Understanding the importance of aquatic habitats and migration strategies in the conservation of spotted flycatchers (*Muscicapa striata*)

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Declaration

I declare that the work in this thesis is my own and has not been submitted elsewhere for the award of any other degree.

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Abstract

Despite declines of Afro-Palearctic migrants spanning decades, little progress has been made in understanding the causes of population trends for most species. The complex annual cycle of migratory birds means that factors affecting population trends may act across an enormous geographic scale, but much research remains focussed on the breeding grounds due to limitations in tracking technology. Many migratory birds are insectivorous, and recent research suggests that aquatic habitats may play a crucial role by supplying nutrients through aquatic insect emergence, which is particularly relevant given reported declines in terrestrial insects. The spotted flycatcher (*Muscicapa striata*) is an obligate insectivorous Afro-Palearctic migrant in urgent need of conservation action, having declined by 93% in the UK since 1967. This thesis explores the role of aquatic habitats and the subsidies they provide in the ecology of spotted flycatchers, and aims to enhance our understanding of their movements outside the breeding season. In a UK-wide study, we found that occupancy and colonisation were positively correlated with river density, and loss was less likely when river density was high. At a local scale in Cumbria, we found that spotted flycatcher nests were more likely to occur near rivers, but this did not appear to influence nest survival, which was primarily driven by predation. However, adults and chicks were in better body condition when their blood contained higher concentrations of fatty acids associated with aquatic habitats, and nests that weren't predated were more likely to fledge chicks during periods of higher aquatic insect availability. We also tracked individuals throughout a full annual cycle and present the first detailed account of spotted flycatcher migration and overwintering behaviour. We found that the species predominantly migrates in short hops between the UK and Namibia, necessitating access to frequently distributed high-quality habitats. Overall, we find that aquatic habitats may provide important refugia for insectivorous birds, and that broad-scale conservation strategies across the entire range may be most effective for this species and others facing similar challenges.

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Statement of authorship

This thesis is prepared in the alternative format as a series of four papers presented in Chapters 2 to 5, with some intended for submission to peer-reviewed journals or currently under review. These chapters have co-authors in addition to my supervisory team at Lancaster University, the contributions of all co-authors is set out below using the CRediT taxonomy. Chapters 1 and 6 are introductory and discussion chapters and are not intended for submission.

Chapter 2 – *in review – Conservation Biology*

Catrin F Eden, Simon Gillings, Richard K Broughton, Bart Donato, Chris M. Hewson, Stuart P Sharp. **The role of freshwater availability and terrestrial land cover in the distribution of a declining terrestrial, insectivorous bird.**

Catrin F Eden: conceptualisation, methodology, formal analysis, writing – original draft; **Simon Gillings**:- methodology; **Richard K Broughton**: conceptualisation, supervision, writing – review and editing; **Bart Donato**: conceptualisation, supervision, writing – review and editing, funding acquisition; **Chris M Hewson**: conceptualisation, supervision, writing – review and editing; **Stuart P Sharp**: conceptualisation, methodology, supervision, writing – review and editing, funding acquisition.

Chapter 3 – *in preparation*

Catrin F Eden, Richard K Broughton, Bart Donato, Chris M. Hewson, Stuart P Sharp. **Terrestrial and aquatic habitat characteristics associated with nest-site selection and breeding success in spotted flycatchers (*Muscicapa striata*)**

Catrin F Eden: conceptualisation, investigation, methodology, formal analysis, writing – original draft; **Richard K Broughton**: conceptualisation, supervision, writing – review and editing; **Bart Donato**: conceptualisation, supervision, writing – review and editing, funding acquisition; **Chris M Hewson**: conceptualisation, supervision, writing – review and editing; **Stuart P Sharp**: conceptualisation, investigation, supervision, writing – review and editing, funding acquisition.

Chapter 4 – *in review – Oecologia*

Catrin F Eden, Richard K Broughton, Bart Donato, Chris M. Hewson, Caroline Isaksson, Stuart P Sharp. **Cross-system transfer of fatty acids from aquatic insects supports terrestrial insectivore condition and reproductive success.**

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Chapter 5 – *in preparation*

Catrin F Eden, Frédéric Jiguet, Gaspard Baudrin, Richard K Broughton, Bart Donato, Stuart P Sharp, Lee Barber, Malcolm Burgess, Joan Castelló, James Kennerley, Michael Holdsworth, Chris M. Hewson. **Migration strategy and seasonal movement patterns in spotted flycatchers (*Muscicapa striata*)**

Catrin F Eden: conceptualisation, investigation, methodology, formal analysis, writing – original draft; **Frédéric Jiguet:** funding acquisition; **Gaspard Baudrin:** formal analysis; **Richard K Broughton:** supervision, writing – review and editing; **Bart Donato:** supervision, funding acquisition, writing – review and editing; **Stuart P Sharp:** supervision, investigation, funding acquisition, writing – review and editing; **Lee Barber, Malcolm Burgess, Joan Castelló, James Kennerley & Michael Holdsworth:** investigation; **Chris M. Hewson:** conceptualisation, supervision, investigation, methodology, writing – review and editing.

Chapter 1 General introduction

1.1. Introduction to Afro-Palearctic migrants

Migratory animals are a vital component of ecological functioning; they have a significant influence on community structure through the transfer of nutrients and diseases, predation of local resources and provision of prey to local predators (Bauer and Hoye, 2014; Whelan *et al.*, 2015). Approximately 2.1 billion passerine and near-passerine birds link Europe and Africa by migrating between the two continents each year along what is known as the Afro-Palearctic flyway (Hahn *et al.*, 2009; Newton, 2023). This is one of the largest migratory systems in the world, yet it is under threat from land use, hunting and climate change (Bairlein, 2016; Newton, 2023). Accordingly, several Afro-Palearctic migrants are in decline, particularly long-distance migrants, which have declined to a greater extent than European resident species and short-distance migrants wintering in northern Africa (Thaxter *et al.*, 2010; Vickery *et al.*, 2014).

Understanding the drivers of migrant declines is complicated by the large geographic range and interdependence of different life stages (Newton, 2023). For example, factors reducing the quality of wintering grounds may not only influence overwintering survival but may also lead to birds arriving at their breeding grounds in poor condition, with knock-on effects for productivity (i.e. carry-over effects) (Norris *et al.*, 2004; Finch *et al.*, 2014). Moreover, until recently, the weight of tracking devices was limited to larger species, and so much of our understanding for smaller passerines was restricted to the breeding grounds (Vickery *et al.*, 2014). Consequently, despite our awareness of the problem spanning decades, there has been little progress in identifying strategies to reverse the declines (Vickery *et al.*, 2023).

A review of the potential causes of Afro-Palearctic migrant declines suggested that multiple factors across the entire migratory cycle may be involved (Vickery *et al.*, 2014), and these factors may affect population trends simultaneously or synergistically. Numerous studies have related population trends to habitat quality and land use change in wintering areas (Sanderson *et al.*, 2006; Hewson and Noble, 2009; Thaxter *et al.*, 2010; Ockendon *et al.*, 2012) and on the breeding grounds (Thaxter *et al.*, 2010; Morrison *et al.*, 2013). Moreover, conditions at stopover sites have been linked to survival (Blackburn and Cresswell, 2016) and breeding success (Finch *et al.*, 2014). Global insect declines that coincide with increasing agricultural intensification may have important implications across the entire range of Afro-Palearctic migrants (Warren *et al.*, 2001; Conrad *et al.*, 2004; Biesmeijer *et al.*, 2006; Hallmann *et al.*, 2017), most of which are insectivorous at some point in their annual cycle. Additionally, weather patterns that are tightly coupled with food availability are being altered by climate change, and have been shown to impact migratory species on the breeding grounds, wintering grounds, and on migration (Schaub *et al.*, 2011; Ockendon *et al.*, 2014; Shipley *et al.*, 2020). Finally, unsustainable hunting levels have been linked to declines in some species (Jiguet *et al.*, 2019; Moreno-Zarate, Arroyo and Peach, 2021). Together, this range of pressures underscores the complexity of migratory bird declines and the potential for various factors to affect species in distinct ways.

Multi-species studies have demonstrated species-specific responses to factors such as land use types and climate change (Ockendon *et al.*, 2014; Beresford *et al.*, 2019; Barnes *et al.*, 2023), highlighting a need for autecological studies to identify factors related to species-specific declines. The urgency of action also varies between species, which are declining at different rates (Sanderson *et al.*, 2006). For some species, it may be necessary to test conservation actions before the most important demographic drivers are identified, but this could lead to valuable time and resources being wasted if actions are misplaced due to a lack of information (Vickery and Adams, 2020). Hence, research should aim to fill knowledge gaps about the species of highest conservation concern, so that interventions to ameliorate declines, which may benefit multiple species (Morrison *et al.*, 2022), can be more accurately targeted.

1.2. The spotted flycatcher

The spotted flycatcher (*Muscicapa striata*) is a species of long-distance migrant passerine, breeding across the whole of Europe and wintering in sub-Saharan Africa (Cramp and Perrins, 1993). It is one of the most rapidly declining Afro-Palearctic migrants that breeds in the UK and is in urgent need of conservation action (Stanbury *et al.*, 2021). Autecological studies for this species are sparce, limiting our ability to make recommendations for reversing its decline. The species is declining across its European range (PECBMS, 2025), but trends are most severe in the UK, suggesting that there are factors affecting the UK population exclusively, or that Europe-wide factors are exacerbated at the western edge of the species' range in the UK. It is an obligate insectivore, feeding almost exclusively on flying insects, yet has rather generalist habitat requirements (Cramp and Perrins, 1993), making it a good representative of food availability across a range of habitats. Hence, understanding factors related to the demographic rates of this species in the UK has the potential to benefit other populations as well as other insectivorous Afro-Palearctic migrants, making it an excellent focus for research.

1.2.1. Taxonomy and appearance

Five subspecies are recognised across Europe but the focus of this study, and the only subspecies found in the UK, is the nominate *Muscicapa striata striata* (Cramp and Perrins, 1993). Being sexually monomorphic, adults of both sexes have dull brown-grey upperparts and off-white foreparts mottled with brown streaks, particularly on the chin and breast. The appearance of juveniles more strongly represents their common name, with plumage of upperparts buff with dark brown margins giving a truly 'spotted' appearance. In the field, spotted flycatchers may also be identified by their characteristic 'sallying' flight, in which they fly up from perches in pursuit of insects, before returning to their perch to consume their prey (Cramp and Perrins, 1993).

1.2.2. Diet

Spotted flycatchers are aerial insectivores, capturing insects in flight after taking off from perches such as tree branches, bushes, fences or other man-made structures (Cramp and Perrins, 1993). The diet of spotted flycatchers is relatively plastic, being driven by local abundances of insect groups. Hymenoptera (particularly Formicidae) appear to dominate the diet of Algerian birds (Boukhemza-Zemmouri *et al.*, 2011), whereas Diptera dominated in one UK study (Davies, 1977). The foraging success of spotted flycatchers is largely determined by insect activity (Davies, 1977), which in turn is heavily influenced by the weather (Taylor, 1963). In times when weather conditions are sub-optimal (e.g. rain, cold), spotted flycatchers can be observed feeding from the ground or gleaning insects from tree canopies, though these strategies are much less efficient and prolonged bouts may lead to chick starvation (Davies, 1977). They have also been observed consuming a small amount of fruits during the autumn migration, although insects continued to make up c.90% of the diet during this period and so are by far their most important food source (Hernández, 2009).

1.2.3. Habitat

The diet and feeding strategy of spotted flycatchers determines their habitat requirements, which are rather flexible in comparison with other species. Despite sometimes being classified as a woodland specialist (e.g. DEFRA, 2025), they can be found in most habitats with sufficient perches to hunt from and open space to pursue insects (Cramp and Perrins, 1993; Kirby *et al.*, 2005; Randler, 2013). During the breeding season, spotted flycatchers can be seen in woodland edges, farmland, gardens, parks and riversides, and tend to avoid completely open areas or dense woodland (Cramp and Perrins, 1993). In Africa, the habitat occupied is equally as broad and appears determined by the presence of perches and open glades for hunting (Cramp and Perrins, 1993). During the breeding season, they also require natural or man-made ledges to build loose, open-cupped nests. Examples include forks of tree branches, crevices in trees or on walls, and in creeping plants such as ivy (*Hedera spp.*) (Cramp and Perrins, 1993; Clarke, 2005; Kirby *et al.*, 2005). Spotted flycatchers are remarkably tolerant of human disturbance and frequently nest on houses and in gardens, positioning them as an ideal species to foster community engagement and interest in conservation (Clarke, 2005).

1.2.4. Migration

Movements of spotted flycatchers have not been well studied, and most of our knowledge is based on a limited number of ringing recoveries (n = 6278) compared to other migratory species (e.g. 98762 for Pied Flycatchers *Ficedula hypoleuca*) and observational studies (Franks *et al.*, 2022). The limited recoveries of ringed birds suggest that there is a migratory divide at approximately 12°E; birds from the UK and far west of Europe appear to travel south-southwest through France and Iberia and then south across the Sahara and into West Africa before continuing further south (Cramp and Perrins, 1993; Elphick, 2007; Franks *et al.*, 2022). Conversely, birds breeding in northern and eastern Europe travel south-southwest through Italy and Greece, and then across the Sahara (Cramp and Perrins, 1993; Elphick, 2007; Franks *et al.*, 2022). In winter, spotted flycatchers may track the rains in a southerly direction through Africa, with birds only found in the southernmost regions between December and February during the peak of the rainy season (Kok *et al.*, 1991; Cramp and Perrins, 1993; Dunning *et al.*, 2016).

Spotted flycatchers are one of the latest arriving migrants in Europe (Huin and Sparks, 2010), departing Africa between late February and March and arriving at their breeding grounds between May and June where they remain until autumn (August–October) (Kok *et al.*, 1991; Cramp and Perrins, 1993). The timing of departure from the wintering grounds appears to be more strongly controlled by day length (Lofts and Marshall, 1960; Kok *et al.*, 1991) than environmental conditions (e.g. as is found for more northerly wintering species (Robson and Barriocanal, 2011)), and consequently the timing of arrival to the breeding grounds shows little change over time (Huin and Sparks, 2010; Finch *et al.*, 2014). It has been proposed that they carry out an itinerant (short-hop) migration i.e. they stop and fuel frequently rather than storing large fat deposits and undertaking a few long journeys (Biebach, 1985; Cramp and Perrins, 1993), although this assumption has not been confirmed by tracking studies. The recent advancement of tracking technologies has exposed more detail of the annual cycle. One study revealed that flights over the Sahara Desert extended over 24 hours, suggesting flexibility in the migration strategy, and contrasting with previous assumptions (Biebach, 1985; Jiguet *et al.*, 2019a; Dufour *et al.*, 2024). So far, there have been no detailed descriptions of the spatio-temporal movements of spotted flycatchers throughout the annual cycle, limiting our understanding of the most appropriate measures to protect them.

1.2.5. Population trends

The entire European population of spotted flycatchers has declined by 56% on average since 1980 (PECBMS, 2025), though this number may be strongly influenced by the UK population that has declined more severely. On the western edge of its range, in the UK, the species has declined by 93% since 1967 (Fig. 1.1a, BTO, 2024), and as such they are red-listed in the Birds of Conservation Concern (Stanbury *et al.*, 2021). Other Afro-Palearctic migrants sharing similar habitats e.g. pied flycatchers are also declining, but to a lesser extent (BTO, 2024). Similarly, other species migrating to the humid zones of Africa have also declined, but the declines are less severe (e.g. barn swallow *Hirundo rustica*) (BTO, 2024). As such, spotted flycatchers are the most rapidly declining Afro-Palearctic passerine in the UK.

Declines have been inconsistent across different time scales and regions, suggesting that multiple factors may have contributed. Though spotted flycatchers have been declining since long-term monitoring began (Hagemeijer, 1997), the trend has been most severe since the mid-1980s (Fig. 1.1a, BTO, 2024). Records from the *Bird Atlas 2007–11*, which collates systematically collected citizen science data, show that spotted flycatchers can be found in 10 x 10 km survey squares (hectads) across most of the UK (Balmer *et al.*, 2013). Colonisation of hectads between the 1970s and 2010s occurred mostly north of the Central Belt in Scotland, though a few hectads were colonised in England, Wales and Ireland (Fig. 1.1b, Balmer *et al.*, 2013). Losses were concentrated around cities in England and Scotland and along the east coast of Great Britain (Balmer *et al.*, 2013). Despite most hectads remaining occupied between the two surveys, the relative abundance within those squares reveals a more concerning trend. The number of occupied 2 x 2 km squares (tetrads) within each hectad has reduced across most of the UK, with increases restricted to Scotland and Ireland (Fig 1.1c, Balmer *et al.*, 2013). Thus, while the distribution of

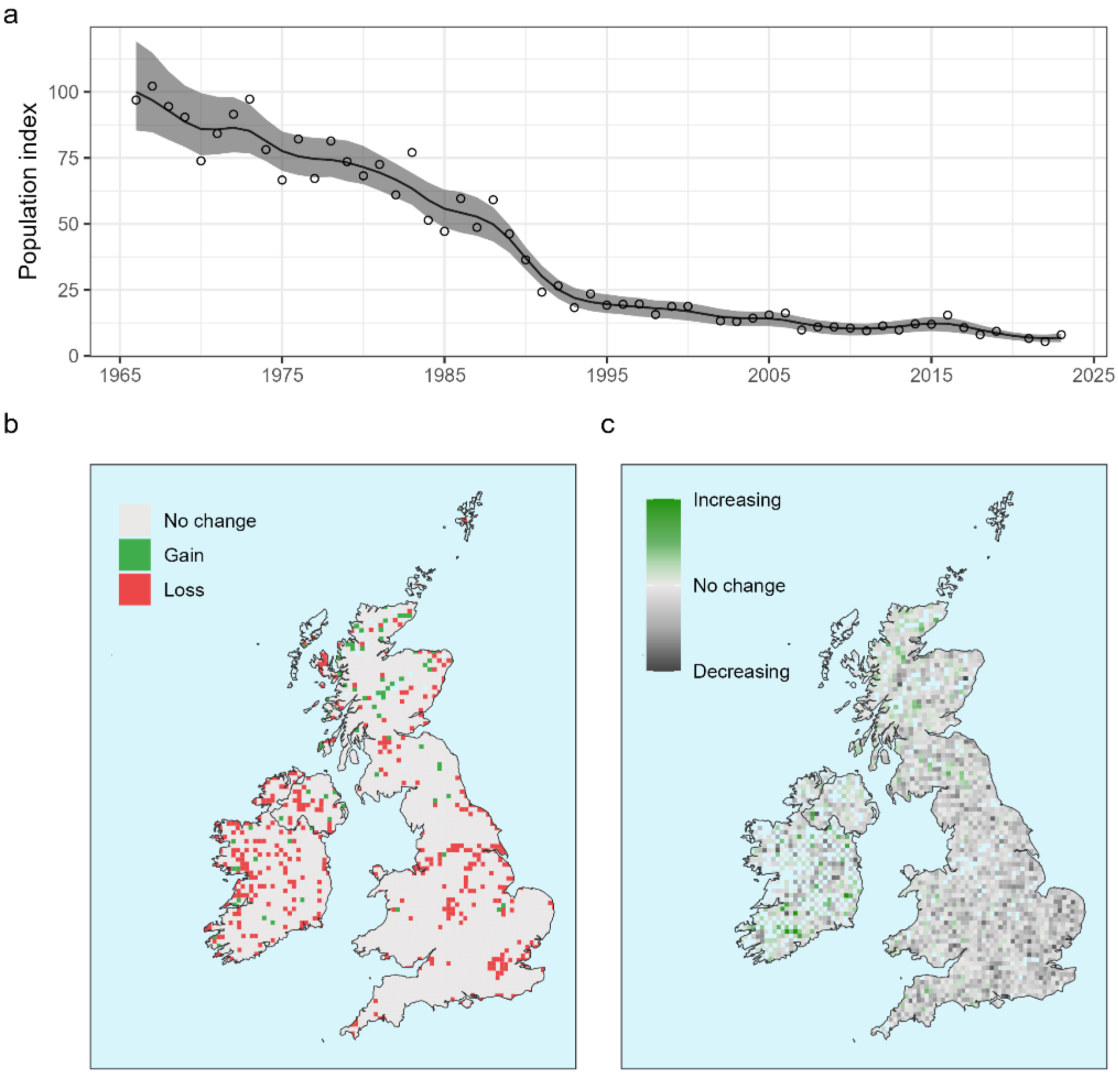


Figure 1.1. Population trends and distribution change of spotted flycatchers in the UK. (a) breeding bird survey smoothed index of spotted flycatcher population change in the UK between 1967 and 2022, (b) change in occupancy of 10 x 10 km squares between 1970 and 2010, and (c) change in proportion of occupied 2 x 2 km squares within each 10 x 10 km square (relative abundance) between 1970–2010. Light blue (empty squares) in b and c represent squares with insufficient data (Balmer *et al.*, 2013; BTO, 2024).

spotted flycatchers has not changed greatly between 1970–2010, their density has decreased considerably.

Trends are negative throughout most of the UK, with limited spatial variation other than around cities, suggesting that factors affecting the decline of spotted flycatchers must be broad ranging, either acting throughout the whole of the UK or occurring elsewhere in the annual cycle. Population trends are a function of survival (juvenile and adult) and productivity (breeding success), and understanding the factors affecting either of these demographic rates can reveal potential causes of decline. However, unveiling the drivers of demographic trends for migratory species is complicated by the interconnectedness of different phases in the annual cycle. For example, carry-over effects from poor conditions on migration can negatively impact productivity (Finch *et al.*, 2014). Additionally, the synchronicity of factors influencing productivity and survival can drive population trends; for example, willow warblers (*Phylloscopus trochilus*) have more favourable population trends in the north west of their UK range, where years with high productivity coincided with years of high survival (Morrison *et al.*, 2016). Moreover, the cause of decline is likely a combination of several factors interacting synergistically. For example, the impact of arriving to the breeding grounds in poor condition is likely to be exacerbated if arriving into poor quality habitat (Morrison *et al.*, 2013), and the influence of predation is intensified when populations are already depleted (Newton, 1998).

1.3. Potential factors related to the decline of spotted flycatchers

To date, relatively few studies have sought to investigate the drivers of decline in spotted flycatchers, despite an urgent need for conservation action. Almost all research has been concerned with conditions on the breeding grounds, probably due to the limitations in tracking technology. Nest predation has been identified as an important determinant of productivity, accounting for the majority of nest failures in southern and central England (Kirby *et al.*, 2005; Stevens *et al.*, 2007). Accordingly, Stoate and Szczur (2006) found that during periods of predator control in central England, their study population experienced high levels of nest survival (77%) that coincided with more favourable population trends in that region. In contrast, Freeman et al., (2003) found no change in national nest failure or productivity over the period of their study, but they identified first-year survival as a potential driver of declines. Climate change has also been recognised as a threat to spotted flycatchers (Pearce-Higgins, 2021), whose productivity has been shown to vary with environmental conditions on migration (Finch *et al.*, 2014) and on the breeding grounds (O'connor and Morgan, 1982). The locality of studies makes it difficult to generalise some findings, and as the species continues to decline, there is a need to update our knowledge base and expand the reach of our understanding by conducting research on a broader scale. The following sections explore factors that may be linked to demographic rates in this species, with a focus on predation and the factors affecting the availability of food, predominantly on the breeding grounds.

1.3.1. Nest predation

Open-cup nesting species are at risk of nest predation from avian and mammalian predators and generally experience higher levels of predation compared to cavity nesting species due to their exposure. Though open-cup nesters have adapted to these conditions, changes in predation rates due to ecological conditions or predator community shifts may negatively impact population trends, particularly for species already in decline (Newton, 1998). A recent meta-analysis identified avian predators as the most frequently encountered predator type for arboreal, open-cup nesting species such as the spotted flycatcher, though the findings were based on a small number of studies (Barton *et al.*, 2025). Predation by avian predators was the main driver of low productivity in farmland and woodland in southern England (Stevens *et al.*, 2007). Eurasian jay (*Garrulus glandarius*) accounted for 12 of 17 avian depredation events (Stevens *et al.*, 2010), but whether this pattern extends beyond southern England is unclear. Several potential spotted flycatcher nest predators have increased in the UK, including carrion crows (*Corvus corone*), jays and jackdaws (*Corvus monedula*) (Roos *et al.*, 2018). Inflated predation pressure has been proposed as a potential driver of declining woodland bird populations (Fuller *et al.*, 2005), but a multi-species review of studies assessing the relationship between population trends and nest predators found little support for this theory (Roos *et al.*, 2018). Nonetheless, identifying the underlying causes of population trends is complicated by the number of factors that may be influencing productivity and survival synchronously, and the potential time lag in their cause and effect (Souchay *et al.*, 2018).

Reproductive rates for spotted flycatchers in farmland and woodlands in southern England were recently shown to be insufficient for achieving a stable population growth rate (Burgess *et al.*, 2025), and so protecting nests from predators is likely to be beneficial. Lethal predator control is effective at a local scale in the short-term (Stoate and Szczur, 2006), but the resources, costs and ethical considerations associated make it an unsustainable long-term solution. Thus, managing the landscape in such a way that reduces predation pressure, such as increasing the availability of vegetation cover for nests and juveniles, may be a more achievable goal (Vitz and Rodewald, 2006; Bellamy *et al.*, 2018; Roos *et al.*, 2018). Accordingly, more research is needed to understand how fine-scale habitat characteristics are associated with nest predation rates.

1.3.2. Food availability and land use

As an obligate insectivore, global insect declines are highly likely to affect spotted flycatchers, but a lack of long-term insect monitoring hampers our ability to test this empirically. Agricultural management has been implicated as the main driver of the 'insect apocalypse', primarily due to intensification of management (Habel *et al.*, 2019; Sánchez-Bayo and Wyckhuys, 2019). Intensive practices include a shift from mixed cropping to farm specialisation, increased fertiliser, pesticide and herbicide use, increased stocking densities and a reduction in the proportion of uncultivated areas (Newton, 2004). Application of non-selective pesticides reduces insect populations (Sotherton and Self, 2000; Bright *et al.*, 2008; Goulson, 2013), while homogenisation of agricultural landscapes through mechanisation, herbicide and fertiliser application reduces the diversity of food plants and habitats available for insects (Vickery *et al.*, 2001; Newton, 2004; Britschgi *et al.*, 2006). Consequently, agricultural intensification has been linked to dramatic losses of farmland and insectivorous birds (Siriwardena *et al.*, 1998; Donald *et al.*, 2001; Denerley *et al.*, 2019)

Bird abundance and breeding success of some species is higher on less intensively managed farms as a result of increased insect habitat and abundance (Peach *et al.*, 2001; Britschgi *et al.*, 2006; Wilkinson *et al.*, 2012), suggesting that reduced invertebrate abundance could be driving population declines through reduced productivity. Agri-environment schemes incentivise the use of more nature-friendly farming practices, and whilst these have shown local successes (Wilkinson *et al.*, 2012; Bellamy *et al.*, 2022), national populations of birds continue to decline, suggesting that the reach of the schemes may be insufficient. As the dominant land use type in western Europe, the impacts of agriculture on insect abundance may extend beyond the farmland boundary, particularly if population sinks (farms) outweigh the sources e.g. uncultivated areas (Hale and Swearer, 2016). Indeed, a 75% decline in insect biomass in protected areas in

Germany was attributed to farmland impacts extending into the surrounding landscape (Hallmann *et al.*, 2017).

Insect and insectivorous bird declines may also be related to changes in woodland management since the mid 20th Century (Hopkins and Kirby, 2007). Conifer plantations now make up approximately half of the woodland cover in Britain (Forest Research, 2023), but this non-native, homogenous habitat type may be of poor quality for insects and insectivorous birds (Pedley *et al.*, 2019). Geographic variation in the changes to broadleaved woodlands makes it difficult to generalise about the factors influencing woodland insect and bird populations (Amar *et al.*, 2010). A trend towards canopy closure and more shaded woodland (Hopkins and Kirby, 2007; Amar *et al.*, 2010) has probably made woodland patches unsuitable for insects (Thomas *et al.*, 2015) and therefore spotted flycatchers and other species foraging in open woodland (Hopkins and Kirby, 2007). The most significant trend, perhaps, is the replacement of oak trees (*Quercus* spp.) with ash trees (*Fraxinus* spp.) that have fewer invertebrate associations (Southwood *et al.*, 1982; Amar *et al.*, 2010; Mitchell *et al.*, 2019), but it is unclear whether the overall abundance of insects has been greatly affected. The sparsity of long-term insect monitoring within woodlands makes it difficult to assess trends in woodland invertebrates and their effects on insectivorous birds. Most research has been focussed on more charismatic insects such as Lepidoptera (Habel *et al.*, 2019) and the birds that consume their larvae (e.g. Burgess *et al.*, 2018). However, these findings have less relevance for aerial insectivores feeding predominantly on numerous flying insect groups, highlighting the limits of broadly categorising species as insectivores.

1.3.3. Climate change

Climate change has been linked to the abundance and distribution of insects (Burns *et al.*, 2016), and as such has potential to work synergistically with the impacts of land use change to alter the availability of food for insectivorous birds. Notably, earlier spring onset has led to a mismatch between the timing of insect peaks and their predators (Thackeray *et al.*, 2016), with migratory species adjusting the time of their arrival to the breeding grounds to coincide with earlier food peaks (Newson *et al.*, 2016). Short-distance migrants have advanced their arrival times more than long-distance migrants (Rubolini *et al.*, 2007; Møller *et al.*, 2008; Both *et al.*, 2010; Saino *et al.*, 2011; Newson *et al.*, 2016), presumably because long-distance migrants rely on daylength, rather than environmental conditions, to initiate migration (Kok *et al.*, 1991). Species that have adjusted their arrival the least have the most unfavourable population trends (Møller *et al.*, 2008; Both *et al.*, 2010; Saino *et al.*, 2011; Newson *et al.*, 2016), but it is unclear whether this relationship is causative.

For aerial insectivores that are less reliant on short, seasonal bursts of Lepidopteran larvae (e.g. Both *et al.*, 2006), or species that can adapt their diet to local conditions (Mallord *et al.*, 2017), the effects of climate change may be more strongly related to variations in food availability caused by unpredictable weather conditions, rather than phenological mismatch (Martay *et al.*, 2023). For example, the availability of flying insects in England tends to peak before the arrival of spotted flycatchers and extends beyond their departure (Martay *et al.*, 2023), so it is unlikely that they would arrive at a period of low relative insect abundance. However, local climate has strong potential to influence the temporal availability of flying insects by modifying their activity, so an increase in the frequency and persistence of wet, windy, cold or hot weather could be detrimental (Taylor, 1963; Tøttrup *et al.*, 2012; Irons *et al.*, 2017; Shipley *et al.*, 2020). Accordingly, weather conditions on the breeding grounds (Irons *et al.*, 2017) and on migration (Briedis *et al.*, 2017) have been linked to the productivity and survival of migrant birds.

1.4. Aquatic subsidies

Freshwater habitats are an important but under-considered source of flying insects for insectivorous vertebrates. Emergent aquatic insects provide an important resource for terrestrial predators that live within riparian habitats (Polis *et al.*, 1997; Henschel *et al.*, 2001), and also supplement the diets of species not restricted to riparian habitats (Iwata *et al.*, 2003). The peak of aquatic insect emergence is asynchronous with terrestrial insect emergence, offering increased temporal availability of food as well as increased abundance (Nakano and Murakami, 2001; Uesugi and Murakami, 2007). In addition to providing additional quantity of food, aquatic subsidies also provide better quality food. Aquatic insects contain highly unsaturated fatty acids (HUFAs), which are rare in the terrestrial environment and cannot be synthesised from molecular precursors efficiently by many species (Twining *et al.*, 2018a, 2019; Moyo, 2020). HUFAs have several important functions in vertebrates, including brain development, muscle growth and metabolism (Speake and Wood, 2005; Weber, 2009; Arnold *et al.*, 2015; Dyall, 2015). Accordingly, tree swallow (*Tachycineta bicolor*) and eastern phoebe (*Sayornis phoebe*) chicks experimentally supplemented with HUFA-rich diets grew quicker and larger than chicks provided with diets rich in HUFA precursors but not HUFAs (Twining *et al.*, 2016b, 2019). Moreover, a higher quality diet prior to laying may allow females to produce greater clutch sizes or eggs of higher quality (Monaghan *et al.*, 1998), but the effects of aquatic subsidies on adult condition are yet to be investigated.

Using foraging observations to identify prey types, Iwata et al.,(2003) estimated that aquatic subsidies made up 82.3% of flycatcher (Muscicapinae) diets, whilst Nakano & Murakami (2001) estimated that the average contribution of aquatic subsidies to annual energy budgets was between 7.4% and 98.2% depending on the predator species. Similarly, aquatic insect prey made up between 2.0% and 96.4% of pied flycatcher nestling diets. Jackson et al., (2021) found that the contribution of aquatic subsidies declined from early spring to late summer, suggesting that aquatic subsidies may be particularly important at the start of the breeding season. Correlative studies have demonstrated that the abundance of insectivorous birds in riparian zones peaks in areas, and at times, of higher emergent insect abundance (Gray, 1993; Murakami and Nakano, 2002; Uesugi and Murakami, 2007; Chan *et al.*, 2008). Similarly, the biodiversity in riparian woodlands exceeds that of non-riparian woodlands in a highly-modified landscape (Bennett *et al.*, 2014), suggesting the potential for riparian habitats to act as refugia. However, the impact of birds exploiting aquatic resources on demographic rates is unclear and research is limited to a few studies in the USA. For example, the state-level population trends of several aerial insectivores associated with riparian habitats were positively correlated with the availability of large-bodied aquatic insects (Manning and Sullivan, 2021). Another study found that tree swallow chicks were more likely to fledge when aquatic insect, but not terrestrial insect, abundance was higher (Twining *et al.*, 2018b). Nestling condition and fledging probability of the same species were found to respond positively to the cover of ponds in the landscape (Berzins *et al.*, 2022). In Europe, aquatic insects appear to have increased in abundance (van Klink *et al.*, 2020), and so freshwater habitats may support insectivorous populations in areas where terrestrial resources are depleted, but this work needs to be extended to different species with varying life-history traits before generalisations can be made.

1.5. Thesis structure and aims

The aim of this thesis is to broaden and update our knowledge on the ecology of spotted flycatchers, and identify factors related to productivity in the UK, which may be used to inform conservation interventions. Few studies have investigated the potential for aquatic subsidies to improve productivity, and so this thesis aims to reveal the relationship between spotted flycatchers and aquatic habitats, utilising rivers as a case study. Productivity may be a more feasible conservation target for many Afro-Palearctic migrants due to the comparative ease of implementing mitigation on the breeding grounds (Morrison *et al.*, 2022), and accordingly, the majority of this thesis relates to the breeding grounds. However, Chapter 5 aims to provide a detailed description of the migratory routes and behaviour of the spotted flycatcher, with the hope that this will inform future research targeting the non-breeding season.

In Chapter 2, the relationships between land cover types and breeding distribution are investigated across Great Britain at a national scale. In Chapter 3, this focus is narrowed to a population in Cumbria, where the aim is to understand if relationships identified at the national scale also explain local variation in nest-site selection and nest survival. The association of fine-scale habitat characteristics, including the presence of rivers, creepers and canopy cover, with nest-site selection and nest success are explored. In Chapter 4, the scale is narrowed further to understand how the availability of aquatic subsidies is related to adult and chick body condition and overall breeding success. Finally, in Chapter 5 the scope is widened, to reconstruct the spatial and temporal movements of the spotted flycatcher throughout the annual cycle. The initial aim of this chapter was to investigate how the availability of aquatic subsidies on the breeding grounds impacts migratory behaviour, but low recapture rates of the tagged birds led to insufficient sample sizes. Nonetheless, the species' migratory strategy is described in detail for the first time, greatly enhancing our knowledge about where spotted flycatchers spend their time outside of the breeding season, and thereby helping to identify the most suitable conservation strategies for this species.

Chapter 2 The role of freshwater availability and terrestrial land cover in the distribution of a declining terrestrial, insectivorous bird

2.1. Abstract

Insectivorous, Afro-Palearctic migrant birds provide cross-border ecosystem services, but many are declining rapidly. The complex life cycle of migrant birds makes it difficult to target conservation actions, but understanding where they spend time during the breeding season can help indicate where those actions will be most effective. We used the spotted flycatcher (*Muscicapa striata*), an Afro-Palearctic migratory insectivore in decline across Europe, as a model to understand how changing distribution patterns during the breeding season are associated with habitat. We tested how aquatic and terrestrial land cover data were related to the distribution of spotted flycatchers within 2 km x 2 km survey squares across Britain, and how river density and land cover change were associated with distribution change between surveys in 1990 and 2010. Squares with higher proportions of urban land cover were less likely to be occupied (odds ratio (OR) 0.7), whilst squares with greater river density (OR 1.19) and a higher proportion of freshwater (OR 1.06), broadleaf woodland (OR 1.2) and improved grassland (OR 1.24) were more likely to be occupied. Greater river density was associated with a lower probability of loss (OR 0.8) from a square between survey periods, and a higher probability of colonisation (OR 1.25). Loss was associated with increases in urban land cover (OR 1.17) and, unexpectedly, colonisation was negatively associated with increases in woodland (OR 0.91) and standing freshwater (OR 0.94). Our study suggests that habitat creation is unlikely to provide sufficient benefits for some insectivorous birds in the timeframe needed for population recovery, and so efforts should be focussed on the protection and improvement of established habitats. Rivers were strongly associated with the presence and persistence of the spotted flycatcher, and understanding how this relationship could be incorporated into the conservation management of other terrestrial species should be a priority.

2.2. Introduction

Management actions are urgently needed to counteract long-term declines of Afro-Palearctic migrant birds, most of which rely on insects at some point during the annual cycle (Vickery *et al.*, 2023). Difficulties in understanding the drivers of decline arise from the complex life cycle and wide spatial range occupied by these birds, breeding in one continent and overwintering in another (Newton, 2007). Climate change and land use change are regularly cited as important factors in the species' declines, but there is little consensus on the individual mechanisms involved (Vickery *et al.*, 2023; Suggitt *et al.*, 2023).

The effects of land use change may be more directly managed than those of climate change, and so they present a more achievable short-term conservation focus. Land use change can affect Afro-Palearctic migrants across the entire flyway; in Africa, the suitability of land cover for long-distance migrants has decreased (Howard *et al.*, 2020), and, in Britain, changing management of woodland (Amar *et al.*, 2006; Holt *et al.*, 2011) and farmland (Bowler *et al.*, 2019) have had negative impacts on some species. Much of the research to date has focussed on understanding drivers of population change on the breeding grounds, with limited attention paid to the wintering grounds due to a scarcity of information on their specific locations (Vickery and Adams, 2020; Vickery *et al.*, 2023). Hence, management actions to improve productivity on the breeding grounds present a more achievable and potentially more effective strategy to improve population trends than attempts to improve survival on the wintering grounds (Saether and Bakke, 2000; Morrison *et al.*, 2016), provided that no density-dependent effects are operating elsewhere in the annual cycle that could undermine the efficacy of such actions, or even result in unintended negative consequences (Taylor and Norris, 2007).

Insectivorous birds consume huge amounts of invertebrates, so the degradation of this system could have serious implications for ecosystem functioning and biological pest control (Nyffeler *et al.*, 2018; Roseo *et al.*, 2024). Afro-Palearctic migrants that feed on insects have undergone more severe declines than other foraging guilds (Sanderson *et al.*, 2006). Declines have also been observed in non-migratory European (Bowler *et al.*, 2019) and North American (Tallamy and Gregory Shriver, 2021) insectivores, suggesting shared pressures across the globe. These losses likely follow worldwide crashes in terrestrial insect abundance, which have been associated with land use change and agricultural intensification (Hallmann *et al.*, 2017; Sánchez-Bayo and Wyckhuys, 2019; Reif and Hanzelka, 2020). For example, the distribution of the common cuckoo (*Cuculus canorus*), a declining Afro-Palearctic migrant reliant predominantly on Lepidoptera larvae during the breeding season, appears to have shifted away from agricultural lowland in response to reduced food availability (Denerley *et al.*, 2019). Conversely, aquatic insects may provide an increasingly important food source as their numbers have increased in Europe since the early 2000s, perhaps due to regulations on water quality and warmer temperatures (van Klink *et al.*, 2020; Qu *et al.*, 2023).

The flux of emergent aquatic insects into terrestrial habitats represents an important ‘aquatic subsidy’ for insectivores that has received little attention (Lafage *et al.*, 2019). The exploitation of these resources by insectivorous birds is evidenced by their greater abundance near to rivers and streams and increased predation of flying insects in these areas (Murakami and Nakano, 2002; Iwata *et al.*, 2003; Bradbury and Kirby, 2006). This behaviour may positively influence population dynamics, particularly in resource-limited populations (Richardson *et al.*, 2010). As well as providing additional food, freshwater may subsidise terrestrial habitats by offering food of higher nutritional quality (Moyo *et al.*, 2017). Aquatic insects are richer in essential omega-3 fatty acids (Moyo *et al.*, 2017; Twining *et al.*, 2019), which have been associated with improved breeding success in some birds (Twining *et al.*, 2018b). Moreover, the timing of aquatic insect emergence is asynchronous with the peak of terrestrial insect emergences, increasing the temporal coverage of food (Nakano and Murakami, 2001). This could be a key driver of more favourable population trends among Afro-Palearctic migrants occupying freshwater habitats, perhaps buffering against phenological mismatch (Both *et al.*, 2010). Thus, an examination of the use of freshwater habitats would provide greater understanding of the population dynamics of migratory insectivorous birds.

Several studies have investigated local breeding habitat associations of Afro-Palearctic migrants (Stevens *et al.*, 2007; Mallord *et al.*, 2016), but few have assessed the landscape-scale associations (but see Denerley et al. 2019), limiting the spatial interpretation of results. Similarly, examinations of the relationship between insectivorous species and freshwater habitats have been limited to local populations (Berzins *et al.*, 2022) or small geographical ranges (Iwata *et al.*, 2003).

Here, we tested whether terrestrial and freshwater land cover predict the British breeding distribution of the spotted flycatcher (*Muscicapa striata*), nationally the most rapidly declining insectivorous Afro-Palearctic migrant bird (Burns *et al.*, 2020). Conservation actions are urgently needed for this species, which declined by 92% in the UK between 1967 and 2020 (Woodward *et al.*, 2020). Understanding trends within the British population may inform practices to avert further declines in the European population, which has decreased by 56% since 1980 (PECBMS, 2025). Spotted flycatchers have three main fine-scale structural habitat requirements during the breeding season: a perch to hunt from, open space to hunt flying insects, and ledges or shallow cavities for nesting (Cramp and Perrins, 1993). Previous studies suggested predation pressure, particularly in woodland and farmland, could be linked to declining breeding success at the local scale (Stoate and Szczur, 2006; Stevens *et al.*, 2007). However, understanding the drivers of change at a national scale may help identify habitat pressures shared across Europe, making the findings relevant to wider populations. Furthermore, given the species' widespread distribution and utilisation of diverse habitats, including woodland, farmland and rural settlements, an understanding of the species' decline will offer insights into the declines in other insectivorous migrants, such as swifts (*Apus apus*) and house martins (*Delichon urbicum*) (Burns *et al.*, 2020).

Using comprehensive national atlas surveys of breeding birds in Britain, we quantified the relationships between freshwater habitats and terrestrial land cover types with occupancy in 2 km x 2 km tetrads to understand recent habitat associations. We then investigated how changes in land cover between two time periods were related to occupancy change during the same period. We assessed the relationship for all suitable land cover types, including agricultural land, woodland, grassland, freshwater and urban land. Although climate change is likely to have had an important effect on the distribution of spotted flycatchers, the aim of this study was to identify specific land use types positively associated with continued occupancy and colonisation, or negatively associated with loss of occupancy, thereby indicating priority land use types for protection or creation. Specifically, we aimed to (1) quantify habitat associations with occupancy during the breeding season at a national scale, (2) examine how changes in land cover are related to changes in occupancy between 1990 and 2010, and (3) assess the importance of freshwater habitats for this insectivorous bird species at a national scale.

2.3. Methods

2.3.1. Occupancy and occupancy change data sources

The occupancy of spotted flycatchers in 2 km x 2 km tetrads in Britain during two survey periods was extracted from the 1988–91 and 2008–11 British Trust for Ornithology (BTO) Bird Atlases (Gibbons, 1993; Balmer *et al.*, 2013), hereafter BA1990 and BA2010. During the spring breeding seasons of 1988–91 and 2008–11, volunteers recorded the presence of all bird species along transects within tetrads on two separate visits, achieving near-total coverage for Britain (Gillings *et al.*, 2019). Each visit lasted one hour during BA1990, but for BA2010 there was an option for volunteers to visit for an additional hour. To ensure standardisation, we only included records from the first hour in BA2010.

The recorded presence of spotted flycatchers in tetrads surveyed during BA1990 and BA2010 was extracted as a measure of occupancy or apparent absence for each period. Results from BA2010 were used to understand the most recent predictors of occupancy, whereas the difference in occupancy between BA1990 and BA2010 was used to explore associations with occupancy change. Presence and absence data from each atlas period were used to assign categories of colonisation (absent 1990, present 2010), loss (present 1990, absent 2010), persistence (present 1990 and 2010), or absence (never present) to each tetrad. To maximise the proportion of breeding birds and minimise the inclusion of transient birds (i.e. birds migrating through a square), presence was only included for tetrads that had probable or confirmed breeding evidence for the encompassing 10 km x 10 km square (Balmer *et al.*, 2013). The chance of recording the same bird in adjacent squares was minimal, as the majority of foraging occurs within 50 m of the nest during the breeding season, with occasional foraging trips of up to 200 m (Davies, 1977). Two datasets were created from the categorised squares: one to test the probability of colonisation, which included all squares from which birds were absent during BA1990, and one to test the probability of loss, including only those squares in which birds were present during BA1990.

2.3.2. Environmental data sources

To identify factors associated with spotted flycatcher distribution and change, we derived a set of covariates describing the environmental conditions in each surveyed tetrad. Mean elevation for each tetrad was calculated using the ASTER Global Digital Elevation Model V003 (NASA/METI/AIST/Japan Space systems and U.S./Japan ASTER Science Team, 2019).

Latitude and longitude of the central point of each tetrad were also extracted. The proportions of 13 habitats in each tetrad were calculated using the UKCEH land cover map for 2007 (LCM2007; Morton et al., 2014): urban, unimproved grassland, improved grassland, heathland, saltwater, rock, sediment, bog-fen, montane, freshwater, coniferous woodland, broadleaf woodland and arable. These habitats were condensed from 20 broad habitat types (Supp. Table 2.1) classified using satellite data. For all analyses we used the land cover map most closely representing the Atlas survey period (i.e. LCM 2007 for analysis of 2010 occupancy).

Land cover change was calculated using the UKCEH Land Cover Change 1990–2015 dataset (Rowland *et al.*, 2020) as the proportion of each land cover type in 2015 subtracted from the proportion in 1990 (Supp. Table 2.2, Supp. Figure 2.1). These data were provided as a 25 m raster and report land use cover in six simplified, but comparable, land cover types across the UK: woodland, urban, arable, grassland, freshwater and other.

As spotted flycatchers are typically associated with broadleaf woodland, rather than coniferous woodland, the change in proportion of coniferous and broadleaf woodland were extracted from the detailed maps of LCM1990 and LCM2007, as changes in the methods used to classify these habitats was likely minimal. River density in each tetrad was calculated as the length of river (km) per km^2 of the tetrad using the vector lines shapefile from the UKCEH Digital River Network Of Britain (1:50,000) (UKCEH, 2000). There should be minimal overlap between the freshwater and river variables, as the former only included standing and running water bodies > 0.5 ha or > 50 m wide, representing mainly still open water, whereas the river density was derived from the 1:50000 Ordinance Survey map.

2.3.3. Data analysis - Model construction

Statistical analyses were carried out using R (V4.3.1; R Core Team, 2020) and the '*lme4'* package (Bates *et al.*, 2015). GLMMs with a binomial error structure and logit link function were used to test the association between environmental variables and occupancy or occupancy change. Three separate models were tested: one testing the recent environmental correlates of occupancy (2010 occupancy model), and two occupancy change models testing correlates of loss and colonisation between BA1990 and BA2010.

To account for maximal spatial associations unrelated to land cover, such as climate or geography, all models included an interaction between latitude and longitude, and a second-order polynomial term for elevation. Additionally, the encompassing 100 km x 100 km square for each tetrad was included as a random effect to further account for geographical trends unrelated to land cover. Explanatory variables were scaled, centred and tested for collinearity prior to model fitting. For the 2010 occupancy global model we excluded habitats that would be unsuitable for flycatchers (e.g. heathland) to reduce overfitting. The global model included river density, urban, improved grassland, unimproved grassland, arable, broadleaf woodland, coniferous woodland and freshwater cover.

The global models for occupancy change included river density and the changes in proportions of woodland, arable, freshwater and urban land. To avoid ambiguity, the land cover change category ‘other’ was excluded. Grassland cover change was highly correlated with arable cover change (r = 0.79), and so only arable change was included (as the alternative model including grassland failed to converge). Change in proportions are constrained by original proportions and so effects may be reflective of original proportions rather than absolute change. We checked for correlations between original proportions and proportion change values and found no correlation between the original proportion and change in proportion of any land cover types, suggesting the effect of original proportions to be minimal. As we were specifically interested in the effect of change, we chose to include only proportion changes in the models. To examine whether woodland effects were driven by a specific type of woodland, a version of the best model (see *model selection & validation* below) was tested using the individual changes in proportions of coniferous and broadleaf woodland, instead of the combined, simplified woodland variable. Both woodland types responded similarly, and so the simplest model is presented.

2.3.4. Data analysis - Model selection and validation

Prior to model selection, the residuals of all global models were checked for divergence from the model assumptions. For each model the ‘dredge’ function from the MuMin package (Bartoń, 2023) was used to select the combination of variables with the lowest AIC value (i.e., the best-fitting model). The 100 km x 100 km random effect and latitude, longitude and elevation were retained in all models. The predictive accuracy of the best models was then tested using 10-fold cross-validation. First, all tetrads were randomly allocated to one of 10 subsets of data (folds). To ensure a representative sample of Britain in each fold, folds were allocated at the level of each 10 km x 10 km square. This approach ensured that each subset was representative of the overall geographic distribution within Britain. The model was tested 10 times in total, once for each subset after training on the remaining nine.

For each fold of validation, the area under the receiver operating characteristic (ROC) curve (AUC) was calculated using the *'pROC'* package (Robin *et al.*, 2011). AUC is a measure of predictive accuracy incorporating model sensitivity (true positive rate) and model specificity (true negative rate), ranging between 0.5 and 1. An AUC of 0.5 depicts a model assigning outcomes at random, whereas an AUC of 1 depicts perfect predictability. Average AUC ± standard deviation of the 10 folds is reported.

2.4. Results

2.4.1. 2010 occupancy model

Overall, 34,708 tetrads were included in the 2010 occupancy model. The global model was the best-fitting model, with an AICc value 5.46 lower than that of the second-best model (Table 2.1). Mean AUC for this model was 0.67 (± 0.02). Spotted flycatchers were negatively associated with urban land cover but positively associated with all other land cover types (Table 2.1, Fig 2.1). The strongest positive association was with improved grassland, followed by broadleaf woodland and river density (Table 2.1, Fig 2.1a,d,g). Arable land, coniferous woodland, unimproved grassland and freshwater were also positively associated with flycatcher occupancy, but their effect sizes were smaller in comparison (Table 2.1, Fig 2.1c,e,f,h).

Table 2.1. Model estimates of generalized linear mixed model for the probability of tetrads being occupied by spotted flycatchers in 2010. Bold text denotes statistical significance.

Predictors	**Odds Ratios (95% confidence interval)**	***p***
(Intercept)	0.12 (0.11 – 0.14)	**<0.001**
Longitude	0.94 (0.86 – 1.03)	0.213
Latitude	1.18 (1.06 – 1.32)	**0.003**
Longitude * Latitude	1.08 (0.99 – 1.18)	0.095
Mean elevation (m)	1.27 (1.18 – 1.38)	**<0.001**
Mean elevation (m)^2	0.79 (0.76 – 0.83)	**<0.001**
River density (km/km^2)	1.19 (1.14 – 1.24)	**<0.001**
% Urban	0.70 (0.64 – 0.76)	**<0.001**
% Freshwater	1.06 (1.03 – 1.10)	**<0.001**
% Improved grassland	1.24 (1.17 – 1.32)	**<0.001**
% Unimproved grassland	1.09 (1.04 – 1.15)	**0.001**
% Arable	1.13 (1.04 – 1.24)	**0.007**
% Broadleaf wood	1.20 (1.15 – 1.25)	**<0.001**
% Coniferous wood	1.10 (1.05 – 1.14)	**<0.001**
N_{centad}	41	
Observations	34708	
Marginal R^2 / Conditional R^2	0.137 / 0.158	

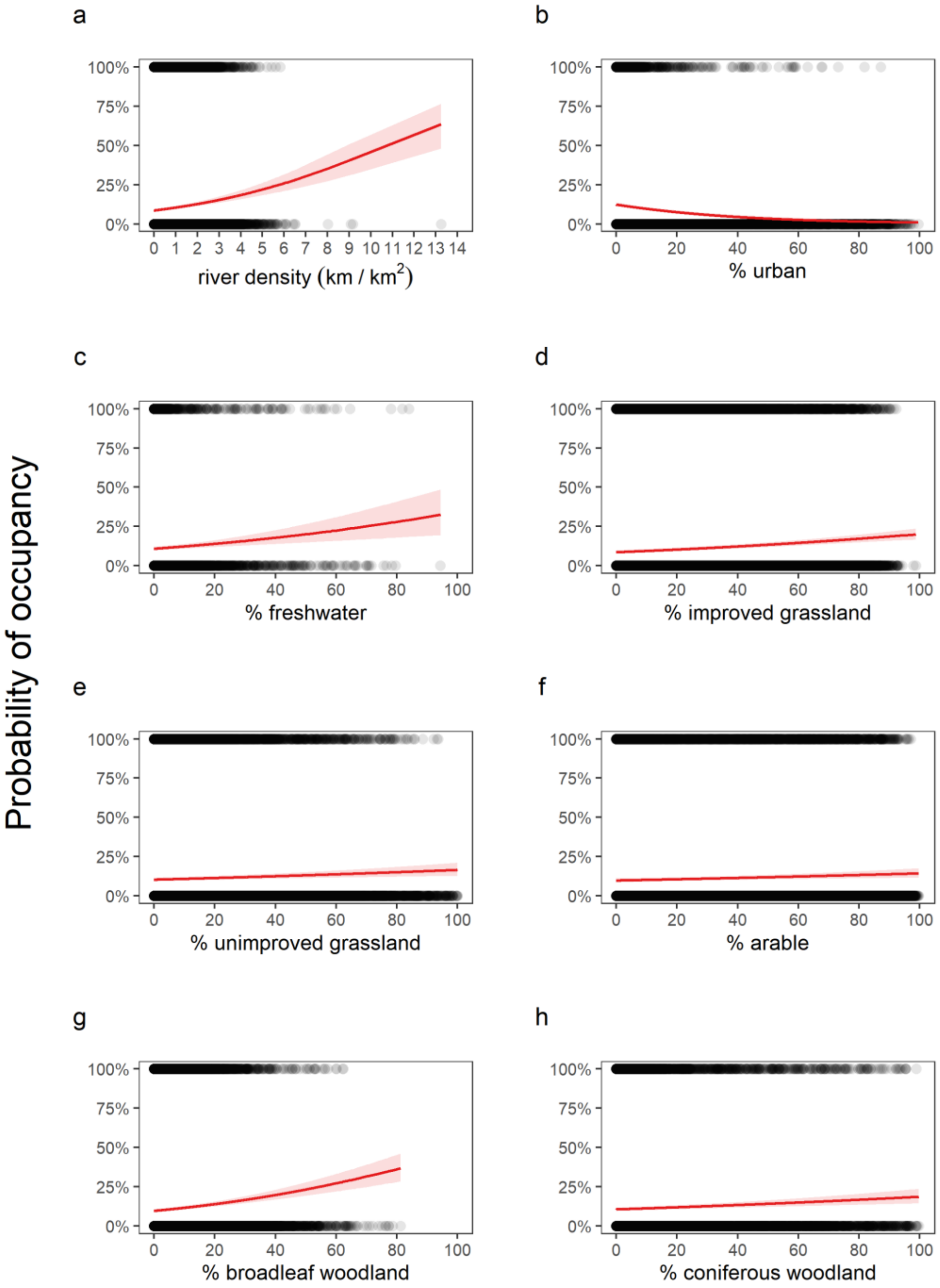


Figure 2.1. Predicted probability (red lines) and standard error (shading) of spotted flycatchers occupying a tetrad in response to different land cover types. Black points signify raw data.

2.4.2. Colonisation

In total, 20,951 tetrads were included in the colonisation model; 19,465 squares never had spotted flycatchers present and 1,486 were colonised between BA1990 and BA2010 (Fig. 2.2a). The best model for colonisation retained all land cover change variables and river density (Table 2.2). Mean AUC for the model was 0.7 (± 0.02). After accounting for the effects of latitude, longitude and elevation, urban land cover change had the strongest negative effect: tetrads with a greater increase in urban land cover were less likely to have been colonised (Table 2.2, Fig. 2.2f). Colonisation was also less likely in tetrads that had a larger increase in woodland cover (Table 2.2, Fig. 2.2c), which was the same for both coniferous and broadleaf woodland change (data not shown). The same was found for freshwater cover, though the relationship was weaker and uncertainty greater (Table 2.2, Fig. 2.2e). River density had the strongest positive effect, with tetrads containing a higher density of rivers more likely to have been colonised by spotted flycatchers (Table 2.2, Fig. 2.2b). Arable land cover change was also associated with a higher probability of colonisation, although this effect was weak (p = 0.06; Table 2.2, Fig. 2.2d).

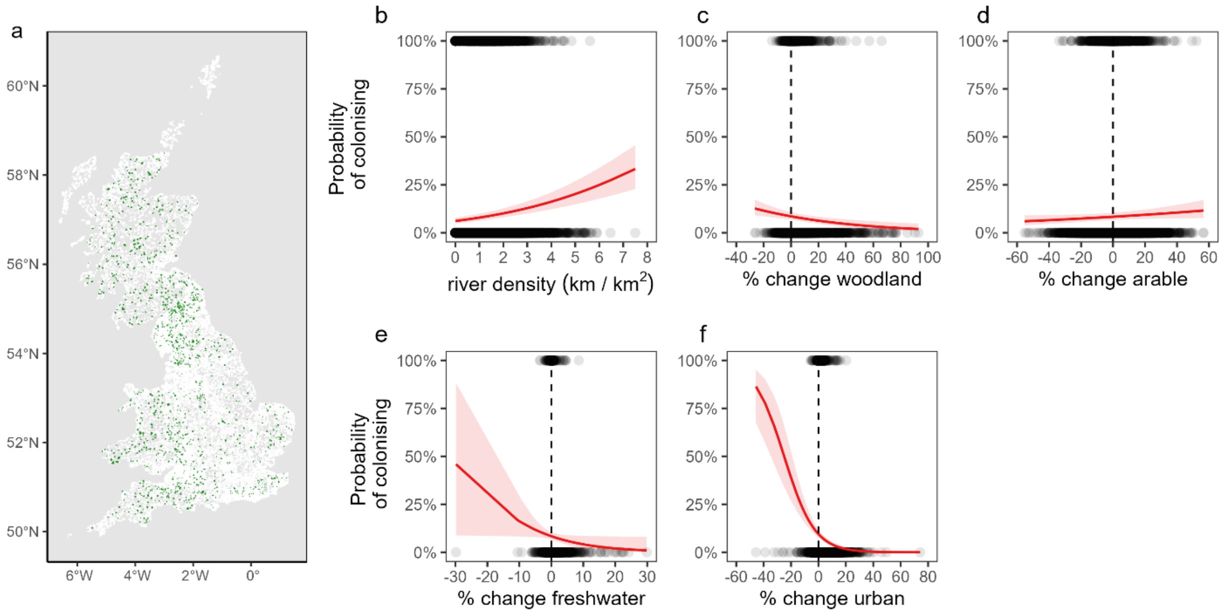


Figure 2.2. Distribution of squares colonised by spotted flycatchers (a) and predicted probability of colonising squares based on river density (b), change in woodland (c), arable (d), freshwater (e) and urban (f) land cover. On the map (a) colonisation is represented in green, absence in white, and tetrads not included in grey. In b–f, lines and shading represent predicted probability and standard error. Black points signify raw data. Dashed lines indicate the point of no change.

Table 2.2. Model estimates of generalized linear mixed models testing the associations between environmental and land cover variables and spotted flycatcher colonisation and loss. Bold denotes significant effect.

	Colonisation		Loss	
Predictors	**Odds Ratios (confidence interval)**	***p***	**Odds Ratios (confidence interval)**	***p***
(Intercept)	0.09 (0.07 – 0.12)	**<0.001**	6.74 (6.07 – 7.48)	**<0.001**
Longitude	0.96 (0.82 – 1.14)	0.654	1.04 (0.94 – 1.15)	0.427
Latitude	0.83 (0.68 – 1.02)	0.072	0.90 (0.81 – 1.01)	0.075
Longitude * Latitude	1.25 (1.07 – 1.46)	**0.005**	1.10 (1.00 – 1.20)	**0.043**
Mean elevation (m)	1.68 (1.51 – 1.86)	**<0.001**	0.62 (0.56 – 0.70)	**<0.001**
Mean elevation $(m)^2$	0.65 (0.61 – 0.69)	**<0.001**	1.18 (1.12 – 1.24)	**<0.001**
River density (km/km^2)	1.25 (1.17 – 1.32)	**<0.001**	0.80 (0.74 – 0.87)	**<0.001**
% change freshwater	0.94 (0.88 – 1.00)	**0.043**	1.12 (1.01 – 1.24)	**0.038**
% change urban	0.74 (0.68 – 0.80)	**<0.001**	1.17 (1.06 – 1.29)	**0.002**
% change woodland	0.91 (0.86 – 0.96)	**0.001**		
% change arable	1.06 (1.00 – 1.12)	0.060		
N	52_{centad}		46_{centad}	
Observations	20951		7356	
Marginal R^2 / Conditional R^2	0.173 / 0.288		0.097 / 0.100	

2.4.3. Loss

In total, 7,356 tetrads were included in the loss model; spotted flycatchers were lost from 6,390 tetrads between BA1990 and BA2010 and were present in 966 tetrads during both periods. The best model for loss had a mean AUC of 0.67 (± 0.03). Arable and woodland cover change were not retained in the best model (Table 2.2). After accounting for the effects of latitude, longitude and elevation, the strongest effect on loss was river density, which was associated with a lower probability of loss from a tetrad (Table 2.2, Fig. 2.3b). A greater increase in urban land was associated with a higher probability of flycatcher loss (Table 2.2, Fig. 2.3d). The same was found for freshwater cover, but with greater levels of uncertainty (Table 2.2, Fig. 2.3c).

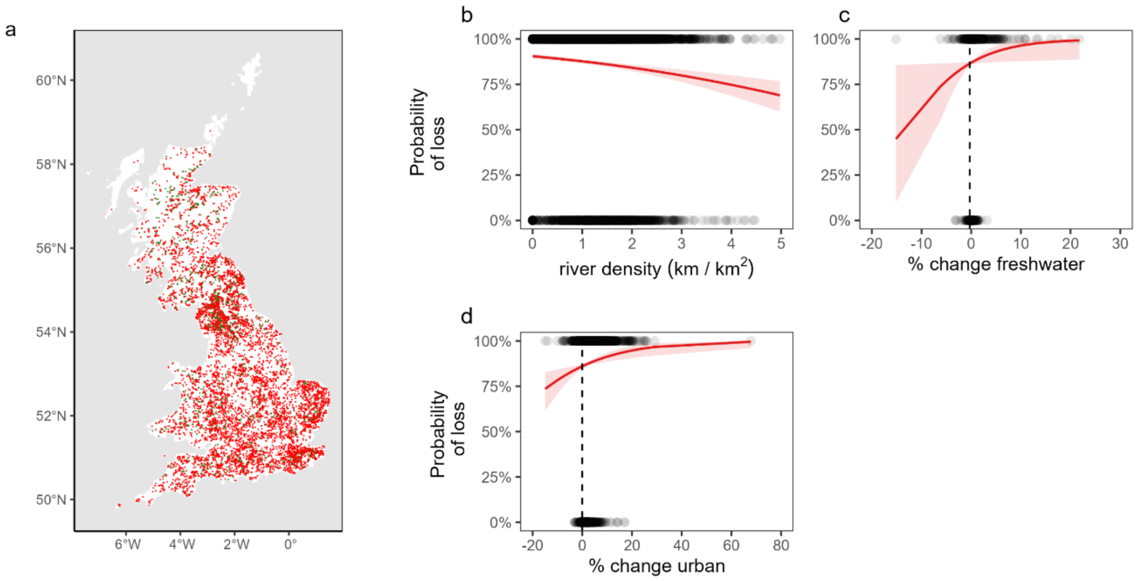


Figure 2.3. Spatial distribution of spotted flycatcher loss (a) and predicted probability of loss from squares determined by river density (b), change in freshwater (c) and urban (d) cover. On the map (a) loss is represented in red, persistence in green and tetrads not included in white. Lines on b–d represent predicted probability and highlighted areas represent standard error. Black points signify raw data. Dashed lines represent the point of no change.

2.5. Discussion

Spotted flycatchers were present in areas containing a range of habitats, including improved grassland, running and standing freshwater, and broadleaved woodland. Most of the land cover variables had weak effects on the presence of flycatchers. River density was an important factor in all three models, highlighting a relationship that has been largely overlooked for terrestrial species. Our results also demonstrated a strong aversion to urbanisation, which was associated with a lower probability of occupancy and colonisation, and was strongly associated with the loss of flycatchers from survey squares. Although habitat change was associated with the loss of flycatchers in Britain, the low variation explained by the model indicates that multiple factors are operating, likely across the entire range. Nonetheless, the results highlight habitats where conservation actions are most likely to be influential, with an emphasis on the importance of still and running freshwater habitats. Despite accounting for spatial factors in the model to disentangle the influence of land cover, land cover is not randomly distributed across Britain and so some residual spatial or climatic influences may still be reflected in the land cover results.

2.5.1. Urbanisation

Urban areas are associated with numerous ecological novelties, including non-native species, impervious surfaces, high density infrastructure and high human disturbance (Evans *et al.*, 2009). These environmental changes result in altered ecosystem functioning, with higher temperatures, greater fragmentation, more pollution and reduced biodiversity (Grimm *et al.*, 2008; Fenoglio *et al.*, 2021). Previous research has demonstrated the avoidance of urban areas by insectivorous birds (Máthé and Batáry, 2015), likely driven by reduced food availability and suitability (Teglhøj, 2017; Narango *et al.*, 2018). Similarly, our occupancy model demonstrated a clear avoidance of squares with a higher urban coverage, and urban expansion led to lower probabilities of colonisation and higher probabilities of loss. Urban areas will continue to expand (Seto *et al.*, 2012; Ministry of Housing, Communities and Local Government, 2024), so urban planning should accommodate greater biodiversity by providing more greenspaces and connectivity through habitat corridors (Beninde *et al.*, 2015). Moreover, identifying which habitats are most beneficial to insectivorous species is essential for protecting them from urbanisation.

2.5.2. Agricultural land cover

Agricultural land covers at least 40% of Britain and is somewhat protected from urban development due to its economic importance (Marston *et al.*, 2023). However, of the declining insectivorous birds in Europe, those occupying farmland have undergone the largest declines (Bowler *et al.*, 2019), owing to large-scale insect declines related to agricultural intensification, including increased pesticide and fertiliser application (Vickery *et al.*, 2001; Hallmann *et al.*, 2017; Seibold *et al.*, 2019). Conversely, less intensive management can benefit insects and insectivores by allowing greater structural diversity (Britschgi *et al.*, 2006; Hannappel and Fischer, 2020). We found only weak effects of arable land cover change on spotted flycatcher distribution change, which is difficult to interpret due to its collinearity with grassland cover change. Nonetheless, improved grassland had the strongest positive association with flycatcher occupancy, whereas arable land cover was only weakly associated with occupancy.

Improved grassland is often created by conversion of semi-natural grassland (Suggitt *et al.*, 2023) and so it is unsurprising that insectivorous species that utilise these habitats are retained in less natural grassland types. Additionally, the spectral classification of improved grassland in the UKCEH dataset encompasses a range of management intensities, including low intensity management with a likely higher insect abundance (Benton *et al.*, 2002; Britschgi *et al.*, 2006; Morton *et al.*, 2014). For example, management regimes with uncut margins and in-field woody vegetation support a greater diversity of plants, invertebrates and birds (Keenleyside and Costa Domingo, 2023). Moreover, much of the improved grassland in this study is likely to be accompanied by grazing livestock, which may support insectivorous species. Invertebrates attracted to livestock or dung provide an additional food source (Møller, 2001), whilst other farmland features associated with livestock (e.g. barns and hedgerows) may act as perches or nest sites for some species. Hence, with appropriate management, grasslands may be important habitats for insectivores, and promoting economically viable management that also promotes biodiversity should be a priority.

2.5.3. Broadleaf and coniferous woodland

Woodland management also has important implications for declining birds. In Britain, woodland cover has almost tripled since the beginning of the 20th century, from 4.7% in 1905 to 13.4% in 2023 (Forest Research, 2023). Our occupancy model demonstrated a clear preference by spotted flycatchers for tetrads with a higher proportion of broadleaf woodland, but colonisation was less likely in tetrads that had gained more woodland, and this effect was similar for broadleaves and conifers. While spotted flycatchers are generally associated with broadleaf woodland, new woodlands in this study had only 20 years to mature during the two survey periods. Young plantations provide a lower abundance of flying insects and lack the structural features required for spotted flycatcher nesting, whereas mature woodlands are typically more structurally and biologically diverse (Fuller *et al.*, 2014; Whytock *et al.*, 2018; Seibold *et al.*, 2019). Hence, the protection of established woodlands, as well as allowing younger woodlands to mature, is likely to be more beneficial for spotted flycatchers than planting new woodlands, at least in the short term.

2.5.4. Freshwater

For insectivorous birds, healthy freshwater habitats provide a periodic surplus of high quality food in the form of emergent aquatic insects (Manning and Sullivan, 2021; Berzins *et al.*, 2022). In addition, the peaks of terrestrial and aquatic insect abundance are asynchronous, creating a greater temporal availability of food, which may help to buffer a declining population by improving chick growth and fledging success (Nakano and Murakami, 2001; Twining *et al.*, 2016b, 2018b). Both et al. (2010) demonstrated how insectivorous migrants have more favourable population trends in marshland areas compared to terrestrial, which may be due to the extended availability, increased abundance or higher nutritional quality of food (Chapter 4), or a combination of these factors.

In accordance with this, we found that spotted flycatchers were slightly more likely to occupy squares with a higher proportion of standing freshwater, but areas where freshwater had increased had a negative impact on colonisation and loss. This suggests that, like woodlands, newly created or modified standing freshwater habitats might not be as beneficial as established ones. New or modified freshwater habitats may be associated with other unfavourable conditions, but finer scale field research is needed to understand the drivers of this relationship.

In contrast to standing freshwater, river density had one of the highest effect sizes in all three models. Insectivorous bird abundance has been shown to be greater adjacent to rivers compared to terrestrial habitats at a local scale (Iwata *et al.*, 2003; Uesugi and Murakami, 2007), and our results demonstrate that this effect expands to the landscape scale. For each 1 km of river per km^2 of landscape the probability of colonisation increased by 31% and the probability of loss decreased by 25%, suggesting strong potential for riverine habitats to attract and conserve insectivorous species. Given that aquatic habitats are threatened by both land management and climate change (Lafage *et al.*, 2019; van Rees *et al.*, 2021), the restoration and protection of these waterbodies, and their surrounding habitats, should be a conservation priority.

Key factors influencing river quality and biodiversity include climate change, anthropogenic wastewater discharge and agricultural pollution, with the latter having a substantial impact (Whelan *et al.*, 2022). Promoting freshwater-friendly farming practices, such as buffer margins around waterbodies, could enhance terrestrial and aquatic habitats for insects, ultimately benefiting insectivorous species (Keenleyside and Costa Domingo, 2023). Our results suggest that improving the availability of freshwater within or adjacent to land already utilised by insectivorous birds, such as agricultural grassland and woodland, may have disproportionate benefits. For example, appropriately managed agricultural ponds, likely excluded from our analysis due to their size, are associated with improved breeding success and survival of some species (e.g. Tree swallows *Tachycineta bicolor*; Berzins *et al.*, 2022). Additionally, restoring natural hydrology by blocking ditches may improve breeding densities of species with a preference for freshwater habitats (Hoover, 2009). Hence, incorporating freshwater systems into conservation management for declining species offers an opportunity for wide reaching benefits, especially given the importance of freshwater for human health and economies (Lynch *et al.*, 2023).

2.6. Conclusion

Our study highlights an important association between the presence and persistence of a declining, insectivorous bird and the availability of river habitats across Britain, which supports similar findings from North America (Berzins *et al.*, 2022) and Asia (Iwata *et al.*, 2003). Due to the scale of this study, we are unable to make conclusions about the mechanisms driving the relationship, which could be due to the biological or physical structure of riverine environments. Hence, future work should aim to study the fine-scale relationships between insectivorous species and river habitats, for example, by investigating the relationship between factors associated with riverine habitats and breeding success. Nonetheless, these findings may have major implications for the design of conservation interventions, given the lack of focus on aquatic habitats for terrestrial species, and we hope that these results serve as encouragement to investigate this relationship further.

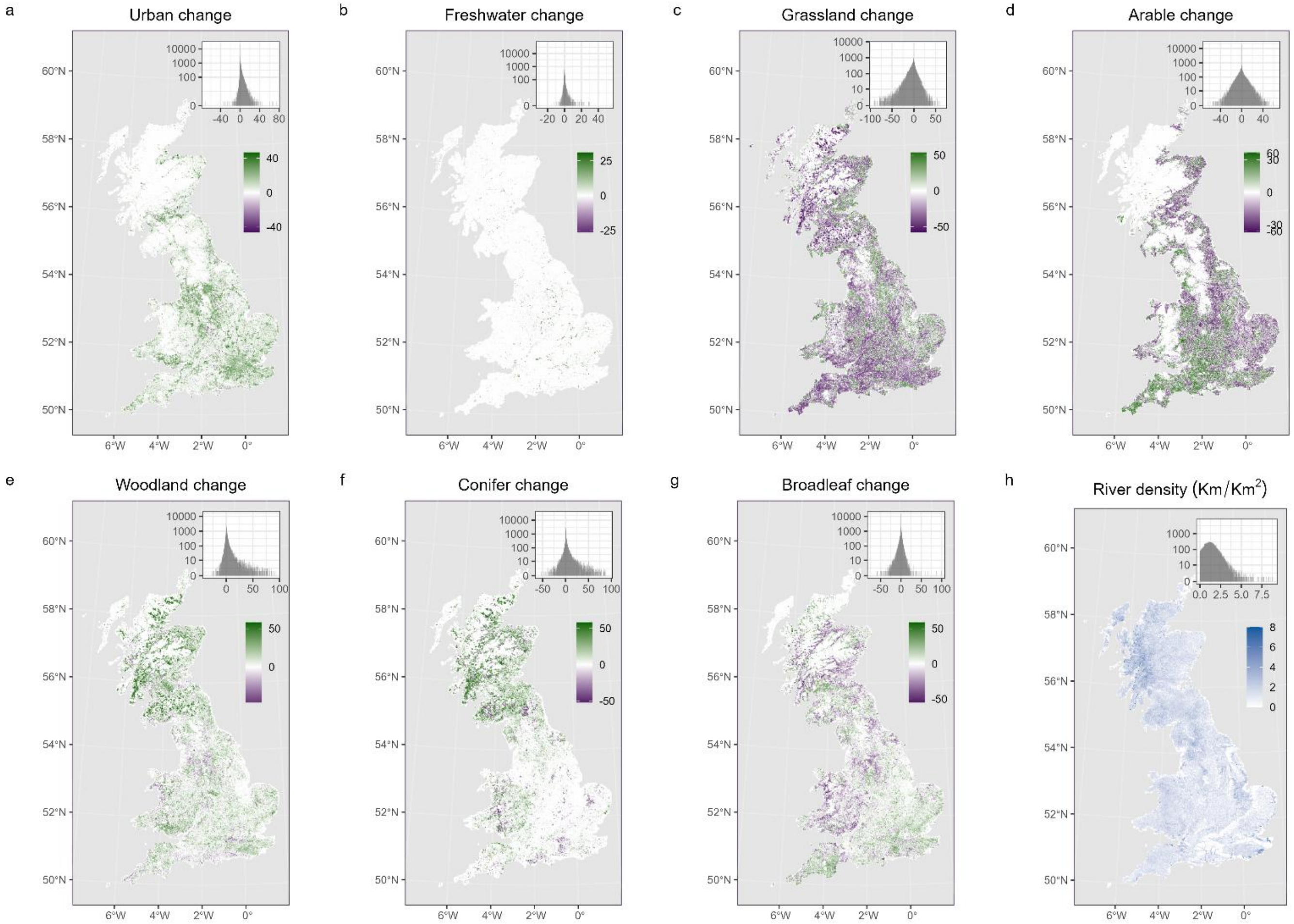
Supplementary material

Supplementary Table 2.1. Habitat variables for the 2010 occupancy model were created from 20 broad habitat types provided in the LCM2007 dataset that were further condensed into 13 habitats.

Condensed variable	**Broad habitat types included**
Broadleaf woodland	Broadleaved, Mixed and Yew Woodland
Coniferous woodland	Coniferous Woodland
Arable	Arable and Horticulture
Improved grassland	Improved Grassland
Unimproved grassland	Neutral grassland Calcareous grassland Acid grassland Rough Grassland
Bog / Fen	Bog Fen, Marsh and Swamp
Heathland	Dwarf Shrub Heath
Urban	Built-up Areas and Gardens
Freshwater	Freshwater
Sediment	Supra-littoral Sediment Littoral Sediment
Saltwater	Saltwater
Montane	Montane Habitats
Rock	Inland Rock Supra-littoral Rock Littoral Rock

Supplementary Table 2.2. Variation in land cover change variables and river density for the entire period included in the colonisation and loss models.

	Min	**Median**	**Mean**	**Max**
Grassland change (%)	-93.03	-1.36	-3.02	53.92
Arable change (%)	-55.28	0	-0.28	60.33
Broadleaf change (%)	-53.41	0.04	-0.12	38.79
Freshwater change (%)	-29.80	0	0.08	29.88
Conifer change (%)	-44.30	0	1.14	87.48
Urban change (%)	-45.58	0.52	1.61	74.23
Woodland change (%)	-26.41	0.48	1.75	93.03
River density (Km/Km^2)	0	1.15	1.21	8.03



Supplementary Figure 2.1. Maps showing the change in proportion of a) urban, b) freshwater, c) grassland, d) arable, e) conifer and broadleaf woodland combined, f) conifer, and g) broadleaf land cover in tetrads across Great Britain. Panel h shows river density, which represents the overall density for the entire period rather than a change variable. Data in panels a–g has been pseudo-log transformed for visualization. Inset shows the same data in a histogram.

Chapter 3 Terrestrial and aquatic habitat characteristics associated with nest-site selection and breeding success in spotted flycatchers (*Muscicapa striata*)

3.1. Abstract

Understanding the drivers of declines in many Afro-Palearctic migrant birds remains a key conservation challenge. The spotted flycatcher (*Muscicapa striata*) requires urgent interventions, especially in the UK where the species has declined by 93% over the last 60 years. Given major shifts in habitat characteristics caused by land use change during the period of decline, understanding how habitat is related to breeding success may inform conservation action. Here, we investigated the habitat characteristics related to nest-site selection, hatching success and breeding success in this species by monitoring nests between 2022 and 2024 in Cumbria, UK. Specifically, we tested the effects of vegetation structure and river proximity on nest-site selection and nest failure rates during the egg and chick stages. The results showed that spotted flycatchers were more likely to nest in sites with an intermediate tree/shrub canopy cover (22% ± 7%), and sites closer to rivers. Despite an apparent selection for nest sites close to a river, river proximity was not strongly correlated with failure at either nest stage. Nest failure at the egg stage was influenced by the structure that nests were built on; nests on buildings had lower daily failure rates (0.028 egg stage, 0.021 chick stage) than nests on trees and other structures (0.047 egg stage, 0.028 chick stage), but failure away from buildings was ameliorated for nests concealed in creeping plants (e.g. ivy *Hedera* sp.). Predation was the main cause of failure at both stages, and nest failure rates were similar to those published from elsewhere in England. Interventions to reduce the impact of predation may be key to supporting population levels in this species, and we discuss how management of ivy could be directed to achieve this.

3.2. Introduction

The decline of Afro-Palearctic migrant bird species has been well-documented, but few studies have identified the underlying causes, particularly for long-distance migrants wintering in the humid zone of Africa (Sanderson *et al.*, 2006; Vickery *et al.*, 2023). Several mechanisms related to population trends and demographic rates have been identified, including rainfall in the Sahel (Ockendon *et al.*, 2014), conditions on migration (Finch *et al.*, 2014) and poor breeding success (Morrison *et al.*, 2016), but these effects vary between species. The spotted flycatcher (*Muscicapa striata*) is one of the fastest declining Afro-Palearctic migrants in the UK, having declined by 56% across its European breeding range between 1980 and 2023 (PECBMS, 2025) and by 93% in the UK between 1967 and 2022, prompting it to be assigned to the red list of Birds of Conservation Concern (Stanbury *et al.*, 2021; BTO, 2024).

Spotted flycatchers have widely been associated with woodland but can be found in a range of habitats and are best considered a habitat generalist, only appearing to avoid habitats that are completely open (e.g. moorland) or closed (e.g. dense woodland) (Cramp and Perrins, 1993). They are an obligate insectivore and feed predominantly on flying insects. Consequently, their structural habitat requirements on the European breeding grounds include open space in which to feed, a perch to hunt from, and a cavity or a ledge to nest on (Davies, 1977; Cramp and Perrins, 1993). Their formerly wide geographical range in the UK has contracted by 10% over the last 40 years, with territories lost mainly from the east coast and urban areas (Balmer *et al.*, 2013). Densities of this species have decreased in all habitat types, suggesting that they may be facing problems elsewhere during the annual cycle, or broader problems such as national insect declines (Newson *et al.*, 2009).

There has been little consensus on the underlying cause of declines from the few studies investigating the demographic trends of spotted flycatchers, largely due to a paucity of suitable information. A lack of understanding of the areas occupied outside of the breeding grounds limit the ability to study drivers outside of the breeding season, but the declines of the 1960–1970s coincided with drought in the Sahel (Hewson and Noble, 2009), demonstrating how issues on migration could influence population trends. In an integrated population model built on UK-wide citizen science data, Freeman and Crick (2003) found no difference in adult survival or breeding success between 1965 and 1996, but suggested that post-fledging survival could have driven negative population trends. Conversely, using data collected the same way, Baillie et al. (2006) noted a decrease in egg-stage failure but an increase in chick-stage failure between 1966 and 2004, which could be related to a reduction in nestling survival. Indeed, widely reported crashes in insect abundance are likely to have affected this species (Conrad *et al.*, 2004; Hallmann *et al.*, 2017; Sánchez-Bayo and Wyckhuys, 2019; van Klink *et al.*, 2020), particularly during chick rearing when demand for resources is high. Moreover, Stevens et al. (2007) and Stoate and Szczur (2006) suggested that predation may be a problem for this species, particularly for pairs nesting in woodland and farmland habitats. Spotted flycatchers and other open-cup nesting species are naturally vulnerable to nest predation due to the exposure of nests to predators. A recent meta-analysis identified avian predators as the most frequently encountered predator type for species nesting in trees (Barton *et al.*, 2025). Though these species have evolved under high levels of predation, additional demographic pressures and shifts in predator communities can lead to negative population trends (Newton, 1998). Consequently, re-analysis of nesting data indicated that the productivity of spotted flycatcher populations in England were insufficient to sustain a stable population (Burgess *et al.*, 2025), suggesting that actions to improve breeding success could ameliorate the negative trends.

In a recent study of the land cover types related to distribution changes of spotted flycatchers in the UK, river density was identified as an important factor related to occupancy and colonisation, but inference was limited by the spatial resolution of the study (2 km x 2 km survey squares) (Chapter 2). Rivers and riparian woodland may provide refugia for species impacted by land use modification (Bennett *et al.*, 2014), but this may be an artefact of suitable vegetation structure being retained near rivers, rather than the habitat there being of higher quality. However, aquatic habitats such as rivers have higher abundances of insects (Uesugi and Murakami, 2007) and insects of higher nutritional quality (Moyo *et al.*, 2017), and this has been shown to improve the breeding success of some insectivorous birds (Twining *et al.*, 2018b). Hence, understanding the apparent attraction of spotted flycatchers to freshwater habitats may reveal important ecological connections that have previously been overlooked.

While factors across the entire annual cycle may influence population trends, measures to improve breeding success offer a feasible conservation target that may benefit multiple species (Morrison *et al.*, 2021). To date, studies of breeding success in spotted flycatchers have been undertaken in southern and central England (e.g. Stoate and Szczur, 2006; Stevens et al., 2007), yet drivers may vary between localities (e.g. Morrison et al., 2016). Moreover, all of the published demographic rates for this species originate from data collected over a decade ago. As demographic rates may be influenced by environmental factors that vary considerably between years (e.g. food availability), a more recent insight into the species' breeding success is required, particularly in view of the spotted flycatcher's ongoing rapid decline. In this study, spotted flycatchers were studied in northern England, where relative abundance has declined at a similar rate to the rest of England, but is higher than the relative abundance found in most of southern and central England (Balmer *et al.*, 2013). Population trends of other Afro-Palearctic migrants appear more favourable in the north than the south of the UK, which may be related to differences in land management or climate (Morrison *et al.*, 2013).

The aim of this study was to understand the habitat characteristics related to nest-site selection and breeding success in spotted flycatchers. We aimed to understand whether the apparent selection for rivers at a large spatial scale (identified in Chapter 2) was detectable at a fine spatial scale, and if so, whether the species was drawn to rivers due to the retention of suitable habitats or whether the affinity could be explained regardless of the structural suitability of the habitat. We also aimed to understand the fine-scale habitat characteristics related to breeding success, in the hope of identifying achievable suggestions for conservation interventions. Finally, we compare our findings to previously published results on this species to understand whether any variation in breeding success may explain regional differences in relative abundance.

3.3. Methods

3.3.1. Study site and nest monitoring

Field work was undertaken within an 11 km radius of Sedbergh, in the Yorkshire Dales National Park, in Cumbria, UK (54.323559, -2.528300). The study area is primarily upland pasture, grazed by livestock, with frequent farmsteads, villages, small pockets of woodland and numerous rivers and streams. We monitored 186 spotted flycatcher nesting attempts in the breeding seasons (May–August) of 2022, 2023 and 2024. Suitable habitats were considered as anywhere with potential nest sites and perches e.g. areas with trees, walls, buildings, excluding completely open areas such as moorland and open grassland. Suitable sites were identified during a systematic breeding bird survey of the study site in 2022. Flycatchers were searched for regularly in all patches of suitable habitat (at least every other week), and we searched for nests in all areas where flycatcher pairs were detected. Nests were located by observing the behaviour of pairs e.g. following them back to the nest, or by cold searching potential nest sites. Once found, the location of nests was recorded using a Garmin eTrex 22x handheld GPS. Nests were checked at least once per week and, to ensure accurate ageing of nestlings, the frequency of checks was increased to every two days when hatching was imminent. We recorded the location, date the first egg was laid (first egg date), clutch size, hatch date, number of hatchlings, and fledging success (i.e. whether or not at least one chick fledged). Dates were back-calculated where nests were found at later stages e.g., during incubation or with chicks present, based on an egg-laying rate of 1 egg per day and an incubation period of 13 days (Cramp and Perrins, 1993). The structure that the nest was built onto was recorded (e.g. wall, tree, building), as well as the presence of creeping plants (ivy (*Hedera* sp.), Virginia creeper (*Parthenocissus quinquefolia*), hydrangea (*Hydrangea* sp.) and wisteria (*Wisteria* sp.)). All handling was carried out by Catrin Eden and Stuart Sharp under license from the British Trust for Ornithology.

Remote sensing data were used to characterise the habitat around nests using QGIS (QGIS Development Team, 2025). The distance of each nest to the nearest river was calculated using the UKCEH digital river network shapefile (UKCEH, 2000). Lidar point cloud data for the study site were used to describe the structure of habitats surrounding nests. Point cloud data collected during the winter at a density of 1 point per square metre and a vertical accuracy greater than 15 cm were downloaded from the National Lidar Programme (DEFRA, 2021). Nest buffers of 50 m were selected based on previous observations of spotted flycatcher territory size (Davies, 1977). Using the *LidR* package in R (Roussel and Auty, 2025), the habitat was stratified into three layers based on previous woodland bird studies in the UK: field layer (<1 m), understory layer (>1 m and < 8 m) and overstory layer (> 8 m) (Broughton *et al.*, 2012). The proportion of each layer within nest buffers was calculated as well as the average height of the overstory layer. The standard deviation of vegetation height was calculated because structural diversity may influence spotted flycatcher nest-site selection (Kirby *et al.*, 2005). Finally, canopy cover was calculated as the proportion of cover from vegetation >1 m.

3.3.2. Nest selection analysis

To investigate the habitat preferences of spotted flycatchers, 300 random points at least 10 m apart were generated within the smallest convex polygon enclosing known nest sites and their 50 m buffers, to represent available habitats. To avoid inclusion of highly inappropriate habitats i.e. completely open areas with no potential nest sites or perches, the random points were restricted to elevations representative of those where true nests were found (<270 m). Habitat characteristics for these available points were then generated using the same method as for true nests.

The influence of habitat characteristics on the probability of nesting was quantified using a binomial model with each nest (used) and random point (available) included as the response variable. A global model was then constructed including mean elevation, river distance and canopy cover as explanatory variables. All of the structural variables derived from the point cloud data were correlated and so only canopy cover was included. Canopy cover at extreme values (i.e. no trees or dense trees) would likely be avoided by spotted flycatchers, so a quadratic term was included. An interaction term between river distance and canopy cover was included to investigate whether the potential affinity to rivers was driven by the presence of trees in these habitats.

3.3.3. Nest failure analysis

Nest failure rates were calculated for all nests with sufficient data (n = 178) using a Mayfield logistic regression (Mayfield, 1975), with failure / success as the response variable and the number of exposure days as the denominator. A separate model was constructed for the egg stage (laying and incubation) and chick stage, as the drivers of nest failure may differ between stages. Overall nest survival was then calculated based on a period of 17 days for the egg stage (4 egg-laying days based on median clutch size for the study population +13 days of incubation) and 13 days for the chick stage (Cramp and Perrins, 1993). Initially, simple logistic regression models were constructed to acquire mean nest failure rates under different scenarios. An intercept-only model was used to obtain average failure rates across the entire season, and models with either year or habitat were constructed to obtain average rates per year or per habitat. Subsequently, a global model for each stage was constructed to measure the statistical influence of different drivers of nest failure. The global models included year, canopy cover, habitat type (building or other), presence of creepers and distance from a river as explanatory variables. An interaction between canopy cover and distance from a river was included as well as a three-way interaction between habitat, creepers and year. This three-way interaction was intended to allow for variation in mortality between years e.g. in relation to poor weather conditions. As nest survival may vary throughout the season, particularly during the chick stage, a global model including first egg date was also evaluated on a smaller sample of data for which first egg dates were available (egg stage n = 85, chick stage n = 68).

All continuous variables were scaled and centred prior to inclusion in the models. The residuals of all global models (nest selection and nest failure) were checked for divergence from the model assumptions. To reduce overdispersion, data in the egg and chick failure models were filtered to only include nests with more than 2 and 4 exposure days, respectively. First egg date was not retained in either of the top model sets so results presented include all nests for which sufficient data were available (egg stage n = 107, chick stage n = 76). The *MuMIn* package (Bartoń, 2023) was used to apply an information-theoretic model selection approach by fitting all possible combinations of variables. All candidate models within <2 delta AICc of the best fitting model were averaged to account for model selection uncertainty. We present the coefficients and standard errors from the full averaged models, rather than conditional averaged models, to obtain the most conservative estimates of coefficients.

3.4. Results

3.4.1. Nest selection

Density plots of used and available nest sites showed that the habitat characteristics of spotted flycatcher nests were distributed differently to the randomly distributed loacations that were available across the study site (Fig. 3.1). The final averaged model for nest-site selection retained all variables included in the global model (Table 3.1). Nests were found at elevations lower than the average available (Table 3.1). There was support for the independent selection of river distance and canopy cover, which were both retained in the top model set. The quadratic effect of canopy cover demonstrated that areas with intermediate levels of canopy cover were most likely to be selected as nest sites, and the linear effect of river distance demonstrated that nests were more likely to be found closer to a river (Table 3.1). The interaction between canopy cover and river distance was retained in the averaged model, but the estimated effect size was not significant.

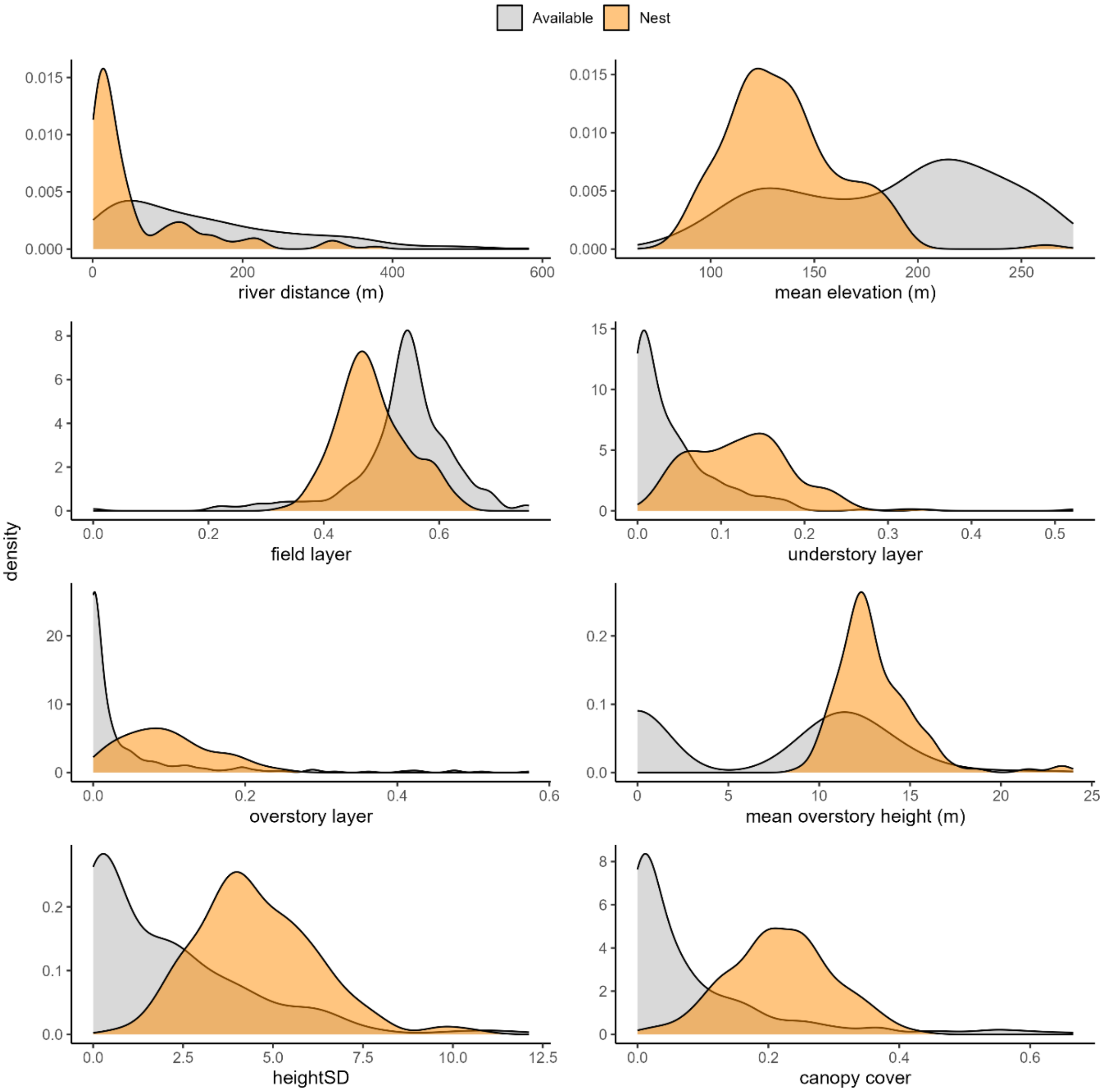


Figure 3.1. Density plots of habitat variables considered for spotted flycatcher nest-site selection modelling. Orange shading represents the density of observed nests, grey shading represents the density of random points (available habitats). Overlapping densities suggest use of available habitats (no preference) whereas diverging densities infer preferential selection for characteristics. Note differences in x and y scales.

Table 3.1. Output from the final averaged generalised linear model investigating drivers of nest-site selection in spotted flycatchers.

	Estimate	Std. Error	Adjusted SE	z value	*p*
Intercept	-0.954	0.224	0.225	4.244	**<0.001**
Canopy cover	3.035	0.378	0.379	8.006	**<0.001**
Canopy cover^2	-1.387	0.242	0.243	5.719	**<0.001**
Mean elevation	-1.062	0.220	0.220	4.821	**<0.001**
River distance	-0.420	0.219	0.219	1.914	0.056
Canopy cover:River distance	-0.261	0.297	0.297	0.880	0.379

3.4.2. Nest failure

Daily nest failure varied between years, but differences were not significant. The daily failure rate for the entire study period was 0.036, equating to a 33% chance of nest success over the entire nest period (Table 3.2). Egg stage failure rate was 0.042 on average, amounting to a 48% chance of survival for the complete egg stage (Table 3.2). Average daily failure rates for the chick stage were slightly lower than the egg stage (0.027), equating to a 70% chance of survival. Nest survival was higher on buildings than other structures (e.g. trees, bridges) in both stages (Fig. 3.2, Table 3.2), and this difference was significant when included as the only explanatory variable. The cause of failure was known for 70 nests of 94 that failed over the study period. Nests with unknown causes of failure were often inaccessible and monitored from a distance. Of all the nests monitored, 9.6% were found with dead young in the nest, 14.9% were abandoned at the egg stage and 50% were predated (i.e. nests were found destroyed or prematurely empty). Predation was the main cause of failure at both the egg-stage (59.6% of all nests with known failure stage) and chick-stage (40.7% of all nests with known failure stage).

Several variables were retained in the full averaged model for egg stage nest failure (Table 3.3). There was a significant interaction between habitat type and year, whereby nests on buildings were more likely to fail than nests in other habitats in 2024 (Table 3.3, Fig. 3.2). There was moderate support for the interactive effect of habitat and the presence of creepers, which suggested that the probability of failure for nests on buildings was not influenced by creepers, but nests in other habitats were less likely to fail when they were concealed in creepers (Table 3.3, Fig. 3.2).

Table 3.2. Average daily failure rates and overall probability of spotted flycatcher nest survival at different nest stages and on different structures.

	Egg stage daily failure (overall nest survival)	Chick stage survival daily failure (overall nest survival)	Whole nest period daily failure (whole period survival)
Buildings	0.028 (53%)	0.021 (76%)	0.028 (42%)
Other	0.047 (44%)	0.028 (69%)	0.044 (26%)
All nests	0.042 (48%)	0.027 (70%)	0.036 (32%)

Nest failure during the chick stage was not associated with the same factors that were correlated with egg stage failure. The full averaged model included habitat type, canopy cover, river distance and the presence of creepers, as well as an interaction between canopy cover and river distance (Table 3.3). However, estimated effect sizes were small and standard errors large, indicating low confidence for the effect of these variables (Table 3.3)

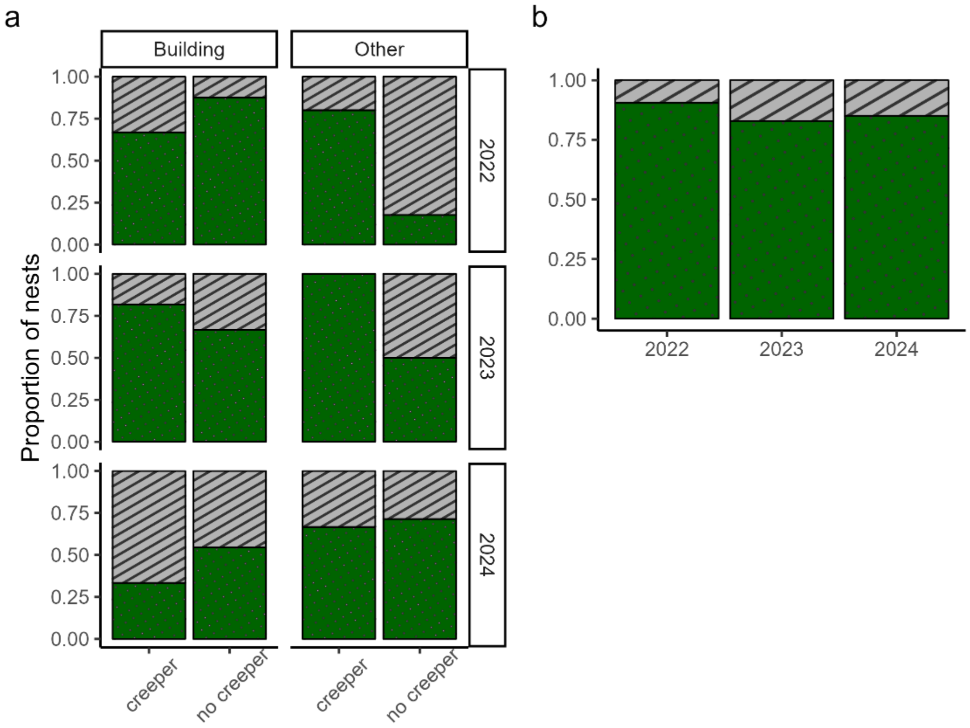


Figure 3.2. Raw proportions of failed (grey, striped) and successfully (green, dotted) hatched (a) and fledged (b) spotted flycatcher nests in Sedbergh between 2022 and 2024. Hatched nests are separated by habitat type (building, other) and the presence of a creeper around the nest. Fledging success displays only nests that successfully hatched.

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Table 3.3. Estimated and standard errors of spotted flycatcher nest failure rates from Mayfield logistic regression investigating drivers of egg stage and chick stage failure rates. Bold text denotes p < 0.05.

	Estimate	**Std. Error**	**Adjusted SE**	**z value**	***p***
Egg failure					
(Intercept)	-4.141	0.868	0.878	4.715	**< 0.001**
Creeper [no creeper]	-0.1	0.708	0.717	0.139	0.889
Habitat [other]	0.244	1.104	1.118	0.218	0.828
Year [2023]	0.157	0.993	1.004	0.156	0.876
Year [2024]	1.357	0.88	0.891	1.523	0.128
Creeper [no creeper]:Habitat [other]	1.782	0.966	0.978	1.823	0.068
Habitat [other]:Year [2023]	-1.298	1.015	1.028	1.263	0.207
Habitat [other]:Year [2024]	-2.497	0.973	0.985	2.535	**0.011**
Creeper [no creeper]:Year [2023]	0.264	0.797	0.803	0.329	0.742
Creeper [no creeper]:Year [2024]	-0.107	0.596	0.602	0.177	0.860
Canopy cover	-0.028	0.113	0.114	0.248	0.804
Chick failure					
(Intercept)	-5.191	0.844	0.854	6.078	**< 0.001**
Habitat [other]	0.679	0.884	0.892	0.762	0.446
Canopy cover	0.256	0.506	0.511	0.501	0.616
River distance	-0.817	1.043	1.054	0.775	0.438
Creeper [no creeper]	0.083	0.335	0.339	0.245	0.807
Canopy cover:River distance	0.859	1.253	1.260	0.682	0.495

3.5. Discussion

The aim of this study was to identify habitat characteristics related to nest-site selection and breeding success in spotted flycatchers in northern England. Our results demonstrate an apparent preference for nesting near rivers, which was not driven solely by the presence of trees. However, the same characteristics were not related to breeding success and so the underlying reason for this could not be established with our analysis. Predation was the main cause of known nest failure, accounting for 67% of failed nests where the cause of failure was known, emphasising a need to understand whether management to moderate the impacts of predation could improve population trends. We found that egg-stage and chick-stage failure were driven by different habitat characteristics, which most likely reflects the variation in causes of failure or success at these stages.

Nest site selection was related to both canopy structure and river distance independently, suggesting that spotted flycatchers were drawn to both characteristics individually, rather than one because of the other. Although the high density of rivers in our study site may have inflated the apparent strength of the relationship with river proximity, the pattern remains consistent with broader ecological trends. Previous research in southeast Australia has demonstrated that biodiversity is higher in riparian woodland compared to terrestrial woodland (Bennett *et al.*, 2014). Similarly, we found that at a national scale, spotted flycatchers were more likely to occupy and colonise, and were less likely to be lost from, survey squares with a higher density of rivers (Chapter 2). In the UK, buffer strips adjacent to rivers retain natural vegetation while large amounts of the remaining land is converted for agricultural use, so the affinity of flycatchers for rivers could therefore be driven by the availability of suitable nesting sites in these areas (i.e. mature trees). Nevertheless, the results of this study demonstrate that flycatchers independently select for both intermediate tree cover and sites closer to a river.

Aquatic insects emerging from rivers offer extra food of higher nutritional quality, which may disproportionately benefit insectivorous species (Chapter 5, Moyo *et al.*, 2017). Previous research demonstrated that tree swallow (*Tachycineta bicolor*) and eastern phoebe (*Sayornis phoebe*) chicks grew heavier when supplemented with essential highly-unsaturated fatty acids (HUFAs) (Twining *et al.*, 2016b, 2019), which are found at greater concentrations in aquatic compared to terrestrial insects. Hence, selection for nests nearer to rivers may benefit populations improving chick growth and condition. Yet, we found only weak evidence for the effect of river distance on fledging success, suggesting that the effect was either minimal, masked by other factors, or occurring outside of the nestling period. For example, the impact of river distance may not have been detected in this study due to the measurement of breeding success as a binary variable (no chicks fledged or at least one chick fledged). We were unable to accurately measure the number of chicks fledged in this species, as approaching the chicks near to the time of fledging can cause them to fledge prematurely ('explode'), and it is not possible to count the number of chicks that died prior to fledging as adults often remove dead chicks from the nest (pers. obs.). Additionally, the availability of aquatic insects to chicks may not be accurately represented by river distance, as it can vary depending on the timing of nesting, hydrological characteristics of different stretches of river, and the feeding behaviour of parents. Yet, in a study investigating the impacts of HUFA concentrations on the body condition of spotted flycatchers, we found that chicks with higher HUFA concentrations had higher body condition scores (Chapter 4). Body condition is positively related to post-fledging survival in chicks (Naef-Daenzer *et al.*, 2001), and so the benefits of river distance may not be observed until after the nestling phase, which could not have been detected in the present study.

During this study, spotted flycatchers were observed most frequently in areas with small clusters of mature trees, often adjacent to or within farmland, and were observed at the lowest densities in woodlands (pers. obs.). Although nests in woodland were more difficult to locate, the detection of flycatchers within woodland (i.e. by sound) was comparable to other habitats. Our observations contrast with previous work that found higher densities of spotted flycatchers in woodlands than farmland (Benson and Williamson, 2009). Our nest-site selection results confirm our observations, showing that spotted flycatchers at our study site nested in areas with a maximum of 42% canopy cover (mean 22% ± 7%). Previous work has highlighted the potential for changes in woodland management to have influenced declines in woodland birds (Amar *et al.*, 2006), and our results indicate that management to achieve a medium level of canopy cover may be most attractive to this species. However, many of the canopy structure characteristics in our study were correlated, and so it is unclear whether selection was specifically for canopy cover or other related structural characteristics.

Daily failure rates and overall nest survival were similar to those reported from central England (Kirby *et al.*, 2005). Likewise, we also found differences between nests on buildings and nests on other structures. Nest survival on buildings in our study site was lower than reported in the south of England (42% vs. 59%), but nest survival on other structures was similar to those reported for woodland and farmland (Stevens *et al.*, 2007). Estimates of nest failure rates from volunteer nest records are considerably lower than we found in our study (BTO, 2024), indicating a likely bias towards nests found at later stages and recorded in gardens. Moreover, sample sizes for the estimates are low (typically $n < 100$) and may be biased towards areas where the species is found at higher densities, increasing the ease with which nests can be found. Of published estimates, by far the highest nest survival rate was reported in central England during a period of predator control (77%), and this dropped significantly when predator control ceased (Stoate and Szczur, 2006).

Predation was the main cause of nest failure during both nesting stages in our study. It was also the main driver of nest failure in southern England, with most predation being caused by corvids (Stevens *et al.*, 2010) and occurring during the egg stage (Burgess *et al.*, 2025). Population modelling showed that these nest survival rates are inadequate to sustain a stable population, suggesting that reducing nest failure could ameliorate the population decline observed in spotted flycatchers, though these results are geographically limited (Burgess *et al.*, 2025). Open cup nesting species are naturally vulnerable to predation, and consequently adapted to low nest survival (e.g. Jara et al., 2020), but the impact of predation may be exacerbated if predator populations become inflated e.g. due to a reduction in apex predators, and/or if populations are already in decline (Newton, 1998). Several potential predators of avian nests have increased in the UK (e.g. jay *Garrulus glandarius*), and some populations of predators are found at higher densities in the UK than continental Europe (e.g. carrion crow *Corvus corone*) (Roos *et al.*, 2018). Lethal predator control has demonstrated positive effects on nest survival (Stoate and Szczur, 2006), but given that the impact of different predators may vary locally this is not an ethical or feasible method of improving breeding success at a national scale.

The majority of nests in southern England were predated by jays, but the distribution of jays is not uniform across the UK (Balmer *et al.*, 2013), and they were infrequently seen in our study site. We were only able to identify the predator responsible for one predation event during our study, and this was a domestic cat (*Felis catus*). Cats were also responsible for 3 of 20 predation events in southern England (Stevens *et al.*, 2010). The impact of domestic cats as non-native predators is a debated topic (Palmer, 2022), and empirical evidence for their effect is lacking (Lockwood *et al.*, 2025). However, studies quantifying the number of animals killed by cats rely on them returning to their homes with their prey, and so likely severely underestimate the true effect. Nonetheless, without definitive evidence for the species responsible for nest predation nationally, efforts are better targeted at protecting nests from predators, rather than unethically targeting a wide range of potential predator species.

Non-lethal predator control such as placing guards or fences around nests may be equally successful as lethal predator control (Major *et al.*, 2015), although most experiments are restricted to ground nesting species whose nests may be more easy to access and protect (Gautschi *et al.*, 2024). Several monitored nests in our study were inaccessible due to their height (up to 12 m), and the unpredictability of the habitat surrounding nests would make it difficult to design a universal cage or guard. However, habitat management to influence the complexity and availability of natural cover for nest sites to reduce predation rates could potentially serve as a natural method of non-lethal predator control (Bellamy *et al.*, 2018), though a better understanding of habitat-predator relationships may be required (Maag *et al.*, 2022).

In this study we found that away from buildings, nests that were concealed in creeping plants were more successful than exposed nests. We were unable to model the availability of creepers in our nest-site selection model, but in central England the majority of nests were in creeping plants, suggesting an attraction of this species to creepers (Kirby *et al.*, 2005). Nests in creeping plants were more difficult to locate and so were presumably less likely to suffer from predation. The benefit of ivy for pollinators and other insects is well understood (Jacobs *et al.*, 2009; Garbuzov and Ratnieks, 2014), but there has been little focus on its benefits for nesting birds. Walls covered with creeping plants (green walls) in urban areas host a number of breeding birds and attract greater diversity than areas without green walls (Chiquet *et al.*, 2013; Oloś, 2023). In Europe, authors call for the protection of ivy due to its provision of food and shelter for numerous species, and its association with unmanaged woodland (Kajtoch *et al.*, 2023; Wyka *et al.*, 2023). However, despite the potential for the encouragement of creeping plants in woodlands to support several declining woodland bird species, ivy on trees is frequently removed or killed in the UK. Hence, more research is needed to support the benefit of ivy for declining woodland bird species in order to inform future management practices.

Importantly, nest predation was not the only cause of nest failure in our study. Several nests were abandoned at the egg stage or found with dead chicks in the nest. Anecdotally, nest abandonment and chick mortality appeared to be related to environmental conditions. For example, 11 of the 14 abandoned nests were found in 2024, when several pairs initiated clutches in early June during a period of warm, dry weather that was followed by a prolonged period of cold and wet weather. The effect of cold weather during the breeding season has been demonstrated for tree swallows, which are also aerial insectivores. Pairs that initiated breeding before the last cold spell of the year fledged on average one less chick than nests started after the cold spells had ended (Shipley *et al.*, 2020). Indeed, insect activity is reduced in poor weather, and so daily trends in insect activity may be equally as important as long-term abundance trends. Long-term monitoring of local insect availability and weather conditions are needed to better understand their impact on breeding success in this and other declining insectivores.

3.6. Conclusions

Our research adds to the emerging recognition of the value of freshwater habitats for species traditionally considered as terrestrial, but further investigation is needed to understand what drives these relationships. In particular, future work should consider how broader landscape features, such as river density, may influence habitat selection and contribute to observed patterns. Our findings reinforce previous research that demonstrates predation as a major driver of breeding success in spotted flycatchers, and although it is unclear whether predation is the underlying cause of population declines, habitat management to reduce its impact may ameliorate population trends. Nest survival was higher on houses, but we reveal an important role of ivy in providing nest concealment and improving the survival of nests away from houses. We encourage future research to validate these findings on a national scale to inform targeted conservation actions that promote ivy growth as a natural nest protection measure.

Chapter 4 Cross-system transfer of fatty acids from aquatic insects supports terrestrial insectivore condition and reproductive success

4.1. Abstract

Cross-system fluxes of aquatic insects rich in highly unsaturated fatty acids (HUFAs), specifically eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA), may subsidise insectivorous vertebrates facing terrestrial insect declines. The benefits of high HUFA diets, such as improved growth and immunocompetence, have previously been demonstrated for riparian insectivores. The potential for aquatic insects to benefit generalist species remains unmeasured in the wild yet is necessary for informing land management practices. Using the spotted flycatcher (*Muscicapa striata*), a habitat-generalist, insectivorous bird, as a model, we tested how blood plasma HUFA concentrations and the ratio of ω-6:ω-3 fatty acids were related to the body condition of 14 adults and 84 chicks in the wild. We measured how variation in HUFAs and ω-6:ω-3 was related to river proximity, to test whether higher HUFA concentrations were related to aquatic insect availability. We also tested how these relationships may extend to population dynamics by monitoring flying insect availability throughout two breeding seasons and assessing whether this predicted reproductive success. EPA and ω-6:ω-3 were positively correlated with body condition in chicks and adults, and both were correlated with river proximity. Breeding success was positively correlated with aquatic insect availability, suggesting that access to high HUFA diets could be beneficial at the population level. Our results demonstrate the potential for aquatic subsidies to buffer populations of terrestrial insectivores, highlighting how the maintenance or creation of high-quality freshwater habitats may be promoted in a conservation context for non-aquatic species.

4.2. Introduction

The flow of insects from aquatic to terrestrial habitats may provide an important, yet often overlooked, resource for terrestrial insectivores. Aquatic habitats offer a relatively higher abundance of insect biomass and a greater temporal availability of insects due to the addition of emergent aquatic insects and their asynchronous peaks (Nakano and Murakami, 2001; Uesugi and Murakami, 2007; Twining *et al.*, 2018b). Numerous terrestrial consumers are known to take advantage of these aquatic subsidies, including spiders (Marczak and Richardson, 2007), reptiles (Marczak and Richardson, 2007), and birds (Uesugi and Murakami, 2007). Some species are explicitly riparian and rely heavily on aquatic subsidies, while others travel in response to ephemeral insect emergences (Gray, 1993). Hence, considering aquatic and terrestrial habitats separately is over-simplistic, and quantifying the contribution of aquatic systems to the terrestrial environment could improve our understanding of food webs and the extent to which restoration or creation of aquatic habitats should be considered for terrestrial species.

In addition to supplementing insect quantities, aquatic subsidies also carry nutritional benefits. Aquatic primary producers, which are consumed by herbivorous aquatic insects, contain high levels of omega-3 (ω-3) highly-unsaturated fatty acids (HUFAs), specifically eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA; Parmar et al., 2022), which are essential nutrients, i.e., they cannot be synthesised endogenously (Gladyshev *et al.*, 2013). This is in contrast to terrestrial primary producers, which are only able to synthesise the HUFA precursor alpha-linolenic acid (ALA; Gladyshev et al., 2013). Demand for dietary HUFAs is dependent on the endogenous ability to elongate ALA into EPA or DHA, which is consequently determined by evolutionary history and trophic niche. For example, many aquatic animals with reliable access to dietary HUFAs have limited capacity to synthesize HUFAs from ALA, whereas terrestrial generalists have a greater capacity for conversion (Twining *et al.*, 2016a). Nonetheless, dietary acquisition of HUFAs may be favourable in any circumstance due to the energetic cost of conversion (Twining *et al.*, 2018a).

HUFAs have a number of important physiological roles, including maintenance of neuronal membranes, immune function, and anti-inflammatory responses (Larsson *et al.*, 2004; Twining *et al.*, 2016a). DHA has a unique role in brain development and functioning, whereas EPA, the most abundant HUFA in aquatic insects (Parmar *et al.*, 2022), has an important role as a precursor for DHA (Dyall, 2015). Deprivation of HUFAs has been shown to negatively influence a range of physiological functions in humans and other animals, including growth and vision (Twining *et al.*, 2016a). In addition to the absolute concentration of HUFAs, the quantity of ω-6 fatty acids relative to ω-3 fatty acids (ω-6:ω-

3) has important implications for health. ω-6 fatty acids dominate in terrestrial food webs, to the extent that the ω-6:ω-3 signature can be used to differentiate between aquatic and terrestrial diets (Koussoroplis *et al.*, 2008). The ω-6 fatty acid linoleic acid (LA) has the potential to decrease HUFA synthesis by competing with ALA for enzymes and transporting systems (Brenna *et al.*, 2009). For example, domestic chickens (*Gallus gallus domesticus*) fed higher ω-6:ω-3 diets showed lower HUFA synthesis and deposition compared with those fed a low ω-6:ω-3 diet (Ibrahim *et al.*, 2018). Additionally, the balance of ω-6 and ω-3 fatty acids can determine levels of inflammation and oxidative stress, by mediating the balance of pro-inflammatory (ω-6) and anti-inflammatory (ω-3) molecules (Larsson *et al.*, 2004; Isaksson, 2015).

Terrestrial insects are reported to be in decline globally (Hallmann *et al.*, 2017; Sánchez-Bayo and Wyckhuys, 2019), yet one meta-analysis found that freshwater insect abundances may be increasing (van Klink *et al.*, 2020). Therefore, the disproportionate contribution of HUFAs from aquatic insects (Twining et al., 2019; Parmar et al., 2022; Shipley et al., 2022) may offer an offset for insectivorous species with well-documented declines across Europe (Møller *et al.*, 2021) and North America (Tallamy and Gregory Shriver, 2021). However, the capacity for dietary HUFAs to benefit insectivorous species is dependent on their ALA to HUFA conversion efficiency; those with high efficiency may not be limited by HUFAs as they may acquire enough via ALA conversion. For example, tree swallow (*Tachycineta bicolor*) and Eastern phoebe (*Sayornis phoebe*) chicks have been experimentally shown to benefit from increased HUFA diets, which resulted in improved growth, immunocompetence and metabolism (Twining *et al.*, 2016b, 2019). However, both of these species are commonly associated with riparian habitats (Schukman *et al.*, 2011; Twining *et al.*, 2019), and so the benefits observed may be due to high reliance on dietary HUFAs and consequential low ALA to HUFA conversion efficiency. In contrast, a study of blue tits (*Cyanistes caeruleus*), a generalist species found in both aquatic and terrestrial habitats, concluded that nestlings were not limited by dietary HUFA availability due to their capacity to synthesise DHA from ALA, though the physiological impact of higher HUFA diets on nestlings was not reported (Twining *et al.*, 2021). Hence, understanding if the advantages of dietary HUFA acquisition are limited to riparian species is key to determining whether aquatic subsidy provision might benefit a wider range of species.

So far, the understanding of the direct impact of HUFAs on insectivorous bird health has been driven by experimental laboratory studies, and those linking aquatic subsidies with reproductive success are limited to correlational studies. For example, breeding success in tree swallows was positively correlated with the availability of ponds and aquatic insects (Twining *et al.*, 2018b; Berzins *et al.*, 2021), and we previously demonstrated that spotted flycatcher (*Muscicapa striata*) occupancy was positively correlated with the density of rivers (Chapter 2). However, more detailed studies are required to determine whether the correlations have arisen from the nutritional benefits of aquatic subsidies or by habitat complexity and other confounding factors associated with these habitats.

In this study, we investigate the importance of aquatic subsidies in the wild, specifically for a species that is not frequently associated with freshwater habitats. By doing so, we aim to illuminate the potential benefits of providing high-quality aquatic habitats for terrestrial species. We used the spotted flycatcher as a model species, owing to its strict insectivorous diet but use of both aquatic and terrestrial habitats (Cramp and Perrins, 1993; Stevens *et al.*, 2007). We assessed how chick and adult body condition varied with fatty acid composition, specifically the HUFAs EPA and DHA and ω-6:ω-3. To ensure that the fatty acid concentrations observed were predominantly a result of diet rather than conversion, we also investigated how river proximity was related to fatty acid composition. Finally, we examined how breeding success varied with the availability of aquatic insects to investigate whether the effects observed were sufficient to influence population dynamics.

We predicted that higher HUFA and lower ω-6:ω-3 would result in better body condition of spotted flycatchers. We expected that HUFA concentrations would decrease and ω-6:ω-3 would increase for nests further away from rivers, which would imply that the composition was being driven by aquatic insects. Finally, we predicted that the availability of aquatic insects would be positively correlated with breeding success.

4.3. Methods

4.3.1. Study species

The reliance of spotted flycatchers on flying insects, alongside rapid insect declines, may be associated with the species' 93% decline in the UK since the 1960s (BTO, 2024) and

56% decline across its European breeding range (PECBMS, 2025). Spotted flycatchers frequently occur along riverbanks with suitable perch sites and use riparian and wetland areas on their wintering grounds in Africa (Cramp and Perrins, 1993). However, they are not exclusively riparian and can be found in a range of wooded and semi-wooded habitats, including parkland, farmland and woodland (Stevens *et al.*, 2007). During the breeding season, most foraging trips occur within 50 m of the nest, but occasional flights of up to 200 m can occur during incubation (Davies, 1977).

4.3.2. Nest monitoring and sampling

Field work was undertaken within an 11 km radius of Sedbergh, in the Yorkshire Dales National Park, UK (54.323559, -2.528300) (Supp. Fig. 4.1). The study area is primarily upland pasture, grazed by livestock, with frequent farmsteads, villages, small pockets of woodland and numerous streams and small rivers. We monitored 128 spotted flycatcher nesting attempts between May and August in 2023 and 2024 (Supp. Fig. 4.1). GPS coordinates of nests were later used to calculate the distance to the nearest river using ArcGIS and the CEH river networks dataset (UKCEH, 2000). We searched for nests in all areas where flycatcher pairs were detected. Nests were checked at least once per week, and, to ensure accurate aging of nestlings, the frequency of checks was increased to every other day when hatching was imminent. We recorded the date the first egg was laid (first egg date (FED)), clutch size, hatch date, number of hatchlings, fledging success and the number of chicks present 1–3 days prior to fledging for all nests where possible. Dates were back-calculated where nests were found at later stages e.g., during incubation or with chicks present, based on an incubation period of 13 days. Chicks were aged ± 1 day based on body size and feather development. At 7 days old (hatch day = day 0), individual British Trust for Ornithology (BTO) metal rings were fitted and biometric measurements taken. Each chick was weighed ± 0.1 g using an electronic balance and tarsus length recorded ± 0.1 mm by measuring from the inter-tarsal joint to the joint between tarsus and toes using dial callipers. Adults were captured using a combination of mist nets and spring-loaded ‘perch traps’ at varying stages of nesting. BTO metal rings and a unique combination of two or three anodised-metal colour rings were fitted to each adult and biometrics measured the same way as for chicks. Biometric measurements of adults and chicks were later used to calculate a scaled body mass index (SMI; hereafter body condition) by standardising the mass of all birds to the mean mass of sampled birds with a scaling exponent estimated from standardised major axis (SMA) regression of mass against tarsus length (Peig and Green, 2009). In 2023 only, up to 100 µL of blood was extracted from the brachial vein of adults and chicks with 26G x 13 mm Microlance^{TM} hypodermic needles and 75 x 1.15 mm heparinised capillary tubes. Blood samples were centrifuged immediately (10 mins at 6000 RPM) to separate red blood cells from plasma. Plasma and red blood cells were pipetted into separate vials and stored on ice until they could be transferred to a -20 ˚C freezer on the same day. Once fieldwork was complete, all samples were sent to the lab and stored at -80 ˚C until analysis. All handling and capture was carried out under license from the British Trust for Ornithology. Blood sampling was carried out by Catrin Eden and Stuart Sharp under ethical approval from Lancaster University and licensed by the UK Government's Home Office and Natural England.

4.3.3. Insect monitoring

Flying insects were trapped using flight intercept traps hung from trees from May to August in each year (Knuff *et al.*, 2019). Four traps were placed at each of two sites with high spotted flycatcher occupancy. Two of these traps were hung adjacent to a river and two were hung approximately 80 m from the same river. Insects were trapped in 1 L bottles containing 60 mL propylene glycol, 40 mL water and a drop of liquid detergent. Traps were emptied weekly and insects decanted through a 1 mm sieve and stored in 100% ethanol until sorting and identification. Non-flying insects were discarded and the remaining insects identified to order level and their body length measured ± 1 mm. Due to time constraints it was not possible to identify insects to family level and so Ephemeroptera, Plecoptera and Trichoptera were classified as aquatic and all other insects were classified as terrestrial. Biomass was later calculated using allometric equations based on order and body length (Hódar, 1996; Ganihar, 1997; Sabo *et al.*, 2002).

4.3.4. Fatty acid extraction and gas chromatography/mass spectrometry (GC/MS)

Fatty acids were extracted from blood plasma using previously published methodology (Andersson *et al.*, 2015; Eikenaar *et al.*, 2022). Briefly, lipid extraction of up to 5 µL plasma was performed for 1 hr using 50 µL of chloroform:methanol (2:1 v/v) with 33.3 ng/µL of internal standard methyl cis-10-heptadecenoate (purity >99%, Aldrich). Base methanolysis was then used to convert fatty acid moieties in the solvent to fatty acid methyl esters (FAMEs) by adding 100 µL of 0.5 M KOH in methanol and placing samples in the oven for 1hr at 40 ˚C. The reaction was halted by neutralising the base with 100 µL 0.5

HCl in methanol and FAMEs separated by adding 300 µL heptane. The polar layer was removed and samples were washed twice with H_2O, with removal of the polar layer between each wash. Then the heptane including the FAMEs were dried with anhydrous sodium sulfate before concentrating the heptane phase under N_2. The FAME extracts were then quantified using Agilent 5975 MS coupled to an Agilent 6890 GC equipped with an HP-INNOWax column (30 m x 0.25 mm i.d., and 0.25 µm film thickness; Agilent). In total, 20 fatty acids were identified by comparing mass spectra with known retention times of synthetic standards.

4.3.5. Data handling and statistical analyses

All statistical analyses were carried out in R version 4.3.1 (R Core Team, 2020) using the Bayesian package *brms* (Bürkner, 2021). In all cases, model fit was checked by comparing the posterior predicted distribution to the observed data, and chain convergence assessed visually and using the R-hat value. Default priors were used for all models, and hypothesis testing was based on model estimates and the overlap of 90% credible intervals (CRIs) with 0. Four chains were run for 4000 iterations with a burn-in of 1000 and thinning interval of 1. Effect sizes are reported as the median of the posterior distribution and 90% CRIs, unless otherwise stated.

4.3.5.1. Fatty acid analysis

We calculated relative proportions for the 20 fatty acids by dividing the area for each individual fatty acid peak with the sum of all fatty acid peaks (Supp. Table 4.1). Absolute fatty acid concentration was calculated by dividing the fatty acid peak area by the internal standard peak area, then multiplying by the internal standard concentration (33.3 ng/µL), and finally dividing by the sample plasma volume. Here, we present the absolute concentrations of highly unsaturated ω-3 fatty acids eicosapentaenoic acid (EPA), docosahexaenoic acid (DHA) and the ω-6:ω-3 ratio.

To test for correlations between HUFAs and ω-6 :ω-3 with the dependent variable body condition, we used generalised linear (adults) and generalised linear-mixed models (chicks) fitted with a Gamma distribution and log link function. Brood ID was included as a random effect in models for chicks to account for non-independence among individuals within the same nest. We did not include brood ID as a random effect in adult models as sample size was small and not all adults sampled were pairs (i.e. identified with the same brood ID). We created two models investigating the relationship with body condition; one for the response to HUFA concentrations (EPA and DHA) and one for the response to ω-6:ω-3.

To investigate the influence of river proximity on fatty acid concentrations we constructed individual GLMMs for EPA, DHA and the ω-6:ω-3 ratio which included age (adult / chick), river proximity (m) and year as fixed effects and brood ID as a random effect. All models were fitted using a Gamma distribution and log link function.

4.3.5.2. Breeding success analysis

We tested the relationship between breeding success and aquatic insect availability using four breeding success metrics: clutch size, number of hatchlings, fledging success (a binary measure of whether at least one chick fledged from a sampled nest), and the number of chicks fledged (the number of chicks present 1–3 days prior to fledging). For all analyses we excluded nests that were known to have been predated. We included year as a factor in all models to account for environmental differences between years.

Daily aquatic and terrestrial insect availability was calculated using data from flight intercept traps. Insects < 2 mm were removed from the analysis as these were mostly small, unfavourable Diptera (e.g., Nematocera) which are unlikely to be eaten by spotted flycatchers (Davies, 1977) and had a strong influence on the overall biomass due to large emergences following heavy rainfall at some sites. Weekly samples were standardised by dividing the biomass of insects with the length of time the trap was active. Data from both sites were pooled into terrestrial (traps 80 m from river) and river catches as both sites showed similar temporal trends. We then calculated a 7-day moving average to estimate daily insect availability for every day between the first and last insect sample for aquatic and terrestrial insects from both river and terrestrial traps. We extracted terrestrial insect biomass from the terrestrial traps and aquatic biomass from the river traps for use in the analyses.

Each breeding success metric was modelled with the appropriate distributions and tested for correlations with insect biomass corresponding to the appropriate period for the life stage (Table 4.1). Despite clutch size being most commonly modelled using a Poisson distribution, we found that a Gaussian model most accurately predicted the distribution of our clutch size data (Table 4.1). Default link functions were used for all models. Both hatching success and number of fledglings models were weighted by clutch size, as this allowed the greatest sample size to be tested (e.g. in comparison with weighting the number of fledglings with the number of hatchlings). Interactions were only retained where 90% credible intervals did not overlap 0.

4.4. Results

4.4.1. Fatty acids

4.4.1.1. HUFA concentrations

Fatty acid composition was calculated for 14 adult spotted flycatchers and 84 chicks from 25 broods. Chick condition was positively correlated with plasma EPA concentration (effect size: 0.04, 0.01–0.06) but not DHA concentrations (effect size: -0.01, -0.03–0.00; Table 4.2, Fig. 4.1a–b). Adults showed a similar trend but 90% CRIs overlapped 0 for both HUFAs (Figs. 4.1c–d, Table 4.2). EPA concentration was higher in chicks than adults (effect size: -0.63, -0.89 – -0.37), ranging from 4.92 ng/µL to 289.59 ng/µL in chicks (mean: 112.37 ng/µL) and 104.88 ng/µL to 368.87 ng/µL (mean: 196.40 ng/µL) in adults (Fig. 4.1e, Table 4.2). The opposite effect was found for DHA, which ranged from 4.05 ng/µL to 172.40 ng/µL in chicks (mean: 61.10 ng/µL) and 29.84 ng/µL to 131.78 ng/µL (mean: 53.48 ng/µL) in adults, though there was considerable overlap between the two (Fig. 4.1f, Table

Table 4.1. Model-fitting distributions, sample sizes and corresponding period for which insect biomass was calculated for GLMs testing the effect of insect biomass on clutch size, hatching success, fledging success and number of fledglings. Weighted binomial models were all weighted with clutch size. FED = first egg date.

Breeding metric (n)	Insect data period	Model fitting distribution	Fixed effects tested
Clutch size (63)	7 days prior to FED	Gaussian	Year, first egg date, aquatic insect biomass, terrestrial insect biomass
Hatching success (42)	FED to 1 day prior to hatch date	Weighted binomial	Year, aquatic insect biomass, terrestrial insect biomass, aquatic insect biomass*distance from river
Fledging success (59)	Hatch date to 13 days after hatch date	Bernoulli	
Number of fledglings (30)	Hatch date to 13 days after hatch date	Weighted zero-inflated binomial	

4.2). EPA concentration clearly decreased as distance from the river increased (-0.14, -0.26 – -0.02) but no effect of river proximity was found for DHA (Figs. 4.1e–f, Table 4.2).

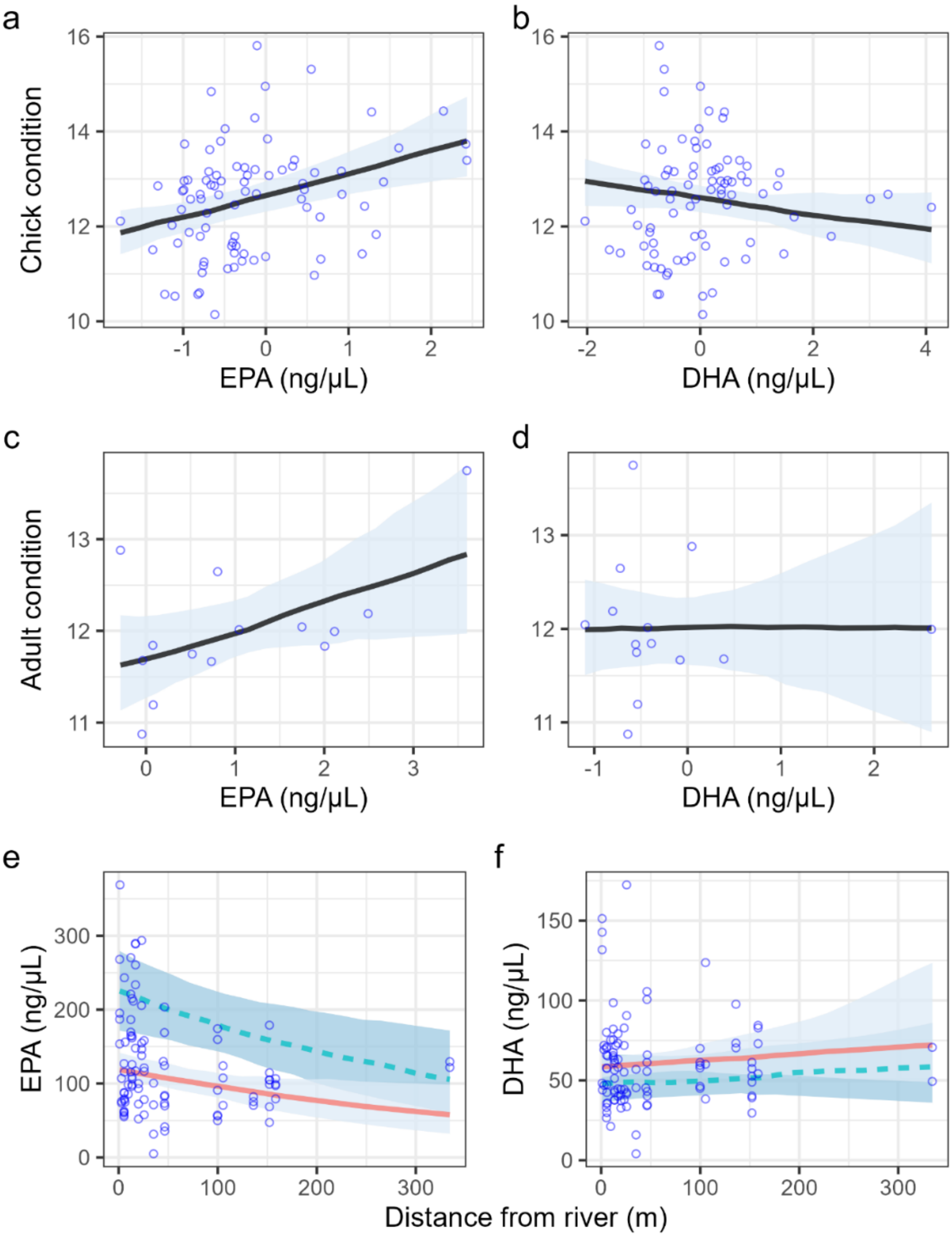

Figure 4.1. Highly unsaturated fatty acid (HUFA) concentration is correlated with body condition of spotted flycatcher chicks (a,b), adults (c,d) and proximity to rivers (e,f). Open circles show raw data, solid lines and shaded areas represent the median of the expected posterior predicted distribution and 90% CRIs. In plots e,f unbroken orange lines represent chicks and broken blue lines represent adults. X axes in plots a–d show mean-centred values.

Table 4.2. Summary of results for Bayesian generalised linear and generalised linear mixed models testing the relationship between spotted flycatcher body condition and fatty acid concentration, and the relationship between fatty acid concentration and proximity of nests to rivers. All models including chick data were modelled with a brood ID random effect to account for repeat sampling. Bold denotes 90% CRIs not overlapping 0.

Chick condition	*Estimates*	*CRI (90%)*	Marginal R^2 / Conditional R^2
Intercept	**2.54**	**2.52 – 2.56**	0.104 / 0.496
DHA (ng/µL)	-0.01	-0.03 – 0.00	
EPA (ng/µL)	**0.04**	**0.01 – 0.06**	
Random Effects			
σ^2	0.52		

Adult condition	*Estimates*	*CRI (90%)*	R^2 Bayes
Intercept	**2.46**	**2.41 – 2.50**	0.352
DHA (ng/µL)	0	-0.04 – 0.04	
EPA (ng/µL)	0.03	0.00 – 0.06	

EPA (ng/µL)	*Estimates*	*CRI (90%)*	Marginal R^2 / Conditional R^2
Intercept	**5.31**	**5.09 – 5.53**	0.262 / 0.622
Distance from river	**-0.14**	**-0.26 – -0.02**	
Age [Chick]	**-0.63**	**-0.85 – -0.42**	
Random Effects			
σ^2	2407.87		

DHA (ng/µL)	*Estimates*	*CRI (90%)*	Marginal R^2 / Conditional R^2
Intercept	**3.88**	**3.67 – 4.11**	0.039 / 0.258
Distance from river	0.04	-0.05 – 0.14	
Age [Chick]	0.23	0.00 – 0.45	
Random Effects			
σ^2	186.35		

Chick condition	*Estimates*	*CRI (90%)*	Marginal R^2 / Conditional R^2
Intercept	**2.53**	**2.51 – 2.55**	0.080 / 0.458
Ω6:Ω3	**-0.03**	**-0.04 – -0.01**	
Random Effects			
σ^2	0.49		

Adult condition	*Estimates*	*CRI (90%)*	R^2 Bayes
Intercept	**2.49**	**2.45 – 2.52**	0.067
Ω6:Ω3	-0.01	-0.05 – 0.03	

Ω6:Ω3	*Estimates*	*CRI (90%)*	Marginal R^2 / Conditional R^2
Intercept	**0.3**	**0.20 – 0.41**	0.163 / 0.674
Distance from river	**0.09**	**0.02 – 0.16**	
Age [Chick]	-0.07	-0.17 – 0.02	
Random Effects			
σ^2	0.07		

4.4.1.2. ω-6:ω-3

The ratio of ω-6:ω-3 had a negative correlation with chick body condition (-0.03, -0.04– -0.01), but this was not found for adult condition (Figs. 4.2a–b, Table 4.2). No distinct difference was observed between the ω-6:ω-3 ratio in chicks and adults, which ranged from 0.65 to 2.35 (mean: 1.30) in chicks and 0.87 to 2.04 (mean: 1.40) in adults (Fig. 4.2c, Table 4.2). River proximity had a strong correlation with ω-6:ω-3, which increased with distance from the river (0.09, 0.02– 0.16; Fig. 4.2c, Table 4.2).

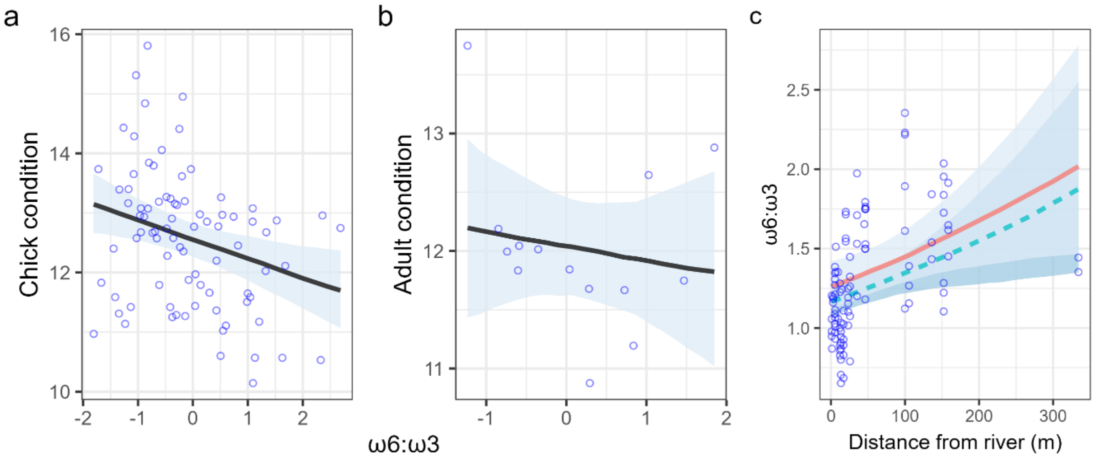

Figure 4.2. Correlation between ω-6:ω-3 ratio and body condition (a,b) and river proximity (c) in spotted flycatcher chicks and adults. Blue circles represent raw data. Lines and shaded areas represent the median of the expected posterior predicted distribution and 90% CRIs. X axes in plots a–b show mean-centred values. In (c) the continuous orange line represents the predicted trend for adults and the dashed blue line represents chicks.

4.4.2. Breeding success

There was a relatively strong correlation between first egg date (FED) and both aquatic and terrestrial insect biomass (Pearson's correlation -0.50 and -0.63, respectively), and so we compared three models that included FED (FED-only model), aquatic biomass + terrestrial biomass (insect-only model) or FED + aquatic biomass + terrestrial biomass (insect and FED model). Year was included as a fixed effect in all three models. The FED-only model accounted for more variation than the insect-only model (Bayes R^2: 64.7 vs 0.26) and performed equally to the insect and egg model (Bayes R^2: 64.8). Thus, the FED model was selected as the most likely, as clutch size is known to decrease later in the season regardless of environmental conditions (Stevens et al., 2007). We found no evidence that aquatic biomass during the incubation period influenced hatching success, but aquatic biomass during the chick growth stage was positively correlated with fledging success and the number of fledglings, depending on how close the nest was to a river (Fig. 4.3, Table 4.3). Greater aquatic insect biomass resulted in a greater probability of fledging at least 1 chick, and the strength of this effect was greater further away from rivers (Fig. 4.3a, Table 4.3). Conversely, the effect of aquatic insects on the number of fledglings was greater when the nest was closer to a river (Fig. 4.3b, Table 4.3). The effect was positive for both fledging success (Supp. Figure 4.2) and number of fledglings up until approximately 50 m from a river (Supp. Figure 4.3).

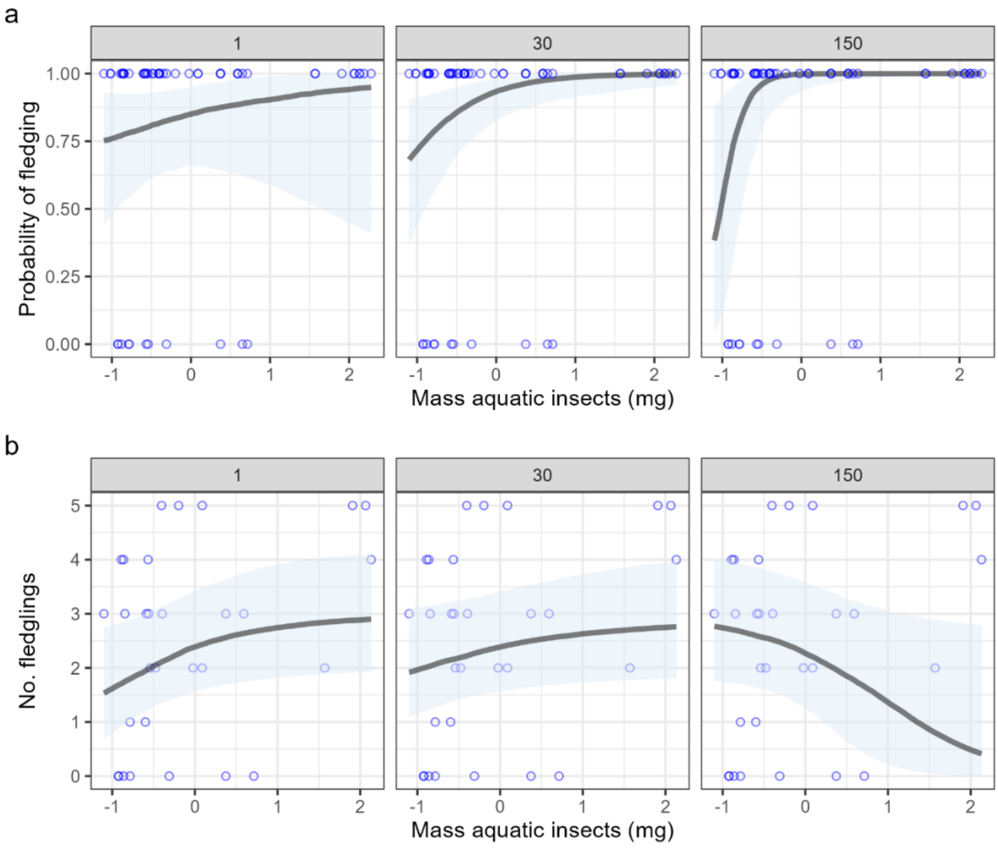

Figure 4.3. The probability of spotted flycatcher nests fledging (a) and the number of fledglings (b) in relation to the mass of aquatic insects during the nestling period for nests 1, 30 and 150 m from a river. Blue circles represent raw data. Lines and shaded areas represent the median of the expected posterior prediction and 95% CRIs. Titles above each plot represent distance from the river (m) for which the prediction was made. All x axes show mean-centred values.

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Table 4.3. Summary of models testing the relationship between insect availability and four different breeding success variables. Models were fit using Bayesian generalised linear mixed models in the R package *brms*. Bold denotes 90% credible intervals not overlapping 0.

Clutch size			
Predictors	*Estimates*	*CRI (90%)*	R^2 Bayes
Intercept	**5.81**	**5.54 – 6.07**	0.655
egg1	**-0.03**	**-0.04 – -0.03**	
year [2024]	**-0.31**	**-0.50 – -0.13**	
Hatchlings	*Log-Odds*	*CRI (90%)*	R^2 Bayes
Intercept	**1.36**	**0.94 – 1.80**	0.327
year [2024]	0.65	-0.14 – 1.48	
Mass aquatic insects during laying period	0.32	-0.08 – 0.73	
Mass terrestrial insects during laying period	0.21	-0.24 – 0.69	
Fledging success	*Log-Odds*	*CRI (90%)*	R^2 Bayes
Intercept	**3.34**	**2.02 – 5.30**	0.172
year [2024]	-0.97	-2.32 – 0.29	
mass aquatic insects during growth period	**2.35**	**0.76 – 4.68**	
distance from river	**2.15**	**0.34 – 5.32**	
mass terrestrial insects during growth period	-0.72	-1.54 – 0.00	
mass aquatic insects during growth period:distance from river	**2.69**	**0.33 – 6.26**	
Number of fledglings	*Log-Odds*	*CRI (90%)*	R^2 Bayes
Intercept	**1.39**	**0.68 – 2.15**	0.130
year [2024]	-0.13	-1.13 – 0.89	
mass of aquatic insects during growth period	0.24	-0.39 – 0.94	
distance from river	-0.01	-0.74 – 0.91	
mass terrestrial insects during growth period	0.13	-0.43 – 0.70	
mass aquatic insects during growth period :distance from river	**-1.27**	**-2.40 – -0.29**	

4.5. Discussion

Our results show that access to dietary HUFAs during the breeding season was positively correlated with the condition and breeding success of a non-aquatic, generalist insectivorous bird. Variation in EPA concentration and ω-6:ω-3 in chicks and adults was explained by distance to a river, suggesting a substantial contribution of aquatic insects to these values, and this was supported by a higher fledging success at nests exposed to a greater biomass of aquatic insects. The apparent absence of an effect from DHA, either on body condition or relative to river proximity, was contrary to our expectations and is discussed below. These results suggest that the previously reported positive influence of river density on habitat occupancy by spotted flycatchers (Chapter 2) may at least be partly explained by improved breeding success resulting from access to better food quality, and not just a potential consequence of variation in habitat structure.

Our confirmation that body condition in both chicks and adults increased with concentrations of EPA and lower ω-6:ω-3 was in line with expectations. Twining et al. (2016b) showed that, under laboratory conditions, tree swallow chicks fed low amounts of high HUFA diet grew heavier than chicks fed a large amount of low HUFA diet, suggesting that quality is more important than quantity, at least during early development. However, various other factors contribute to chick development in the wild, e.g. predation risk and parental quality (Remeŝ and Martin, 2002), which could mask or dilute the benefits of a high-quality diet. For the first time in wild birds, we show that EPA concentration is positively related to body condition, a commonly used proxy for health and post-fledging survival (Naef-Daenzer *et al.*, 2001; Ronget *et al.*, 2018; Evans *et al.*, 2020). Moreover, fledging success was greater in nests exposed to a higher aquatic insect biomass during the chick development period, suggesting that the positive effect of dietary HUFAs may scale up to the population level.

It is likely that the limited sample size in the adult models (n = 14) reduced the power to detect an effect, although the trend was the same as that for chicks. The influence of HUFAs on adult birds has been largely overlooked in the context of aquatic subsidies, but the potential importance of ω-3 fatty acids for migration has been demonstrated in other species (Weber, 2009). For example, semipalmated sandpipers (*Calidris pusilla*) switch to feeding exclusively on DHA-rich prey prior to migration, which is thought to improve migration performance through increased metabolism efficiency and endurance in flight muscles (Weber, 2009). Additionally, improved body condition in adults with higher EPA concentrations may enhance survival (Blums *et al.*, 2005) or breeding success (Kouba et al., 2021). These results highlight the importance of high-quality diet throughout the lifecycle, and future research should aim to explore the long-term impact of high-quality diet on adult insectivorous birds.

The apparent lack of an effect of DHA on body condition in either adults or chicks, and the lack of a correlation with river proximity, was surprising given the importance of DHA in brain development and functioning. However, demand for DHA during the early developmental stages is high in altricial species, which undergo rapid brain growth between hatching and fledging (Speake and Wood, 2005), and so DHA deposition is likely highly regulated. Whilst aquatic insects contain higher concentrations of DHA than terrestrial insects, Twining et al. (2018a) calculated that this amount was still insufficient to meet dietary demand, and so a large proportion of DHA is likely acquired through elongation of EPA. Therefore, although aquatic insects provide higher DHA potential through a higher EPA contribution, conversion is likely constrained to necessary levels and DHA immediately transported to where it is required (i.e. the brain), which would result in less variation in the blood pool (sampled in this study).

Differences in HUFA concentrations between chicks and adults may suggest preferential feeding of high-quality food items to chicks. Spotted flycatchers have been observed selectively feeding chicks larger insects (Davies, 1977), but it is unclear whether specific orders or families with differing HUFA potential are selected. Significantly lower EPA concentrations and marginally higher DHA concentrations in chicks (Fig. 1e–f) may have resulted from preferential feeding of DHA to chicks by adults. However, high DHA demand during development may lead to higher EPA to DHA conversion in chicks compared to adults, which would lead to higher DHA and lower EPA concentrations in the blood. Thus, a more detailed understanding of EPA to DHA conversion and of the insect species eaten by adults and chicks is required to explain these trends.

The ω-6:ω-3 ratio had a similar effect on chick condition to EPA, which is unsurprising given the biological mechanisms influenced by ω-6:ω-3. Firstly, ω-6 competes with ω-3 for binding sites (Twining *et al.*, 2016a), and so higher ω-6:ω-3 ratios can lead to lower deposition of EPA and DHA in muscles (Ibrahim *et al.*, 2018). Moreover, ω-6 is pro-inflammatory whilst ω-3 is anti-inflammatory, and so the ratio between the two can determine the levels of inflammation and oxidative stress in the body (Larsson *et al.*, 2004; Isaksson, 2015). Here, we demonstrated that the proximity to rivers, a proxy for aquatic insect availability, was negatively associated with ω-6:ω-3. Though we were unable to trace the origins of fatty acids in our study (e.g., through isotope labelling), the relationship between plasma EPA and ω-6:ω-3 with river proximity implies that aquatic insects likely drove the variation in fatty acid content.

Although we did not measure the ALA to EPA conversion efficiency of spotted flycatchers, previous work has suggested that other generalist species are less likely to be limited by dietary HUFAs as they have better conversion efficiency than species reliant on aquatic resources (Twining *et al.*, 2021). However, our results suggest that, although not limited, generalist species may still benefit from higher quality food. Most aquatic insect deposition occurs within 0.5 m of the river, though some species range further than 500 m (Muehlbauer *et al.*, 2014). The maximum distance of a flycatcher nest from a river in our study was 334 m, which exceeds the average distance that spotted flycatchers travel from their nests to feed (Davies, 1977), and so the lower EPA concentrations measured in samples furthest from rivers are likely to be the result of a combination of ALA conversion and a small contribution of aquatic insects. Chicks nearer to rivers in our study benefited from better access to aquatic insects and their high EPA content. They were in better condition than chicks that had access to a lower quantity of aquatic insects, suggesting potential for HUFA-rich aquatic subsidies to benefit insectivorous species, regardless of dietary niche.

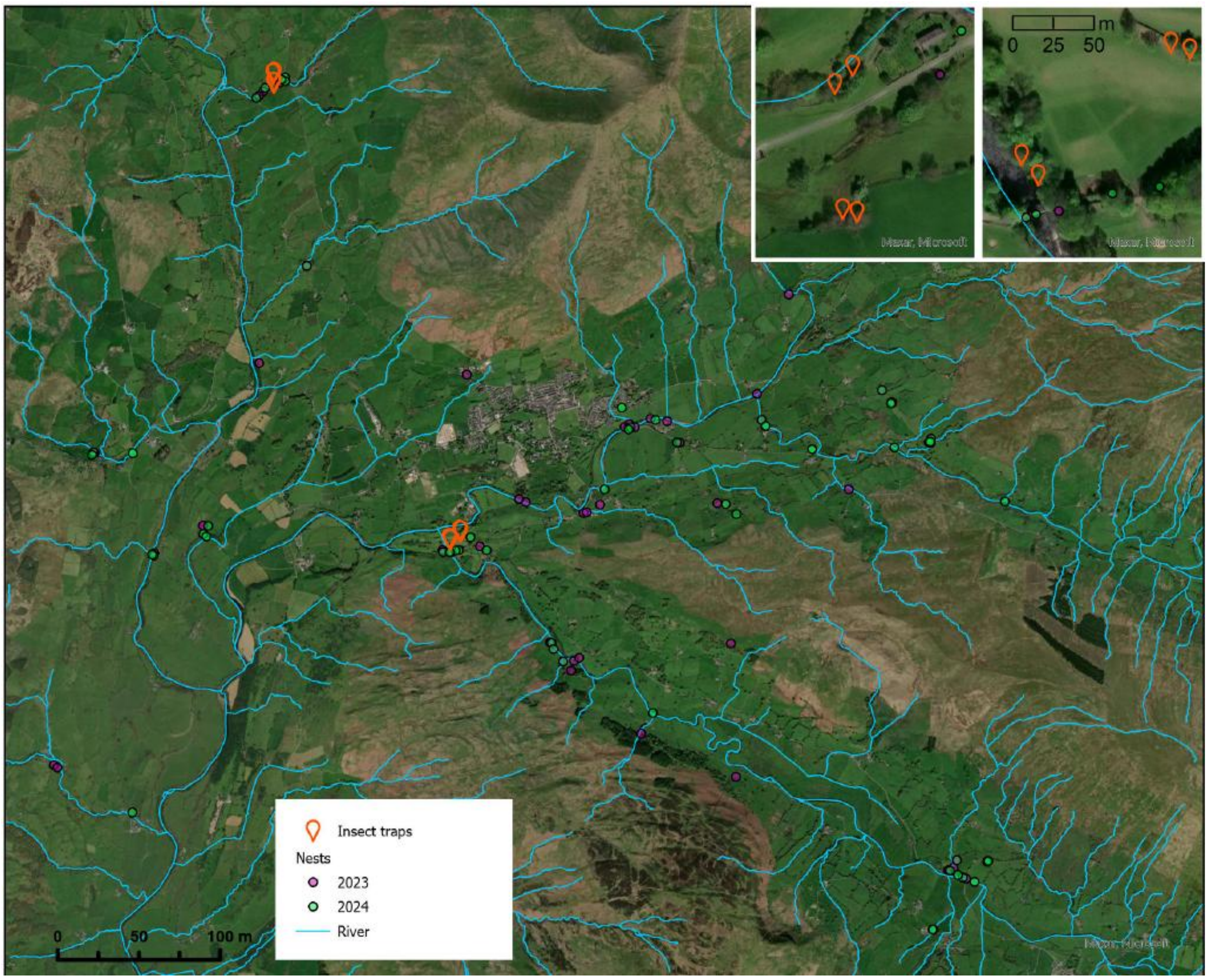
The results of our breeding success analyses further emphasise the importance of aquatic subsidies for generalist insectivores. The driver of opposing interactions between river proximity and aquatic insects for productivity is unclear, but may be a result of the study design. Aquatic insect abundance was measured adjacent to rivers, and so most accurately reflects the availability of aquatic insects for nests closer to rivers, whereas the availability of insects to nests further away from rivers is confounded by various factors including insect species and river productivity (Muehlbauer *et al.*, 2014). Nests within 50 m of rivers responded positively to higher aquatic insect abundance (Appendix B, Figs B2, B3), which clearly demonstrates the benefit of having access to high-quality food during the nesting phase. Though this study focussed solely on river systems, similar benefits may be obtained from other wetland habitats that support emergent aquatic insects, such as lakes and ponds. For example, one study found that insect biomass was 25-fold higher around well-managed ponds (Lewis-Phillips *et al.*, 2020) and Berzins et al., (2021) found that tree swallow recruitment and chick condition was positively related to the abundance of surrounding ponds. Given the relative ease of introducing ponds into the landscape, these features may offer an effective way to disproportionately benefit insectivorous populations.

Humans have strong potential to disrupt overall HUFA export from aquatic habitats via land use and climate change. Increased frequency of droughts and both agriculture and pollution have potential to alter the abundance and community structure of aquatic invertebrates (Ledger *et al.*, 2013; Van Dijk *et al.*, 2013; Stenroth *et al.*, 2015; Manning and Sullivan, 2021; Powell *et al.*, 2024), which may differ in their HUFA composition (Parmar *et al.*, 2022). Additionally, the timing of aquatic insect emergence has become earlier and more concentrated as a result of climate change (Shipley *et al.*, 2022), increasing the pressure for consumers to synchronise with high-quality food peaks. As our study took place in an area of relatively high water quality (Powell et al., 2023 - Fig. S6), within a limited distance from a river, studies incorporating a wider range of habitats and availability of aquatic subsidies are required to fully understand the consequences of disrupting the availability of high-HUFA diets for generalist species in the wild.

4.6. Conclusion

Our study is the first to examine the role of aquatic insects and their nutritional composition on a Palearctic insectivorous bird. Though the ability to synthesize HUFAs endogenously, and so the requirement for dietary HUFAs, may vary between species, direct consumption may still be energetically favourable. As the spotted flycatcher is not exclusively riparian, it is likely that it has sufficient ability to synthesize HUFAs from precursors, yet benefits were still apparent from direct consumption, demonstrating significant potential for aquatic insects to improve breeding success and alter population trends via improved food quality. Future studies should aim to extend this understanding to other insectivorous species that are currently undergoing rapid declines across Europe and North America. Gaining a better understanding of the consequences of limiting these resources may help to quantify the potential of introducing (e.g., pond creation) or improving (habitat management) aquatic systems as a conservation measure for terrestrial species.

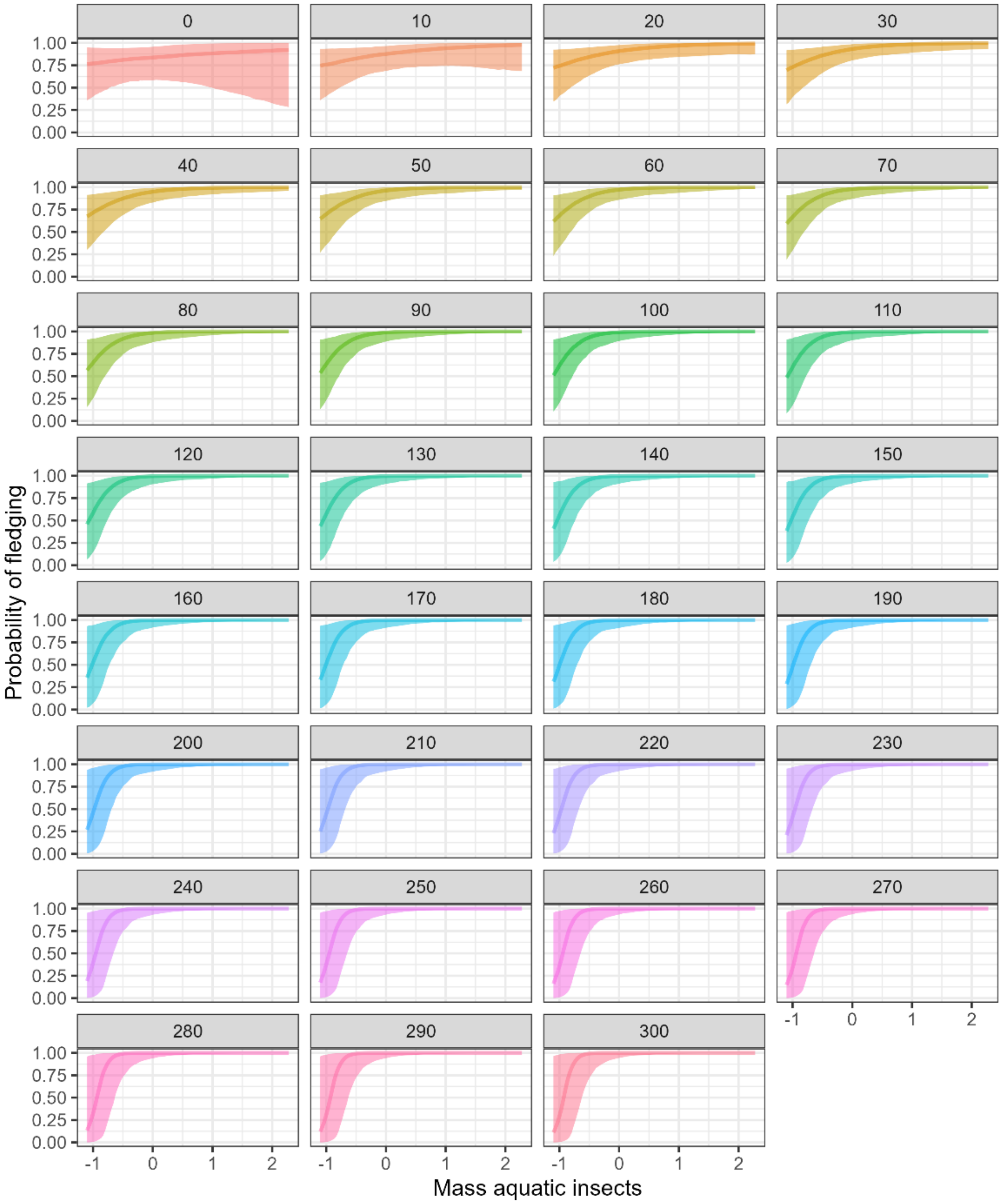
Supplementary material



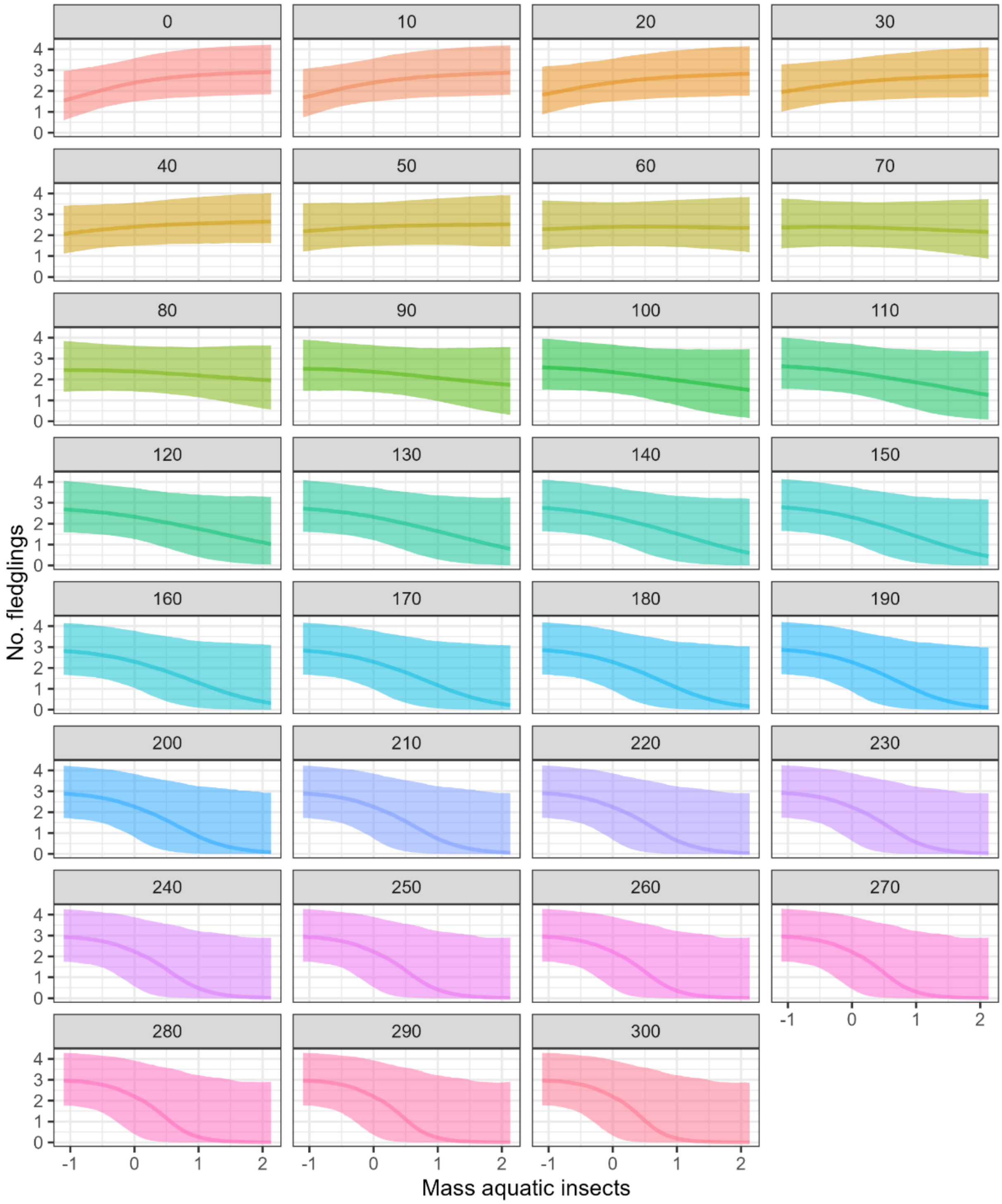
Supplementary Figure 4.1. Aerial view of study site in Sedbergh, Yorkshire Dales National Park, UK (54.323559, -2.528300). Monitored nests are shown as purple (2023) and green (2024) circles. Locations of insect traps are shown as red markers, in both the main map and the inset. Rivers are shown as blue lines. A large proportion of the area is roughly grazed upland, which is unsuitable for spotted flycatchers, Sedbergh was chosen as a study site due to its relatively high density of spotted flycatchers. Monitoring took place in the valleys of Sedbergh, which are predominantly utilised for pastoral farmland and rural settlements and are delineated by second- and third-order streams and rivers.

Supplementary Table 4.1. Mean and SD of percentage of fatty acids in blood plasma of 14 spotted flycatcher adults and 84 7-day old chicks.

	Mean (SD)	
Fatty acid	**Adults (%)**	**Chicks (%)**
12:0 Lauric acid	0.15 (0.08)	0.33 (0.40)
14:0 Myristic acid	1.50 (0.28)	2.22 (1.55)
15:0 Pentadecanoic acid	0.22 (0.06)	0.19 (0.08)
16:0 Palmitic acid	18.66 (1.85)	20.47 (3.58)
16:1(n-9) Hypogeic acid	0.36 (0.09)	0.41 (0.17)
16:1(n-7) Palmitoleic acid	11.70 (2.57)	12.32 (3.48)
17:0 Heptadecanoic acid	0.60 (0.13)	0.62 (0.17)
18:0 Stearic acid	12.64 (1.10)	13.68 (1.32)
18:1(n-9)	16.18 (1.42)	18.24 (2.85)
18:1(n-7) Vaccenic acid	1.43 (0.62)	2.32 (0.84)
18:2(n-6) Linoleic acid	11.95 (2.19)	9.26 (1.73)
18:3(n-3) Alpha-linolenic acid	5.03 (1.82)	4.54 (2.06)
20:0 Arachidic acid	0.14 (0.06)	0.18 (0.21)
20:1(n-9) Gondoic acid	0.04 (0.02)	0.09 (0.05)
20:3(n-6) Dihomo-gamma-linolenic acid	0.43 (0.13)	0.51 (0.20)
20:4(n-6) Arachidonic acid	8.19 (1.43)	6.01 (1.83)
20:5(n-3) Eicosapentaenoic acid	7.19 (2.45)	4.40 (1.75)
22:4(n-6) Adrenic acid	0.23 (0.44)	0.13 (0.05)
22:5(n-3) Docosapentaenoic acid	1.37 (0.35)	1.64 (0.52)
22:6(n-3) Docosahexaenoic acid	1.99 (0.82)	2.45 (0.92)



Supplementary Figure 4.2. Predicted probability of fledging at least 1 chick from 0 to 300 m from a river. Lines denote median of the posterior distribution and shaded areas represent 95% CRIs. Plot titles represent proximity to rivers (m). X axis has been mean-centred.



Supplementary Figure 4.3. Predicted number of fledglings from 0 to 300 m from a river. Lines denote median of the posterior distribution and shaded areas represent 95% CRIs. Plot titles represent proximity to rivers (m). X axis has been mean-centred.

Chapter 5 Migration strategy and seasonal movement patterns in spotted flycatchers (*Muscicapa striata*)

5.1. Abstract

Understanding the full annual cycle of declining migratory birds is essential for their protection. As well as knowledge of where birds go and the routes they take, identifying the strategy used to complete migration informs us about their needs outside the breeding season. Here, we reconstructed the migration of 19 spotted flycatchers (*Muscicapa striata*) from the UK, where the species has undergone significant declines, using light-only (GLS) and multi-sensor geolocators (MGLS). We used acceleration, light and atmospheric pressure data from four recovered MGLS tags to define the timings of movements and locations of stopovers. We compared these trajectories with GLS tracks, which were available for more individuals (n = 15) but provide lower spatio-temporal resolution. Both tag types provided spatially similar results; birds took an extensive western detour from the shortest distance between wintering and breeding grounds, travelling southwest through the Iberian peninsula and then along the coast of West Africa, before travelling south into northern Namibia. Short-hop migration was the dominant strategy, with birds flying over 10,000 km between England and northern Namibia in 43 ± 4 migratory flights in autumn and 38 ± 6 migratory flights in spring. Autumn migration took 106 ± 9 days, whereas spring migration was faster (68 ± 22 days), enabled by spending less time at staging sites and making continuous flights of up to 45 hours directly across the Sahara Desert. This study provides the first detailed description of the full migratory route of UK-breeding spotted flycatchers and highlights the need for broad-scale conservation strategies for this species, which relies on regularly distributed, good quality habitat for refuelling during frequent stopovers.

5.2. Introduction

Over two billion birds utilise the Afro-Palearctic flyway each year to migrate between breeding areas in Europe and wintering areas in Africa (Hahn *et al.*, 2009). Many long-distance migrants (i.e. those migrating between Europe and Sub-Saharan Africa) have undergone greater declines than most short-distance migrants and non-migratory species

(Gregory *et al.*, 2023), leading to an urgent need to understand the full annual cycle of these birds. Despite interest in migration spanning over a century, the fine-scale examination of the full migratory cycle of individual birds has been limited to larger species until recently, due to the weight of tracking devices. Advances in tracking have provided insights into locations occupied during longer stopovers (e.g. Lemke et al., 2013), but reconstruction of the migratory route is hampered by the spatio-temporal limitations of these analyses (Lisovski *et al.*, 2012). As a result, the specific migration routes and stopover locations of many species are yet to be uncovered (Beresford *et al.*, 2019; Vickery *et al.*, 2023), despite their potential to influence survival (Blackburn and Cresswell, 2016) and breeding success (Finch *et al.*, 2014).

As well as an understanding of the geographic locations used by birds outside of the breeding season, the migration strategy used may influence which type of conservation actions will be most effective (Vickery *et al.*, 2023). For example, 'capital' migrants that fuel up in discrete stopover locations prior to long, direct journeys will benefit from conservation in discrete locations that are used for fuelling (Zhang *et al.*, 2021). Meanwhile, short-hop ('income') migrants, which don't carry large fat reserves and rely on multiple refuelling sites along the journey, are likely to benefit from broader-scale conservation strategies that increase the probability of birds finding good quality habitat and sufficient fuel along the migration route (Evans and Bearhop, 2022).

The spotted flycatcher (*Muscicapa striata*) is a migratory species in need of urgent conservation action, having declined by 93% in the UK since 1969 (BTO, 2024), and by 56% more widely in Europe since 1980 (PECBMS, 2025). The causes of this decline remain uncertain, and drivers may exist across the entire range from Europe to southern Africa (Cramp and Perrins, 1993). As with many other migratory species, the majority of research to date has investigated drivers of decline on the breeding grounds, with nest predation being highlighted as a potentially important factor in the UK (Stoate and Szczur, 2006; Stevens *et al.*, 2007, 2010). In addition, using an integrated population model, Freeman and Crick (2003) suggested that post-fledging mortality could have driven the negative UK population trends. This mortality could occur on the breeding grounds, during migration or on the wintering grounds. Given that the UK's spotted flycatchers have been declining for over half a century (BTO, 2024), it is likely that multiple factors have contributed, either synchronously or at different periods.

Our ability to assess potential drivers of population trends outside of the breeding grounds is limited by the lack of detailed descriptions of the migratory route of spotted flycatchers. Much of the research so far, on spotted flycatchers and other small migratory passerines, has been based on light-level geolocation. Light-level geolocators fitted to birds measure light intensity at fixed time intervals, which can later be related to local twilight times and used to estimate the longitude and latitude of stationary periods (Lisovski *et al.*, 2012). This method is of limited use during the peak of most species' migration (e.g. Burgess et al., 2022), as during the equinox there is insufficient latitudinal variation in sunrise and sunset times. The accuracy of light-level geolocation can also vary depending on species-specific behaviour, as weather, vegetation and topography influence the intensity of light recorded and consequently the precision of estimations (Lisovski *et al.*, 2012). Moreover, many passerines migrate at night, and so the timing of flights can only be estimated for flights lasting longer than the whole night.

Multi-species and multi-population light-level tracking studies that include spotted flycatchers have presented a western migration route similar to many other Afro-Palearctic migrants breeding in western Europe (Jiguet *et al.*, 2019a; Baudrin, 2024; Dufour *et al.*, 2024). However, these studies lack detailed descriptions of individual routes, and the limited spatio-temporal resolution provides little insight into the underlying migration strategies or the specific stopover sites used along the route. Spotted flycatchers are unusual among migrants in that they do not appear to build up large fat reserves before migration; while many migrant species were caught in the Sahara desert with elevated body masses during autumn migration, spotted flycatchers were recorded at weights similar to those during the breeding season (Bairlein, 1992). Consequently, it was previously assumed that spotted flycatchers undertook a short-hop migration, making use of oases within the Sahara for frequent refuelling (Biebach, 1985; Bairlein, 1992), but no tracking studies have confirmed this. Instead, light-level tracking has recently unveiled that most individuals undertook long-haul flights over the Sahara during spring migration (Jiguet *et al.*, 2019a; Dufour *et al.*, 2024), suggesting that their migration strategy may be adaptable.

More recently, multi-sensor loggers containing barometers, accelerometers and light sensors have been used to investigate breeding behaviour, flight timings, migratory strategies and stopover locations of several migratory species (Lathouwers *et al.*, 2022; Nussbaumer *et al.*, 2023a; Rime *et al.*, 2023; Jiguet *et al.*, 2025). This method allows greater spatio-temporal resolution, by accurately recording the movement of species (acceleration data) and aligning the pressure data recorded by the tags with global atmospheric datasets (Nussbaumer *et al.*, 2023b). In this study, we utilise multi-sensor loggers (MGLS) and light-level geolocators (GLS) to reconstruct and describe in detail the migratory route of spotted flycatchers breeding in the UK for the first time. A small sample of retrieved MGLS tags allowed us to use this high-resolution data to validate and complement the trajectories reconstructed from light-level data, whilst providing additional information beyond the resolution of light-level analyses. Overall, we aimed to generate novel information on the spotted flycatcher's migration strategy, stopover locations, timing of migration, the routes taken and the difference between autumn and spring migrations.

5.3. Methods

5.3.1. Multi-sensor geolocator deployment

Multi-sensor geolocators (Migrate Technology Ltd, model CARP30Z11-DIP; weight 0.44g) were fitted to spotted flycatchers in Sedbergh, England (54.323559, -2.528300) in 2023 using leg loop harnesses (total weight 0.48g). These recorded maximum light every 5 minutes and pressure, temperature and acceleration every 20 minutes. Birds were captured at their breeding territories to ensure maximum chance of retrieval, as this species frequently returns to the same breeding site each year. Birds were captured using mist nets, spring-loaded perch traps and, in some cases, sound lures. All captured birds were fitted with a British Trust for Ornithology (BTO) metal ring and a unique combination of two anodised metal colour rings. Of 37 birds captured in 2023, 20 were fitted with geolocators, whilst the other 16 were fitted with colour rings, but no tags, to serve as a control group. The average body mass of captured birds was 15.1 ± 1.1 g SD. Search effort at all sites remained consistent in 2024 allowing comparison of return rates between control and tagged birds. Three of the 17 control birds were resighted in 2024, whilst 7 of 20 tagged birds were resighted, suggesting that tag deployment did not have a negative impact on spotted flycatcher survival. We recaptured four of the tagged birds, whilst the other three were either never resighted a second time (n = 1) or nests failed and adults could not be relocated (n = 2).

5.3.2. Multi-sensor geolocator data analysis

We used the package *GeoPressureR* V3.3.4 (Nussbaumer and Gravey, 2022) in R V4.3.1 (R Core Team, 2020) to follow steps outlined in the *GeoPressure manual* (Nussbaumer and Nussbaumer, 2024) to reconstruct the trajectories of birds carrying MGLS tags. Here, we outline the main steps of the method, and readers are directed to Nussbaumer et al. (2023a, 2023b) for more detail about the implementation.

First, accelerometer and pressure data were used to manually label stationary periods and periods of flight for each bird. Stationary periods were characterised by relatively stable pressure measurements and sporadic but short bouts of activity. Migratory flights were characterised by sharp reductions in pressure, relating to the change in altitude associated with migratory flights, and consistently high acceleration readings. Pressure timeseries of stationary periods were then matched to the hourly 0.5 x 0.5° resolution ERA5 surface level pressure dataset (Copernicus Climate Change Service, 2023) to produce a probability map of the birds position. We then created a probability map based on light data using the threshold method, based on the distribution of zenith angle of all twilights recorded during a calibration period of known locations (i.e. locations of tag deployment and retrieval, see Nussbaumer et al., 2023a). Finally, each bird's trajectory was constructed following the Hidden Markov Model (HMM) presented in Nussbaumer et al. (2023b). The observation model within the HMM, which defines the likelihood of observing a measurement at a given position, used the likelihood maps constructed using pressure and light data. The movement model, which defines the probability that a bird was able to fly the distance between two consecutive stationary points, utilised data on flight duration (defined during labelling, based on pressure and acceleration data). The parametric equation of movement was based on groundspeed and was defined as the cubic root of the mechanical power required for the average groundspeed calculated for each transition, accounting for the average size and shape of a spotted flycatcher. We fixed the same probability of groundspeed to 15 km/h to account for short local/exploratory flights. Using this model, we generated for all stationary periods over 14 hours (1) the most likely trajectory i.e. the set of positions that maximise the joint probability of the trajectory, (2) the marginal probability map corresponding to the marginal distribution of the HMM, and (3) 100 simulations of the trajectory. To measure the extent of detours, we first generated the great circle distance (shortest route) between the breeding and the wintering grounds (the longest stationary period in Africa). We then generated the distance travelled as the cumulative distance between stationary periods lasting longer than 0.9 days from the most likely trajectory. Detour distance was calculated as the difference between the distance travelled and the great circle distance. Values presented are mean ± standard deviation (SD) unless otherwise stated.

5.3.3. Light-level geolocator deployment

Light-level geolocators were deployed at various locations in two regions of England: 38 in eastern England (Cambridgeshire, where the species is declining) and 43 in southwest England (Devon, where the population trend is more positive) during 2016 and 2018, with a respective 15 and 16 of these being recaptured in a subsequent year. An additional 20 birds were tagged in Devon only in 2019, with 5 being recaptured the following year.

Thirty-five control birds were caught and fitted with metal rings but not tagged in both Cambridgeshire and Devon across 2016 and 2018, with 15 and 13, respectively, being sighted or trapped in a subsequent year. Three of 20 control birds marked in Devon in 2019 were resighted or recaptured the following year. Each bird received either a red or blue anodised metal BTO ring identifying birds belonging to the tagged and control cohorts. In 2016, we deployed Migrate Technology Intigeo-W30Z11-DIP geolocators weighing 0.36 g including harnesses, but the data quality from these light-stalkless tags was insufficient for analysis in FlightR (Rakhimberdiev *et al.*, 2017), which was necessary due to the migration strategy the birds employed. Consequently, only data from light-stalked tags deployed in 2018–19 were used. These were Migrate Technology P30Z11-7-dip weighing 0.4g including the harness, which amounted to 2.5–3.13% of the birds' body weight (average mass14.3g). Across all years and sites, the return rates of tagged birds (38%) versus control birds (40%) indicated no negative impacts of tag deployment on survival.

5.3.4. Light-level geolocator analysis

The trajectories of light-level tags were calculated using twilight times inferred using the threshold method (Lisovski and Hahn, 2012) and calibration periods defined from known locations. The FLightR package was then used to reconstruct the trajectory of the tags (Rakhimberdiev *et al.*, 2017); see Baudrin (2024) for a full description of the methods used. Trajectories were successfully constructed for 15 of the retrieved tags. We used the median estimated locations for stationary periods of at least 1.5 days using a minimum 0.1 probability of movement. The distance between each successive movement and the cumulative distance of each migration was also calculated. Complete autumn migration was estimated for all tags, though two tags were excluded from distance comparisons due to spurious longitudinal movements likely caused by geolocation error. Full spring migration was estimated for three tags, but only two were used for distance calculations due to spurious longitudinal movements estimated for one tag. Stopover sites were initially categorised as breeding (> 49 ° N), wintering (minimum latitude) and migration (any stops between the breeding and wintering site). However, some trajectories included multiple long (> 20 days) stopovers in southern Africa and so all stopovers over 40 days that were initially categorised as migratory were categorised as wintering locations.

The performance of light-level geolocators was compared with MGLS tags using non-parametric Mann-Whitney tests. We tested for statistical differences between the estimated number of days taken to carry out migration, number of stops taken from the breeding to wintering grounds, duration of stops, distance between estimated stop locations and total distance travelled from breeding site to first wintering site.

5.4. Results

5.4.1. Migration trajectory: stopovers and timings (MGLS tags)

All four retrieved MGLS tags recorded data for the entire annual cycle and were used for estimation of stopover locations from June 2023 to June 2024 (Fig. 5.1). Three spotted flycatchers departed their breeding sites in late August and the other departed on the 3rd of August 2023. All birds carried out an intermittent autumn migration, moving in a south-westerly direction through France, Spain and Portugal before taking longer flights to reach Mauritania and Senegal. Most birds appeared to then track the southern coast of west Africa until they reached Nigeria. One bird (CM546; Fig. 5.1) appeared to take a more direct, inland route from Mauritania/Senegal to Nigeria. From Nigeria, all birds followed the western coast down into Angola, where they stayed for 17–38 days before heading into Namibia. Departure time from this extended stopover took place between the 18th of November and the 3rd of December, and arrival into the wintering grounds in Namibia occurred between the 30th of November and the 6th of December. The birds utilised a clear wintering location in northern Namibia, where they remained for between 105 and 111 days.

Spring migration was initiated between the 17th and 23rd of March 2024, and had a similar trajectory to the route taken in autumn, but with different stopover locations. In West Africa, birds stopped in Liberia, Sierra Leone and Guinea before taking an easterly shortcut directly over the Sahara Desert (Fig. 5.1). Crossing of the Sahara Desert was relatively synchronous between 3 birds, which departed between the 11th and 12th of May, whereas the other bird departed earlier on the 25th of April (CM557; Fig. 5.1). All birds stopped in the Atlas Mountains following the Sahara crossing, before proceeding into Portugal or Spain (Fig. 5.1). The return journey through France and across the English Channel closely resembled the autumn route in reverse (Fig. 5.1).

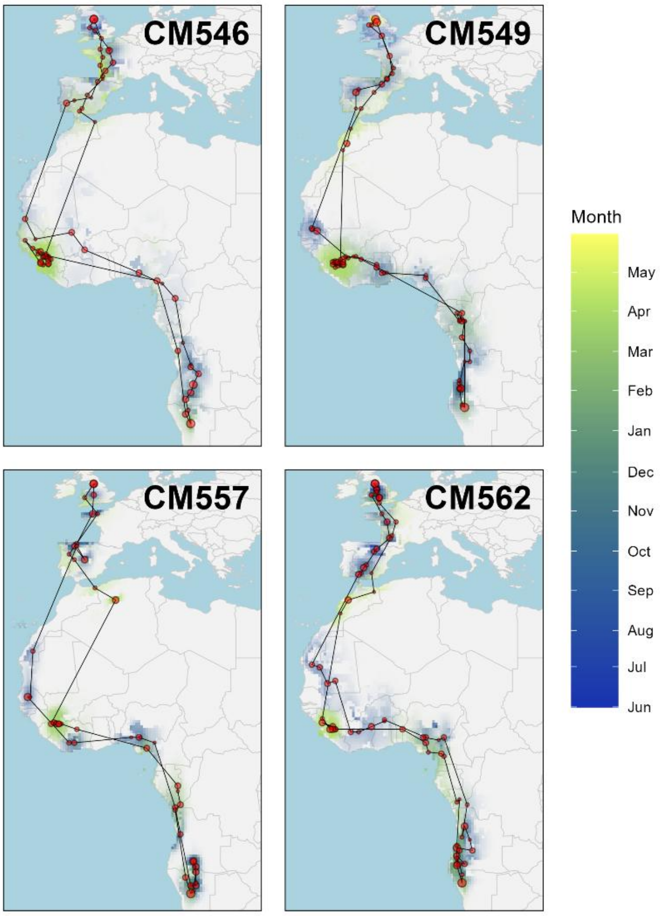


Figure 5.1. Median latitude and longitude of 100 simulated trajectories and stopover locations of spotted flycatchers tracked using multi-sensor geolocators in Cumbria, UK. Point size represents the logged duration of each stopover. Shading opacity represents the marginal probability of each bird's position, and the colour represents the time of the year, with autumn migration in blue and spring migration in green.

5.4.2. Migration strategy: number of stops, flights and detour extent (MGLS tags)

The number and duration of stops and flights in each season are summarised in Table 5.1. The number of stopovers over 24 hours ranged from 10 to 25. Autumn migration took longer than spring migration (106 vs 63 days), and took more stops to complete (Table 5.1, Fig. 5.2). Refuelling stops in spring were shorter than autumn, resulting in the birds spending less than half the time refuelling during spring than they did in autumn (Table 5.1, Fig. 5.2).

Variation in flight distance was high in both seasons (Table 5.1). Spring migration took slightly fewer flights than autumn, but these flights were longer and covered greater distances (Table 5.1), including a non-stop flight of 40–45 hours over the Sahara Desert. In autumn, almost all flights were initiated after 17:55 UTC (median 19:30 UTC) and lasted between 1 and 21 hours (Table 5.1, Fig. 5.3). Most flights ended early in the morning (median 04:19 UTC) but a few continued into the day during the Sahara crossing (Fig. 5.3). Spring departure and take off times were similar to autumn (median take off 19:46 UTC, median landing 04:47 UTC), although one bird was recorded initiating a 10.7 hour flight at 12:17 UTC (Fig. 5.3). This flight took place south of the Sahara but was not immediately before or after the Sahara crossing (start: 7.75 ° N, 13.25 ° W, end: 9.75 ° N 10.75 ° W) i.e. it was not a flight following a short rest stop where the bird may have been grounded.

Table 5.1. Summary of the number, duration and length of stopovers and flights recorded for spotted flycatchers equipped with multi-sensor (MGLS) and light-level (GLS) geolocators in England. Flight metrics are calculated using accelerometer data and so are presented for MGLS tags only.

	Autumn		**Spring**	
	MGLS	**GLS**	**MGLS**	**GLS**
No. stops†	17 (6)	6.7 (1.4)	9.5 (0.6)	8.3 (1.5)
Total time spent at stopovers (days) †	77 (9)	44 (13)	26 (6)	38 (15)
Avg. stop duration (days) †	4.5 (6.7)	7.0 (4.8)	2.8 (1.2)	4.3 (0.9)
Total duration (days)	106 (9)	61 (14)	63 (8)	68 (22)
Avg. distance between stops (km)	676 (648)	977 (705)	983 (1126)	1230 (544)
Avg. flight duration (hrs)	7.7 (3.6)	NA	8.6 (6.3)	NA
No. migratory flights	43 (4.3)	NA	38 (6)	NA
Great circle distance (km)	8479 (169)	7943 (849)	8479 (169)	7943 (849)
Total distance travelled (km)	12162 (835)	10612 (973)	11336 (325)	10605 (399)
Detour distance (km)	3682 (785)	2596 (754)	2857 (413)	2335 (9)

†Includes stops > 24 hours for MGLS and >36 hours for GLS

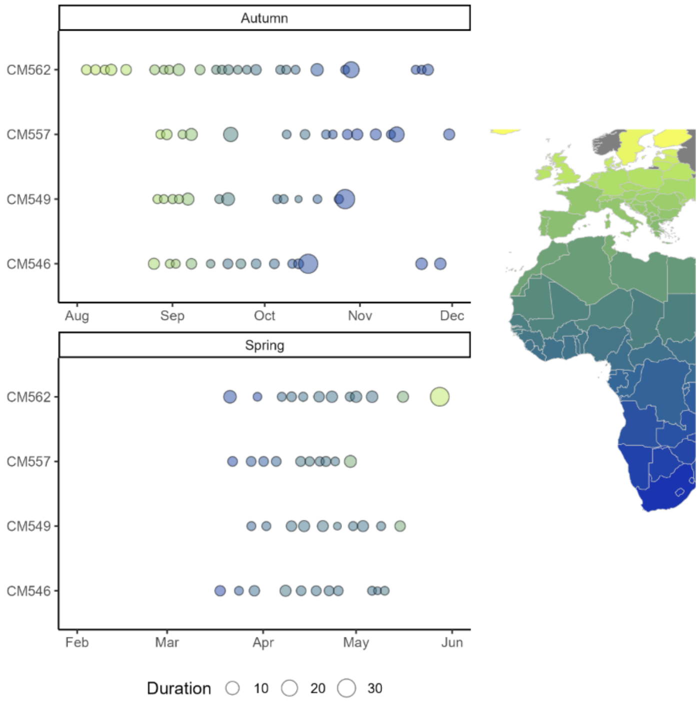


Figure 5.2. Stopover duration and timing of spotted flycatchers tracked using multi-sensor geolocators in Cumbria, UK. Points are located at the start of each stationary period and their size represents the duration of the stopover. Colours represent latitude as shown on the map. Only stopovers over 24 hours have been included and breeding and wintering residences are not shown.

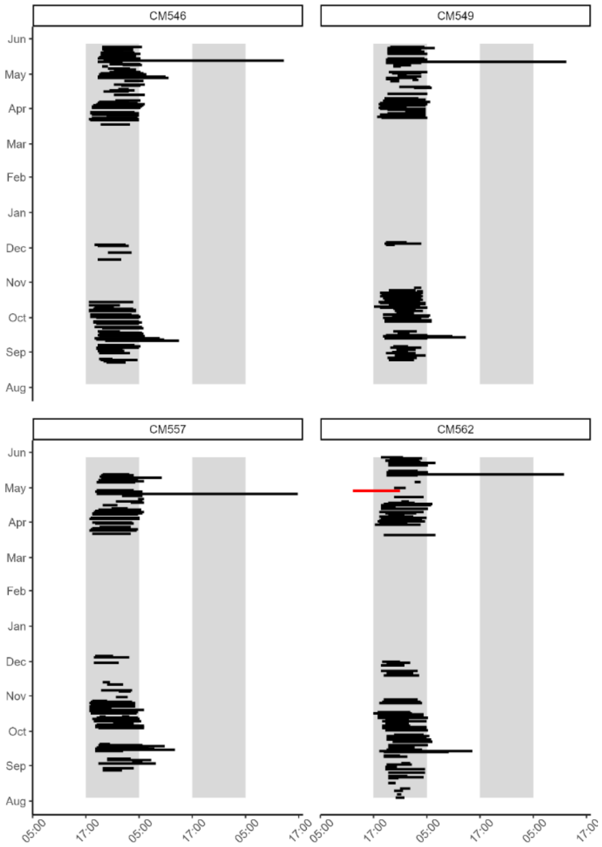


Figure 5.3. Diurnal pattern of flight activity over the year based on accelerometer data from spotted flycatchers tagged with multi-sensor geolocators in Cumbria, UK. Grey shading represents night (17:00 to 05:00 UTC). Red line in data for tag CM562 highlights single flight initiated during the day.

Birds deviated west of the great circle route in both seasons (Table 5.1, Fig. 5.4), adding 2791–4564 km to the great circle route in autumn and 2452–3418 km in spring. Detour distance was less in spring than in autumn for all but one MGLS tagged bird, which travelled 88 km further in spring (CM549; Fig. 5.1).

5.4.3. Trajectory validation and comparison using GLS tags

Trajectories constructed using the light-only geolocators were similar to those constructed using pressure data (Fig. 5.4), albeit simplified in comparison as stationary periods were limited to a minimum of 1.5 days. Variation in departure from the breeding grounds was slightly larger for GLS tagged birds (SD 14 days), though most departed in either late August or early September (median: 23rd August, range: 20th July–10th September).

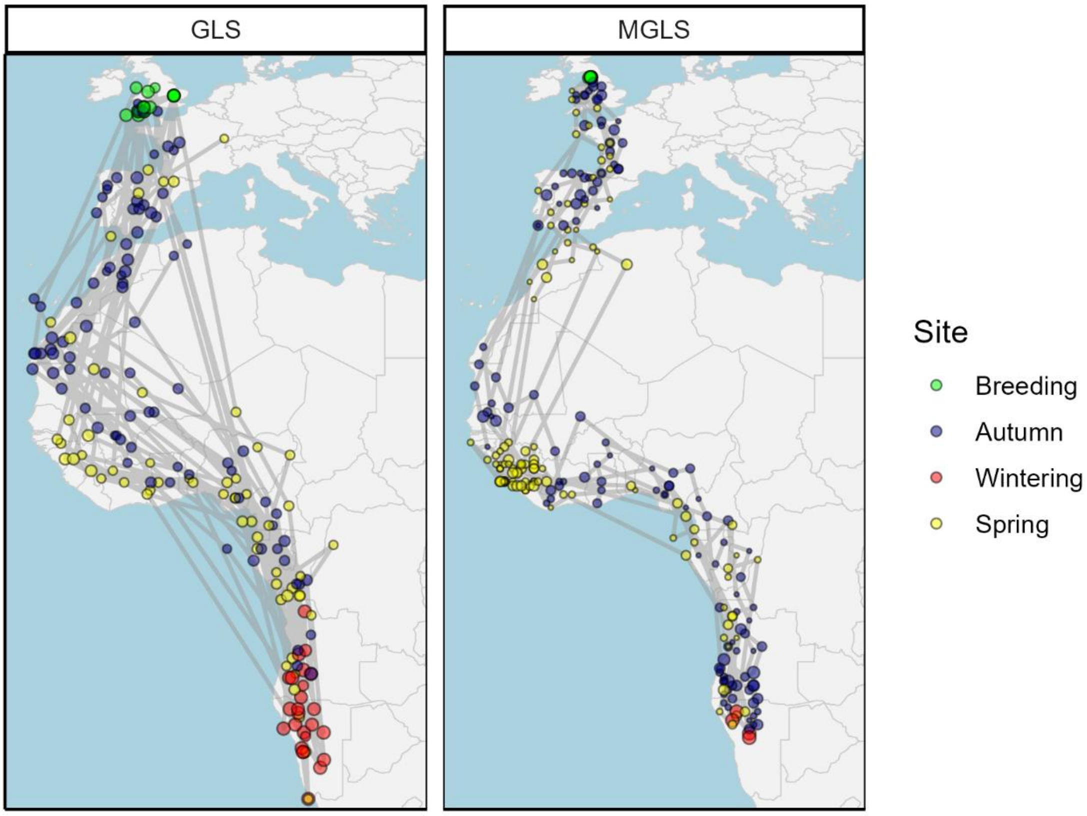


Figure 5.4. Trajectories and stopovers of spotted flycatchers tracked using light (GLS, left panel) and multi-sensor geolocators (MGLS, right panel) in the UK. Point size represents the logged duration of the stationary period, which is a minimum of 1.5 days for GLS tracks and 14 hours for MGLS tracks. GLS trajectories represent the median of the estimated latitude and longitude of staging sites, whilst MGLS trajectories represent the most likely path (see methods for full details).

Arrival at the wintering grounds was earlier than for MGLS tags and ranged between the 11th of October and the 1st of January (median 28th October, SD 76 days). Median wintering latitude and longitude did not differ significantly from those estimated for MGLS-tagged birds (Fig. 5.4). The duration of autumn migration was shorter than for MGLS tagged birds ($Z = -3.3519$, $p < 0.001$; Fig. 5.5a) and comprised significantly fewer stopovers than were recorded by MGLS tags ($Z = -3.4397$, $p < 0.001$; Fig. 5.5b). The average time spent at stopovers was significantly longer than was recorded for MGLS tags ($Z = 2.1349$, $p = 0.033$; Fig. 5.5c), and the distance between stopovers was significantly longer ($Z = 2.504$, $p = 0.008$; Fig. 5.5d).

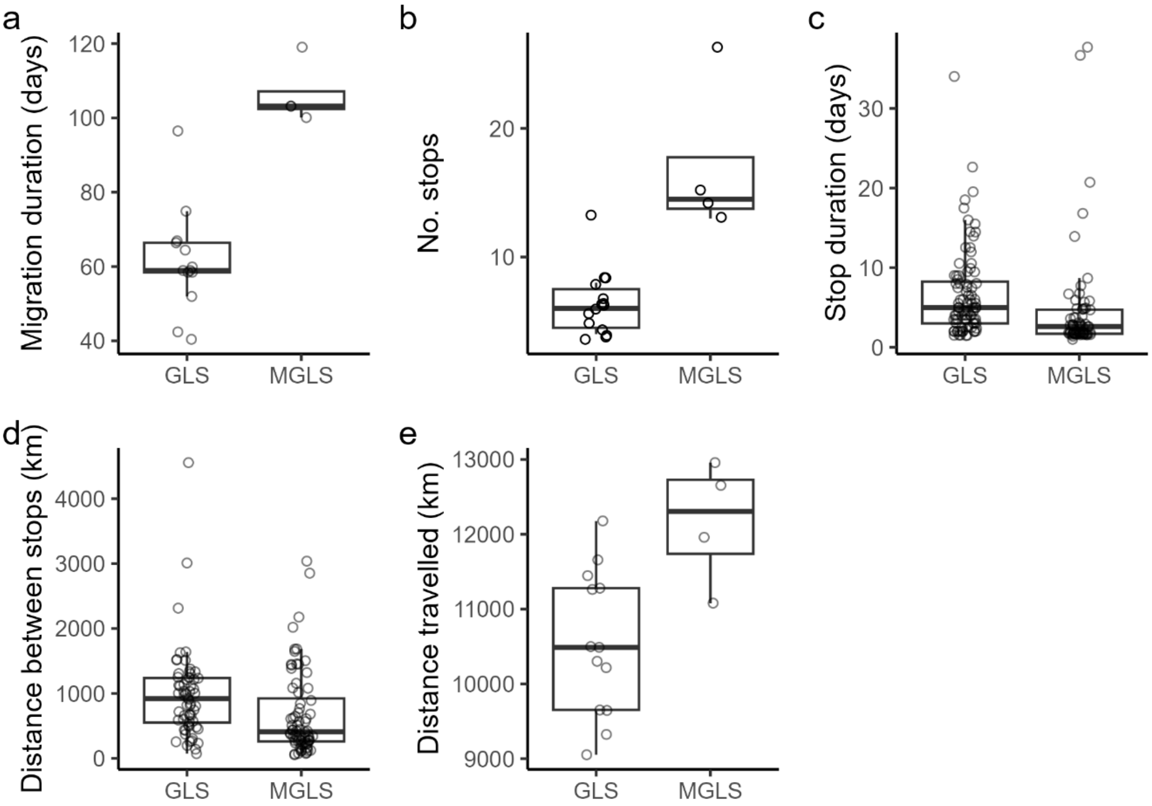


Figure 5.5. Comparison of autumn migration between light only geolocators (GLS) and multi-sensor geolocators (MGLS) fitted to spotted flycatchers in England. The number of days taken (a), the number of stops taken (b), the duration of stops (c), distance between estimated stop locations (d) and total distance travelled from breeding site to first wintering site (e). Wintering site is defined as sites used for >40 days (excluding breeding grounds) for GLS and the site with the longest stationary duration for MGLS.

We excluded three light-only GLS tags from distance calculations due to unrealistic reconstructed longitudinal movements. Stopover duration was on average 6 days shorter than in autumn, but the total average duration for migration was slightly longer than autumn (Table 5.1). The great circle distance between breeding sites and the final wintering residence was longer for MGLS than GLS tags (Table 5.1), reflecting the c.250 km distance between breeding sites in northwest England and Cambridgeshire/Devon. The total distance travelled in autumn was significantly longer for MGLS tagged birds ($Z = -2.454$, $p = 0.010$; fig. 5.5e). Only 3 GLS tags could be used to reconstruct the trajectory of the full spring migration and so no statistical comparisons were made between tag types. Spring migration was initiated between the 9th of February and the 4th of April (median 25th March, SD 28 days). Arrival back into the UK took place between the 1st and 19th of May (median 16th May, SD 10 days). Both GLS tagged birds included in the spring distance calculations recorded journeys at least 700 km shorter in spring than in autumn.

5.5. Discussion

In this study we aimed to reconstruct the detailed spatio-temporal aspects of the migration of spotted flycatchers using data from multi-sensor and light-level geolocators. We confirmed that the UK population of the species utilises a short-hop, itinerant strategy throughout most of the migration, with the exception of the Sahara Desert crossing, when birds carry out longer flights. Activity data allowed reconstruction of movements at an unprecedented high temporal resolution, revealing the precise (± 20 min) timing of key events such as Sahara crossings and the arrivals and departures to and from wintering and breeding grounds. Notably, we identified a period of prolonged residency at the wintering site that was previously undocumented. Comparison of MGLS data with GLS data showed a broad spatial concordance, while also demonstrating the clear advantage of MGLS in capturing higher spatial and exceptionally high temporal resolution. Estimating stopovers of less than 24 hours allowed us to reduce the gaps between known locations, leading to a more accurate and detailed depiction of the migration route.

The discovery that short-hop migration is the dominant strategy used by spotted flycatchers validates previous assumptions based on limited migratory fuelling (Bairlein, 1992), and may be related to flight energetics. Flight is more energetically expensive at greater mass (Lindstrom and Alerstam, 1992; Klaassen and Lindström, 1996), and lighter birds are able to take-off more quickly than heavier birds (Kullberg *et al.*, 2002; Forrester and Martin, 2025). This may be particularly relevant for spotted flycatchers, whose foraging success is likely to decline with increased mass, as foraging involves repeatedly taking off explosively from perches in pursuit of aerial insects. Moreover, conversion of protein-rich insects to fat stores for endurance flights is a costly process (Jenni-Eiermann and Jenni, 2025), and so short-hop migration is likely the most functionally advantageous strategy for spotted flycatchers.

All four spotted flycatchers equipped with multi-sensor loggers in our study carried out flights exceeding 40 hours during the spring Sahara crossing and flights exceeding one night during autumn (Fig. 5.3), consistent with findings from other studies (Jiguet *et al.*, 2019a; Dufour *et al.*, 2024), the former including some data from light-level GLS which is presented here. While these results confirm the species' capacity for sustained flight, they contrast with its typical short-hop migration strategy and insectivorous diet (Jenni-Eiermann and Jenni, 2025). Most long-distance migrants rely on fruit-rich diets before long flights to maximise fat stores and support metabolic shifts that prioritise flight over digestion (Hume and Biebach, 1996; Jenni-Eiermann and Jenni, 2025). Although spotted flycatchers have been observed consuming berries during autumn migration (Hernández, 2009), Biebach (1985) found that autumn migrants carried similar body mass to individuals on the breeding grounds, indicating limited pre-migratory fat deposition. However, observations of higher body mass in spring suggest that fuelling strategies may vary seasonally (Moreau and Dolp, 1970). MGLS data in our study showed no evidence of extended stopovers pre- or post-Sahara crossing, as stopover durations were comparable to those throughout the rest of the spring migration (max 6.7 days near the Sahara vs. max 8.4 days in the spring). This discrepancy highlights the need for further field observations, particularly during spring migration, to better understand the physiological and behavioural adaptations that support barrier crossings in this species.

Ensuring sufficient resources during migration may explain the species' choice of migratory routes and timing. An extensive western detour was observed in both seasons in birds tracked with both light- and multi-sensor geolocators, increasing the overall distance between breeding and wintering grounds. Such detours are typically favoured when fuelling opportunities are better along the longer route or when time constraints are relaxed (Alerstam, 2001). In autumn, the absence of time pressure to reach the breeding grounds and availability of better quality habitat along the West African coast may explain the preference for this route. In spring, however, time pressure to reach the breeding grounds often leads to shorter or faster migrations (Nilsson *et al.*, 2013). Accordingly, spotted flycatchers in our study reduced their spring migration duration by approximately 40%, primarily by shortening stopovers. Interestingly, the direct Sahara crossing in spring reduced the total distance by only ~7%, suggesting that time minimisation alone does not explain the long non-stop flights observed. This raises the question as to why energetically demanding non-stop flights are favoured in spring but not autumn, which may be related to seasonal differences in food availability or wind patterns (Schmaljohann *et al.*, 2009; Mondain-Monval *et al.*, 2024).

The trajectory taken by spotted flycatchers suggests that the birds track rain, and the food availability that it provides, in short hops along the western edge of Africa and then into southern Africa, where rain peaks between January and March (Dunning *et al.*, 2016). The reliance of migratory birds on rainfall and water availability is demonstrated by the rapid decline of Afro-Palearctic migrants following drought in the Sahel region, which was not restricted to species typically associated with aquatic habitats or birds overwintering in that region (Hewson and Noble, 2009; Ockendon *et al.*, 2014; Zwarts *et al.*, 2023). Rainfall drives food availability via vegetation productivity, but this link is increasingly vulnerable to shifts in climatic patterns, habitat modification and water extraction, particularly in semi-arid regions such as the Sahel (Thorup *et al.*, 2017; Telenský *et al.*, 2020; Robertson *et al.*, 2024).

Our ability to investigate how climate change and land use have influenced the temporal and spatial availability of good quality habitats for Afro-Palearctic migrants has been limited by the coarse resolution of previous tracking studies (Vickery *et al.*, 2023). Our study provides the temporal and spatial resolution necessary to begin linking migratory behaviour and population trends with finer resolution land use and climate data. For example, prior to crossing the Sahara Desert, all of our MGLS-tagged birds spent time in Guinea, Sierra Leone and Liberia. These areas are under increasing pressure from anthropogenic activities in these regions, such as deforestation, which has potential to modify the water regime by reducing rainfall (Duku and Hein, 2021). Given the role of water and aquatic systems in supplementing food during breeding (Chapter 4, Twining *et al.*, 2018b) and migration (Weber, 2009), future research should focus on how the availability of these resources is changing, and how such changes may have influenced population trends over time.

Reliable and frequently distributed food sources are vital for short-hop migrants, such as spotted flycatchers, which may arrive at stopover sites with insufficient fuel reserves to continue onward migration. When high quality habitats are sparsely distributed, or their quality has recently changed, birds may arrive at poor quality sites where mortality risk is high (Oppel *et al.*, 2015). Such risk may be even greater for juveniles migrating independently with no prior migration experience (Cresswell, 2014), and could be linked to the suggestion that post-fledging mortality might explain the decline in spotted flycatchers (Freeman and Crick, 2003). Hence, our findings reinforce the need for broad-scale, landscape-level conservation strategies that maintain resource availability across migratory routes, rather than focusing solely on discrete protected areas. Understanding how this can be achieved whilst balancing the needs of communities reliant on the land should be a conservation priority.

Our comparison of multi-sensor and light-level tags highlights the substantial benefits of incorporating additional sensors for tracking small migratory birds. While both tags revealed broadly similar migration routes, MGLS provided significantly higher spatio-temporal resolution. Pressure data enabled reconstruction of much shorter stationary periods, allowing for a more detailed reconstruction of trajectories and stopover behaviour. Accelerometer data greatly improved confidence in the timing of movements, enabling precise estimates of departure and arrival times. This improved resolution has important ecological implications. For instance, light-only tags recorded several extended stopovers in Namibia and Angola but did not clearly identify a single wintering site (Fig. 5.4). In contrast, MGLS data revealed a distinct, prolonged winter residency, as well as a separate extended stopover prior to arrival at the wintering grounds. These differences are likely artefacts in GLS data caused by variable shading conditions at the wintering site being misinterpreted as different sunrise/sunset times, which can lead to the estimation of multiple stationary periods. Without accelerometer data, it would have been possible to misinterpret the birds' winter behaviour as continuous resource tracking, which is seen in other species (Norevik *et al.*, 2019). These findings underscore the value of multi-sensor tags for studies of migratory phenology and habitat use. By providing a more accurate picture of where birds are and when they are there, MGLS technology enables more informed conservation planning, particularly in identifying critical stopover and wintering sites.

5.6. Conclusions

Our study provides new, detailed insight into the migratory behaviour of the spotted flycatcher and highlights the benefit of using multi-sensor geolocators to record migration in smaller passerines. We clearly demonstrate that this species adopts a short-hop strategy to undertake an exceptionally long-distance migration, extending the distance further by taking an extensive detour in both seasons. The extensive detour is presumably driven by the need for a frequent distribution of good quality habitats, emphasising that broad conservation initiatives across West Africa and southern Europe are most likely to benefit this species. Moreover, our results reveal that spotted flycatchers spend approximately half of their lifetime on migration, emphasising the importance of understanding this period of the annual cycle. Our detailed presentation of the stopovers used by this species provides the basis for future studies, such as those combining high resolution land use and climate data to understand drivers of population change.

Chapter 6 General discussion and conclusions

6.1. Summary of thesis aims

Despite a 93% decline in the UK since 1967, we have limited knowledge of the ecology of spotted flycatchers and the factors affecting their population trends. Multiple factors are likely to have contributed to the population trends of this, and other, Afro-Palearctic migrants, and these factors may have varied throughout the period of decline. A few autecological studies exist from southern and central England, conducted over a decade ago (Kirby *et al.*, 2005; Stoate and Szczur, 2006; Stevens *et al.*, 2007), but the relevance of the findings to other regions is unclear. Additionally, a lack of understanding about the non-breeding season of this species severely limits our ability to infer potential factors related to migration or the wintering grounds, despite repeated calls for greater focus on this period to better understand migrant population trends (Marcacci *et al.*, 2023; Vickery *et al.*, 2023). Recent studies have emphasised the importance of aquatic habitats and the nutritional subsidies they provide as valuable resources for terrestrial birds (Bennett *et al.*, 2014; Lewis-Phillips *et al.*, 2020; Berzins *et al.*, 2022), an emerging area of research that may be particularly relevant for declining insectivorous migrants in light of global reductions in terrestrial insect populations (van Klink *et al.*, 2020). Hence, the aim of this thesis was to update and broaden the knowledge surrounding this species, with the hope of identifying factors that could be used to inform conservation. We aimed to reveal how spotted flycatchers interact with aquatic and terrestrial habitats at a national and local scale, and the potential implications. We also aimed to reveal the movements of spotted flycatchers outside of the breeding season, as descriptions of the species' non-breeding behaviour are currently limited to a few observational studies and ring recoveries (e.g. Biebach, 1985; Hernández, 2009).

6.2. Discussion of key findings

6.2.1. Terrestrial habitat characteristics related to spotted flycatcher distribution and breeding success

Until now, most research on the habitat associations of spotted flycatchers has been limited to multi-species or local-scale studies. However, the distribution and densities of spotted flycatchers is not uniform across the UK, suggesting that geographic variation in land cover types or climate may be related to variation in occupancy. In Chapter 2, we found that distribution change was associated with changes in land use between 1990 and 2010 (Figs. 2.2–2.3). Several land cover types were associated with the distribution and distribution change of spotted flycatchers, including woodland, farmland and urban cover (Figs. 2.1–2.3). Areas that were predominantly urban or had experienced increases in urban cover were less likely to have birds present and more likely to have lost them between the two time points. The unsuitability of these habitats for spotted flycatchers is most likely related to food availability, rather than human disturbance, as the species is well known for nesting around humans and anthropogenic structures (Clarke, 2005). The replacement of natural and semi-natural habitats with impervious surfaces and non-native plant and animal species leads to a dramatic reduction in biodiversity and abundance and, consequently, food availability for all but a few insectivorous species (Aronson *et al.*, 2014; Fenoglio *et al.*, 2021). With urban expansion inevitable due to human population growth, it is crucial to identify other valuable habitat types for insectivorous species so that these environments can be protected from urban development.

The distribution, colonisation and loss of spotted flycatchers were only weakly related to several terrestrial land cover types, emphasising the generalist nature of this species, despite it often being classified as a woodland specialist (Tables 2.1–2.2). Spotted flycatchers were less likely to colonise areas where broadleaved woodland had increased, and this result probably reflects the preference of this species for mature rather than new-growth trees. Woodland management has changed considerably over the last century, and the structure and composition of woodlands varies throughout the UK, making it difficult to generalise from such broad categorisations as broadleaved and coniferous woodland (Amar *et al.*, 2010). Nonetheless, woodland was associated with poor breeding success in one study (Stevens *et al.*, 2007), and similarly in Chapter 3, we found that spotted flycatchers were less likely to nest in areas with a high proportion of canopy cover (Fig. 3.1, Table 3.1), suggesting that woodland may actually be a poor habitat for this species.

Monitoring nests at our study site in Cumbria revealed extremely low densities of spotted flycatchers in woodland blocks, but a high affinity with trees. Mature trees in other habitats (e.g. riverbanks, roadsides, churchyards) were regularly used for nesting, demonstrating the importance of retaining mature trees outside of woodlands. In Chapter 3, we found that ivy on these trees (and some other structures) had potential to conceal nests from predators, and we highlight the potential for this plant to act as natural predator control. This has important management implications, as the killing and removal of ivy from trees is common practice in the UK, which appears primarily driven by a need for 'tidiness'. Authors from other countries call for ivy to be protected, due to its associations with food and shelter for several species (Kajtoch *et al.*, 2023). In the UK, where populations of some predator species are inflated (Roos *et al.*, 2018), ivy could provide vital refuge for open-cup nesting species with low nest survival rates.

6.2.2. Aquatic habitat characteristics related to spotted flycatcher distribution and breeding success

The importance of aquatic habitats for terrestrial species remains largely under-researched, but a few studies highlight the potential importance of these habitats for biodiversity (Bennett *et al.*, 2014; Lewis-Phillips *et al.*, 2020). Given global declines in insect populations, aquatic habitats may serve as important refugia, as the abundance of aquatic insects appears to be increasing (van Klink *et al.*, 2020). Aquatic insects are rich in omega-3 highly unsaturated fatty acids (HUFAs), which are rare in terrestrial environments but essential for key physiological functions such as tissue growth and brain function (Twining *et al.*, 2016a). Thus, aquatic habitats not only offer a greater abundance of food but also provide food of higher nutritional quality.

In Chapter 2, we revealed that spotted flycatcher distribution is related to river density on a national scale (Figs. 2.1–2.3). Areas with a higher density of rivers were more likely to have been colonised by spotted flycatchers and less likely to have lost them, concurring with previous studies that found higher biodiversity in riparian compared to terrestrial habitats (Bennett *et al.*, 2014). However, interpretation of these findings was limited by the coarse scale of the study (2 x 2 km squares). In Chapter 3, we demonstrated that this relationship was evident at a finer scale – nests in our study site were more likely to be found closer to a river (Table 3.1). In this study we found no evidence that river proximity was related to overall nest survival (i.e. the probability of fledging at least one chick), but in Chapter 4 we revealed that the concentration of HUFAs in chick and adult blood was positively related to body condition (Fig. 4.1). As chick body condition is positively related to post-fledging survival (Naef-Daenzer *et al.*, 2001), our results suggest that aquatic subsidies have potential to improve demographic rates. This study was the first to test the association of HUFA concentrations with body condition in a wild bird species, and our results support previous laboratory findings in other species (Twining *et al.*, 2016b).

Despite an apparent increase in aquatic insects, aquatic habitats are under threat from anthropogenic activities (van Rees *et al.*, 2021). Only 14% of rivers and 14% of lakes in England are classified as having good ecological status, largely due to physical modifications and the deposition of chemicals and nutrients from farms and urban areas (DEFRA, 2025a). Pollution of waterways leads to a change in aquatic community composition, for example, a shift from the dominance of large-bodied invertebrate groups (e.g. Plecoptera, Trichoptera) to small-bodied invertebrate groups (e.g. Nematocera) which are less strongly associated with aerial insectivores (Kraus *et al.*, 2014; Stenroth *et al.*, 2015; Larsen *et al.*, 2016; Manning and Sullivan, 2021). Climate change also has potential to alter the structure and function of aquatic communities, by increasing water temperature and modifying hydrological properties (Ledger *et al.*, 2013; Greenwood and Booker, 2016). Hence, our research reiterates the urgency to protect rivers and other waterways, which provide vital resources to humans, animals and plants.

6.2.3. Exposing the non-breeding movements of spotted flycatchers breeding in the UK

Limitations in tracking technologies have historically hindered our understanding of the non-breeding movements of several small passerine birds. Consequently, identifying the locations used by migratory birds during the non-breeding season is repeatedly highlighted as a research priority for declining populations (Marcacci *et al.*, 2023; Vickery *et al.*, 2023). Most of our knowledge of spotted flycatchers outside of the breeding grounds has been based on a few observational and ringing studies (Biebach, 1985; Bairlein, 1992; Hernández, 2009). Yet, due to the interrelation of different life stages, understanding where migratory species spend their time, and how they get there, is essential for developing effective conservation strategies (Evans and Bearhop, 2022; Marcacci *et al.*, 2023).

In Chapter 5, we revealed the detailed movements of spotted flycatchers throughout the full annual cycle for the first time. New tracking technologies allowed migration trajectories to be constructed at a relatively fine spatial resolution and an extremely fine temporal resolution. We were able to quantify the number and length of stops and flights, confirming that short-hop migration is the primary mode of travel, as was previously assumed (Biebach, 1985). However, we also revealed the species' flexibility in migration strategy by demonstrating that all tracked birds undertook long non-stop flights of 40–45 hours during the spring migration. Previous work led to the conclusion that spotted flycatchers were unique in their lack of pre-migratory fuelling (Biebach, 1985), but undertaking such a long continuous flight must require considerable amounts of energy, suggesting adaptability in their fuelling strategy. Most field observations are restricted to the autumn migration, but our findings reveal the need for more field studies aimed at elucidating the species' behaviour during spring migration, particularly the habitats used and the extent of pre-migratory fuelling undertaken.

We also demonstrated a substantial detour from the direct route between the UK and the wintering grounds in Namibia. In spring, spotted flycatchers travelled along the western edge of West Africa, east across the southern coast of West Africa and then south from Nigeria into Namibia (Fig. 5.1). This trajectory was reversed in autumn, although birds tended to stop in different locations between seasons. The detour likely reflects the species' need for regularly distributed patches of habitat with good food availability, which are more likely to occur along the coastal perimeter of West Africa than in the Sahara Desert. Our demonstration of seasonal variation in stopover locations has important implications for future research aiming to understand the relationship between migration and population trends. Overall, our findings highlight the need for broad-reaching conservation initiatives for this species, which is more likely to benefit from a greater continuity of high-quality habitat patches than from improvements to a few isolated sites.

6.3. Directions for future research

This thesis has advanced our understanding of spotted flycatcher ecology and highlighted the potential significance of aquatic habitats for this species. Nevertheless, the limited body of research on this species means that our knowledge remains incomplete. Many of our findings inspire new directions for future research, both on this species and on other insectivorous birds facing similar challenges.

6.3.1. Investigate the importance of aquatic subsidies at a larger scale

While our findings align with previous research emphasising the importance of aquatic subsidies for insectivorous bird species (Bennett *et al.*, 2014; Manning and Sullivan, 2021), the scale of the results makes it challenging to assess how access to these subsidies might influence national population trends. In the USA, the population trends of several aerial insectivore species were positively related to the abundance of emergent aquatic insects at the state-level (Manning and Sullivan, 2021), though species-specific responses introduce complexity. In the UK, national-scale data on aerial insect trends at the order level are unavailable, and so proxies must be used (e.g. river density, Chapter 2), which complicates interpretation. Therefore, future research should aim to upscale the field studies undertaken in Chapters 3 and 4 to a broader geographical scale, potentially incorporating population-level metrics alongside individual or nest-level trends. The high density of rivers within our study site meant that all nests were located within 300 m of a river, and the homogeneity of surrounding land cover limits our ability to assess variation between rivers. Consequently, expanding these studies to areas with greater variability in river proximity and adjacent land cover types would be valuable.

6.3.2. Assess the importance of alternative sources of aquatic insects

Whilst this thesis focuses on aquatic subsidies produced by rivers, it would be useful to expand this research from rivers to other aquatic features such as ponds. Tree swallow (*Tachycineta bicolor*) productivity was positively related to the abundance of ponds in an agricultural landscape in Canada (Berzins *et al.*, 2022), and restored agricultural ponds in the UK were associated with higher biodiversity than abandoned ponds (Lewis-Phillips *et al.*, 2020). The ability to add ponds to the landscape, as opposed to the impossibility of increasing the availability of rivers, makes it a feasible and attractive method to introduce high quality food into an insect depleted landscape. Initiatives currently underway in the UK to restore farmland ponds (e.g. https://norfolkponds.org/) offer an ideal field experiment to test the impact of pond availability and restoration on the population trends or demographic rates of insectivorous birds. Expanding this research to several species could also greatly enhance our understanding of which priority species might benefit from the availability of aquatic subsidies.

6.3.3. Investigate the importance of ivy as a natural nest protection measure

Improving the reproductive success of spotted flycatchers could have positive implications for population trends (Burgess *et al.*, 2025). Interventions to improve breeding success may be more feasible than targeting other demographic rates i.e. survival, particularly when there is clear spatial variation in productivity (Morrison *et al.*, 2022). Our study found similar nest survival rates and productivity estimates (e.g. clutch size) to other studies in the UK, suggesting low spatial variation in productivity. However, given the extent of decline in the UK compared to continental Europe, it is reasonable to assume that habitat quality across the UK may be poor for this species, and that population trends may be improved by enhancing productivity. This may be achieved by improving nest survival rates, which are heavily impacted by predation events (Chapter 3; Stoate and Szczur, 2006; Stevens et al., 2007). Lethal predator control is neither feasible nor ethical without a clear understanding of which specific predators are responsible for nest failure and whether predation is the primary driver of population declines. Therefore, non-lethal measures to protect nests from predators are a more appropriate and precautionary approach. Spotted flycatchers do not readily take up nest boxes, and those that do seem vulnerable to predation (Clarke, 2005), though this is likely dependent on the positioning and concealment of boxes. Cup-shaped artificial nests (or coconut shells) appear to be taken up more readily, and can be easily concealed in creeping plants, although the frequency of use in our study meant that it was not possible to test their impact on nest survival. Nest protection measures used for other open cup nesting species include placing fences or guards around ground and shrub nests (Major *et al.*, 2015; Gautschi *et al.*, 2024), but the accessibility of spotted flycatcher nests greatly reduces the practicality of these methods.

Our research highlighted the underappreciated potential for ivy and other creeping plants to provide valuable nest concealment from predators outside of gardens (Chapter 3), a finding that warrants further investigation. Creeping plants are frequently used as nest substrates by spotted flycatchers (Clarke, 2005; Kirby *et al.*, 2005), but the availability of this habitat may be at risk as ivy removal is commonplace in the UK. Future studies should aim to assess productivity across a range of sites, with a particular focus on comparing the success of nests concealed by ivy versus those that are exposed. Ivy removal could have negative implications for spotted flycatcher breeding success if it results in greater exposure to predators, and so understanding the importance of this resource could provide essential evidence to inform more effective habitat management practices that support the species' recovery.

6.3.4. Refine our understanding of the relationship between population trends and non-breeding habitat and climate.

Understanding how climate and land cover interact across the annual cycle to determine the productivity and survival of spotted flycatchers is critical in informing where conservation might be most effective. Previous studies have use remote sensing data to compare the impacts of land use and climate on Afro-Palearctic migrants (e.g. Howard et al., 2020), but their conclusions are constrained by limited knowledge of the birds' precise spatial and temporal distribution outside of the breeding season. Now that we have a clearer understanding of the spatio-temporal distribution of spotted flycatchers during the non-breeding season (Chapter 5), we have the necessary information to retest for climatic and land-related drivers of population trends. The reconstructed trajectories of spotted flycatchers may now also be used to determine the most appropriate locations for field work in Africa, which could be used to identify fine-scale priority habitats related to high-risk migratory movements i.e. crossing the Sahara Desert.

6.3.5. Investigate determinants of variation in population trends between continental Europe and the UK

Spotted flycatchers are declining at a slower rate in Europe than in the UK, and are of a more favourable conservation status (Birdlife International, 2021; BTO, 2024; PECBMS, 2025), suggesting that demographic rates may be lower for the UK population than those in other European countries. Understanding whether the factors affecting populations in continental Europe are the same as those in the UK would greatly enhance our knowledge of the most appropriate interventions, but no other European demographic rates have been published. Moreover, understanding the drivers of demographic rates in other European countries could help pinpoint the stage of the annual cycle that may have driven declines. Therefore, monitoring of spotted flycatcher nests across Europe should be encouraged, and could be achieved by collaborating with European institutions to improve inclusivity and strengthen knowledge exchange.

6.4. Overall conclusions

This study has demonstrated an apparent preference of spotted flycatchers for aquatic habitats, specifically rivers, which appears driven by the superior food quality in these environments. This study also provided the first detailed description of the species' migration route and timing, significantly advancing our understanding of its behaviour and distribution during the non-breeding season. Although we did not directly investigate drivers of population trends and so cannot infer specific causes of decline, we identified factors related to nest survival and productivity, which are directly linked to population dynamics. Indeed, multiple factors are likely contributing to the overall population trend, and conservation efforts may be more effectively directed toward identifying practical strategies to support population recovery, rather than focusing on historical causes of decline that may no longer be reversible within the timescale required to protect this species in the UK.

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