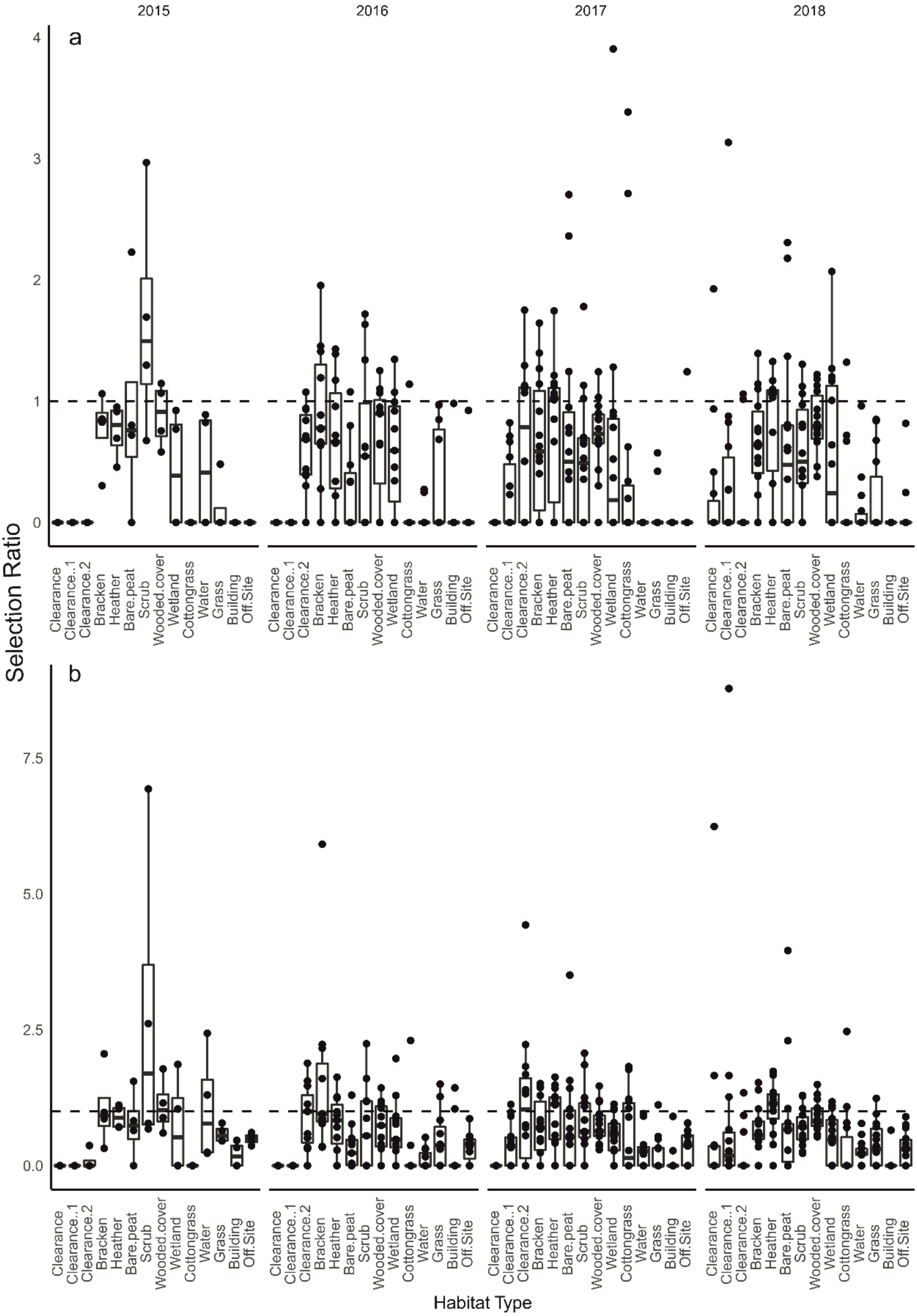


Figure 3.2: Median habitat selection ratios for individual nightjars (n =45) within a): 50% home range on Hatfield and Thorne Moors 2015-2018, and b): 95% home range on Hatfield and Thorne Moor 2015 – 2018. Data plotted on a square root scale for visibility. Boxes represent Inter-Quartile Ranges and whiskers extend to 1.5 x IQR. Black dashed line at 1 represents line of selection (above = selected for; below = avoided).

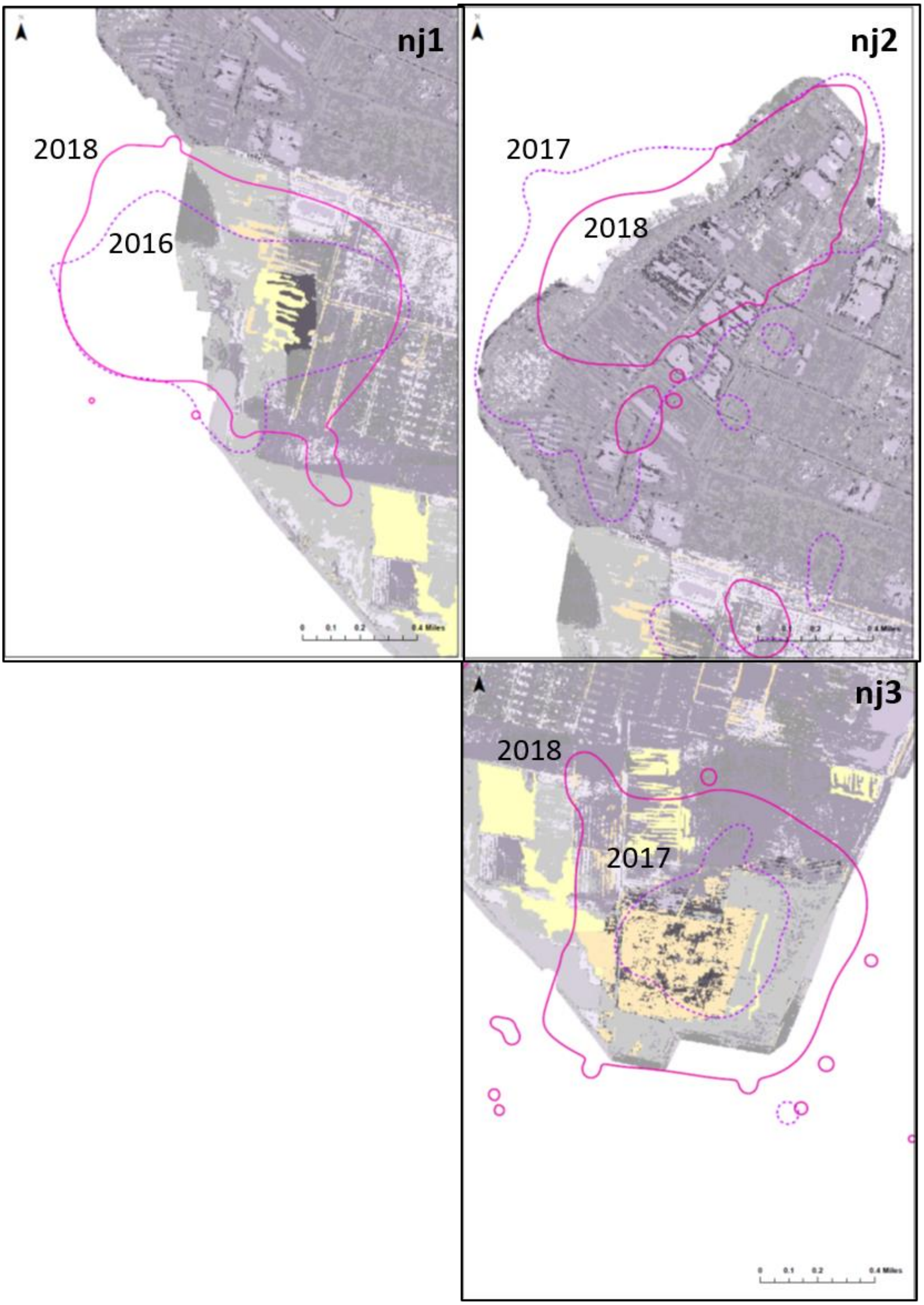


Figure 3.3: Home ranges of the three birds for which two years of tracking data were gained, displaying high levels of overlap between years. Dotted purple lines represent the first year of tracking (2016/2017) and dark pink lines represent the second year of tracking (2018).

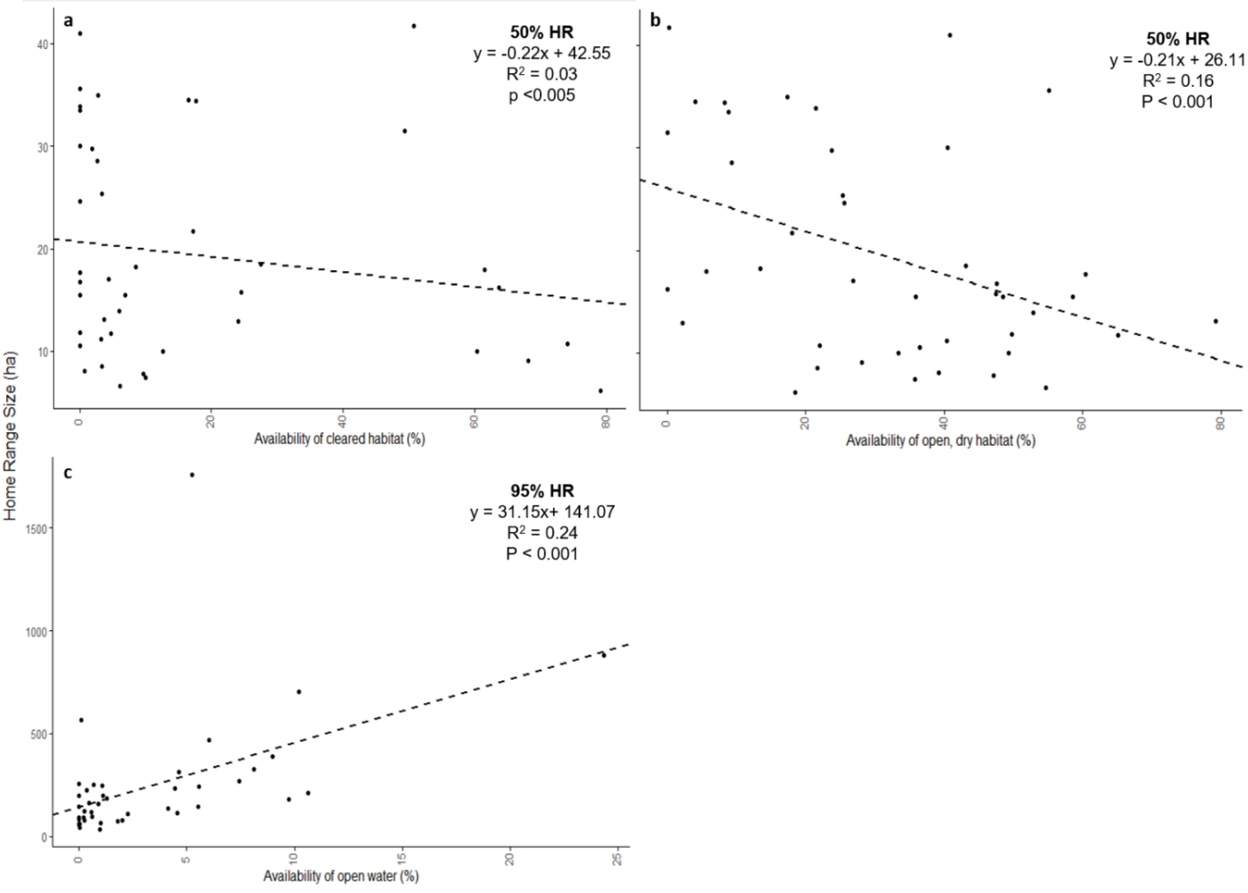


Figure 3.4: Linear relationship between a) 50% home range size (hectares) and availability of open, dry habitat (%); b) 50% home range size (hectares) and availability of cleared habitat (%); c): 95% home range size (hectares) and availability of open water (%).

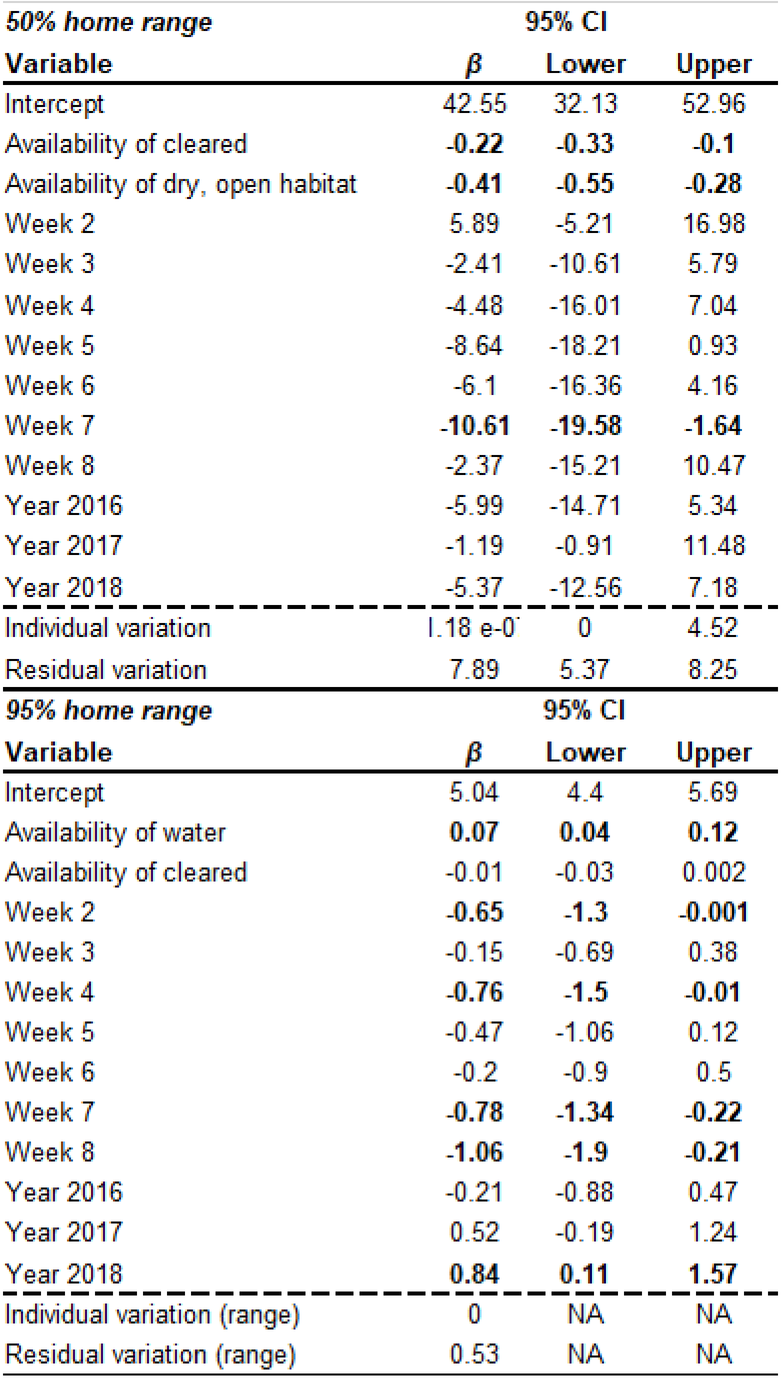
3.4.3. Movement and habitat selection between sexes

Nightly distances travelled differed significantly between the sexes; male nightjars travelled significantly further than females (t-test; t = -4.89, df = 199, p = 2.12e-06). However, this did not translate to a difference in size between male and female home ranges at either the core (50%) or wider (95%) home range (t-test; 50%: t = 0.42, df = 25, P= 0.68; 95%: t = 0.66, df = 30, p = 0.51).

3.4.4. Habitat heterogeneity

Habitat heterogeneity varied between individuals, ranging from 3 patches of different classes of habitat per 100 hectares, to 42 per 100 hectares. Home ranges tended to be smaller where habitats were more diverse and heterogeneous, which varied between years ($F_{4,26}$: 4.37, p: 0.008; Figure 3.5).

Table 3.2: Coefficients and 95% Confidence Intervals from the linear mixed models (lowest AIC value) used to test for functional responses in 50 and 95% nightjar home range size to habitat availability and over time. Coefficients and confidence intervals for models of functional responses in the 95% home range are model-averaged estimates for all models within Δ 2 of top model. Random effects are below the dotted line (Individual, week of the breeding season and residual). Random effects of averaged models are reported as a range of values. Significant results are highlighted in bold.



50% home range		**95% CI**	
Variable	***β***	**Lower**	**Upper**
Intercept	42.55	32.13	52.96
Availability of cleared	**-0.22**	**-0.33**	**-0.1**
Availability of dry, open habitat	**-0.41**	**-0.55**	**-0.28**
Week 2	5.89	-5.21	16.98
Week 3	-2.41	-10.61	5.79
Week 4	-4.48	-16.01	7.04
Week 5	-8.64	-18.21	0.93
Week 6	-6.1	-16.36	4.16
Week 7	**-10.61**	**-19.58**	**-1.64**
Week 8	-2.37	-15.21	10.47
Year 2016	-5.99	-14.71	5.34
Year 2017	-1.19	-0.91	11.48
Year 2018	-5.37	-12.56	7.18
Individual variation	1.18 e-0	0	4.52
Residual variation	7.89	5.37	8.25

95% home range		**95% CI**	
Variable	***β***	**Lower**	**Upper**
Intercept	5.04	4.4	5.69
Availability of water	**0.07**	**0.04**	**0.12**
Availability of cleared	-0.01	-0.03	0.002
Week 2	**-0.65**	**-1.3**	**-0.001**
Week 3	-0.15	-0.69	0.38
Week 4	**-0.76**	**-1.5**	**-0.01**
Week 5	-0.47	-1.06	0.12
Week 6	-0.2	-0.9	0.5
Week 7	**-0.78**	**-1.34**	**-0.22**
Week 8	**-1.06**	**-1.9**	**-0.21**
Year 2016	-0.21	-0.88	0.47
Year 2017	0.52	-0.19	1.24
Year 2018	**0.84**	**0.11**	**1.57**
Individual variation (range)	0	NA	NA
Residual variation (range)	0.53	NA	NA

As home ranges increased, birds became more selective with higher selection ratios in larger home ranges (F1,29: 6.45, p: 0.02; Figure 3.5) although this relationship was weaker than that of home range and habitat heterogeneity, skewed slightly by some more extreme values.

Table 3.3: Coefficients and 95% confidence intervals from the top two averaged linear models (Δ < 3), to test for functional responses in mean distance travelled (metres) to woodland and cleared habitat availability. * = 95% confidence intervals do not overlap zero.

		95% CI	
Variable	***β***	**Lower**	**Upper**
Intercept	3.968	3.772	4.164
Availability of water	0.01	-0.001	0.021
Availability of cleared	-0.001	-0.007	0.003
Availability of open, dry	0.002	-0.001	0.005
Availability of woodland	-0.001	-0.005	0.003
Availability of wetland	0.001	-0.002	0.006
Individual variation (range)		(0.000 - 0.000)	
Residual variation (range)		(0.022 - 0.023)	

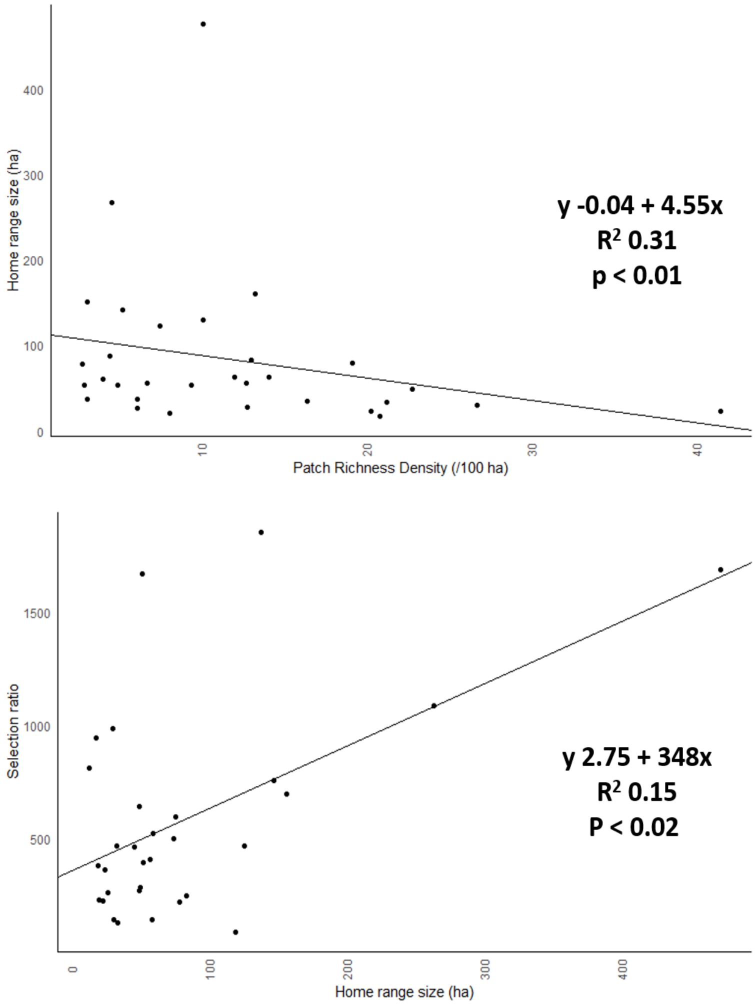


Figure 3.5: Relationships between (top): home range and habitat heterogeneity as measured by patch richness density (patches of different habitat types per 100ha) and (bottom): selection ratio.

3.5. Discussion

3.5.1. Habitat selection

In line with previous studies, more nightjars selected for drier habitats (Alexander and Cresswell 1989; Jenks *et al.*, 2014; Sharps *et al.*, 2015), when using the population mean. However, the birds in this population displayed high individual variability in selection for both dry and wetland-dominated habitat, which was contrary to my expectations. Use of unexpected habitats was also found by Evens *et al.*, (2017), demonstrating this species' ability to be flexible according to the distribution of food resources (which may not be habitat-specific) or potentially accessibility (Sharps *et al.*, 2015). Variation between individuals implies that the population as a whole is generalist, able to exploit multiple habitat types through differential habitat selection (Kotler and Brown, 1988).

Over the period of habitat change from 2015 to 2016/2017, cleared habitat increased in availability and nightjars present in these manipulated areas selected for this habitat type intensely. However, this did not occur within the majority of the population. Preference for open areas that have been provided by new clearance work has been reported previously (Wichmann 2004; Verstraeten *et al.*, 2011; Sharps *et al.*, 2015). These areas provide desirable nesting habitat as well as good foraging habitat, and this multi-functionality potentially explains strong use by many individual birds in this study. Against expectations, selection for woodland did not increase over time, despite the decrease in its availability within home ranges. This perhaps implies there is a threshold amount of woodland needed within their home range (Angelstam *et al.*, 2003; Zielewska-Büttner *et al.*, 2018), which is met by most of the individuals here.

In comparing birds across breeding seasons, I have shown intra-individual consistency in both home range placement and habitat selection. The population appears variable and generalist, but these individuals appear consistent and therefore specialist, which potentially indicates that this is a population with a broad niche, consisting of individuals with narrow habitat niches (Wilson and Yoshimura, 1994). It also highlights the presence of strong site-fidelity, which in contrast to specific habitat-type fidelity, has been shown to influence reproductive success (Patrick and Weimerskirch, 2017). With the exception of one of the individuals, the habitat selection ratios do not change between years, despite significant habitat change within the home range of one of the birds, which suggests that site or territory fidelity regardless of habitat type, is more important. Despite this being based only on three birds, I believe this is a good example of within-individual consistency alongside strong between-individual variation (R. A. Phillips *et al.*, 2017) that is common in site-faithful long distance foraging birds, particularly where individuals have been successful in breeding in previous seasons (Wakefield *et al.*, 2015).

3.5.2. Functional responses in home range size and travelling distance

Functional responses were apparent for the whole population. The absence of individual variation in functional responses in home range size and travelling distance contradicts the significant individuality present in the habitat selection analysis. This suggests that although individual preferences for certain habitat types exist, there are foraging-related constraints that ultimately determine the utility of an area, which should be taken into account when managing for this species. Contrary to my hypotheses, the more cleared habitat available, the smaller the home range. Habitat management can result in direct habitat loss, but clear-felling areas can also create ‘novel’ areas of habitat that attract animals (Hodson, Fortin and Bélanger, 2010) by changing both structure and food resources. That the relationship was stronger within the core home range, suggests that newly cleared areas were able to provide both appropriate nesting and foraging habitat, implying multi-functional value of these areas. In contrast, the increase in home range size and distance travelled per night with an increase in the amount of open water present indicates a lack of suitability of these areas for foraging. This is presumably related to both the abundance of prey and the specific taxa present that are more likely to be chironomids and diptera that are more commonly preyed upon by bats (Rydell *et al.*, 1996).

Presence of woodland habitat, again contrary to my expectations, was not significantly influential for home range size. Birch woodland has a high invertebrate diversity (Webb, Clarke and Nicholas, 1984), particularly of beetles and moths, preferred by nightjars (Sharps, 2013), meaning the birds should not have to travel as far to find substantial foraging resources. That there was no apparent substantial functional relationship between nightjar home range and woodland habitat availability, supports my earlier statement related to habitat threshold amounts and potentially points to other influences such as density dependence and conspecific interactions that I have not included here, due to a lack of information.

3.5.3. Movement and habitat selection between sexes

Whilst the overall distance travelled per night by females was significantly shorter than males, female home ranges were not significantly smaller. This may relate both to the need for the female to undertake rapid, efficient foraging because of incubation responsibility, but also the ranging, territorial defence behaviour of the male (Sharps *et al.*, 2015). My data showed that females still made relatively long-distance foraging trips, but that these were made less frequently and were very direct. Therefore, although total distance travelled was much less, their area of interest was the same size.

3.5.4. Habitat heterogeneity influences

That home ranges decreased in size with more heterogeneous environments suggests that higher heterogeneity in habitat type, and presumably structure, is beneficial for species diversity (as highlighted by Cramer and Willig, 2002). If more diverse habitat types and structures are beneficial for nightjar prey, and allow generalist and specialist foraging nightjars to coexist, this reduces the need to forage further afield (Wilson and Yoshimura, 1994). Birds with larger home ranges were apparently more specialist, with higher selection ratios in larger home ranges. This indicates that although they are covering a wider area during their foraging, they actually only use specific areas within this, rather than using what is available as more generalist birds would do, resulting in smaller home ranges.

3.6. Conclusions

This chapter provides evidence of the need to include individual-level information on habitat selection along with population-scale functional responses (Leclerc *et al.*. 2016) to fully appreciate the use of a site and its resources by a population. Using the mean alone to understand resource requirements is not always sufficient to represent the range of individual variation present in a population. I have tracked over 40 individuals during a period of landscape change to explore patterns of habitat selection across the population, as well as functional responses that might present evidence of trade-offs between habitat use and foraging needs. Although mean habitat selection values supported previously gathered information, habitat preferences varied significantly at the individual level, which contributed to apparent population generalism. Analysing behavioural responses to landscape change through movement and home range, provided evidence of both broader functional responses across a population and individual habitat relationships, important for flexibility of the population in the context of future habitat and climate change.

Chapter 4: The environmental factors driving nightjar foraging behaviour and the relationship with prey availability and accessibility.

4.1 Abstract

Efficient foraging movements enable animals to acquire maximum energy gain for minimum energy expenditure. Identifying environmental correlates of foraging behaviour can help to understand the drivers of animal foraging decisions and the potential fitness consequences should conditions change. Here I investigate the direct and indirect environmental factors that influence European nightjar (*Caprimulgus europaeus*) foraging, how they allocate their time and whether these decisions might be influenced by habitat change.

I analysed nocturnal activity of the European nightjar, using Hidden Markov models. Nightjar movement patterns, including changes in movement behaviours, were driven by vegetation structure, including NDVI, and the lunar cycle, with a weak additional effect of temperature. Birds foraged for a decreased proportion of time when the moon at its brightest (>90% full), indicating a trade-off between prey availability, predation risk and visibility that may reflect reduced effort. All behaviours differed significantly between sexes.

Male nightjars foraged for more time (33%) than females (19%), reflecting differences in the biological roles of males and females, although this varied during the course of the breeding season (variation of week of the breeding season 0.76 (95% CI: 0 – 1.65). Foraging time increased when more cleared habitat was available within nightjar home ranges, potentially reflecting reduced effort or increased competition by conspecifics that may infer higher habitat quality and therefore a need for managers to maintain sufficient areas of these habitat types.

4.2 Introduction

4.2.1. Foraging behaviour

Optimal foraging theory focuses on the need for animals to maximise the rate of energy intake by foraging under profitable conditions in the most profitable places (Kamil and Roitblat, 1985). However, animals are constrained in their foraging by morphological and behavioural traits, which can be inherited or alternatively, shaped by the environment in which they live now or in which they developed (Fawcett, Marshall and Higginson, 2015; Toscano *et al.*, 2016). Physiology, including factors such as wing morphology (Cooke *et al.,* 2014) and sensory mechanisms such as vision and echolocation (Brigham and Barclay, 1995), as well as diet (Morse, 2003), can constrain an animal to foraging in certain locations or during limited time periods. Environmental factors such as the proximity of nesting and foraging habitats (including sufficient prey resources; Evens *et al.,* 2018), predation risk (Portugal *et al.,* 2019) and disturbance (Lowe *et al.,* 2014; Lesmerises *et al.,* 2018), will also impact where and when animals choose to forage. To identify the most profitable foraging locations on a more localised scale, animals use cues that relate to prey aggregations such as bathymetry (Wells, Angel and Arnould, 2016) or specific types of vegetation (Ciechanowski *et al.*, 2008; Downs *et al.*, 2016b), collectively termed local enhancement (Wells, Angel and Arnould, 2016). Insectivorous species are particularly constrained by high spatially- and temporally- stochastic prey sources (Cucco and Malacarne, 1996). As such, these species have developed rapid behavioural responses to short term fluctuations in prey abundance in order to maximise opportunity (Macarthur and Pianka, 1966) and efficiency (Andersson, 1981). These rapid responses take the form of behavioural trade-offs to mitigate constraints, and might include travelling further to access more profitable prey (Paiva *et al.,* 2010; Masse *et al.,* 2013) or altering diet to incorporate more numerous but less nutritious prey, when preferred prey are low (Imber, 1975; Pyke, Pulliam and Charnov, 1977). For example, the Spotted flycatcher (*Muscicapa striata*) alters its foraging mode from an energy-efficient sit-and-wait strategy when prey are plentiful, to more costly active foraging when the temperature drops and prey are less numerous (Davies, 1977). Whinchats (*Saxicola rubetra*) preferentially foraged in habitat that provides the ‘cheapest’ movement, i.e. the lowest resistance, but rapidly expanded their home range to include less preferable and less efficiently navigated foraging areas, when prey decrease (Andersson, 1981).

Compensatory behaviour in response to short term environmental fluctuation has also been measured in seabirds, many of which will adjust trip duration according to the distribution of prey resources or weather conditions, in order to maintain consistent foraging quality (Mullers *et al.*, 2009; Gulka and Davoren, 2019). Broader seasonal or cyclical cues, such as the tide and the moon (Rubolini *et al.,* 2015), may also influence behaviour by changing predation threat (Lang *et al.,* 2006; Prugh and Golden, 2014), or by increasing foraging efficiency through reduced competition or increased opportunity (Imber 1975; Roeleke *et al.*, 2018; Trevail *et al.*, 2019).

Animals already constrained to limited foraging circumstances due to evolved adaptations, such as nocturnal or insectivorous animals, may be strongly influenced by changes in environmental conditions (English, Nocera and Green, 2018; Both *et al.*, 2010), as such species have limited opportunity to adjust their use of space or the timing of their foraging (Aldridge and Brigham, 2008; Roeleke *et al.*, 2018). They may therefore employ foraging strategies that allow them to capitalise on periods of profitable conditions (Schifferli *et al.*, 2014; ‘reduced effort hypothesis’). However, some changes in the environment such as habitat loss, might push animals to forage up to and potentially beyond their physiological limits, provoking adverse fitness effects (Boyd *et al.*, 2014; Franci *et al.*, 2015b). For example, Stanton *et al.* (2017) found that Purple martins (*Tachycineta bicolor*), constrained to a short breeding season by migration and transient prey, possessed higher oxidative stress levels following increased foraging trips where agricultural intensity increased. Elevated stress levels were directly related to decreased insect biomass and in combination, these two elements led to a reduced return rate of individuals to the area to breed, thus demonstrating the demographic impacts of forced foraging behaviour change.

Climate and landscape change risk disrupting the predictability of the more fine-scale temporal fluctuations in environmental conditions (Kamil, 1985), including cues that indicate prey abundance and therefore profitable foraging areas (Pirotta *et al.*, 2018). To this end, it is important to understand which factors, such as spatial and temporal environmental heterogeneity, most strongly correlate with foraging behaviour (Franke, Caelli and Hudson, 2004; Boyd *et al.*, 2014; Bennison *et al.*, 2017; Pirotta *et al.*, 2018).

4.2.2. Nocturnal foraging adaptations

Although there are some formulated hypotheses about nocturnal movements (Saldaña-Vázquez and Munguía-Rosas, 2013; Rubolini *et al.*, 2015; Roeleke *et al.*, 2018), overall there is limited information on the foraging behaviour and habitat use of many nocturnal species, as these animals are often secretive and difficult to observe (Nichols and Alexander, 2018; Karelus *et al.*, 2019). For species that are visual predators, increased visibility with increased moonlight (the ‘visual-acuity’ or ‘foraging-efficiency’ hypothesis; Imber, 1975; Rubolini *et al.*, 2015), can elevate foraging levels on lighter nights and is described as ‘lunarphilic’ behaviour. Rubolini *et al.* (2015) described an increased number of dives and an extended foraging period on moonlit nights by Scopoli’s shearwater (*Calonectris diomedea*), as a response to increased pelagic prey presence at the sea surface.

Conversely, many bat species adjust their movements to avoid stronger moonlight, behaviour which is thought to be associated with higher predation risk. Thus, they become ‘lunarphobic’, although this varies significantly among species (Appel *et al.*, 2017; Roeleke *et al.*, 2018; Musila *et al.*, 2019). Roeleke *et al.* (2018) found that noctule bats (*Nyctalus noctula*) decreased their flight altitude when moonlight was most intense. Gannon and Willig (2006), Elangovan and Marimuthu (2001) and Reith (1982) also all found decreased foraging activity in bats with increased light levels. A non-exclusive alternative is that some nocturnal invertebrates are less active during the full moon, than during the new moon (Lang *et al.,* 2006), although this varies between habitats, species, with weather conditions and geographical location (McGeachie, 1989; Rydell *et al.,* 1996; Jetz *et al.,* 2003). Nocturnal foragers therefore face a number of constraints and trade-offs that will determine foraging behaviour on any given night.

4.2.3 Nightjar foraging behaviour

The Caprimulgids – nightjars - are a nocturnal group of insectivorous birds described by multiple studies as being ‘lunarphilic’ (Mills, 1986; Pople, 2003; English *et al.*, 2016). Strong synchronisation with the moon has been described in studies of breeding nightjars where several species lay their eggs in time for the eggs to hatch during the full moon to increase foraging opportunities (Brigham and Barclay, 1992; Perrins and Crick, 2019; English, Nocera and Green, 2018). Increased displaying and foraging with elevated lunar illuminance has also been reported by Mills (1986) and Woods and Brigham (2008), in the male Common poorwill (*Phalaenoptilus nuttallii*). More generally, nightjar foraging is concentrated at dusk and dawn, thought to be due to increased moth activity levels (Mills, 1986; Cleere and Nurney, 1998; Jetz, Steffen and Linsenmair, 2003; Reino *et al.*, 2015). It is clear that the relationship between lunar illuminance and foraging is complex (Brigham & Barclay, 1992; Brigham *et al.,* 1999). As nightjars predate the same prey as bats (mainly Lepidoptera and Coleoptera), some of the ecological constraints to nightjar foraging are expected to be similar, although clearly the primary mechanism by which bats capture their prey, and the threat of predation, is significantly different (Rydell *et al.,* 1996). Although nightjars will also be subject to predation, this is less likely to be during foraging as their main predators are thought to be mammalian (foxes, badgers), and they are therefore more likely to be predated whilst resting on the ground (Sharps *et al.,* 2015). Nightjars should increase foraging activity to coincide with the highest levels of moth activity (English, Nocera and Green, 2018). This may therefore require the birds to make a trade-off between this higher insect availability and more efficient conditions for foraging, where better visibility on lighter nights will be counteracted by lower activity levels of moths (Jetz, Steffen and Linsenmair, 2003; Woods and Brigham, 2008; Evens, Beenaerts, *et al.*, 2017b).

The European nightjar (*Caprimulgus europaeus)* is a migratory insectivore that previous studies have identified as dependent on a high biomass of flying insects (English *et al.*, 2016; Sharps *et al.*, 2015; Henderson, Hunter and Conway, 2018; Evens *et al.*, 2017), in close proximity to sufficient suitable nesting habitat, to reduce physiological stress whilst provisioning young (Evens *et al.*, 2018). Nightjars mostly inhabit heathlands and woodland mosaics (Bright *et al.*, 2007; Sharps, 2013; Verstraeten, Baeten and Verheyen, 2011; Sierro *et al.*, 2001) and this habitat selection, coupled with a dependence on moths, a declining group, make it vulnerable to changes in land use and climate (Eaton, Aebischer, Brown, Hearn, *et al.*, 2015). There is little information on precise nightjar foraging patterns (Palmer and England, 2002; Jackson, 2003; Jenks, Green and Cross, 2014; Evens *et al.*, 2017) because of their cryptic nature. There is even less information on how foraging in response to weather and other environmental conditions, such as habitat, might interact with a cyclical recurrence such the lunar cycle, which would provide an insight into foraging trade-offs they might be making.

Given the decline in invertebrate populations worldwide (Vogel, 2017; Powney *et al.*, 2019), in conjunction with habitat loss (IPBES, 2019), it is important to know what drives nightjar foraging behaviour in response to changing conditions (English, Nocera and Green, 2018; English *et al.*, 2016). In the UK, nightjars are vulnerable (Eaton *et al.* 2015), due to habitat loss, prey decline and threats encountered on migration (Vickery *et al.*, 2014; Nebel *et al.* 2010). As a predator of unpredictable, ephemeral prey, nightjars may allocate more time to foraging in more productive habitats or under more productive conditions, to reduce foraging effort and compensate for poor conditions that might occur in the future (Godfrey and Bryant, 2000; Schifferli *et al.* 2014). If nightjars spend longer foraging in poor conditions, this might negatively impact their breeding success or survival; Bryant and Westerterp (1983) found that poor weather conditions leading to a lack of prey for House martins (*Delichon urbica*), directed this species to use an energy-minimizing strategy whereby they reduced foraging time in these poor conditions and compensated when conditions were good and stores of fat could be developed. Gathering information on which conditions influence behavioural change, such as increased or decreased foraging time, can allow us to identify conservation management options, such development of specific vegetation types and structures to provide good quality foraging resources.

4.2.4 Modelling foraging behaviour

Movement ecology is a growing area and one of the more popular, accessible and applicable methods to the large amount of GPS data now being produced, is the Hidden Markov Model (HMM; Langrock *et al.*, 2012; Michelot, Langrock and Patterson, 2016; Patterson *et al.*, 2017). The models run on the assumption of inferred, unobserved behavioural states, alongside observed GPS fixes (Langrock *et al.*, 2012). States should represent reasonable approximations of different animal behaviour, based on the structural components of the tracks (step length, turning angle; Langrock *et al.*, 2012; Michelot,Langrock and Patterson, 2016). Most commonly these are resting, foraging or searching, and commuting or navigation (Joo *et al.*, 2013), but essentially any number of states can be inferred, as long as the result is biologically interpretable (Pohle *et al.*, 2017; McKellar *et al.*, 2015). Multiple studies have reported the use of HMMs with tracking data and have highlighted their ease of use and ability to accurately quantify movement and feeding behaviour of a variety of species (Joo *et al.*, 2013; Bennison *et al.*, 2018; Ngˆ, 2018; Zhang *et al.*, 2019). Using HMMs, Trevail *et al.* (2019a) found that kittiwake (*Rissa tridactyla*) responses to the tidal cycle were enhanced by other environmental heterogeneity, whilst Towner *et al.* (2016) identified previously unknown foraging modes that differed between adult white sharks (*Carcharhodon carcharias*). As demonstrated in these studies, extensive movement data can be directly linked to environmental correlates and can provide new, readily-interpretable information about use of resources (Whoriskey *et al.*, 2017).

4.2.5. Study aims

I aimed to identify the drivers of nightjar movement behaviour, in the context of habitat change, over a period of four years. As nocturnally constrained visual predators, I hypothesised that the most significant factors influencing nightjar movement would be those influencing foraging visibility and accessibility, as well as availability of prey resources. Broadly, nightjars appear constrained by light levels, as a more illuminated moon creates better visual conditions for the birds in line with the ‘foraging efficiency’ or ‘reduced effort’ hypothesis (Schifferli et al 2014), so I expected the intensity of the moon related to its phase would significantly influence the division of behaviours over time. However, as they prey primarily on moths, which are reported to be averse to the full moon and as nightjars can potentially succumb to predation themselves, I expected a reduction in foraging during the brightest stages of the lunar cycle (English, Nocera and Green, 2018), representing a trade-off between the reduced effort and predation risk hypotheses (Imber, 1975).

Habitat type is known to affect nightjar distribution, as good quality habitat not only provides nest sites (Camacho, 2014; Troscianko *et al.*, 2016), but also prey resources (English *et al.*, 2016). Previous studies have highlighted that nightjars struggle to forage in heavily vegetated areas despite high moth densities in these locations (Sharps *et al.*, 2015). Therefore, secondly, I expected more foraging to occur in semi-open areas of habitat, where prey resources are more accessible, although potentially at lower density. Using moth trapping data collected onsite (see Chapter 5 for details), I observed a difference in moth beta diversity between habitat types but also large variance and overlap, so whilst I expected an effect of habitat type and NDVI on foraging and other behaviour, I anticipated it would relate more to structure and therefore accessibility, than to prey composition or diversity. This therefore represents a trade-off between higher energy gain but less accessible areas, and lower energy gain in more accessible areas, that could also pertain to the reduced effort hypothesis.

Thirdly, I expected temporally-variable weather conditions to influence both the birds' behaviour. I specifically asked if nightjars would increase time allocated to foraging with an increase in temperature and/or a decrease in rainfall, under the reduced effort hypothesis. Fourthly, I hypothesised that males and females would differ in proportion of time allocated to various behavioural states. Due to their differing roles during breeding, time spent foraging would be higher in males and time spent in a sedentary, resting state would be higher in females, as they are incubating or brooding chicks. Finally, I expected to see an increased proportion of time spent foraging in 2018 compared to other years, as by this time the amount of foraging resources had declined on the breeding site, due to extensive birch scrub removal.

4.3 Methods

4.3.1. Study site

The Humberhead peatlands is located in South Yorkshire (53° 38' 17, 0° 53' 50) and is one of the more northerly breeding sites for European nightjars in the UK. It is dominated by *Betula* woodland, *Calluna* heathland, open bare peat, as well as wetter areas dominated by *Eriophorum* and *Sphagnum*. The site has undergone a substantial amount of landscape change in the last few years, including felling of large areas of birch woodland and increasing of wetland areas through water management. Breeding birds exist across all but the wettest areas of the site and are concentrated in areas dominated by heather and birch scrub.

4.3.2. GPS tracking

From 2015 to 2018 I deployed archival miniaturised GPS tags onto the tails of breeding European nightjars. Accurate fixes were collected every 3 minutes (2015 to 2016) and every 5 minutes (2017 and 2018) from 21:00 to 05:00. I retrieved data from 42 adult male (n = 26) and female (n = 16) nightjars, with data ranging from 2 to 17 nights. From this data I estimated the mean hourly distance travelled by each individual, to observe patterns of activity during the night.

4.3.3. Environmental data

To relate nightjar movement behaviour to external influences, I acquired lunar illuminance (proportion of moon illuminated) for each date of the tracking data using package 'lunar' (Lazaridis, 2014). Although the strength of light from the moon will be tempered by the level of cloud cover, unfortunately this was not readily collected by the weather station close to Hatfield and Thorne Moors. I also obtained Normalised Difference Vegetation Index (NDVI) from the Sentinel-2 satellite (Drusch *et al.*, 2012) was acquired using Google Earth Engine (Gorelick *et al.*, 2017). NDVI represents the density of green vegetation and runs from -1 to +1, where values between -0.1 and -1 represent water, 0 represents bare ground and values close to +1 represent heavily wooded areas. NDVI allowed me to supplement the habitat category information obtained from the UAV as discussed in Chapter 3, as each habitat would contain a range of NDVI values representing better the structure and composition of the habitat. I acquired a mean NDVI value for each month of my study, excluding 2015 for which NDVI data was averaged over June and July due to problems with the Sentinel 2 data. This was deemed a sufficient timescale over which to observe meaningful changes in vegetation density, due to grass regrowth. Mean NDVI value was extracted per tracking point, in R for use in the HMMs.

To observe the influence of short-term fluctuations, I obtained data on hourly mean values for temperature and wind speed were obtained from the weather station at Doncaster and Sheffield airport, which lies 5 km to the south-west of Hatfield Moor (53.480911, -1.0099621; data obtained through the Met Office Integrated Data Archive System (MIDAS; Met Office, 2012). Data on hourly mean rainfall (in mm) were obtained from the Environment Agency Dirtness Power station (53.579451, -0.86975526; data directly from the Environment Agency). As the GPS data were acquired at a much higher frequency than the weather data, I interpolated the hourly weather data to produce a weather covariate value for each GPS fix, using package ‘rioja’ (Juggins, 2017) in R (v 3.6.1.).

4.3.4. Hidden Markov Models

To identify movement behaviours within nightjar tracking data, I used the package moveHMM (Michelot, Langrock and Patterson, 2016) in R. The GPS fixes were regular with few missing, which made the data suitable for discrete-time movement modelling (Bennison *et al.*, 2018). Any points that were missing or inaccurate were removed from the dataset prior to use. A null model was initially created to verify a ‘stationary’ state, by attaching several active GPS units to stationary marker posts outside in the field and collecting fixes under the same conditions (rate, start time and end time) as the true data. A starting model was then parameterised with values of step lengths (both a mean and standard deviation) and turning angles (mean and concentration of angles), derived from the null model and subsequent exploration of the step lengths and turning angle distributions within the model framework (Michelot, Langrock and Patterson, 2016). Different behaviours are identified using the combination of both step lengths and angles, where shorter step lengths and narrow turning angles are indicative of more tortuous movement, such as foraging (Bennison *et al.* 2018). Conversely, longer step lengths and shallower turning angles should represent more directed movement, such an animal travelling over an unfavourable area (Michelot *et al.*, 2017). As my data were collected over two different sampling regimes, three- and five-minute fix frequencies, these were modelled separately by year, in order to avoid confounding differences between years with regime-related variation in step length and turning angle.

Initial testing highlighted the superior structure of a three-state model (resting, foraging, travelling), over a two-state model (resting, other) using AIC value comparison. Following Michelot, Langrock and Patterson (2016) and Pohle *et al.*, (2017) I attempted to interpret the different numbers of states related to the ecology of nightjars. As rapid, aerial foragers, with the ability to switch behaviours, I deemed the three-state model to be correct. Environmental covariates were then included in the model using a standard formula notation '~'. I ran a model for each month for each environmental value alone, as well as a model using quadratic lunar illuminance ('lunar^2') and a two-covariate model of lunar illuminance and NDVI, as the two most influential parameters in all model sets. The step length error structure was gamma, the turning angle distribution was von Mises and I employed the Viterbi algorithm to define the states (Michelot, Langrock and Patterson, 2016; Michelot *et al.*, 2017). Relative strength of models was judged using AIC value and maximum log likelihood and model fit assessed through pseudo-residuals (Michelot, Langrock and Patterson, 2016). Once the best model had been chosen, the state assigned to each GPS fix was extracted from the model and combined with the tracking data and environmental covariate values for further analysis.

4.3.5. Behavioural analysis

I extracted all points from the HMMs once they had been designated with a behavioural state and calculated how much time (i.e. the percentage of points) was allocated to each behaviour. Data were not numerous enough to use mixed effects models for individual-level analysis. I used a generalised linear model (GLM), with gamma error structure and log link function, to test for significant differences in time allocated to all three behaviours, between sex, month and year firstly to identify broad patterns that might account for any responses to environmental covariates. As I previously found that habitat selection was not equal across the population, instead being very variable between individuals (Chapter 3), I wanted to identify if there was any foraging behaviour-specific variation present in habitat use. I used the extracted foraging points as above and tested for significant differences, using a linear model, in the number of points allocated to foraging behaviour between the different habitat categories.

Next, I wanted to identify how foraging behaviour specifically (as opposed to travelling and resting) changed with environmental covariates. For this I used square-root transformed time spent foraging to test for influences of the lunar and habitat conditions (lunar illuminance (%) and NDVI on the amount of time allocated to foraging, during the tracked period, accounting for phenological change by including week of the breeding season within a linear model.

Using both habitat category and NDVI provides a multi-dimensional view of habitat use by the nightjars, by considering both vegetation type (e.g. dominant species) and the structure and condition of the vegetation. Habitat category was assigned based on vegetation type and structure using a combination of high-resolution photography and ground truthing, but NDVI uses infrared reflectance based on vegetation density, or lack thereof. This means that multiple habitat types can contain similar levels of NDVI and vice versa (Figure 4.1). Whilst NDVI may potentially be a more accurate way of classifying vegetation structure, there is added value from knowing the vegetation type, because of species-specific plant-moth associations.

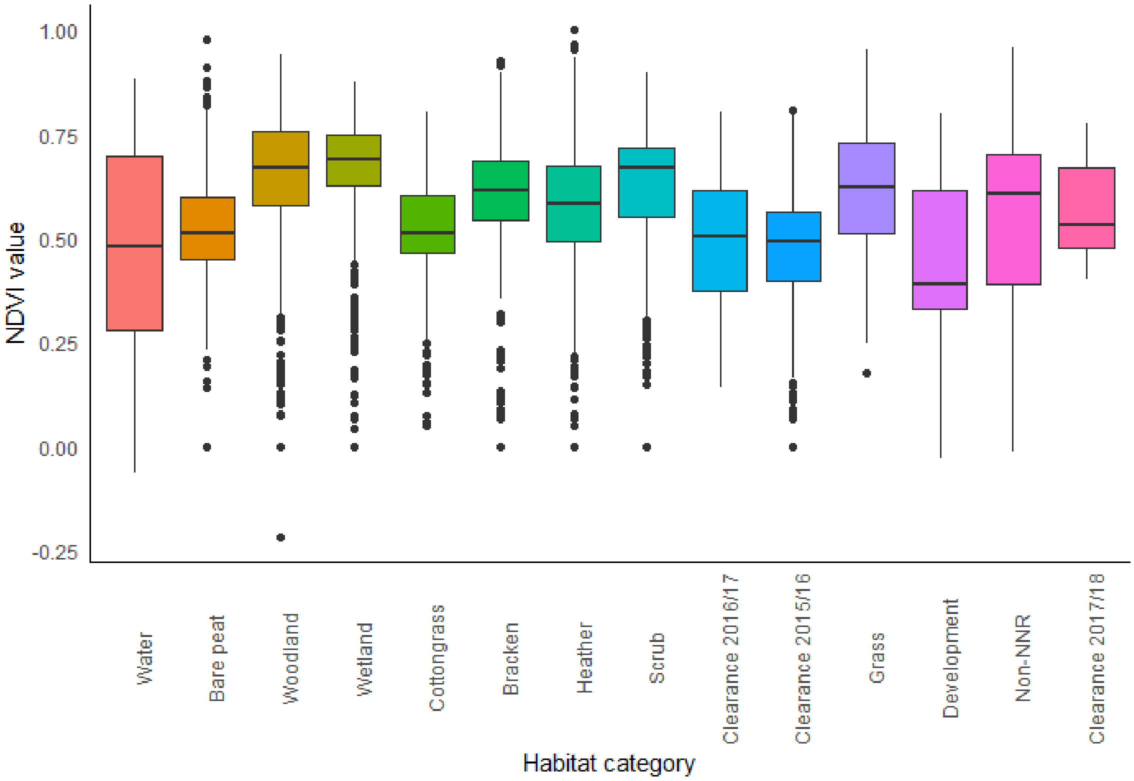


Figure 4.1: Median and range of NDVI values incorporated within each UAV-designated habitat category within the habitat map used for habitat selection and movement analysis of nightjars on Thorne and Hatfield Moors.

As I found significant influences of the availability of particular habitat types on the size of the home range in Chapter 3, I also incorporated habitat availability values here, to identify any effect of these on time allocated to foraging. I also added year into the global model as a fixed effect and week of the breeding season as a random effect, to account for phenological variation and change over time. Week of the breeding season also helped to account for sex-related differences, as sex could not be added into the model when week of the breeding season was used as a random effect due to singular fit at the boundary. Male and female data were modelled together as separately the data were not robust enogh (i.e. did not contain enough points). To reach an optimal minimal AIC and residual variance, signifying goodness of fit, I removed terms singularly. Simulated residuals were calculated and plotted through 'DHARMa' (Hartig, 2016) in R. Model selection tables were produced using MuMIn in R (Barton, 2015).

4.4 Results

4.4.1. Nightjar movement behaviour

Hidden Markov models distinguished three distinct behavioural modes, which equated to resting (overall mean step length: 9.53m +/- SD 6.51), foraging (86.67m +/- SD 89.77) and travelling (371.71m +/- SD 409.77; Figure 4.2). Mean step lengths and angles varied between months and years (Appendix V; Figure 7.6) and had high standard deviations, causing a large amount of overlap between the three states. States 1 and 2 were interpreted as resting and foraging phases, possessed almost identical angle structure (both close to -π/π), differing only in the step lengths. The resting phase incorporated some minor GPS error, making it particularly small and tortuous. Step lengths in state 3 (travelling or commuting) were longer and the angles were shallower, but even in this state, angles close to -π/π were present (Appendix V; Figure 7.6).

NDVI was a key factor in all models; (Appendix V; Figure 7.7). In all months and years, except July 2016, lunar illuminance was also a key factor that influenced movement behaviour (Table 4.1). The relationship with lunar illuminance varied between months and years; most commonly the relationship was non-linear (Appendix V; Figure 7.8). In July 2016 temperature and NDVI together were most important (Table 4.1). Increased temperatures specifically were correlated with more nightjars switching behaviours (i.e. becoming more active). In July 2018, the HMMs run with NDVI + lunar illuminance and NDVI alone were within Δ 2 AIC of each other. I subsequently used the outputs from the two-covariate model for further analysis, as this combination of factors is thought to be more comprehensive in its interpretation of nightjar behaviour (English, Nocera and Green, 2018).

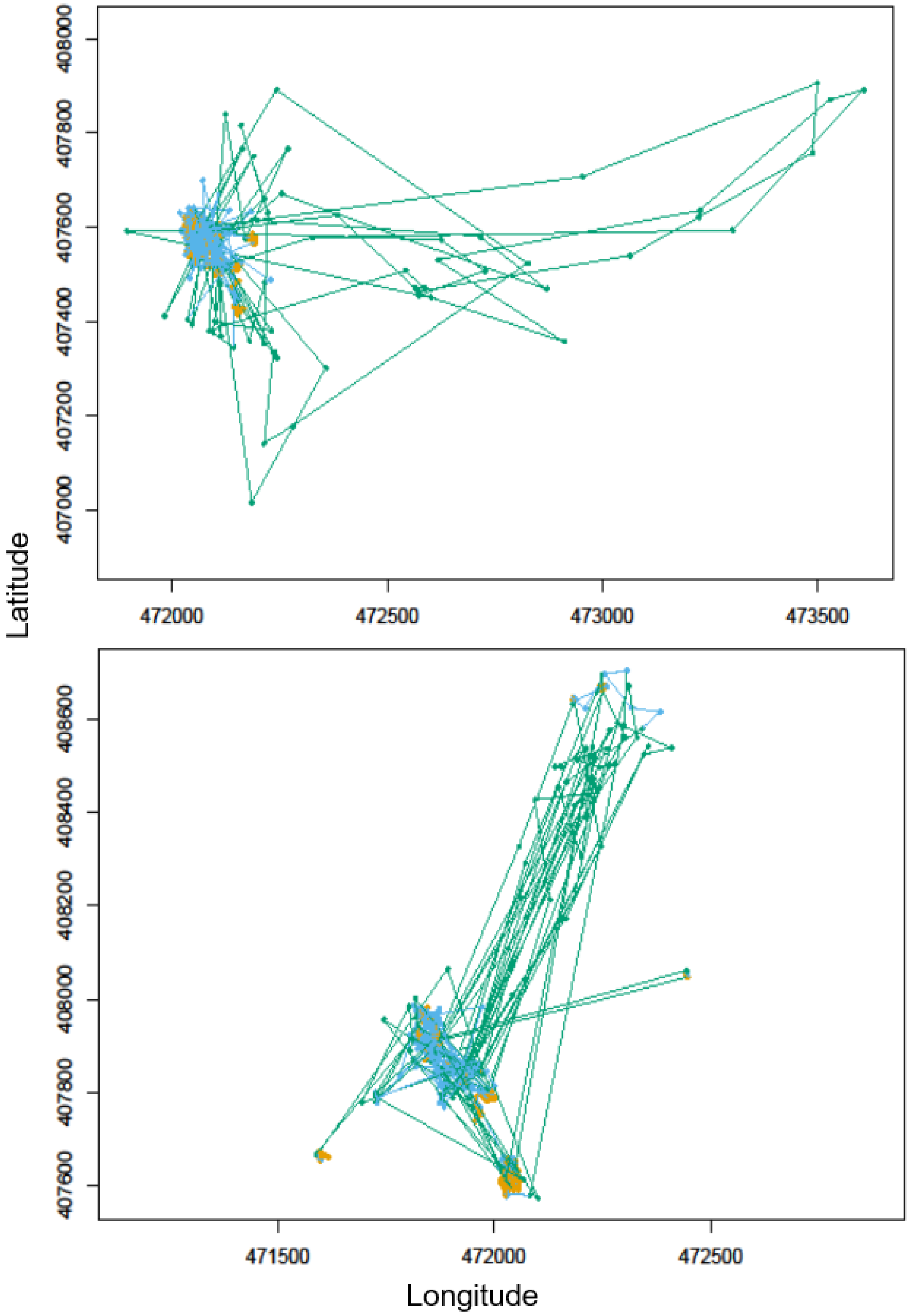


Figure 4.2: Examples (n = 2) of nightjar GPS tracks. Both sets of tracks were collected over 6 days in 2016, coloured according to the state assigned by the Hidden Markov Models. Orange = state 1) resting; Blue = state 2) foraging; Green = state 3) travelling.

Points represent fixes collected every 3 minutes and are plotted in British National Grid units.

Table 4.1: AIC values from 3-state (resting, foraging, travelling) Hidden Markov Models produced using GPS tracking data from European nightjars (n = 42) and run separately for each month (June/July) and year (2015 – 2018). Lowest AIC value, i.e. best model, in bold. ‘3 state’ indicates model run with no addition of covariates. Each covariate added in preceeded with ‘+’. ‘Temp’: temperature in °C; ‘lunar’: lunar illuminance value (percentage moon illuminated); ‘NDVI’: Normalised Differential Vegetation Index; ‘lunar^2’: quadratic relationship with lunar illuminance.

	2015	**2016**	**2016**	**2017**	**2017**	**2018**	**2018**
Model	*All*	*June*	*July*	*June*	*July*	*June*	*July*
3 state	46727.8	66172.93	40743.77	97876.6	52428.6	117482.3	54933.3
+ Temp	46733.45	66170.73	40712.59	97861.5	52429.5	117476.3	55517.2
+ lunar	46695.01	66069.05	40749.38	97880.5	52412.2	117482.8	54930.5
+ NDVI	46709.6	66072.27	40743.99	97862.4	52375.2	117477.2	**54898.9**
+ Temp + NDVI	46718.09	66068.33	**40710.57**	97850	52373.5	117454.2	54909.1
+ Temp + lunar	46699.77	66072.52	40721.74	97865.8	52413.4	117474.1	54940.9
+ NDVI + lunar	46663.9	**66003.92**	40749.07	97863.6	52365.9	117459.3	**54899.1**
+ NDVI + lunar^2	**46654.44**	66012.19	40736.26	**97835.6**	**52363.1**	**117451**	54906

4.4.2. Movement behaviour influences

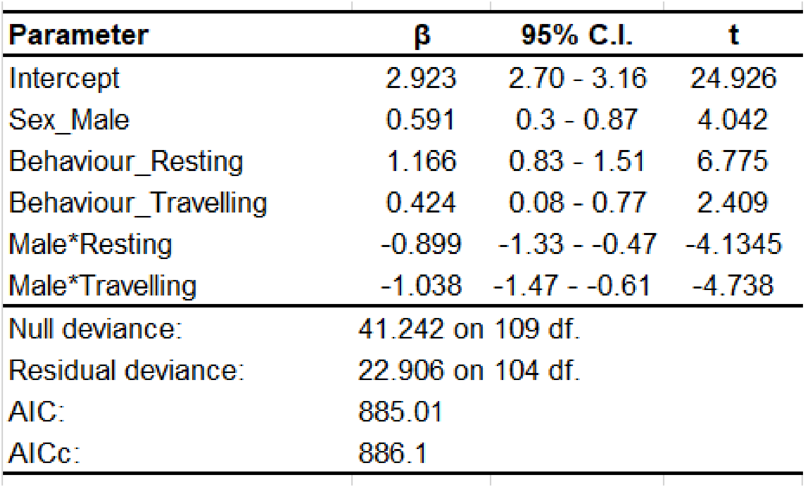
I found that behaviour type varied significantly between habitat types ($F_{13,28}$: 7.56, p = 4.2e-06). Most foraging activity took place in areas of heather and two-year-old clearfell (Figure 4.3), whilst heather, woodland and new clearfell were heavily used for resting behaviours. As with overall habitat selection chapter 3, there was significant overlap (Figure 4.3; Appendix V); i.e. no single habitat type was used above all others for any of the activities.

Significant sex differences were found in the allocation of time to different behaviours, identified using a GLM (Table 4.2). Males spent significantly more time foraging (33.6%) than females (18.6%, Figure 4.4). Females spent significantly more time resting (59.7%) than males (43.9%) and significantly more time travelling (F: 28.4%; M: 18.2%; Figure 4.4, Table 4.3). Year was not retained in the top model, as although there is variation between years, the differences explained by sex are much stronger.

Table 4.2: Model selection table of Generalised Linear Models (GLMs) to test for differences in the allocation of time between different behaviours, sex, month and year. df = degrees of freedom; loglik = log likelihood of the model; AICc = Akaike's information criterion corrected for small sample size; Delta AIC = difference in AIC between best model and current model; Weight = Akaike weight. Model with lowest AICc and highest weight in bold.

Parameters	df	loglik	AICc	Delta AIC	Weight
Sex * Behaviour_type	**7**	**-435.5**	**886.1**	**0**	**0.68**
Sex * Behaviour_type + Month	8	-435.4	888.3	2.15	0.23
Sex * Behaviour_type + Year	10	-434.3	890.9	4.77	0.06
Sex * Behaviour_type * Month	13	-431.2	892.1	6.05	0
Sex + Behaviour_type	5	-447.7	906.1	20.01	0
Sex + Behaviour_type + Month	6	-447.8	908.3	22.24	0
Sex * Behaviour_type * Year	25	-425.3	916	29.89	0

Table 4.3: Model coefficients and 95% confidence intervals from the Generalised Linear Model (GLM) with lowest AICc in Table 4.2. testing for differences in the allocation of time between different behaviours by European nightjars.



Parameter	β	95% C.I.	t
Intercept	2.923	2.70 - 3.16	24.926
Sex_Male	0.591	0.3 - 0.87	4.042
Behaviour_Resting	1.166	0.83 - 1.51	6.775
Behaviour_Travelling	0.424	0.08 - 0.77	2.409
Male*Resting	-0.899	-1.33 - -0.47	-4.1345
Male*Travelling	-1.038	-1.47 - -0.61	-4.738
Null deviance:	41.242 on 109 df.		
Residual deviance:	22.906 on 104 df.		
AIC:	885.01		
AICc:	886.1		

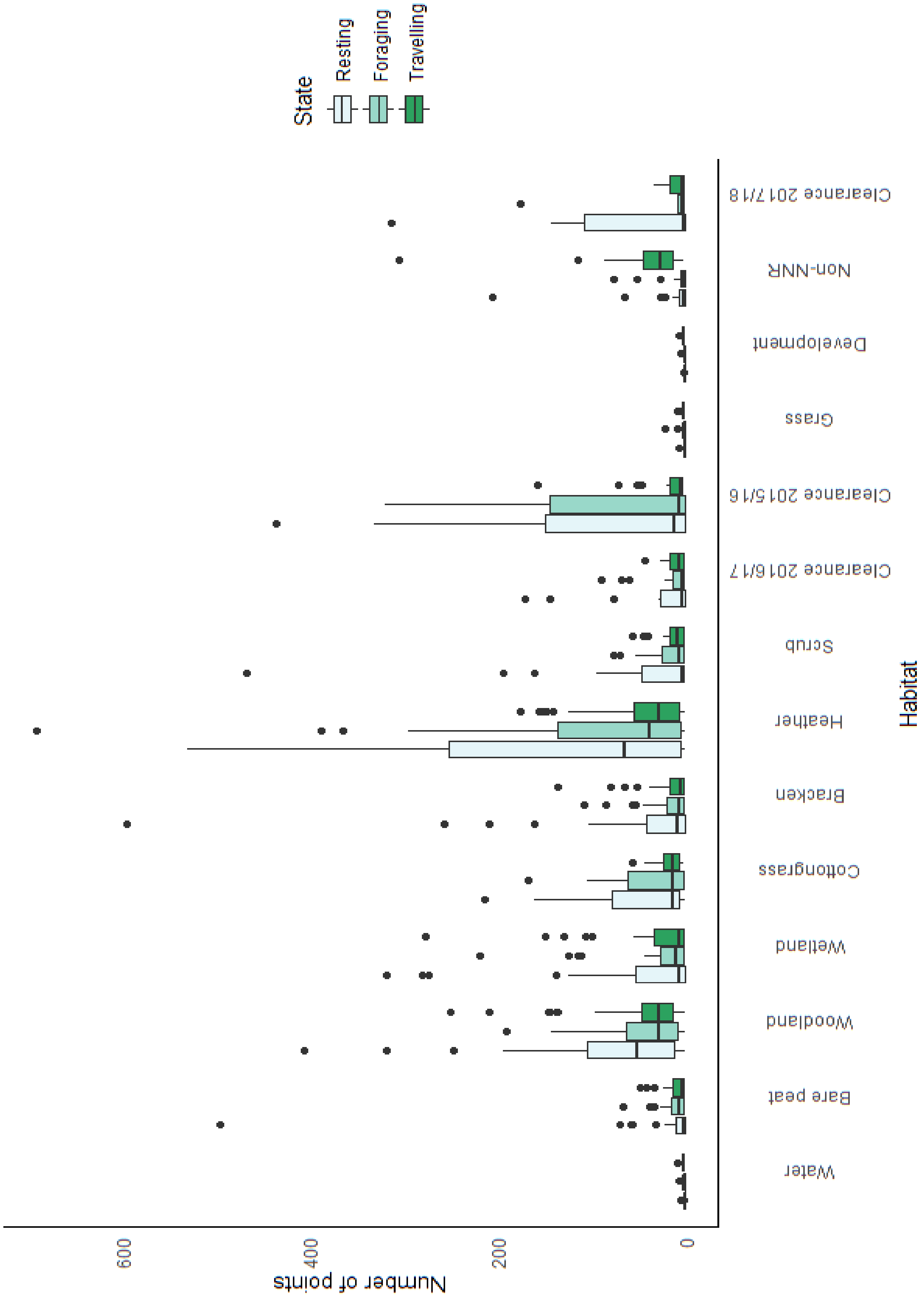


Figure 4.3: Comparison of the median number (bold line, plus interquartile range) of tracking points identified as ‘resting’, ‘foraging’ and ‘travelling’ between each habitat category (for categorisation details see Chapter 3).

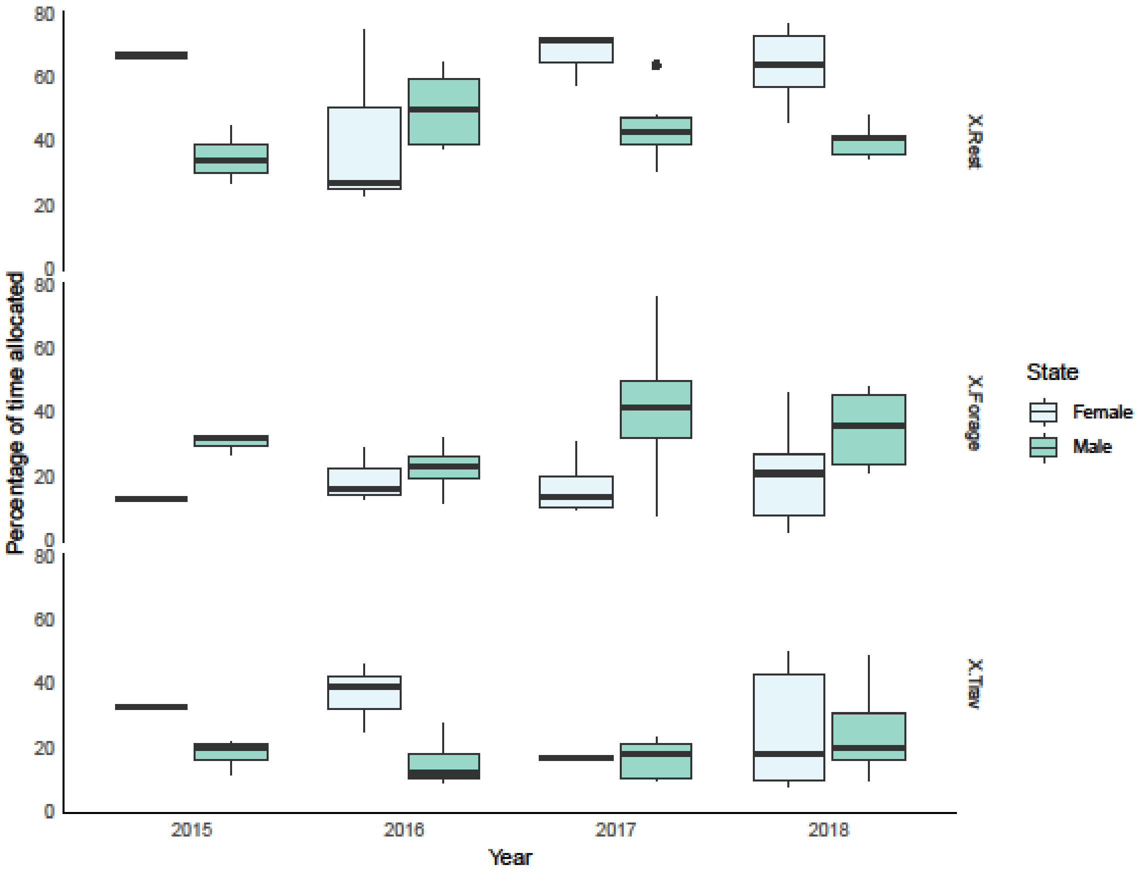


Figure 4.4: Percentage time allocated by female (F) and male (M) nightjars to resting, foraging and travelling in each of 4 years (2015 - 2018, n = 42).

4.4.3 Foraging influences

Having ascertained that NDVI and lunar illuminance were important factors in delineating and altering behaviour, I tested the influence of these variables specifically on the proportion of time spent foraging, uing GLMs. Points identified as foraging were extracted and analysed using GLMs to investigate correlations with environmental covariates. Two models with the lowest AIC values were within Δ 2 AIC of each other but were not model averaged, due to the fit of the residuals with the extra explanatory variable (here, lunar illuminance; coefficients and confidence intervals in Table 4.5). There was a weak negative relationship where birds allocated less time to foraging when the moon was full (Figure 4.5a; Tables 4.4 & 4.5). This was not significant but did help to explain some of the variation. Most foraging took place in semi-open vegetation (mean NDVI: 0.57, +/- SD 0.17). Time allocated to foraging was weakly but positively related to NDVI and temperature, but neither NDVI nor temperature was retained in the final model.

When habitat availability within home ranges was included, the amount of cleared habitat significantly improved the fit of the models. Individuals that had more cleared habitat and more open, dry habitat (heather and early successional peat) allocated more time to foraging (Table 4.5; Figure 4.6).

4.4.4. Influences of phenology and sampling regime

Including week of the breeding season as a random effect helped to explain a large amount of variation among birds and meant the effect of year became completely insignificant (Tables 4.4 & 4.5). The conditional R^2 value, which represents the variation explained by both the fixed effects and the random effects was 0.4, much higher than the marginal R^2 value of 0.16, which represents only the fit of the fixed effects within the model. Sampling regime was accounted for by including the two regimes in the model as a fixed binary effect (3 minute interval vs 5 minute interval). Step length was shown to be significantly different between the two regimes, which could therefore have influenced the resulting foraging behaviour (Welch’s two-sample t-test: t: -18.03, df = 32859, p <2.2e-16). Sampling regime was an important factor in the linear mixed models, and the increase from 3 to 5 minute intervals caused an apparent increase in time spent foraging.

Table 4.4: Model selection table for linear models testing the influence of environmental conditions and habitat availability on the amount of time spent foraging in European nightjars. Models with lowest AIC and highest weight highlighted in bold.

Fixed effects	Random effects	df	logLik	AICc	Δ	weight
Cleared% + Sampling regime	Week	5	-69.98	151.7	0	0.54
Lunar% + Cleared% + Sampling regime	Week	6	-69.37	153.2	1.53	0.25
NDVI + Cleared% + Sampling regime	Week	6	-69.95	154.4	2.69	0.14
Lunar% + Cleared% + Sampling regime + Water%	Week	7	-69.36	156.1	4.45	0.06
Lunar% + Sampling regime	Week	5	-74.17	160	8.34	0.01
NDVI + Sampling regime	Week	5	-74.47	160.6	8.94	0.01
Lunar% + NDVI + Sampling regime	Week	6	-74.15	162.7	11.02	0
Lunar% + NDVI + Sampling regime + Year	Week	9	-72.98	169.6	17.92	0

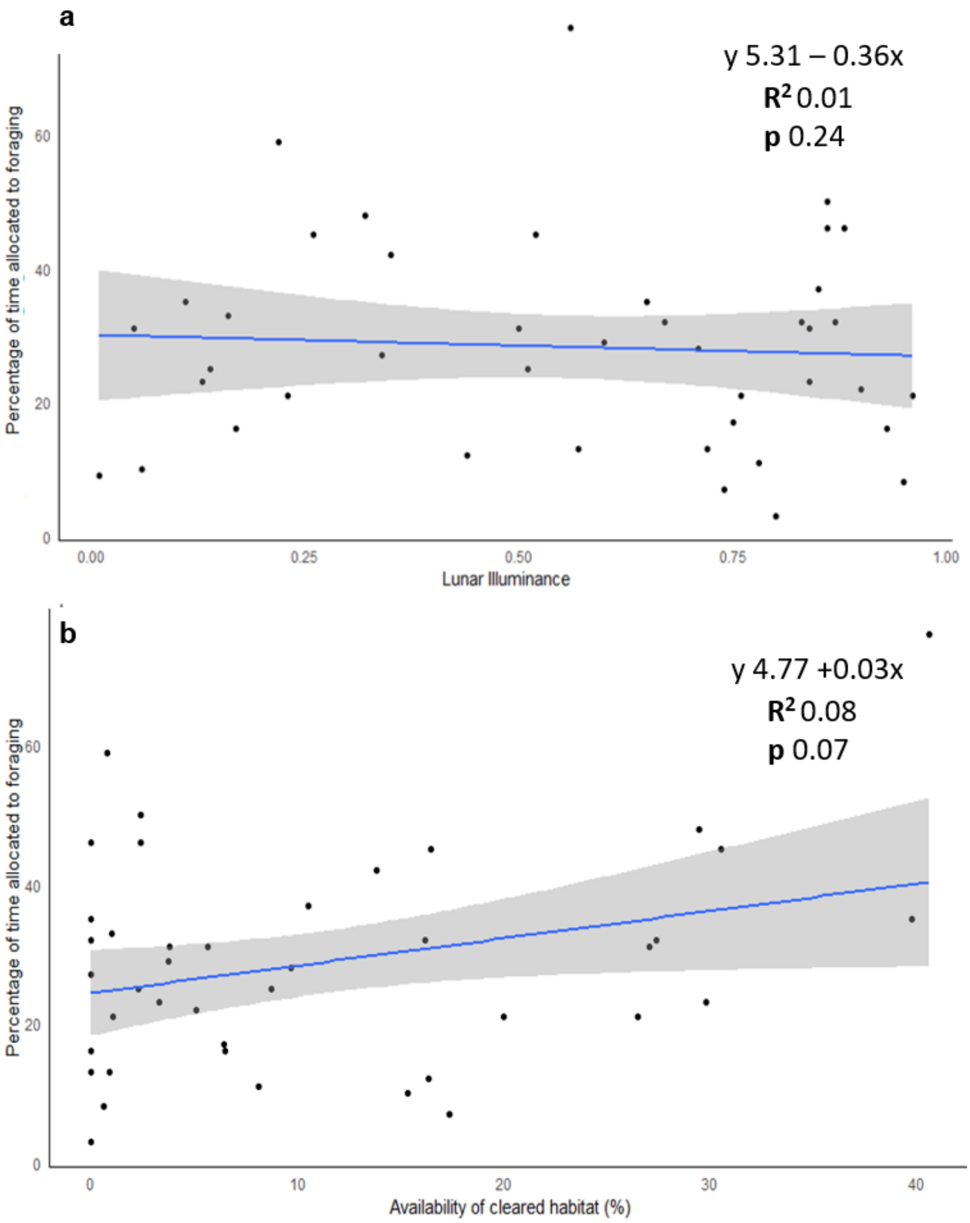


Figure 4.5: Relationship between the time allocated to foraging per bird (percentage of points) and a) lunar illuminance (percentage moon illuminated) and b) percentage availability of cleared habitat (within 95% home ranges). Plotted with regression line and 95% confidence intervals.

Table 4.5: Model coefficients and 95% confidence intervals for the model with the lowest AIC value. Models tested for an influence of environmental covariates on foraging time of nightjars. Cleared habitat % = availability of habitat types within individual nightjar home ranges. Lunar % = lunar illuminance, i.e. percentage of moon face illuminated. Regime = Sampling regime, binary factor.

Parameter	**Estimate**	**95% CI**
Fixed effects		
Lunar %	-0.785	-2.161 - 0.651
Cleared %	0.027	-0.007 - 0.062
Sampling regime	0.818	-0.15 - 1.738
Random effects	**S.D.**	**95% CI**
Week	0.754	0 - 1.65
Residual	1.183	0.942 - 1.551

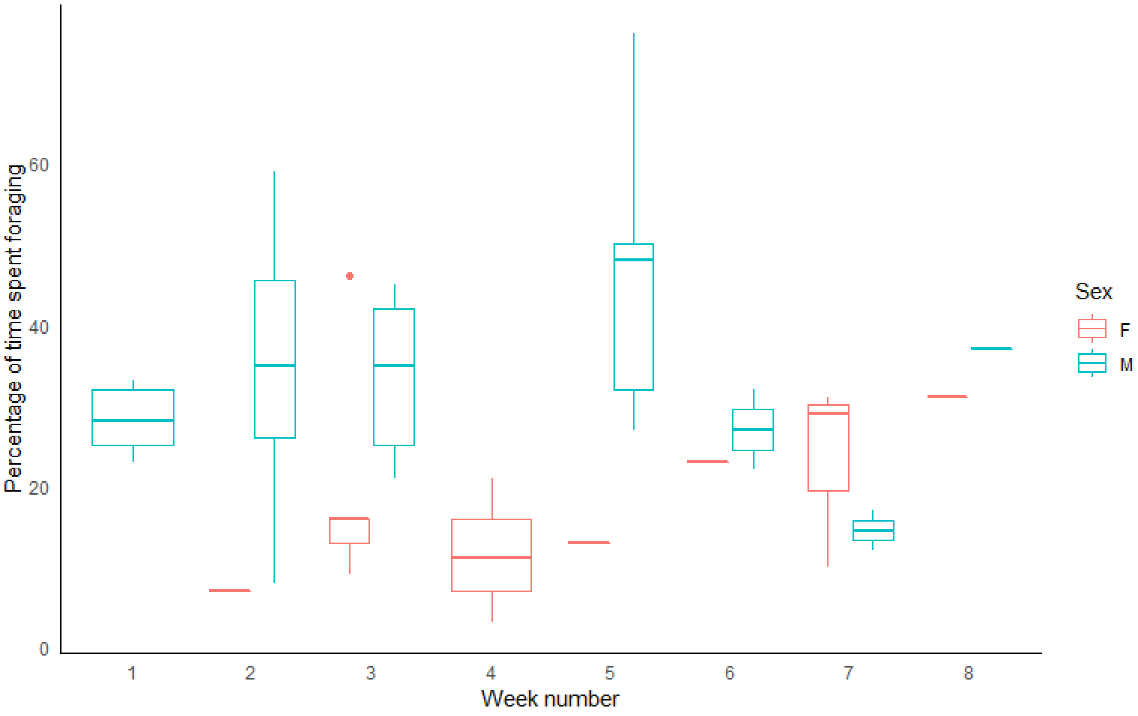


Figure 4.6: Relationship between time allocated to foraging per bird (percentage of points) and week of the breeding season (numbered from the first week where GPS tags were deployed onto birds.

4.5 Discussion

4.5.1. Influence of environmental conditions on behaviour

Nightjar behaviour varied according to spatial and temporal environmental conditions of their breeding area, and these relationships changed during the course of the breeding season according to the week during which the birds were tracked. Males spent significantly more time foraging than females, and females spent significantly more time resting. Considering foraging time alone, time spent foraging increased when there was more cleared habitat in the individual's home range, the overall proportion of which increased during the course of the study. Time spent foraging decreased when the moon was at its brightest, although this relationship was not significant.

Previous literature has identified the stage of the moon as an important cue for breeding and foraging nightjars and indeed, for other nocturnal (Prugh and Golden, 2014; Appel *et al.*, 2017) and diurnal animals (York, Young and Radford, 2014). Stronger moonlight should benefit nightjars by increasing their visual acuity, thus reducing foraging effort (Saldaña-Vázquez and Munguía-Rosas, 2013; Schifferli *et al.,* 2014; Rubolini *et al.,* 2015;). However, moths are lunarphobic and increased moonlight will change their behaviour, therefore requiring nightjars to trade-off between conditions that promote moth activity and those that enable better foraging efficiency through increased visibilty. Nightjars select for larger specimens (Csada, Brigham and Pittendrigh, 1992, and Chapter 5) and have sensitive retinal structures adapted for low light (Nicol and Arnott, 1974). Thus, they should be able to see larger moth species at lower light levels (Brigham & Barclay, 1995) and may therefore not be too compromised by foraging at lower light levels. There were limitations of using lunar illuminance data alone, but unfortunately this data was not available at the weather station used here. Portugal *et al.* (2019) found that Barnacle geese (*Branta leucopsis*) produced physiological responses that were strongest during a supermoon, where lunar distance was at its lowest, the moon was full and cloud cover was low, highlighting the importance of the interactions between separate cyclical and non-cyclical elements.

Habitat composition and structure has been shown to provide both costs and benefits of foraging in aerial predators (Wichmann, 2004; Sharps *et al.*, 2015; English *et al.*, 2016; Evens *et al.*, 2017; Winiger *et al.*, 2018), reflecting the amount of food and the birds' manoeuverability. Here, nightjars foraged in habitats with NDVI values that represent open scrub areas and heather dominated patches, that should promote greater visibility through reduced density of vegetation (Brigham & Barclay, 1995; Sharps *et al.*, 2015). Nightjars also allocated significantly more time to foraging when there was more cleared habitat within their home range. Although well-vegetated areas hold suitable plant species for breeding moths, thus forming rich prey resources (Evens *et al.*, 2018; Winiger *et al.*, 2018), these patches can be costly for aerial predators such as nightjars, because there may be limited visibility and accessibility (Sierro *et al.*, 2001; Sharps *et al.*, 2015). This indicates a trade-off between prey abundance and accessibility in use of habitat types. An increase in foraging time in particular habitats may also be a product of competition. If habitat quality is higher, such that it provides an adequate trade-off between prey abundance and accessibility, conspecific competition will increase (Kotler and Brown, 1988; Trevail *et al.,* 2019b). This may then drive an increase in foraging activity ('increased effort hypothesis' – Schifferli *et al.,* 2014), as birds compete for prey items. Previous work in Chapter 3 showed that an increased amount of cleared habitat resulted in smaller home range size, suggesting that these habitats are good quality, relieving the need to travel further to acquire profitable resources (Trevail *et al.,* 2019b).This would then support a hypothesis of increased competition because of a higher number of individuals inhabiting the area, leading to increased foraging time.

It is potentially surprising that there was not a stronger relationship between foraging time and temperature, given that previous studies of both bats and moths highlight this as a strongly influential variable (McGeachie, 1989; Ciechanowski *et al.*, 2008; Betzholtz and Franzén, 2013). However, temperature was not particularly variable between years and I only tracked birds for short periods during the full summer, rather than over a wider range of temperatures or seasons. Additionally, the scale at which the temperature data was collected does not necessarily match that of the nightjars, nor their prey, which presumably respond to very small scale topographical and vegetation-related changes in temperature on the moors. Nightjars became more active when the temperature increased, perhaps matching increased activity of particularly the larger moths (Yela., 1997; Betzholtz and Franzén, 2013). This occurrence of increased activity levels concurs with previous studies on nightjar calling behaviour, which becomes longer and more frequent with higher temperatures (Middleton *et al,* 2018). Despite the lack of significance of temperature overall, it is likely that it interacted with vegetation density and structure on a much more localised spatial scale, where vegetated areas provide shelter and warmth and therefore a higher abundance of larger moth species (Bowden and Dean, 1977; Merckx *et al.*, 2010, 2012; De Smedt *et al.*, 2019). It is possible that the effect of the vegetation may mask the effects of the temperature and wind, related to the different spatial scales at which the data has been collected.

4.5.2. Variation in behavioural patterns between sexes

I found clear sex differences using the HMMs in the allocation of time to different behaviours, which represented their different roles during the breeding season and potentially also different stages of the breeding season, where birds with older chicks allocate more time to foraging. Not only do males conduct extensive territorial displays (Mills, 1986; Jenks, Green and Cross, 2014), females, in contrast, only leave the nest for a limited time at dusk and dawn whilst incubating the eggs (Cross *et al.*, 2005). Females therefore spent significantly less time in the ‘active’ foraging state and significantly more time in the resting state. However, they may be employing a sit and wait foraging strategy, whilst on, or close to the nest, an activity that would be represented by the resting state. This represents an energy efficient/ time-minimizing strategy whilst incubating (Schoener, 2003). Such sex differences in behaviour could explain lower female common poorwill field metabolic rate found in a previous study (Thomas, Brigham and Lapierre, 1996).

4.5.3. Variation between weeks and with habitat change

Contrary to my predictions, the proportion of time spent foraging did not increase over time and infact variation in foraging time was accounted for by incorporating week of the breeding season into the model. This week by week variation also cancelled out the significant sex differences in time spent foraging (*not* time allocated to different behaviours overall, as described above), indicating phenological change, which was not synchronised across all birds, as the effect of week by week variation was not linear. As the amount of dense birch woodland decreased across the site, I expected nightjars to forage for longer as sources of prey would have decreased and consequently moth availability in clear cut areas would be much lower (Summerville, Bonte and Fox, 2007; Fuentes-montemayor *et al.*, 2012). This was not the case, which may relate to section 4.4.1. where I discuss the effects of vegetation structure on the ability of nightjars to forage efficiently. Moth community composition post-clearfell is thought to develop alongside the composition of the ground-flora (Summerville and Crist, 2002). Areas on the Humberhead peatlands that have begun to regenerate following clearance in 2016 and 2017 are now layered with new growth *Erica tetralix* and *Calluna vulgaris*. This suggests that resources on the site may have become more plentiful or more accessible, which should impact on the amount of energy expended by birds in search of prey. In Belgium, nightjars commuted long distances to find adequate foraging habitat where functional habitat types were strictly segregated. In some locations mean foraging distance was >3km, and this substantial distance concurrently increased stress levels (Evens *et al.*, 2018). In comparison, birds here rarely travelled >1km away from the NNR and overall travelling activity significantly decreased with increased habitat heterogeneity over time.

4.5.4. Behavioural state modelling

HMMs applied to the nightjar data have allowed the fine-scale identification of nocturnal behaviours, which have previously only been measured via direct observation over short timeframes or in small areas, and by using calling level as a proxy for overall activity level, in previous studies (Mills, 1986; Brigham and Barclay, 1992; English *et al.*, 2016). I identified three behavioural modes; resting (small steps, sharp turning angles), foraging (longer steps but equally sharp turning angles) and travelling (long steps, shallow angles), however the differentiation between resting and foraging states is of interest and of some potential confusion here and is thus worth discussing, to provide more context.

Nightjars are variously described as ‘sit-and-wait’ or sallying foragers (Brigham and Barclay, 1992; Bayne and Brigham, 1995; English *et al.*, 2016), and aerial foragers i.e. they capture prey on the wing (Brigham and Barclay, 1992). This means the distinction between resting and foraging states is not always clearly defined. Resting behaviour, denoted by the HMMs as short movements of ~8 metres between points, could represent nightjars perching, flying out to take a moth, and then returning to the perch, given that the time between points is 3 to 5 minutes. This is substantially different from the model-specified foraging behaviour (~80 metre steps between points) but is still important prey-capture behaviour. In turn, the foraging state potentially includes the territorial ranging behaviour of the male, which may or may not include some foraging. Interpretation of HMMs therefore requires biological knowledge of the species that statistical delineation of movement behaviours cannot incorporate. Given the regularity and frequency of the data, it is a useful tool for understanding fine-scale movement behaviour in nightjars. It is still important to understand how the change in sampling frequencies between years influences step length and turning angle. Step length was more strongly affected by the increase in fix interval, perhaps unsurprisingly. An increase in the time between fixes extended mean step length by 39%; similarly strong responses were not seen in relation to the turning angles. Consequently sampling regime became and important variable in the linear models, also accounting for some of the year-to-year change that occurred.

4.6 Conclusions

Nightjars allocated more time to foraging in conditions that increased foraging efficiency, both in relation to direct impacts on the birds and also indirectly through the activity and abundance of their prey. Nightjars responded to a cyclical cue and foraged more at lunar light levels that traded-off increased visibility and prey availability. Nightjars also concentrated their foraging in areas containing vegetation that provided efficient movement, supporting the reduced effort hypothesis. Overall nightjars foraged more in areas dominated by semi-open levels of vegetation and increased their foraging in open areas with low vegetation. These results indicate that foraging efficiency is important for nightjars, which is understandable given their short breeding season and variable food source. As they exploit ephemeral prey, adjusting their behaviour in response to both stochastic, localised and broader, cyclical cues, can provide aerial foragers with optimal foraging conditions. These results have implications for conservation management, where maintenance of semi-open areas should be pursued, to improve conditions for efficient foraging by increasing accessibility of mobile moths and potentially decreasing the distance between nesting and foraging habitats.

Chapter 5: Environmental and temporal variability in the diet of a cryptic, nocturnal insectivore.

5.1 Abstract

Many species are reliant on prey that are vulnerable to environmental changes, particularly insectivorous aerial foragers, such as bats, hirundines and caprimulgids. For such species a sharp decline in invertebrate abundance and diversity in the past decades may have induced a change in diet composition that could be a driver for observed changes in population dynamics. According to optimal diet theory, species such as insectivores that consume naturally fluctuating prey resources, i.e. insects, should have a broad, flexible population niche, potentially driven by individual specialisation. Here, I analysed dietary composition and variation of the European nightjar (*Caprimulgus europaeus*) on a northern breeding site in the UK from 2015 – 2018, to obtain a measure dietary breadth and identify individual differences. I also quantified variation in diet between years. Composition of faecal pellets from nests and roosts was compared with composition of prey availability to identify diet selection by nightjars.

I applied high-throughput metabarcoding to 130 faecal samples, which identified 625 unique molecular operational taxonomic units (MOTUs), 65% of which I identified to species. Diet composition varied significantly between years and months and was broader in 2017, compared to other years. This indicated a wide population niche, able to expand in response to changes in availability or abundance of prey, potentially related to weather conditions or habitat change. Where species were identifiable, the most common species were all >40mm wingspan and were present across 40 – 50% of the samples, indicating favoured items within a flexible niche. Faecal samples were significantly more likely to contain moths with a wingspan of >60mm and significantly fewer moths <25mm, indicating size bias that varied between months and years. Population niche width appeared to be driven by inter-individual variation in diet, indicating flexibility or responses to competition on the breeding site. This flexibility should enable the population to adjust their diet in response to changes in environmental conditions in the future, particularly where phenological changes in prey species could drive a shift in peak emergence times of favoured items.

5.2 Introduction

The conservation of vulnerable species requires a thorough understanding of factors that influence survival and productivity (Ando *et al.*, 2013; Idaghdour, Broderick and Korrida, 2003). One such factor is diet, since the acquisition of sufficient food resources is important for maintaining body condition and provisioning offspring (Will *et al.*, 2015, Trevelline *et al.*, 2016). Knowledge of dietary composition and diversity can provide evidence regarding the status of a population, for example the quality of the foraging habitat (Clare *et al.*, 2014). This can also help to deduce how varied or flexible a population's diet is and allow us to infer how flexible it is likely to be in response to anthropogenic change (Howells *et al.*, 2017). Often predators reliant on ephemeral prey have adapted to align their breeding with peaks in preferred prey resources (Jetz *et al.,* 2003; although see Dunn *et al.,* 2011). However, climate change has been demonstrated to alter the timing of these peaks (Nebel *et al.,* 2010; Møller, 2013), which subsequently creates a mismatch between the predator and its prey (Saino *et al.,* 2011). Although some species have been able to shift the timing of their breeding to account for this mismatch (English *et al.,* 2017), others may be partially or completely unable to (Both *et al.,* 2010; Charmantier *et al.,* 2019). These species may need to find alternative ways of adjusting to these changes, such as by increasing their flexibility and the range of prey that they take (Orlowski *et al.,* 2014). Variation in prey availability is likely to affect certain groups of species more acutely than others, for example specialist predators reliant on prey types that are themselves at risk (Andreas, Reiter and Benda, 2012; Stanton, Clark and Morrissey, 2017; Nocera *et al.*, 2012). It is therefore valuable to study diets of species such as insectivores, whose prey are in decline (Spiller *et al.* 2017).

As well as examining diet on a species level, it is also important to consider finer scale variation, as differences between sexes (Downs *et al.*, 2016a; Mata *et al.*, 2016; Thalinger *et al.*, 2018) and between adult and nestling diets (Jedlicka *et al.* 2016, McInnes *et al.,* 2018) have been observed in other species. These differences might relate to alternative foraging strategies (Bell, 1982) and differing energy or nutritional requirements (Thomas, Brigham and Lapierre, 1996; Rocha *et al.*, 2017). Dietary components may also vary between months and years, in line with natural fluctuations in prey availability or related to human-induced habitat change (Durst *et al.*, 2008).

5.2.1. Insectivorous diets

Bird species that rely solely on insect prey resources must respond to localised spatial and temporal changes in prey abundance (Cucco and Malacarne, 1996; Imlay, Mann and Leonard, 2017), as their preferred prey are often patchy in distribution and may change in abundance with both short- and long-term weather conditions (Jarosik and Novak, 1997; Jonason, Franzen and Ranius, 2014). Species that take flying insect prey on the wing (‘aerial insectivores’) such as the barn swallow (*Hirundo rustica*) and the swift (*Apus apus*) are identified globally as being at risk (Nebel, Mills, Mccracken, *et al.*, 2010; Nocera *et al.*, 2012), due in part to the significant decline in insect populations worldwide (Hallmann *et al.*, 2017; van Strien *et al.*, 2019). The dietary composition of aerial insectivorous birds can reflect resource availability potentially resulting from weather conditions that might affect emergence; accessibility, i.e. the ease of catching particular prey items; nutritional content and habitat quality (Garlapow, 2007; English, 2009; Sharps, 2013; Razeng and Watson, 2015). Although there are now many studies available regarding the diet of aerially insectivorous bat species, this has not extended to nocturnal, insectivorous bird species whose diet may differ from bats related to foraging techniques, morphology and energy requirements (Bayne and Brigham, 1995; Brigham and Barclay, 1995). For many species it can be difficult to obtain information due to limitations in acquiring visual observations of feeding and the difficulty in finding and dissecting faecal matter (Mumma *et al.*, 2016; Nielsen *et al.*, 2018), as well as the fact that the soft-bodied moths and flies primarily taken by this feeding guild are not visually identifiable in faecal matter (Razgour *et al.*, 2011; Trevelline *et al.*, 2016).

5.2.2 Diet examination using metabarcoding

In the last two decades, rapid development of molecular techniques such as metabarcoding have become more widely used (Pompanon *et al.*, 2012; Taberlet *et al.*, 2012), allowing researchers to acquire valuable information relevant to species conservation (Gillet *et al.*, 2015; Kress *et al.*, 2015; Gerwing *et al.*, 2016). Metabarcoding allows ecologists to process samples in bulk (Taberlet *et al.*, 2012) and to identify the components of an animal’s diet using short sequences from specific genes that remain in the faecal matter from prey items, known as DNA barcodes (Symondson, 2002; Hebert *et al.*, 2003; Valentini, Pompanon and Taberlet, 2009). Ideal barcodes are short regions with high interspecific diversity but low intraspecific diversity and flanked by highly conserved regions for priming sites. Commonly used barcodes include cytochrome c oxidase subunit I (COI) or the 16S region of mitochondrial DNA and have been effectively used to distinguish between species (Hajibabaei *et al.*, 2006). For example, Mata *et al.* (2016) demonstrated dietary segregation through resource partitioning (Kotler and Brown, 1988) of two species of bat sharing the same foraging area. Trevelline *et al.* (2018) also identified intra- and inter-species resource partitioning in Lousiana waterthrushes (*Parkesia motacilla*), demonstrating within- and between-species flexibility to avoid competition. Metabarcoding has revealed hitherto undocumented but important predator-prey relationships, for example the identification of multiple avian predators of invertebrate pest species (King *et al.*, 2008; Crisol-Martinez *et al.*, 2016; Aizpurua *et al.*, 2018). Compared to other diet analysis methods such as neck collars (Zarzoso-Lacoste *et al.*, 2016; Tanneberger *et al.*, 2017), stomach dissection and visual dissection of faecal matter (Graclik and Wasielewski, 2012; Mumma *et al.*, 2016), molecular methods are non-invasive and can be more comprehensive (Ji *et al.*, 2013; De Barba *et al.*, 2014; Krehenwinkel *et al.*, 2017). This allows researchers to observe animals at a distance and then collect faeces, without coming into contact with the animal (McInnes *et al.*, 2016; Thalinger *et al.*, 2018), which is particularly beneficial for vulnerable or secretive species.

Although substantial development has occurred in metabarcoding techniques, there are still limitations relating to quantification, species-level identification and contamination (Alberdi *et al.*, 2018). In many cases, taxon-specific primers are able to resolve diet down to species level (Metzker, 2010; Alberdi *et al.*, 2012). However, there is still uncertainty around the ability to directly quantify the biomass and frequency of each species present (Bowles *et al.*, 2011; Thomas *et al.*, 2016; Deagle *et al.*, 2018). Elbrecht & Leese (2015) found a strong positive relationship between specimen biomass, related to individual body size, and the number of sequencing reads obtained overall, but this varies between target taxa and can also vary between primer pairs used; thus, caution is required (Piñol, Senar, & Symondson, 2018). PCR amplification bias (i.e. preferential amplification of certain species related to changes in annealing temperature and cycle number; Alberdi *et al.*, 2018; Krehenwinkel *et al.*, 2018) is a limitation for accurate quantification of DNA in faeces, which can be biased towards particular groups, e.g. Hymenoptera (Brandon-Mong *et al.*, 2015). Quantification can also be hindered by a lack of reference sequences (Burgar *et al.*, 2014; Sullins *et al.*, 2018) and PCR inhibition from soil or bird bacteria (Zarzoso-Lacoste, Corse and Vidal, 2013; Vestheim and Jarman, 2008).

Faeces is a difficult substance from which to extract prey DNA, as the DNA is degraded by microbial activity and outcompeted by the predator’s own DNA (Deagle, Eveson and Jarman, 2006; Kamenova *et al.*, 2018). Degradation can also depend on how faeces is collected and stored (Demay *et al.*, 2013; Deagle, Eveson and Jarman, 2006; Krehenwinkel *et al.*, 2018; Alda, Rey and Doadrio, 2007), the weather conditions the faeces is exposed to prior to collection (Oehm *et al.*, 2011) and the method of extraction (Schiebelhut *et al.*, 2017; Li *et al.*, 2003; Djurkin Kusec *et al.* 2015). Avian faeces is an especially challenging material from which to extract DNA, due to the high concentration of uric acid (Kohn and Wayne, 1997; Eriksson *et al.*, 2017), which inhibits extraction and amplification of DNA (Vo and Jedlicka, 2014). Indeed, Sullins *et al.* (2018) retrieved arthropod DNA from just 96/314 samples of Lesser prairie grouse (*Tympanuchus pallidicinctus*) faeces, whilst Idaghdour, Broderick and Korrida (2003) could not obtain any predator DNA from around 10 out of 34 samples due to sample degradation, despite the fact that predator DNA should be far more numerous than that of the prey species (Deagle, Eveson and Jarman, 2006). Despite these limitations, metabarcoding of faecal samples has the potential to increase our knowledge of diet for species, especially for species with diverse diets that include many small and soft bodied prey.

5.2.3. The European nightjar

The European nightjar (*Caprimulgus europaeus*) is a nocturnal insectivore of conservation concern in the UK (Eaton *et al.*, 2015). The limited diet information available has been obtained through stomach content analysis and visual analyses of faeces from this and similar species in North America (Sierro *et al.*, 2001; Sharps, 2013; Knight *et al.*, 2018). Nightjars primarily feed on moths, beetles and flies (Cramp, 1985; Sharps, 2013), although this is dependent on location (Jackson, 2000). Given the clear importance of habitat for invertebrate populations (Fuentes-Montemayor *et al.*, 2012, Sullins, 2018), any change in habitat composition or configuration (e.g. removal of invertebrate-rich vegetation), could lead to a substantial decline in numbers of invertebrates and have subsequent effects on nightjar populations.

5.2.4. Aims

In order to understand any change in nightjar diet during a period of significant habitat change related to peatland restoration, I aimed to analyse the diet of a subset of individual European nightjars on a UK breeding site. I did this using metabarcoding techniques, which have not been published before in this species, and which should allow us to identify previously indistinguishable nightjar prey items that are soft-bodied and thus degraded due to digestion. Previous studies have highlighted that nightjars select for larger moths, due to both nutritional value (Bell, 1990; Razeng and Watson, 2015) and the greater ease of spotting larger individuals in low light (Bayne and Brigham, 1995; Brigham and Barclay, 1995). Therefore, to understand if any size selection took place, I used moth traps to obtain a measure of prey availability across the sites. Moth traps, although low-powered, should provide a reasonable representation of moth availability in a limited area despite different responses to light by different species (Baker and Sadovy, 1978; Merckx *et al.*, 2014) and have been used to quantify prey availability in other nightjar studies (Sharps, 2013; Henderson, Hunter and Conway, 2018).

Firstly, I wanted to quantify individual-level diversity and composition of diet. I expected diet to vary among individuals, as individuals vary in their habitat preferences (see Chapters 2 & 3). However, at a population level, I hypothesised that nightjars would specialise on larger moths, in line with the literature (Cramp, 1985; Sharps, 2013). If nightjars are specialising on larger moths, I would expect to see a difference between diet composition and prey availability in terms of size, where faecal samples contain a higher proportion of larger-bodied specimens than is apparently available. Secondly, I wanted to understand if there was any difference between male and female dietary composition that may be related to their differing roles during parental care, rather than size dimorphism, which is not present between male and female nightjars (M. Delaunay, *pers comm*; unpublished ringing data, this study). I hypothesised that as females spend only a short time foraging due to their role in incubation, they would be less targeted in their foraging, and as a result would display a larger dietary diversity than males, a difference which may be particularly strong during periods of bad weather if females are more constrained due to incubation of eggs or increased levels of chick brooding. Lastly, I expected to see a change over time due to the removal of large areas of vegetation and weather variation between years (Clare *et al.*, 2011, 2014). Large areas of clearfell have been created annually on the breeding site, which are known to influence both composition and abundance of moths (Stanton, Clark and Morrissey, 2017). I expected to see a decline in diet diversity because of the reduction in area of the richest moth resources, i.e. birch woodland (Winiger *et al.*, 2018). Weather, and thus emergence and activity of moths, can vary substantially throughout the breeding season and between years. Nightjars are constrained in their breeding due to migration, and arrive in the UK in May and June, raising one or two broods prior to return migration in September. This short window should coincide with peaks of preferred moth prey, particularly larger specimens which are more active when temperatures are higher, and weather is more stable (Jones and Cresswell, 2010). Therefore, unseasonal or prolonged periods of poor weather during the breeding season (e.g. decreased temperatures, high rainfall) may cause a deficit of food, illiciting a change in the diet of the nightjars, potentially where individuals become more generalised and more similar in their dietary choices, due to a narrower range of available species (Kotler and Brown, 1988; Orlowski *et al.,* 2014).

5.3 Materials and methods

5.3.1. Faecal sample collection

Nightjar faecal samples were collected during the breeding season (June to August, 2015 to 2018) and were obtained from daytime roosts and nests. Nightjars form discrete spherical pellets, which were placed into sterile, 30ml tubes with cocktail sticks, then labelled with a number, the date, location and the sex of the bird, identified visually in the field. Multiple pellets were collected where available, but I prioritised fresh samples; very dry and desiccated samples were not collected due to DNA degradation. Fresh samples were identified by their colour and consistency, being softer than older pellets and darker in colour. Samples were stored in a -20°C freezer temporarily, then -80°C for longer term storage. All lab work took place at the NERC Biomolecular Analysis Facility (NBAF) within the Department of Animal and Plant Sciences, at the University of Sheffield.

5.3.2. Prey availability

I obtained an index of invertebrate prey availability on the breeding site using 15W actinic moth traps, placed at eight locations on each of Thorne and Hatfield Moors (total N = 16; Figure 5.1). Four sites were trapped during alternate weeks and the range of sites was designed to cover all major habitat types and structures. I recorded numbers of species and individuals, calculated species diversity (Simpson's dominance; Morris *et al.* (2014) and also allocated species to a size category (in mm; <25, 25-30, 30-40, 40-50, 50-60, or >60) based on Townsend and Waring (2014).

Figure 5.1: Actinic moth traps in different habitat types on Thorne and Hatfield Moors, South Yorkshire. Moth traps were placed in all main habitat categories on a rotational weekly basis to obtain a measure of prey availability that might influence nightjar diet. Bulb strength: 15W.

5.3.3. DNA extraction

DNA was extracted from faecal samples using the QIAmp DNA Fast Mini Stool Kit (Qiagen, Germany), following the human DNA extraction protocol (Figure 5.2), adapted to suit more highly degraded DNA from bird faeces by increasing the amount of sample (300mg vs standard 220mg) and inhibitex buffer used (1.4ml vs standard 1ml; Figure 5.3). Samples were also incubated for an increased amount of time after the lysis buffer was added (20 minutes vs. standard 10 minutes), to increase the number of cells broken down from the sample and increase DNA yield. DNA extracts were quantified using a Fluostar Optima (BMG Labtech, Germany) and kept in a -20°C freezer until PCR.

Figure 5.2: Example of nightjar faecal pellet under initial dissection in a plastic weighing dish, prior to DNA extraction. White substance is hardened urea. On the right hand side is a parasitic worm found within the sample.

5.3.4. PCR

Primers were chosen for PCR-testing for their specificity, i.e. they targeted invertebrates, as well as their ability to amplify degraded DNA (Zeale *et al.*, 2011; Clarke *et al.*, 2014; Alberdi *et al.*, 2018), as faeces contains a very small amount of mitochondrial DNA to enable species identification (Hebert *et al.*, 2003). Suitable primers were chosen to target fragments of 100 to 180 base pairs (bp), since fragments below 100 bp may not be distinguishable from the primers or may not target a varied enough region to allow species-identification (Deagle *et al.*, 2014). Suitable candidates and combinations were chosen for testing from numerous COI and 16s short primers in the literature; all sets targeted between 127 and 313bp regions, were either invertebrate-specific or universal, and targeted COI and 16s genes. Two commonly-used primers targeting the COI gene ('Uniminibar' in Meusnier *et al.*, 2008; 'ZBJ' in Zeale, Butlin, Barker, Lees, & Jones, 2011) were not compatible with my samples, creating lots of primer dimer (interactions that occur within the primers themselves during PCR, leading to erroneous sequence creation; Brownie *et al.,* 1997) and only sporadic amplification across groups. Instead, the 16s region amplified by 16sINS1Short F and R (156bp, Clarke, Soubrier, Weyrich, & Cooper, 2014) was identified through initial PCR testing as more likely to provide even amplification across all samples. I ran a temperature-gradient PCR from 55 – 70°C with a series of faecal samples, moth and nightjar positive samples to counteract the preferential amplification of predator DNA, and determined an ideal temperature of 62°C, where moth control samples amplified but nightjar did not. Following these steps, PCR products were visualised on a 1% agarose gel with a 100bp ladder to verify amplification success (Figure 5.4).

5.3.5. Reference DNA library

To create a reference 16S sequence library representative of some of the assemblage present on the site, against which I could compare the sequencing reads once produced, DNA was extracted from 81 specimens of 80 species of moths and beetles, collected from moth traps at the Humberhead Peatlands. Specimens were identified to species using Townsend and Waring (2014). Extractions were carried out following an Ammonium acetate precipitation method (Bruford *et al.*, 1998), where a digestion solution, Proteinase K and Ammonium acetate were added to a sample of moth legs and incubated overnight, to penetrate the invertebrates' solid chitin-based exterior. Extracted insect DNA was Sanger-sequenced using an ABI3730 (Applied Biosystems, ThermoFischer Scientific, USA), following PCR (see Appendix I for protocol) using both the *ZBJ* COI primers (Zeale *et al.*, 2011) and the chosen *16S1short* primers (Clarke *et al.*, 2014). Due to the lack of British 16S moth sequences in the GenBank database, verification of species identification by comparing the sequenced moth 16S genes against COI sequences was necessary. Almost all British moth species has a COI sequence present in the global database, and these were identified using BLAST (Altschul *et al.*, 1990). Once verified, 16S sequences were submitted to the NCBI GenBank database (consecutive accession numbers: MK620910 – MK620988; Clark *et al.* 2016).

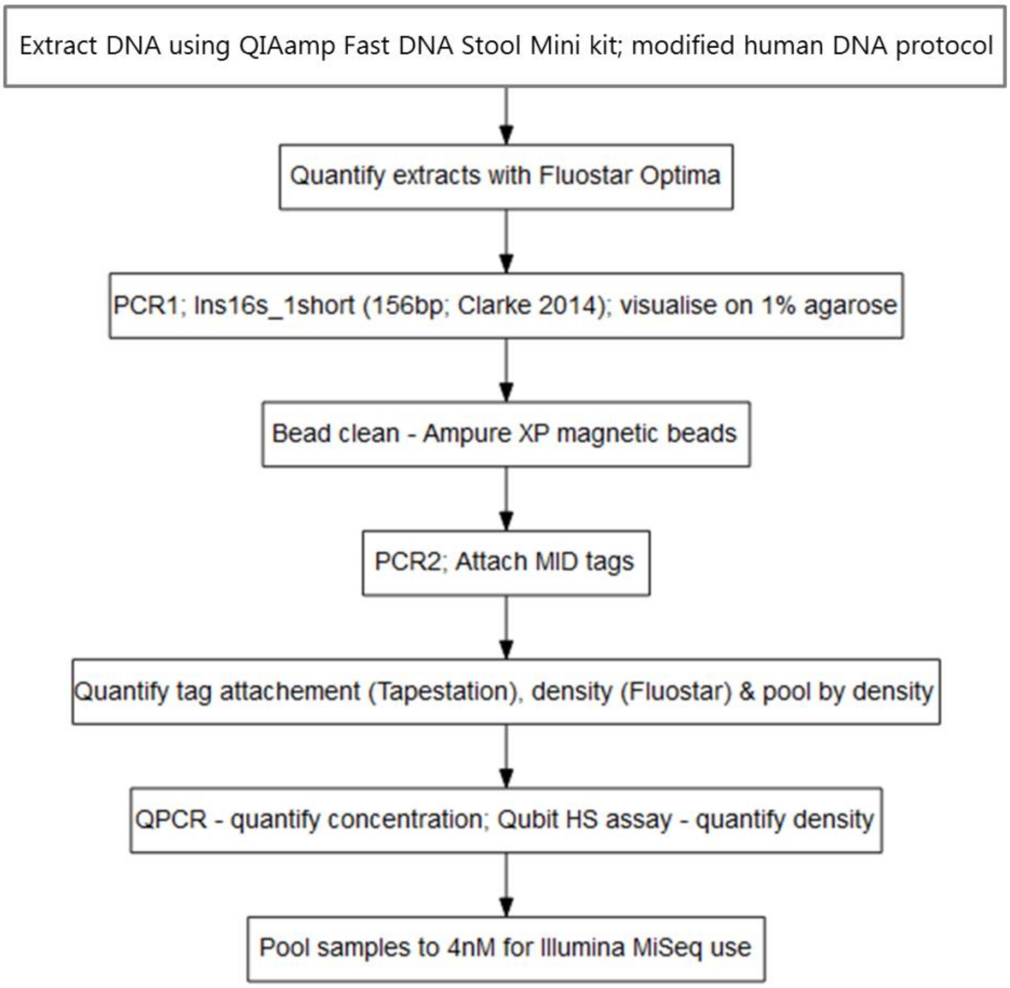


Figure 5.3: Workflow used for faecal sample extraction and sequencing preparation.

5.3.6. Sequencing

Following initial PCR, replicates were cleaned in a multi-step procedure with Ampure XP magnetic beads (Beckmann Coulter, USA; Figure 5.3), to remove DNA fragments of an inappropriate length. Multiplex identified (MID) tags were attached to the bead-cleaned samples through a second PCR procedure to allow individual identification of samples after pooling (Brown *et al.*, 2014; Rennstam Rubbmark, Traugott, Sint, & Horngacher, 2018). A random selection of samples was tested on an Agilent 4200 Tapestation system (Agilent Technologies Inc., USA) to verify attachment of the multiplex identified tags. All samples were quantified on the Fluostar and pooled into 12 libraries of 12 samples by row (individual sample contribution to library dependent on initial density (ng/ul), totalling 20ul).

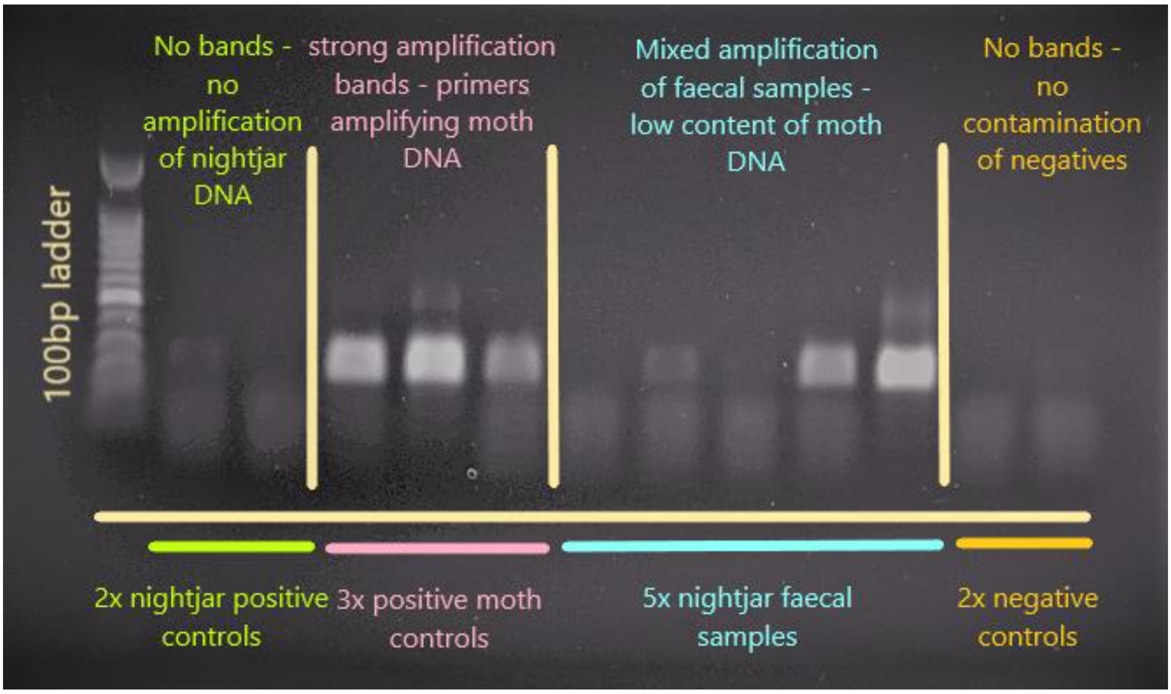


Figure 5.4: Example of gel electrophoresis run at 62ºC to visualise amplification of DNA from nightjar faecal samples using 16S invertebrate-specific primers from Clarke *et al.,* 2014. White bands represent amplification of ~160 base pair long fragments of DNA targeted by the primers. Nightjar and moth positive controls used to confirm amplification of correct taxa DNA.

Next, qPCR was carried out to quantify DNA density in each of the libraries using a QuantStudio 12K Flex Real-Time PCR System (ThermoFischer Scientific, UK). Library samples were tested at three dilutions (1:100, 1:1000, 1:10,000), along with six KAPA qPCR DNA density standards (at concentrations of 20, 2, 0.2, 0.02, 0.002 and 0.0002) and one set of negative controls, in triplicate (thus, n = 108; see Supplementary Information for qPCR run information). The 12 libraries were then pooled into one sample (total volume of 20ul, based on individual library density), which was then quantified on a Qubit Flurometer (Invitrogen, ThermoFischer Scientific, USA), using a high sensitivity assay. Shorter, artefactual sequences were numerous and could not be removed by bead cleaning so were run on an automated gel electrophoresis Blue Pippin (Sage Science, USA), to remove size-selected bands of between 250 and 400bp. In order to achieve the necessary density of 4nM for Illumina sequencing, samples were again tested using qPCR and diluted as necessary. Samples were processed on the Miseq on a 2 x 150bp run with 10% of PhiX added to improve the quality of the results.

5.3.7. Bioinformatics

Bioinformatics to process and quantify the raw reads from the Illumina Miseq took place on the high-powered computer cluster Iceberg at the University of Sheffield (Figure 5.5). I initially evaluated the raw sequence data using FastQC (Andrews, 2010) and removed Illumina adapter sequences and poor-quality reads using Trimmomatic (Bolger, Lohse and Usadel, 2014). Because the data are diet-based and thus have been subject to degradation both during digestion and afterwards during storage and processing, I trimmed reads with a Phred score of <24 within a 4bp sliding window and removed reads with a total length (amplicon + primers) of > 180bp. I aligned reads with Flash (Magoč and Salzberg, 2011), with an allowance of 10% mismatches (i.e. 1 in 10) across the sequence lengths.

I ran the *trim.seqs* function in Mothur (Schloss, 2009) to match the reads to the 16S primer sequences and then remove the primer sequences, leaving only the targeted amplicon. Sequences were clustered in three stages using *Usearch* and *Unoise2* (Edgar, 2013, 2016). First, the dereplication of sequences to leave only unique haplotypes (using: *fastx_uniques*); second, the removal of chimeric sequences (using: *unoise_2*), and third, the clustering of sequences based on a 97% similarity match (Edgar, 2010; Razgour *et al.*, 2011; Alberdi *et al.*, 2018; using: *cluster_fast*).

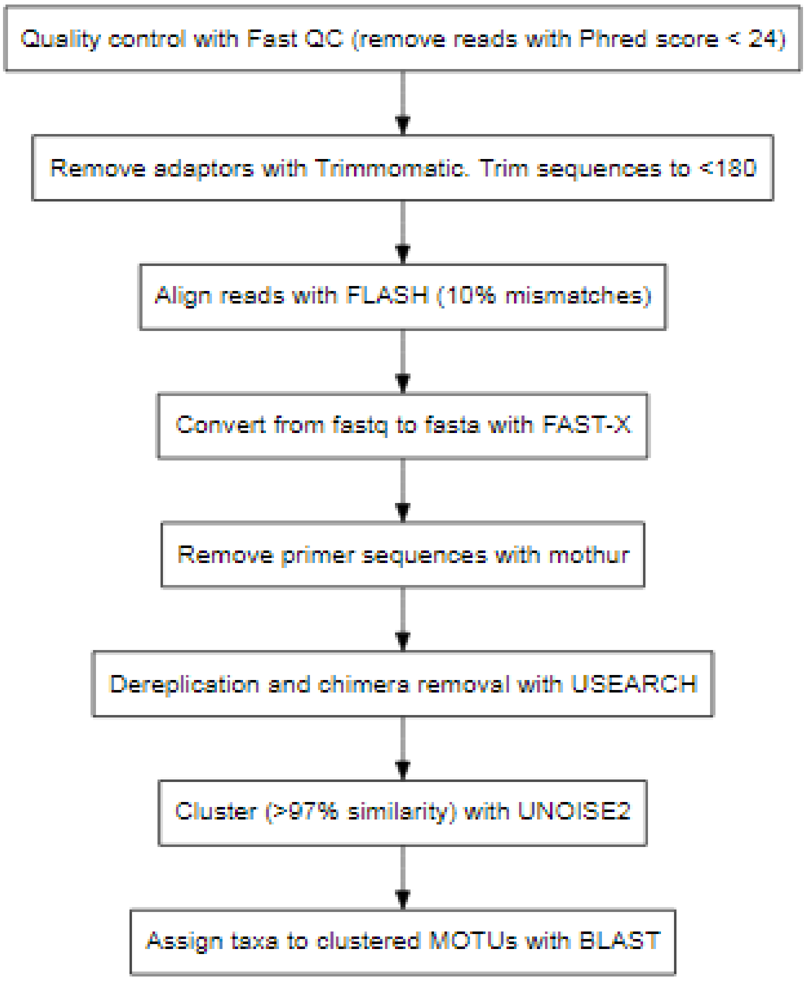


Figure 5.5: Bioinformatics workflow for analysis of NGS sequencing data from nightjar faeces.

Clustered units, commonly referred to as ‘molecular operational taxonomic units’ (MOTUs), were then compared to reference sequences in the NCBI nucleotide database using BLAST (Altschul *et al.*, 1990), with a 95% minimum sequence identity and maximum ‘e-value’ of 0.0001 representing the likelihood of obtaining the sequence by chance. I manually checked the BLAST output and converted the accession numbers to taxonomic identification numbers (or, ‘taxids’) using ‘*esummary’*. I converted resulting taxids using the NCBI taxonomic identifier tool (Sayers *et al.*, 2009) to full taxonomic lineages, to allow MOTUs to be assigned to a taxa. Unfortunately, despite myspecimen additions to the GenBank database, British species of invertebrate (particularly Lepidoptera) are lacking; thus, many MOTUs were assigned to species either not present in the UK or to multiple species with an identical level of certainty. Where this occurred, species were manually assigned to a higher level of classification (i.e. genus, where species could not be clarified, or family, where multiple genera were assigned by BLAST). Therefore for all diversity analyses, I used a matrix of MOTUs, rather than species and/or genera because of the described discrepancy in assigning units. Classifying sequence reads this way allowed me to include all units identified through the clustering process, whether I were able to assign them to a known species or not (Clare *et al.*, 2011; Hawlitschek *et al.*, 2018).

Matrices of final read numbers and presence/absence matrices were finally created in R (v. 3.6). These were used to filter out low reads. Following De Barba *et al.* (2014) I set a sequence threshold of 0.05% of the total sequences per sample and removed MOTUs that did not meet this criteria. False positives (i.e. negative contamination), can occur at multiple stages in the extraction and PCR procedure (Ficetola *et al.*, 2015; Zepeda-Mendoza *et al.*, 2016; Alberdi *et al.*, 2018). Therefore, I used the negative controls to set filtering parameters for all samples (as in De Barba 2014, Porter 2013 and Corse 2017), where the number of reads in the negative controls were subtracted from other samples containing the same MOTUs. Although it reduced the number of samples in the final matrix, caution over false positives is important (Froslev *et al.*, 2017).

5.3.8. Statistical analyses

To understand more about breadth of nightjar diet, I first calculated frequency of occurrence (FOO) as the proportion of samples in which each order was found. As MOTU data cannot reliably be used to assess relative abundance of sequences nor biomass, I used the presence/absence MOTU matrices (produced in section 5.3.7) for all samples across all years to calculate Chao extrapolated species richness index (Chao and Chiu, 2016) and Chao dissimilarity indices in R package ‘vegan’ (functions 'specpool' and 'vegdist'; Oksanen *et al.*, 2019). Both of these methods work with incidence data (i.e. presence/absence data) rather than abundance data and were also chosen for their ability to account for unknown species (Chao, Chazdon and Shen, 2005), which was important here having filtered the data multiple times and potentially having missed certain species during amplification.

As this is incidence data, beta diversity can be reliably calculated (Anderson, 2006a), analogous to compositional differences. To test for significant differences in in beta diversity between subgroups of samples, I used multivariate tests for homogeneity of group dispersions (a principle-components type analysis;

Anderson, (2006a, 2006b)). These multivariate permutation tests take dissimilarity indices (here, Chao dissimilarity indices) and calculate a mean dissimilarity per subgroup and then calculate the distance to the mean from each individual sampling unit (Anderson, 2006a). The tests are able to deal with non-normality, multiple variables and zero-inflation (implemented through function 'betadisper' in vegan; Oksanen *et al.*, 2019). These were followed with multivariate anovas (using ‘adonis’ in ‘vegan’) to explore year, month and sex-related group differences in the means of the dissimilarity indices (McClenaghan, 2019). I estimated confidence intervals related to the mean and group dispersion using Tukey HSD tests.

To explore size composition for the subset of MOTUs identified to species level within each sample, I allocated each species to a size category according to mean wingspan, as with the moth trap catches (see section 5.3.2). To test for significant differences in the frequency of occurrence of different size classes between years I used Kruskal-Wallis rank sum tests, because the proportional data was non-normal and sample sizes were relatively small.

To understand how prey availability varied with environmental covariates, I tested for differences in moth trap diversity (calculated in 5.3.2. using Simpson’s dominance) by year, month and habitat using PERMANOVA. Covariates were: habitat type at trap location (based on the 14 category habitat map, categorised based on vegetation type and structure; details in chapters 2 and 3); nightly mean temperature (degrees celsius, obtained from the Met Office MIDAS database (Met Office, 2012); nightly total rainfall (in mm, obtained from the Environment Agency at Dirtness Power station, unpublished dataset) and lunar illuminance (percentage of moon face illuminated; obtained for each night using R package ‘lunar’, Lazaridis, 2014).

Finally, to test for size selection of moth prey by nightjars, I used proportional Z-tests to compare the frequency of occurrence of each size class found in the faecal samples, to those found in the traps, between years and months.

5.4. Results

I retrieved a total of 13,900,616 reads from 141 faecal samples using the MiSeq. After trimming and clustering, total of 1631 MOTUs were identified. After assignment with BLAST, MOTUs that had been assigned to non-arthropod species, i.e. *Homo sapiens*, *Sus scrofa*, *Columba palumbus* and *Akkermansia sp*, were removed, resulting in a list of 740 MOTUs. After filtering negative contamination and sequences below the minimum sequencing threshold I retained a final total of 625 unique MOTUs from 130 samples (i.e. 11 samples contained no reads). 62 of the 625 MOTUs were present in >5% of the samples; the remaining 563 MOTUs were only present in a minimal number <5% of samples. Of these, 65% of these could be identified to species, 5% to genus, 12% to family and 18% only to order (these were all Lepidoptera).

5.4.1. Diet composition, richness and variation

Lepidoptera were found in 99% of samples and were subsequently the most frequently occurring order. This was followed by Diptera (27%), Coleoptera (9%), Neuroptera (7%) and <1% of both Hemiptera and Hymenoptera (Figure 5.6). Of the sequences identified to species level, the most common species present were *Lathoe populi* (in 43% of samples), *Autographa gamma* (45%), *Euthrix potatoria* (45%), *Lycophotia porphorea* (49%), *Mythimna impura* (50.4%), and *Noctua pronuba* (52%).

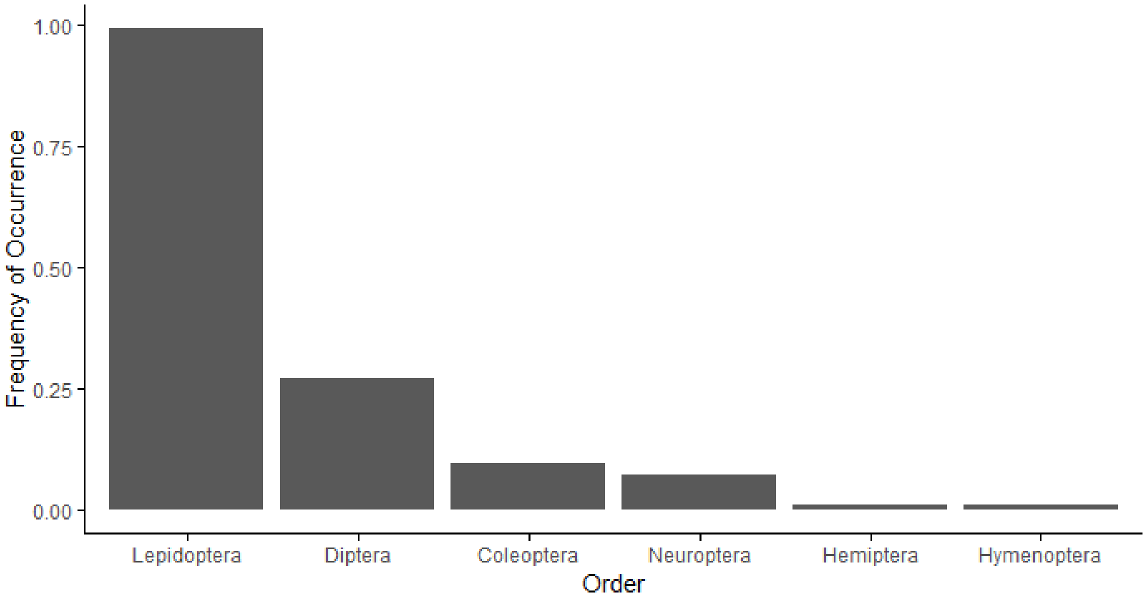


Figure 5.6: Frequency of occurrence (i.e. proportion of samples the order is found in) of each order identified within nightjar diet samples.

Samples contained an average of 15.7 MOTUs (+/- SD 9.6). Mean Chao dissimilarity value was 0.79 (+/- 0.27). Samples did not differ significantly in their composition or dissimilarity between sex (permutation test of homogeneity of variance: Female: n = 60, Male: n = 56; $F_{1,114}$: 0.083, p = 0.774) nor month (June: n = 31, July: n = 57, August: n = 34; $F_{2,119}$: 1.910, p = 0.153; Figures 5.7 a,b, and c). However, there was a significant difference in sample variance between years (permutational test: 2015: n = 8, 2016: n = 21, 2017: n = 39, 2018: n = 62; $F_{3,126}$: 5.342, p = 0.002; Figure 5.7d). The homogeneity of variance tests indicated a significant difference in the distance of the samples from the mean (i.e. the variance) between 2017 and 2018 (Tukey HSD p = 0.002), whereby the samples in 2017 were significantly more variable (i.e. spread out from the mean), compared to 2018. Multivariate anovas confirmed differences in mean sample composition between years (Table 5.1; Figure 5.7d), and also showed that despite variance being similar between months, there was a significant difference between the mean composition of samples from June, compared to July and August (Table 5.1; Figure 5.7d), although the relationship is weaker than that of year (R^2 value for monthly differences: 0.03; R^2 value for yearly differences: 0.15) and there was no interaction. There was no significant difference in mean sample composition between sexes ($F_{1,114}$: 1.29, p = 0.24).

Where I could identify MOTUs to species and therefore allocate an approximate size, I found that most faecal samples contained species with a wingspan of between 30 and 40mm (in 96% of samples), followed by moths with a wingspan of 50 - 60mm (in 74% of samples) and the largest moths (>60 mm wingspan, in 46% of samples). The five most commonly identified species in the samples all had a wingspan of more than 30mm; two of these had a wingspan of more than 50mm (*A. gamma, L. populi*). I identified a linear change over time in the occurrence of the largest moths (>60mm); these were present in a higher proportion of samples in 2018 (66%), compared to all other years (2015: 0%; 2016: 14%; 2017: 36%; X^2: 27.08, df = 3, p <0.0001). Non-linear changes in occurrence of other size categories were also present. Significantly higher numbers of faecal samples contained 40-50mm moths in 2016 (90%) compared to other years (2015: 50%; 2017: 67%; 2018: 53%; X^2: 10.16, df = 3, p = 0.02). Significantly higher numbers of faecal samples contained 30-40mm moths in all years (2016: 100%; 2017: 87%; 2018: 95%) compared to 2015 (63%; X^2: 12.66, df =3, p = 0.005). There were no significant differences in the occurrence of any size category between months, but samples from female nightjars were significantly more likely to contain small moths (<25 mm wingspan; 23%) than males (7%; X^2 = 4.62, df = 1, p = 0.03), but there was no difference in the other size categories.

Table 5.1: Permutational multivariate analysis of variance used to test for significant differences between months and years (separately and the interaction between the two variables) in mean sample composition.

Variable	**Df**	**Sum of Sq**	**F**	**R2**	**P**
Month	2	1.31	2.28	0.03	0.005
Year	3	6.42	7.46	0.15	0.001
Month * Year	5	1.9	1.33	0.05	0.066
Residuals	111	31.85		0.77	
Total	121	41.47		1	

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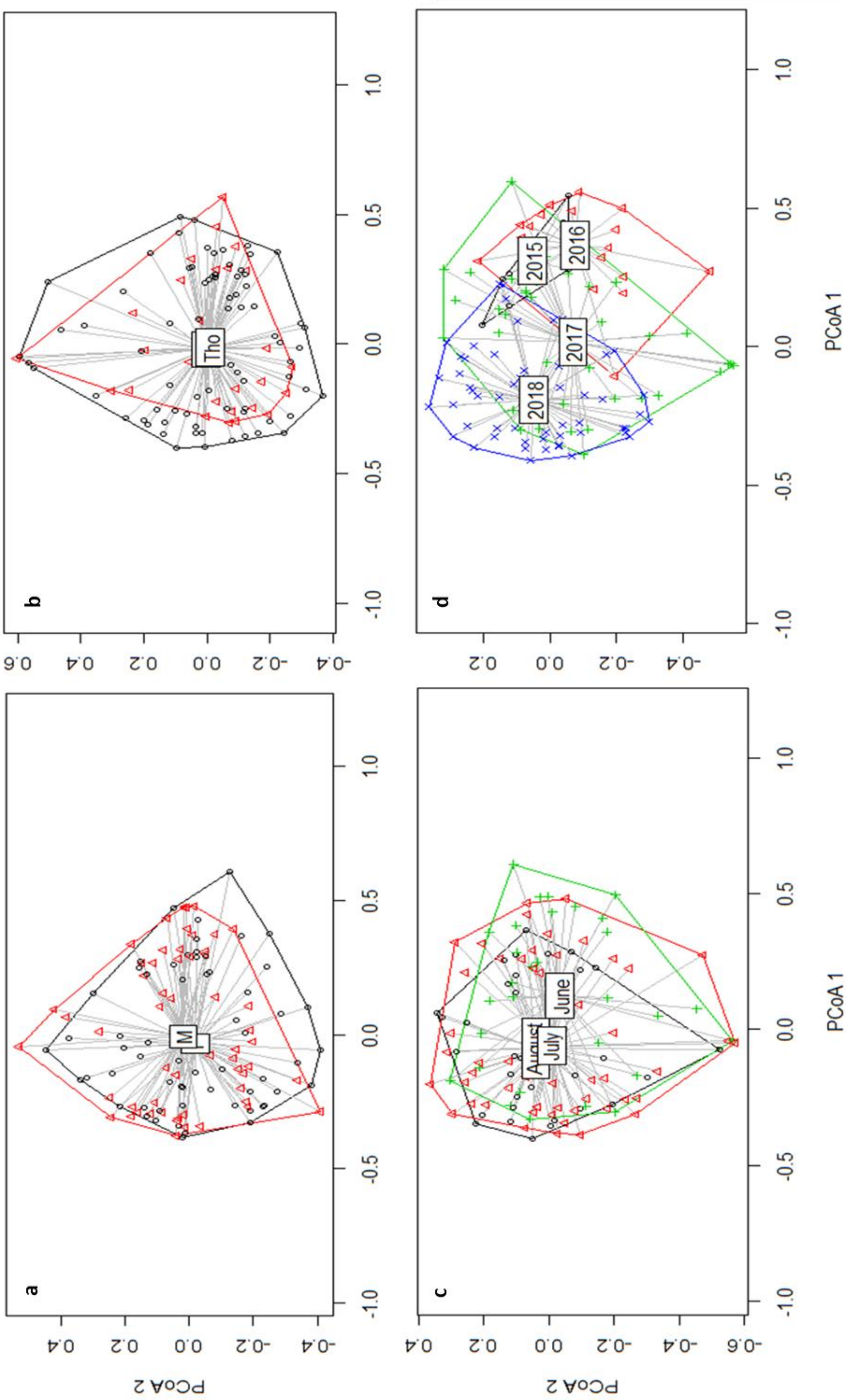

Figure 5.7: Homogeneity of variance analyses represented on principal components axes representing the variance and distribution of faecal sample species composition grouped by a) sex, b) site, c) month, d) year. Sample sizes vary between groups; numbers are included in the text.

5.4.2. Prey availability

To obtain a measure of prey availability, I collected weekly moth trapping data onsite. I captured 3575 insect individuals of 109 species in 135 trapping sessions, during June, July and August 2016- 2018. Significantly higher numbers of moths were trapped in 2017 and 2018 (individuals: $F_{6,165}$: 16.95, $p < 0.0001$; species: $F_{6,165}$: 15.2, $p < 0.0001$). Mean Simpson's dominance was 14.07 (+/- SD 9.23), and was significantly higher in August (18.6 +/- 8.79) than June (7.19 +/- 4.68), and again in 2017 (14.53 +/- 8.69) and 2018 (19.55 +/- 7.84), compared to 2016 (5.28 +/- 4.73), but there was no relationship with temperature, habitat nor lunar illuminance ($F_{13,121}$: 11.17, R^2: 0.55, $p < 2.13e-15$). Mean Bray-Curtis dissimilarity was 0.84 (+/- SD 0.16). PERMANOVA outputs indicated significant effects of all covariates on moth trap dissimilarity indices (Table 5.2), except lunar illuminance. Pairwise permutation tests on the covariates in the PERMANOVA analyses indicated that many of the effects were non-linear and that, as with the faecal samples, there was a large amount of variation within groups, leading to weak R^2 values. This was particularly the case with temperature and rain, where Tukey post-hoc confidence intervals all overlapped zero, indicating non-significance.

Table 5.2: PERMANOVA analysis of Bray-Curtis dissimilarity indices to test for significant differences in moth trap catch dissimilarity between year, month, temperature, rainfall (mm), Habitat type and lunar illuminance (% of moon face illuminated). Signficant results highlighted in bold.

Factor	Df	Sum of Squares	F	R^2	P
Temp	1	1.268	3.91	0.03	**0.001**
Month	2	2.879	4.44	0.06	**0.001**
Year	1	2.589	7.99	0.05	**0.001**
Rain	1	0.673	2.08	0.01	**0.008**
Habitat	8	3.37	1.3	0.07	**0.01**
Lunar %	1	0.503	1.55	0.01	0.052
Residual	120	38.896		0.78	
Total	134	50.179			

Overall, numbers of moths varied significantly between different habitats (Figure 5.8). Woodland and habitat immediately after clearance had significantly fewer moths found in the traps (cleared habitat: β -0.797 +/- se 0.333, t: -2.461, p: 0.02; Woodland: -0.70, t: -1.849, p: 0.07). Whilst mean number of moths was higher in cleared habitat with one year of regrowth, this was not significant (*β:* 0.379, t: 1.15, p: 0.252).

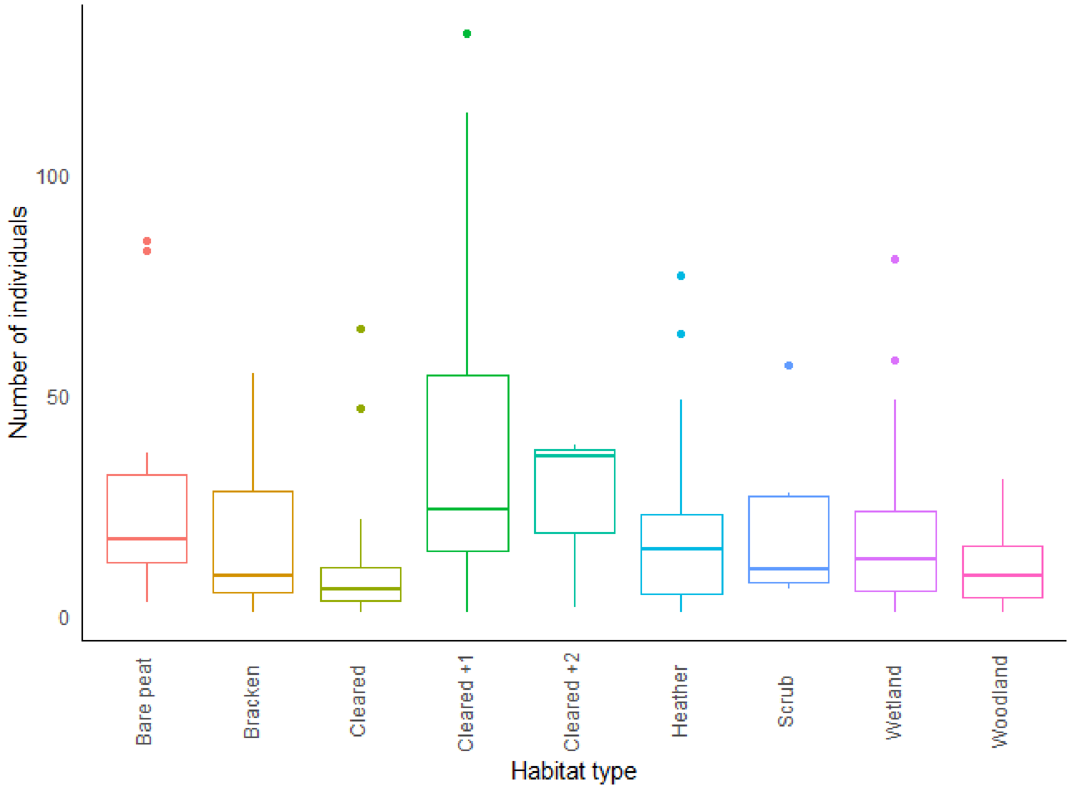

Figure 5.8: Number of individual moth specimens acquired via moth traps in each habitat type. Median line plotted, plus interquartile range and outliers as points.

Significant results appeared when testing for year differences in moth trap sample variance and dissimilarity. All three years were significantly different from each other ($F_{2,132}$: 13.495, p = 0.001; Figure 5.9a) but 2016 displayed the strongest differences, with samples remaining closer to the mean and containing less overlap with 2017 and 2018. June catches, compared to July and August, were also significantly different ($F_{2,132}$: 6.37, p = 0.001; Figure 5.9b). Although habitat emerged as significant in the PERMANOVA, there were also significant differences in the amount of variation (permutational homogeneity of variance test: $F_{8,126}$: 2.23, p = 0.03). This indicated that all habitats contained variable moth trap compositions, and large amounts of overlap (Figure 5.9c).

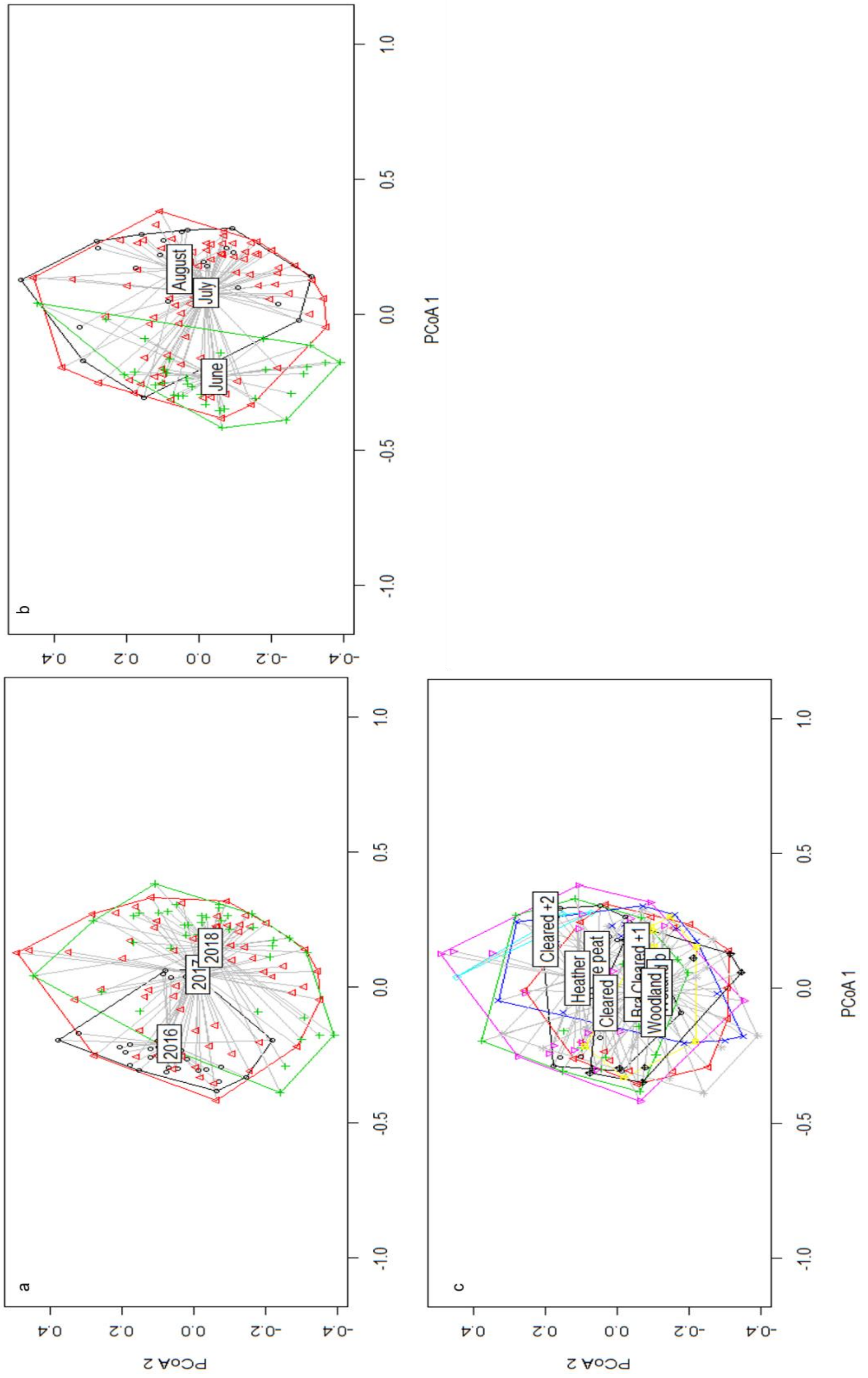

Figure 5.9: Homogeneity of variance analyses presented on principal components axes representing the variance and distribution of moth trap catch composition grouped by a) year, b) month and c) habitat.

5.4.3. Size selection in diet samples compared to prey availability

A higher proportion of nightjar diet samples contained the largest moths (>60mm) compared to the moth trap catches, but the difference was only significant in 2017 (diet samples: 0.4, moth traps: 0.18; X^2: 4.61, df= 1, p = 0.03) and 2018 (diet samples: 0.67, moth traps: 0.34; X^2: 9.5, df =1, p = 0.002; Figure 5.10). In contrast, moth trap catches were more likely to contain smaller moths (<25mm and 25-30mm), but again, the difference was only significant in one year (2018: diet samples <25mm: 0.18, moth traps: 0.49; X^2: 9.55, df =1, p = 0.002; diet samples 25-30mm: 0.72, moth traps: 0.98; X^2: 9.23, df =1, p = 0.002; Figure 5.10).

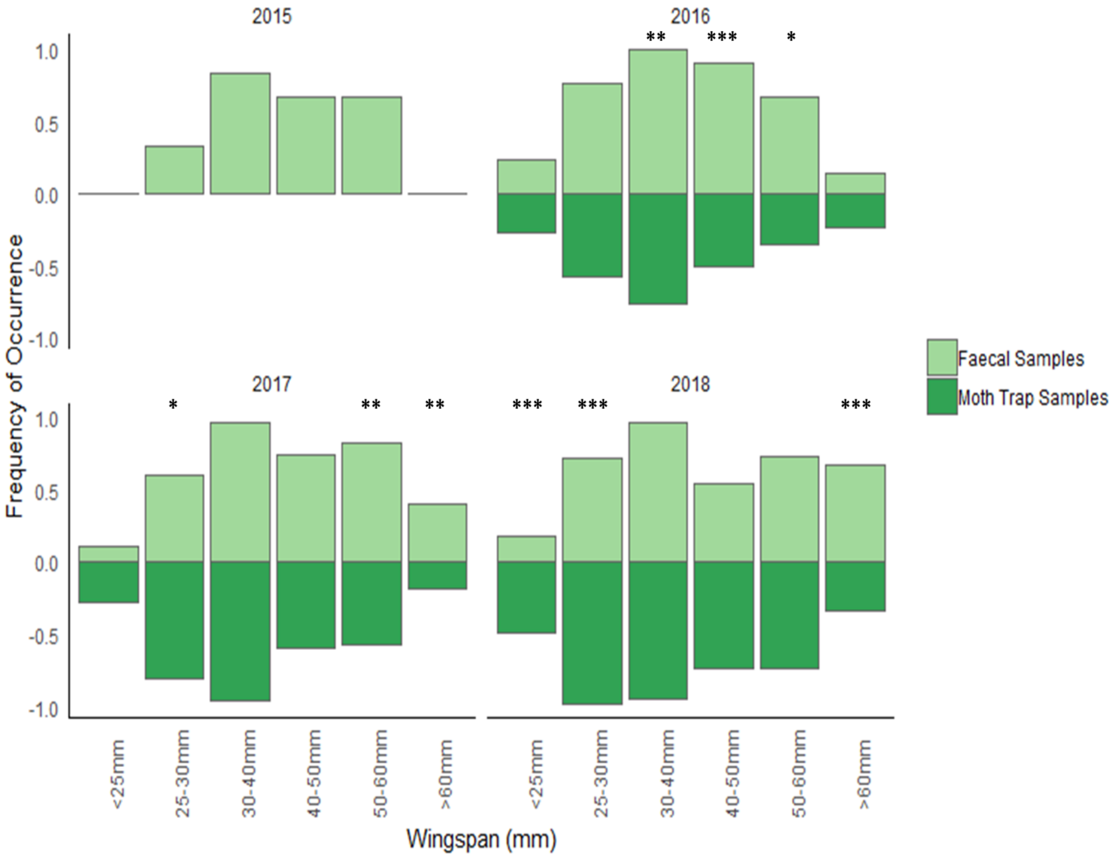

Figure 5.10: Frequency of occurrence, i.e. proportion of each moth size class in diet samples and moth trap catches, for each year. Differences between the faecal samples and moth trap samples were calculated using proportional Z-tests and significance levels are denoted by: * = <0.06; ** = <0.05; *** = <0.01. NB: No moth trapping took place in 2015.

In 2016, faecal samples were significantly more likely to contain 30-40mm and 40-50mm moths (30-40mm: diet samples: 100%, moth traps: 74%; X^2: 4.69, df =1, p = 0.03; 40-50mm: diet samples: 90%, moth traps: 5%; X^2: 6.99, df =1, p =

0.008), but this was not replicated in other years. Across all years, less than 18% of diet samples, contained moths with the smallest wingspan (<25mm).

I also tested for significant differences between months in the frequency of occurrence of different size classes in diet samples and moth traps as I previously found significant differences in their respective beta diversity and variances (see 5.4.1 and 5.4.2). Differences between diet samples and moth trap availability were less clear between months (Figure 5.11). In June and August, diet samples were significantly more likely than moth traps to contain larger moths (June: 50-60mm: diet samples: 22%; moth traps: 4%, X^2: 11.66, df =1, p = <0.001. August: >60mm: diet samples: 15%, moth traps: 3%, X^2: 5.73, df = 1, p = 0.02).

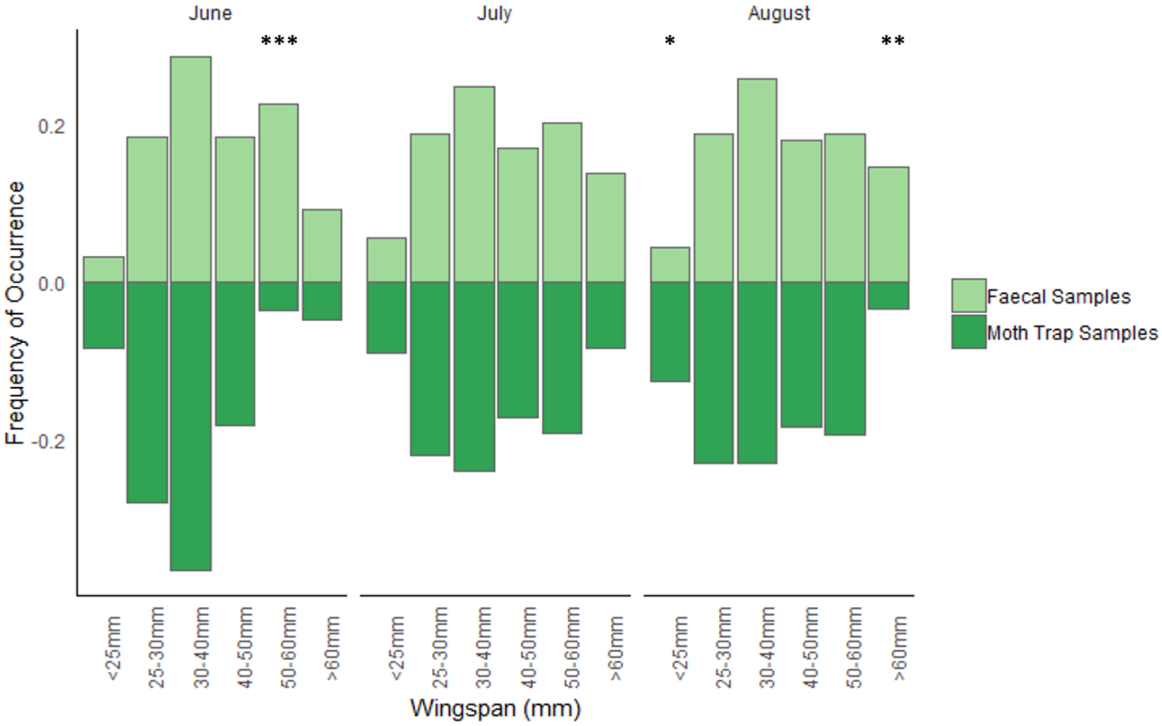

Figure 5.11: Frequency of occurrence for each month. Differences between faecal samples and moth trap samples were calculated using proportional Z-tests, and significance levels are denoted by: * = <0.06; ** = <0.05; *** = <0.01.

5.5 Discussion

Our analyses showed the strongest variation in dietary richness and variance occurred between years. I identified 625 unique MOTUs within 130 faecal samples, with a mean of 15 MOTUs per sample. This shows that diet was broad and variable among individual samples. Samples were more varied in 2017, compared with all other years and mean beta diversity was significantly different between 2017 and 2018. There was also a significant difference in diet beta diversity between months, specifically June compared to July and August, as well as size-biased prey selection, the magnitude of which varied annually and seasonally. Overall, specimens of larger moth species occurred more frequently in nightjar diet samples, than in moth traps, with larger specimens taken more frequently in June and August, compared to their availability. No strong sex differences were identified, although occurrence of smaller moths varied between the sexes and were significantly more likely to be found in female diet samples, than in those from males.

5.5.1. Nightjar niche breadth

I found that individual diet samples had high dissimilarity, demonstrating a broad population niche. Although each pellet provides a single snapshot, this could point to potential individual specialisation, as to my knowledge, none of the samples were from the same individuals (Bolnick *et al.*, 2011) and the study was carried out over four years, with samples from each year. Intraspecific variation in diet is common and can reflect both resource availability and the avoidance of competition through resource partitioning (Kotler and Brown, 1988; Maldonado *et al.*, 2019), or habitat selection, which I found in this population of nightjars (Chapter 3). However, for species exploiting patchy, ephemeral resources as the nightjars are here, it is beneficial to be generalist and flexible to be able to adjust to prey availability and abundance (Maldonado *et al.*, 2019; Szigeti *et al.*, 2019). This is particularly the case with prey such as moths, which can fluctuate with short-term weather conditions (Yela and Holyoak, 1997).

There was a difference among years in sample composition; samples were more varied from each other and further away from the mean in 2017, particularly compared to 2018. This indicates that the population might have responded to variation in prey availability by widening their niche (Maldonado *et al.*, 2017). There was a difference in the mean beta diversity between years, where 2018 was slightly different to all other years in sample composition (although some of this is accounted for by the wide variance within years). There was also a difference in mean beta diversity between months, where June was different in sample composition to July and August. These annual and seasonal differences were consistent, with no interaction. Therefore this suggests that nightjars were responding to changes in prey availability related to emergence times and weather conditions. Annual and seasonal variation in moth community diversity and overall abundance have been shown to be related to variation in climate (Summerville, Bonte and Fox, 2007; Spitzer and Lepg, 2019).

Here, prey availability onsite significantly differed between years, supporting the annual differences in dissimilarity indices. Significantly more moths (both individuals and species) were caught in 2018, in August and when rain was lower, as well as when temperatures were warmer, although this was only weakly significant. Beta diversity of moth trap catches was significantly different between months, especially between June and July/August, as well as in 2017 and 2018, compared to 2016. These changes in moth availability on an annual basis might therefore reflect the changes seen in faecal sample composition, and again indicate the flexibility of the birds in their diet choice, according to availability. It is important to consider that the samples of moths obtained from the light traps, is not representative of total site availability. The traps were comparatively weak (15W actinic bulb), which should mean that all the catches were representative of what was in the immediate area during each capture occasion. Truxa and Fiedler, (2012) found that the attraction radius of low-power traps was often only around 10 metres, meaning there should be little attraction of individuals from adjacent habitats, which would skew the results. Merckx *et al.* (2014) found this to be particularly true for noctuid moths, which were common components of the catches and of the diet samples.

Nightjar diet samples as a whole had high occurrence of moths of > 30mm, which includes up to the largest possible size of around 80-90mm for some *L. populi* individuals. Large moth specimens should provide higher energy gain per item than small moths and this strategy of selecting for larger body size is identified as a foraging strategy in other nocturnal insectivores (Clare *et al.*, 2009; Vesterinen *et al.*, 2016). Contrary to expectation, no significant difference was found between male and female sample diversity (Mata *et al.*, 2016; Knight *et al.*, 2018), nor composition. Female nightjars spend more time on the nest (Chapter 4), particularly during incubation (Sharps *et al.*, 2015), whilst males spend significantly higher amounts of time and, presumably, energy (Thomas, Brigham and Lapierre, 1996), defending their territory. I therefore expected to find that females had more diverse diets, because of their limited foraging opportunity and perhaps because of differing nutritional requirements relating to egg production (Houston, 1997). However, not all females will be incubating during the period when the faecal samples were acquired. Additionally, males also take part in provisioning offspring once they have hatched, which perhaps points towards an overlap in male/female diet.

However, where species could be identified within the samples, female nightjar faecal samples were significantly more likely to contain smaller moths, potentially indicating higher opportunism due to limited foraging time, which I showed in Chapter 4. Foraging theory would suggest that both the shorter handling time of smaller moths and lower selectivity (i.e. they are taking prey more in line with availability) would benefit females in terms of energy gain when they are trying to concentrate on incubating (Pyke, 1984; Schoener, 2003), especially as these moths are more available in June which would often coincide with the start of incubation. However, information is lacking on when in the breeding stage samples were taken, i.e. eggs/incubation or chicks/provisioning, but this higher occurrence of small species may be harder to explain when female nightjars are provisioning rapidly growing chicks that need maximum energy gain, as opposed to just maintaining their own body condition (Paiva *et al.,* 2010).

Dominance of Lepidoptera in nightjar diet has been reported in other studies (Sierro *et al.*, 2001; Sharps, 2013), however this does not hold true for all species of Caprimulgid (Knight *et al.*, 2018), nor for the European nightjar when on its wintering grounds on the African continent (Jackson, 2000), where Coleoptera become much more prevalent. Coleoptera should provide more energy and nutrition for nightjars and therefore should be selected for, as their exoskeletons contain much larger amounts of protein than Lepidoptera (Razeng and Watson, 2015; Bell, 1990). However, this benefit must be traded off with more difficult digestion due to high amounts of chitin (Bayne and Brigham, 1995). That Lepidoptera are so prevalent in the diet of this population may reflect local availability of this prey type (exceedingly high numbers of larger moths, or very few numbers of Coleoptera) and an acclimatisation of the population (Maldonado *et al.*, 2019) to being almost entirely Lepidoptera specialists.

5.5.2. Prey selection by nightjars

Examining dietary and moth trap samples together, it is possible to obtain an estimation of what nightjars are consuming compared to local availability, bearing in mind that not all the MOTUs identified in the diet samples have been translated into species and that as mentioned above, trap catches do not represent entire site availability, but a very localised snapshot of moths. Species that occurred most frequently in the moth traps, occurred most frequently in the faecal samples, suggesting prey availability is important for driving foraging decisions in nightjars (Pyke, 1984). However, moth traps catches contained higher proportions of medium to small moths, whereas faecal samples displayed a slightly larger size bias, with medium to large moths present in almost double the number of diet samples compared to traps. This suggests that relative energy gain of the prey item is also influential, as well as its availability (Pyke, Pulliam and Charnov, 1977), the combination of which should be indicative of some flexibility in niche width (Araújo, Bolnick and Layman, 2011). Nightjars are visual predators and it has been suggested that they preferentially take larger specimens because they are easier to see at low light levels when most of their foraging occurs (Bayne and Brigham, 1995; Brigham and Barclay, 1995). Twilight foraging limits the time available for capturing prey, which should drive size bias upwards in line with the energy maximization – time minimization rule (Schoener, 2003; Pyke, 1984). In a study of foraging Common nighthawks (*Chordeiles minor*) compared with big brown bats (*Eptesicus fuscus*), Aldridge and Brigham (2008) found common nighthawks foraged for less time than expected, given their estimated basal energy requirements. They suggested that they must be taking larger than average prey to reduce time spent foraging (Schoener, 2003), in line with optimal foraging theory (Pyke, 1984; Emlen, 1966). My findings therefore suggest that availability of larger moths might be a strongly influential factor for foraging nightjars and represent their foraging preferences (Araújo, Bolnick and Layman, 2011; Schrimpf, Parrish and Pearson, 2012; Vesterinen *et al.*, 2016).

These results have implications for breeding nightjars in the context of reduced habitat availability, with the added stressor of changing climate. Insect, especially moth, populations globally, and certainly in agriculturally-intensive northern Europe, have declined significantly (van Strien *et al.*, 2019; Hallmann *et al.*, 2017), but declines appear to occur in different species and populations dependent on their current distribution and host plant type, relative to the amount of connectivity between habitats (Fox *et al.*, 2013). Larger-winged moth species are at higher risk of decline, along with those that inhabit woodland, grassland and heathland (Coulthard *et al.*, 2019). Both Thorne and Hatfield Moors are dominated by heather and birch woodland habitat and the nightjar population here is biased towards these larger-winged species. If moth populations continue to decline, disproportionately affecting larger species, this could have implications for nightjars in the future and might cause them to broaden their dietary niche (Pyke, 1984) and/ or force them into undertaking longer foraging trips (Schoener, 2003). Not only is there an overall decline, but many invertebrate species are altering their peak emergence times in response to rising temperatures, and the predictability of emergence is also changing (Charmentier *et al.,* 2019), which could have an effect on a migrating species such as the nightjar such that their temporal constraints related to arrival on the breeding grounds (Jones and Cresswell, 2010) cause a mismatch between arrival and peak prey emergence. This may have repercussions for individual fitness as they struggle to meet energy requirements for themselves earlier in the season (Thomas, Brigham and Lapierre, 1996; Aldridge and Brigham, 2008), or are not able to provide sufficient amounts of energy to their chicks when hatched. As a result, monitoring changes in dietary composition over time in vulnerable species could help to identify potential stressors within the population (Howells *et al.*, 2017).

5.5.3. Limitations of methods

Molecular methods, especially high-throughput sequencing or metabarcoding, has made it possible to identify physically unrecognisable remains of prey specimens for many taxa (Hawlitschek *et al.*, 2018; McClenaghan, 2019; Kartzinel and Pringle, 2015; and many more). Despite the leaps in development in recent years, it is still hindered by a few key challenges. Firstly, contamination of control samples with non-target DNA means that caution must be taken when conducting both the laboratory work and post-sequencing bioinformatics (Zepeda-Mendoza *et al.*, 2016). Although metabarcoding should be able to identify less common species, contamination and the subsequent filtering thresholds that must be taken to produce confident results, can sometimes remove these rare sequences especially if these are also representative of small specimen size. This may then have effects on the size categories represented from the final outputs. Secondly, a lack of reference sequences for particular groups of species in global databases (such as NCBI Genbank used for BLAST processing) means that species-level identification is not available for a relatively high proportion of MOTUs (Hebert and Gregory, 2005; Wilson *et al.*, 2011). Although we are still able to assess sample richness, variation and changes between months or years, understanding the ecological information that comes with a species-level assignment is invaluable (Hebert *et al.*, 2003).

Additionally, between- and within-sample variation in MOTU composition and diversity have been found in recent molecular studies (Alberdi *et al.*, 2018; Mata *et al.*, 2018), meaning that to obtain a more reliable estimate of diet, multiple samples from the same individual over a period of time should be taken. For more informed studies on individual specialisation in diet, longitudinal data (as opposed to a ‘snapshot’ of diet richness) are needed (Araújo, Bolnick and Layman, 2011; Bolnick *et al.*, 2011).

5.6. Conclusions

This work highlights the utility of faecal metabarcoding as a way of assessing the diet of the European nightjar and expands on previous visual dissection of faecal pellets. Improvement of these methods is still needed, particularly where reference sequences that make species-level identification possible are lacking. European nightjars breeding on Thorne and Hatfield Moors displayed a preference for Lepidoptera over other flying insects and for those species with a mean wingspan of >30mm. Nightjars appeared to select prey based on availability and size; their diet was composed of the most frequently occurring size classes, but with a bias towards larger items. Diet varied between single samples, displaying high overall dissimilarity, and was also significantly different between years, indicating population flexibility through individual variation and in response to seasonal and annual environmental variation. Whilst the population is able to adjust its diet apparently in response to variation in prey availability as a consequence of varying environmental conditions, ultimately they are reliant on there being a sufficient population of aerial insects, which are declining in abundance due to climate change and habitat loss. Therefore, it is important from a conservation perspective, to manage for a variety of habitat types and structures that can produce a wide variety of species throughout the breeding season, in order to reduce the unpredictability of emergences related to a changing climate. A mosaic of habitats that can provide the vegetation types and structures for this should help to maintain the flexibility observed in this population of nightjars, helping them to adjust to further environmental changes.

Chapter 6: General discussion

Species can respond to environmental change by altering their behaviour. Information on changing behaviour can provide a multitude of benefits for conservation, for example understanding how different individuals respond to changes in resource availability, which can identify the sections of the population most at risk from habitat loss or degradation (Mitchell and Biro, 2017; Saltz *et al.*, 2018). The need for data on behavioural responses to change will only increase, as more novel climatic and environmental conditions emerge (Noonan *et al.*, 2018; Buchholz *et al.* 2019), to which species are not adequately adapted. For species with limited ranges, or which are habitat specialists, it is of the utmost importance that we understand how species respond to environmental change, as far as is possible, so that conservation managers and researchers can implement appropriate conservation management actions.

I sought to understand how the European nightjar, an obligate insectivore and long-distance migrant, would respond to changes in habitat type and structure, as well as other temporally-varying environmental factors. This nightjar population displayed high individual variation and used multiple, and on occasion unexpected, habitat types. Home range sizes changed according to habitat type; specifically they decreased when newly cleared areas were more available, and increased when they encompassed mostly wet habitat. Nightjar movement behaviour changed with habitat type and was also driven by other temporally-varying environmental conditions. The individual variation seen in nightjar resource selection was also present in their foraging behaviour and in their diet. Individuals ate a wide variety of moths, although there were common items found in 40 – 50% of samples, displaying a broad population niche.

Here I link the findings from each chapter to broader ecological and behavioural consequences for this nightjar population and I expand on one of the clearest outcomes of this work, that not only was individual variation high in this population of nightjars, but that it was more pronounced in particular circumstances. I have used a combination of resource selection measures, diet and movement analysis, which has produced a multi-faceted study to inform nightjar conservation through an understanding of flexibility in habitat use, niche breadth and effects of external stimuli on foraging. This work has also benefited from the use of multiple recent technological developments, namely accurate, miniaturised GPS tracking devices and metabarcoding techniques that allowed me to test several hypotheses regarding nightjar behavioural ecology in more depth and detail than previous studies were able to.

6.1. Thesis summary

In Chapter 2, I found mixed results when estimating home range size at varying sampling frequencies and durations. The largest amount of variation was attributed to individuals, but there was also variation related to the week of the breeding season and the tracking parameters that indicated a need to analyse tracking data from individuals over the same length of time. There is disagreement in the literature over how best to collect and model fine-scale tracking data, particularly for a central place forager such as the nightjar, which displays rapidly changing, diverse movement patterns in response to patchy resource distribution. The substantial individual variation indicates that researchers should maintain the individual as their level of analysis unless population consistency can be demonstrated. Thus, incorporation of among-individual differences should be the standard when undertaking tracking studies (Montgomery *et al.*, 2018). GPS data are numerous and complex and therefore should be analysed at the scale of the autocorrelation, so that movements can be interpreted correctly and the data can be used to analyse individuals comparatively, or to modify future tracking schedules. I recommend that GPS data be collected at a scale and over a timeframe that is relevant and related to the home range size of the study species in question, and that if movement patterns are the end goal, particularly for a rapidly foraging animal such as the nightjar, that data is collected more frequently. If general habitat patterns over multiple seasons or years is the primary aim, then data can be collected less frequently as a robust understanding of the habitat selection strength can still be obtained.

In Chapter 3, I analysed individual variation in habitat selection, and how this changed between years, sites and sexes. I explored the contribution of individual variation to the population mean as well as overall population responses, by testing for significant differences in home range size between habitats. Individual nightjars significantly differed from one another in their habitat choice and several individuals displayed strongly divergent responses to varying habitat types, including recently manipulated clearfell. Individual variation in nightjar habitat selection led to an apparent lack of selection at a population level (as in Karelus *et al.*, 2016), indicating an overall generalist population comprised of speialists, where nightjars exploited a variety of habitat types. I identified apparent individual specialisation, i.e. extremely strong selection for one habitat type by an individual, as well as more generalist habitat use, i.e. use of multiple habitat types relatively evenly. Within-population variation may indicate specialisation of individuals as a result of competition (as shown by western gulls (*Larus occidentalis*) in Shaffer *et al.*, 2017), which can drive segregation as a way to improve foraging efficiency in individuals (van den Bosch *et al.*, 2019). Coexistence of generalists and specialists can occur in a structurally diverse environment (Kotler and Brown, 1988; Polito *et al.*, 2015; Patrick and Weimerskirch., 2017) that contains a number of habitat types able to sustain both specialists that prefer one habitat type, and flexible generalists that are able to move between many habitat types (Garrick *et al.*, 2006; Wilson and Yoshimura, 1994). Species exploiting fluctuating and stochastic prey should develop and maintain a number of generalist individuals, which are able to respond to rapid or short-term changes with little cost associated with habitat switching (Wilson and Yoshimura, 1994). Although specialising in one habitat type should improve efficiency and therefore fitness (Weimerskirch 2007; Patrick and Weimerskirch, 2007), these individuals may struggle to adjust their behaviour if things change (Garrick *et al.*, 2006). That this nightjar population appears to contain both specialists and generalists should indicate an ability to persist in novel conditions, as at least some of the individuals will be able to exploit them (Lescroël *et al.*, 2010; Foster, 2013) and be able to buffer the population (Phillips *et al.*,2017). Fitness outcomes of birds studied in this population could not be obtained during the course of this study. Robust measures of breeding success for example were not numerous enough to allow analysis, due to the inability to find nests of known birds, and to calculate true measures of success of the nests that were found.

Within-population variation has implications for population flexibility and dynamics in response to habitat change, if certain phenotypes, e.g. more plastic individuals (Dingemanse and Wolf, 2013; Hall and Chalfoun, 2019) are more profitable in novel environments (Smith and Blumstein, 2008). This may lead to long term changes in the behaviour of the population (Stamps, Briffa and Biro, 2012; Stamps and Biro, 2016) Repeated measurements from individuals are needed to understand the extent of plasticity within individuals. Here, within-individual between-year consistency was displayed in three individuals that were caught in multiple years. These individuals displayed consistent movement and habitat selection behaviour between years, and the birds exploited almost identical home range areas, indicating a tendency for strong site fidelity, that might be more important than specific habitat preferences (as in Patrick and Weimerskirch, 2017). This is typical of many long-distance migrants, which return to the same breeding territory every year. If individual differences are consistent over time, i.e. individuals are different but aplastic, if the environment changes this might disrupt the heritability of particular phenotypes (Saltz *et al.*, 2018). If the environment is the same this should promote the use of equivalent habitats to increase foraging efficiency (Patrick and Weimerskirch, 2017; van den Bosch *et al.*, 2019). If the environment becomes more temporally and spatially unpredictable, which may occur with managed habitat change and is predicted to occur with climate change (Noonan *et al.*, 2018), increasingly generalist behaviour might develop throughout the population to facilitate persistence (Killen *et al.*, 2013; Hall and Chalfoun, 2019). Among-individual differences in habitat selection also promoted a population-level functional response to varying habitat types. Home range size changed across the population in response to the proportion of clear-felled and wetland habitats within the home range, indicating that there were common constraints on the ability of birds to meet their needs in certain habitat types, for example prey availability or competition. Nightjars had larger home ranges in wetter areas, but smaller ranges in clearfelled areas. This result was supplemented by the finding that home ranges also decreased where habitat was more heterogeneous; i.e. patchier areas induced higher generalism amongst individuals, whilst specialist individuals searched over a wider area but only foraged very locally This might indicate that patchier areas with plenty of cleared habitat type provided more better quality resources, allowing nightjars in these areas to reduce the time allocated to travelling and searching for transient resources (Chalfoun and Schmidt, 2012). Following optimal foraging theory, animals should forage further away when resources nearby are depleted or of poor quality, or when competition is high (Andersson, 1981). To compensate for the extra distance travelled to sites of better quality, they should forage for longer (Macarthur and Pianka, 1966; Krebs and Cowie, 1976), resulting in an increased home range. If this is the case, then individual differences in habitat selection may be more the result of intra-population competition for areas of higher resource quality (Goss-Custard *et al.*, 2006). Stronger competitors that are better able to acquire and exploit higher-quality areas might do so due to age (Marchetti, 1989), or other behavioural and physiological characteristics (e.g. metabolic rate Bouwhuis *et al.*, 2014; Holtmann, Lagisz and Nakagawa, 2017) and these individuals might therefore dictate future population success (Lescroël *et al.*, 2010). Personality-related traits such as boldness, have also been shown to influence the size of home ranges and conspecific competition (Schirmer *et al.*, 2019).

Individual habitat preference may also have developed through a natal habitat preference mechanism (Stamps and Swaisgood, 2007). Nightjars are site faithful and I have retrapped many chicks on the Humberhead Peatlands that have returned the following year (see Chapter 1). If there is flexibility in natal habitat preference, this could induce use of novel environments that appear through habitat manipulation by returning birds. If not, and these individuals move breeding sites, this may prohibit recruitment of these individuals into the population. However, further study is needed here, and the potential maladaptive habitat selection that could occur, should modified environments represent their preferences, but do not actually provide good quality habitat (Stamps and Swaisgood, 2007).

Further to the examination of broad habitat selection patterns, I examined temporal factors influencing foraging behaviour in nightjars in Chapter 4. The main drivers of nightjar foraging behaviour were those influencing foraging ability along with prey accessibility and availability, representing both reliable circadian variations and more stochastic factors. Whilst this was true across the population, there was individual variation in the magnitude of the response to abiotic and biotic stimuli, as well as variation by month and year, potentially related to broader-scale, seasonal, climatic variables (Erickson and West, 2002). Nightjars appeared to make efficiency- and resource-related trade-offs, whereby time allocated to foraging decreased during the full moon. Although a brighter moon should provide them with better visibility (Rubolini *et al.*, 2015), moth activity will be lower under brighter conditions, driving nightjars to increase their efforts during periods of favourable conditions, reported as the reduced effort hypothesis (Bryant and Westerterp, 1983; Godfrey and Bryant, 2000). A reliable variance, such as the lunar cycle, can be used by the nightjars along with more stochastic variables, to fine-tune their foraging activities (Kamil and Roitblat, 1985). Higher energy expenditure and more time was allocated to foraging in favourable conditions in house martins (Bryant and Westerterp, 1983), which increased their foraging during periods when insect numbers (particularly large specimens) were more available, rather than increasing foraging efforts in poor conditions (also known as the increased effort hypothesis).

Nightjars mostly foraged in semi-open areas of vegetation, despite previous studies indicating that abundance of moths is higher in heavily vegetated areas (Sharps *et al.,* 2015). However, manoeuvrability is lower in thick woodland, thus, they preferentially foraged in areas with the most efficient, ‘cheapest’ movement (Andersson, 1981), relative to moth abundance. When NDVI values were aligned with the habitat map created in Chapter 3, these areas primarily correspond to heather and two-year old clearfell, which have a layer of ground vegetation, but minimal cover of mature trees. Post-clearance monitoring has shown that moth numbers and community composition depends on a substantial layer of ground vegetation (Summerville and Crist, 2002), making these areas not only accessible, but also profitable foraging areas. This highlights cleared areas as a particularly positive development for the nightjars and reinforces the idea that a mosaic of varying habitats can benefit the population as a whole. The foraging data analysed with HMMs in Chapter 4, supported the substantial variation in habitat type found in Chapter 3 but also suggested common features (vegetation structure and climatic variables) to which the whole population might respond. Therefore, particular habitat type or structure inhabited by nightjars might represent better quality areas, individual specialisation related to food choice or metabolic rate, or as I suggested earlier, competition-related spatial segregation. If resource composition and diversity do differ between habitat types, this can also drive habitat selection through individual dietary preferences.

High among-faecal-sample dissimilarity found in Chapter 5 and indicated a broad population dietary niche that might represent competition-related specialisation (Maldonado *et al.*, 2017), or inherent differences in metabolic rates (Holtmann, Lagisz and Nakagawa, 2017; Maldonado *et al.*, 2019). Understanding prey consumption by predators can support differences seen in habitat selection and can elucidate mechanisms of coexistence, such as resource partitioning (Kotler and Brown, 1988). If diet is variable within a population in terms of species composition, then individuals themselves may also be generalist (a monomorphic population; Roughgarden 1974) or they may be specialised (polymorphic population). Nightjars exploit food resources that vary greatly both spatially and temporally, which should encourage generalist phenotypes (Cucco and Malacarne, 1996; Orłowski and Karg, 2013). Flying insect prey are also likely to be influenced by variable weather conditions on a daily and seasonal basis (Erickson and West, 2002). Therefore, nightjars should be able to identify profitable areas and exploit the most profitable, abundant resources at that time (Pyke, 1981). Individuals may select for specific characteristics of prey, for example size, flight speed or accessibility of prey (Kotler and Brown, 1988), as these factors facilitate prey capture (Cryan, Stricker and Wunder, 2012; Rubolini *et al.*, 2015).

I found that where I was able to identify moth prey species and assign them to a size category, nightjars consumed sizes in line with availability overall, but also displayed a bias towards larger specimens. Selection for larger items aligns with optimal foraging theory, where the food items that provide most energy gain, i.e. larger items, should be preferred, up to the point where handling cost overtakes the energy gained (Davies, 1977; Krebs, Stephens and Sutherland, 1983; Kotler and Brown, 1988). Smaller prey were taken more frequently by nightjar females, despite the lower energy gain of these items. This might indicate that abundance of prey within the environment is a driver for foraging behaviour and that as with some seabirds, nightjars can be ‘facultative’ specialists (Wells, Angel and Arnould, 2016), maximising their opportunity to gain energy by reducing their search time and thus taking the more available resources. Higher availability and lower handling time might be especially important for females, which have a limited time available in which to forage and will need to forage in poor conditions to maintain both their own condition and that of their offspring (Krebs and Cowie, 1976). The dietary analysis in my study indicates the potential for nightjars to respond positively to habitat change, if the population is, as it appears to be, generalist. However, reduction of flying insects is well documented and the decline is biased towards larger specimens (Moller, 2013; Coulthard *et al.*, 2019). This reduction may force increased selection of smaller, less profitable moths and consequently might negatively impact nightjar energetics and therefore population dynamics if energetic requirements are not equal across the population (Smith and Blumstein, 2008; Mullers *et al.*, 2009; Kelly *et al.*, 2013).

There are a number of relationships here that make understanding of nightjar foraging rather complex. Ultimately there is the need to obtain maximum energy for minimum expenditure influences (Krebs, Stephens and Sutherland, 1983; Ford, 2016). Thus, environmental conditions that influence temporal heterogeneity in prey availability are particularly important. These external conditions function alongside individual ability to acquire and exploit profitable resources, which may change with age and breeding status (Killen *et al.*, 2013). However, without a measure of how changing resource availability influences nightjar fitness, it is hard to make an assessment of future population stability (Matthiopoulos *et al.*, 2015; Cattarino, McAlpine and Rhodes, 2016). Novel environmental conditions in different habitats can induce contextual responses of individuals (Toscano *et al.*, 2016; Owen, Swaisgood and Blumstein, 2017). Understanding context is particularly relevant when considering multiple novel stressors (Sih, Ferrari and Harris, 2011), such as climate change coupled with habitat loss (Noonan *et al.*, 2018) that might interact (differently, in different populations), to amplify an animal's behavioural response (Hale, Piggott and Swearer, 2017; Owen, Swaisgood and Blumstein, 2017).

6.2 Future research needs

Given the presence of several different influential elements on individual differences in nightjar behaviour above, I feel that the next step for this research would be to produce quantitative information on energy expenditure and fitness to link behaviour to population dynamics (Dolman and Sutherland, 1995). Numerous tracking studies are now collecting individual fitness-related information such field metabolic rate, daily energy expenditure, and combining these data with information on reproductive success (Elliott *et al.*, 2013, 2014). Although a population might present several different behavioural phenotypes, inferring flexibility and adaptability to change, the cost of such plasticity can be high (Patrick and Weimerskirch, 2017; Saltz *et al.*, 2018; Hall and Chalfoun, 2019), which might adversely impact those individuals. Differences between individuals in metabolic rates can themselves be a cause of inter-individual differences in behaviour (Bouwhuis *et al.*, 2014; Holtmann, Lagisz and Nakagawa, 2017), which can then create a feedback loop through influence of behaviour on other stress and fitness related measures such as oxidative stress and glucocorticoid levels (Costantini, 2008; Jenni-Eiermann *et al.*, 2008; Davies and Deviche, 2014; Tarjuelo *et al.*, 2015; Will *et al.*, 2015). Measuring stress through feathers, blood or faecal corticoids has been shown to provide a measure of how successfully an animal is managing its position in the landscape in terms of disturbance and, particularly importantly here, habitat quality (Coppes *et al.*, 2018). Subsequently, this could provide useful information to link foraging behaviour and habitat selection to population fitness. Development of a conservation physiology framework is ongoing (Cooke *et al.*, 2013, 2014) and exploration of fitness metrics could provide much needed confirmation of the inferences from behavioural work.

6.3 Study limitations

There are a number of limitations in this study that relate both to the difficulty of studying such a cryptic species and to a lack of technological development. Nightjars' small size means that the attachment of accelerometers in combination with GPS units to concurrently measure movement behaviour and vital rates is essentially impossible. However use (and rapid development) of these devices is promising as a non-invasive way of obtaining information on energetics that could provide further information on the mechanisms behind behavioural differences and how these link to reproductive success. Behavioural change in response to one or more stimuli can provide a good indication of species needs, but to truly understand the outcome of these stimuli, we need to understand how it impacts the heritability of behavioural and fitness traits through reproduction and recruitment. There was no robust measure of success in my study, due to difficulties in locating nests of known individuals and uncertainty over true success or failure of nests because of movement of the parents and juveniles away from a known nest location. Therefore direct links from foraging behaviour to reproductive success and survival could not be made, which limits the predictability of outcomes. Ideally, known individuals would always be linked to nests with known outcomes, but the nightjars cryptic ecology prohibited this from occurring consistently across all tagged individuals.

Additionally, although metabarcoding of faeces has improved dramatically in recent decades, there are still limitations due to the coverage of the DNA database and the efficacy of extracting highly degraded DNA. As with tracking technology, these are expected to improve and to decrease in cost in the near future.

6.4 Concluding remarks

This thesis has contributed to knowledge on both broader scale habitat use and specific foraging needs of an understudied insectivorous bird. My work has highlighted trade-offs made by the nightjars and that the flexibility observed has the potential to drive population stability. Our ability to track known individuals provides us with the opportunity to explore the contribution of individual behaviour to population responses to environmental heterogeneity (Goss-Custard *et al.*, 2006; Forsman and Wennersten, 2016). Nightjars in this population can clearly use multiple habitat types to successfully breed, including those considered atypical. This variation can be maintained by providing a mosaic of habitats across their breeding site, thus encouraging multiple phenotypes to settle and breed, hopefully maintaining a population that can cope with change. Objective quality of both different habitat types and individuals inhabiting them is not currently known, however population-wide functional responses show that there may be inherently better areas that mean that individuals expend less energy acquiring profitable prey, leading to fitter, more successful individuals. Although nightjars are very mobile, travelling long distances across inhospitable areas has been shown to increase stress. Extra stress from increased foraging distance, coupled with the decline in flying insects globally, indicates the need for managers to maintain sufficient patches prey resources, close to nightjar nest sites, in order to facilitate their populations. Managers should use the differences observed in home range size, to create more areas of habitat that encourage smaller home ranges, as a proxy for energy expenditure.

Further information is needed on the level of flexibility and the subsequent outcomes for populations. Populations often contain inherent flexibility (Ofstad, 2019), but pressures from environmental disturbance might drive an increase particular phenotypes to become more flexible (Garrick *et al.*, 2006). Flexibility appears high here, potentially due to the atypical nature of the site and the disturbance the site has gone through. If this flexibility is also present in other sites in the UK, this might provide positive indications of population stability nationwide. Qualification of habitat use variability across different populations would be a valuable tool in ensuring population maintenance in a variety of different locations, particularly in light of significant climate and land use changes that impact upon animal populations.

7. Appendices

7.1 Appendix I

Examination of autocorrelation structure including time to independence using variogram and correlogram tools within package ‘ctmm’ (Fleming *et al.,* 2015, 2017).

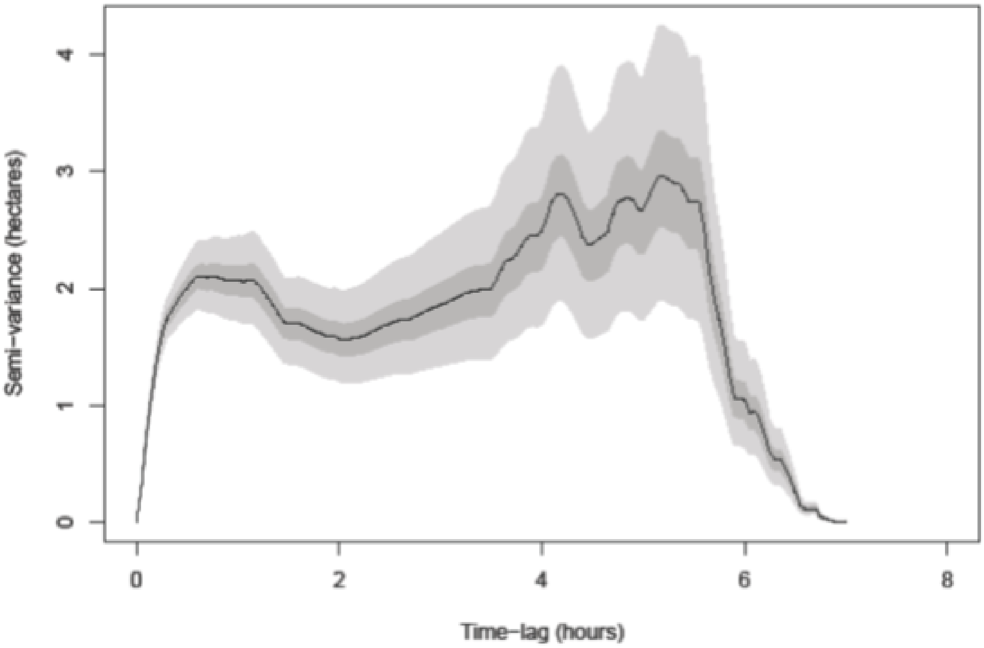

Figure 7.1: An example of a variogram produced using GPS data from one nightjar individual, using the package ‘ctmm’. The variogram shows the semi-variance function (SVF), a measure of autocorrelation that represents the distance travelled within the sampling interval chosen, plotted against the time-lag of the GPS data. The SVF typically asymptotes with autocorrelation, following the steep ascending slope that represents strong velocity autocorrelation. Point of asymptote should be used to identify time to independence (in the figure above, it is around 30 minutes) in order to correctly run methods that require independent sampling points.

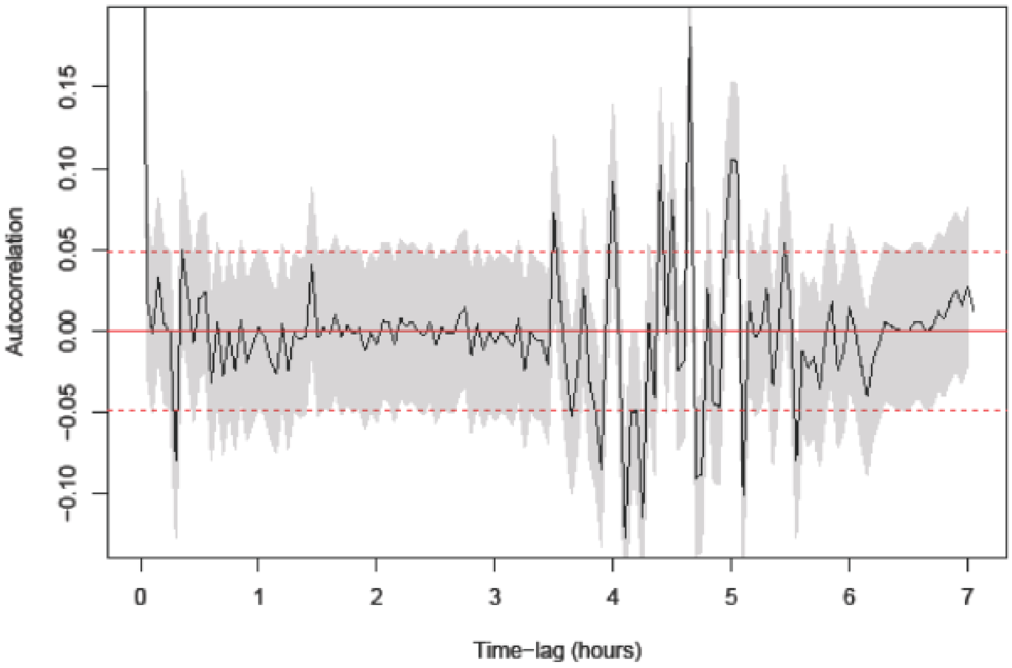

Figure 7.2: An example of a correlogram of the autocorrelation structure produced from the same nightjar individual. Correlograms display the level of autocorrelation plotted against the time-lag (in hours) of the data. Red dashed lines represent confidence intervals and align with ‘normal’ levels of autocorrelation (Fleming *et al.,* 2017).

Table 7.1: ‘Autocorrelated Kernel Density Estimators’ (AKDE) home range sizes in hectares, with standard deviation**.** Samples sizes vary between subsets. For 16 and 10 fixes per hour, n=9; for 12 and 6 fixes per hour, n=23; for 4 fixes per hour, n =32. For the tracking duration subsets; 3 days, n =64; 6 days, n = 32.

	At a fix rate of:						***At a subset of:***	
	16/ hour	**12/ hour**	**10/ hour**	**6/ hour**	**4/ hour**	**All**	**3 days**	**6 days**
Mean AKDE (ha)	50.02	106.21	41.39	128.94	102.09	91.66	77.03	62.36
(+/- S.D.)	39.88	125.85	32.92	131.92	109.75	104.58	81.67	49.66

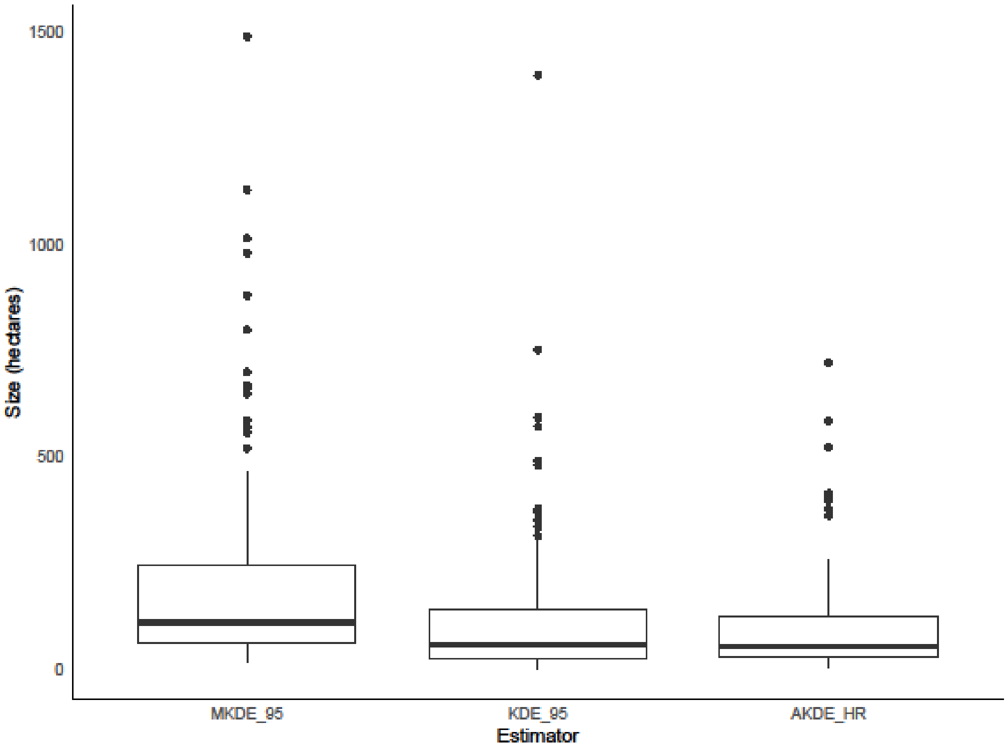

Figure 7.3: Size variation in hectares, within and between MKDE, KDE and AKDE home range estimators. MKDE_95 = Movement based kernel density estimate (95% level); KDE_95 = conventional kernel density estimate (95% level); AKDE_HR = Autocorrelated kernel density estimate (95% level). Boxes display means, 1st and 3rd interquartile ranges; filled points = outliers.

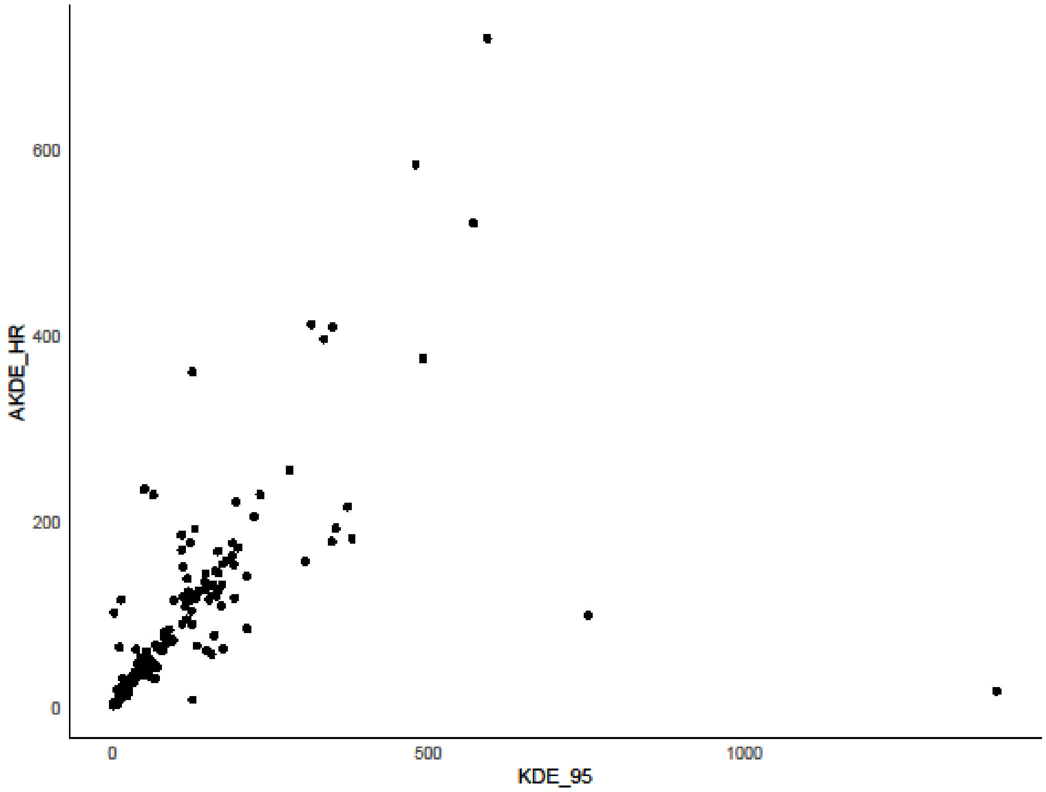

Figure 7.4: Comparison of home range sizes estimated by KDE and AKDE. Direct comparison of estimated size of individual nightjar home ranges, at each fix rate and tracking duration subset, as well as the full dataset. Home ranges calculated at the 95% level.

7.2 Appendix II

Model selection tables for linear mixed models produced to test effects of tracking parameters on two home range estimators and their respective habitat selection estimates. Models reduced by AICc and df; where models were within delta AIC2 models were averaged.

Table 7.2: Model table for MKDE Home range as the response variable. 'logLik.' = Log likelihood; 'dev' = model deviance; Wi = Akaike weights. Model with lowest AICc highlighted in bold.

Fixed Effects	Random Effects	df	logLik	AICc	Δ AIC	weight
Fix Rate + Days + Dominant habitat	**Individual (intercept) + Days (slope) / Week number**	**17**	**-106.53**	**250.80**	**0.00**	**0.63**
Fix Rate + Days + Dominant habitat + Number of fixes	Individual (intercept) + Days (slope) / Week number	18	**-106.53**	253.30	2.47	0.18
Fix Rate + Days + Dominant habitat + Number of fixes + Site	Individual (intercept) + Days (slope) / Week number	19	-106.12	255.00	4.15	0.08
Fix Rate + Days + Dominant habitat + Number of fixes + Site + Temp	Individual (intercept) + Days (slope) / Week number	20	-106.08	257.40	6.61	0.02
Fix Rate + Days + Dominant habitat + Number of fixes + Site + Temp + Year	Individual (intercept) + Days (slope) / Week number	23	-104.55	262.20	11.34	0.00

Table 7.3: Model table for KDE home range as the response variable. ‘logLik.’ = Log likelihood; ‘dev.’ = model deviance. Wi = Akaike weights. Model(s) with lowest AICc value in bold.

Fixed Effects	Random Effects	df	logLik	AICc	Δ AIC	weight
Days + Dominant habitat	**Individual (intercept) + Days (slope) / Week number**	**16**	**-129.47**	**294.3**	**0.00**	**0.42**
Days + Dominant habitat + Site	**Individual (intercept) + Days (slope) / Week number**	**17**	**-128.64**	**295**	**0.77**	**0.29**
Days + Dominant habitat + Number of fixes	Individual (intercept) + Days (slope) / Week number	17	-129.37	296.5	2.25	0.14
Days + Dominant habitat + Number of fixes + Site	Individual (intercept) + Days (slope) / Week number	18	-128.38	297	2.74	0.11
Days + Dominant habitat + Number of fixes + Site + Temp	Individual (intercept) + Days (slope) / Week number	19	-128.25	299.2	4.98	0.04
Days + Dominant habitat + Number of fixes + Site + Temp + Fix Rate	Individual (intercept) + Days (slope) / Week number	20	-128.14	301.6	7.30	0.01
Days + Dominant habitat + Number of fixes + Site + Temp + Year	Individual (intercept) + Days (slope) / Week number	23	-127.24	307.6	13.29	0.00

Table 7.4: Model table for MKDE-derived Selection Ratio as the response variable. 'logLik.' = Log likelihood; 'dev.' = model deviance. W_i = Akaike weights. Model with lowest AICc in bold.

Fixed Effects	Random Effects	df	logLik	AICc	Δ AIC	weight
Fix Rate + Days + Number of fixes + Site	**Individual (intercept) + Days (slope) / Week number**	**10**	**-110.44**	**242.20**	**0.00**	**0.39**
Days + Number of fixes + Site	**Individual (intercept) + Days (slope) / Week number**	**9**	**-111.72**	**242.50**	**0.31**	**0.33**
Fix Rate + Days + Number of fixes + Site + Year	Individual (intercept) + Days (slope) / Week number	13	-107.63	243.50	1.28	0.20
Fix Rate + Days + Number of fixes + Site + Year + Temp	Individual (intercept) + Days (slope) / Week number	14	-107.42	245.40	3.22	0.08

Table 7.5: Model selection table for KDE-derived Selection Ratio as the response variable. 'logLik.' = Log likelihood; 'dev.' = model deviance. W_i = Akaike weights. Model with lowest AICc in bold.

Fixed Effects	Random Effects	df	logLik	AICc	Δ AIC	weight
Days + Number of fixes + Site	**Individual (intercept) + Days (slope) / Week number**	**9**	**-101.02**	**221.10**	**0.00**	**0.41**
Days + Number of fixes	**Individual (intercept) + Days (slope) / Week number**	**8**	**-102.29**	**221.40**	**0.34**	**0.34**
Days + Number of fixes + Site + Year	Individual (intercept) + Days (slope) / Week number	12	-98.47	222.80	1.71	0.17
Days + Number of fixes + Site + Year + Fix Rate	Individual (intercept) + Days (slope) / Week number	13	-98.41	225.00	3.91	0.06
Days + Number of fixes + Site + Year + Fix Rate + Temp	Individual (intercept) + Days (slope) / Week number	14	-98.34	227.20	6.13	0.02

7.3. Appendix III

Table 7.6: Model selection table for all response variables analysed at a subsampled rate of 32 fixes per hour for direct comparison. Models reduced by AICc and df. ‘logLik.’ = Log likelihood. Model(s) with lowest AICc in bold; where within Δ2 AIC, model averaged coefficients are obtained and reported in the text**.**

MKDE Home Range

Fixed Effects	Random Effects	df	logLik	AICc	Δ AIC	weight
Temp + Year	**Week number**	**7**	**-39.06**	**96.78**	**0.00**	**0.72**
Temp + Year + Number of fixes	Week number	8	-38.53	99.3	2.53	0.20
Days + Temp + Year + Number of fixes	Week number	9	-38.31	102.8	6.02	0.04
Site + Temp + Year + Number of fixes	Week number	9	-38.33	102.8	6.07	0.04
Days + Site + Temp + Year + Number of fixes	Week number	10	-38.13	106.7	9.96	0.01
Days + Dominant habitat + Site + Temp + Year + Number of fixes	Week number	18	-33.89	156.4	59.62	0.00

KDE Home Range

Fixed Effects	Random Effects	df	logLik	AICc	Δ AIC	weight
Days + Number of fixes	**Week number**	**5**	**-46.08**	**104.5**	**0**	**0.76**
Days + Number of fixes + Temp	Week number	6	-45.95	107.3	2.79	0.19
Days + Number of fixes + Temp + Year	Week number	9	-42.03	110.3	5.78	0.04
Days + Number of fixes + Temp + Year + Site	Week number	10	-42.02	114.5	10.05	0.01
Days + Number of fixes + Temp + Year + Site + Habitat	Week number	18	-39.96	168.5	64.07	0.00

MKDE Habitat Selection

Fixed Effects	Random Effects	df	logLik	AICc	Δ AIC	weight
Days + Temp	**Week number**	**5**	**-28.9**	**70.4**	**0**	**0.47**
Days + Site + Temp	**Week number**	**6**	**-27.6**	**70.7**	**0.30**	**0.40**
Days + Temp + Year	Week number	8	-25.48	73.49	3.10	0.10
Days + Site + Temp + Year	Week number	9	-24.83	76.23	5.83	0.03
Days + Site + Temp + Year + Number of fixes	Week number	10	-24.71	80.4	10.02	0.00

KDE Habitat Selection

Fixed Effects	Random Effects	df	logLik	AICc	Δ AIC	weight
Site	**Week number**	**4**	**-32.1**	**73.68**	**0.00**	**0.88**
Site + Year	Week number	7	-29.82	78.3	4.61	0.09
Site + Year + Number of fixes	Week number	8	-29.12	80.5	6.81	0.03
Site + Year + Number of fixes + Temp	Week number	9	-28.63	83.4	9.76	0.01
Site + Year + Number of fixes + Temp + Days	Week number	10	-28.63	87.7	14.05	0.00

AKDE Home Range

Fixed Effects	Random Effects	df	logLik	AICc	Delta AIC	weight
Year	**Week number**	**6**	**-41.63**	**98.6**	**0**	**0.631**
Year + Temp	**Week number**	**7**	**-41**	**100.7**	**2.04**	**0.228**
Year + Temp + Days	Week number	8	-40.93	104.1	5.5	0.04
Year + Temp + Site	Week number	8	-40.99	104.2	5.62	0.038
Temp + Site + Days	Week number	6	-44.57	104.5	5.87	0.034
Year + Temp + Site + Days	Week number	9	-40.93	108	9.41	0.006
Year + Site + Days + Dominant habitat	Week number	16	-37.9	144.1	45.43	0
Year + Temp + Site + Days + Dominant habitat	Week number	17	-37.85	153.4	54.79	0

7.4. Appendix IV

Table 7.7: Vegetation categories defined during the habitat map creation process and their associated number coded into the raster file.

Number	Vegetation type
1	Open water – significant pools; do not dry out in summer.
2	Bare peat – unvegetated peat; sometimes pooled with water overwinter.
3	Wooded cover – primarily birch trees of >2 metres tall. Covers mature scrub, as well as woodland.
4	Wetland vegetation – a combination of species that can tolerate high groundwater level, including *Juncus* spp., *Eriophorum* spp., sedges, willow and some birch.
5	Cottongrass – *Eriophorum* dominated areas – often bordering open pools or on deeper, wetter peat. Contains large amounts of *Sphagnum* – perhaps closest to ‘true bog’.
6	Bracken – drier areas including ‘baulks’ and some cleared areas, dominated by bracken.
7	Heather – areas representing more ‘wet heath’ type habitat with heather of varying age and condition.
8	Scrub – areas covered by young, re-growing birch scrub, often with little other ground vegetation.
9	Clearance (2016/17) – > 1 year old clearance. Low levels of ground vegetation, still newly lying brash and/or chippings.
10	Clearance +1 (2015/16) – >2 year old clearance; often becoming dominated by bracken and rhododendron regrowth depending on thickness of brash layer.
11	Grass – Often external to the NNR (, but also present on Lindholme Island.
12	Building – Only present on Hatfield due to tarmacked roads through to peat works.
13	Off Site – covers all areas not included within the boundary of the NNR including agricultural land, urban development and old industry.
14	Clearance (2017/18) – Newly cleared habitat, only present on Hatfield in 2018.

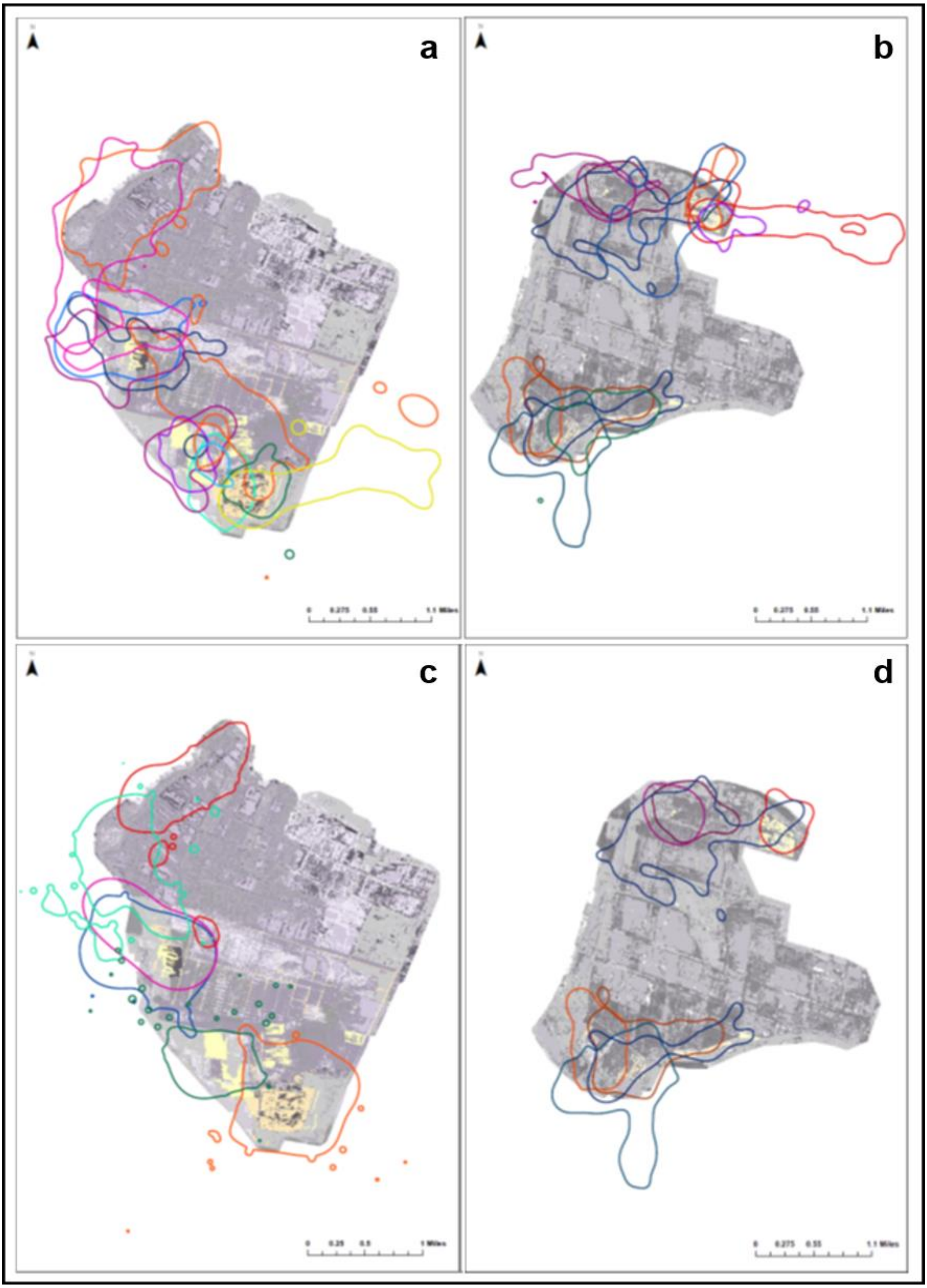

Figure 7.5: Nightjar 95% home ranges on a) Thorne Moor, 2016 & 2017; b) Hatfield Moor 2016 & 2017; c) Thorne Moor 2018; d) Hatfield Moor, 2018, created using the MKDE method in R. Different colours represent different individual birds.

Table 7.8: Coefficients and 95% confidence intervals from linear models used to test for differences in availability of different habitat types within nightjar home ranges between year and level (core 50% / wider 95%) of home range (HR). Significant results are delineated in bold italics.

		Woodland		(log) Scrub		Open, dry		(log) Clearance		(log) Wetland	
Parameter		***β***	**(95% CI)**	***β***	**(95% CI)**	***β***	**(95% CI)**	***β***	**(95% CI)**	***β***	**(95% CI)**
Intercept		33.49	(22.14 - 44.85)	1.67	(0.9 - 2.44)	36.11	(19.55 - 52.67)	0.12	(-1.03 - 1.28)	0.63	(-0.72 - 1.98)
Year 2016		-9.68	(-22.53 - 3.42)	-0.51	(-1.38 - 0.37)	-7.39	(-26.12 - 11.67)	***1.69***	***(0.34 - 2.98)***	0.91	(-0.58 - 2.4)
	2017	***-20.9***	***(-33.51 - -8.39)***	-0.18	(-1.00 - 0.7)	-5.74	(-24.03 - 12.56)	***2.28***	***(1.02 - 3.56)***	1.35	(-0.12 - 2.8)
	2018	***-17.08***	***(-29.61 - -4.63)***	-0.03	(-0.88 - 0.81)	0.99	(-17.29 - 19.08)	***1.8***	***(0.55 - 3.08)***	1.05	(-0.38 - 2.51)
95% HR		3.59	(-0.00 - 7.18)	0.04	(-0.18 - 0.25)	-3.52	(-8.31 - 1.27)	-0.08	(-0.35 - 0.2)	0.002	(-0.17 - 0.17)
Individual variation		90.49	(6.73 - 12.92)	0.46	(0.5 - 0.9)	205.6	(10.65 - 19.14)	1.1	(0.8 - 1.38)	1.73	(1.06 - 1.68)
Residual variation		69.1	(6.86 - 10.36)	0.25	(0.41 - 0.62)	123.2	(9.17 - 13.79)	0.41	(0.53 - 0.8)	0.15	(0.32 - 0.49)

7.5. Appendix V

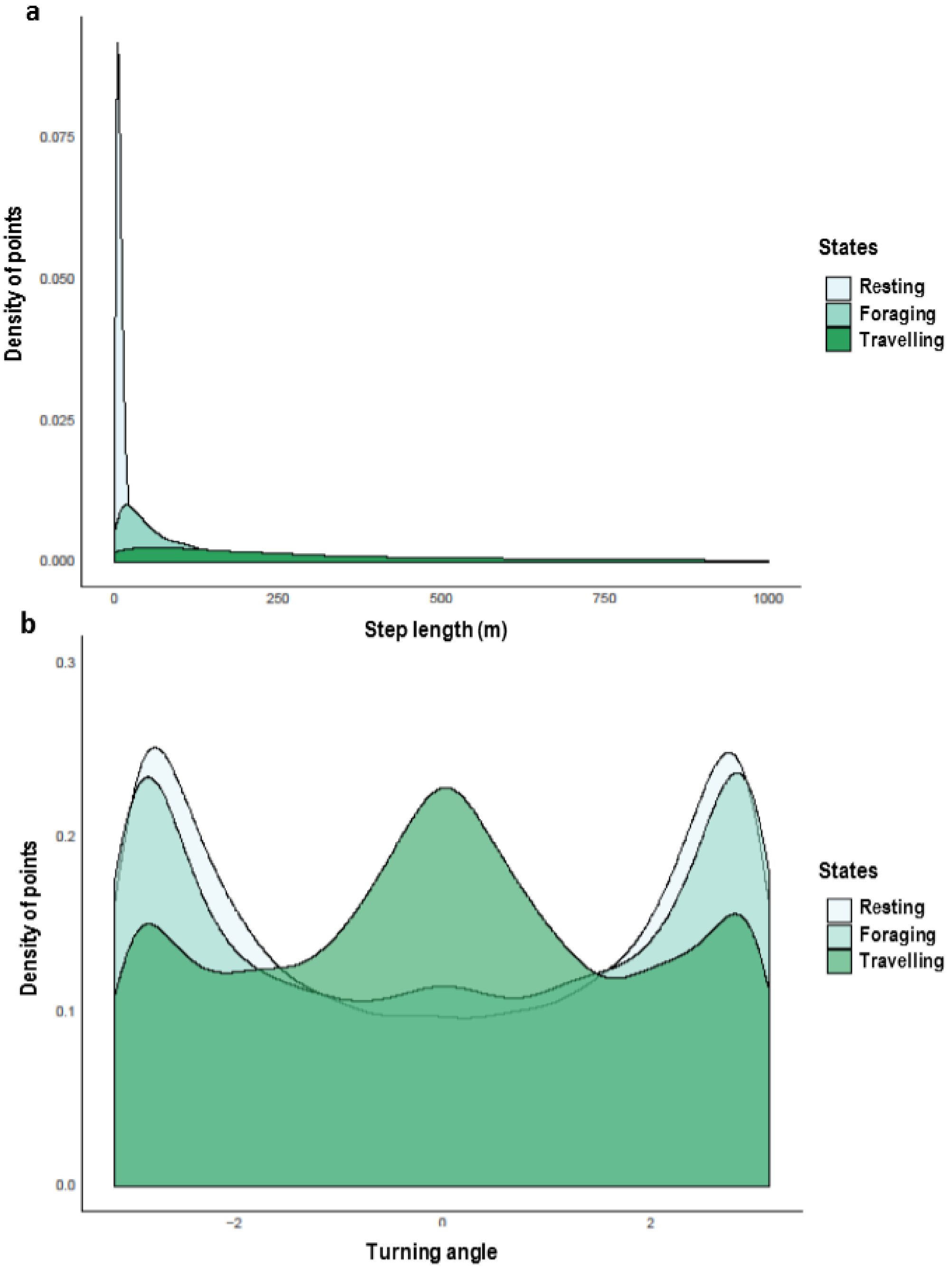

Figure 7.6: Density of a) step lengths and b) turning angles for each of the three behavioural states identified from the Hidden Markov Model, pooled across all models.

Table 7.9: Mean (+/- standard deviation) step lengths and mean (+ concentration) turning angle values for nightjar GPS data within HMMs run by month and year

		Step length		***Angle***	
	Year	***Mean***	***SD***	***Mean***	***Concentration***
State 1	*2015*	8.442	5.009	3.096	0.64
	2016 June	8.422	5.532	3.125	0.644
	2016 July	6.566	3.729	-3.011	0.579
	2017 June	11.182	7.669	-3.049	0.582
	2017 July	9.97	6.812	-3.119	0.557
	2018 June	10.333	6.912	-3.118	0.648
	2018 July	9.191	6.067	3.14	0.742
State 2	*2015*	31.082	24.166	-3.081	0.829
	2016 June	48.653	43.007	2.992	0.779
	2016 July	15.463	8.52	-3.128	1.011
	2017 June	123.46	116.863	3.026	0.391
	2017 July	97.251	94.38	-3.096	0.567
	2018 June	92.377	87.707	3.139	0.628
	2018 July	69.434	68.679	3.095	0.372
State 3	*2015*	252.709	270.911	-0.131	0.099
	2016 June	314.081	326.584	-0.021	0.306
	2016 July	133.458	144.919	3.074	0.159
	2017 June	469.107	471.545	1.207	0.11
	2017 July	523.815	591.353	-0.062	0.394
	2018 June	425.248	444.299	0.281	0.062
	2018 July	496.32	447.197	-1.348	0.064

Table 7.10: Regression coefficients for state transitions produced by HMMs run by month and year (June & July 2015 - 2018). State codes: ‘1’: Resting, ‘2’: Foraging, ‘3’: Travelling. Transition indicates change of behaviour from one state to another; i.e. ‘1 -> 2’: Resting -> Foraging.

		State transition					
		1 -> 2	***1 -> 3***	***2 -> 1***	***2 -> 3***	***3 -> 1***	***3 ->2***
2015	**Intercept**	-7.847	-0.193	-2.563	-3.256	-3.211	-4.883
	Lunar ^2	-0.914	-1.299	0.715	0.304	1.345	2.581
	NDVI	7.05	-1.248	0.427	1	1.893	2.466
2016	**Intercept**	-5.31	-8.087	-1.338	-7.812	-0.728	1.847
June	**Lunar**	2.106	9.105	-0.821	-1.657	0.315	-2.43
	NDVI	3.334	-5.197	1.164	12.929	-2.843	-4.086
2016	**Intercept**	0.344	-5.881	0.566	0.716	-3.63	-2.81
July	**Temp**	0.807	0.215	0.244	0.891	0.345	0.297
	NDVI	-3.749	5.812	-3.324	-2.897	2.561	0.513
2017	**Intercept**	-1.423	-1.291	-1.129	-11.451	-2.223	-2.568
June	**Lunar ^2**	1.193	5.995	1.146	1.212	-1.498	-13.141
	NDVI	-0.508	-2.215	-1.165	14.607	0.358	-0.533
2017	**Intercept**	0.424	-3.594	0.218	-2.444	-2.498	-4.084
July	**Lunar ^2**	2.093	-0.301	4.198	-3.717	2.047	-5.455
	NDVI	-3.717	1.305	-2.005	0.504	3.372	-0.511
2018	**Intercept**	-5.169	-1.758	-1.894	0.105	-2.448	-0.974
June	**Lunar ^2**	2.014	2.028	0.575	2.549	-2.766	2.306
	NDVI	5.006	-1.013	0.224	-2.703	-0.772	-1.237
2018	**Intercept**	-2.31	3.653	-3.791	-14.505	-2.988	-4.44
July	**Lunar**	0.206	0.412	-0.272	0.964	0.492	0.708
	NDVI	0.356	-13.4	4.921	20.163	1.86	4.287

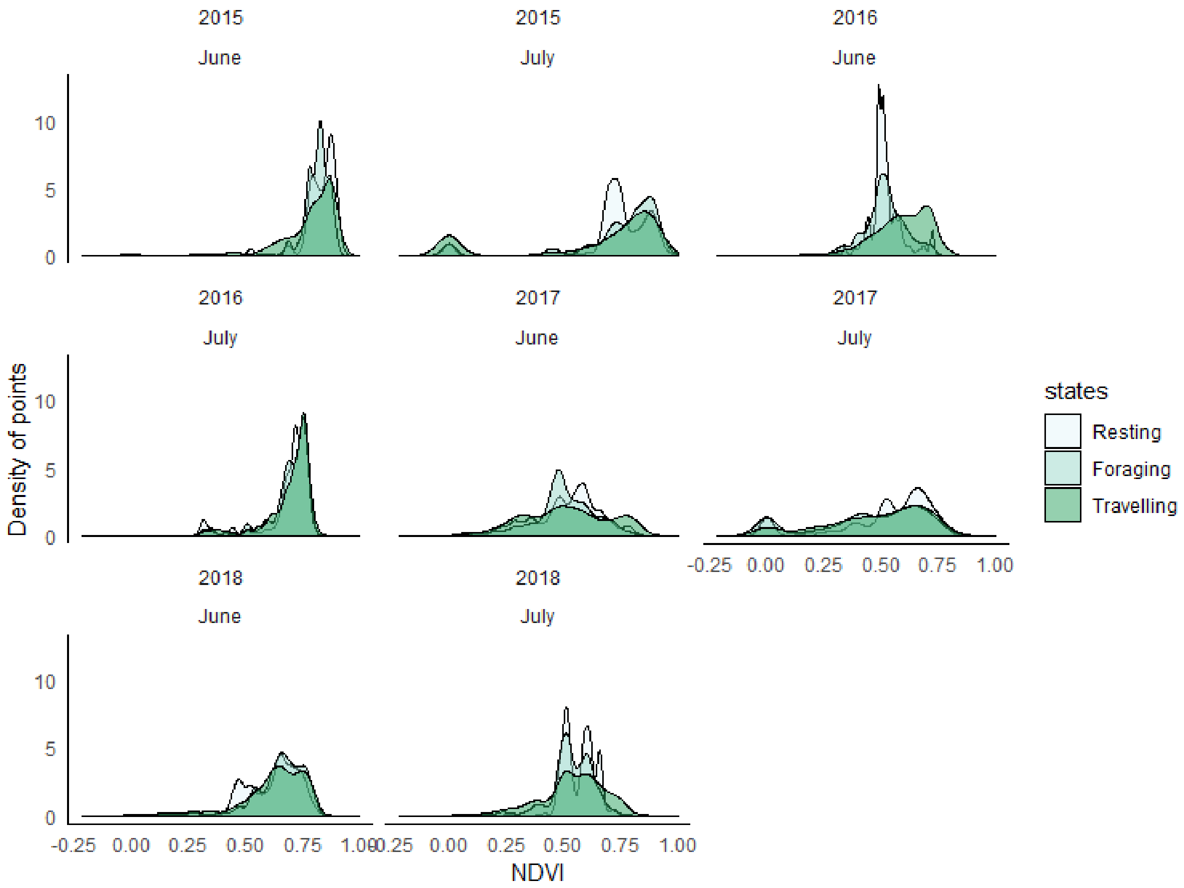

Figure 7.7: State point densities produced by the HMMs (i.e. the probability of being in one of three states; Resting, foraging or travelling), at different levels of Normalised Differential Vegetation Index (NDVI), by month in each year. Values of NDVI run from -0.25 indicating no vegetation, to +1 indicating heavily vegetated areas.

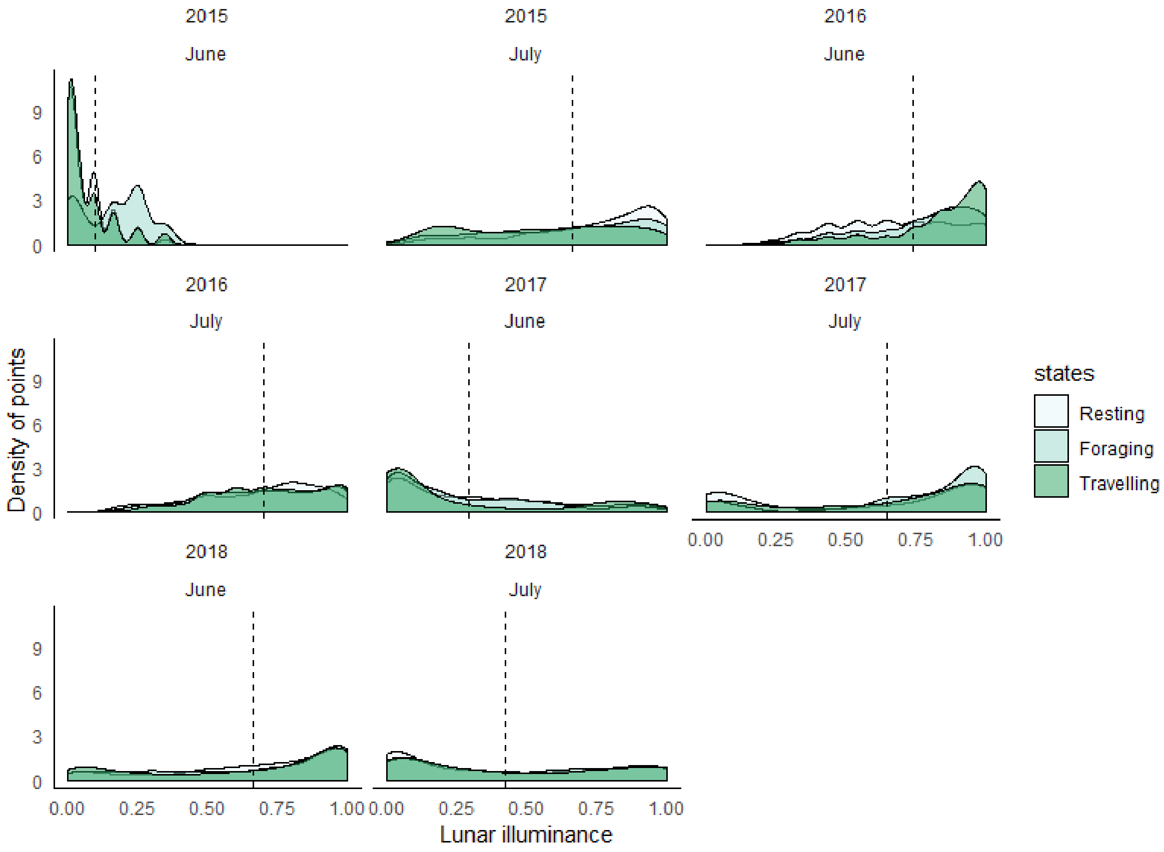

Figure 7.8: State probability densities produced by the HMMs (i.e. the probability of being in one of three states; Resting, foraging or travelling), at different levels of lunar illuminance (% face of moon illuminated) for each month and year combination modelled. Dashed vertical line represents the mean lunar illuminance level per month and year.

Table 7.11: Coefficients and 95% confidence intervals from linear model testing for significant differences in points identified as foraging behaviour between habitat types.

Habitat	β	Lower CI	Upper CI
Water	0.64	0.07	1.21
Bare peat	1.31	0.5	2.12
Woodland	2.41	1.67	3.16
Wetland	1.44	0.65	2.23
Cottongrass	1.91	0.86	2.97
Bracken	1.5	0.75	2.25
Heather	2.67	1.92	3.42
Scrub	1.49	0.73	2.26
Clearfell +1	1.18	0.27	2.09
Clearfell +2	1.9	1.03	2.77
Grass	0.09	-0.78	0.96
Development	-0.19	-1.44	1.07
non-NNR	0.34	-0.41	1.1
Clearfell	1.17	-0.16	2.51

Residual standard error: 1.5
R^2: 0.25

7.6. Appendix VI: PCR procedures

Faecal sample initial PCR

All PCR amplifications were run at a reaction volume of 20ul containing:

10ul Qiagen MasterMix,

6ul ddH20,

1ul each of the forward and reverse primers,

2ul template.

PCR program

Initial denaturation: 95 ºC for 15 minutes

Then 40 cycles of:

95 ºC for 30 seconds,

62 ºC for 30 seconds,

72 ºC for 30 seconds,

Final annealing at 72 ºC for 10 minutes.

PCR procedure for attaching MID tags for Illumina Sequencing

8ul cleaned template (these are pooled PCR products from faecal samples)

10ul Qiagen MasterMix,

1ul each of forward and reverse primer

(this makes 144 combinations of forward- (Fi5) and reverse-tags (Ri7) at a concentration of 2uM).

Initial denaturation: 95 ºC for 15 minutes

Then 10 cycles of:

98 ºC for 10 seconds,

65 ºC for 30 seconds,

72 ºC for 30 seconds

Final annealing at 72ºC for 5 minutes.

QPCR quantification of samples

Make three independent dilutions of each pooled sample library; 1:100 (1ul of template to 99ul of buffer), 1:1000 (1ul of first dilution into 9ul of buffer) and 1:10000 (1ul of template from second dilution into 9ul of buffer).

Add 8ul of SYBR mastermix into 96 well plate, with either:

2ul KAPA BIOsystems standards,

2ul library dilutions,

2ul dilution buffer (negative control) = total reaction volume 10ul.

QPCR program:

Initial denaturation: 95 for 5 minutes

Then 35 cycles of:

95 for 30 seconds

60 for 45 seconds.

7.7: Appendix VII: Raw data

Table 7.12: Summary of nesting data collected during the study from a) 2015 – 2017 (n = 29), b) 2018 (n = 20). Nest IDs beginning with H = Hatfield; those beginning with T = Thorne. Contents column indicates contents of nest upon initial discovery.

a)

Nest	Date located	Site	Contents	Habitat type	Revisit date	Hatched	Fledged
H1_15	09/06/2015	Packards Heath	Eggs (1)	Heather (mature)	15/06/2015	0	NA
H2_15	09/06/2015	Packards Heath	Eggs (2)	Heather/Birch scrub	15/06/2015; 02/07/2015; 14/07/2015; 19/07/2015	2	2
H3_15	30/06/2015	Triangle Woods	Eggs (2)	Birch scrub clearing	14/07/2015; 23/07/2015	2	2
H4_15	15/07/2015	Packards Heath	Eggs (2)	Birch scrub clearing	23/07/2015	0	NA
H5_15	18/07/2015	Poor Piece	Chicks (1)	Bare peat/Birch saplings	-	1	1
H1_16	07/06/2016	Packards Heath	Eggs (2)	Birch scrub clearing	16/06/2016	0	NA
T1_16	17/06/2016	Greenbelt	Eggs (2)	Bracken/bare ground	27/06/2016; 08/07/2016	2	2
H2_16	21/06/2016	Packards Heath	Eggs (1)	Birch scrub clearing	07/07/2016; 11/07/2016; 20/07/2016	2	2
H3_16	24/06/2016	Triangle Woods	Eggs (2)	Bare peat /Birch saplings	-	0	NA
H4_16	24/06/2016	Triangle Woods	Eggs (2)	Birch brash/ heather	-	0	NA
H5_16	29/06/2016	Poor Piece	Eggs (1)	Bare peat /Birch	07/07/2016; 14/07/2016	2	2
H6_16	01/07/2016	Stainforth	Eggs (2)	Birch brash/ heather	09/07/2016; 13/07/2016	2	Unknown
T2_16	05/07/2016	Angle Drain	Chicks (2)	Bracken/bare ground	15/07/2016	2	2
T3_16	16/07/2016	Canal One	Eggs (2)	Bracken/bare ground	20/07/2016; 28/07/2016	2	2
H1_17	08/06/2017	Belton Moor	Eggs (2)	Bracken/ Heather	16/06/2017; 27/06/2017	2	2
T1_17	14/06/2017	Durham's Gardens	Chicks (2)	Bracken/bare ground	20/06/2017; 30/06/2017	2	2
H2_17	22/06/2017	Packards Heath	Eggs (2)	Heather/ Birch scrub	03/07/2017; 16/07/2017	2	2
H3_17	28/06/2017	Poor Piece	Eggs (2)	Bare ground/ *Molinia*	05/07/2017; 12/07/2017	2	Unknown
H4_17	01/07/2017	Stainforth	Eggs (2)	Heather/ Birch brash	12/07/2017; 28/07/2017	2	Unknown
T2_17	29/06/2017	Snaith & Cowick	Eggs (2)	Heather/ Moss	02/07/2017; 08/07/2017; 16/07/2017	2	Unknown
H5_17	05/07/2017	Moor Bank	Chicks (2)	Bare ground/ Birch saplings	07/07/2017; 19/07/2017	2	2
T3_17	07/07/2017	Elmhirst	Eggs (2)	Bracken/ bare ground	14/07/2017; 26/07/2017	2	Unknown
H6_17	12/07/2017	Belton Moor	Eggs (1)	Bracken/ bare ground	20/07/2017; 03/08/2017	1	1
H7_17	19/07/2017	Packards Heath W	Chicks (2)	Heather/ Bare ground	24/07/2017; 28/07/2017	2	Unknown
H8_17	20/07/2017	Stainforth	Chicks (2)	Birch scrub/ bare ground	28/07/2017	2	1
T4_17	25/07/2017	Greenbelt	Eggs (2)	Bracken/ bare ground	02/08/2017; 10/08/2017	2	1
T5_17	02/08/2017	Greenbelt	Eggs (2)	Birch scrub/ bare ground	10/08/2017	0	NA
H9_17	03/08/2017	Belton Moor	Eggs (2)	Heather/ Bare ground	12/08/2017; 19/08/2017	2	Unknown
T6_17	04/08/2017	Casson's Marsh	Chicks (2)	*Rhod*. brash/ bracken	09/08/2017; 14/08/2017	2	1
T7_17	09/08/2017	Casson's Marsh	Eggs (1)	*Rhod*. brash/ bracken	14/08/2017	0	NA

b)

Nest	Date located	Site	Contents	Habitat type	Revisit dates	Hatched	Fledged
T1_18	6/11/2018	Northern Goole Moor	2 eggs	Bare ground and leaf litter, birch trees (c. 1.5m), heather.	6/30/2018	Unknown	Unknown
H1_18	6/12/2018	Packards	2 eggs	Brash 50%, bare ground 40%, bracken 10%.	6/21/2018	2	2
H2_18	6/13/2018	Stainforth	1 egg.	Brash 40%; Birch 10%; Heather 50%.	14/6/18. 21/6/18	Failed	NA
T2_18	6/18/2018	Snaith & Cowick Moor	2 eggs	Heather, bare ground.	25/6/18 & 4/7/18	2	2
H3_18	6/21/2018	Kilham	2 eggs	Bare ground/leaf litter 60%; birch 30%, heather 10%	7/6/2018	2	2
T3_!8	6/28/2018	Snaith & Cowick Moor	1 chick	Heather, birch scrub (c. 1.5m), brash/leaf litter.	7/4/2018	1	Unknown
T4_18	6/29/2018	Elmhirst	2 eggs	Bracken, bare ground	31/7/17 & 10/8/17	2	2
H4_18	6/30/2018	Triangle Woods	1 egg, 1 cl	Bare ground 65%; Heather 25%; Birch 10%	6/7/18.	2	Unknown
T5_18	7/3/2018	Durham's Gardens	2 eggs	Rhododendron scrub, brash and leaf litter.	10/7/18 & 20/7/18	2	2
H5_18	7/4/2018	Belton	2 chicks	Brash 20%. Bracken 80%	None	2	2
H6_18	7/5/2018	Packards	2 eggs	Bare ground 20%. Heather 60%, Birch 20%.	9/7/18.	2	2
H7_18	7/10/2018	Packards	2 chicks	Heather 40%, Leaf litter/ bare ground 60%. Large pine 5-7m tall.	None	2	2
H8_18	7/10/2018	Packards	2 chicks	Heather 40%, Leaf litter 40%, bare ground 20%.	None	2	2
T6_18	7/11/2018	Snaith & Cowick	1 egg	Heather, bare ground, brash.	20/7/18 & 1/8/18	2	2
H9_18	13/7/18.	Belton	1 egg	Bracken 35%; Birch shrubs 35% (1.5m tall); bare ground 30%.	7/18/2018	0	0
H10_18	7/18/2018	Packards	1 egg	Heather 60%, bare ground 35%, birch 5%.	28/7/18. 2/8/18.	2	1
T7_18	7/18/2018	Snaith & Cowick	2 eggs	Heather, Birch trees (2m), bare ground	7/28/2018	0	0
H11_18	8/1/2018	Moor Bank	2 chicks	Heather 40%, Moss 25%, Brash 35%,	None.	2	2
H12_18	8/6/2018	Packards	1 chick	Bracken 35%; brash 65%.	None.	1	1
H13_18	8/8/2018	Kilham North	1 egg	Heather 70%, bare ground 20%, birch 10%.	8/14/2018	0	0

Table 7.13: Home range raw data for all birds tagged and retrieved from 2015 – 2018. Hat = Hatfield; Tho = Thorne. Level = 50% (X50) or 95% (X95) home range level.

Individual	Site	Sex	Year	Level	Size (ha)
LH30214	Hat	Male	2015	X50	33.84
LH30214	Hat	Male	2015	X95	702.8425
LH30216	Hat	Female	2015	X50	10.505
LH30216	Hat	Female	2015	X95	94.28
LH30217	Hat	Male	2015	X50	15.465
LH30217	Hat	Male	2015	X95	65.875
LH30221	Hat	Female	2016	X50	13.95
LH30221	Hat	Female	2016	X95	147.01
LH30223	Hat	Male	2015	X50	16.735
LH30223	Hat	Male	2015	X95	114.9625
LH30235	Hat	Male	2016	X50	10.72
LH30235	Hat	Male	2016	X95	197.06
LH30237	Hat	Male	2016	X50	29.78
LH30237	Hat	Male	2016	X95	213.66
LH30238	Hat	Male	2016	X50	6.2
LH30238	Hat	Male	2016	X95	55.22
LH30239	Hat	Male	2016	X50	9.97
LH30239	Hat	Male	2016	X95	62.77
LH30241	Hat	Female	2016	X50	30.02
LH30241	Hat	Female	2016	X95	144.83
LH30252	Hat	Male	2017	X50	13.1
LH30252	Hat	Male	2017	X95	92.54
LH30269	Hat	Male	2018	X50	15.5
LH30269	Hat	Male	2018	X95	313.4
LH30272	Hat	Female	2018	X50	33.5
LH30272	Hat	Female	2018	X95	880.5
LH30273	Hat	Female	2018	X50	17
LH30273	Hat	Female	2018	X95	250.8
LH30278	Hat	Female	2018	X50	35
LH30278	Hat	Female	2018	X95	566.5
LH30281	Hat	Female	2017	X50	15.74
LH30281	Hat	Female	2017	X95	243.82
LH30283	Hat	Male	2017	X50	18.5
LH30283	Hat	Male	2017	X95	185.1
LH30284	Hat	Male	2017	X50	11.7
LH30284	Hat	Male	2017	X95	74.49
LH30288	Hat	Male	2017	X50	11.8
LH30288	Hat	Male	2017	X95	469.78
LH30289	Hat	Female	2017	X50	9.1
LH30289	Hat	Female	2017	X95	63.03
LJ25651	Tho	Male	2018	X50	34.5
LJ25651	Tho	Male	2016	X95	162.13
LJ25651	Tho	Male	2018	X95	224.1
LJ25659	Tho	Male	2016	X95	76.74
LJ25661	Tho	Female	2017	X50	34.4
LJ25661	Tho	Female	2017	X95	196.42
LJ25663	Tho	Male	2016	X95	41.57
LJ25664	Tho	Male	2016	X95	36.24
LJ25667	Tho	Female	2016	X95	134.56
LJ25672	Tho	Male	2017	X50	17.96
LJ25672	Tho	Male	2017	X95	109.83
LJ25676	Tho	Female	2017	X50	35.55
LJ25676	Tho	Female	2017	X95	327.97
LJ25681	Tho	Male	2017	X50	40.97
LJ25681	Tho	Male	2018	X50	15.5
LJ25681	Tho	Male	2017	X95	1757.5
LJ25681	Tho	Male	2018	X95	178.7
LJ25685	Tho	Male	2017	X50	12.94
LJ25685	Tho	Male	2017	X95	159.41
LJ25687	Tho	Female	2017	X50	21.68
LJ25687	Tho	Female	2017	X95	124.83
LJ25689	Tho	Male	2017	X50	16.24
LJ25689	Tho	Male	2018	X50	41.7
LJ25689	Tho	Male	2017	X95	80.52
LJ25689	Tho	Male	2018	X95	245.1
LJ25690	Tho	Male	2017	X50	31.5
LJ25690	Tho	Male	2017	X95	255.23
LJ65131	Hat	Male	2018	X50	7.8
LJ65131	Hat	Male	2018	X95	90.4
LJ65132	Hat	Male	2018	X50	6.6
LJ65132	Hat	Male	2018	X95	60.3
LJ65150	Hat	Female	2018	X50	10
LJ65150	Hat	Female	2018	X95	82.5
LJ65151	Hat	Male	2018	X50	25.4
LJ65151	Hat	Male	2018	X95	267.1
LK48111	Hat	Male	2018	X50	24.6
LK48111	Hat	Male	2018	X95	387
LK48113	Tho	Male	2018	X50	17.7
LK48113	Tho	Male	2018	X95	235.1
LK48114	Tho	Female	2018	X50	8.1
LK48114	Tho	Female	2018	X95	117.6

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