Ollscoil na hÉireann, Corcaigh

National University of Ireland, Cork

The spatial ecology and conservation of an important game bird in Ireland: the Eurasian woodcock

Thesis presented by

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for the degree of

Doctor of Philosophy

University College Cork

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April 2024

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Declaration

This is to certify that the work I am submitting is my own, was led by me, and has not been submitted for another degree, either at University College Cork or elsewhere. All external references and sources are clearly acknowledged and identified within the contents. I have read and understood the regulations of University College Cork concerning plagiarism and intellectual property.

Abstract

A wide range of species are targeted by human hunters, including those with uncertain or poor conservation status. However, the direct and indirect effects of this exploitation can be complex and are often poorly understood. The Eurasian woodcock (hereon woodcock) is a largely migratory ground-nesting bird in the family Scolopacidae associated with forested habitat, and is commonly hunted by humans across its European range. The direct and indirect effects of hunting on this species are generally poorly known, and it can be difficult to study owing to its elusive and crepuscular habits. On the island of Ireland, the woodcock population comprises both resident breeding birds and migratory overwintering birds which originate from areas such as Fennoscandia, the Baltic States and Russia. The breeding population is thought to have declined in recent decades, with available evidence suggesting a range contraction of over 70% between 1968 and 2011, whilst trends for migratory birds are unknown. However, the species is popular among hunters in Ireland, and no information exists as to how hunting activity affects its population or ecology.

To address these knowledge gaps, this research had four main objectives:

i. Establish an understanding of the current distribution and abundance of breeding woodcock in Ireland, and the environmental drivers that influence these, through a nationwide 'roding' survey from 2017 to 2021 and a two-step species distribution modelling (SDM) method.
ii. Explore whether hunting and bird age affected the survival of non-breeding woodcock using radiotelemetry to monitor the fates and activity of 168 tagged birds across three hunted and three not hunted sites.
iii. Explore whether hunting and bird age affected the use of space and movement ecology of non-breeding woodcock using global positioning system (GPS) tracking of 42 birds across three hunted and three not hunted sites.
iv. Assess woodcock habitat preferences in the context of heterogenous Irish landscapes, and explore whether hunting affects habitat preferences using GPS tracking of 42 birds across three hunted and three not hunted sites.

These objectives produced the following key results:

i. National roding survey results and SDM outputs estimated that breeding woodcock are more widespread in Ireland than recently reported, with a population estimate of 27,434 males (95% CL: 16,947 - 36,288). Bioclimatic variables, including precipitation and temperature seasonality and mean winter temperature, were important determinants of woodcock distribution, whilst forest habitat availability and composition at different landscape scales significantly influenced their abundance.

ii. Survival of overwinter woodcock across the six sites was high relative to the findings of comparative studies, with an estimated monthly survival rate during the hunting open season of 98.0%. The predominant cause of recorded mortality was hunting, followed by natural predation. Too few mortalities were recorded to meaningfully investigate the effect of hunting and bird age on mortality rates.

iii. Both hunting and bird age affected the use of space and movement ecology of non-breeding woodcock. Hunted and juvenile birds recorded larger diurnal and nocturnal home ranges than not hunted and adult birds, respectively, and hunting disproportionately affected adult woodcock commuting movements. Juveniles showed a slightly higher level of localised exploratory movement than adults.

iv. Diurnal and nocturnal habitat preferences of non-breeding woodcock were ranked. Hunting affected habitat preference, with hunted birds showing greater preference for broadleaved forest and less preference for hedgerows and scrub; these three habitats were of equal importance to not hunted birds. Nocturnally, hunted birds showed greater preference for grassland habitats at night and lower preference for closed habitats.

The results are discussed in the context of wider knowledge of woodcock and other species, and the scope for further research and species monitoring effort is explored. This research provides novel information and methodology with international appeal on the spatial ecology and impacts of human activity on this species. It is hoped that this work will contribute to the implementation of sustainable landscape and species management practices with a view to reducing human impacts on the natural world.

Acknowledgements

What a fantastic experience I have had over the course of this project! Firstly, I would like to thank my principal supervisor, Prof. John Quinn, for his guidance, enthusiasm, wise words, and - not least - patience over the course of the past five years. Undertaking a PhD not long after graduating from my bachelor's degree was a huge challenge in many ways and there were some testing moments, but John never lost his faith in my ability to keep going and gently but surely steered me to see it through to the end. For that I am ever grateful; thanks John!

I would also like to thank my secondary supervisors: Dr. Andrew Hoodless for his insight and expertise in all things woodcock, and Dr. Paul Holloway for his crucial help with data analysis, GIS, species distribution modelling, and wonderfully constructive feedback in the latter stages.

There are many people without whose contributions this project would not have been possible. In particular, thanks to the guys at the NARGC, most of all Ray Devine, Dan Curley, Seamus O'Brien and Richie Delaney for your more-than-enthusiastic financial, practical and moral support and hospitality throughout the project. A huge thanks also to David Tierney and Sinéad Cummins at the NPWS for your financial and advisory support, and to the other members of the committee, Luke Harman, John Wilson and Brian Caffrey who helped steer the project in its early stages.

Thank you to Jessica Perrott, who laid the foundation of the project before I took it on, and I am grateful to everybody from all walks of life who volunteered their time to undertake the roding surveys. Thanks to Chris Heward for hosting me at GWCT HQ in Fordingbridge and training me in tagging woodcock. Thanks also to Mark Jessopp for lending me his VHF receiver and antenna, which got an awful lot of use. A special thanks to Luke Harman for joining me on so many long, gruelling, soaking, muddy winter nights in some godforsaken fields, tagging and recapturing woodcock and straining our ears to hear VHF beeps over the howling of the wind. Let's do it again sometime! A shout-out to the others who assisted me in the field: Alan McCarthy, Jamie Darby, Kieran Lawrence and John O'Neill. Thanks to local gun-club members, particularly Aiden Boyle, Kevin Barry and James Coffey, for showing me around your club grounds and for your hospitality and co-operation during field seasons, Thanks to landowners, in particular to Nicholas and Colleen Lowry and Conor Duggan, for kindly hosting us on your land for winter fieldwork. Of course, once the fieldwork ended, I am indebted to Tom Reed, Jamie Darby and Shane Somers for helping me get to grips with modelling and data presentation in R.

So many friends and family have wholeheartedly supported me over the course of this project and beyond. My 'A Team' ringing buddies Sam and Paloma (and Lucy!) Bayley, Alan McCarthy, Clare Heardman, Ian McDermott, Domhnall Finch, Luke Harman, Shane Somers, Róisín Towe, Jenny Coomes, Joanne Monaghan and Cormac Quirke – thanks for so many fantastic days and nights catching and ringing all manner of amazing birds and really enriching my time since moving to West Cork! Thanks to Kendrew Colhoun for managing to keep me extra-busy with amazing side-projects – some incredible experiences and memories. A shout out to some friends from afar whom I have unfortunately rarely or never had the chance to see over the course of my PhD: Catherine West, Jonnie Fisk, Ben Porter and Paul Leafe, the latter two who introduced me to nocturnal bird lamping and sparked my love for woodcock ringing. John and Georgina Young, visits to your epic swift colony (its awesomeness rivalled only by your warm friendship, hospitality and support) have been true highlights of each year. Thanks Cathal and Fiona Noonan for being the very best landlords I could have hoped for over this time; may your farm forever flourish with beautiful wild nature, including its healthy population of woodcock!

To my mother, Rosemary, and my father, John; to David, Andrew, Judith, Ben, Merryn, Granny Audrey and Uncle David; and to Susan and Klaus, thank you for your unwavering love, support and encouragement through all of this!

Finally, thank you Hannah for sharing this journey with me. I'd be lost without you! You are stronger than you know and I have drawn so much inspiration from your tenacious resolve to do the right thing at all times, to rise to a challenge with dignity and poise, and to see a task done well and thoroughly to the end. I am so proud of you, and I am so grateful to have your pride, patience and love in return.

This thesis is dedicated to Douglas Boyes (1996 – 2021)

"*Now fades the glimmering landscape on the sight,*

And all the air a solemn stillness holds,

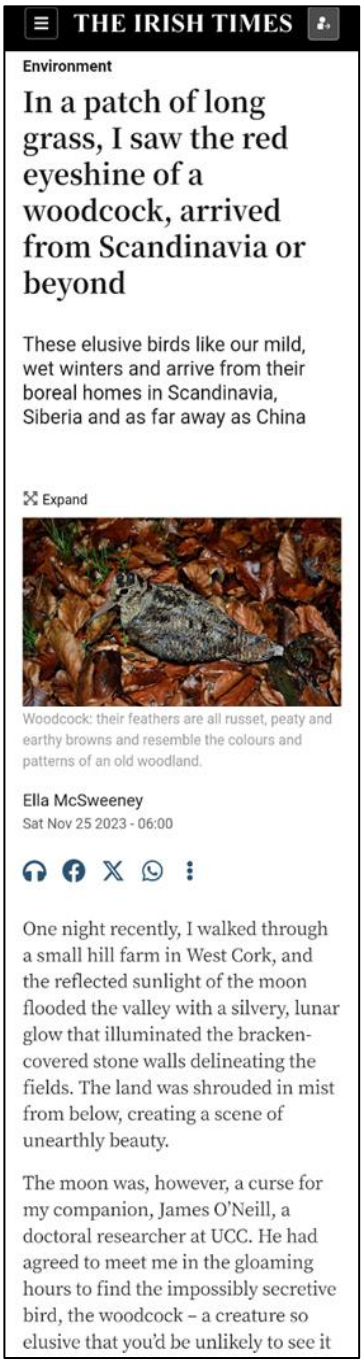
Save where the beetle wheels his droning flight

And drowsy tinklings lull the distant folds.

"Truly, we field lepidopterists are more fortunate than most of our fellow-men; for we experience pleasures that are beyond the imaginings of more 'earthy folk'. As the day draws to a close and our fellow-beings begin to think only of rest and recreation within doors, a growing anticipation wells through us, no matter how tired we may be, as we sense the advent of a new phase in our quest for moths. And, once started, all the way to the wood we are possessed by that subtle and pleasantly thrilling expectation which prevents the moth hunter's enthusiasm from being damped by the most unpropitious of seasons. Yes, we are fortunate indeed…"

P.B.M. Allan, *Moths and Memories*

Public outreach



THE IRISH TIMES

Environment

In a patch of long grass, I saw the red eyeshine of a woodcock, arrived from Scandinavia or beyond

These elusive birds like our mild, wet winters and arrive from their boreal homes in Scandinavia, Siberia and as far away as China

Expand

Woodcock: their feathers are all russet, peaty and earthy browns and resemble the colours and patterns of an old woodland.

Ella McSweeney
Sat Nov 25 2023 - 06:00

One night recently, I walked through a small hill farm in West Cork, and the reflected sunlight of the moon flooded the valley with a silvery, lunar glow that illuminated the bracken-covered stone walls delineating the fields. The land was shrouded in mist from below, creating a scene of unearthly beauty.

The moon was, however, a curse for my companion, James O'Neill, a doctoral researcher at UCC. He had agreed to meet me in the gloaming hours to find the impossibly secretive bird, the woodcock – a creature so elusive that you'd be unlikely to see it

James O'Neill – PhD student at University College Cork and one of the foremost woodcock specialists in Ireland

Medium

Of Woodcock and worms

Anthony McGeehan · Follow
7 min read · Mar 19, 2019

Listen Share

There are three of us. I keep glancing behind to keep an eye on Bruce Mactavish, my Canadian buddy, who thought that armour-plated safety boots would be suitable. Instead, he is labouring under the weight of concrete shoes. Always ahead, James O'Neill is our young and sprightly leader. We follow and periodically pause as he illuminates the greensward with a spotlight. He is hoping to catch the sparkle of eye-shine from a Woodcock probing for worms. By day, Woodcock melt among dank undergrowth. Their plumage is cryptic. For hours, the phantom presses itself flat. Feathers blend among mouldering leaves, twigs and bits of bark. Woodcock are masters of mimicking the environment. Observers remarked that the bird does not even blink, lest the action might shatter the illusion of a mottled, inanimate object.

Chapter 1: Introduction

Global biodiversity is currently under serious threat, with a rate of change in nature across the world over the past 50 years that is unprecedented in human history (IPBES, 2019). Indeed, the rate of species loss is so elevated that some claim that earth's sixth mass extinction event is underway (Cowie, Bouchet and Fontaine, 2022). With growing human population, economies and trade, and thus an increasing demand for resources, the main direct drivers behind biodiversity loss are all anthropogenic in origin (IPBES, 2019). These are, in order from highest to lowest impact: 1) changes in land- and sea-use; 2) direct exploitation of organisms, such as harvesting, hunting, fishing; 3) climate change, which, as well as being a direct driver, also exacerbates the impact of other drivers; 4) pollution, for example chemical, untreated waste, plastics, atmospheric emissions, oil spills and agricultural run-off; 5) alien and invasive species introduced accidentally and deliberately by humans to new locations. Given the worrying current and projected rates of biodiversity loss (Pereira et al., 2020) and the critical importance of healthy, functioning ecosystems for the wellbeing of human populations, there has been increasing interest in the conservation and restoration of species and ecosystems across the world, such as international calls to allocate at least half the earth's surface for nature conservation (Watson and Venter, 2017).

Whilst current total conservation effort is not nearly enough to reverse global biodiversity loss (Dinerstein et al., 2017), there are many examples of projects which deliver successful conservation outcomes (reviewed in Langhammer et al., 2024). Forming the basis of much conservation efforts are appeals to authority and stakeholder engagement on a range of power hierarchy levels, from individual stakeholders and landowners to world leaders and governments, to enact and enforce actions and policies that benefit wildlife. For example, a successful campaign in Nepal for a government ban on the veterinary drug diclofenac, along with farmer engagement and education, has resulted in partial recovery of vulture populations (Prakash et al., 2012; Galligan et al., 2020). Practical work directly targeting organisms and ecosystems can also be critically important actions in conservation and include, for example, ranger patrols guarding wildlife from poaching (Moore et al., 2018), sympathetic habitat and landscape management such as through managed nature

reserves or agri-environment schemes (Kleijn and Sutherland, 2003; Batáry et al., 2015), effective captive breeding and/or reintroduction of species (Griffiths and Pavajeau, 2008; Evans et al., 2009; Leus, 2011), or direct management of invasive or problematic species (Russell and Holmes, 2015; Doherty et al., 2017; Laidlaw et al., 2021). Finally, effective conservation research is crucial in order to identify threats and challenges, understand the ecological factors involved, suggest appropriate conservation measures, and to monitor population statuses and ecosystem health (Williams, Balmford and Wilcove, 2020). This thesis focuses on establishing an understanding of the national conservation status and the ecological and anthropogenic factors influencing the spatial ecology of a species currently of uncertain conservation status.

1.1 Use of space by animals

Spatial ecology is an umbrella term encompassing a variety of subdisciplines that study how ecological processes relate to space. All aspects of ecology are influenced by space to some extent, and therefore it is crucial that any planning for wildlife conservation and nature-sympathetic land management must consider the spatial patterns of individual organisms, populations, communities and ecosystems. Specifically, my thesis focuses on two closely intertwined modes of animal space use on a seasonal basis: in geographical space (species distribution, movement, home ranges) and in environmental space (habitat selection, environmental drivers of spatial distribution).

1.1.1 Estimating species distributions

Here, I define a species' range as the geographic limits of its occurrence, and the distribution of a species as the arrangement of its population, or populations, across space that takes into account the structure of occurrence at different spatial scales. These can be considered at different temporal scales, from seasonal to multi-year time periods. As changes in a species' range or distribution are often used to assess conservation status on global to local scales (IUCN, 2012; Gilbert, Stanbury and Lewis, 2021), an understanding of how a species is distributed is crucial for informing conservation or population management. The distribution of a species is a complex

expression of its unique ecology and evolutionary history (Brown, 1995) and may be understood through the species niche concept, defined by Hutchinson (1957) as "… the hypervolume defined by the environmental dimensions within which that species can survive and reproduce". Soberon and Peterson (2005) expand further on this by introducing the biotic, abiotic and movement (BAM) conceptual framework. This states that the 'realised niche' of a species is determined mainly by the intersection of geographic regions with favourable biotic and abiotic factors. When the accessibility of geographic space to a species' capacity for movement, either by natural dispersal or anthropogenic introduction, is also considered, these factors interact with varying strengths at different scales to produce the geographic distribution of a species.

Species' distributions can be estimated in a number of ways using species occurrence datasets. Grid-based mapping of species occurrence is commonly used in atlas projects dealing with large numbers of species within major taxonomic groups (e.g. Balmer et al., 2013; Lysaght and Marnell, 2016; Randle et al., 2019), and is undertaken by dividing the geographical region of interest into a series of grid cells. Species occurrence data may be compiled systematically or opportunistically and is often generated by hundreds or thousands of volunteer amateur observers. Where a positive record intersects with a grid cell, that cell is marked as 'present' for that species. Less commonly, quantitative data can also be represented in gridded maps using the number of records or number of individuals recorded. With coarser grid resolution there is increased confidence that a lack of observation of the species represents a true absence, as larger grid cells have greater average sampling effort per cell (Franklin 2010). This method of estimating species' distributions has clear drawbacks (reviewed in Donald and Fuller, 1998; Franklin, 2010). Occurrence datasets comprising opportunistic species records are often used, but these usually lack counts of zero and can be biased by spatially heterogenous observer effort. To some extent, such bias can be negated at coarser grid scales. However, the coarse resolution of grid cells provides little ecological information on how species are distributed according to environmental factors on finer scales, which limits its usefulness for conservation or monitoring purposes. In addition, when occurrence data collection effort for atlas projects deals with a wide range of taxa, the survey methods used may be more unsuitable for reliably detecting particular species due to rarity, elusiveness, or habitat specificity. Therefore, these species may be particularly under-represented by grid-based atlas projects and

can require specialised, species-specific survey methodology undertaken by trained personnel to collate sufficient species occurrence datasets (Black, 2020).

Species distribution modelling (SDM) represents a powerful set of analytical techniques commonly used in conservation science that are able to address some of the drawbacks of grid-based distribution mapping. They enable detailed exploration of the spatial relationships between a species and environmental characteristics (Franklin, 2010). Modelled relationships can then be projected to estimate distribution across poorly sampled regions to inform conservation decisions such as the identification of locations of previously unknown populations (e.g. Wilson, Roberts and Reid, 2011; Moradi et al., 2019). Additionally, models may be projected temporally, using historical or predicted environmental data to estimate how species may respond to changes in the environment (Araújo and New, 2007; Lambert, Cawkwell and Holloway, 2021).

The inclusion of suitable environmental data is critical to the success of SDMs. Given the complex and dynamic interplay of biotic, abiotic and movement factors that determine the actual distribution of a species at different scales (Soberon and Peterson, 2005), it is difficult to characterise the precise niche of a species from available environmental data. However, digital geospatial datasets have steadily become more available over the past twenty years, which allows for the construction of reasonably accurate SDMs for some species. For example, the online Worldclim resource provides current, historical and future estimations of global surface climatic variables, derived from the interpolation of global weather station data (https://worldclim.org; Fick and Hijmans, 2017). Remote sensing can provide fine-scale topographical, landcover, vegetation type and disturbance datasets with high sampling density. As SDM techniques improve and the distributions and ecologies of more species are understood, important biotic interactions can be included in models more than ever before (e.g. Giannini et al., 2013; Leach, Montgomery and Reid, 2016).

The type and quality of species occurrence data is an important consideration when constructing SDMs. Model method and performance can be limited if data collection is not specifically designed for SDM or related purposes. Records from opportunistic sources such as the global biodiversity information facility (GBIF; https://www.gbif.org) may be cost free to the modeller but they can suffer from

sampling bias and are sometimes aggregated to coarse grain scale. Furthermore, their reliability can often be called into question and careful data cleaning measures are usually required as spatial errors can degrade the performance of SDM. Such data sources usually provide 'presence only' data, which fails to include information on species absence. To utilise presence-only data in commonly used SDM methods such as maximum entropy (MAXENT), pseudoabsences (or background points) must be randomly generated. These represent the available environment, which may not correspond with true absence, and are accompanied by a number of model assumptions that are frequently violated leading to incorrectly interpreted outputs (Yackulic et al., 2013). It is therefore preferable to use presence-absence datasets when possible, which may be generated through survey methods specifically designed for the species in question.

When quantitative species occurrence data are gathered, it may be possible to model the relationships between species abundance and environmental variables as part of SDM. Projection of these models can sometimes generate population estimates but is a rare application of SDMs as it requires quantitative species occurrence data which includes true absences, and ideally should be validated using independent data (Lee-Yaw et al., 2022).

1.1.2 Movement Ecology

Movement is a fundamental characteristic of life on earth and is inherently spatial in nature. Understanding the causes, patterns and consequences of movement is an important element of species conservation and ecosystem restoration, as these play a fundamental role in determining the fate of individual organisms and in shaping ecological processes. While studies of movement have long been a focus of ecology research, advances in tracking technology have seen a rapid expansion in the field over the past two decades, leading to basic scientific advances in animal ecology as well as contributing to applied species conservation (Kays et al., 2015; Katzner and Arlettaz, 2020; Nathan et al., 2022).

Nathan et al. (2008) lay out a framework for understanding the drivers of organismal movement, based on the interplay of four fundamental components: i) internal state (why move?); ii) motion (how to move?); iii) navigation (when and where to move?); and iv) the external and environmental factors that affect movement. Whilst this

paradigm can be used to understand animal movement at all scales, it is helpful to broadly categorise strategies of animal movement phases that contribute to the lifetime track of an individual (Table 1.1; Dingle, 2014). An animal may employ different

Table 1.1. A simplified taxonomy of movement phase strategies and behaviours contributing to lifetime tracks (adapted from Dingle, 2014).

Movement strategy		Characteristics	Example
Movements resource or home range-directed			
Sedentism		Stationary, no displacement	
Station keeping		Movements keeping organism in its home range	
	Kinesis	Non-directional changes in rate of movement or turning in response to stimulus	Moth flight in a pheromone 'plume'
	Taxis	Directed movement toward a stimulus source	Insect moving toward light (positive phototaxis);
	Foraging	Reiterative movement in search of resources; ceases when resource encountered	Searching behaviour for food, mate or reproductive site
	Commuting	Predictable movement between patches of resources on a regular short-term basis; ceases when resource encountered	Diel vertical movement by plankton; deer moving between forest and open habitats at dusk
	Territorial behaviour	Patrolling territorial boundary; agonistic response to neighbours and/or intruders	Many examples across taxa
Ranging		Exploratory movement across a domain; ceases if suitable home range located	Postnatal dispersal; nomadism; exploratory movement away from home range
Movements not directly responsive to resources or home range			
Migration		Undistracted, often relatively long-distance movement to new domain; cessation promoted by movement itself. Responses to resources or home range suspended or suppressed	Annual flights of birds between breeding and non-breeding grounds; movements to breed by diadromous fish
Evasion		Directed movement away from threat	Prey evading pursuing predator
Movements not under control of organism			
Accidental displacement		Organism does not initiate movement. Movement stops when organism leaves transporting vehicle	Storm vagrancy in birds; oceanic rafting event
Assisted transport		Accidental or deliberate anthropogenic movement	Conservation introductions; biological control species; accidental invasive species introduction

movement strategies based on its capabilities at different stages of its life cycle, and/or on the basis of internal state (need to feed, reproduce, or defend territory), biotic interactions, or environmental conditions. For example, marine animal species with pelago-benthic life histories have sedentary adult stages, whilst their larvae disperse widely on ocean currents and driving their geographical distributions (Allen, Metaxas and Snelgrove, 2018). Many migrant birds undertake long-distance migratory journeys twice per year, yet may otherwise remain in separate, stable home ranges for the duration across each of the breeding and non-breeding seasons (e.g. Olalla-Kerstupp et al., 2015; Blackburn and Cresswell, 2016).

In this thesis, the study of movement largely focuses on those that occur within such seasonal home ranges. Most animals reside, for at least some portion of their lives, within relatively restricted home ranges, inside which an individual travels to access resources needed for survival and reproduction (Burt, 1943). Animal home range size varies depending on species characteristics, temporal scale and external ecological conditions, and range from no larger than the span of the organism in sedentary species, to thousands of square kilometres in the case of pelagic seabirds (e.g. Karris et al., 2018). However, the applied concept of 'home range' is subjective and there is no consensus on precise definition (Laver and Kelly, 2008; Horne et al., 2020); suitable methods of estimating home range area from spatial location data vary widely and depend on ecological context and the research questions being asked. Popular methods include minimum convex polygons (MCP) and kernel density estimators (KDE), but a range of others are available (Horne et al., 2020).

1.1.3 Field methods for studying animal movement

Animal movement has been studied using a variety of field-based techniques; mark-recapture (or individual recognition) is the most basic and long-standing method used. For example, a form of this, bird ringing/banding, has been used to study avian migration and movement since 1900 (Jespersen and Tåning, 1950) and continues to the present day. Although such methods have contributed hugely to our collective knowledge about bird movements (https://www.migrationatlas.org; Spina et al., 2022; also Thorup et al., 2014) as well as for other animal groups, such as fish and cetaceans (McGarvey and Feenstra, 2002; Carpinelli et al., 2014), the return rates of recoveries are often low compared to the number of individuals marked or catalogued, and can

be heavily geographically or seasonally biased (Robinson, Grantham and Clark, 2009). Sampling density is also usually low because often only two location data points per recovered individual are available, these being the location of initial capture and marking, and the location of recovery. This generally makes these methods most suitable for studying long-distance movements or site fidelity at the population level.

The advent of using very high frequency (VHF) radio telemetry to study animal ecology began from the 1960s (Lord, Bellrose and Cochran, 1962). This method normally requires manual tracking and triangulation of tagged animals via handheld radio-receivers; sampling density and schedule therefore depend on the resources that observers can commit to recording the location of each tagged individual in a study. The relatively low power and short-distance range of VHF radio signals used in the study of wildlife movement ecology means that its use is largely limited to studying relatively restricted home range movements of animals, as highly mobile individuals will quickly pass out of range from the observer. However, a recent and rapidly evolving application of radiotelemetry technology for studying movement has developed in the form of the Motus wildlife tracking system (https://www.motus.org; Taylor et al., 2017). This uses an extensive network of strategically placed ground-based radio receivers which can detect corresponding radio-tagged animals at a range of up to 20km. Extremely lightweight tags allow animals as small as large insects to be tracked as they move distances from local to inter-continental scales, though short deployment times due to small battery capacities remains an important limitation.

Additional methods of tracking animal movements have been developed, such as Argos Doppler-shift based satellite positioning (https://www.argos-system.org), or geolocators, which use the relative timing of sunset and sunrise on each day to estimate a rough geographical location (Lisovski et al., 2020). However, these methods can be subject to substantial location error, with that of Argos transmitters measured in hundreds of metres to tens of kilometres, and that of geolocators measured in hundreds of kilometres, as well as being rendered ineffective in polar latitudes and during equinox periods (Vincent et al., 2002; Phillips et al., 2004; Fudickar, Wikelski and Partecke, 2012; Rakhimberdiev et al., 2016; Irvine et al., 2020; Halpin et al., 2021). Thus, these methods are best suited for studying long-distance migration rather than fine-scale, local movements. Since the early 2000s, the use of global positioning system (GPS) has rapidly expanded in wildlife research (Cagnacci et al., 2010;

Tomkiewicz et al., 2010), with devices becoming more cost- and power-effective and gradually smaller, allowing for safe deployment on delicate animals such as small birds (e.g. (Geen, Robinson and Baillie, 2019; Pedersen, Thorup and Tøttrup, 2019; Bolton, 2021) or for the combination with other biologging sensors such as accelerometers, immersion loggers or small cameras to produce complementary datasets which help monitor the animal and its behaviour (Moll et al., 2007; Brown et al., 2013; Berlincourt, Angel and Arnould, 2015; Carneiro et al., 2022). GPS can determine geographical position with high precision and accuracy on predetermined or remotely programmable schedules, while location data may be transmitted and received remotely via satellite, cellular networks or radiotelemetry. For these reasons, GPS tracking is an equally suitable method for studying movements at a wide range of spatial and temporal scales, from high-intensity, short-fix-interval behavioural studies on a local scale (e.g. Bergen et al., 2022) to global, long distance migration studies (e.g. Wong et al., 2022).

1.1.4 Habitat use by animals

Habitat selection is a complex process by which an organism chooses a habitat by locating an area that is physically, chemically and biotically suitable for its survival and/or reproduction. As resources are distributed heterogeneously across landscapes, habitat use by an animal is closely associated with its movement ecology because an animal must move during the process of habitat selection (Van Moorter et al., 2016). Habitat preference can be defined as the likelihood that a resource will be occupied as a result of habitat selection, if habitats are offered up equally (Johnson, 1980; Manly et al., 2002); in practice, this can differ from the actual likelihood of occupation as habitats are rarely equally available in a landscape (Fieberg et al., 2021).

Studying habitat use requires a determination of an animal's movements and recording the habitats that they occur in over sufficient periods of time. The simplest method of doing this is by direct observation (e.g. Economakis and Lobel, 1998; Young and Schlesinger, 2015). However, this can only be done under certain circumstances. It is usually not possible to identify individual animals, and nocturnal behaviour or individuals in habitats offering poor visibility cannot easily be observed. Elusive or highly mobile species cannot readily be observed much of the time, and the act of observing may change the behaviour of individuals. More effective on a landscape

scale is the use of VHF radiotelemetry, though similar issues can occur with highly mobile species moving out of range, the need to triangulate simultaneously to determine location (Schmutz and White, 1990), or behavioural change through disturbance when tracked animals are approached to confirm their location and habitat (Kenward, 2001). As previously outlined, GPS allows for scheduled, highly precise and accurate location data from individuals to be remotely collected and transmitted at a range of spatial and temporal scales. However, GPS devices have limited functionality within some habitats, such as dense vegetation, due to reduced communication ability with satellites, particularly if the animal remains stationary.

One of the most important methods for analysing animal location data to identify habitat preferences are resource-selection-function models (named habitat-selection-functions in Fieberg et al. (2021)). These use logistic regression to compare environmental variables, such as habitat type, at locations visited by an animal against those at a set of background locations assumed available to the animal (Boyce and McDonald, 1999; Manly et al., 2002). This requires environmental datasets comparable to those used in SDM, which have become more available in recent years. Such models can be adapted for use at different spatial scales (DeCesare et al., 2012), to include random and fixed effects accounting for ecological dynamics (McLoughlin et al., 2010; Fieberg et al., 2021), and in some cases can be used to predict species abundance or incorporated into SDM (Johnson and Gillingham, 2008; Boyce et al., 2016; McCabe et al., 2021).

1.2 Effects of hunting on wildlife

Exploitation is second most important driver of global biodiversity loss (IPBES, 2019). Hunting of wildlife by humans occurs globally and is an important mode of the direct exploitation of wildlife, particularly for mammals and birds. Reasons for hunting vary and can overlap. These include subsistence and resource gathering for trade, recreation, pest control and wildlife management (Hitchcock, 2000; Rao et al., 2010; Garshelis, Noyce and St-Louis, 2020; Bichel and Hart, 2023). Methods of hunting and the range of animal species hunted also vary widely geographically, depending on local faunal diversity and human culture, with many countries setting legal boundaries determining which, when and how species may be hunted, often with

a goal of sustainable hunting management. Hunting can have both direct and indirect effects on the population dynamics and ecology of target species. The impacts of these may vary depending on factors such as hunting effort and intensity, species population size, status and fecundity, and other anthropogenic or natural pressures that populations face. Where the impacts of hunting are studied, it is important to attempt to quantify the spatial and temporal intensity of hunting to then allow the design of studies to appropriately examine the effects on target species.

1.2.1 Direct effects

Direct effects of hunting come about through mortality of individuals in a population that are directly killed by humans. Species may be exploited sustainably when overall mortality rates remain lower than long-term reproduction rates, and populations can remain stable but below ecological carrying capacities (Caughley and Sinclair, 1994). When harvest rates are too high, the direct consumptive effect of hunting on wildlife will contribute to population declines or extinction when species' recruitment rates cannot replenish populations sufficiently. Across human history, a number of species and populations have gone extinct where the cause has been attributed at least in a large part to the direct effects of over-exploitation; well-known examples include the dodo *Raphus cucullatus* (Turvey and Cheke, 2008), the Caribbean monk seal *Monachus tropicalis* (Baisre, 2013; Jørgensen, 2021), and the passenger pigeon *Ectopistes migratorius* (Cuker, 2020). Overhunting is still listed as one of the main threats to global biodiversity (IPBES, 2019), with many extant animal populations and ecosystems remaining in a depleted or declining state as a result of historical or current overexploitation (e.g. Thiollay, 2006; Corlett, 2007; Freeman, 2008; Wilkie et al., 2011; Benítez-López et al., 2017; 2019).

Hunting mortality can be additive (maximal) or compensatory (minimal) to natural mortality (Burham and Anderson, 1984; Boyce, Sinclair and White, 1999; Sutherland, 2001; Grzegorczyk et al., 2024). Additive mortality occurs where hunting mortality occurs in addition to normal rates of death by natural causes and annual survival decreases linearly with increasing harvest. Compensatory mortality occurs when survival rates increase in the remaining population as harvest rates increase (up to a threshold), or hunting mortality is balanced by compensatory natality: increased reproduction rates in remaining individuals. Proving either type is notoriously difficult

but, in reality, hunting mortality is probably rarely fully compensatory (Sutherland, 2001; Pöysä, 2004; Péron, 2013) though partial compensatory hunting mortality has sometimes been suggested to occur, such as in waterfowl (Burham and Anderson, 1984; Péron, Nicolai and Koons, 2012) and willow ptarmigan *Lagopus lagopus* (Pedersen et al., 2004; Sandercock et al., 2011). On the other hand, many works suggest that commonly hunted species experience largely additive mortality, highlighting the need for careful and adaptive hunting management particularly when hunting is carried out primarily for leisure (e.g. Dusek, Wood and Stewart, 1992; Smith and Willebrand, 1999; Gauthier et al., 2001; Bender et al., 2004; Duriez et al., 2005a; Zbinden et al., 2018, reviewed in Cooch et al., 2014).

1.2.2 Indirect effects

Indirect effects of hunting encompass human-induced changes to population dynamics and species ecology that occur beyond the initial offtake from direct hunting mortality. For example, in some instances, hunting may have a 'superadditive' effect on species' mortality rates, where hunting indirectly causes additional natural mortality, for example through increased likelihood of natural predation following behavioural changes (Gehr et al., 2018), or through social or demographic perturbance (Milner, Nilsen and Andreassen, 2007).

Where selective hunting occurs with a focus on particular age, sex or phenotypic classes, resulting demographic changes can impact the size and evolutionary trajectory of populations (reviewed in Coltman et al., 2003; Milner, Nilsen and Andreassen, 2007; Grzegorczyk et al., 2024). For example, high harvesting pressure from trophy hunting on mature males in polygynous species can result in strongly female-skewed sex ratios, low average age of males and perturbed social structures. This, over particular thresholds, can have a number of knock-on effects such as delayed birth rate or body mass development, skewed offspring sex ratios, and sexually selected infanticide, often resulting in lower fecundity or recruitment (Solberg et al., 2002; Milner-Gulland et al., 2003; Milner, Nilsen and Andreassen, 2007; Frank et al., 2017). Whilst intentional selection, for instance harvesting only individuals with the most extravagant features such as large size, horns, tusks or plumes for trophies, may lead to evolutionary shrinkage of those features (Pigeon et al., 2016; Festa-Bianchet, 2017), unintentional selection may also have evolutionary consequences. For example,

phenological traits such as migration timing, or personality traits such as boldness, can make some individuals more vulnerable to harvest, negatively selecting against those traits (Quinn et al., 2007; Ciuti et al., 2012a; Madden and Whiteside, 2014). Unintentional selective removal of individuals in poor condition (e.g. Dufour, Ankney and Weatherhead, 1993; Christensen, 2001; Guillemain et al., 2007) can also have phenotypic consequences as it may raise the average fitness of the remaining population.

Trait-mediated indirect effects on a species are those that influence and modify traits such as behaviour, phenology or life history in a population. Such effects have been widely observed as a result of natural predation on prey populations, and indeed can have a greater ecological impact than the direct, lethal effects of a predator (Brown, Laundré and Gurung, 1999; Peacor and Werner, 2001). An important indirect effect arises when individuals change their behaviour to avoid mortality as a response to perceived predation risk resulting in a 'landscape of fear', where trade-offs arise between safety and the ability to successfully forage or reproduce (Brown, Laundré and Gurung, 1999; Laundre, Hernandez and Ripple, 2010; Bleicher, 2017). In some cases, this can have important and far-reaching ecological ramifications such as trophic cascades (Schmitz, Krivan and Ovadia, 2004; Fortin et al., 2005; Ripple et al., 2016).

The 'landscape of fear' as a result of human activity such as hunting can equal or surpass the indirect effects of natural predation on target species (Frid and Dill, 2002; Ciuti et al., 2012b; Proudman et al., 2020). Target species commonly modify their behaviours in response to human hunting pressure. Vigilant behaviour increases because of hunting, which may interfere with time available for foraging or rest (Benhaiem et al., 2008; Casas et al., 2009; Proudman et al., 2020). Similarly, a higher propensity to undertake greater evasive movements can be energetically costly (Béchet, Giroux and Gauthier, 2004; Casas et al., 2009; Reimers et al., 2009). The ability to make up for lost foraging time can depend on the energetic cost of the disturbance and the feeding strategy of the species, with some, such as wigeon *Mareca penelope*, unable to fully compensate even for a single hunting disturbance event in a day (Madsen and Fox, 1995). Where hunting is too intensive, denial of access to important foraging areas and increased energy expenditure can contribute to exhaustion and starvation (Meile, 1991; Madsen and Fox, 1995). In addition, potential

carryover effects can affect animals in non-hunting periods, such as reducing breeding success and recruitment (Juillet et al., 2012).

Spatial behaviour and movement can be strongly influenced by hunting. In some cases, particularly in highly mobile species such as waterfowl or wading birds, individuals will simply vacate the general area, often displacing to inhabit comparatively safer sanctuaries at least until the threat of hunting has passed (Madsen, 1998; Evans and Day, 2001; 2002; Casas et al., 2009). This can alter activity patterns: sanctuaries may not offer sufficient foraging opportunities and therefore animals may have to limit feeding activity in more productive hunted areas to the hours of darkness when hunting does not occur (Casazza et al., 2012). Infrequent movement events such as migration or dispersal may also be affected, with hunting triggering early migratory movements (Rivrud et al., 2016), or increased dispersal into unoccupied territories left by harvested individuals which may increase gene flow (Chen et al., 2023). Where long-distance movement or displacement is not part of an animal's behavioural response to hunting activity, changes in fine-scale habitat selection and diel activity patterns often occur instead. For example, under hunting pressure, many terrestrial species prefer to take refuge in thick vegetation and limit activity in open habitats to hours of darkness, often with a trade-off against foraging opportunities (Kilgo, Labisky and Fritzen, 1998; Kamei et al., 2010; Saïd et al., 2012; Lone et al., 2015).

1.3 The woodcocks: an overview

The genus *Scolopax*, in the shorebird family Scolopacidae, contains eight species of mainly forest-dwelling birds called woodcocks. Six of these (Amami woodcock *S. mira*, Bukidnon woodcock *S. bukidnonensis*, Javan woodcock *S. saturata*, Moluccan woodcock *S. rochussenii*, New Guinea woodcock *S. rosenbergii* and Sulawesi woodcock *S. celebensis*) are residents within highly restricted ranges, each occurring allopatrically on separate islands or island groups in eastern and southeast Asia and Oceania (Del Hoyo, Collar and Kirwan, 2020; Fjeldså and Kirwan, 2020; Van Gils and Wiersma, 2020; Van Gils, Wiersma and Kirwan, 2020a; 2020b; 2020c). The remaining two species have larger global ranges and are mostly migratory. The American woodcock *S. minor* is a resident or short-distance migrant found across much of eastern North America (McAuley, Keppie and Whiting Jr., 2020), while the

Eurasian woodcock *S. rusticola* is the most widespread species, occurring widely across the Palaearctic as a resident and a short- or long-distance migrant (Van Gils, Wiersma and Kirwan, 2020b; Birdlife International, 2024).

The woodcocks are unusual in their predominantly forest and woodland habitat preferences compared with the majority of the Scolopacidae. Most of the 90 extant species in this family are strongly associated with open habitats; e.g. beaches and rocky shores, tidal flats, grasslands or open ocean in the non-breeding season, and nesting on alpine or arctic tundra, grasslands, heath, peatlands or dwarf scrub. Aside from the woodcocks, only a small number of rare snipe species (*Gallinago imperialis* and *Coenocorypha* spp.) habitually live in wooded habitats (Parker, et al., 1985; Poulsen, 1993; Higgins and Davies, 1996), though the Tuamotu sandpiper *Prosobonia parvirostris* and overwintering bristle-thighed curlew *Numenius tahitiensis* will regularly forage and perch within the relative safety of native forest on remote Pacific islands and atolls (Howell, 2014). Additionally, some sandpipers of the genus *Tringa* are known to breed in semi-open boggy forests, even nesting within the branches of trees, though otherwise use open habitats (Pulliainen and Saari, 1991; Zwdárek, 1999; Houston, 2012; Maslovsky et al., 2023). As the habitat preferences and lifestyle of woodcocks are almost unique within the family, they have come to occupy a specialist 'woodland wader' niche and have become highly adapted for this lifestyle.

Differing predation pressures and the enclosed nature of terrestrial, wooded habitats compared to ancestral open habitats seems to have driven the evolution of highly cryptic plumage (Figure 1.1.A) and elusive behaviours in woodcocks. When approached, woodcocks will only take flight at very close range, otherwise they remain motionless or will creep away through thick undergrowth, relying on their camouflage to avoid detection. Much of their activity typically takes place during the hours of twilight and darkness (Hirons, 1980; Stribling and Doerr, 1985; Duriez et al., 2005c; Braña, Prieto and González-Quirós, 2010). Their anatomy reflects this crepuscular and nocturnal lifestyle, and includes a long, downward-angled bill with large eyes placed laterally and high in the skull (Figure 1.1.A), giving a comprehensively multi-directional visual field (Martin, 1994). Along with high scotopic retinal sensitivity (Rojas et al., 1999), this allows woodcocks to remain vigilant for predators whilst their head is lowered as they forage by probing the ground with their bill to find prey using tactile and chemical cues. The bulk of woodcock diet

consists largely of earthworms Lumbricidae with smaller proportions of other invertebrates, at least in the American and Eurasian species (Miller and Causey, 1985; Hoodless and Hirons, 2007; Bende and László, 2022). Despite predation risks, the thermoregulatory advantages of living in sheltered wooded habitats mean that woodcocks have relatively low energy requirements compared to other wader species living in exposed environments (Duriez et al., 2004). In common with some other camouflaged, crepuscular and nocturnal birds such as nightjars Caprimulgidae; (Aragonés, Reyna and Recuerda, 1999) or true owls Strigidae (Penteriani et al., 2007; Bettega et al., 2013), woodcocks exhibit pale feather patches that contrast strikingly with the rest of the cryptic plumage, which, in the case of the Eurasian woodcock, are 30% more reflective of light than any previously measured feather (Dunning et al., 2023). These are located on the undersides of the tail feather tips (Figure 1.1.B) and, although normally hidden, can be suddenly revealed, which may serve as a means of communication and signalling to other woodcocks in dimly lit conditions, or a predator distraction display (Hagen, 1950; Ingram, 1974; Hirons, 1980; Dunning et al., 2023).

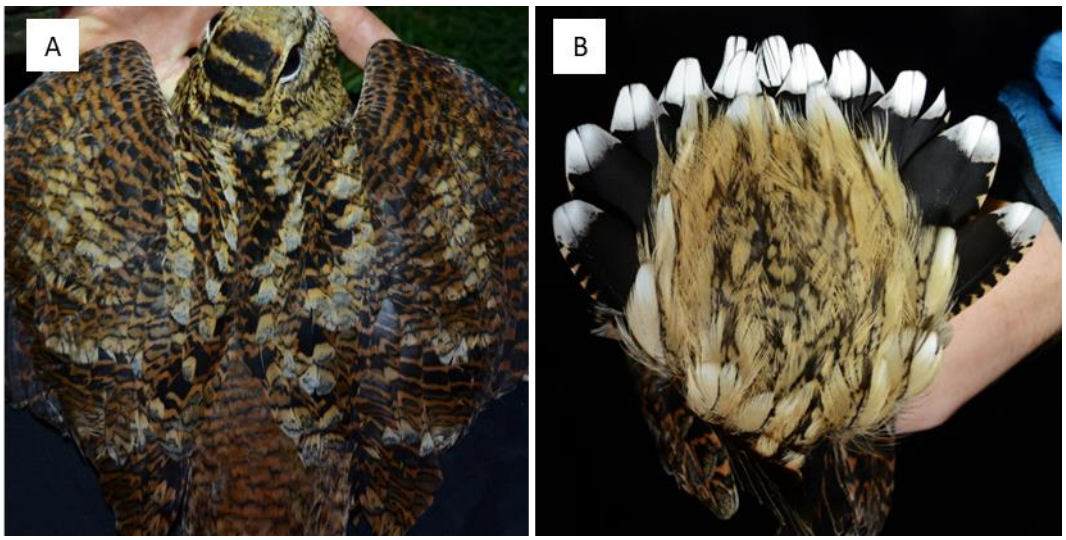


Figure 1.1. Photographs of a Eurasian woodcock captured for tagging purposes, showing: A) the cryptically patterned plumage and eyes laterally-placed on the head; B) the striking, white undersides of the tail feather tips. Images by J. O'Neill.

Due to their elusive habits and preferences for closed, wooded habitats, woodcocks are relatively difficult birds to study, but are popular amongst wild game hunters in many parts of their ranges. Little is known about the conservation status and population sizes and trends of the six island endemic woodcock species. The Amami and Moluccan woodcocks are each estimated to have populations of fewer than 10,000 and 20,000 individuals, respectively, and are both thought to be in decline (Delany, 2006; Sugimura et al., 2014), with both being listed by the International Union for Conservation of Nature (IUCN) as 'vulnerable' (IUCN, 2016a; 2021). Little or no data exist for the Bukidnon, Javan, New Guinea or Sulawesi woodcocks though habitat loss and human exploitation remains a concern for some populations (Patandung et al., 2019; IUCN, 2023a; 2023b). The American and Eurasian woodcocks are culturally and economically important as game species, and so have attracted greater levels of detailed study. Both are listed by the IUCN as 'least concern' (IUCN, 2016b; 2020). The American woodcock has a large estimated population of 3.5 million individuals, though it is also experiencing a significant long-term population decline largely driven by habitat loss (Gutowsky et al., 2020; IUCN, 2020; Seamans and Rau, 2023). The status of the Eurasian woodcock, on the other hand, is thought to be stable overall, with an estimated global population of 10-26 million individuals, though some local populations are in decline or their status is unknown (IUCN, 2016b; Wetlands International, 2024).

1.4 Study species: the Eurasian woodcock

1.4.1 Range and Migration

The Eurasian woodcock is the focal species of this thesis and is hereon referred to as 'woodcock'. Its breeding range stretches from northern Japan in the east, across much of the taiga and temperate forests of Asia and Europe, to Ireland and northern Spain in the west, with outlying populations in the Caucasus, the Balkans, the Atlantic archipelagos of the Azores, Madeira and the Canary Islands, and across the Himalayan and Tien Shen mountain ranges (Figure 1.2; Van Gils, Wiersma and Kirwan, 2020d; Birdlife International, 2024). Woodcock on the western fringes of their breeding range such as in Great Britain and Ireland, northern Spain and the Atlantic archipelagos, are mainly resident or undertake only infrequent or short annual movements (Bannerman

and Bannerman, 1963; Hoodless and Coulson, 1994; Powell, 2012; Braña et al., 2013; Andrade et al., 2022). Those that breed further north and east are, for the most part, strictly migratory to avoid inhospitable frozen winter weather, overwintering in the milder climates of western Europe, the Mediterranean (including parts of North Africa), Anatolia, India, Sri Lanka, mainland south-east Asia and south-eastern China, South Korea and Japan (Van Gils, Wiersma and Kirwan, 2020d). To date, most studies on the ecology and conservation of woodcock focus on European populations, with relatively few little known about populations from the east of their global range.

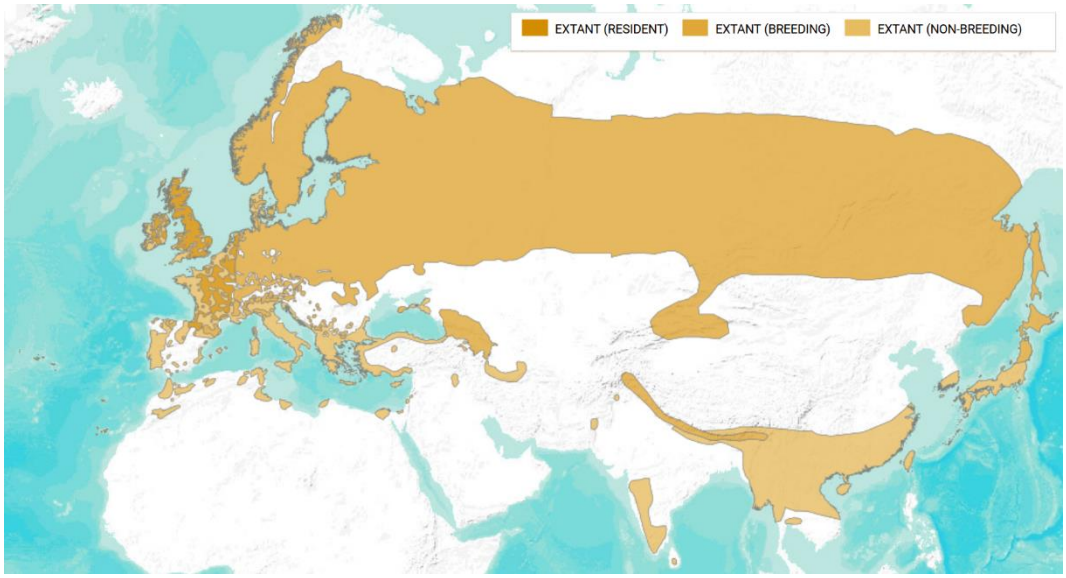


Figure 1.2. Map showing the global range of the Eurasian woodcock (from Birdlife International, 2024; IUCN 2016b).

Migrant woodcock usually show strong fidelity to breeding and wintering sites between years, as well as migration routes (Hoodless and Heward, 2019; Tedeschi et al., 2020), which is a common habit amongst the Scolopacidae (e.g. Olalla-Kerstupp et al., 2015; Lourenço et al., 2016; Summers et al., 2023). Ringing recoveries, satellite telemetry and stable isotope analyses show that migratory connectivity in this species is weak, with a high degree of mixing of individuals from different breeding populations on non-breeding grounds (Hoodless and Coulson, 1994; Powell, 2012; Hobson et al., 2013a; 2013b; Hoodless and Heward, 2019). For example, of 60 overwintering birds satellite-tagged in a variety of locations in Great Britain and Ireland, spring migration destinations were spread across nine countries, from Great

Britain (i.e. resident birds), across Fennoscandia and the Baltic states, to three birds that travelled to central Russia, the latter a result of migration distances of around 6,300 km (Figure 1.3; Hoodless and Heward, 2019). Such weak migratory connectivity likely results in the high genetic diversity observed across the mainland European breeding population (Trucchi et al., 2011), and may improve their ability to evolve adaptive responses to changing selection pressures (Webster et al., 2002). Notably, in contrast, the resident woodcock populations on the Azores show low but consistent genetic differentiation from mainland populations, indicating restricted levels of gene flow and recent divergence (Andrade et al., 2022). It is not currently known whether climate change has had, or will have, an effect on woodcock migratory behaviour. However, it has been shown that woodcock migration is significantly influenced by local weather conditions (Birtsas et al., 2013; Le Rest et al., 2019; Bende, Faragó and László, 2023). For example, higher air temperatures and tail-winds greatly increase the likelihood of spring migratory movements, whilst greater air humidity reduces the likelihood (Le Rest et al., 2019). Therefore, it seems likely that climate change and associated changes in annual weather patterns may impact the migration phenology and distances travelled by woodcock.

Figure 1.3. Map showing winter (blue), stopover (grey), and breeding (orange) sites of 52 migratory Eurasian woodcock satellite tagged in Great Britain and Ireland. Breeding sites are geographically widely distributed, indicating weak migratory connectivity (from Hoodless and Heward, 2019).

1.4.2 Non-breeding ecology

Post-migration, when woodcock have settled at overwintering sites, individual birds usually remain within a limited home range for the duration of the winter, which can vary in size to a recorded maximum of 6.03 km^2 (Wilson, 1983; Duriez et al., 2005d; Powell, 2012). Periods of particularly cold weather can force birds to undertake long-distance 'escape' flights, returning to normal home ranges when conditions improve again (Péron et al., 2011; Guzmán, Caro and Arroyo, 2017; Hoodless and Heward, 2019). Within a home range, most activity is restricted to a variable number of regularly revisited core areas; those used during the hours of daylight are often different to those used nocturnally (Duriez et al., 2005d; Powell, 2012). (Duriez et al., 2005d) found that strategies of diurnal and nocturnal core area use varied by individual, with some using only a single, unique diurnal or nocturnal core area throughout the winter, whilst those that used multiple core areas used them alternately or, more rarely, successively (never returned to a previously used core area); differences in diurnal strategies could be linked to prey availability, individual foraging efficiency or disturbance (Duriez et al., 2006).

In landscapes with mild, oceanic climates, woodcock commonly use different habitats during the day compared to the hours of darkness (Wilson, 1983; Duriez et al., 2005b; Powell, 2012). By day, densely vegetated and wooded habitats such as forest, scrub or hedgerows are primarily used, which provide shelter and protection from predators. Although feeding activity is most prevalent at night in winter, woodcock also habitually forage during the day (Duriez et al., 2005c) and so it is believed that, to an extent, prey availability drives specific diurnal habitat selection. Broadleaved woodlands with dense shrub-layer vegetation and soil with high degrees of well-mixed organic matter (mull humus), particularly wet woodland, are favoured, owing to their higher biomass of earthworms (Duriez et al., 2005b; Powell, 2012). Suitably dense hedgerows were also an important diurnal habitat, but mature coniferous forest was typically rarely used. At night, woodcock frequently use open habitats, most favouring grazed pastures and meadows due to their high abundances of earthworms (Duriez et al., 2005b; Powell, 2012). Other habitats used included arable farmland and ungrazed grassland, while birds sometimes remained in woodland at night (discussed below). On Sado Island, Japan, cultivated rice fields constitute the main known nocturnal foraging habitat for woodcock (Okahisa, Okahisa and Odaya, 2019). The risk of

predation, particularly from avian predators, is significantly lower in open habitat at night than during the day, though woodcock remain at risk from mammalian predators (Duriez et al., 2005a). Little is known about woodcock habitat preferences in locations with warmer, drier climates, and it is possible that in such areas, birds remain in wooded habitats at night more frequently.

At dusk, woodcock may commute between diurnal and nocturnal locations. Commute flights and different nocturnal habitats potentially present higher energetic costs and higher risk of predation than remaining in wooded habitats (Duriez et al., 2005a; Braña, Prieto and González-Quirós, 2010). Therefore, a bird's decision whether to commute each evening is likely to be based on weather conditions and the trade-off between starvation and predation risk, and it will commute only if its energetic requirements have not been fulfilled during the hours of daylight immediately prior (Duriez et al., 2005c). Where a bird has fed sufficiently by day, it will remain in its diurnal location. This can be relatively rare, with the number of nocturnal radiotelemetry locations from three separate studies recorded in woodland being 12-15%, and 57-58% of birds remaining within woodland at least once, with some individuals remaining in forest much more frequently than others (Duriez et al., 2005c; Powell, 2012; Ferrand et al., 2013; also see Duriez et al., 2005b). Commute flights take place shortly after sunset, the precise timing of which is determined by a trade-off between predator avoidance and the need to forage, with birds tending to move earlier in the evening relative to sunset during periods of migration, colder temperatures and darker, overcast conditions (Braña, Prieto and González-Quirós, 2010). Commute distances can be highly variable, with reported means ranging from 259 to 1,113 metres, and maximum distances of 4,417 to 5,135 metres (Duriez et al., 2005d; Powell, 2012; Guzmán, Caro and Arroyo, 2017).

1.4.3 Breeding ecology

Woodcock begin breeding activity in the early spring; when males undertake 'roding' display flights to advertise themselves to females. Exact commencement dates in Europe depend on latitude and longitude, with roding seen as early as mid-January in the resident population in Azores (Machado et al., 2006), but usually begins in April in migrant populations in northern and eastern countries such as Sweden (Marcström, 1986); activity generally ceases by July in all European breeding populations. Roding

consists of visual and vocal display: wide patrolling flights are undertaken by males typically over forest canopy at dusk and dawn, often following open forest features such as rides or clearings, and is accompanied by a two-part 'grunt-squeak' call repeated every few seconds (Hirons, 1980; Hirons and Owen, 1982). Individual males may be identified by their vocal signature with the help of sound recording technology (Hoodless et al., 2008) and have been shown to use a number of sites within a season (Bristow et al., 2023). Several males may have overlapping roding grounds and directly compete with each other (Hirons, 1980; Bristow et al., 2023), in what seems to be an 'extended lek' mating system. The mean area used by roding woodcock in an evening ranges from 0.88 – 1.29 km^2 (Hirons, 1983; Heward, 2020) but can use large areas (>7 km^2) over the course of a season (Sládeček et al., 2023). Mating strategies vary widely in the Scolopacidae, and like several other species, woodcock have a polygamous strategy where competition between males is high, individual mating success rates are variable, and paternal care for offspring is non-existent (Hirons, 1980; Hirons and Owen, 1982).

Females have an extended nesting season from March until early August, with northern and eastern populations in Europe commencing later in April (Hirons and Owen, 1982; Hoodless and Coulson, 1998; Machado et al., 2006; Bende and László, 2021). The possibility of females producing a second brood after successfully fledging a first brood is a subject of discussion but does not yet appear to be definitively proven (reviewed in Bende and László, 2021). Two to five, but typically four, eggs in a clutch are laid on the ground, with an average incubation period of 21.9 days (Hoodless and Coulson, 1998; Bende and László, 2021). With a diet consisting mainly of earthworms (Hoodless and Hirons, 2007), chicks develop rapidly, and are able to fly after 20 days of age, becoming independent after 35-42 days (Hirons, 1983).

Similarly to the non-breeding season, in March adult woodcock are mainly found in wooded habitat during the day and can use open grassland habitats at night. However, the frequency of nocturnal use of open habitats decreases considerably as the breeding season progresses to July, with birds opting to remain within woodland at night more often, reflecting increased diurnal activity and seasonal changes in relative prey availability (Hirons and Owen, 1982; Hirons, 1983; Hoodless and Hirons, 2007; Braña et al., 2013). Open, sparse forest is a favoured nocturnal habitat (Sládeček et al., 2023). A heterogenous landscape with a high proportion of total forest cover appears to be

important for supporting higher densities of breeding woodcock, which can use a wide variety of woodland types but prefer young deciduous forests, particularly those dominated by birch *Betula*, with dense shrub- and ground-level vegetation cover (Hoodless and Hirons, 2007; Braña et al., 2013; Heward et al., 2018; Sládeček et al., 2023). On the south-western fringes of the breeding range, altitude also appears to be an important determinant of breeding woodcock distribution in a landscape, with higher abundances found at higher elevations, probably reflecting the importance of cooler, wetter climatic conditions for this species (Brüngger and Estoppey, 2008; Braña et al., 2013).

1.4.4 Conservation status and hunting

Globally, the conservation status of the woodcock is considered to be stable with an extremely large range and population size, so the IUCN lists it as a species of least concern (IUCN, 2016b). In Europe, it is also considered stable (Wetlands International, 2024), but regional population trends are generally poorly known; it appears to be stable or increasing as a breeding species in Russia (Fokin and Blokhin, 2013), and Fennoscandia (Valkama, Vepsäläinen and Lehikoinen, 2011; Lindström et al., 2015) , but declining in the United Kingdom and Ireland (Colhoun and Cummins, 2013; Heward et al., 2015; 2024; Gilbert, Stanbury and Lewis, 2021). In France, it has previously been reported as stable (Gossmann and Ferrand, 1998; Ferrand et al., 2008), but more recently, reported as declining (Boussac, 2018). Most breeding survey schemes use species-specific methods focusing on the detection of roding male woodcock at dusk, which can be used to produce quantitative datasets for studying abundance patterns and generating population estimates (e.g. Hoodless et al., 2006; 2009; Machado et al., 2008a; 2008b; Braña et al., 2013; Fokin and Blokhin, 2013; Heward et al., 2015; 2018). Even less is known about the status of non-breeding populations as there are few robust monitoring networks owing to the difficulty in surveying this species in winter. However, as far as I am aware there is no published evidence for any serious declines on a large scale and it is reported to be stable in countries such as France and Italy (Ferrand et al., 2008; Tuti et al., 2023).

Woodcock are a traditional quarry species for wild game hunters across much of their European range. Timing of legal hunting open seasons vary by country, generally following the seasonal movements of the species. Where woodcock are mainly

summer breeding visitors, the hunting season primarily spans late summer and early- to mid-autumn, with an additional spring open season targeting roding males in some parts of Russia when even more birds may be taken than in the autumn (Blokhin, Mezhnev and Fokin, 2006). Where woodcock are primarily an overwintering or resident species, the main hunting period takes place during the late autumn and winter months, as late as the end of February in France. Similarly, restrictions on numbers to be hunted vary by country, with some allowing unrestricted hunting, whilst others impose bag limits such as three birds per hunter per day in Portugal (Rodrigues et al., 2018); the same rule applies in western France as well as a maximum of thirty birds per hunter per season (Duriez, Eraud and Ferrand, 2006). The total number of woodcock taken by hunters each year varies by country, with a total European estimate of 3-4 million (Ferrand and Gossmann, 2001); of those 736,000 – 1,200,000 are taken in France alone (Ferrand and Gossmann, 2000; Aubry et al., 2016). The annual harvest in the United Kingdom has been estimated to be 140,000 - 180,0000 from 2004 to 2016 (Aebischer, 2019), decreasing to 62,000 – 140,000 since 2018 (McNicol, Ellis and Madden, 2024), whereas in Germany, the annual harvest normally ranged between approximately 7,800 and 12,200 since 2012/13 (Deutscher Jagdverband, 2023).

The effects of hunting on woodcock populations and ecology are poorly known and require better understanding to inform effective conservation measures. Survival rates can be lower where hunting takes place, particularly in juveniles, with hunting being the predominant known cause of mortality (Tavecchia et al., 2002; Duriez et al., 2005a; Guzmán, Caro and Arroyo, 2017; Prieto et al., 2019); it has thus been suggested that hunting mortality may be additive to natural mortality. In parts of Russia, when hunting seasons were cancelled due to viral disease pandemics in humans in 2006 and 2020, spring roding intensity (and presumably woodcock abundance) significantly increased above levels seen in seasons before and after the hunting bans (Blokhin and Artemenkov, 2023). This suggests that woodcock populations may be limited by hunting to some extent. Effects of hunting on ecology and behaviour have barely been studied; the only example used radiotelemetry to track a single site in France using radiotelemetry to track birds through the winter hunting season (Ferrand et al., 2013). They found little effect of hunting on daily use of space, and only limited increases in diurnal movement and home ranges from ‘controlled disturbances’, where birds were deliberately flushed every day to simulate more intense hunting disturbance.

1.4.5 Woodcock in Ireland

Ireland hosts both a resident breeding population of woodcock and a migratory, overwintering population. The status of the breeding population is poorly known, and until now has only been monitored via the three breeding bird atlases of Great Britain and Ireland which attempted to map the ranges of all British and Irish breeding birds via gridded distribution estimation at a resolution of 10 km (Sharrock, 1976; Gibbons, Reid and Chapman, 1993; Balmer et al., 2013). While woodcock remained a widespread breeding species, between the first (1968-72) and third (2007-11) atlases, breeding woodcock range appeared to contract by over 70% in the Republic of Ireland (Figure 1.4), earning its place on the 'red list' of birds of conservation concern (Colhoun and Cummins, 2013; Gilbert, Stanbury and Lewis, 2021). While the survey methods used were similar between the atlases, they were not species-specific and mainly focused on detecting a wide range of largely diurnal species, which are unreliable for detecting elusive and crepuscular species such as woodcock (Hoodless et al., 2006). It is also unknown if crepuscular or nocturnal survey effort across Ireland was similar between the atlases. Therefore, while it is probable that breeding woodcock have indeed declined in Ireland, the true status, distribution and size of the breeding woodcock population in Ireland is still poorly understood.

Large numbers of migrant woodcock spend the winter in Ireland. However, there is no national monitoring scheme for these, and knowledge of their national and local distribution and abundance is limited to anecdotal experience accumulated mostly by hunters in the field, which can be unreliable. In Britain, the wetland bird survey (WeBS) includes woodcock as a countable species through the year, and reports highly variable winter numbers between years, with an apparent increasing trend since 1975 (Woodward et al., 2024). However, the methodology used in WeBS is unsuitable for a species with such elusive and strongly terrestrial habits, and it is difficult to distinguish detection effect from true population trends. Until now, only two small-scale studies have investigated the non-breeding ecology of woodcock in Ireland; Wilson (1980; 1983) used ringing recoveries and radiotelemetry to track the movements, site fidelity and habitat use of overwintering birds, laying the foundations for our current knowledge of woodcock non-breeding ecology. Given the unique composition of Irish landscapes, with relatively low proportions of broadleaved forest and extensive improved pasture, hedgerow networks and peatlands (Carlier et al.,

2021; DAFM, 2023), it may be important to quantify habitat use by woodcock to inform improved countryside management practices.

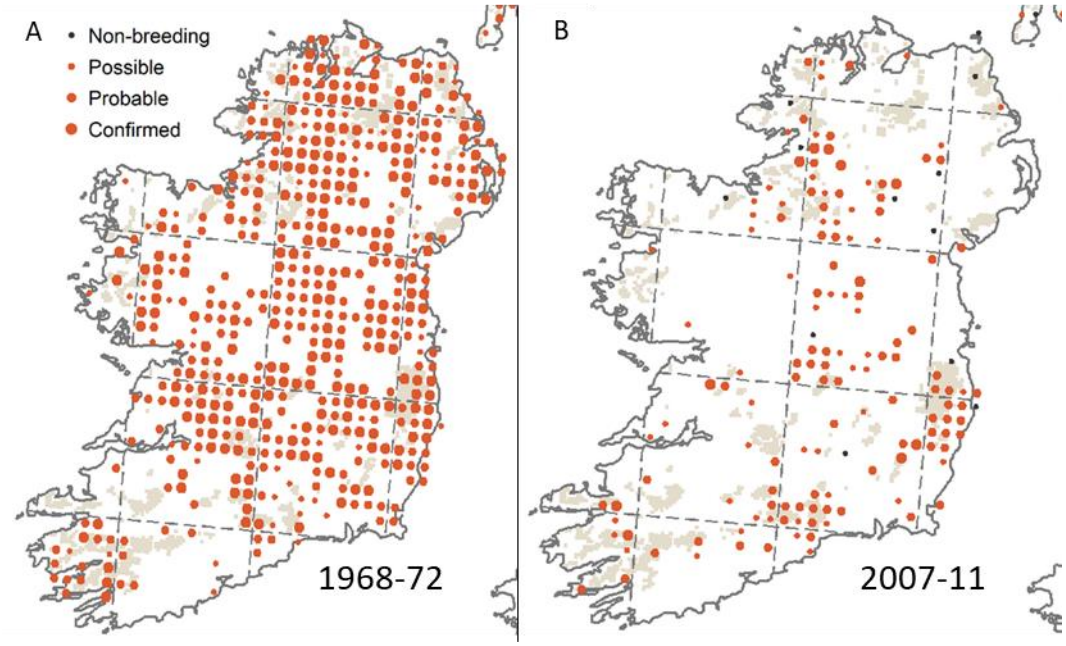


Figure 1.4. Recorded grid-based distributions of woodcock in Ireland from A) the first (1968-72) and B) the third (2007-11) breeding bird atlases of the United Kingdom and Ireland in 1968-72, suggesting a possible range contraction by over 70% in the intervening period (from Sharrock (1976) and Balmer et al. (2013)).

Woodcock hunting is a popular and traditional rural pursuit in Ireland (McKelvie, 1990). Much hunting is undertaken by local gun clubs or syndicates, who hunt using traditional 'rough shooting' methods, using 'beating' gundog breeds such as English springer spaniel or cocker spaniel to extensively and indiscriminately flush wildlife from tracts of thick vegetation into the path of the hunter. The use of pointing dog breeds such as setters, which detect and can discriminate birds by scent, alerting the hunter before the quarry is flushed, is less common, unlike in other countries such as France and Italy where these breeds are predominantly used (McKelvie, 1990). Shooting can also be offered on a commercial basis to paying clients, who may use rough hunting methods, or driven shooting, where teams of 'beaters' drive birds toward shooters, who remain stationary or slow-moving. However, little information exists on the quantity of woodcock taken annually, the number of hunters who target woodcock, or the distribution and intensity of hunting efforts, as hunters are currently

not officially obliged to submit such information. It follows that the direct and indirect effects of hunting on the breeding and non-breeding populations and ecology of this species in an Irish context are also unknown.

1.5 Research aims and thesis structure

The main aim of this research is to improve the understanding of the conservation status and spatial ecology of breeding and non-breeding Eurasian woodcock in Ireland, as well as exploring the impacts of human activity on the species, given its uncertain national conservation status and cultural importance as a hunted species. Specifically, this thesis seeks to address three central research topics, with a chapter devoted to each and produced in the style of journal articles. The thesis structure, research topics and questions are summarised as follows.

Chapter 2: Modelling the distribution and abundance of breeding Eurasian woodcock across Ireland

Little is known about which environmental factors drive the distribution and abundance of breeding woodcock across most of its range. In Ireland, its breeding distribution is imperfectly understood and no population estimate exists. To address these knowledge gaps, the research questions explored are: i) how do climatic variables drive the distribution of breeding Eurasian woodcock? ii) how do climatic and landscape-scale land cover variables influence breeding Eurasian woodcock abundance? iii) what is the current distribution and abundance of breeding Eurasian woodcock in Ireland? Through the coordination of a national volunteer-based survey of roding male woodcock, a species occurrence dataset was compiled. From this, a two-step species distribution modelling method was performed using bioclimatic and landcover variables to provide an estimate of the national distribution and population size of breeding woodcock. To my knowledge this is the first time this method has been applied to a bird species on a national scale.

Contributions: **James O'Neill**: conceptualisation, methodology, writing (original draft); **John Quinn**: conceptualisation, writing (review and editing), supervision; **Andrew Hoodless**: conceptualisation, writing (review and editing), supervision; **Paul**

Holloway: methodology, writing (review and editing), supervision; **Jessica Perrott**: conceptualisation, methodology: **Jamie Darby**: methodology.

Chapter 3: The effects of hunting and bird age on survival, movement and use of space in non-breeding Eurasian woodcock

Like many terrestrial bird species commonly targeted by hunters, very little is known about how hunting affects the space use and movement ecology of woodcock. To explore this, the research questions are: i) what are the survival rates and causes of mortality of non-breeding Eurasian woodcock at hunted and not-hunted sites? ii) what are the effects of human hunting activity on the spatial behaviour of non-breeding Eurasian woodcock? iii) what are the effects of bird age on the spatial behaviour of non-breeding Eurasian woodcock? GPS and radiotelemetry tracking of individual birds at multiple hunted and not-hunted sites were used to provide insights into winter woodcock survival and spatial ecology, with an emphasis on investigating the effects of hunting.

Contributions: **James O'Neill**: conceptualisation, methodology, writing (original draft); **John Quinn**: conceptualisation, writing (review and editing), supervision; **Andrew Hoodless**: conceptualisation, writing (review and editing), supervision; **Paul Holloway**: methodology, writing (review and editing), supervision; **Luke Harman**: methodology; **Shane Somers**: methodology.

Chapter 4: The effects of hunting on habitat preferences of non-breeding Eurasian woodcock across a heterogenous landscape in Ireland

There are concerns that much habitat of importance to non-breeding woodcock has been lost across Ireland in recent decades. In addition, it is not known how hunting may affect the habitat preferences of woodcock. To help inform sustainable landscape and hunting management practices, the research questions explored are: i) what are the diurnal and nocturnal habitat preferences of non-breeding Eurasian woodcock in diverse farmed landscapes in the context of continued agricultural intensification? ii) what are the effects of human hunting on habitat preferences of non-breeding Eurasian woodcock? iii) what are the effects of bird age on habitat preferences of non-breeding Eurasian woodcock? GPS tracking of individual birds was used to provide insights into the differential habitat use of woodcock at multiple hunted and not-hunted sites.

Contributions: **James O'Neill**: conceptualisation, methodology, writing (original draft); **John Quinn**: conceptualisation, writing (review and editing), supervision; **Andrew Hoodless**: conceptualisation, writing (review and editing), supervision; **Paul Holloway**: methodology, writing (review and editing); **Luke Harman**: methodology; **Shane Somers**: methodology.

Chapter 5: Synthesis

This final chapter summarises the key results of this thesis and offers a speculative discussion of the findings within the context of wider research on this and other species, as well as an exploration of the scope for future research.

Contributions: **James O'Neill**: conceptualisation, writing (original draft); **John Quinn**: writing (review and editing), supervision; **Paul Holloway**: writing (review and editing), supervision.

Chapter 2: Modelling the distribution and abundance of breeding Eurasian woodcock across Ireland

Abstract

Establishing the abundance and distribution of species is central to conservation biology. Species Distribution Models (SDMs) are a useful tool set for this purpose, especially for rare or elusive species for which limited species occurrence data exist. The Eurasian woodcock *Scolopax rusticola* (hereon woodcock) is an elusive woodland-dwelling bird species that is not captured by general bird population monitoring schemes and therefore its population size and conservation status are poorly known in many areas. Here, a species distribution modelling approach was used to estimate the abundance and distribution of woodcock at a national scale. Survey data collected over three years from 238 randomly-selected woodland sites in Ireland using a species-specific protocol was analysed in two steps. First, presence/absence data were used to fit an ensemble SDM to estimate the national range, using bioclimatic variables. Second, relationships between woodcock abundance, climatic and habitat variables were modelled (conditional on presence) and projected across the estimated range to generate estimates of national distribution and population size. Approximately 49% of variation in abundance was explained by the explanatory variables, including mean summer temperature, area of forest cover and forest species and age composition at different landscape scales. The model suggested that breeding woodcock are more widely distributed in Ireland than previously reported, though lends support to a recent range contraction. We generated a national population estimate of 27,434 males (95% CL: 16,947 - 36,288), the first such national estimate for any bird species produced in this way, as far as we are aware. Our results indicate that the breeding distribution of this elusive species is determined by a complex interplay of climate throughout the year and landscape-scale habitat factors. Future changes may be difficult to accurately predict, though increasing rates of afforestation using mixed and broadleaved species is likely to benefit this species. However, this may be negated by the effects of climate change which may have already contributed to the observed range contraction.

2.1 Introduction

Understanding what influences the distribution, abundance and population trend of a species is fundamental for informing population management and conservation efforts (Goldsmith, 2012), particularly at a time when global biodiversity is at high risk from human activity (IPBES, 2019). Rates of loss are particularly striking in forest ecosystems (Giam, 2017; Daskalova et al., 2020), where even minimal anthropogenic disturbance can have disproportionately large impacts on a species' conservation status (Betts et al., 2017). Long-term monitoring schemes have shown that many European woodland birds have declined since 1980, with habitat specialist, insectivorous and ground-nesting species particularly strongly impacted due to landscape-scale changes to resource availability or predation risk (Gregory et al., 2007; Bowler et al., 2019; Stanbury et al., 2021), while climate change may also present a significant threat to some species (Leech and Crick, 2007). In addition, woodland specialist birds are important indicator organisms for assessing the impacts of change on forest ecosystems due to their complex ecological requirements, and the relative ease with which they may be surveyed (e.g. Lindenmayer, McIntyre and Fischer, 2003; Betts *et al.*, 2006; MacKay, Allard and Villard, 2014; Porro, Chiatante and Bogliani, 2020). However, where a species is elusive, it can become difficult to accurately evaluate its conservation status or identify the drivers of population and distributional change (Black, 2020).

Species Distribution Models (SDMs) represent a powerful set of analytical tools that allow detailed exploration of the spatial relationships between species and characteristics of their environment such as climate or habitat (Franklin, 2010). At a range of scales, these relationships can be projected to estimate a species' distribution and, in some cases, variations in density and abundance (Tôrres et al., 2012; Krüger et al., 2018), as well as forecasting or hindcasting spatial effects of environmental change (Holloway, Miller and Gillings, 2016). SDMs have regularly been used to highlight the potential impact of climate change on bird species' distributions, with many expected to respond by undergoing range shifts. For some, this may mean a contraction or loss of climatically suitable range (Marini et al., 2009; Matthews et al., 2011; Velásquez-Tibatá, Salaman and Graham, 2013; Coxen et al., 2017; Freeman, Sunnarborg and Peterson, 2019). For others, it may create new opportunities for range expansion into new climatically suitable areas (Matthews et al., 2011; Melles et al.,

2011). Such shifts in range will likely be further influenced by a range of interrelated ecological variables, such as species traits, competition, and habitat availability and connectivity as per the biotic, abiotic and movement (BAM) theoretical framework (Soberon and Peterson, 2005). Therefore, climatically derived SDMs should result in more ecologically realistic projections if these details can be taken into account (Van Der Putten, Macel and Visser, 2010; Meier et al., 2012; Mpakairi et al., 2017; Reino et al., 2018).

SDMs have often been used to further understand how woodland bird species may distribute themselves in a landscape according to forest habitat availability, composition and quality, which can inform land management and conservation (Mitchell, Lancia and Gerwin, 2001; Brotons, Herrando and Pla, 2007; Ferraz et al., 2012; Zuckerberg et al., 2016; Porro, Chiatante and Bogliani, 2020). The identification of previously unknown, potential high-priority areas for conservation is another important application of this method (Moradi et al., 2019). Furthermore, SDMs can be used to predict how populations may respond to land-use and habitat changes. For instance, habitat creation policies are expected to increase the range of specialist forest bird species by around 23.7% in a highly fragmented landscape in Brazil (Ferraz et al., 2012). While SDMs are often used to model the distributions of specialist, endangered, elusive or inaccessible species (Wilson, Roberts and Reid, 2011; Lavers et al., 2014; Fournier et al., 2017; Krüger et al., 2018), robust models crucially require sufficient high-quality species occurrence data, ideally including true absences, which can be challenging to obtain for such species (e.g. Wintle *et al.*, 2005). As such, most studies use presence-only data or machine learning, which can impede interpretation of important ecological processes determining the distributions (e.g. Angelieri *et al.*, 2016; Mi *et al.*, 2017; Dias *et al.*, 2023). Targeted efforts to engage fieldworkers to undertake specialised, species-appropriate methods may be required to collect sufficient presence/absence data for monitoring elusive or obscure species using SDMs.

In some cases, SDMs may offer the added possibility of modelling population density and abundance. This is a much less developed function of SDM methodology, as many extrinsic factors can influence abundance which cannot all be fully captured in an SDM; as such, it has been suggested that SDMs may be better at predicting upper limits of abundance (VanDerWal et al., 2009) and indeed, in some cases, SDMs are

poor at predicting abundance (e.g. Oppel et al., 2012). However, up to 70% of single-species studies that modelled abundance using SDMs have been validated by independent data (Lee-Yaw et al., 2022), particularly where quantitative data were collected and/or two-step methods combined separate probability of presence and abundance models (e.g. Boulangeat, Gravel and Thuiller, 2012; Mellin *et al.*, 2012).

The Eurasian woodcock (hereon woodcock) is a forest-dwelling bird found widely across the Palaearctic and represents an example of a species that cannot be reliably surveyed using commonly used bird survey methods such as daytime transects (Bibby, 2000). As well as being largely nocturnal, they are shy and highly camouflaged in their preferred dense woodland habitat, taking flight during the day only at very close range. As such, relatively little is known about the population trends of this species across its range, though it is reported to be stable across Fennoscandia (Lindström et al., 2015) and in France (Gossmann and Ferrand, 1998), but declining in Great Britain (Heward et al., 2015; 2024). In the Republic of Ireland (hereon Ireland), the woodcock is a widespread breeding species but is thought to be in decline (Colhoun and Cummins, 2013; Gilbert, Stanbury and Lewis, 2021). Although it is a culturally important quarry species for hunters in the non-breeding season, there is currently no national monitoring scheme with a focus on this species. The breeding bird atlases of the United Kingdom and Ireland, which consist of three comprehensive volunteer-based surveys for all breeding bird species between 1968 and 2011 (Sharrock, 1976; Gibbons, Reid and Chapman, 1993; Balmer et al., 2013), suggest a breeding range contraction of >70% over a span of 40 years in Ireland (Figure 1.4). This resulted in the woodcock's placement on the 'red list' of species of conservation concern (Colhoun and Cummins, 2013; Gilbert, Stanbury and Lewis, 2021).

The reasons for these recorded range contractions are unknown. Given their specific habitat and dietary requirements during the breeding season (Hirons and Johnson, 1987; Hoodless and Hirons, 2007), and their vulnerability as ground-nesting birds, woodcock are likely to be sensitive to habitat change. Whilst forest cover only represents 11.6% of its land area and remains highly fragmented, Ireland has seen rapid afforestation in recent decades with a strong focus on commercial softwood plantations harvested via clearfelling (DAFM, 2023). However, as breeding woodcock are reported to prefer deciduous woodland over conifers, and such plantation forestry largely lacks the preferred habitat heterogeneity (Hirons and Johnson, 1987; Hoodless

and Hirons, 2007; Heward et al., 2018), this afforestation may have only provided limited benefit so far, especially if current forest management practices are not sympathetic to the needs of breeding woodcock (Fuller et al., 2007). Climate and weather may play an important role in determining breeding distribution; there is evidence that summer weather conditions, such as temperature and precipitation, affect breeding success (Guzmán and Arroyo, 2015; Le Rest et al., 2019), whilst the species' distribution on the south-western continental fringes of its global breeding range is limited to cool, damp mountainous regions, suggesting climatic restrictions (Machado *et al.*, 2008a; Braña *et al.*, 2013). This species can also be heavily exploited by hunters during the legal open season. Whilst it is likely that, like British breeding woodcock, those in Ireland are largely non-migratory, it is likely that most of those harvested in recent years are migrants from the continent (Hoodless and Coulson, 1994), though the possibility that hunting may have contributed towards localised declines in the breeding population cannot be ruled out. Ultimately, it is difficult to know whether the breeding bird atlases, which largely relied on general, non-specific survey methods focusing on diurnal species, were able to capture the true nature of recent distributional changes given the elusive habits of the species, despite observers being encouraged to undertake dusk visits for the most recent atlas.

The current distribution, population and species-environment relationships remain poorly known for breeding woodcock, especially in Ireland. To address these knowledge gaps, we co-ordinated a national species-specific survey undertaken from 2017 to 2021, producing an occurrence dataset consisting of quantitative presence records (counts of roding males), as well as true absences. We used a two-step modelling approach: firstly, we used these data in an ensemble SDM to investigate relationships between bioclimatic variables and probability of presence, as well as estimating the national breeding range. Secondly, we modelled the relationships between woodcock abundance and bioclimatic and habitat variables, conditional on presence, using generalised additive modelling (GAM). Finally, we project the GAM across the estimated range and generate a distribution projection and sum all predicted density values to produce a population estimate. Importantly, we also hope this study 1) serves as a baseline against which future survey efforts may be compared to generate reliable population trends for monitoring purposes, and 2) helps demonstrate

the proficiency of this two-step method for predicting population estimates of elusive species more generally.

2.2 Methods

2.2.1 Roding surveys

Woodcock are most conspicuous when males undertake 'roding' display flights in search of receptive females from late February to mid-July with a peak in May and June (Figure 2.1; Hoodless et al., 2006). Roding flights are undertaken in circuits above the forest canopy, where the males repeatedly emit a distinctive two-toned call, consisting of a short series of low-pitched grunts followed immediately by a high-pitched squeak. This behaviour lasts for only an hour or so at dusk, meaning that one site per evening can be surveyed by a single observer, and forms the basis for most breeding surveys across parts of its European range (Hoodless *et al.*, 2006, 2009; Machado *et al.*, 2008a, Machado *et al.*, 2008b; Fokin and Blokin, 2013; Heward *et al.*, 2015).

Figure 2.1. A roding male woodcock seen during a survey in county Clare in 2019.

A total of 2,783 potential survey areas were generated randomly across forest cover on the island of Ireland using ArcGIS Pro v.3.1.0. As it is thought to be the minimum forest area required to support breeding woodcock (Fuller, 1982), only continuous blocks of forest over 10 hectares were used to generate potential survey areas. Potential survey areas comprised circular areas 2 km in diameter to maximise the

chance that a suitable survey watch point could be found within, and were spaced apart by at least 1km to avoid duplication of survey zones (Heward et al., 2024). Forest cover was based on land cover data provided by Coillte, the Forestry Division of the Irish Governmental Department of Agriculture, Food and the Marine (DAFM), and the Forest Service of the Northern Ireland Governmental Department of Environment, Agriculture and Rural Affairs (DAERA).

Potential survey areas were made publicly available online where volunteers could select them and register their intent to survey. Chosen survey areas were usually selected by volunteers due to proximity and convenience, though there was no obvious bias towards areas of higher human habitation. Prior to undertaking surveys, surveyors were asked to choose an appropriate observation point within or adjacent to the largest block of forest within their chosen survey zone(s), and that provided a reasonable view of the sky over the local forest area.

Surveys were conducted in 2017, 2019 and 2021. In each year, the survey period ran from 1st May to 30th June, coinciding with the seasonal peak period of roding woodcock activity (Hoodless et al., 2006). Each survey site was surveyed once, twice, or ideally three times during the survey period. All surveys were conducted from the same observation point within each survey area. Surveys commenced fifteen minutes before sunset and ran for seventy-five minutes. During this period, each woodcock seen or heard was registered. If two woodcock were seen at once, they were recorded as two separate registrations. Data were submitted through an online application, by email or by post. Unfortunately, although attempts were made to engage enough volunteers in Northern Ireland, there were insufficient data collected to include that region in this study. Verification and cleaning of survey data was undertaken. Where details submitted by surveyors were questionable, for example if the count of registrations appeared unrealistically large, or they had recorded woodcock in unexpected locations, attempts were made to contact the surveyors to verify the information. Where appropriate, incorrect data were corrected (n = 8) whilst unverifiable data records were excluded (n = 10).

In addition to surveys, an effort was made to collate casual records of woodcock submitted by observers in the breeding season (15th April to 15th July) between 2017 and 2021 inclusive. These records provided additional presence data that was used

primarily to illustrate the extent to which our approach identified the entire breeding range.

2.2.2 Explanatory variables

The nineteen raster datasets representing historical (near-current) bioclimatic variables (Table A.1) from 1970-2000 at 30 arc seconds were obtained from Fick and Hijmans (2017). Bioclimatic variables represent ecologically relevant climate information, such as annual and quarterly precipitation and temperature averages, ranges and seasonality. These were then resampled to ensure a consistent 1 km^2 resolution across the study area for integration into the SDM. These are the best available relevant bioclimatic data, and for the purposes of this study, they represent current bioclimatic variables in Ireland.

Forest land cover data for 2020 in vector format for Ireland was obtained from Coillte, the Forestry Division of the DAFM, and the 2018 Corine Land Cover Inventory (European Environment Agency, 2019). Although the latter source is considered less precise and thematically coarse (Grafius et al., 2016; Lambert, Cawkwell and Holloway, 2021) it was used to identify the few significant areas of forest not included in the former two datasets. All these sources were then collated to produce a single forest land cover dataset for the island of Ireland. Blocks of forest land cover were categorised according to type, similar to standard Irish forestry categories (Keane, Mason and Pfeifer, 2018): 'coniferous' (comprising ≥75% coniferous trees), 'broadleaved' (comprising ≥75% broadleaved trees), and 'mixed' (comprising a mix of coniferous and broadleaved trees where neither type exceeds 75%). Forest land cover was further categorised by majority tree age following the method of Keane, Mason and Pfeifer (2018): 'prethicket' (less than 8 years), 'thicket' (8 to 20 years), and 'mature' (more than 20 years, closed canopy). For the purposes of this study, forest land cover in the 'prethicket' category was excluded from subsequent analysis as it overwhelmingly comprised newly-planted forestry; given its open nature often dominated by herbaceous vegetation, scrub or bare ground and that it is most preferred by species associated with open or shrubby habitat (Wilson et al., 2009; O'Connell et al., 2012), it is unlikely to represent suitable habitat for roding woodcock.

To provide a measure of potential human disturbance such as recreation and dog-walking, urban settlement was included as a land cover category. Urban land cover

data for Ireland were obtained from the 2018 Corine Land Cover Inventory (European Environment Agency, 2019). To represent significantly built-up urban settlement areas, the following Corine land cover categories were collated: Continuous urban fabric; Discontinuous urban fabric; Industrial or commercial units.

The following land cover vector datasets were produced: i) all forest; ii) coniferous forest; iii) broadleaved forest; iv) mixed forest; v) mature forest; vi) thicket-stage forest; vii) urban settlement. From these, habitat raster datasets were generated, each corresponding to a separate habitat variable, with cell size resolution of 10 meters across the land area of Ireland (Figure 2.2).

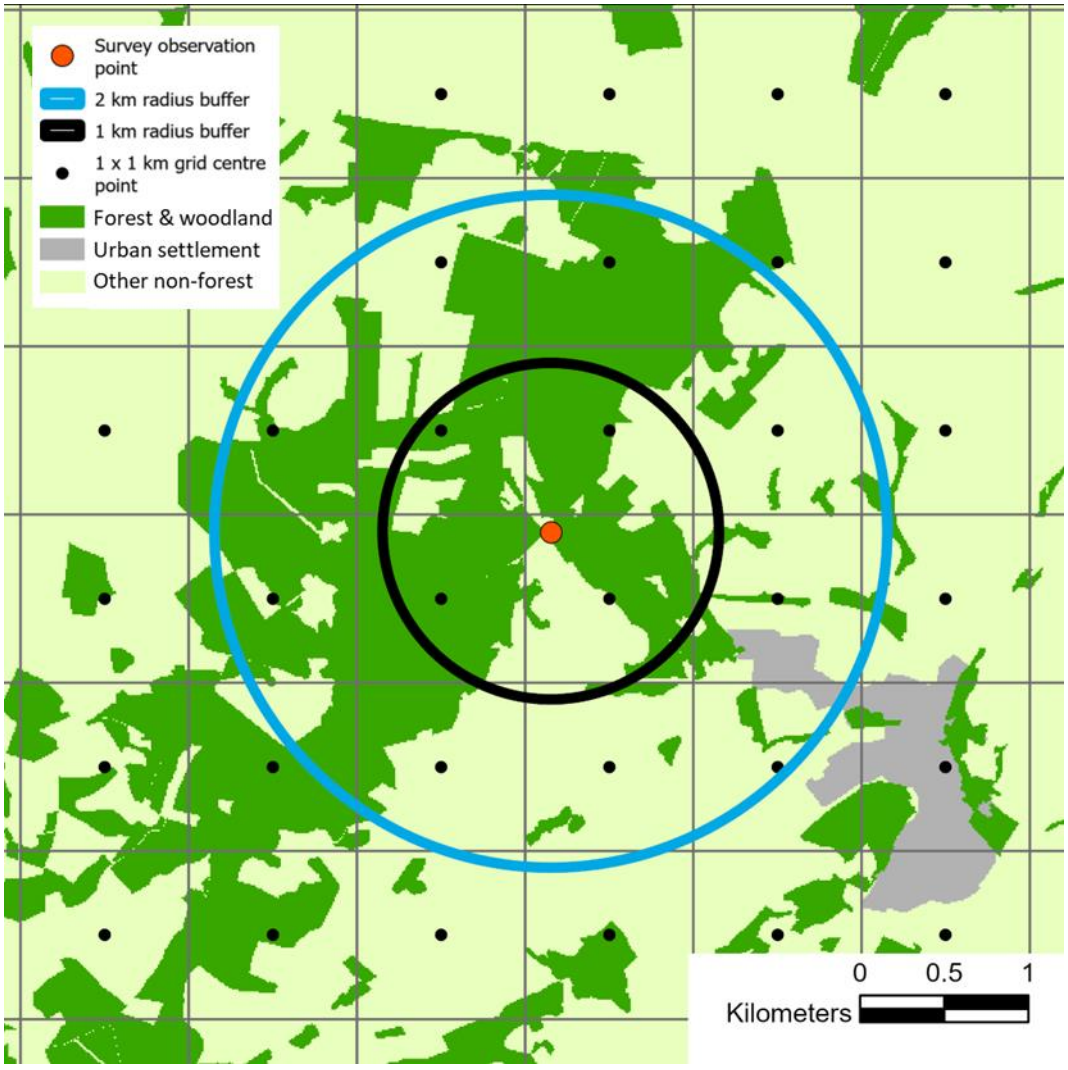


Figure 2.2. A map showing a roding woodcock survey site. Examples of map features generated during data preparation and analysis are shown, including: the survey observation point and its surrounding 2 km and 1 km buffer zones; the 1 km^2 grid and grid-square centre points which overlay the entire land area of Ireland; and habitat category rasters (forest & woodland, urban settlement and other non-forest habitat types). For figure simplification, all forest and woodland types were combined into a single category.

2.2.3 Model 1: Probability of presence and range estimation

Figure 2.3 provides a methodological workflow of the two-step SDM framework used in this study.

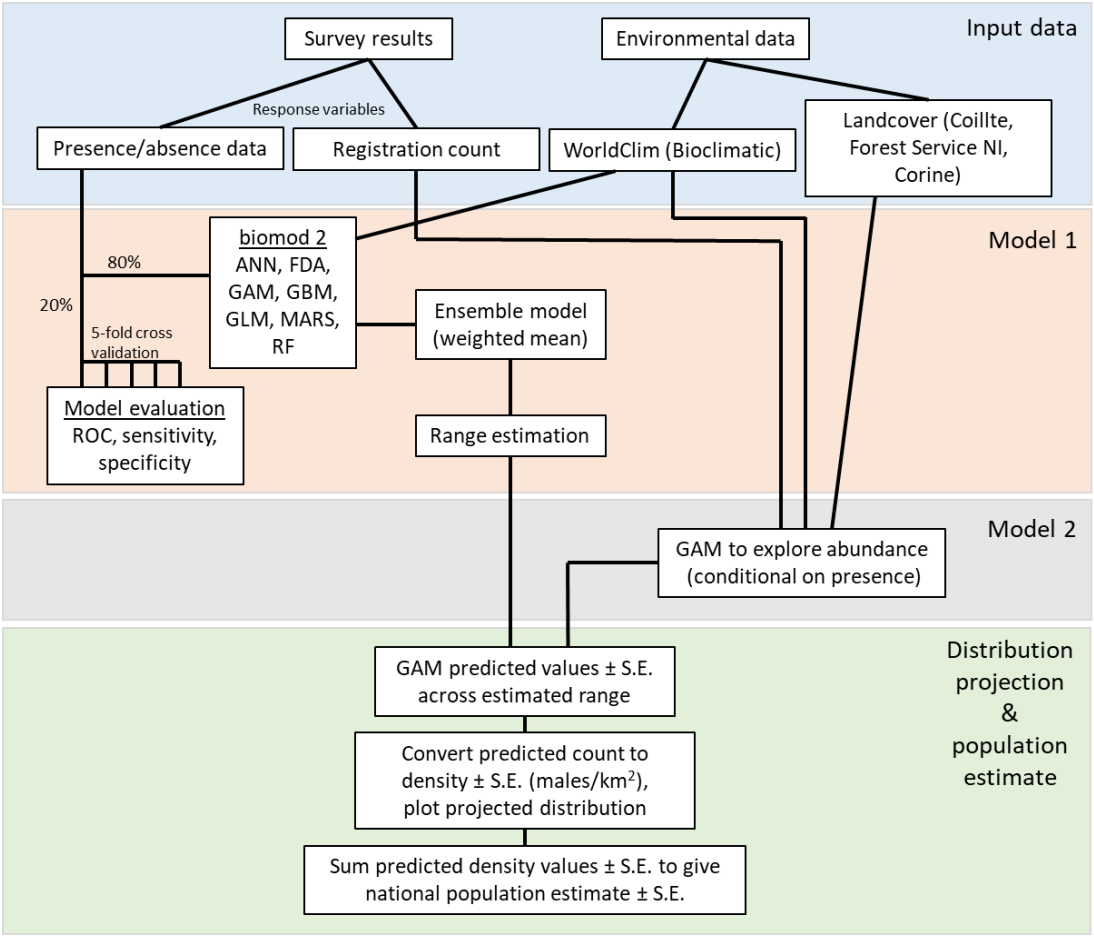


Figure 2.3. Conceptual workflow of the species distribution modelling framework implemented in this study.

To estimate the species' breeding range in Ireland, a SDM was produced using the 'biomod2' package (Thuiller et al., 2009) in R v.4.1.2 (R Core Team, 2021). 'Biomod2' allows for the construction of a single-algorithm distribution model as well as consensus (ensemble) distribution models, which have been shown to significantly increase the accuracy of SDM projections (Comte and Grenouillet, 2013). The response variable comprised a binary dataset of occupied (1) and unoccupied (0)

surveyed sites, the status at each designated as '1' if woodcock had been observed during at least one visit, or '0' if woodcock had not been recorded on any visit. Due

to repeat visitation for over 88% of survey sites (Table 2.1), we have much greater confidence that 0 likely represents true absences, compared to arbitrary pseudo-absences commonly generated at random to provide a negative class in presence/absence SDMs. Explanatory variables for the national model were bioclimatic only and were chosen based on ecological relevance and correlation values (threshold: r = 0.7) to remove collinearity between covariates (Table A.2). As a result, five bioclimatic variables were chosen to include in the modelling analysis: Bio3 (isothermality), Bio10 (mean temperature of warmest quarter), Bio11 (mean temperature of coldest quarter), Bio12 (annual precipitation) and Bio15 (precipitation seasonality).

An ensemble model was constructed from seven modelling techniques with default parameters: Artificial Neural Network (ANN), Flexible Discriminant Analysis (FDA), Generalised Additive Models (GAM; using the package 'mgcv'; Wood, 2011), Generalized Boosting Models (GBM), Generalised Linear Models (GLM), Multiple Adaptive Regression Splines (MARS) and Random Forests (RF). Five-fold cross-validation was undertaken for each model type to avoid possible spatial autocorrelation between training and evaluation data (Thuiller et al., 2009), training the models on 80% of the data and testing the data on the remaining 20% to evaluate accuracy.

The final ensemble projection was generated using a weighted mean method in 'biomod2', based on the AUC values of each individual model run, where those with higher AUC scores had more influence in determining final values. Model accuracy was determined by the average area under the curve (AUC) of a receiver operating characteristic (ROC) statistic, the power to predict presences (sensitivity) and the power to predict absences (specificity). Model projections were generated as continuous values between 0 and 1, representing probability of presence. A binary transformation was applied to the weighted mean projection to generate an 'estimated range', where the threshold was based on the prevalence of occupied sites as a proportion of the total set of surveyed sites (Franklin, 2010).

Mean variable importance for each single-algorithm model was returned by 'biomod2'. Variable importance for the ensemble model was calculated by multiplying the weightings used for the ensemble forecasting with the variable

importance scores for individual models. Resulting values for each variable were summed to produce the weighted mean importance (Fletcher et al., 2016).

2.2.4 Model 2: modelling abundance

The relationships between woodcock abundance and explanatory variables across survey areas were explored using a general additive model (GAM) approach with the 'mgcv' package (Wood, 2011) in R v.4.1.2 (R Core Team, 2021), which allows for a flexible framework that can detect whether a non-linear or linear fit is more suitable for each covariate. This part of the analysis was conditional on presence: only survey sites that intersected with the estimated range produced by Model 1, or those that did not intersect but did record roding woodcock, were included. In addition, only those that received at least two visits were included. From each site, the maximum number of total registrations of woodcock across visits was used as the response variable. The maximum registration counts were used as they are thought to provide the best index of male abundance at a site (Hoodless et al., 2006; 2008). As the response variable used in the GAM was a count of integers, and included a number of zeros that may have arisen for mixed reasons, a 'zero-inflated Poisson' distribution was chosen (Loeys et al., 2012).

Explanatory variables included both bioclimatic and land cover (forest and urban) covariates, and were chosen based on ecological relevance. To explore the importance of habitat on woodcock abundance at different spatial scales, circular buffers of radii 2 km and 1 km were created around each survey site (Figure 2.2). For each buffer size, the following land cover variables were calculated from the habitat raster layers for each survey site: i) total forest cover as a percentage of total buffer area; ii) coniferous, broadleaved and mixed forest cover each as a percentage of total forest cover; iii) mature forest cover as percentage of total forest cover; iv) Total urban settlement area as a percentage of total buffer area. In addition, values corresponding to the distances from each survey site to the nearest urban area over 0.5 km^2. To facilitate model projection, a grid of 1 km^2 squares was generated across the entire land area of the country (Figure 2.2), and corresponding values for each habitat and bioclimatic variable were generated for the centre points of each grid square.

Correlation matrices using Pearson's correlation tests were produced between all bioclimatic variables and between all land cover variables (Table A.3; Table A.4);

where two variables had high correlation values ($r > 0.7$), one was excluded to remove collinearity and ensure variable independence. There was strong collinearity between similar variables each calculated within 1 and 2 km buffer scales (r = between 0.76 and 0.94). At both buffer scales, proportions of broadleaved and coniferous forest were overall strongly negatively correlated ($r = 0.90$ and 0.91 at 1 km and 2 km scales, respectively); therefore, broadleaved forest was excluded as a variable as it was generally less common than coniferous forest. After testing for collinearity, five bioclimatic variables of a total of nineteen were considered, including Bio3 (isothermality), Bio4 (temperature seasonality), Bio10 (mean temperature of warmest quarter), Bio11 (mean temperature of coldest quarter) and Bio12 (annual precipitation). X and Y coordinates were also included as an explanatory variable to account for spatial autocorrelation (Renner et al., 2013; Heinänen et al., 2017). To test whether potential population fluctuation from year to year affected the counts, year of survey was included as a categorical variable. Smoothed terms of each predictor variable were considered significant when $p < 0.05$, and the deviance explained by the model was used as a measure of model fit. Model selection began by excluding explanatory variables that returned non-existent or weak relationships which were not ecologically meaningful. The 'dredge' function in the R package 'MuMin' was used as a guide where different models produced by all possible combinations of variables under consideration were ranked by the Akaike Information Criterion (AIC). The model with the lowest AIC score was selected as the best model. By this stage, five variables were included: one bioclimatic (Bio10), three land-cover (forest cover within 2km, proportion of forest that was coniferous within 1km, proportion of forest that was mature within 1km) and X/Y coordinates.

2.2.5 Distribution projection and population estimate

The selected model was used to project the distribution of breeding woodcock across Ireland. The 'predict.gam' function in the 'the 'mgcv' package (Wood, 2011) in R v.4.1.2 (R Core Team, 2021) was used to predict fitted values corresponding to estimated maximum registration counts (R), along with standard errors (SE_R). This was done for all 1 km^2 squares with more than 0.1 km^2 of forest (considered to be the minimum forest area required to support breeding woodcock; Fuller, 1982), which fell within the 'estimated range' produced in Model 1. Whilst the observed roding activity

of male woodcock is dependent on population density, the relationship between the total registration count and the number of individuals encountered is non-linear (Hoodless et al., 2008). Thus, these predicted values were used to estimate the density of male woodcock across the modelled distribution, following the methods and justification detailed in Hoodless et al., (2008) and Heward et al., (2015), where estimated maximum registration counts (R) were used to estimate the number of individual males (N), using the equation $N = 0.74R^{0.708}$. As the mean area used by roding woodcock each evening as measured by radio- and global positioning system (GPS) tracking has been reported to be 0.88 km^2 - 1.29 km^2 (Hirons, 1980; Heward, 2020), it was assumed that the estimated number of individual males encountered is approximately equivalent to the density of males per km^2. Estimated density confidence limits (CL_D) were computed using:

$$CL_D = 0.74(R \pm (SE_R \times 1.96))^{0.708} \qquad Eq.1$$

Any lower confidence limit estimates computed as negative values were capped at zero.

To generate a national population estimate, density estimates (N) from every 1 km^2 square projected as present by Model 1, with more than 0.1 km^2 of forest, were summed. Similarly, the upper and lower 95% confidence limits of the population estimate were computed by summing the upper and lower estimated density confidence limits (CL_D), respectively, from every relevant 1 km^2 square.

2.3 Results

2.3.1 Roding surveys

Following data cleaning, a total of 238 random sites were surveyed at least once across Ireland, of which 88.2% received a minimum of two visits (Table 2.1). 125 (53%) sites were found to be occupied by woodcock of which 91% received at least two visits, and 46% received the recommended three visits. Occupied sites were widely spread geographically, although were less frequent across much of the west of Ireland, particularly the south-west and north-west (Figure 2.4). Across survey sites, forest structure was well represented relative to overall proportional availability of forest type (coniferous, broadleaved and mixed) and age (mature vs thicket; Table A.5).

Table 2.1. A summary of the sites surveyed for roding woodcock, including detail for year of survey and number of visits. No site was surveyed over multiple years.

	2017	2019	2021	Total
One visit	3	3	22	28
Two visits	40	50	52	142
At least three visits	19	17	32	68
Total	62	70	106	238

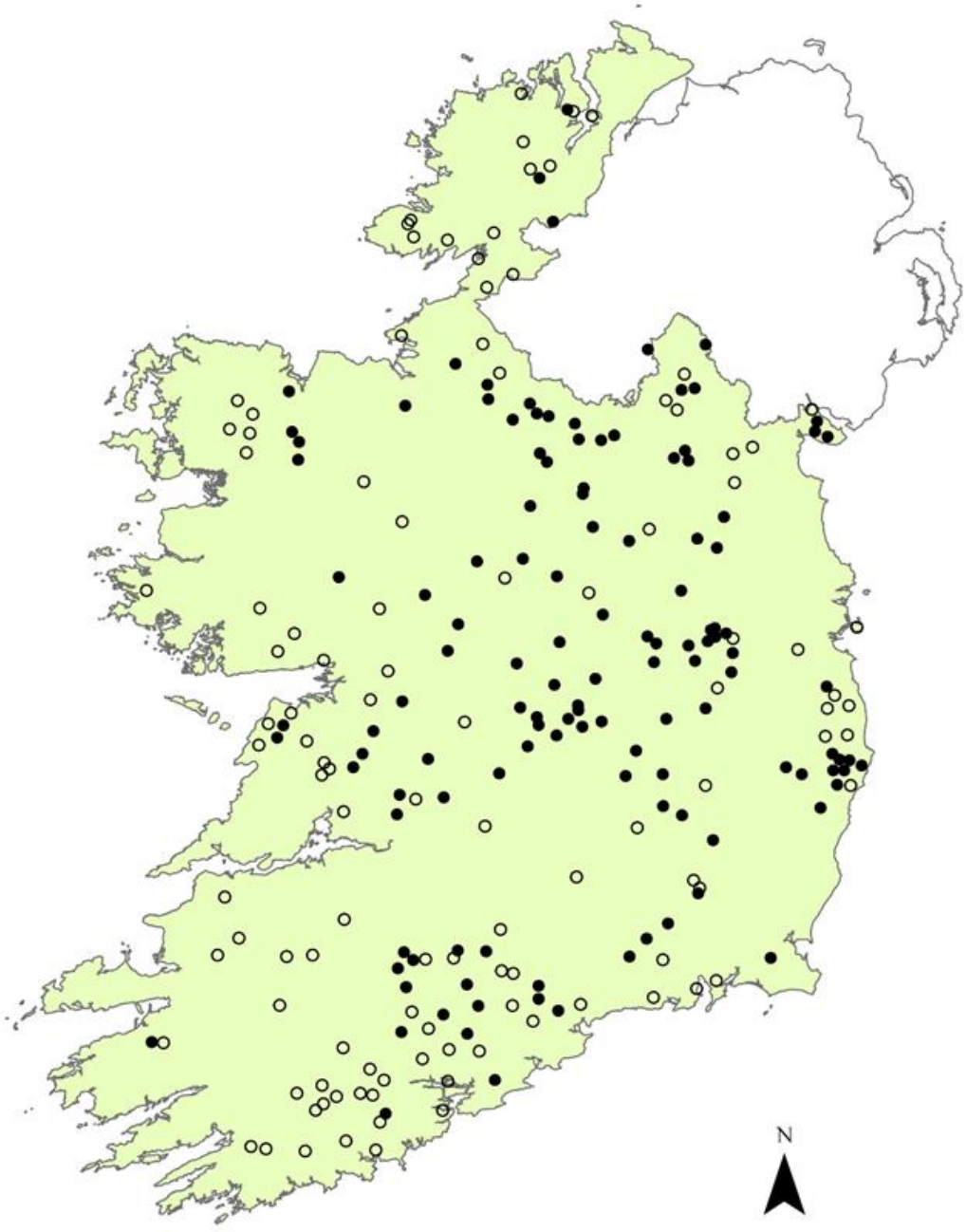


Figure 2.4. Location of sites occupied (filled circles) and unoccupied (open circles) by breeding woodcock in 2019, 2017 and 2021, based on surveys of roding males in 238 randomly selected forest sites that constituted at least 0.1km^2 continuous tree cover.

2.3.2 Model 1: probability of presence and range estimation

The estimated range of breeding woodcock in Ireland was modelled with relatively high predictive accuracy using five bioclimatic explanatory variables. The mean AUC score of each modelling method in cross-validation runs always exceeded 0.74 (Table 2.2). The mean-weighted ensemble model produced the highest AUC and specificity score, although it also produced the lowest sensitivity score.

Table 2.2. Mean accuracy metrics for the different model types used in 'biomod2' as well as the combined ensemble model. AUC = area under the curve.

Model	AUC	Sensitivity	Specificity
GLM	0.74	78.4	69.1
GAM	0.81	79.2	80.0
FDA	0.79	74.4	80.0
MARS	0.80	74.4	82.7
RF	0.81	76.0	79.1
GBM	0.83	76.0	83.6
ANN	0.78	78.4	78.2
Ensemble	0.90	73.2	90.0

The three most important predictor variables (Bio 15, Bio 11 and Bio 3) accounted for 84.64% of the sum of the importance values of all variables (Table 2.3). The response curve plot (Figure 2.5) for Bio 15 (precipitation seasonality) suggests that breeding woodcock tend to be found where there is relatively low seasonal variation in rainfall, ideally where variation in total monthly precipitation is between 18 and 24% of mean monthly precipitation over the course of the year. The response curve plot (Figure 2.5) for Bio 11 (mean temperature of coldest quarter) suggests that breeding tends to occur in areas where mean winter temperatures do not exceed 5.4°C. The response curve plot (Figure 2.5) for Bio 3 (isothermality; a measure of daily temperature oscillation relative to annual temperature oscillation, indicating temperature seasonality) suggests that breeding woodcock tend to occur where the mean monthly diurnal temperature range is more than 40% of the maximum annual temperature range, i.e. in areas with comparatively lower seasonal changes in temperature.

Table 2.3. Mean variable importance scores, presented as a % of the sum of all variable importance scores for each modelling method as produced by 'biomod2'. In bold are the three most important variable scores for the mean-weighted ensemble model. Bio10 = Mean temperature of warmest quarter; Bio11 = Mean temperature of coldest quarter; Bio12 = Annual precipitation; Bio15 = Precipitation seasonality (coefficient of variation); Bio3 = Isothermality (mean diurnal temperature range divided by annual temperature range)

Variable	Ensemble	GLM	GAM	FDA	MARS	RF	GBM	ANN
Bio10	12.71	8.16	16.68	14.82	21.87	12.87	9.63	4.21
Bio11	**31.45**	49.86	32.21	26.28	20.85	36.23	43.64	16.93
Bio12	2.66	0.00	1.06	0.00	0.00	6.79	2.18	7.74
Bio15	**35.98**	15.05	30.73	43.02	42.90	30.18	31.06	55.28
Bio3	**17.21**	26.92	19.31	15.88	14.37	13.93	13.49	15.84

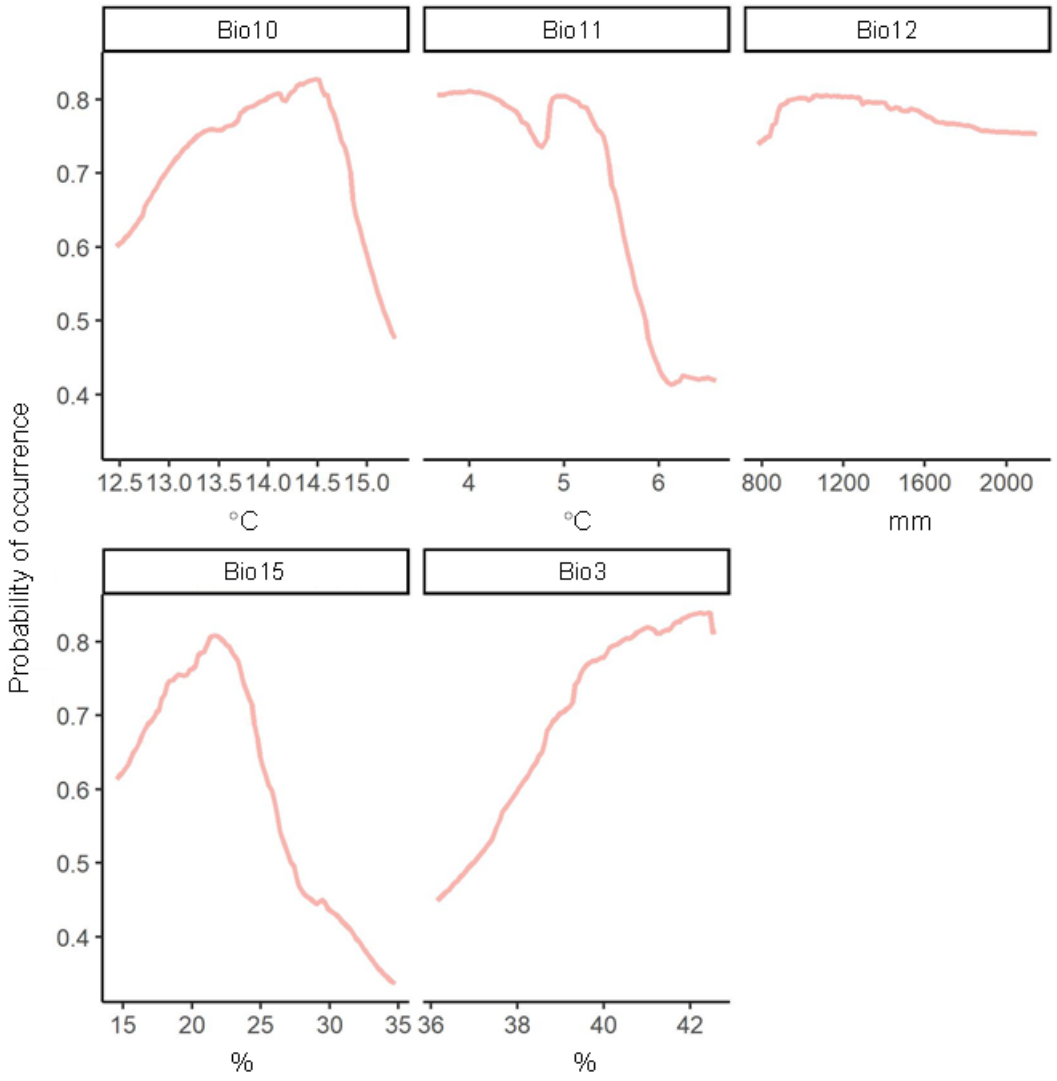


Figure 2.5. Response curve plots for each predictor variable used in the mean-weighted ensemble model in 'biomod2'. Bio10 = Mean temperature of warmest quarter; Bio11 = Mean temperature of coldest quarter; Bio12 = Annual precipitation; Bio15 = Precipitation seasonality (coefficient of variation); Bio3 = Isothermality (mean diurnal temperature range divided by annual temperature range).

The model output and estimated range suggest that breeding woodcock are likely to be present across much of the east, midlands and north-west of Ireland, and extend as far south as Waterford and East Cork, while they are unlikely to be found across most of the west, particularly the south-west, and Donegal (Figure 2.6.A and B).

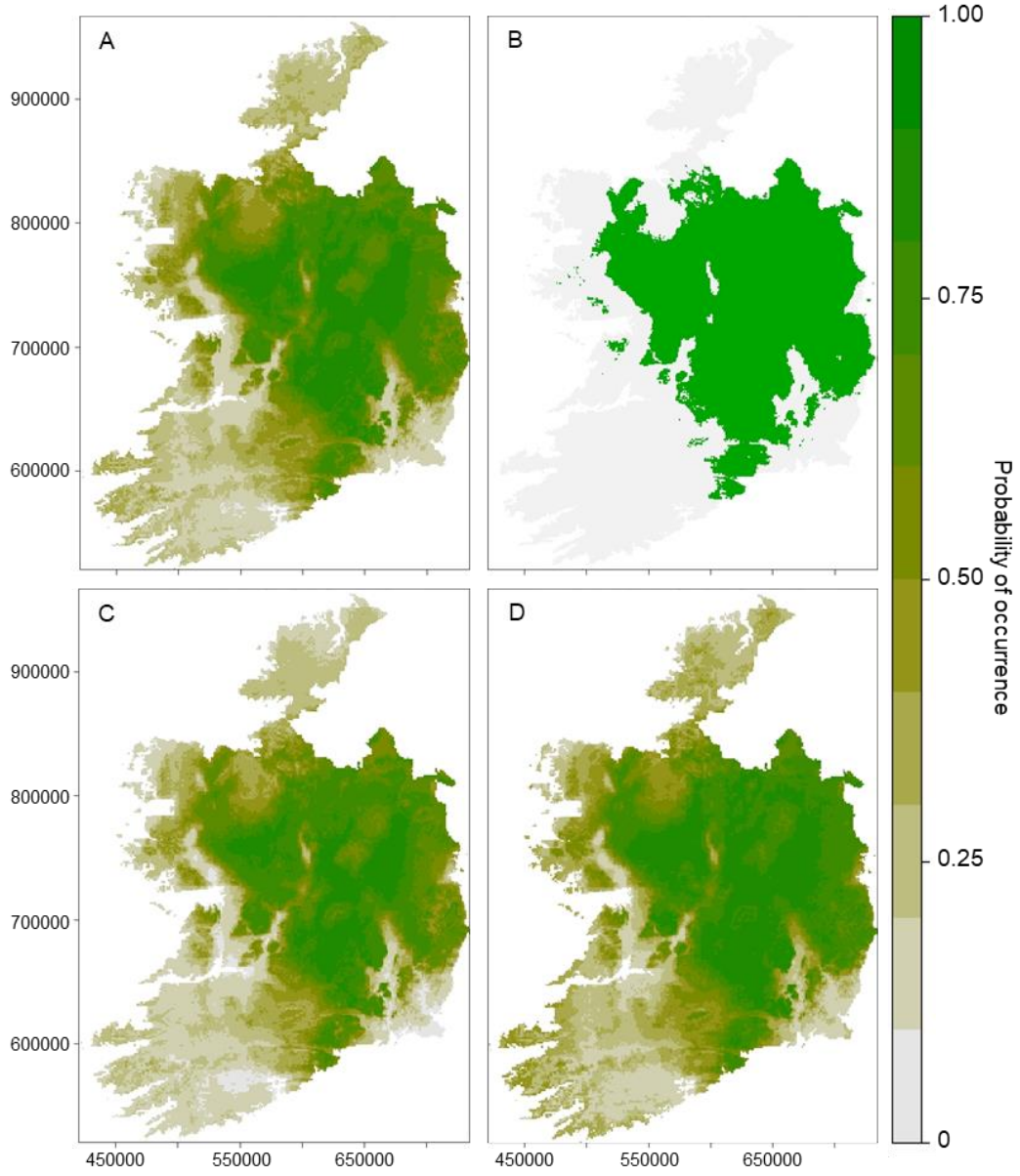


Figure 2.6. Species distribution model output maps showing the probability of occurrence of breeding woodcock in Ireland, based on surveys undertaken at 238 randomly selected woodland sites, produced using the package 'biomod2' in R: **A**) mean-weighted projection; **B**) an estimated species range generated from a binary transformation (threshold based on prevalence of occurrence = 0.53) of the mean-weighted projection to 'presence' (1) and 'absence' (0); **C**) Lower confidence limit projection; **D**) Upper confidence limit projection. Map coordinates are Irish Transverse Mercator (ITM).

2.3.3 Model 2: relationships between abundance and explanatory variables

After data cleaning, only counts from survey sites that fell within the estimated range from Model 1 or those that detected the presence of woodcock (n = 133) were used to explore relationships between woodcock abundance and explanatory variables (Figure 2.7). The selected GAM explained 48.9% of deviance and five of six explanatory variables had a significant effect on the response variable (Table 2.4); notably, year of survey had no significant effect ($p > 0.05$) and was not included in the selected model with the lowest AIC value. Observed and model predicted values were strongly positively correlated ($r = 0.70$, $p < 0.01$; Figure 2.8).

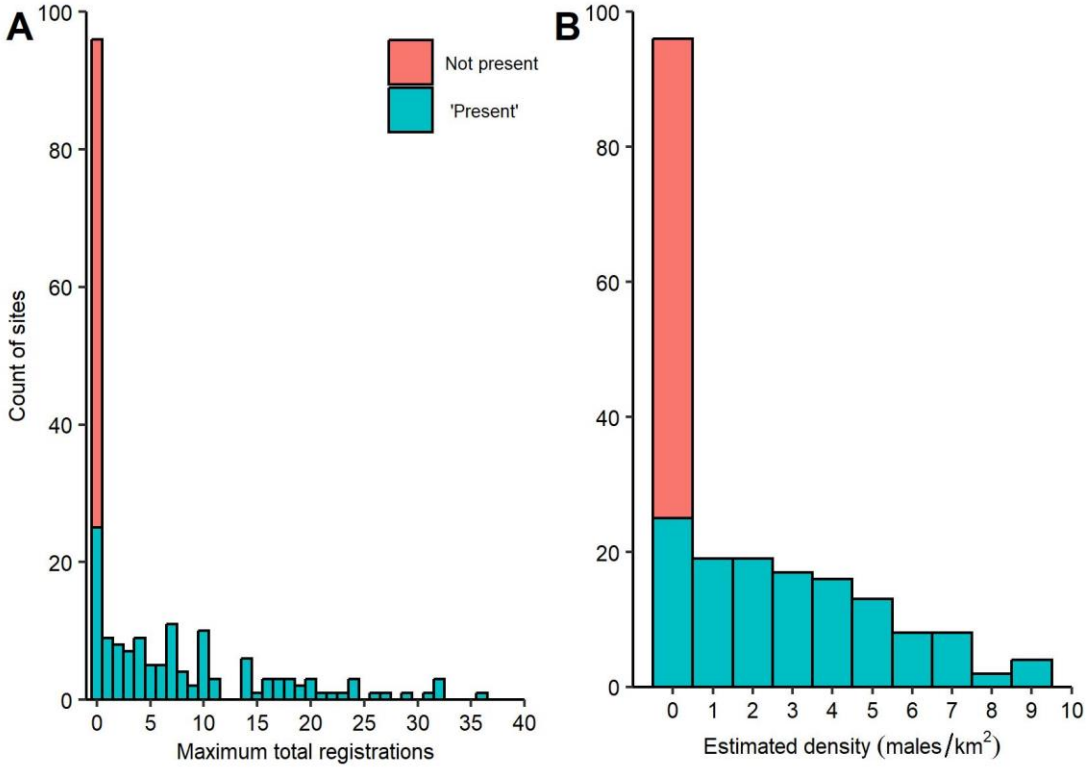


Figure 2.7. Histograms of (**A**) maximum total registration counts (R) from randomly-selected survey sites in Ireland in 2017, 2019 and 2021 at which repeat visits occurred (n = 204); and of (**B**) estimated density of male woodcock (N) at same survey sites derived from the equation $N=0.74R^{0.708}$ (Hoodless *et al*., 2009). In orange are sites that fall outside the estimated range from Model 1 where no woodcock were detected ('not present', n = 71); in blue are sites that fall within the estimated range or, if outside, detected the presence of woodcock ('present', n = 133).

Table 2.4. Summary of the explanatory variables included in a generalised additive modelling analysis with a zero-inflated Poisson distribution. The response variable was the maximum total registration count (R) from each survey site (n = 133). The four variables that had the most impact on R are highlighted in bold.

Explanatory variable	Edf	Ref. df	Chi.sq	p-value
Coordinates (X/Y)	**23.82**	**29**	**183.91**	**<0.001**
Bio10 (mean temperature of warmest quarter)	1.56	4	5.137	0.023
Area of forest cover within 2km	**3.72**	**4**	**50.47**	**<0.001**
Proportion of forest that is coniferous within 1km	**2.34**	**4**	**38.39**	**<0.001**
Proportion of forest that is mature within 1km	**3.43**	**4**	**24.727**	**<0.001**
Distance to nearest settlement over 0.5 km^2	< 0.01	4	0.00	0.326

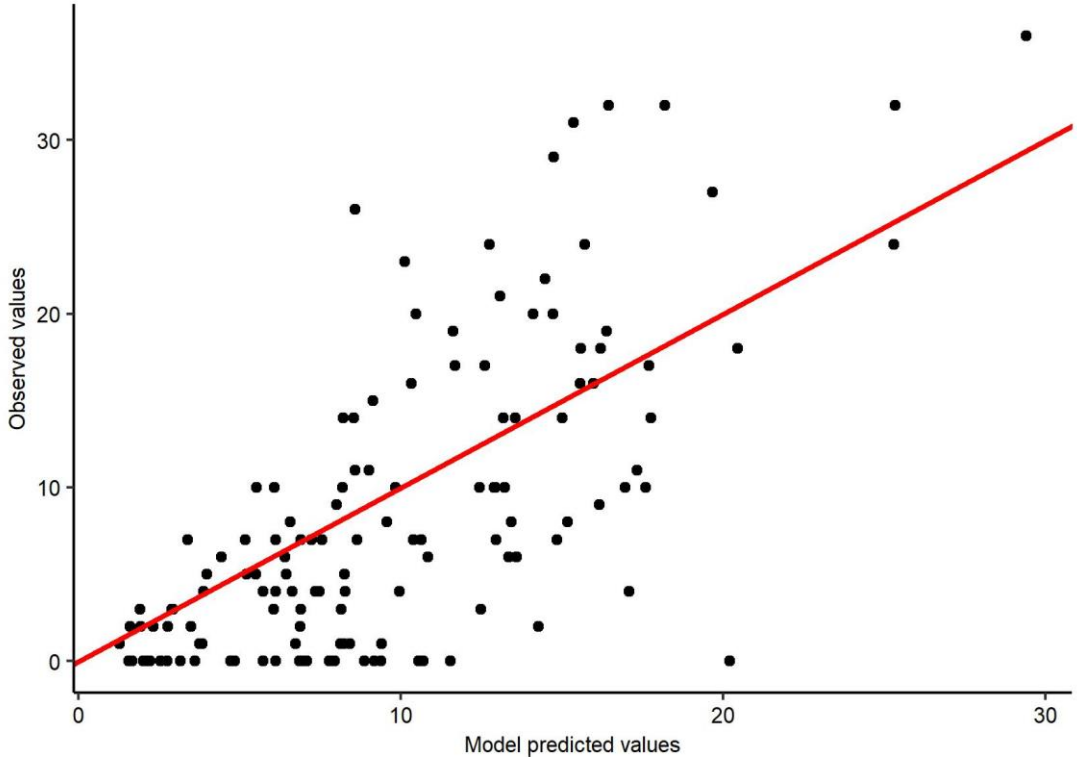


Figure 2.8. The relationship between observed values and model predicted values from the selected GAM for the response variable (maximum total registration count (R); r = 0.70, p < 0.01, n = 133). A red line with slope = 1 is shown for reference.

The selected model suggests that woodcock abundance was influenced by geographical location, as represented by the X/Y coordinates variable, where the highest densities tend to be found across the midlands north to county Monaghan, the east of counties Clare and Limerick and north-east county Cork, and the south-east (Figure 2.9.A). Geographical location in Ireland is not likely to directly influence

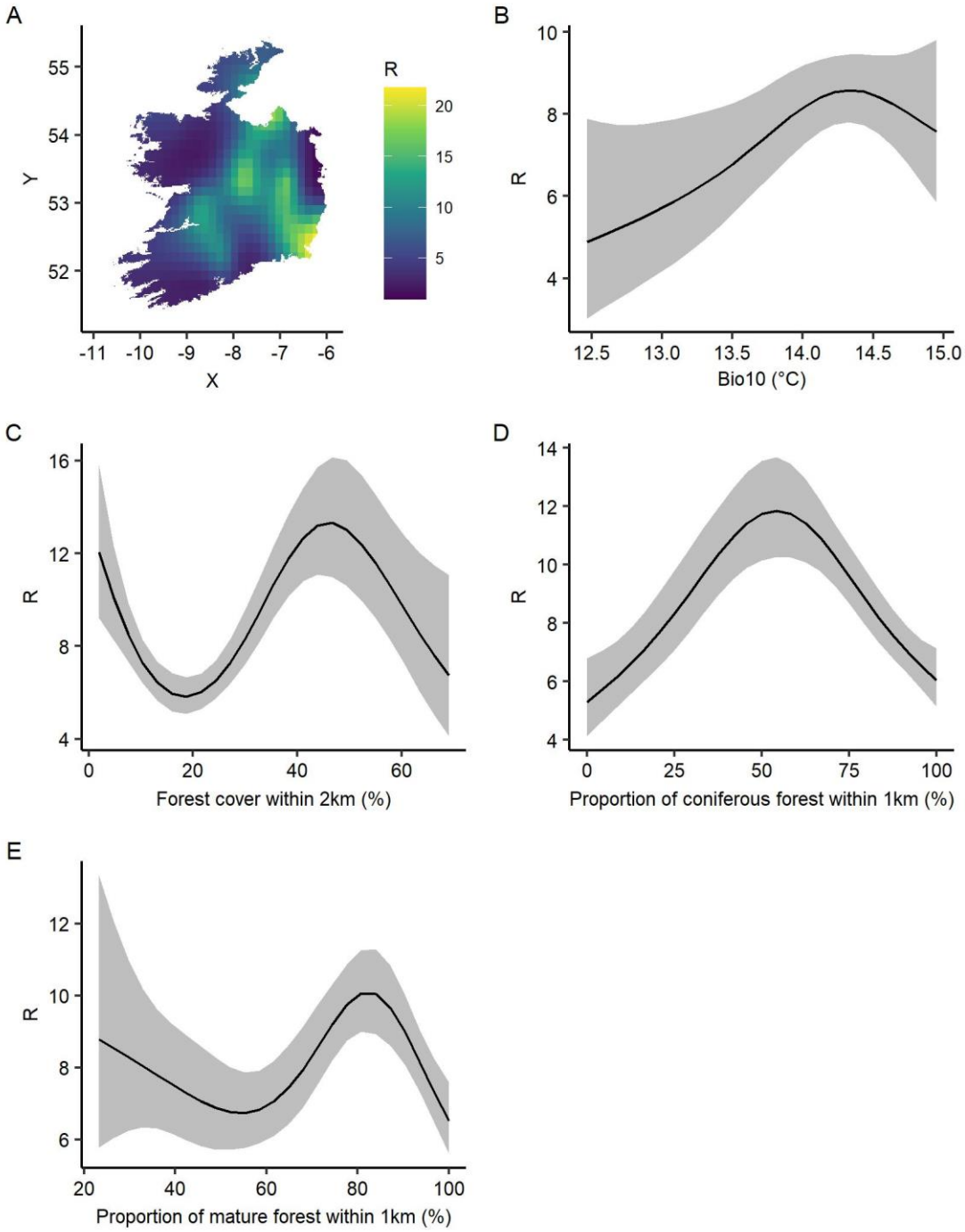


Figure 2.9. Response curves from the selected GAM showing significant relationships between the response variable (R) which corresponds to a maximum count of woodcock registrations, and predictor variables: (**A**) X/Y coordinates, here represented as longitude and latitude on the x and y axes, respectively; (**B**) Bio10 (mean temperature of warmest quarter); (**C**) Proportion of 2km radius buffer area comprising forest cover; (**D**) Proportion of all forest cover area as coniferous within 1km radius buffer; (**E**) Proportion of all forest cover as mature closed canopy (>20 years old) within 1km buffer. Shaded areas represent ±95% confidence intervals.

abundance, so it likely represents a combination of factors not otherwise sufficiently accounted for by other model variables. One bioclimatic variable was shown to significantly influence abundance, Bio10 (mean temperature of warmest quarter), suggesting that there was an increase in woodcock abundance with an increase in mean summer temperature, peaking where temperatures were higher than 14.0°C (Figure 2.9.B). However, this had relatively little impact and greater uncertainty compared to the landcover variables.

Woodcock abundance was strongly influenced by the area of forest cover within 2km of the survey site (Figure 2.9.C). Abundance peaked where forest cover comprised 40-50% of the total area. Abundance also appeared to increase when forest cover fell below 15%, although this may be an artefact and is discussed below. Composition of forests within 1km of the survey sites also significantly influenced woodcock abundance. Abundance peaked where the proportion of forest cover that was coniferous was 50-60%, decreasing to either side of these values (Figure 2.9.D), suggesting that high proportions of coniferous forest have a negative influence. The same may not be true for low proportions of coniferous forest as this relationship may result from poor representation of sites with low proportion of coniferous forest. Similarly, abundance peaked where 75-85% of forest within 1km was mature (> 20 years old), with greater uncertainty where < 55% of forest was mature (Figure 2.9.E).

2.3.4 Distribution projection and population estimate

The estimated distribution of breeding woodcock in Ireland (Figure 2.10) indicates that, where suitable habitat exists, they are most abundant across the midland counties, north to the borders of Monaghan and Cavan with Northern Ireland, west to Roscommon and the Slieve Aughty uplands in east Clare and south Galway, south into north Tipperary and Kilkenny, as well as around south Wicklow, north Wexford and Carlow. Elsewhere, in the extremities of their breeding range, woodcock typically exist at lower densities. Some areas where breeding woodcock were recorded during the survey time periods were not represented by the SDM. These areas include the inner Iveragh and Beara peninsulas of county Kerry, east Cork and Limerick, east Donegal, and south-east Wexford. These are shown as outlier records in Figure 2.10 for illustrative purposes. Based on our method, the total population estimate for

breeding woodcock in Ireland over the period from 2017 to 2021 is approximately 27,434 males (95% CL: 16,947 - 36,288).

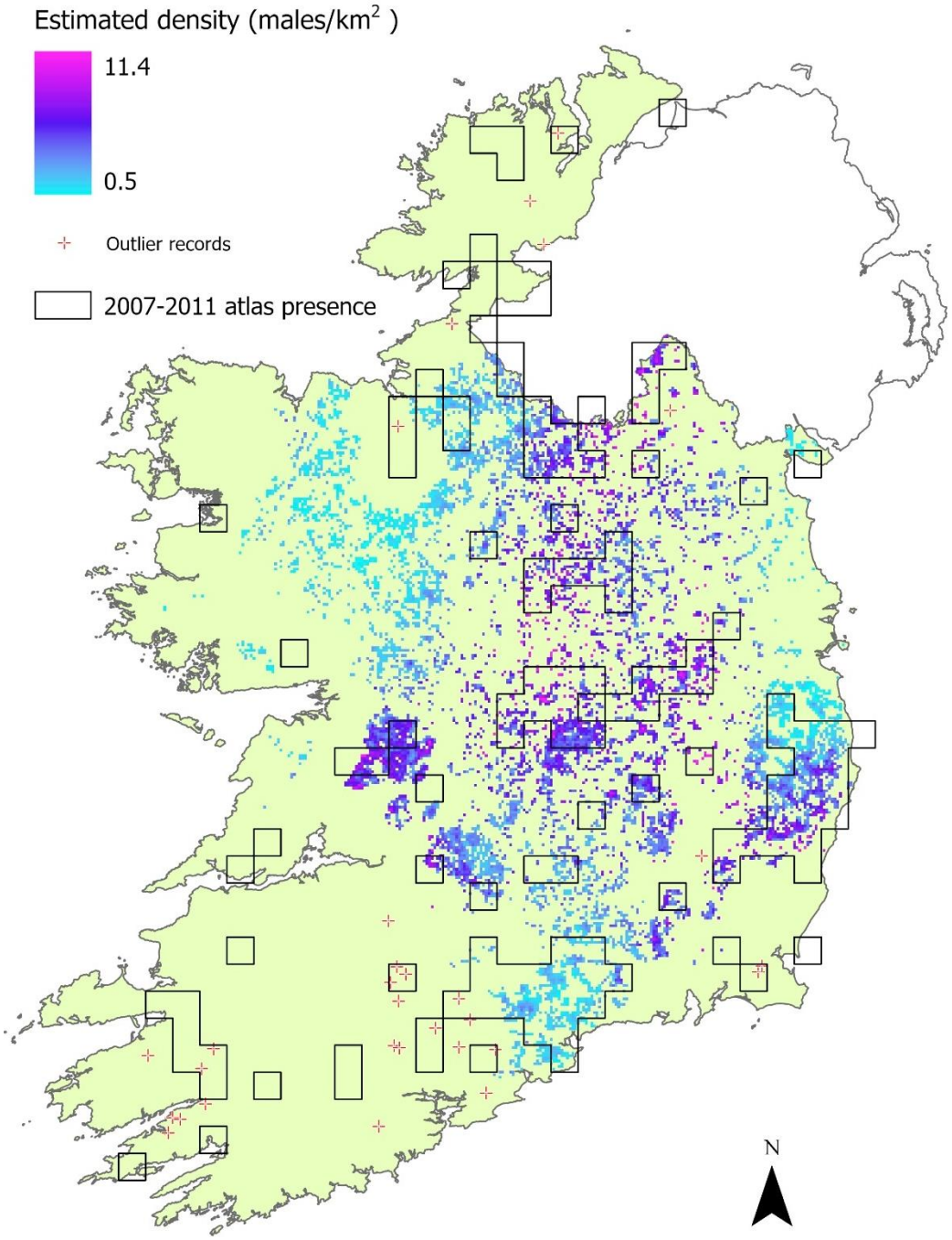


Figure 2.10. Estimated distribution of breeding woodcock in Ireland, produced from density estimates predicted from a GAM using five explanatory predictor variables for 1 km^2 squares with at least 0.1 km^2 woodland across the estimated range (produced using 'biomod2'; Figure 2.6.B), based on surveys undertaken at 133 separate randomly-selected sites in May and June of 2017, 2019 and 2021. Outlying records of birds displaying breeding behaviour, including occupied survey sites and casual sightings from the same time periods, which were located at least 5km from the estimated distribution, are included for illustrative purposes. The outlines of the 10 x 10 km squares where woodcock were recorded for the 2007-11 atlas are overlaid so this estimated distribution may be compared against the previously known distribution.

2.4 Discussion

In this study we used a two-step modelling approach to improve our understanding of the drivers behind breeding woodcock distribution and abundance, as well as to generate national distribution and population estimates. We present the results of a national survey using repeat visits, true absences, and quantitative species records. Our model outputs suggest that woodcock are still a widespread breeding species, and that a complex set of relationships with climatic and habitat variables influence the species' distribution and abundance.

2.4.1 Effects of climate on distribution

The Irish breeding population of woodcock is probably largely non-migratory (Hoodless and Coulson, 1994) and this explains why we found that climatic conditions throughout the year were influential. Woodcock were more likely to be found where mean winter temperatures did not exceed 5.4°C (Bio11, Figure 2.5) and were most likely to occur, and were most abundant, where mean summer temperatures were above 14°C (Bio10, Figure 2.5; Figure 2.9.B). Similarly, the relationships for Bio15 (precipitation seasonality) and Bio3 (isothermality) (Figure 2.5) suggest that woodcock prefer areas where there is relatively lower seasonal variation in rainfall and temperature, respectively. These patterns agree with the breeding distribution reported in other regions on the south-western fringes of its global range, where woodcock are restricted to mountainous regions (Machado et al., 2008a; Braña et al., 2013), which likely experience cooler, wetter summer conditions.

The ecological drivers of these relationships are likely linked to energetics and prey availability. Our survey sites, distributed widely across Ireland, had a mean summer temperature of between 12.5 and 15.0°C (Bio10, Figure 2.5; Figure 2.9). That the likelihood of occurrence and abundance peaked at the higher end of this range suggests that woodcock prefer warmer areas which allows for greater energetic efficiency, given that they are thermo-neutral at about 17.5°C (Duriez et al., 2004). Climatic effects on prey availability at different stages of the breeding and non-breeding cycle are also likely critical. On the one hand, one might expect higher prey abundance where there is higher precipitation, since earthworms retreat deeper in the soil when dry (Hoodless and Hirons, 2007), and more reliability where there is lower seasonal variation in precipitation and temperature (Bio 15 and Bio3, Figure 2.5); indeed, chick survival

may be lower in years with low June rainfall (Hirons, 1983). Conversely, areas with favourable winter conditions such as warmer, wetter regions in the west may attract larger numbers of migratory woodcock, potentially resulting in increased intra-species competition for resources outside the breeding season. This may explain why woodcock are less likely to occur in areas where mean winter temperatures did not exceed 5.4°C (Bio 11, Figure 2.5), which was an important influence on distribution (Table 2.3). Little is known about the extent to which individuals of this species compete with each other for resources in the winter, though the possibility of social dominance hierarchies has been suggested to occur (Duriez et al., 2005d; Powell, 2012). Whatever the mechanisms, ours is the first study to show that climatic conditions across the year influence the breeding distribution and abundance of this species.

With predicted increased seasonal variation featuring warmer, wetter winters and hotter, drier summers (O'Brien and Nolan, 2023), climate change may drive range shifts in the future, and could explain the withdrawal of woodcock from the extremities of the 1968-72 range, particularly the west (Sharrock, 1976; Balmer et al., 2013) which experiences the mildest and wettest winters. However, predicting these shifts are likely to be difficult against the potential ability of the species to adapt its phenology or migratory strategy, or concurrent changes in suitable habitat availability.

2.4.2 Effects of habitat on distribution

Our results suggest that woodcock abundance is significantly impacted by landscape-scale land cover and habitat. Woodcock are known to prefer large areas (> 0.8km^2) of woodland habitat (Fuller, 1982; Heward et al., 2018) but also require reasonable access to some areas of open foraging habitat, such as pasture, for at least part of the breeding season (Hoodless and Hirons, 2007), as well as through the winter (Hoodless, 1994; Duriez et al., 2005b; Powell, 2012). Our finding that woodcock appear to prefer landscapes where 40-50% of the area within 2 km of a survey site (equivalent to 5.0-6.3 km^2) is forested (Figure 2.9.C) supports this, and likely represents a reasonable balance between patches of forest, ideally well-connected to each other, and open habitat. There was no significant relationship between abundance and the area of forest within a 1 km^2 square. This suggests that the availability of forest habitat in the wider landscape is more important, likely forming more resilient woodcock populations compared to smaller or more isolated patches of woodland. The apparent increase in

abundance where the proportion of forest cover within 2km falls below 15% (Figure 2.9.C) seems to be an artefact, perhaps because of increased detectability and observation bias at small woodland patches, which warrants further investigation by improving an understanding of the relationship between the number of roding registrations and the actual number of individuals under varying landscape habitat compositions.

Breeding woodcock in Great Britain have been shown to prefer more heterogeneously structured forest (Heward et al., 2018) as a range of different habitats are used throughout the breeding cycle, including open clearings and rides, open growth and dense young sapling thickets (Hirons and Johnson, 1987; Hoodless and Hirons, 2007). Our results support this generality because we found that the proportion of forest area that was coniferous vs. deciduous and the proportion of forest area that was mature within 1 km buffers were important (Figure 2.9.D and E). Abundance peaks at intermediate values for each variable, suggesting a preference for forests with a mix of deciduous and coniferous types, and trees of different ages supporting previous findings.

Unexpectedly, abundance decreases as the proportion of forest area that is coniferous decreases (Figure 2.9.D). Woodcock have been shown to prefer broadleaved over coniferous forest, particularly in well-forested landscapes (Heward et al., 2018), whilst Hoodless and Hirons (2007) found that birds living in landscapes with predominantly coniferous forest used home ranges with high proportions of young birch relative to overall availability. Whilst the proportion of broadleaved species in new Irish forestry is rapidly increasing, the national forest estate is dominated by non-native conifer species, particularly in well-forested landscapes (DAFM, 2023). Coniferous plantations make up 69.4% of the national forest estate and by their nature tend to be more homogeneous in age and structure than semi-natural woodlands. This is reflected in our results by the density plots for the proportions of coniferous and broadleaved forest variables within the 1 km scale buffers (Figure A.1.C and D) which show that landscapes where a higher proportion of forest area was broadleaved were poorly represented, especially where the total area of forest cover was high. Thus, more targeted work may be required to establish more accurate relationships between woodcock abundance and woodland type and structure.

2.4.3 Projected distribution and population estimate

The range of breeding woodcock in Ireland has been suggested to have contracted between 1968-72 and 2007-11 (Sharrock, 1976; Balmer et al., 2013). On the one hand our results support this. Many regions, particularly across the west in areas such as west county Galway, south county Mayo or much of county Donegal, where this species was widely recorded in 1968-72 (Figure 1.4.A), are apparently unoccupied or unlikely to be occupied (Figure 2.10). However, our model output (Figure 2.10) indicates that breeding woodcock may be more widespread and abundant when compared with the contrastingly patchy recorded distribution of woodcock in the most recent atlas (Figure 1.4.B, Figure 2.10; Balmer et al., 2013), and may not have contracted their range by as much as 70% as recently suggested (Colhoun and Cummins, 2013; Gilbert, Stanbury and Lewis, 2021). We suspect that this may be explained by the species' secretive nature and the focus in atlas surveys on general diurnal bird surveys, rather than woodcock specific methods. In addition, our results suggest that the catastrophic declines seen in most other ground-nesting wader species in Ireland, most of which breed on farmland or coastal habitats (Gilbert, Stanbury and Lewis, 2021) rather than in woodland habitat, has not occurred in woodcock which appear still to be widespread and locally common across much of Ireland, where climate and habitat allow. Nevertheless, their populations have undeniably been under pressure in the past, and may well continue to be in the future, so there is a strong need to repeat the approach in this at practicable intervals to reliably establish population trends, complementing a similar monitoring framework established in the United Kingdom (Hoodless et al., 2009; Heward et al., 2015).

National breeding population estimates for birds can be calculated in a number of ways according to species, data availability and region (e.g. Musgrove et al., 2013; Woodward et al., 2020). However, SDMs are rarely used for the purpose of calculating national abundance of any bird species, although some studies utilising SDMs focus on a local scale (e.g. Arneill, 2018). No previous estimates of breeding woodcock population size in Ireland exist but our estimate of 27,434 males is approximately half that of the latest estimates for Great Britain in 2013 and 2024 (55,241 and 50,750 males, respectively; (Heward et al., 2015; 2024), which used the same field-based survey methods but a different, regional averaging, analytical approach. Our estimate

is credible given the differences in land area, forest cover and composition, and human population density between the two regions. On the other hand, the confidence intervals are relatively large, which is inevitable because the GAM is based on a modest sample size and explained around half of the variance. Where the observed maximum registration counts were zero, the model always predicted values above zero (Figure 2.8), suggesting that it may have overestimated the population size to an extent. Similarly, the estimates assumed a previously reported relationship between the maximum number of registrations per survey and the number of males found within that 1 km^2 square (Hoodless et al., 2008), which is likely to vary in response to landscape feature composition and warrants further work. However, although some regions were poorly covered, the ensemble SDM method showed high accuracy (Table 2.2) and is a well-established technique that can help in such cases where species occurrence data is unevenly distributed (e.g. Marini et al., 2010; Breiner et al., 2015).

2.5 Conclusion

The results here demonstrate the utility of species-specific survey methodology, high-quality species occurrence data, and SDMs for elucidating the population size and drivers of spatial distribution in rare or elusive species. Our models suggest that predicted increases in broadleaved and mixed species forest (DAFM, 2023) will benefit this species, but that these gains could be neutralised by losses linked to climate change, which may already have contributed to range contractions. Although the breeding population does not appear to have suffered the same catastrophic declines in other sympatric wader species, their cultural and ecological importance means that populations and habitats need to be monitored. We also suggest that the two-step modelling approach here using bioclimatic and land cover variables may represent a useful method for estimating national abundance and distribution for comparable species that are difficult to monitor.

Chapter 3: The effects of hunting and bird age on survival, movement and use of space in non-breeding Eurasian woodcock

Abstract

Human disturbance, such as that caused by recreational hunting, can alter the space use and movement behaviour of species, with potential knock-on impacts on population dynamics. To date, surprisingly little work has been done to assess impacts of hunting disturbance on the spatial ecology of terrestrial birds. Similarly, age can have a dramatic influence on spatial ecology; in birds, juveniles often present markedly different use of space compared to adults. The Eurasian woodcock *Scolopax rusticola* (hereon woodcock) is an important game species in Western Europe. Here, we used radio telemetry at three hunted and three control (not hunted) sites to monitor the fates of 168 tagged overwintering woodcock, 43 of which also provided detailed global positioning system (GPS) location data. GPS tags took multiple diurnal and nocturnal locations per day with an average deployment duration of 64 days. Linear and generalised linear mixed models were used to explore the interacting effects of time of day (day/night), age and hunting disturbance on home ranges, commuting behaviour, and fidelity to roosting and foraging sites. The majority of mortality events recorded were due to hunting, but overall estimated monthly survival rates were high over the hunting open season (98.0%). Age and hunting activity both affected movement ecology. While woodcock generally showed high fidelity to both diurnal and nocturnal locations, juveniles used larger diurnal and nocturnal home ranges, were more likely to commute further between diurnal and nocturnal locations, and displayed a greater degree of localised exploratory movement compared to adults. Birds that experienced hunting activity had larger diurnal home ranges at the landscape-scale, with a carry-over effect of larger nocturnal home ranges, and were more likely to commute greater distances, but did not use larger overall home ranges. Hunting activity also disproportionately affected aspects of the movement ecology of adults. These effects contrast with the more dramatic relocation response to hunting seen in many other quarry species. Our results increase our understanding of the effects of hunting on the spatial ecology of terrestrial avian quarry species.

3.1 Introduction

Animal movement and space use is driven by the interplay of four basic components (Nathan et al., 2008). Three of these (internal state, motion capacity and navigation capacity) are affected by individual attributes such as species, age, experience, sex and personality traits (reviewed in Shaw, 2020). The fourth component relates to the influence of abiotic and biotic external factors, including resource and habitat distribution and accessibility (Fahrig, 2005; Doherty and Driscoll, 2018), perceived predation risk, and inter- and intra-specific competition (Abe and Shimada, 2015; Pérez-Barbería et al., 2015; Austin et al., 2021; Williams et al., 2024). Recent advances in tracking technology have enabled novel research into the spatial ecology of a wide variety of species (Hebblewhite and Haydon, 2010; Williams et al., 2020). However, our knowledge of how one anthopogenic external factor, human hunting, impacts movement and use of space remains limited for most commonly targeted quarry species.

Although the direct impact of hunting mortality on populations can be substantial, especially when unmanaged (Cullen, Bodmer and Valladares Pádua, 2000; Benítez-López et al., 2017), indirect effects such as disturbance can be equally if not more important. For example, the landscape of fear (Laundre, Hernandez and Ripple, 2010) can lead to so-called trait mediated indirect effects on prey species, which can have an equal or greater impact on spatial behaviour and fitness than the effect of natural predators (Frid and Dill, 2002; Ciuti et al., 2012b). Fear of hunting by humans can also lead to similar coarse or fine scale changes in the movement of game species, which respond by choosing to spend more time in more inaccessible areas with restricted hunting activity, often as a trade-off against access to important resources for survival or resulting in higher energy costs during daily movements (Bonnot et al., 2013; Lone et al., 2015; Nickel et al., 2021; Mols et al., 2022).

In birds, relatively little is known about the effects of hunting disturbance on behaviour and spatial ecology, particularly for different demographic (e.g. age or sex) groups within a population, and most work to date deals with waterbirds. Hunting can cause redistribution in both quarry and non-quarry species, which relocate to safer spaces and can sometimes limit foraging activities to the hours of darkness (Madsen and Fox, 1995; Casazza et al., 2012; McDuie et al., 2021). For example, shooting has been

shown to significantly affect the distribution of diving ducks, where birds were far more likely to use refuges or offshore waters at times when hunting activity was high, and quickly returned to preferred inshore habitats when the shooting season ceased or on days when hunting activity was low, such as midweek periods (Evans and Day, 2001; 2002), suggesting an ability to rapidly respond to changes in hunting mortality risk. Similarly, creation of new waterfowl refuges in Denmark resulted in the redistribution of geese and dabbling ducks into these areas resulting in higher species richness, indicating that hunting activity generally displaces quarry species, though effects can be variable and dependent on context, hunting intensity, and species involved (Bregnballe and Madsen, 2004).

Much less is known about the response of species in terrestrial environments. Comparative radio-tracking studies showed that forest grouse species such as willow ptarmigan *Lagopus lagopus* that were exposed to hunting and recreational disturbance did not leave or change their home ranges, but changed their preferences to less-disturbed areas or made more use of denser habitats (Olsson, Willebrand and Smith, 1996; Brøseth and Pedersen, 2010). On a farmland site in France, quarry species that included golden plover *Pluvialis apricaria* and lapwing *Vanellus vanellus*, as well as a non-quarry species, little bustard *Tetrax tetrax*, each showed strong behavioural responses to hunting activity, including increased vigilance and flight probability, as well as relocation to, and increased use of, non-hunted refuges for daytime roosting; it is not known how nocturnal behaviour was affected (Casas et al., 2009).

Age can affect an animal's spatial ecology because of factors such as accumulated life experience and foraging efficiency (Missagia et al., 2015; Van Den Hout et al., 2016; Battley et al., 2020), different resource requirements (Ficetola, Pennati and Manenti, 2013; Lim, Yong and Christy, 2016), or the ability to deal with intraspecific competition (Cresswell, 1994; Caldow et al., 1999). These effects can manifest as differences in home range size (Cederlund and Sand, 1994; Saïd et al., 2009) or spatial segregation at a range of scales, from regional or latitudinally in some wide-ranging species (Ketterson and Nolan, 1983; Nebel et al., 2002; Missagia et al., 2015; Pettex et al., 2019), to local or micro-habitat scales (Catry et al., 2004; Ficetola, Pennati and Manenti, 2013; Pelletier et al., 2014). In birds, young individuals of long-lived species with an extended immature period usually display transient, exploratory behaviour with large home ranges, a period when they gain important experience, avoid

intraspecific competition and assess potential future breeding or overwintering sites (Whitfield et al., 2009; Krüger, Reid and Amar, 2014). In some species, such as shorebirds in the family *Scolopacidae*, adults generally show strong fidelity to breeding and non-breeding sites (e.g. (Olalla-Kerstupp et al., 2015; Lourenço et al., 2016; Schwemmer et al., 2021), reflecting accumulated experience and dominance. Conversely, after their initial postnatal migration to the non-breeding range, juveniles are generally less site-faithful with larger home-ranges, exploring widely and 'sampling' habitats before settling at a non-breeding site to which they will be loyal for the rest of their lives (Warnock and Takekawa, 1996; Lourenço et al., 2016; Battley et al., 2020). Juveniles can also be less proficient at foraging and are often vulnerable to dominance and exclusion by adults into unfavourable spaces with fewer resources or higher predation risk (Groves, 1978; Warnock, 1990; Cresswell, 1994; Van Den Hout et al., 2014).

The Eurasian woodcock *Scolopax rusticola* (hereafter 'woodcock') is a nocturnal, elusive and largely migratory bird in the family *Scolopacidae,* and is a popular quarry species in Western Europe. Recorded survival rates in the non-breeding season vary by location, weather conditions and age class, with some authors noting concern over low survival at least in local populations ((Hoodless and Coulson, 1994; Tavecchia et al., 2002; Duriez, Eraud and Ferrand, 2006; Aradis et al., 2008). Little is known about how hunting affects mortality rate, though Duriez, Eraud and Ferrand (2006) suggest that hunting mortality can be additive to natural mortality. During the day in the non-breeding season, woodcock use thickly-vegetated habitats such as forest, hedges and scrub, but at night they commonly occupy open habitats (e.g. grassland), commuting between diurnal and nocturnal locations at dusk and dawn (Duriez et al., 2005b). Both habitat types can be important for foraging during the day and night (Duriez et al., 2005a, c). Previous radio-tagging studies in winter show high fidelity to both nocturnal and diurnal locations within a season but also considerable individual variability in space use (Wilson, 1983; Duriez et al., 2005b; Powell, 2012; Ferrand et al., 2013). Little work has been done to investigate the effects of hunting or age on the behaviour of the woodcock. Ferrand et al., (2013) found little impact of either hunting or age among 54 woodcock over three seasons, although this study was undertaken at a single site.

Here, we use global positioning system (GPS) tracking and very high frequency (VHF) radio telemetry on non-breeding woodcock to compare, at hunted and not hunted sites: i) survival rates and causes of mortality, and ii) spatial behaviour using multiple metrics linked to home range size, commuting flights, and exploratory behaviour. Given that hunting occurs exclusively during daylight hours, we hypothesised that diurnal distributions would be most affected, with increases in home range area and unsettled behaviour, but we also tested for similar carry-over effects to nocturnal patterns, which could arise, for example, if disturbance during the day changed which locations were optimal for foraging. In addition, we explored how spatial ecology differed between adult and juvenile age groups with the expectation that juveniles would show a higher degree of unsettled or exploratory behaviour, and whether they may therefore be unequally affected by hunting disturbance.

3.2 Methods

3.2.1 Study sites

Fieldwork was undertaken at six locations on the island of Ireland, in counties Cavan, Cork, Kerry and Tyrone, over the course of three consecutive winter seasons: 2019-20, 2020-21 and 2021-22 (Figure 3.1,Table 3.1). Two fieldwork sites were used per season, one of which was 'hunted' and the other 'not hunted'. Hunted sites were visited by hunters who targeted woodcock using traditional Irish rough shooting methods, which included the use of dogs, mainly English Springer Spaniels, to find birds in densely-vegetated habitats such as hedges, scrub and forest edges, and flush them into the path of the hunters. The 'not hunted' sites were left relatively undisturbed as landowners did not permit hunting activity, though this did not exclude the potential for poaching. The open season for hunting woodcock in the Republic of Ireland falls between 1 November and 31 January each season, and no hunting took place during the hours of darkness.

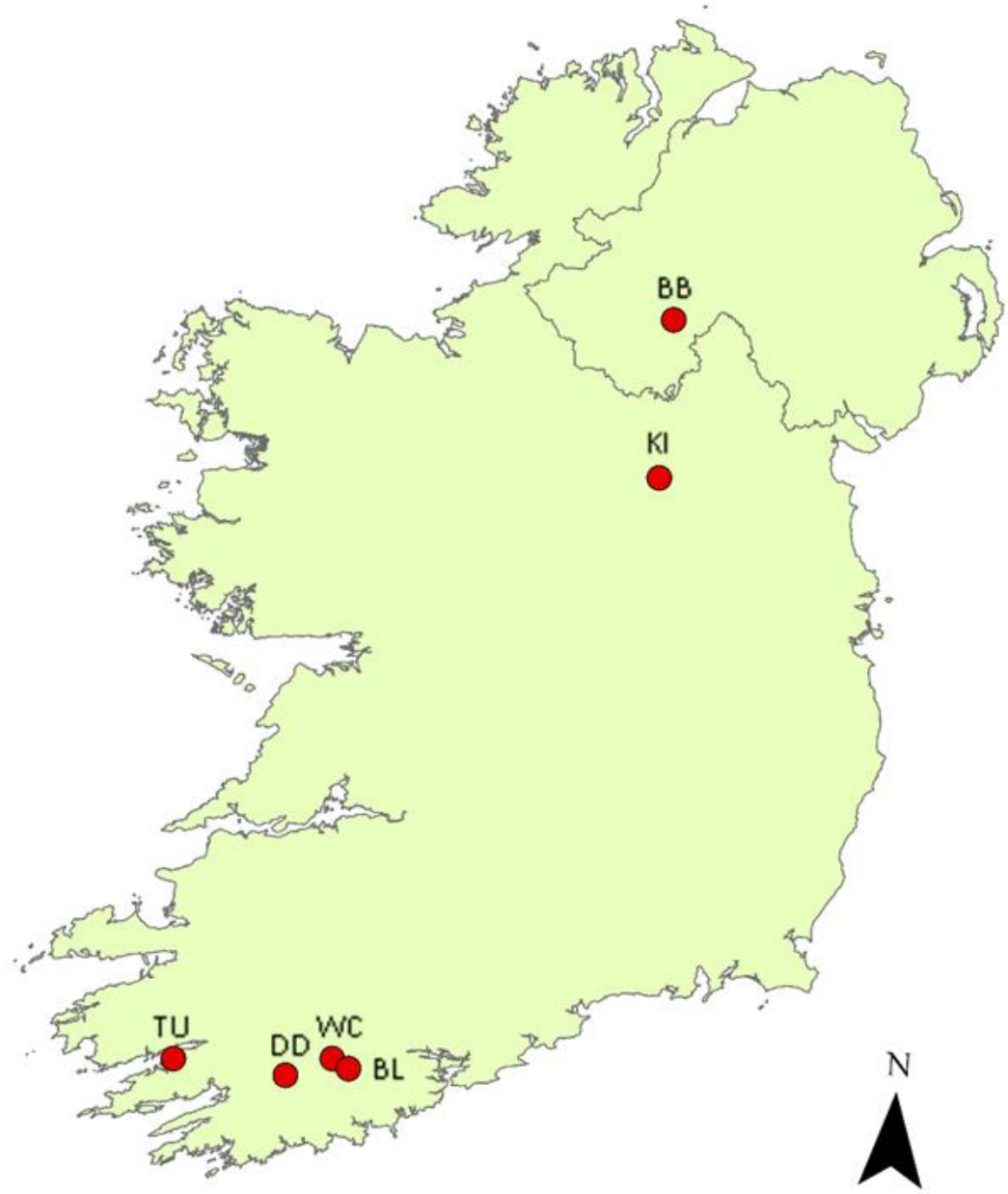


Figure 3.1. Location of study sites where woodcock were tagged and monitored across three winter seasons from 2019 to 2022 (Table 3.1).

Sites were selected where there was sufficient habitat to support good numbers of woodcock; where necessary, nocturnal counts on pasture at prospective sites were undertaken using thermal imaging to confirm their presence in sufficient numbers prior to tagging. Hunted sites were selected where a good relationship had been established with local hunters to ensure frequent communication about the extent of hunting activity and any recoveries of tagged or ringed birds. Based on information provided by hunters, hunted sites were subject to variable hunting activity until the 31

Table 3.1. Overview of sites where woodcock were tracked with VHF radio transmitter tags or combined GPS logger/VHF radio transmitter tags. Metrics used in the survival analysis, as well as estimated monthly survival rates recorded within the hunting open season, are included.

Site Code	County	Season	Site Hunted	Number tagged	By end 31st January (end of hunting open season)					Number GPS tagged	Usable GPS datasets retrieved
					Number included in survival analysis	Total bird-days (*t*)	Deaths (*y*)		Estimated monthly survival rate (S_{mon})		
							Hunted	Predation			
BB	Tyrone	1	No	35	35	1708		1	0.983	10	7
KI	Cavan	1	Yes	35	28	1480	1		0.980	11	8
WC	Cork	2	No	35	34	1714			1.000	10	6
BL	Cork	2	Yes	36	33	1475	2		0.960	11	5
DD	Cork	3	No	15	14	586	1		0.950	15	9
TU	Kerry	3	Yes	12	11	413			1.000	12	8
All				**168**	**155**	**7376**	**4**	**1**	**0.980**	**69**	**43**

January of each tag deployment season, among which the sites that were hunted least (BL and TU) were visited at least 5 times, whilst the site that was hunted most (KI) was visited at least once or twice per week (8-16 times) by multiple hunters in different areas of the site. It is unknown how much hunting took place at each site before the tags were deployed. At one not hunted site (DD) a tagged bird was strongly suspected to have been shot by a hunter on the fringe of the site; in this case the GPS tag was retrieved but had malfunctioned shortly after deployment and provided insufficient data. Though contact could not be made with the hunter in question, they are not thought to have hunted within the main site area.

3.2.2 Tagging procedure and data retrieval

All work was conducted under permits issued by the National Parks and Wildlife Service (Ireland) and the British Trust for Ornithology (BTO; UK). Between 12 and 36 woodcocks were tagged at each site, with a total of 168 birds tagged with VHF transmitters across the six sites (Table 3.1). Of these, 69 (42 adults, 27 juveniles) were additionally mounted with GPS loggers. Tagging took place in the month of December each season: season 1 (2 to 15 December); season 2 (3 to 17 December); season 3 (16 to 22 December). Whilst the hunting open season had begun for woodcock on 1st November, and birds were present on sites from late October, the timing was chosen to maximise the chances of tagging only birds that had fully settled on their wintering grounds, as opposed to passage migrants that could have moved away after capture. Birds were mainly captured at night in open habitats, using a bright torch and hand-net, although some were captured using mist nets as they flew over fields at dusk (Figure 3.2.A). They were each fitted with a numbered metal ring issued by the BTO, and morphometric measurements were taken. The age of each bird was determined as juvenile (hatched within that calendar year) or adult (hatched in the previous calendar year or before) using wing feather characteristics and moult status (Ferrand and Gossmann, 2009; Demongin, 2016).

The tags used were ‘very high frequency’ (VHF) radio transmitters (5.5g glue-on model; Perdix Wildlife Supplies, UK). A number of these were additionally combined with GPS data loggers (PinPoint 50, Lotek Wireless Inc., UK) forming a maximum combined mass of 7.5-8.1g (<2.5% of the bird’s body mass, mean = 331g). This arrangement allowed for real-time tracking of the VHF signals to monitor the fate of

each bird and to increase the likelihood of physical retrieval of the GPS loggers. The VHF transmitter component produced a single VHF pulse every 1.6 seconds (bandwidth 149-151MHz), and included a 'mortality indicator', which presented as a repeated double VHF pulse after 18 hours of the tag experiencing no movement. Tags were fitted with a small piece of cotton gauze and attached using cyanoacrylate glue to a small area of feathers and skin on the birds' backs, positioned over the front of the synsacrum (Figure 3.2.B). This unobtrusive method of attachment was temporary and tags would eventually have been discarded as a result of the birds' moult or preening action.

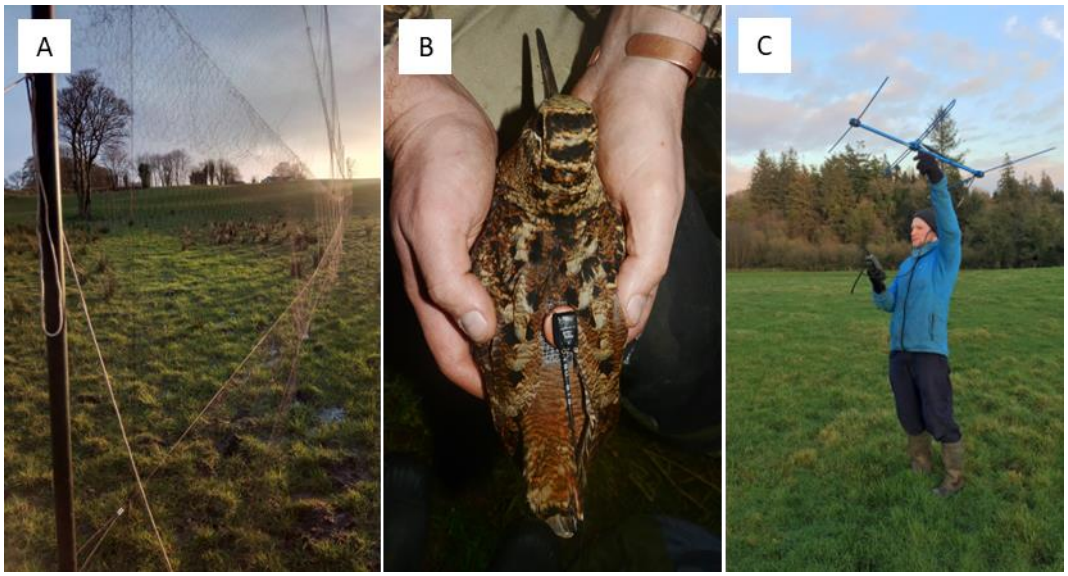


Figure 3.2. Fieldwork in action: **A**) a mist net set at dusk across a field known to be used by woodcock, in the hopes of capturing low-flying commuting birds; **B**) a captured woodcock mounted with a double-unit VHF-GPS tag; **C**) tracking VHF radio-tagged birds using a radio-receiver unit and antenna.

During season 1 and 2, tags were programmed using Pinpoint Host software (Lotek Wireless Inc., UK, version 2.15.4.0) to take a GPS locational fix four times per day; two nocturnal (04:00 and 21:00) and two diurnal (09:00 and 15:00). During season 3, tags were programmed to take an additional four locations per day, resulting in eight locations in a 24-hour period; four nocturnal (00:00, 04:00, 06:00 and 21:00), three diurnal (09:00, 12:00 and 15:00) and one which transitioned from nocturnal through dusk to diurnal as the season progressed (18:00).

At least once per week through each winter season, sites were revisited in attempts to re-locate each tagged bird via VHF telemetry, monitoring their activity status and

approximate location (Figure 3.2.C). If a mortality indicator was detected, suggesting the tag had been discarded or the bird had died, attempts were made to find and retrieve the tag and record the status of the bird and cause of death if possible or appropriate. When tags had been discarded or gone 'missing' either due to birds permanently emigrating from the sites or VHF tag failure, birds were removed from the study or 'censored'. Where GPS tags had not been retrieved before 15 February of each season, we attempted to recapture each bird either using mist nets at dusk, or a torch and hand net at night. Upon recapture of a bird, the GPS logger was retrieved before immediate release. Recapture efforts continued until either all GPS loggers had been retrieved, or the woodcock had departed on their spring migration whereby it was assumed that any tags remaining deployed were lost.

Of the total number of GPS tags deployed, 7 birds (five adult and two juvenile) left the sites altogether either immediately or shortly after tagging either as a response to capture or because they were still migrating, an additional 7 tags were otherwise not retrieved, 5 tags malfunctioned, 6 were prematurely discarded, and 1 bird prematurely died (hunting mortality). Forty-three birds (26 adults, 17 juveniles) yielded useful GPS datasets (Table 3.1). Mean GPS logger deployment duration was 63.7 days (min = 18, max = 104). After GPS data had been retrieved from each site where hunting activity had taken place, the respective hunters were consulted and shown the diurnal tracking data. They were able to confirm if individual woodcock had likely been exposed to hunting activity based on whether their locations coincided with the areas where the hunters were active. This allowed us to categorise the status of each bird more accurately in relation to whether it had inhabited areas within sites that experienced hunting (n = 17) or were not hunted (n = 25). One 'hunted' site (TU) included four birds that were considered unlikely to have experienced hunting activity, as the areas they used during the day were not visited by hunters due to inaccessibility or proximity to residential buildings, and were classified as 'not hunted'. All birds at the not hunted sites were classified as 'not hunted' and we were assured this was true based on conversations with landowners, local hunters or from personal knowledge. One woodcock (BB6) was diurnally located in an area several kilometres from the tagging site where it was unknown if woodcock hunting activity took place and was excluded from all modelling analyses.

3.2.3 Survival analysis

We used the Mayfield method, originally developed for analysing nesting success in birds but which can be extended to radio telemetry data analysis (Trent and Rongstad, 1974; Heisey and Fuller, 1985), to provide simple approximations of survival for focal periods between the earliest date of tag deployment (2-17 December) and the end of the hunting open seasons (31 January) for each site as well as across all sites. This method assumes that the mortality rate remains constant over time, which is reasonable here given the relatively short focal periods and consistently mild weather conditions experienced at the sites over the three study seasons. Birds that were censored before each first re-location visit to a site (n = 13) were excluded from this analysis. We estimated mean daily survival (μS_i) using the following equation:

$$\mu S_i = \frac{t - y}{t}$$

where, within the focal period, t is the total combined number of bird-days (days that living birds were known to be mounted with functioning VHF units), and y is the number of deaths that occurred. As Aradis et al. (2008) calculated monthly survival estimates for overwintering woodcock for their and others' studies (Tavecchia et al., 2002; Duriez, Eraud and Ferrand, 2006), to allow for comparison we also report the estimated monthly survival rates for each site and across all sites. Monthly survival estimates (S_{mon}) were obtained by raising estimated mean daily survival to a power equal to the number of days in a month (thirty after Aradis et al., 2008), for example as follows:

$$S_{mon} = (\mu s_i)^{30}$$

We did not extrapolate estimated survival rates or use encounter data from past the end of the hunting open seasons because in practice the mortality rate may not have remained constant across the open and closed seasons if hunting mortality was additive to natural mortality, violating the assumption of the Mayfield method for estimating survival rates. There were too few deaths recorded to reliably examine the effects of hunting and age on survival rate.

3.2.4 Spatial analysis

Raw GPS location data were plotted (projected coordinate system: IRENET95 Irish Transverse Mercator) and examined in ArcGIS Pro v. 3.0 (ESRI, Redlands, CA, U.S.A.). Data with low GPS accuracy were excluded by filtering out GPS locations where the number of satellites used to generate the location was fewer than four, or where Horizontal Dilution Of Position (HDOP) > 10, as location error can increase significantly above this value (Recio et al., 2011). Locations were categorised as diurnal or nocturnal based on the daily time they were generated. Those generated at 18:00 during season 3 were excluded from these analyses as these transitioned from nocturnal to diurnal across the duration of the season. Particular attention was paid to locations generated immediately after tag deployment; consecutive locations that appeared to fall outside the apparent regular home ranges of each bird indicating a behavioural reaction to capture and tagging, were excluded from main analyses (n = 103, from 22 birds). In these cases, it took between less than a day to four days for behaviour to return to normal. Where two birds each made a brief, apparently erratic, long-distance movement from the tagging sites (i.e. further than 10km) in the middle of the winter season, the corresponding location data points (n = 16) were also excluded from the main analyses as these represented highly unusual movements.

After data preparation, a total of 8,772 GPS locations (2,012 diurnal, 6,760 nocturnal) were obtained from the 43 birds. Thirty-four percent of diurnal fixes and ninety-four percent of nocturnal fixes were successful; the disproportionately low success rate of diurnal GPS locations can be attributed to birds often choosing to diurnally inhabit densely-vegetated habitats, which reduces communication ability between GPS satellites and the tags. For the purposes of investigating the effects of hunting and age, all GPS locations that fell within the months of February and March, i.e. the closed season for hunting, were excluded. This, along with the exclusion of data from BB6, left 6,400 GPS locations (1,507 diurnal, 4,893 nocturnal) that fell within the hunting open season for modelling analyses.

Distances between chronologically consecutive locations within each dataset were calculated in ArcGIS Pro v. 3.0. Any distance measurement made between a diurnal location and directly successive nocturnal location, or vice-versa, was identified as a ‘commute’.

Home range metrics for each bird were calculated using the 'adehabitatHR' package (Calenge, 2006) in R v. 4.1.2 (R Core Team, 2021), for two periods: across the entire winter season, and within the hunting open season. Two different methods of estimating home range were chosen to represent different aspects of use of space. To estimate a home range that considers the spread across the landscape, including infrequently visited areas between GPS locations (and by implication, distance between locations), a minimum convex polygon (MCP) was calculated for diurnal, nocturnal, and overall (diurnal + nocturnal) location data for each bird (Figure 3.3.B). To estimate core area used for non-volant activity such as roosting and foraging, we estimated diurnal, nocturnal and overall home ranges using Single-Linkage Cluster Analysis (SLCA; Kenward et al., 2001). This uses nearest-neighbour distances to identify clusters of at least three points around which MCPs are drawn, and estimates a multinucleate home range which excludes areas rarely or never visited in between clusters (Figure 3.3.C). For both methods, subsets comprising 95% of the respective data locations were used to exclude potential extreme outlying locations from significantly inflating home range estimations. Diurnal 95% MCP and 95% SLCA home ranges for birds that recorded fewer than five diurnal locations were not calculated (entire winter season: n = 0; open hunting season: n = 2).

Treating diurnal and nocturnal data separately, clusters of GPS locations were identified (separately across the winter period and within the hunting open season) for each individual in ArcGIS pro (Figure 3.3.D). A cluster represented a core area visited two or more times within a season and was identified when a minimum number of GPS locations (three diurnal and nocturnal for seasons 1 and 2; four diurnal and five nocturnal for season 3) was found within a search distance of 41.4 metres (the upper quartile for distances travelled between successive locations within a nocturnal or diurnal period); where a location was more than 41.4 m from the next-nearest location, it was not included in a cluster. Where a bird recorded fewer than five diurnal locations, diurnal clusters were not identified calculated (entire winter season: n = 0; open hunting season: n = 2).

To measure the extent of exploratory and unsettled movement, two metrics were calculated: i) the proportion of un-clustered locations (i.e. those that were not members of a cluster; Figure 3.3.D), and ii) the proportion of diurnal/nocturnal periods when birds moved between or away from clusters. For i), diurnal values from birds that

recorded fewer than ten diurnal locations were excluded calculated (entire winter season: n = 4; open hunting season: n = 4), while for ii), diurnal values were excluded for birds that recorded fewer than ten diurnal periods with more than one GPS location calculated (entire winter season: n = 6; open hunting season: n = 22).

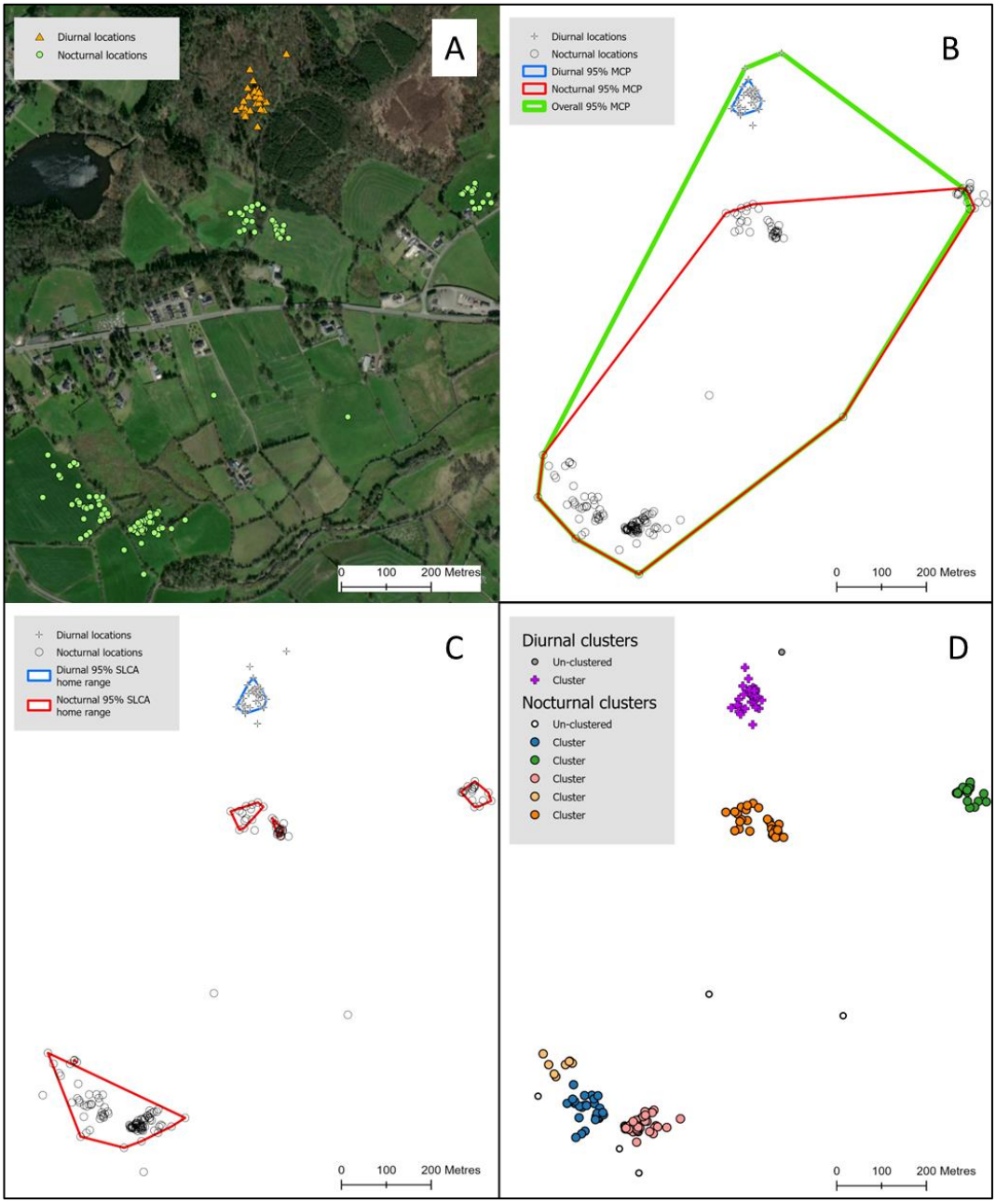


Figure 3.3. Maps demonstrating spatial analysis methods, using GPS data from a single typical example of a Woodcock (BB7): **A**) Satellite image showing GPS data in context of landscape features; **B**) Diurnal, nocturnal and overall 95% Minimum Convex Polygon (MCP) home ranges; **C**) Diurnal and nocturnal Single Linkage Cluster Analysis (SLCA) home ranges; **D**) Diurnal and nocturnal location clusters (indicating preferred core areas used by the Woodcock), as well as un-clustered locations.

3.2.5 Modelling analyses

We used linear mixed models (LMMs) and generalised LMMs (GLMMs) using the 'lme4' package (Bates et al., 2015) in R v. 4.1.2 (R Core Team, 2021) to explore relationships between response variables that captured different aspects of space use and movement behaviour, and hunted status (hunted/not hunted), woodcock age (adult/juvenile) and time of day (day/night) where relevant. These response variables included: i) overall 95% MCP home range; ii) commute distance; iii) likelihood of commuting more than 100 metres; iv) diurnal and nocturnal 95% MCP home range (Ln transformed); v) diurnal and nocturnal 95% SLCA home range (Ln transformed); vi) number of clusters; vii) proportion of diurnal/nocturnal periods when birds moved between or away from clusters; viii) proportion of diurnal/nocturnal un-clustered locations.

To explore the effect of hunting on different age groups, models with response variables ii) and iii) were initially run with an interaction between hunted status and age; if this reported an insignificant relationship the interaction was removed from the model. If an interaction was significant, two post-hoc models were fitted, each treating the hunted and not hunted groups separately. Where metrics were calculated separately for day and night, a similar approach with respect to time of day was taken with response variables iv), v), vi), vii) and viii). To explore whether effects of age or hunted status differed between day and night, each model initially included two separate two-way interactions between time of day and hunted status, and between time of day and age. An interaction between hunted status and age was not included here due to the modest sample size. Where an interaction was significant, two post-hoc models were run, to explore the effects of hunting and age on diurnal and nocturnal data separately.

Nested random effects accounting for site and bird ID were included where appropriate. Diagnostic plots of residuals were generated and examined to ensure assumptions of homoscedasticity and normality were met before model evaluation. To help assess variable significance, the 'lmerTest' package (Kuznetsova, Brockhoff and Christensen, 2017) in R v. 4.1.2 (R Core Team, 2021) was used to add p-values to the mixed model outputs via the 'Satterthwaite's degrees of freedom' method. However, p-values can be notoriously unreliable in mixed modelling and only provide an informal guide to significance and are best used in addition to estimates, standard

error, t-values, and confidence intervals to make informed judgements of significance and evidence of effect (Luke, 2017). Thus we considered that where $p < 0.15$, weak or moderate support for an effect was detected, and where $p < 0.05$, strong support for an effect was detected. Main variable effects and interactions were plotted using the 'ggeffects' and 'interactions' packages, respectively (Lüdecke, 2018; Long, 2019).

3.3 Results

3.3.1 Survival

Within the hunting open seasons, the estimated mean daily survival rate across all sites was 0.9993, which provided a monthly survival estimation of 0.980. Monthly survival estimates for each site varied from 0.950 to 1.000 (Table 3.1). Of the 168 tagged woodcock, 42 were censored before the end of the hunting open seasons. Of these, 29 had prematurely discarded their tag, while 13 were assumed to have emigrated from the study sites or their VHF tag had failed. Three birds that had discarded their tags were subsequently recaptured alive later in the winter and identified by their metal leg-rings. Thus, the fates of 129 birds (76.8%) were known by the end of the hunting open seasons. Five mortality events were recorded within the hunting open seasons; four of these, two adults and two juveniles, were a result of hunting (including one on the fringe of a not hunted site) while one adult was predated by a mammal. It is not known how many unmarked woodcock were additionally taken by hunters at each site. Outside the hunting open season and just prior to the onset of pre-breeding migration in mid- to late March, only two additional mortality events were recorded, both at the same site (BB). These were the result of predation: one juvenile by a sparrowhawk *Accipiter nisus* and one adult by a mammal.

3.3.2 Overall home range and commuting

Throughout the entire winter seasons, woodcock showed considerable individual variation in their use of space across the 24h period (Figure 3.4; median overall MCP home range = 0.289 km^2, IQR = 0.149 – 0.574, range = 0.030 - 9.477, n = 43). Within the hunting open season, there was no evidence that hunted status or age had an effect on overall MCP home range size (Table 3.2.A).

Commute distances also varied substantially (throughout entire winter seasons: median = 481.6 m, IQR = 193.8 - 908.9, range = 0.0 - 6552.6, n = 2,758), as was true for individual mean commute distances (range = 88.8 - 4962.5 m, n = 43). Mean commute distance was strongly correlated with overall 95% MCP home range ($r = 0.90$, $p < 0.01$, $n = 43$). Within the hunting open season, hunted birds undertook significantly longer commute flights than not hunted birds (Table 3.2.B). Age did not significantly affect commute distance and there was no significant interaction between age and hunted status (LMM; $t = -0.92$, $p = 0.352$, B ±SE = -203.60 ±216.09, $n = 2,023$).

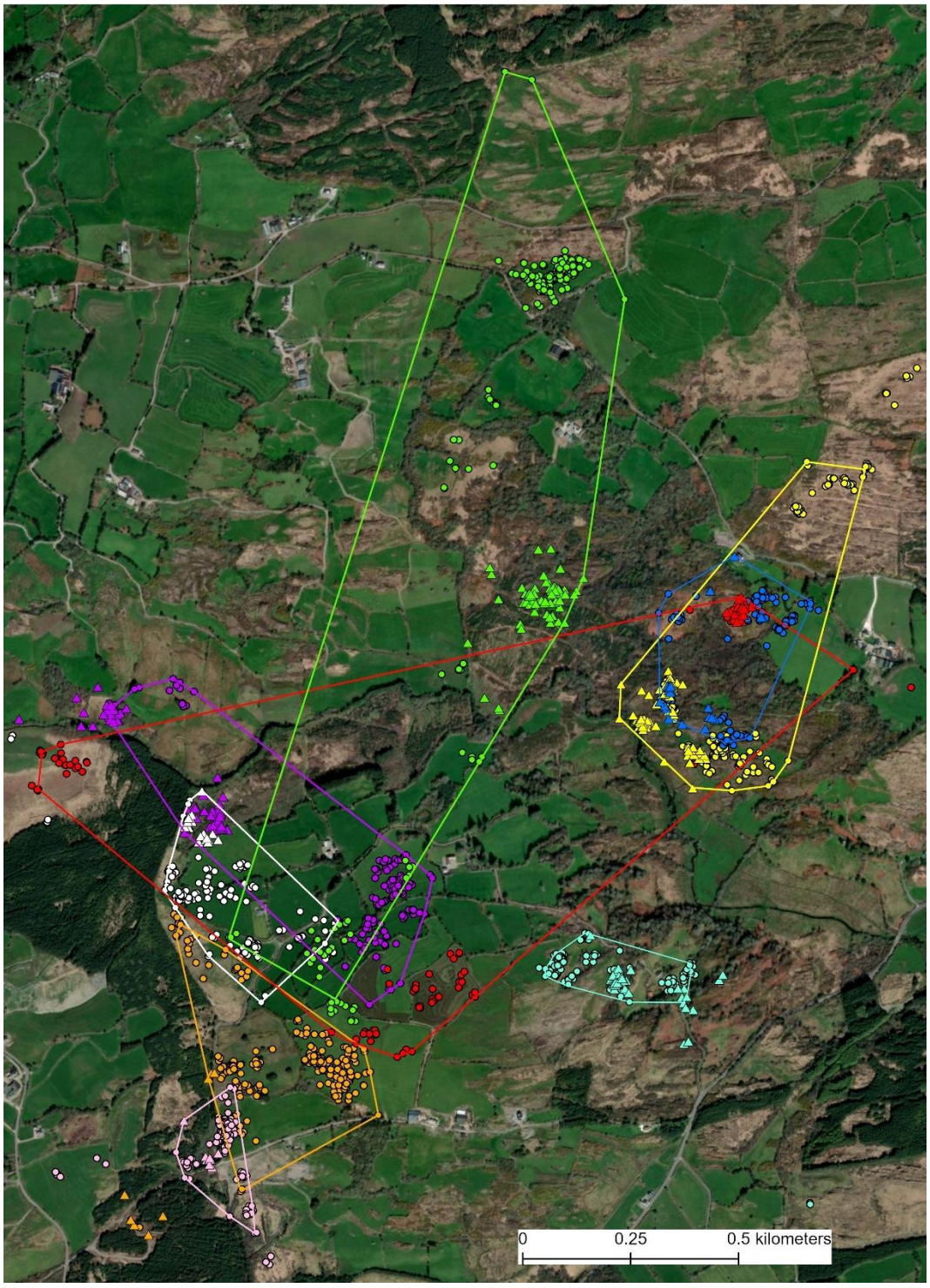


Figure 3.4. Map of a study site (DD) showing overall 95% MCP home ranges, and diurnal (triangle markers) and nocturnal (circle markers) GPS fixes for nine individual woodcock over the course of the 2021/22 winter season. Each individual is represented by a different colour. This shows the unique and limited use of space by each bird and the variation in home range size.

Table 3.2. Mixed model outputs for the relationships between movement/space use metrics and hunted status and age. Where p-values are shown: ** = strongly significant where $p < 0.05$; * = weakly to moderately significant effect where $0.05 < p < 0.15$. Models A and B are linear mixed models; models C, D and E are logistic mixed models with binomial distributions; D (not hunted sites only) and E (hunted sites only) are post-hoc tests of C (hunted/not hunted). For the categorical factors hunted status and age, reference levels were not hunted and adult respectively.

	Response variable	Fixed effect / Random effect	Estimate	SE	df	t-value (z-value)	p-value	Random effect var. (% of total var.)	Random effect std. dev.
A	Overall 95% MCP home range (km^2) (n=42)	Intercept	0.256	0.152	5.546	1.681	0.148		
		Hunted status (hunted)	0.298	0.207	8.553	1.439	0.186		
		Age (juv.)	0.176	0.154	37.984	1.145	0.259		
		Site						(21.19)	0.224
B	Commute distance (m) (n = 2,023)	Intercept	395.56	76.62	39.93	5.162	<0.001**		
		Hunted status (hunted)	113.02	104.73	39.22	1.979	0.055*		
		Age (juv.)	207.22	104.80	39.11	1.078	0.287		
		ID : Site						(50.68)	325.20
		Site						(0.00)	0.00
C	Probability of commuting further than 100 metres (n = 2,023)	Intercept	1.590	0.445		(3.571)	<0.001**		
		Hunted status (hunted)	2.237	0.739		(3.029)	0.002**		
		Age (juv.)	1.134	0.646		(1.752)	0.080 *		
		Age (juv.) × Hunted (hunted)	-2.143	1.077		(-1.989)	0.047*		
		ID : Site						1.979	1.406
		Site						0.137	0.370
D	Probability of commuting further than 100 metres (not hunted n = 1,121)	Intercept	1.589	0.532		2.988	0.003**		
		Age (juv.)	1.238	0.631		1.960	0.049**		
		ID : Site						1.771	1.331
		Site						0.547	0.740
E	Probability of commuting further than 100 metres (hunted, n = 902)	Intercept	3.799	0.571		6.652	<0.001**		
		Age (juv.)	-1.116	0.834		-1.338	0.181		
		ID : Site						1.872	1.368
		Site						<0.001	<0.001

Throughout entire winter seasons, the mean proportion of nights and mornings on which a bird commuted further than 100 metres was 0.85 (n = 43, SD ±0.18, min = 0.17, max = 1.00). Within the hunting open seasons, hunting significantly increased the probability that adults would commute further than 100 m but had no effect on juvenile woodcock (hunted × age, Table 3.2.C; Figure 3.5.B). Among not hunted birds, juveniles were significantly more likely than adults to commute further than 100 m (Table 3.2.D; Figure 3.5.B) but there was no difference between age groups among hunted birds (Table 3.2.E; Figure 3.5.B).

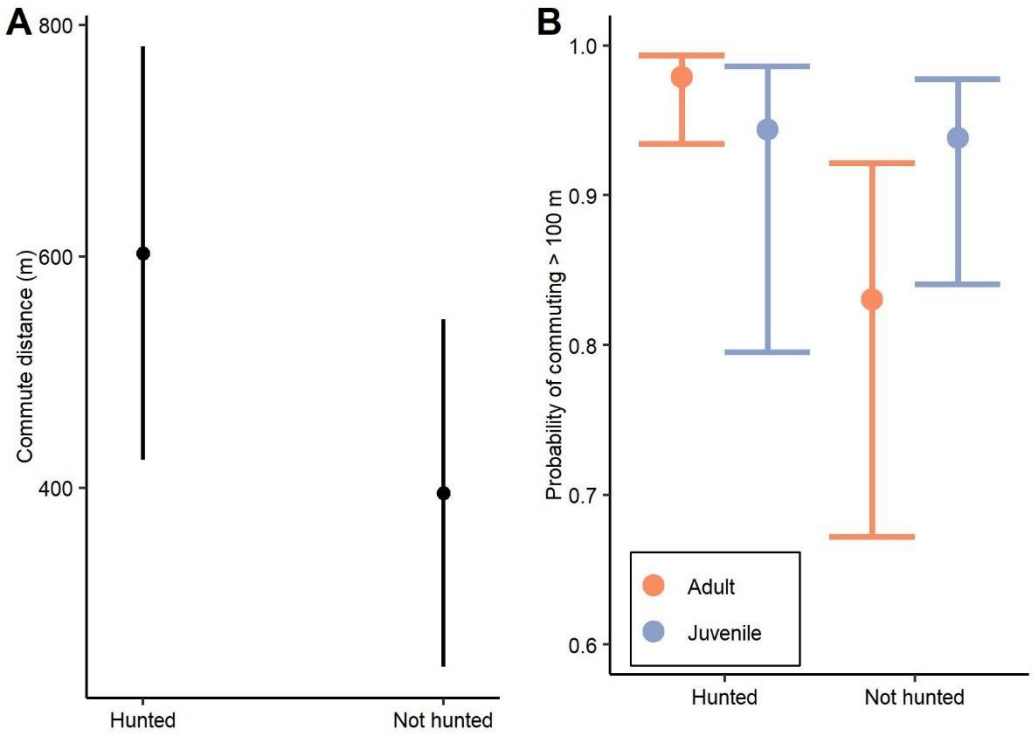


Figure 3.5. Plots generated from linear mixed models showing **A**) the effect of hunting on commute distance (n = 2,023) (Table 3.2.B) and **B**) the interacting effect of hunting and age on the probability of commuting further than 100 metres (Table 3.2.C, D and E). Hunting increased the probability of commuting further than 100 metres for adults but not for juveniles. Bars represent predicted model values.

3.3.3 Diurnal and nocturnal home ranges

Nocturnal MCP home ranges were usually larger than corresponding diurnal MCP home ranges (throughout entire winter seasons: median diurnal 95% MCP home range = 0.015 km^2, IQR = 0.004 – 0.046, range = 0.0003 - 0.420, n = 43; median nocturnal 95% MCP home range = 0.253 km^2, IQR = 0.105 – 0.605, range = 0.014 - 9.415, =

43). Within the hunting open seasons, hunted birds tended to have larger diurnal and nocturnal MCP home ranges than not hunted birds (Table 3.3.A; Figure 3.6.A). In addition, juveniles had larger diurnal and nocturnal MCP home ranges than adults (Table 3.3.A; Figure 3.6.B). There was no significant interaction between hunted status and time of day (LMM of Ln response variable; t = 0.082, p = 0.935, B ±SE = 0.046 ±0.560, n = 82), or between age and time of day (LMM of Ln response variable; t = -0.023, p = 0.981, B ±SE = -0.013 ±0.557, n = 82).

SLCA home ranges were 23 times larger at night than during the day (throughout entire winter seasons: median diurnal SLCA home range = 0.006 km^2, IQR = 0.002 – 0.012, range = 0.0003 - 0.057, n = 43; median nocturnal SLCA home range = 0.14 km^2, IQR = 0.016 – 0.041, range = 0.004 - 0.297, n = 43). Within the hunting open seasons, there was an effect of age on SLCA home range (Table 3.3.B; Figure 3.6.C), though there was no significant interaction between age and time of day (LMM of Ln response variable; t = -0.975, p = 0.336, B ±SE = -0.434 ±0.446, n = 82). There was no effect of hunting on diurnal or nocturnal 95% SLCA home range.

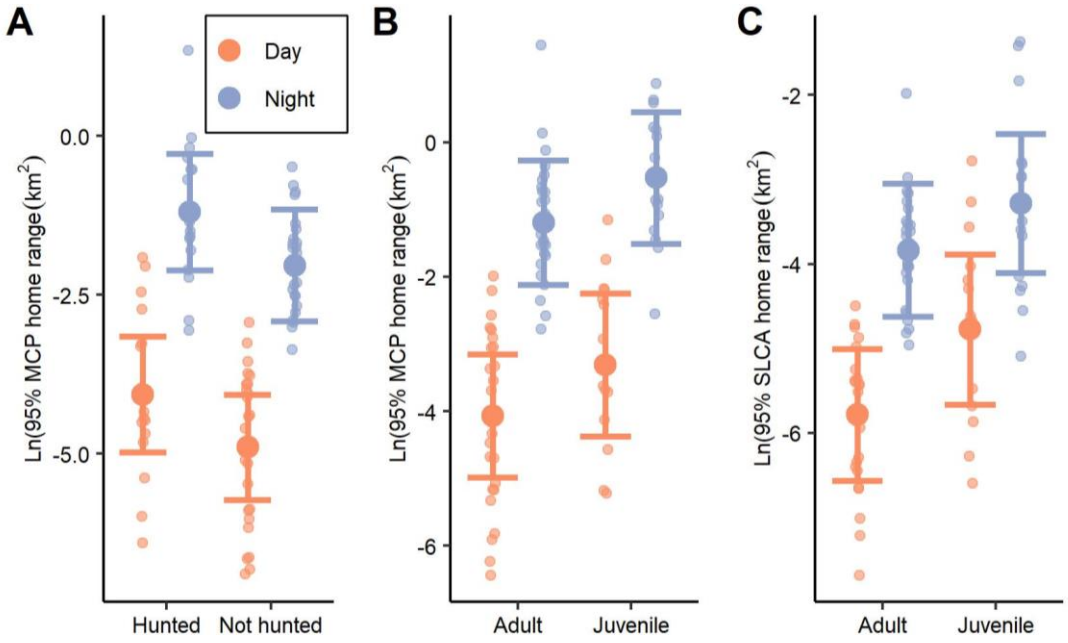


Figure 3.6. Plots generated from linear mixed models, grouped by time of day (day/night), showing **A**) the effect of hunting on 95% minimum convex polygon (MCP) home range (n=82); **B**) effect of age on 95% MCP home range size (n = 82); **C**) effect of age on 95% single-linkage cluster analysis (SLCA) home range area (n = 82). Bars represent model predicted values, while partial residuals are shown as points. The main effects shown in each plot are significant, but no interactions were significant (Table 3.3).

Table 3.3. Linear mixed model outputs for diurnal and nocturnal home ranges. Where p-values are shown: ** = strongly significant where $p < 0.05$; * = weakly to moderately significant effect where $0.05 < p < 0.15$. For the categorical factors time of day, hunted and age, the reference levels were night, not hunted and adult respectively.

	Response variable	Fixed effect / Random effect	Estimate	SE	df	t-value	p-value	Random effect var. (% of total var.)	Random effect std. dev.
A	Ln(95% MCP home range (km^2)) (n = 82)	Intercept	-5.572	0.386	22.252	-14.453	<0.001**		
		Time of day (night)	2.731	0.495	71.861	5.522	<0.001**		
		Hunted status (hunted)	0.844	0.372	5.927	2.265	0.065*		
		Age (juv.)	0.804	0.349	40.872	2.303	0.027**		
		No. of fixes	0.007	0.004	76.966	1.767	0.081*		
		ID:Site						19.19	0.593
		Site						3.04	0.236
B	Ln(95% SLCA home range (km^2)) (n = 82)	Intercept	-5.845	0.331	20.977	-17.649	<0.001**		
		Time of day (night)	1.489	0.399	72.407	3.729	<0.001**		
		Hunted status (hunted)	0.073	0.337	9.624	0.217	0.833		
		Age (juv.)	0.808	0.275	40.376	2.934	0.005**		
		No. of fixes	0.002	0.003	75.893	0.662	0.510		
		ID:Site						12.27	0.386
		Site						8.74	0.326

3.3.4 Cluster analyses

Throughout the entire duration of the winter seasons, woodcock largely limited their distributions to disjunct location clusters dispersed within their respective MCP home ranges, with a variable proportion of GPS locations recorded outside these clusters. Birds usually had more nocturnal than diurnal clusters (throughout entire winter seasons: mean ± SD = 1.605 ± 0.877, range = 1 - 4, n = 42; nocturnal, mean ± SD = 4.209 ± 2.356, range = 1 - 13, n = 43). Within the hunting open seasons, there was no significant effect of bird age or hunted status on the number of clusters (Table 3.4.A), nor was there any significant interaction between time of day and hunting status (LMM; t = -1.397, p = 0.166, B ±SE = -0.961 ±0.688, n = 83), or between time of day and age (LMM; t = -0.486, p = 0.628, B ±SE = -0.332 ±0.682, n = 83).

Birds varied in the extent to which they wandered away from preferred locations, as shown by the proportion of un-clustered locations, but there was no effect of time of day on this variable (throughout entire winter seasons: diurnal median percentage of un-clustered locations = 5.56%, IQR = 3.18 - 15.04, range = 0.00 - 71.43, n = 39; nocturnal median percentage of un-clustered locations = 6.79%, IQR = 4.01 – 11.07, range = 1.21 - 80.85, n = 43). Within the hunting open seasons, there was evidence that juveniles were significantly more likely to have recorded a slightly higher proportion of un-clustered locations than adults (Table 3.4.B; adult median = 0.054, IQR = 0.033 – 0.089, range = 0.000 – 0.294, n = 48; juvenile median = 0.0863, IQR = 0.049 – 0.147, range = 0.000 – 0.702, n = 32). There were no significant effects of time of day or hunted status (Table 3.4.B), nor were there significant interactions between time of day and hunted status (GLMM with binomial distribution; t = -1.263, p = 0.207, B ±SE = -0.302 ±0.239, n = 80) or between time of day and age (GLMM with binomial distribution; t = -0.725, p = 0.237, B ±SE = 0.172 ±0.237, n = 80).

Throughout the entire duration of the winter seasons, birds undertook few long-distance movements during the day or at night. During the day, 91.1% of recorded movements between successive locations were less than 50 m (n = 620 individual movements, min = 0.0 m, max =779.0 m). At night, 66.6% of recorded movements between successive nocturnal locations across all birds were less than 50 m, while 80.5% movements were less than 150 m (n = 5350, min = 0.0 m, max = 6627.6 m).

Table 3.4. Mixed model outputs showing the relationship between cluster analysis metrics and time of day (day/night). Model A is a linear mixed model; models B and C are generalised linear mixed models with binomial distributions. Where p-values are shown: ** = strongly significant where $p < 0.05$; * = weakly to moderately significant effect where $0.05 < p < 0.15$. For the categorical factors time of day, hunted and age, the reference levels were night, not hunted and adult respectively.

	Response variable	Fixed effect / Random effect	Estimate	SE	df	t-value (z-value)	p-value	Random effect var. (% of total var.)	Random effect std. dev.
A	Number of clusters (n = 83)	Intercept	1.488	0.412	83.000	3.613	<0.001**		
		Time of day (night)	1.825	0.631	83.000	2.893	0.005**		
		Hunted status (hunted)	-0.076	0.346	83.000	-0.219	0.827		
		Age (juv.)	-0.004	0.349	83.000	-0.012	0.991		
		No. of fixes	0.007	0.004	83.000	0.920	0.360		
		ID:Site						(0.000)	0.000
		Site						(0.000)	0.000
B	Proportion of un-clustered GPS locations (n = 80)	Intercept	-2.718	0.274		(-10.140)	<0.001**		
		Time of day (night)	0.086	0.117		(0.738)	0.461		
		Hunted status (hunted)	-0.076	0.334		(-0.227)	0.821		
		Age (juv.)	0.475	0.221		(2.153)	0.031**		
		ID:Site						0.311	0.558
		Site						0.183	0.428
C	Proportion of nocturnal periods moved cluster (n = 42)	Intercept	-1.814	0.147		(-12.317)	<0.001**		
		Hunted status (H)	0.151	0.204		(0.741)	0.459		
		Age	-0.028	0.204		(-0.136)	0.892		
		ID:Site						0.277	0.526
		Site						0.000	0.000

Birds were more likely to move between or away from clusters at night than by day (throughout entire winter seasons: median percentage of diurnal periods when birds moved between or away from clusters = 0.0%, IQR = 0.0 – 6.1, range = 0.0 - 33.3, n = 36; median percentage of nocturnal periods when birds moved between or away from clusters = 21.1%, IQR = 11.8 – 28.9; range, 3.1-56.5, n = 43). Within the hunting open seasons, only twenty out of forty-two birds recorded ten or more diurnal periods with more than one GPS location. As such, only nocturnal values were used in this analysis. Neither hunted status nor age had a significant effect on the likelihood of moving between or away from clusters during a nocturnal period (Table 3.4.C).

3.4 Discussion

We examined the effects of hunting and age on the spatial ecology of woodcock in the non-breeding season. Survival rates were high and the mortality observed was caused mainly by hunting (Table 3.1). Birds showed strong fidelity to a variable number of disjunct core diurnal and nocturnal locations (Figure 3.4). Compared to adults, juveniles had larger diurnal and nocturnal home ranges (Figure 3.6.B and C), were more likely to commute further between diurnal and nocturnal areas (Figure 3.5.B), and undertook more wandering, exploratory movements (Table 3.4.B). Birds that experienced hunting had larger diurnal and nocturnal home ranges and tended to commute greater distances than not hunted birds. Adults were disproportionately affected by hunting as they were more likely to commute further than 100 metres between diurnal and nocturnal locations than not hunted adults, whilst there was no difference between hunted and not hunted juveniles (Figure 3.5.B).

3.4.1 Survival and mortality

Although our study examined woodcock survival over a relatively short period of time in the winter, it did so at multiple sites and covered a large part of the hunting open season. Our monthly survival estimate of 0.98 based on data from 155 birds within the hunting open season is higher than equivalent values from other studies that report monthly survival rates of between 0.85 and 0.96 across winter seasons (Tavecchia et al., 2002; Duriez, Eraud and Ferrand, 2006; Aradis et al., 2008) suggesting comparatively low mortality rates at our sites. Due to the small number of mortality

events we recorded, we are not able to conclude whether juveniles are more susceptible to higher mortality rates, but first-year woodcock have been shown to generally have lower survival than adults (Hoodless and Coulson, 1994; Tavecchia et al., 2002; Duriez, Eraud and Ferrand, 2006; but see Aradis et al., 2008). We are confident that censoring of birds was independent of mortality; most birds of unknown fate were a result of premature discarding of the tag. Three cases where birds had prematurely discarded their tags and were subsequently recaptured later in the winter proved that tags were discarded without harm to the birds. A smaller number of birds were assumed to have emigrated from the sites or their VHF tags had failed.

Ireland's mild oceanic climate is likely to contribute to high winter survival rates in woodcock. It has been shown that woodcock suffer higher mortality in winters with severe weather (Tavecchia et al., 2002) but the three seasons of our study were all reasonably mild with few nights falling below 0°C (Table A. 6), which is projected to continue in future winters (O'Brien and Nolan, 2023) and is likely to benefit overwintering woodcock. In addition, Ireland has relatively low predator diversity compared to other regions within the global range of woodcock. Woodland-dwelling birds of prey that can be important predators of woodcock elsewhere, particularly northern goshawk *Accipiter gentilis* (Verdal, 2007), tawny owl *Strix aluco* (Hoodless, 1994; Hoodless and Coulson, 1998) and Eurasian eagle-owl *Bubo bubo* (Lourenço, 2006) are rare or not present in Ireland (Balmer et al., 2013). However, important mammalian predators such as red fox *Vulpes vulpes*, pine marten *Martes martes* and feral cat *Felis catus* are widespread and common in Ireland (Duriez et al., 2005a; Lysaght and Marnell, 2016).

From the 129 known-fate birds by the end of hunting open seasons, four of the five that died had been shot by hunters, indicating that hunting was the main source of mortality at our sites. Previous work suggests that hunting mortality can be additive in woodcock (Duriez, Eraud and Ferrand, 2006), and that it can be strongly additive in other terrestrial game species (Small, Holzwart and Rusch, 1991; Smith and Willebrand, 1999; Sandercock et al., 2011; Zbinden et al., 2018). For example, for willow ptarmigan in central Sweden, monthly survival in the autumn was considerably lower where hunting took place (0.81) compared to not hunted areas (0.91; Smith and Willebrand, 1999), highlighting the need for sensible management of hunting activity to ensure sustainability. Whether additive or compensatory, the impact of hunting was

low at our study sites. Woodcock hunting is undertaken widely across Ireland in the open season, though little is known about the distribution of hunting intensity, which is difficult to quantify (Rist et al., 2008). Most hunting that took place at our hunted study sites was low-intensity rough hunting traditionally practised in Ireland using springer spaniels to indiscriminately locate and flush wildlife across large areas of suitable habitat, which differs from favoured methods in other regions of Europe where the use of pointing dog breeds or driven hunting can be more intense and prevalent (McKelvie, 1990; 1996). We suggest that further research attempting to quantify hunting intensity and exploring in detail the survival rates and causes of mortality at a greater variety of sites with different methods of hunting should be a priority.

3.4.2 Age and space use

The pattern we observed, where woodcock showed strong fidelity to a variable number of disjunct core diurnal and nocturnal locations, high levels of inter-individual variation in home range size and individually-unique use of space (Figure 3.5), matches the patterns seen in previous radio-tagging studies of overwintering woodcock in Ireland (Wilson, 1983), France (Duriez et al., 2005d; Ferrand et al., 2013) and England (Powell, 2012), though the reduced functionality of GPS in densely-vegetated habitats probably limited our ability to draw stronger conclusions from diurnal location data.

In common with other members of the family Scolopacidae, juvenile woodcock showed higher levels of exploratory behaviour and larger diurnal/nocturnal home ranges than adults. This was true during the day and at night (Table 3.3; Table 3.4.B; Figure 3.6.B and C) but it did not result in an increase in overall MCP home range size across day and night (Table 3.2.A; see also Powell, 2012). Thus, juvenile exploratory movements mainly occurred on a small spatial scale within their overall home range. On the one hand this may reflect the inexperienced juveniles sampling and learning about new foraging and roosting locations within their home range. However, it could also be due to intraspecific competition. Little is known about the extent to which woodcock compete for resources in the non-breeding season, though the possibility of social dominance has been raised (Duriez et al., 2005d; Powell, 2012), as has been documented between adults and juveniles in closely related species in the same family

(Groves, 1978; Cresswell, 1994; Van Den Hout et al., 2014). Although they are occasionally encountered in small, loose groups of two, three, or occasionally more (J. O'Neill, personal observation), overwintering woodcock are largely solitary. It is possible that adults, with accumulated experience and strong fidelity to wintering grounds from previous seasons (Tedeschi et al., 2020), are dominant over juveniles, leading to increased unsettled behaviour in juveniles. Like related species such as Eurasian curlew (Jiguet et al., 2023), post-migration juveniles might also sometimes associate with nearby adults to directly benefit from their experience. This may explain the common occurrence of pairs or trios of birds loosely associating together and could result in a higher frequency of 'un-clustered' exploratory locations in juveniles. At sites where there is no hunting activity, juveniles were more likely to commute further than 100 m than adults, implying that they may need to travel more widely to find foraging sites where they can find enough earthworms, as juveniles are less efficient at foraging than adults (Duriez et al., 2005c).

3.4.3 Hunting and space use

Although we believe our sites were not hunted at high intensities, and mortality rates were relatively low, we nevertheless detected significant differences in the movements and space use of woodcock in hunted and not hunted sites. As expected, diurnal MCP home ranges were larger where birds experienced hunting (Table 3.3.A; Figure 3.6.A), which corresponds with previous findings that controlled diurnal disturbance increased diurnal home range and movements, although the same study found no effect of normal levels of hunting on home range size (Ferrand et al., 2013). Unexpectedly, we also found nocturnal MCP home range was higher in hunted sites (Table 3.3.A, Figure 3.6.A). This may result from a knock-on effect of having a larger diurnal home range and/or a response to an increased perceived risk of predation at or near the favoured diurnal locations. We cannot distinguish between the two, but in support of the latter, hunted birds did commute greater distances overall (Figure 3.5.A), and hunted adults were less likely than not hunted adults to remain close (<100 m) to diurnal locations (Figure 3.5.B).

Hunting appeared to disproportionately affect the commuting behaviour of adult woodcock. Where hunting did not take place, adults had a significantly lower chance than juveniles of commuting more than 100 metres (Figure 3.5.B); to save energy,

such short journeys may have been walked, rather than flown. Adults that did experience hunting had a higher probability of commuting further than 100 m compared to not hunted adults, and had no significant difference from that of any juveniles (Figure 3.5.B). Duriez et al. (2005a) found that, in winter, the decision to undertake a commuting flight was taken every evening based on a trade-off between starvation and predation risk; grassland contains considerably higher biomass of food (earthworms) than woodland, but if birds had fed sufficiently well during the day, they would conserve energy and remain in the relative safety of their diurnal location. As juveniles tend to be less efficient at foraging than adults, they may be less likely to meet their daily energy requirements during the day and more likely to undertake commute flights to more productive areas. As such, we suggest that the perceived risk of predation may also influence the decisions regarding commuting flights with a disproportionate effect on adults, arising through an increase in the perceived risk of predation at diurnal locations, carrying over to night-time when birds are less likely to remain close to these diurnal locations.

The effects of hunting on woodcock spatial ecology we report here involved small scale changes in space use within and between diurnal and nocturnal periods, with no difference in overall home range size and little evidence of long-distance avoidance movements. Similar effects were reported for willow ptarmigan, which is also a terrestrial, elusive quarry species that is commonly found in closed habitats (Olsson, Willebrand and Smith, 1996; Brøseth and Pedersen, 2010). That woodcock readily move between densely-vegetated habitats within a restricted range to avoid hunters alludes to the importance of heterogeneous landscapes for this species. The actual mechanism of disturbance provided by hunting seems likely to be the repeated flushing of birds by gundogs. Regular flushing of woodcock has been shown to alter their use of space (Ferrand et al., 2013), and it is possible that a springer spaniel could flush a bird several times in the same day if it does not travel out of the local area.

Hunting likely had a negligible energetic cost for woodcock, not just because we believe hunting intensity was low, but because the distances were short and because suitable foraging habitat appears not to be limited, even in intensive agricultural landscapes where earthworm abundance is generally high (Muldowney et al., 2003; Curry et al., 2008). This contrasts with the effects seen in other quarry species such as waterfowl or terrestrial species in open habitats, which will often quickly relocate to

relatively distant safer sanctuaries or poor-quality habitat to spend daylight hours, sometimes with associated increases in nocturnal foraging activity to compensate for lost foraging time (Madsen and Fox, 1995; Evans and Day, 2001; Bregnballe and Madsen, 2004; Béchet, Giroux and Gauthier, 2004; Casas et al., 2009; Casazza et al., 2012; McDuie et al., 2021). For woodcock, relocating to new areas may be unnecessary for energetic reasons and may present several disadvantages, such as a higher risk of predation or hunting, lack of knowledge of local resources, or increased intra-specific competition, though we cannot discount the possibility that larger movements could occur in more intensively hunted sites. More generally, the costs and benefits of moving long distances in response to hunting are likely to differ among locations, populations and species, and is an area of applied research that could generally improve the management of hunted species.

3.5 Conclusion

This study improves our understanding of how hunting impacts space use by a terrestrial, elusive quarry species, as well as furthering our knowledge of its spatial ecology in the non-breeding season. Though the reduced functionality of GPS in closed habitats probably limited our ability to draw stronger conclusions from diurnal location data, we suggest that the effects of hunting on the spatial ecology of woodcock, i.e. behavioural change without leaving or greatly expanding the overall home ranges, are relatively subtle in comparison to the effects seen in other birds such as waterfowl, which will readily relocate to safer areas under hunting pressure. As expected, juveniles naturally display a greater extent of exploratory and commuting movements than adults, resulting in a disproportionately greater impact of hunting on aspects of the spatial behaviour of adults. We suggest that priorities for future research on this species should include increasing an understanding of winter survival rates and the role that hunting plays in this, as well as exploring the indirect effects of varying intensities of hunting on movements and use of space.

Chapter 4: The effects of hunting on habitat preferences of non-breeding Eurasian woodcock across a heterogeneous landscape in Ireland

Abstract

Most research on the sustainability of hunting has focused on direct impacts on mortality. In birds, indirect impacts are poorly understood, with little known about how hunting disturbance affects habitat preferences. The Eurasian woodcock *Scolopax rusticola* is an important quarry species that is hunted diurnally in Western Europe where it overwinters in high densities. Agricultural expansion and intensification have resulted in loss of their preferred habitats but the extent to which hunting influences usage of these habitats at all times of the day is poorly known. Here, we examined the importance of various habitat types to overwintering woodcock in agricultural bocage landscapes and tested whether human hunting activity affected diurnal and nocturnal habitat preferences. We used Global Positioning System (GPS) devices to track 42 non-breeding woodcock at three hunted and three not hunted sites in Ireland, with an average deployment duration of 64 days between December and early March from 2019 to 2022, largely coinciding with the open hunting season for this species. GPS units recorded multiple diurnal and nocturnal locations per day, which we analysed using habitat-selection function logistic regression models. Diurnally, woodcock preferred roosting in broadleaved and mixed forest, followed by hedgerows and scrub, while coniferous forest was the least-favoured closed habitat type. Nocturnally, birds used a variety of available habitats but mostly favoured grassland habitats. Age of the birds had limited effect on habitat preference. At sites where hunting took place, birds tended to avoid more easily hunted habitats during the day, including hedgerows and scrub, in favour of safer broadleaved/mixed forests; not hunted birds favoured each habitat equally. Although hunting occurs only during the day, birds at hunted sites showed a higher preference for open grassland habitats at night and were significantly less likely to use any closed habitats than were not hunted birds; increased use of open habitats and commuting activity may increase natural predation risk. We suggest that heightened perceived predation risk from hunting is an important factor influencing habitat selection even at night-time when not hunted. Our results emphasise the

importance of indirect effects and carry-over effects of hunting, and underline the need for a mosaic of different wooded and open habitats across the landscape, with an emphasis on broadleaved woodland and hedgerows.

4.1 Introduction

Understanding how species use habitats is a fundamental part of conservation biology. Much research in developed countries over recent decades has focused on understanding the habitat needs of species whose populations have declined dramatically, which has been especially pronounced across agrarian landscapes due to rapid changes in agricultural practices and land-use (De Heer, Kapos and Ten Brink, 2005; Boatman et al., 2007; Kleijn et al., 2009; Seibold et al., 2019; Clough, Kirchweger and Kantelhardt, 2020). Identifying habitat requirements can be challenging because many species are difficult to study, particularly those that are elusive, highly mobile or nocturnal. Additionally, many species require a variety of habitats to access resources needed for survival and reproduction, which may vary with life stage (e.g. Thomas, Simcox and Clarke, 2009), time of day (De Groeve et al., 2023) or by season (Pratt, Smith and Beck, 2019). Maintaining heterogenous agricultural landscapes with sufficient availability of different habitat types can have important consequences for species' abilities to withstand change or other human pressures, such as hunting (Maskell et al., 2019; Martin et al., 2020).

Wild game hunting is a prevalent recreational, cultural, and economic activity in many countries (Arnett and Southwick, 2015; Kupren and Hakuć-Błażowska, 2021). If not managed sustainably, hunting can lead to adverse impacts on quarry populations, either through direct overexploitation (Cullen, Bodmer and Valladares Pádua, 2000; Benítez-López et al., 2017), or through indirect effects caused by disturbance. Hunting disturbance mimics and exacerbates the natural predator-induced 'landscape of fear', leading to changes in the spatial behaviour of individuals in their attempt to reduce their perceived risk of predation, which often involve changes in habitat preferences (Reyna-Hurtado and Tanner, 2005; Laundre, Hernandez and Ripple, 2010; Bonnot et al., 2013; Lone et al., 2015). These behavioural changes may come at a cost to overall fitness, as key resources such as food or shelter may be less accessible (Benhaiem et al., 2008; Lone et al., 2015), resulting in higher energetic costs and reduced ability to

maintain body condition. Thus, hunting disturbance can lead to lower likelihood of survival through starvation or a higher risk of natural predation via superadditive effects (Kilgo, Labisky and Fritzen, 1998; Gehr et al., 2018; Smith, Gaynor and Suraci, 2021).

In birds, hunting disturbance has been shown to strongly affect spatial behaviour and movement ecology, though most work to date has focused on waterbirds (reviewed in Madsen and Fox, 1995; also (Evans and Day, 2001; 2002; Bregnballe and Madsen, 2004; Béchet, Giroux and Gauthier, 2004; Casazza et al., 2012), and few studies have attempted to quantify changes in habitat preferences. One study showed that greater snow geese *Anser caerulescens* tracked using radio telemetry tended to use less energetically productive foraging habitats when subjected to exceptional hunting during spring migration (Béchet, Giroux and Gauthier, 2004). Along with increased evasive flight and decreased time available for foraging, this resulted in a reduction in energy gains for geese at this site in years with hunting. Cox and Afton (1997) and Casazza et al. (2012) both found that habitat selection by radio-tracked overwintering northern pintail *Anas acuta* was strongly affected by hunting disturbance, which greatly increased the diurnal use of non-foraging habitat in sanctuaries compared to the closed season for hunting. At the same time, birds reduced their diurnal use of foraging habitat, which was mainly found outside sanctuaries, with the result that hunting activity effectively limited birds to foraging mainly during the hours of darkness. Little is known about how hunting disturbance affects habitat selection in terrestrial game-bird species, though Whitaker et al. (2006) suggest that based on results from radio telemetry, hunting may force particular age and sex classes of ruffed grouse *Bonasa umbellus* away from otherwise preferred habitats. Thus, there is an urgent need for more research on how hunting affects habitat use in terrestrial game species, especially in agricultural landscapes where habitat change has been particularly marked due to changing practices and intensification.

The Eurasian woodcock *Scolopax rusticola* (hereafter woodcock) is a largely migratory bird found widely across Eurasia, with particularly high non-breeding densities around the Mediterranean and in Western Europe (Cramp and Simmons, 1977), where it is a popular quarry species amongst game hunters in the autumn and winter. During the day, this species typically inhabits densely-vegetated habitats such as forest, hedgerow and scrub, while at night they may use open habitats (e.g. grassland) to forage, with commute flights between diurnal and nocturnal locations at

dusk and dawn (Wilson, 1983; Duriez et al., 2005b; Powell, 2012). A common complaint from local hunters is that much habitat diurnally preferred by this species, such as scrub, hedgerow and semi-natural or wet woodland, has been lost in recent decades to agricultural expansion and intensification (pers. comms), which is borne out by research in Ireland (Devaney, Redmond and O'Halloran, 2015; Green et al., 2021). Bird age (adult vs. juvenile) has been found to have limited effects on habitat selection in woodcock (Duriez et al., 2005b; Powell, 2012) and whilst one prior study has investigated the effects of hunting on their movement ecology (Ferrand et al., 2013), to date no studies have established whether hunting activity affects habitat selection in this species.

This study had two primary aims: i) to establish the importance of various habitat types to overwintering woodcock in diverse 'bocage' landscapes (woodlands and pastures with hedgerows) under the context of continuing agricultural intensification; and ii) to test our hypothesis that human hunting activity affects habitat preferences through disturbance, by tagging birds at separate hunted and not-hunted sites. As hunting occurs exclusively during the day, we expected an effect on diurnal habitat selection but also tested for possible carry-over effects on nocturnal habitat selection. In addition, effects of bird age were also assessed. Our study is an advance over similar studies on the effects of hunting on habitat selection in birds for two reasons. First, previous studies have used radio telemetry, which is both labour intensive and difficult to use at night; here, we use a tracking method that combines global position system (GPS) and radio telemetry, which automatically and continuously collected location data several times per day throughout the winter period. Second, we use habitat-selection function (HSF) analysis, which is an increasingly popular, simple and robust use of logistic regression modelling to explore habitat selection (Fieberg et al., 2021).

4.2 Methods

4.2.1 Study sites

Fieldwork was undertaken at six locations on the island of Ireland, in counties Cavan, Cork, Kerry and Tyrone, over the course of three consecutive winter seasons: 2019-20, 2020-21 and 2021-22 (seasons 1, 2 and 3, respectively; Figure 3.1; Table 3.1). Two fieldwork sites were used per season, one of which was 'hunted' and the other 'not-

hunted'. Hunted sites were visited by hunters who targeted woodcock using traditional Irish rough shooting methods. The 'not-hunted' sites were left relatively undisturbed as landowners did not permit hunting activity, though this did not exclude the potential for poaching. The open season for hunting woodcock in the Republic of Ireland falls between 1 November and 31 January each season. No hunting took place during the hours of darkness.

Sites were selected where there was sufficient habitat to support good numbers of woodcock; where necessary, nocturnal counts on pasture at prospective sites were undertaken to confirm their presence in sufficient numbers prior to tagging. Hunted sites were selected where a good relationship had been established with local hunters to ensure frequent communication about the extent of hunting activity and any recoveries of tagged or ringed birds.

Based on information provided by hunters, hunted sites were subject to variable hunting activity until the 31 January of each tag-deployment season, among which the sites that were hunted least (BL and TU) were visited at least 5 times, whilst the site that was hunted most (KI) was visited at least once or twice per week (8-16 times) by multiple hunters in different areas of the site. It is unknown how much hunting took place at each site before the tags were deployed. The intensity of rough hunting can vary based on hunter effort, but based on information provided by the hunters, we consider the levels of hunting at our hunted study sites to be at relatively low to medium intensities. At one not-hunted site (DD), a tagged bird was strongly suspected to have been shot by a hunter on the fringe of the site; in this case the GPS tag was retrieved but had malfunctioned shortly after deployment and provided insufficient data. Though contact could not be made with the hunter in question, they are not thought to have hunted within the main site area.

4.2.2 Tagging procedure and data retrieval

All work was conducted under permits issued by the National Parks and Wildlife Service (Ireland) and the British Trust for Ornithology (BTO; U.K.). Between 10 and 15 woodcock were tagged at each of six sites, giving totals of 42 adults and 27 juveniles (Table 3.1; Figure 4.1). Tagging took place in the month of December each season. Whilst the open hunting season had begun for Woodcock on 1st November, and Woodcock were present on sites from late October, the timing was chosen to

maximise the chances of tagging only Woodcock that had fully settled on their wintering grounds, as opposed to passage migrants, which could have moved away after capture (Hoodless and Heward, 2019). Woodcock were mainly captured at night in open habitats using a bright torch and hand-net, although some were captured using mist nets as they flew over fields at dusk (Figure 3.2.A). They were each fitted with a numbered metal ring issued by the BTO. The age of each bird was determined as juvenile (hatched within that calendar year) or adult (hatched in the previous calendar year or before) using wing feather characteristics and moult status (Ferrand and Gossmann, 2009; Demongin, 2016).

The tags used were double units consisting of a VHF radio transmitter (5.5g Glue-on Model; Perdix Wildlife Supplies, U.K.) and a GPS data logger (PinPoint 50, Lotek Wireless Inc., U.K.) glued together, forming a maximum combined mass of 7.5-8.1g (<2.5% of the birds' body mass, mean = 331g). This arrangement allowed for real-time tracking of the tag using 'very high frequency' (VHF) signals to increase the likelihood of physical retrieval of the GPS units. The VHF transmitter component, when activated, produced a single VHF pulse every 1.6 seconds (bandwidth 149-151MHz), and included a 'mortality indicator', which presented as a repeated double VHF pulse after 18 hours of the tag experiencing no movement. Tags were fitted with a small piece of cotton gauze and attached using cyanoacrylate glue to a small area of feathers and skin on the birds' backs, positioned over the front of the synsacrum (Figure 3.2.C). This unobtrusive method of attachment is temporary and tags would eventually be shed as a result of the birds' moult or preening action.

Figure 4.1. Nine woodcock captured and each mounted with a double-unit VHF/GPS tag at a study site (DD). These nine birds are the same individuals whose GPS location data is shown in Figure 3.4.

During seasons 1 and 2, tags were programmed using Pinpoint Host software (Lotek, version 2.15.4.0) to take a GPS locational fix four times per day; two nocturnal (04:00 and 21:00) and two diurnal (09:00 and 15:00). During season 3, tags were programmed to take an additional four locations per day, resulting in eight locations in a 24 hour period; four nocturnal (00:00, 04:00, 06:00 and 21:00), three diurnal (09:00, 12:00 and 15:00) and one that transitioned from nocturnal through dusk to diurnal as the season progressed (18:00). Almost all the tags were programmed to begin taking locations from the time of deployment.

The activity status and approximate location of each tagged bird was monitored via VHF telemetry at least once per week through each winter season (Figure 3.2.C). If a mortality indicator was detected, suggesting the tag had been shed or the bird had died, attempts were made to retrieve the tag, and record the status of the bird and tag if possible. For tags that had not been retrieved in this way before 15 February of each season, we attempted to recapture each bird, either using mist nets at dusk or a torch and hand-net at night. Upon recapture of a bird, the GPS logger was retrieved before immediate release. Recapture efforts continued until either all GPS loggers had been retrieved or the woodcock had departed on their spring migration whereby any tags remaining deployed were considered lost and irretrievable.

Of the total number of GPS tags deployed, 7 birds left the sites altogether either immediately or shortly after tagging, an additional 7 tags were otherwise not retrieved, 5 tags malfunctioned, 6 were prematurely shed, and 1 bird prematurely died (hunting mortality). Forty-three birds (26 adults, 17 juveniles) yielded useful GPS datasets (Table 3.1). Mean GPS logger deployment duration was 63.7 days (min = 18 max = 104). After GPS data had been retrieved from each site where hunting activity had taken place, the respective hunters were consulted and shown the diurnal tracking data, and were able to confirm if individual woodcock had likely been exposed to hunting activity based on whether their locations coincided with the areas where the hunters were active. This allowed us to categorise more accurately the status of each bird in relation to whether it had inhabited areas within sites that experienced hunting (n = 17) or were not hunted (n = 25). One hunted site (TU) included four birds that were considered unlikely to have experienced hunting activity and were classified as ‘not hunted. All birds on the not-hunted sites were classified as ‘not-hunted’ and we were assured this was true based on conversations with landowners, local hunters or from

personal knowledge. One woodcock (BB6) was diurnally located in an area several kilometres from the tagging site where it was unknown if woodcock hunting activity took place and was excluded from analyses.

4.2.3 Data preparation

Raw GPS location data were plotted (projected coordinate system: IRENET95 Irish Transverse Mercator) and examined in ArcGIS Pro v. 3.0 (ESRI, Redlands, CA, U.S.A). Data with low GPS accuracy were excluded by filtering out GPS locations where the number of satellites used to generate the location was fewer than four, or where Horizontal Dilution Of Position (HDOP) > 10, as location error can increase significantly above this value (Recio et al., 2011). Locations were categorised as diurnal or nocturnal based on the daily time they were generated. Those generated at 18:00 during season 3 were excluded from these analyses as these transitioned from nocturnal to diurnal across the duration of the season. Particular attention was paid to locations generated immediately after tag deployment; consecutive locations that appeared to fall outside the apparent regular home ranges of each bird, indicating a behavioural reaction to capture and tagging, were excluded from main analyses (n = 103, from 22 birds). Where two birds each made a brief, apparently erratic, long-distance movement from the tagging sites (i.e. further than 10km) in the middle of the winter season, the corresponding location data points (n = 16) were also excluded from the main analyses as these represented highly unusual movements. Thirty-four percent of diurnal fixes and ninety-four percent of nocturnal fixes were successful; the disproportionately lower success rate of diurnal GPS locations can be attributed to Woodcock choosing to diurnally inhabit denser habitats, which reduces communication ability between GPS satellites and the tags. Woodcock generally make few long-distance movements within diurnal or nocturnal periods, usually displacing no further than 50m (see Chapter 3). Therefore, to avoid overfitting for particular habitats, the location dataset was then filtered to only include the two locations per diurnal or nocturnal period with the highest accuracy as measured by HDOP.

After location data preparation, a total of 7,077 GPS locations (1,871 diurnal, 5,206 nocturnal) were obtained from 42 birds. 5,282 locations (74.6%) fell within the months of December and January across the seasons, coinciding with the open season for woodcock hunting. The remainder fell within February and the early days of March,

i.e. the closed season, but were included in the analyses to increase statistical power, as key models failed to converge when these data were excluded. Insufficient data were collected after January 31 to test for differences between the open and closed hunting seasons.

4.2.4 Habitat data and available home ranges

Habitat data were derived from the National Land Cover Map for Ireland 2018 (Tailte Éireann, Dublin, Ireland, 2023). This provided highly detailed landcover category maps of the sites including fine-scale features, such as narrow hedgerows, based on aerial and satellite data from 2018 (Figure 4.2.A). However, it required some manual alteration to correct machine error (e.g. wrongly classifying broadleaved forest as coniferous) and to appropriately update any land-use changes on the sites since 2018. One of the sites (BB; co. Tyrone, Northern Ireland; Figure 3.1) fell outside the geographical scope of the National Land Cover Map for Ireland 2018, which only covered the Republic of Ireland; this site was mapped out manually in ArcGIS Pro, matching the level of detail provided by the National Land Cover Map. Land cover designations were assigned to eight broad habitat categories (Figure 4.2.A): i) coniferous forest (Figure 4.3.A); ii) broadleaved/mixed forest (Figure 4.3.B); iii) hedgerow/treeline (Figure 4.3.C); iv) scrub/bracken (Figure 4.3.D); v) improved grassland (Figure 4.3.C); vi) unimproved/wet grassland (Figure 4.3.E); vii) heath/bog (Figure 4.3.F); viii) other (e.g. open water, urban, artificial surfaces, mudflats, bare rock). These categories were chosen as each represents a potentially important habitat type used by woodcock at different times of the day (Powell, 2012). Here, mixed forest refers to any mature forest interspersed with at least 25% composition of either coniferous or broadleaved species. We include pre-thicket and thicket-stage forest (< 20 years old) in the scrub/bracken category, although little of this existed across the sites. Improved grassland includes both permanent improved pasture and rotational ley; cultivated land was practically absent on the sites. Hereon, densely vegetated habitats (including forest, hedgerow/treeline and scrub/bracken) are referred to as ‘closed’ habitat types, and grassland and heath/bog as ‘open’ habitat.

Since Woodcock commute up to several kilometres between diurnal and nocturnal locations (see Chapter 3; also Duriez et al., 2005c; Powell, 2012), they can travel over large areas of available yet unused habitat within their home ranges. To generate a

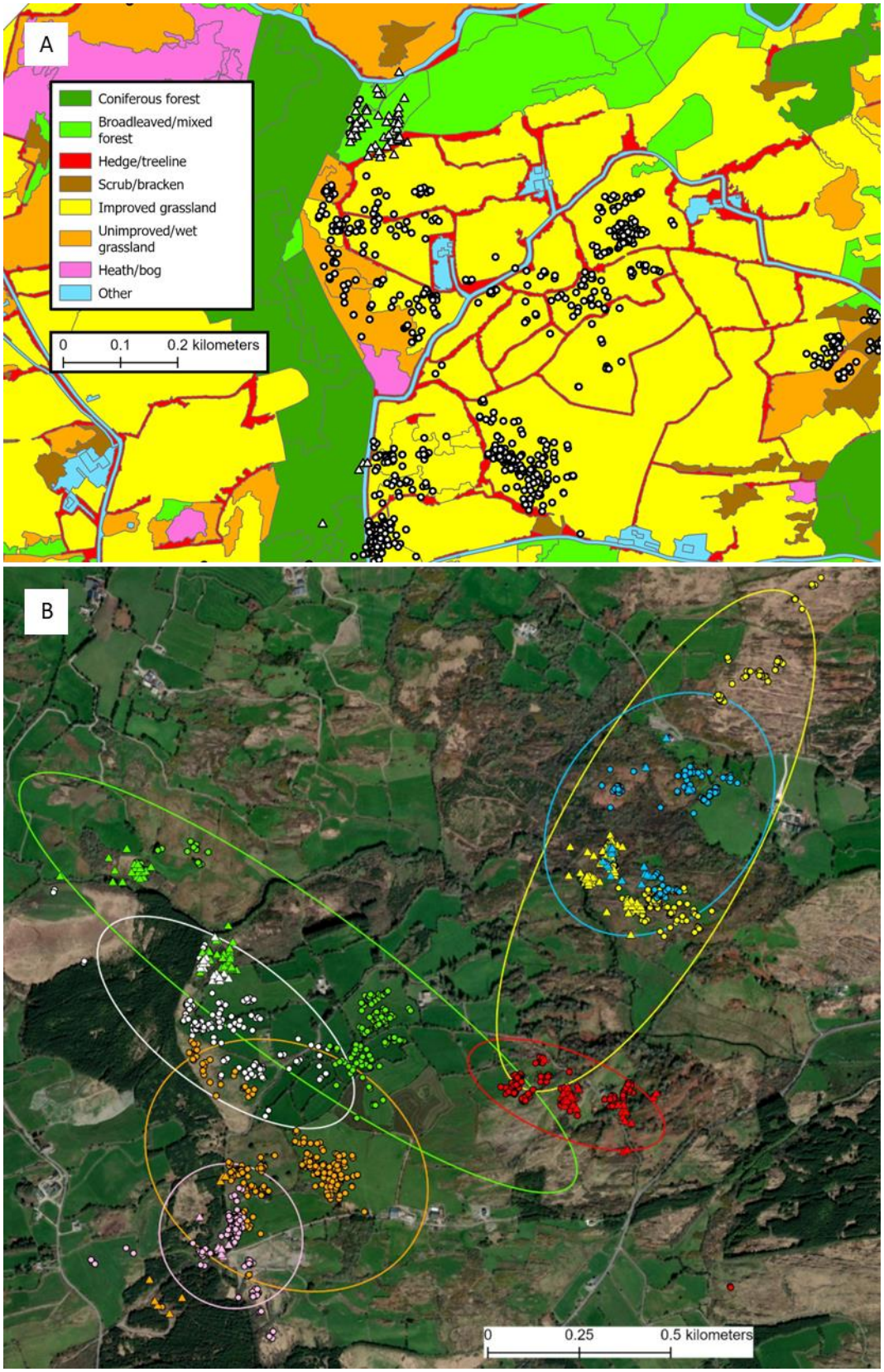


Figure 4.2. Maps of a study site (DD), showing: **A**) mapped habitat categories, each represented by a different colour; the combined diurnal (triangle markers) and nocturnal (circle markers) GPS location data for five birds are shown. **B**) diurnal (triangle markers) and nocturnal (circle markers) GPS location data for seven individual woodcock, as well as directional distribution home range ellipses based on 95% of an individual's GPS locations. Each individual is represented by a different colour.

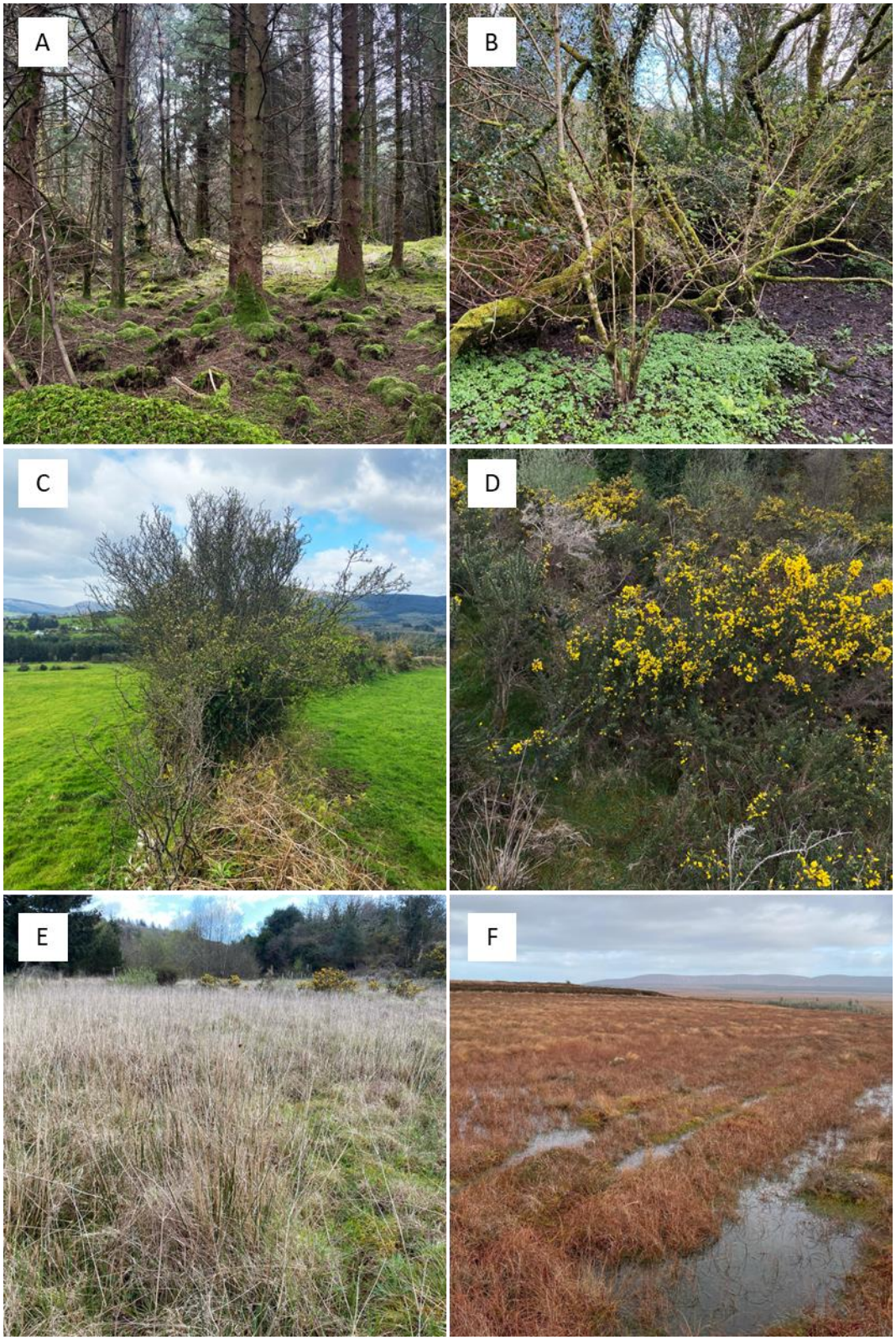


Figure 4.3. Examples of habitats found at study sites: **A**) coniferous forest plantation, mainly composed of Sitka spruce *Picea sitchensis*. Note the general absence of shrub- and ground-layer vegetation; **B**) mixed-species semi-natural broadleaved forest; **C**) improved grassland fields divided by hedgerows; **D**) low scrub, here mainly composed of gorse *Ulex europaeus*; **E**) unimproved wet grassland; **F**) blanket bog; raised bog and wet heath also occur at study sites.

'home range' to serve as the area available to each woodcock, an ellipsoid polygon was drawn for each using the 'Directional Distribution (Standard Deviational Ellipse)' tool in ArcGIS Pro, which calculates the standard deviation of the x and y coordinates from the mean centre to define the dimensions of the ellipse (Figure 4.2.B). Here, the ellipses were based on two standard deviations (95%) of combined diurnal and nocturnal data from each Woodcock that largely encompassed the distributions of the combined location data, and serve as appropriate availability domains. This method was used instead of other more commonly used home range estimation methods such as minimum convex polygon (MCP) and kernel density estimator (KDE) as we judged that it more reliably captured the area available to each bird without being influenced by outlying data points.

Using the 'amt' package (Signer, Fieberg and Avgar, 2019) in R v. 4.1.2 (R Core Team, 2021) 100 random (available) points were generated for each observed location for each woodcock within its respective home range ellipse. Although it has been shown that the number of available points does not strongly impact statistical models (Holloway and Miller, 2014), we chose this ratio following the recommendation by Fieberg et al. (2021) to use the highest ratio of available points to observed without seriously affecting computational speed, as this reduces Monte Carlo error. For both available and observed locations, a habitat variable was created by assigning the intersecting habitat category to each point using the 'sf' package (Pebesma, 2018; Pebesma and Bivand, 2023) in R v. 4.1.2 (R Core Team, 2021). Given the fine spatial scale, imperfectly drawn habitat boundaries, and because diurnal GPS fixes tend to have lower accuracy than nocturnal locations due to satellite signal interference from thick vegetation, any observed diurnal fixes assigned to open habitats that fell less than 10 metres from a closed habitat type (that woodcock are normally expected to inhabit during the day) were reassigned to the nearest habitat of the latter type (n = 166; 8.87%). This can be further rationalised because even if the birds were accurately located at the interface of open and closed habitats, perhaps taking an opportunity to forage in the absence of disturbance, it can be inferred that they are still closely associated with the adjacent forest, scrub, or hedgerow as would be expected. The availability of each habitat was calculated by taking the count of the available locations assigned to each habitat and expressing this as a proportion of the total available

location count; this was done within each individual home range and across the combined area of all home ranges.

4.2.5 Habitat selection functions

Habitat-selection analysis and interpretation was undertaken using a weighted distribution habitat selection function (HSF) method detailed in Fieberg et al. (2021). To perform the HSF, generalised linear mixed models were run (distribution = binomial; link = "logit") using the 'lme4' package (Bates et al., 2015) in R v. 4.1.2 (R Core Team, 2021), using the assignment of available (0) vs. observed (1) as the response variable, with a weight of 5,000 and 1 assigned to available and observed locations, respectively. Habitat was included as a fixed effect. Diurnal and nocturnal data were treated in separate models. Nested random effects accounting for woodcock ID nested within site were included. To explore the potential effects of age and hunting on habitat preference, similar GLMMs were run, first with the inclusion of an interaction between age and habitat, and again where the interaction was between hunted status and habitat. Here, 'coniferous forest' was chosen as the reference habitat category against which to measure the preference of the rest of the habitat categories.

We plotted the habitat selection effects from the models using the 'ggeffects' package (Lüdecke, 2018), and the 'interactions' package (Long, 2019) in R v. 4.1.2 (R Core Team, 2021), for main effects and interaction effects, respectively. These effects are measured using the exponent of the model parameter estimates added to the intercept. Following the interpretation method of Fieberg et al (2021), for each parameter we estimate the 'relative selection' (RS) values, which were calculated by taking the natural exponent of the model estimate alone for a given parameter. This is equivalent to the ratio of the selection effect for that parameter relative to that of the intercept; a higher RS value suggests a higher preference. Since we used coniferous forest as the reference, an RS value of 4 for broadleaved/mixed forest would suggest that, if the two habitat types were equally available, woodcock were four times more likely to select broadleaved/mixed than coniferous forest. Our interpretations are based primarily on these RS values, as selection for each model parameter may be compared against each other and allows habitat preferences to be ranked irrespective of differences in availability of different habitat types. Additionally, in the tables we also report 'relative occupation likelihood', which serves as a multiplicative measure of the

likelihood that a particular habitat at these sites will be occupied relative to the intercept, accounting for unequal availabilities of each habitat. For each parameter, this value was a product of the RS value and the relative availability of the corresponding habitat compared to the reference. Thus, a habitat such as improved grassland may have a low to moderate RS estimate, but as it is more dominant on these specific sites, it could have a higher relative occupation likelihood as the abundance of the habitat meant that it was used more often than if all habitats were equally available.

4.3 Results

4.3.1 Habitat availability

Across the six study sites, woodcock home ranges collectively encompassed a variety of habitats (Table 4.1; Figure 4.4). Overall, the most prevalent available habitat type was improved grassland, though a small number of birds inhabited areas that were dominated by heath/bog, broadleaved/mixed forest, or unimproved/wet grassland. Heath/bog was generally the least common habitat category, being overall 10.45 times less prevalent than improved grassland and absent altogether from two sites. The availability within home ranges did not significantly differ between age or hunted groups for most habitat categories (Mann-Whitney-Wilcoxon tests, $p > 0.05$). However, hunted birds had more hedgerow/treeline ($W = 93$, $p = 0.002$) and less heath/bog ($W = 290$, $p = 0.029$), and tended to have more improved grassland ($W = 139$, $p = 0.076$) available to them than not-hunted birds (Table 4.1; Figure 4.4.A); adults had more broadleaved/mixed forest available to them than juveniles ($W = 295$, $p = 0.024$) and tended to have less heath/bog ($W = 140$, $p = 0.070$) (Table 4.1; Figure 4.4.B), though all of these differences are slight.

4.3.2 General habitat selection

Woodcock showed strong preference for certain habitat types, which differed markedly between day and night (Table 4.2; Figure 4.5). During the day, closed habitat types were favoured (Table 4.2.A; Figure 4.5.A), of which the most important was broadleaved/mixed forest, followed by hedgerow/treeline and scrub/bracken, which were preferred 4.13, 2.33 and 2.21 times more than coniferous forest respectively.

Table 4.1. Proportions of habitat categories available within the home ranges of GPS-tagged woodcock (n = 42), grouped by age (adult or juvenile) and hunted status (not-hunted or hunted). 'Overall' represents the proportion of available habitat across the combined area of all home ranges in that group. Min., median and max. represent the minimum, median and maximum proportions found across individual home ranges from each group. Habitat availability is based on the assignment of habitat types to intersecting randomly-distributed points, of which 100 were generated for each observed diurnal and nocturnal GPS location (n = 7,077) within a corresponding home range.

Habitat	Overall	Adult (n = 26)				Juvenile (n = 16)				Not-hunted (n = 26)				Hunted (n = 16)			
		Overall	Min.	Median	Max.	Overall	Min.	Median	Max.	Overall	Min.	Median	Max.	Overall	Min.	Median	Max.
Coniferous forest	0.070	0.054	0.000	0.042	0.201	0.107	0.000	0.078	0.320	0.086	0.000	0.021	0.320	0.049	0.000	0.041	0.157
Broadleaved/mixed forest	0.174	0.194	0.032	0.199	0.374	0.128	0.000	0.108	0.471	0.188	0.000	0.140	0.374	0.153	0.023	0.142	0.471
Hedgerow/treeline	0.048	0.050	0.000	0.048	0.125	0.044	0.000	0.039	0.080	0.040	0.000	0.055	0.125	0.059	0.020	0.055	0.081
Scrub/bracken	0.047	0.052	0.000	0.028	0.247	0.035	0.000	0.036	0.091	0.056	0.000	0.050	0.247	0.034	0.004	0.028	0.091
Improved grassland	0.459	0.469	0.031	0.477	0.800	0.435	0.000	0.383	0.754	0.410	0.000	0.211	0.716	0.524	0.051	0.549	0.800
Unimproved/wet grassland	0.080	0.081	0.000	0.051	0.516	0.078	0.001	0.086	0.249	0.084	0.000	0.047	0.516	0.075	0.001	0.050	0.249
Heath/bog	0.043	0.026	0.000	0.001	0.217	0.081	0.000	0.024	0.675	0.061	0.000	0.048	0.675	0.019	0.000	0.000	0.217
Other	0.079	0.074	0.003	0.058	0.169	0.093	0.000	0.054	0.327	0.074	0.000	0.032	0.268	0.087	0.003	0.068	0.327

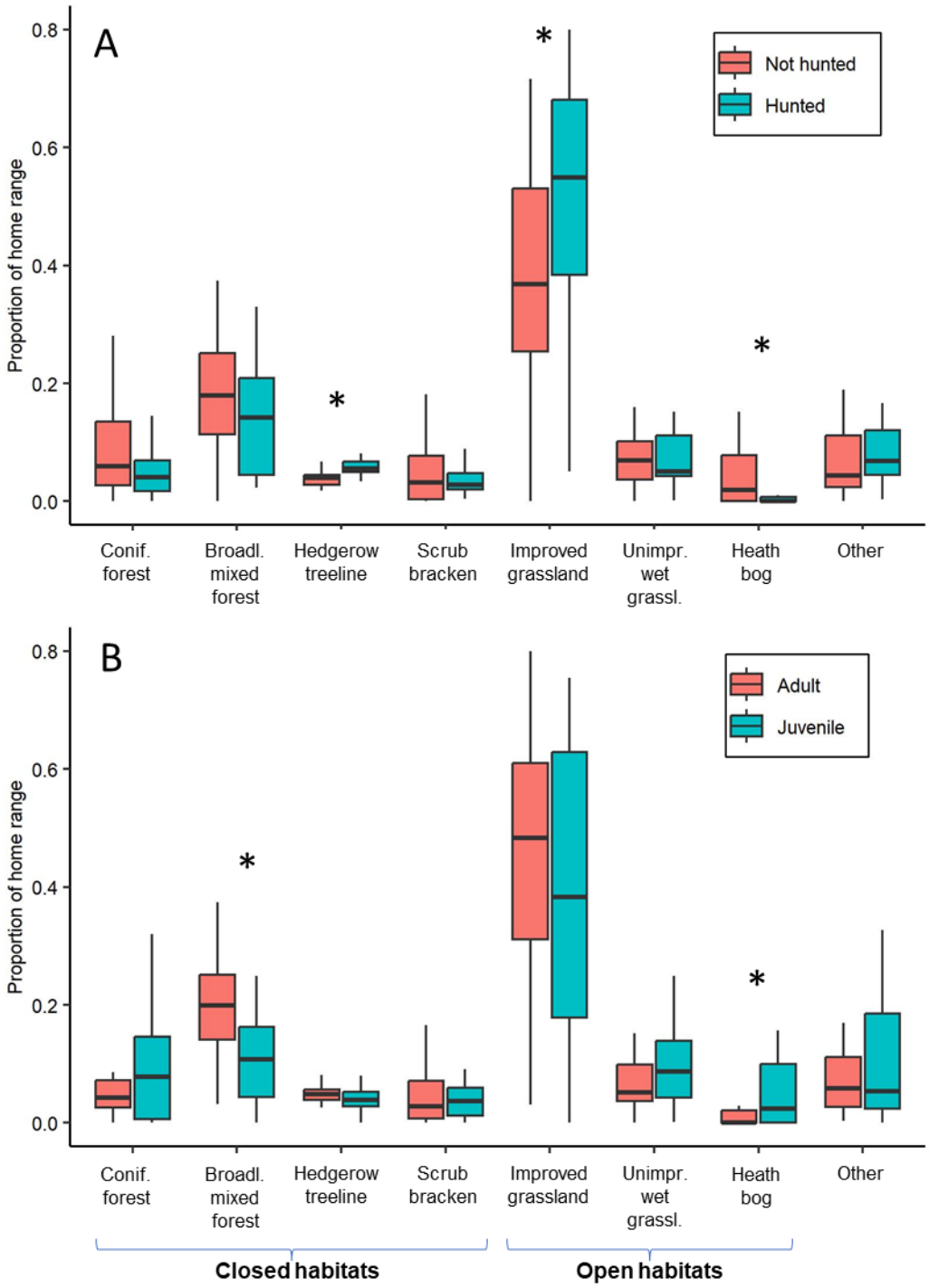


Figure 4.4. The proportion of each habitat category available within the home ranges of 42 tagged woodcock across six sites, based on the assignment of habitat types to intersecting randomly distributed points of which 100 were generated for each observed diurnal and nocturnal GPS location (n = 7,077) within a corresponding home range. Grouped by **A**) hunted status (hunted/not hunted) and **B**) bird age (adult/juvenile). Outlying values not included for increased clarity. Those marked with '*' showed a statistically significant different between groups.

Table 4.2. Outputs and derived values from two habitat selection function models, following the method and interpretation of Fieberg et al (2021), for (A) diurnal (n = 1,871) and (B) nocturnal (n = 5,206) GPS locations from 42 tagged woodcock across 6 sites. 100 random 'available' locations were generated for each observed GPS location within a corresponding home range. 'Coniferous forest' was used as the reference habitat category and serves as the intercept. 'Relative selection' serves as a multiplicative measure of preference compared to the reference; those with higher values are more preferred. 'Relative occupation likelihood' serves as a multiplicative measure of likelihood of occupation compared to the reference when relative habitat availabilities ('relative habitat ratio') across the study sites are accounted for.

	Time	Habitat	n (observed)	% of total observed	Model estimate	S.E.	z-value	p-value	Relative selection	Relative habitat availability	Relative occupation likelihood
A		Coniferous forest (intercept)	136	7.269	-13.021	0.123	-106.25	< 0.001	1.000	1.000	1.000
		Broadleaved/mixed forest	1223	65.366	1.419	0.078	18.097	< 0.001	4.134	2.454	10.144
		Hedgerow/treeline	244	13.041	0.847	0.091	9.313	< 0.001	2.333	0.682	1.591
	Day	Scrub/bracken	196	10.476	0.791	0.099	7.975	< 0.001	2.205	0.668	1.450
		Improved grassland	35	1.776	-3.34	0.15	-22.259	< 0.001	0.035	6.483	0.230
		Unimproved/wet grassland	13	0.695	-2.592	0.227	-11.422	< 0.001	0.075	1.136	0.085
		Heath/bog	17	0.909	-2.396	0.223	-10.769	< 0.001	0.091	0.625	0.056
		Other	7	0.374	-3.248	0.254	-12.768	< 0.001	0.039	1.138	0.044
B		Coniferous forest (intercept)	21	0.403	-15.994	0.077	-208.55	< 0.001	1.000	1.000	1.00
		Broadleaved/mixed forest	267	5.312	1.587	0.063	24.994	< 0.001	4.899	2.454	11.995
		Hedgerow/treeline	161	3.203	2.464	0.062	39.857	< 0.001	11.767	0.682	8.017
	Night	Scrub/bracken	183	3.641	2.486	0.068	36.812	< 0.001	12.012	0.668	7.900
		Improved grassland	3896	77.517	3.442	0.047	72.816	< 0.001	31.260	6.483	202.668
		Unimproved/wet grassland	404	8.038	2.755	0.063	43.601	< 0.001	15.717	1.136	17.851
		Heath/bog	220	4.377	2.56	0.063	40.117	< 0.001	12.932	0.625	7.954
		Other	54	1.074	0.683	0.082	8.281	< 0.001	1.979	1.138	2.234

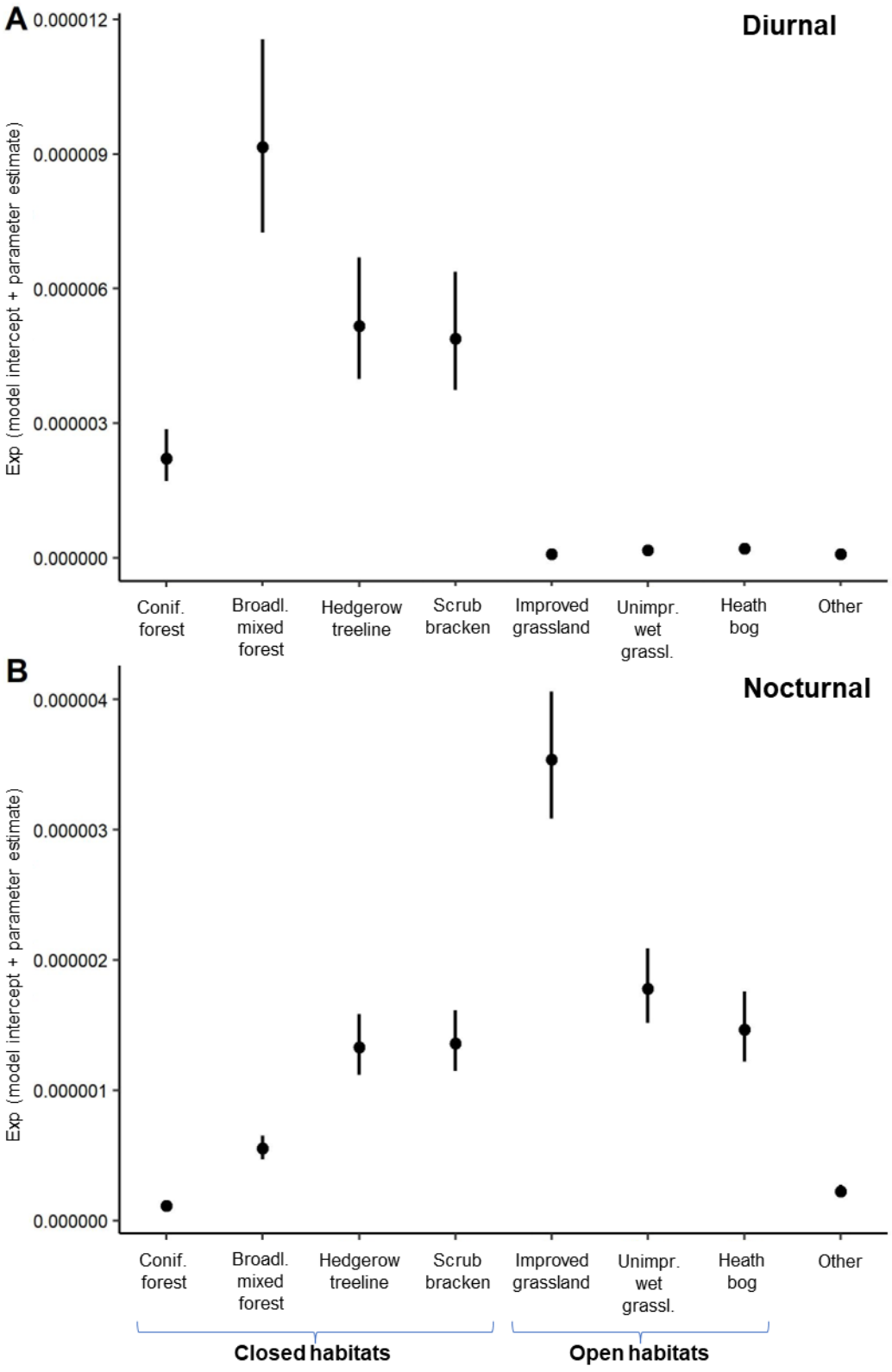


Figure 4.5. Plots derived from two habitat selection function logistic regression models for **A**) diurnal GPS locations (n = 1871) and **B**) nocturnal GPS locations (n = 5206) from 42 tagged Woodcock across six sites. 100 random 'available' locations were generated for each GPS location within a corresponding home range. Y-axis values are derived from the natural exponent of the model intercept + parameter estimates; a higher value indicates greater preference for that habitat category. Bars represent model predicted values ± standard error, corrected for other model factors at their reference category.

During the day, open habitats were largely avoided, although 0.016% of diurnal GPS locations comprised highly accurate (HDOP < 2.0) locations that were recorded in open habitat further than 10 m from forest, hedgerow/treeline or scrub/bracken. Notably, more than half of these locations were assigned to one exceptional juvenile bird (TU7) that was recorded almost exclusively inhabiting the steep, exposed north face of a mountain in habitat largely consisting of bare rock and wet heath on thin, peaty soils. 'Other' habitat types were generally avoided.

At night, a variety of open and closed habitats were used to various extents (Table 4.2.B; Figure 4.5.B). The least important of all nocturnal habitat categories was coniferous forest, which was assigned to just 0.004% of all nocturnal locations. The most important nocturnal habitat was improved grassland, followed by unimproved/wet grassland, which was 0.5 times as likely to be selected than the former. Heath/bog, scrub/bracken and hedgerow/treeline were all approximately equal important. Broadleaved/mixed forest was used sparingly at night, though it was selected for 4.9 times more than coniferous forest. 'Other' habitat types were largely avoided. Of particular note was the activity of one bird (TU5), which regularly used unimproved grassland and wet heath in close proximity to the seashore, and appeared to make occasional nocturnal visits to rocky and shingle intertidal shoreline zones.

4.3.3 Effects of age

Woodcock age had limited effect on diurnal habitat selection. The most preferred habitat for adults was broadleaved/mixed forest, followed by hedgerow/treeline, whilst juveniles most favoured scrub/bracken, followed by broadleaved/mixed forest (Table 4.3.A; Figure 4.6.A). Juveniles preferred scrub/bracken 5.81 times more than adults. Scrub/bracken had a lower relative availability compared to broadleaved/mixed forest (0.28 and 0.29 for juveniles and adults, respectively), so in terms of actual use, scrub/bracken accounted for 21.9% of all juvenile diurnal locations (n = 557) and 5.6% of all adult diurnal locations (n = 1314), whilst broadleaved/mixed forest accounted for 49.7% and 72.0%, respectively. This shows that broadleaved/mixed forest was an important habitat for both age groups, but juveniles had a higher preference for scrub than adults. Adults were 1.45 times more likely to select hedgerows/treelines than juveniles. Coniferous forest was the least preferred closed habitat type for both age groups during the day.

Age also had limited apparent effects on nocturnal habitat selection (Table 4.3.B; Figure 4.6.B). Both age groups had similar habitat preferences, generally following the overall order of preference across all birds (Table 4.2.B; Figure 4.5.B). Most notably, juveniles preferred hedgerow/treeline 1.42 times more than adults, whilst adults preferred scrub/bracken 1.45 times more than juveniles, both of which were opposite to what was found during the day.

4.3.4 Effects of hunting

Hunting affected both diurnal and nocturnal habitat selection (Table 4.4; Figure 4.7). By day, broadleaved/mixed forest, hedgerow/treeline and scrub/bracken were of approximately equal importance to not-hunted birds (Table 4.4.A; Figure 4.7.A). In contrast, birds that experienced hunting strongly favoured broadleaved/mixed forest, selecting this habitat type 3.33 and 8.56 times more than hedgerow/treeline and scrub/bracken, respectively. Preference for coniferous forest did not significantly differ between hunted and not-hunted birds.

Nocturnally, hunted woodcock were significantly more likely to use grassland habitats and significantly less likely to use any closed habitat types than not-hunted birds (Table 4.4.B; Figure 4.7.B). Improved grassland was the most important habitat for both groups, though hunted birds selected for this 1.39 times more than not-hunted birds. Conversely, not-hunted birds were 2.89, 1.44 and 1.43 times more likely to use broadleaved/mixed forest, hedgerow/treeline or scrub/bracken than hunted birds, respectively. Heath/bog was of approximately equal importance for both groups.

Table 4.3. Outputs and derived values from two habitat selection function models, following the method and interpretation of Fieberg et al (2021), for (**A**) diurnal (n = 1,871; adult = 1,314, juvenile = 557) and (**B**) nocturnal (n = 5,206; adult = 3,537, juvenile = 1,669) GPS locations from 42 tagged woodcock (26 adult, 16 juvenile) across six sites, where an interaction term between 'age' and 'habitat' was included. 100 random 'available' locations were generated for each observed GPS location within a corresponding home range for that individual. 'Coniferous forest' and 'Adult' were used as the reference habitat and age categories, respectively, and together serve as the intercept. 'Relative selection' serves as a multiplicative measure of preference compared to the reference. 'Relative occupation likelihood' serves as a multiplicative measure of likelihood of occupation compared to the reference when relative habitat availabilities across the study sites are accounted for. 'Ad/juv selection ratios' serve to compare adult and juvenile values of relative selection for each habitat category. 'Ad/juv relative habitat availability ratios' serve to compare adult and juvenile habitat availabilities relative to the reference. 'Ad/juv relative occupation likelihood ratios' serve to compare adult and juvenile values of relative occupation likelihood for each habitat category.

			Adult (Ad)				Juvenile (Juv)						
	Time	Habitat	Model estimate	p-value	Relative selection	Relative occupation likelihood	Model estimate	Interaction p-value	Relative selection	Relative occupation likelihood	Ad/Juv selection ratio	Ad/Juv relative habitat availability ratio	Ad/Juv relative occupation likelihood ratio
A	Day	Coniferous forest	(intercept)	< 0.001	1.000	1.000	0.224	< 0.001	1.251	2.469	0.800	0.507	0.405
		Broadleaved/ mixed forest	1.407	< 0.001	4.084	14.668	1.585	0.740	4.879	11.552	0.837	1.517	1.270
		Hedgerow/ treeline	0.977	< 0.001	2.656	2.471	0.607	< 0.001	1.835	1.477	1.447	1.156	1.674
		Scrub/bracken	0.093	0.51	1.097	1.054	1.850	< 0.001	6.362	4.069	0.172	1.501	0.259
		Improved grassland	-3.392	< 0.001	0.034	0.292	-3.031	0.570	0.048	0.388	0.697	1.077	0.751
		Unimproved/ wet grassland	-2.576	< 0.001	0.076	0.114	-2.435	< 0.001	0.088	0.126	0.868	1.044	0.906
		Heath/bog	-2.739	< 0.001	0.065	0.031	-1.643	< 0.001	0.193	0.290	0.334	0.322	0.108
		Other	-15.075	< 0.001	< 0.001	< 0.001	-2.013	0.760	0.134	0.230	< 0.001	0.789	< 0.001
B	Night	Coniferous forest	(intercept)	< 0.001	1.000	1.000	-1.686	< 0.001	0.185	0.366	5.399	0.507	2.735
		Broadleaved/ mixed forest	1.138	< 0.001	4.848	11.210	0.930	< 0.001	2.535	6.002	1.231	1.517	1.868
		Hedgerow /treeline	1.860	< 0.001	11.170	5.979	2.211	< 0.001	9.122	7.341	0.704	1.156	0.814
		Scrub/bracken	2.075	< 0.001	10.430	7.644	1.704	< 0.001	5.496	3.516	1.448	1.501	2.174
		Improved grassland	2.920	< 0.001	22.424	160.638	3.006	< 0.001	20.207	162.556	0.917	1.077	0.988
		Unimproved /wet grassland	2.295	< 0.001	11.445	14.920	2.197	< 0.001	8.994	12.961	1.103	1.044	1.151
		Heath/bog	2.052	< 0.001	10.051	3.763	2.087	< 0.001	8.060	12.098	0.966	0.322	0.311
		Other	-0.202	0.063	1.181	1.112	0.549	< 0.001	1.731	2.984	0.472	0.789	0.373

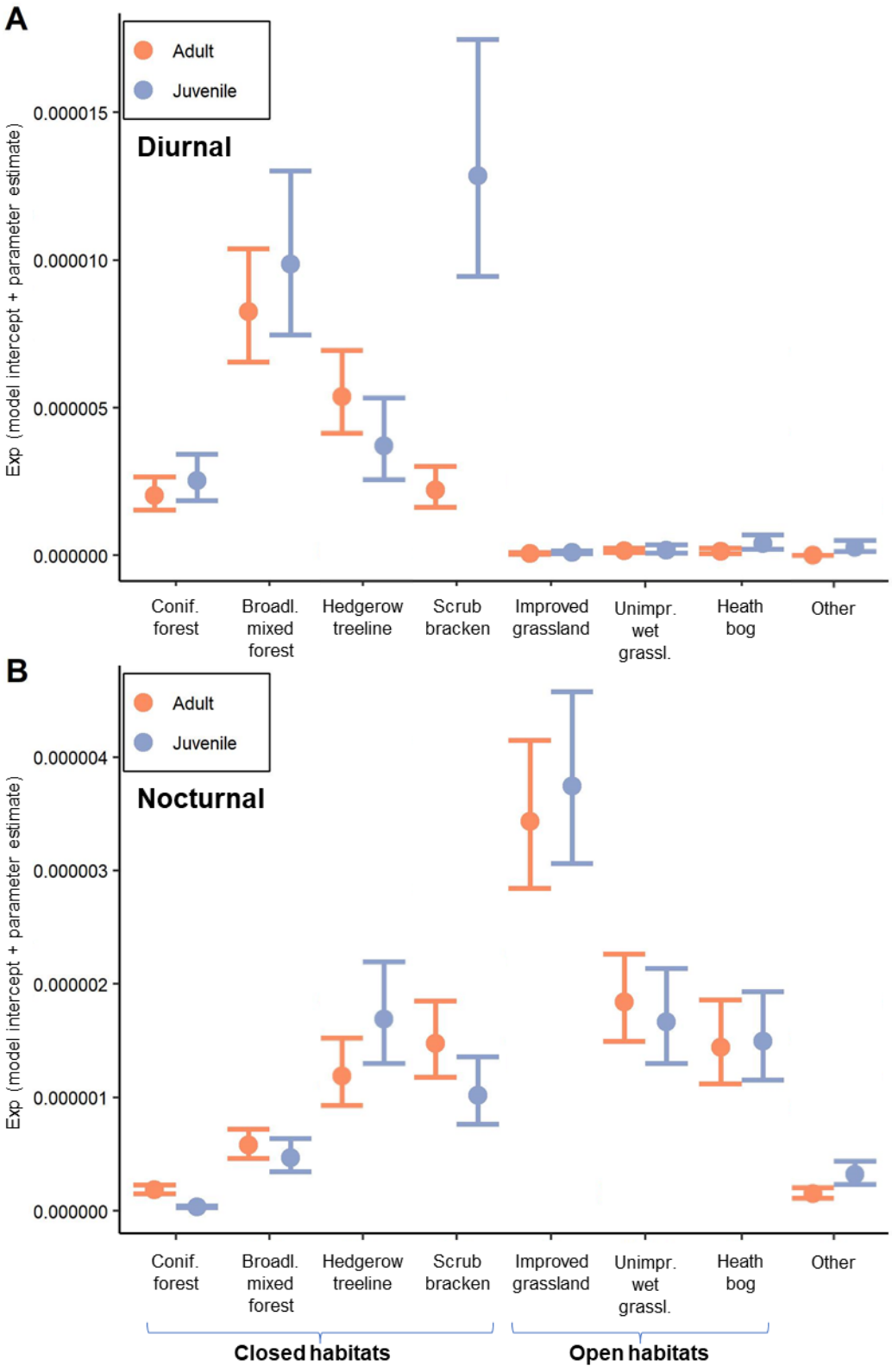


Figure 4.6. Plots derived from two habitat selection function logistic regression models, grouped by age, for (A) diurnal GPS locations (n = 1,871) and (B) nocturnal GPS locations (n = 5,206) from 42 tagged Woodcock across six sites. 100 random 'available' locations were generated for each GPS location within a corresponding home range. Y-axis values are derived from the natural exponent of the model intercept + parameter estimates; a higher value indicates greater preference for that habitat category. Bars represent model predicted values ± standard error, corrected for other model factors at their reference category.

Table 4.4. Outputs and derived values from two habitat selection function models, following the method and interpretation of Fieberg et al (2021), for **A**) diurnal (n = 1,871; not-hunted (NH) = 1,052 , hunted (H) = 819) and **B**) nocturnal (n = 5,206; NH = 3,054, H = 2,152) GPS locations from 42 tagged woodcock (NH = 26 , H = 16) across six sites, where an interaction term between 'habitat' and 'hunted' was included. 100 random 'available' locations were generated for each observed GPS location within a corresponding home range. 'Coniferous forest' and 'NH' were used as the reference 'habitat' and 'hunted status' categories, respectively, and together serve as the intercept. 'Relative selection' serves as a multiplicative measure of preference compared to the reference. 'Relative occupation likelihood' serves as a multiplicative measure of likelihood of occupation compared to the reference when relative habitat availabilities across the study sites are accounted for. 'NH/H selection ratios' serve to compare NH and H values of relative selection for each habitat category. 'NH/H relative habitat availability ratios' serve to compare NH and H habitat availabilities relative to the reference. 'NH/H relative occupation likelihood ratios' serve to compare NH and H values of relative occupation likelihood for each habitat category. 'NH/H selection ratios' serve to compare NH and H values of relative selection for each habitat category.

Time	Habitat	Not-hunted (NH)				Hunted (H)				NH/H selection ratio	NH/H relative habitat availability ratio	NH/H occupation likelihood ratio
		Estimate	p-value	Relative selection	Relative occupation likelihood	Estimate	Interaction p-value	Relative selection	Relative occupation likelihood			
A	Coniferous forest	(intercept)	< 0.001	1.000	1.000	0.069	0.744	1.072	0.611	0.933	1.756	1.638
	Broadleaved/ mixed forest	1.327	< 0.001	3.771	8.236	1.629	0.079	5.099	9.033	0.740	1.233	0.912
	Hedgerow/ treeline	1.327	< 0.001	3.768	1.765	0.427	< 0.001	1.533	1.049	2.458	0.684	1.682
	Scrub/bracken	1.258	< 0.001	3.518	2.277	-0.518	< 0.001	0.596	0.232	5.908	1.663	9.825
Day	Improved grassland	-3.477	< 0.001	0.031	0.147	-3.213	0.450	0.040	0.245	0.768	0.782	0.601
	Unimproved/ wet grassland	-2.192	< 0.001	0.112	0.109	-3.072	0.002	0.046	0.040	2.411	1.121	2.704
	Heath/bog	-2.145	< 0.001	0.117	0.083	-2.059	< 0.001	0.128	0.028	0.918	3.225	2.959
	Other	-2.486	< 0.001	0.083	0.072	-15.823	< 0.001	< 0.001	∞	∞	0.848	∞
B	Coniferous forest	(intercept)	< 0.001	1.000	1.000	-10.087	< 0.001	< 0.001	∞	∞	1.756	∞
	Broadleaved/ mixed forest	1.579	< 0.001	4.848	10.587	0.518	< 0.001	1.678	2.973	2.889	1.233	3.561
	Hedgerow /treeline	2.413	< 0.001	11.170	5.231	2.051	< 0.001	7.775	5.320	1.437	0.684	0.983
	Scrub/bracken	2.345	< 0.001	10.430	6.750	1.985	< 0.001	7.277	2.832	1.433	1.663	2.383
Night	Improved grassland	3.110	< 0.001	22.424	106.689	3.438	< 0.001	31.131	189.362	0.720	0.782	0.563
	Unimproved /wet grassland	2.438	< 0.001	11.445	11.160	2.698	< 0.001	14.856	12.919	0.770	1.121	0.864
	Heath/bog	2.308	< 0.001	10.051	7.129	2.325	< 0.001	10.224	2.248	0.983	3.225	3.171
	Other	0.167	0.189	1.181	1.016	0.834	< 0.001	2.303	2.337	0.513	0.848	0.435

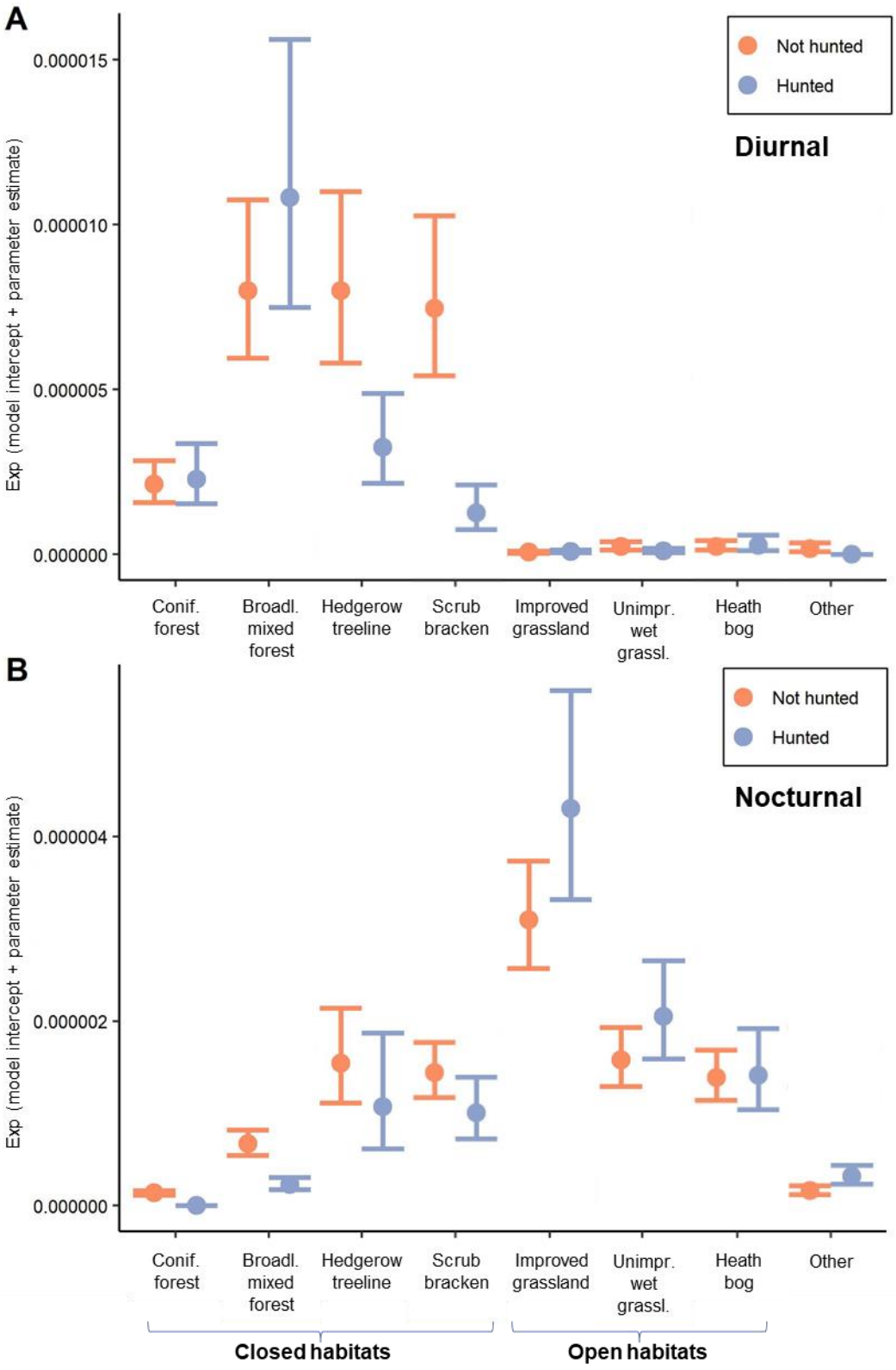


Figure 4.7. Plots derived from two habitat selection function logistic regression models, grouped by hunted status, for (A) diurnal GPS locations (n = 1,871) and (B) nocturnal GPS locations (n = 5,206) from 42 tagged Woodcock across six sites. 100 random 'available' locations were generated for each GPS location within a corresponding home range. Y-axis values are derived from the natural exponent of the model intercept + parameter estimates; a higher value indicates greater preference for that habitat category. Bars represent model predicted values ± standard error, corrected for other model factors at their reference category.

4.4 Discussion

Our primary aims were: 1) to establish the habitat preferences of overwintering woodcock in agricultural bocage landscapes; 2) to examine whether human hunting activity affected diurnal and nocturnal habitat preferences. During the day, birds almost always selected closed habitat types with a strong preference for broadleaved/mixed forest, although hedgerow/treeline and scrub/bracken were also important, while coniferous forest was the least preferred closed habitat (Table 4.2.A; Figure 4.5.A). At night, a variety of open and closed habitats were often used, with a clear preference for open grasslands (Table 4.2.B; Figure 4.5.B). Bird age had limited observed effects on habitat selection (Table 4.3; Figure 4.6). However, both diurnal and nocturnal habitat preferences were affected by human hunting activity (Table 4.4; Figure 4.7), which we suggest can be explained by the trade-off between perceived predation risk and foraging ability.

4.4.1 General habitat preferences

Diurnally, woodcock overall preferred the broadleaved/mixed forest habitat category, followed by hedgerow/treeline and scrub/bracken (Table 4.2.A; Figure 4.5.A), whilst coniferous forest was the least preferred closed habitat type. This corresponds with the findings of comparable studies (Duriez et al., 2005b; Powell, 2012) and probably reflects two qualities of these habitats: extent of ground layer vegetation for cover and prey availability. Mid-rotation and mature coniferous plantation forests in the densely-planted style normally found in Ireland and the United Kingdom, and found on our sites, usually have little shrub- and ground-layer vegetation (Figure 4.3.A; Ferris et al., 2000) and so affords little concealment from aerial or terrestrial predators. In contrast, most of the deciduous and mixed forest found on our sites was natural and semi-natural wet woodland or young plantation, which often possessed thick shrub- and ground-layer vegetation such as brambles *Rubus* spp., bilberry *Vaccinium myrtillus*, willows *Salix* spp. or holly *Ilex aquifolium*, providing effective cover Figure 4.3.B). Similarly, scrub and many hedges across our study sites featured dense shrub- and ground-layer vegetation. With a specialist diet consisting mainly of earthworms, the ability to successfully forage in diurnal habitats has been shown to be an important factor in habitat selection by woodcock (Duriez et al., 2005b; 2005c). Soils with mull humus form, associated with deciduous forest and high earthworm density, are utilised

over those with mors humus form that is associated with coniferous forest, thick litter layers and low soil invertebrate abundance (Jabiol, 1995; Bernier, 1998; Duriez et al., 2005b). Moreover, Duriez et al. (2005a) found that earthworm abundance was strongly linked to levels of shrub-layer vegetation cover. Thus, the use of coniferous forest at our study sites probably reflects instances where birds were able to find patches of suitable shrub-layer vegetation in gaps, firebreaks or on forest boundaries, which could not be identified at the level of accuracy from the GPS locations or habitat mapping.

We expected thick hedgerows with sufficient shrub and ground-layer to be an important habitat given their proximity to earthworm-rich pasture (Holden et al., 2019) and frequent presence of wet features running along or within hedgerows. The incidence of woodcock using hedges/treelines diurnally appeared to be higher on our sites compared to the findings of Duriez et al. (2005a) on their site in Brittany, France. This may reflect differences in the landscape composition between the study areas, for example a generally lower availability of forest across our sites twinned with a higher availability of suitable hedgerows relative to the area of deciduous woodland.

Nocturnal habitat preferences were dominated by improved grassland, followed by unimproved and wet grassland (Table 4.2.B; Figure 4.5.B). This is typical of woodcock in bocage landscapes (Wilson, 1983; Duriez et al., 2005b; Powell, 2012), which commute from diurnal habitats to exploit higher food availability in grasslands as a trade-off against the higher risk of mammalian predation and higher thermoregulatory costs in open habitats (Duriez et al., 2004; Duriez, Eraud and Ferrand, 2006; Braña, Prieto and González-Quirós, 2010). On our sites, 5.7% of GPS nocturnal fixes on our sites were recorded in forest (24.4% availability), compared to about 12% of nocturnal radiotelemetry fixes in forest (about 30% availability) recorded by Powell (2012) in southern England. Duriez et al. (2005b) used activity tilt-switches in tags to show that the decision whether to commute is made each evening, with those that had fulfilled their energy requirements during the day remaining in woodland overnight. This suggests that prey availability in diurnal habitats across our sites, particularly woodland and forest, do not generally provide sufficient feeding and in most instances birds commute to grassland, though the extent to which our birds nocturnally used closed habitats may be under-represented given the limitations of GPS to operate in dense vegetation. Nonetheless, our results show

that, when available, scrub, hedgerows, broadleaved/mixed forests and even heath/bog, which typically have low earthworm availability in peaty soils (Cotton and Curry, 1982), are regularly used nocturnally by woodcock in our study areas, reflecting flexibility to adapt to different habitats and landscapes.

4.4.2 Hunting and habitat use

Birds that experienced hunting activity favoured broadleaved/mixed forest more strongly and had a lower preference for hedgerow/treelines and scrub/bracken during the day compared to not-hunted birds, which favoured each habitat type approximately equally (Table 4.4.A; Figure 4.7.A). Forest is a more difficult habitat for hunting, as flushed birds can quickly be obscured by dense branches or foliage, presenting fewer opportunities for a shot. Hunters tend to focus their activity along hedgerows, scrub and forest edges, where flushed birds are more likely to present a shot in the open. We suggest that an increased perceived risk of hunting mortality during daylight hours causes woodcock to select for the safer option of broadleaved forest at that time. As woodcock are notoriously difficult to shoot (McKelvie, 1996) suggesting that at least a moderate proportion of birds evade hunters, along with the low hunting mortality rates that occurred at our sites (Table 3.1), this seems likely to be through a learned change in individual behaviour, as seen in other game species (e.g. Lone et al., 2015).

Although hunters only target woodcock during the day, this activity appears to have a carry-over effect on nocturnal habitat selection. Our results show that woodcock that experienced hunting activity were less likely to use closed habitats at night, particularly broadleaved/mixed forest, and have a higher preference for open grassland habitats (Table 4.4.B; Figure 4.7.B). Therefore, we suggest that the decision to commute to open habitats is affected not only by prey availability in diurnal habitats, but also by the perceived risk of predation in those habitats. Those that experience even relatively low levels of hunting activity within their diurnal habitats may have an increased perception of predation risk associated with these habitats, which carries over into the hours of darkness and are more likely to switch to grassland habitats at night where actual predation risk may be greater than in closed habitats (Duriez, Eraud and Ferrand, 2006), as well as increased risk associated with commuting flights (Braña, Prieto and González-Quirós, 2010).

The methods of hunting may be important in this regard, as these differ between European countries. In France and Italy, the use of pointing breeds of dogs to seek by scent and point individual birds in appropriate habitats is most common. In Ireland, Springer Spaniels and similar breeds are commonly used to cover a lot of ground, particularly in thick cover, and indiscriminately flush any birds in the vicinity, unlike pointing breeds mainly used in other parts of Europe; this may result in relatively higher levels of disturbance and thus have an increased effect on woodcock behaviour, even with low frequency of hunting events in an area.

4.5 Conclusion

This study is an important addition to the limited body of research regarding how hunting affects habitat use in birds. Like other quarry species, woodcock show a significant behavioural response to hunting pressure, including changes in habitat preferences, with carry-over effects to periods of time when hunting does not take place. Moreover, our results regarding general habitat preferences complement the findings of other habitat selection studies on this species. Together they demonstrate the importance of a varied habitat mosaic within a landscape for supporting overwintering woodcock, with an emphasis on well-managed hedgerows and broadleaved forest; the latter being particularly important where hunting occurs given the increased preference for this habitat during the day in response to hunting pressure.

Chapter 5: Synthesis

5.1 Summary and key results

The Eurasian woodcock *Scolopax rusticola* (hereon woodcock) is a largely migratory, ground-nesting bird in the family Scolopacidae associated with forested habitat, and is commonly hunted by humans across its European range. The direct and indirect effects of hunting on this species are generally poorly known and can be difficult to study owing to its elusive and crepuscular habits.

In the Republic of Ireland (hereon Ireland), the woodcock population comprises both resident breeding birds and migratory overwintering birds which originate from areas such as Fennoscandia, the Baltic States and Russia (Hoodless and Coulson, 1994; Powell, 2012; Hoodless and Heward, 2019). The breeding population is thought to have declined in recent decades, with a comparison of the first and third breeding bird atlases for the United Kingdom and Ireland suggesting a range contraction of over 70% between 1968 and 2011 (Sharrock, 1976; Balmer et al., 2013; Colhoun and Cummins, 2013; Gilbert, Stanbury and Lewis, 2021). However, the elusive nature of the species and the methodology used raise questions as to how reliably the atlases represent the true distribution and trend of the species in Ireland. The woodcock is a popular game species among hunters in Ireland, although little information exists on how many are taken annually or the impacts on populations at local or national scales.

Given its uncertain national conservation status and cultural importance as a hunted species, the main aim of this research was to improve the understanding of the current status and spatial ecology of breeding and non-breeding woodcock in Ireland, and to explore the impacts of human activity on their behaviour and ecology. The key results from each of the preceding three chapters are summarised below.

Chapter 2: Modelling the distribution and abundance of breeding woodcock across Ireland

A national volunteer-based survey of roding male woodcock was coordinated in May/June of 2017, 2019 and 2021. From a potential 2,783 randomly-selected forest sites across Ireland, 238 of these were surveyed with an occupancy prevalence of 53%, producing a quantitative species occurrence dataset that included true absences (Figure

2.4). Using this, a two-step species distribution modelling method was performed (Figure 2.3). The first model used presence/absence occurrence data and bioclimatic variables to generate the probability of presence and the geographical range of breeding woodcock across Ireland with a 1 km^2 resolution (Figure 2.6) This indicated that precipitation and temperature seasonality, and mean winter temperature were important drivers of distribution (Figure 2.5, Table 2.3). The second model explored the relationships between abundance and environmental factors, including bioclimatic and landscape-scale land cover variables, conditional on presence. This indicated that mean summer temperature and availability of forest habitat within the landscape, as well as the forest type and age composition, significantly influenced the abundance of breeding woodcock (Figure 2.9, Table 2.4), with the model explaining approximately 49% of deviance. By projecting the second model across the range estimated by the first model and summing the estimated density of woodcock per km^2, I generated a distribution and population estimate (27,434 males, 95% CL: 16,947 – 36,288) for breeding woodcock in Ireland (Figure 2.10).

Chapter 3: The effects of hunting and bird age on survival, movement and use of space in non-breeding Eurasian woodcock

I used radio telemetry at three hunted and three not hunted sites to monitor the fates of 168 tagged overwintering woodcock, 43 of which also provided detailed global positioning system (GPS) location data (Figure 3.1, Figure 3.2, Table 3.1). GPS tags took multiple diurnal and nocturnal locations per day with an average deployment duration of 64 days. Linear and logistic regression was used to explore the interacting effects of time of day (day/night), age and hunting disturbance on home ranges, commuting behaviour, and fidelity to roosting and foraging sites. Most mortality events recorded were due to hunting, but overall estimated monthly survival rates were high over the hunting open season (98.0%; Table 3.1). Age and hunting activity both affected movement ecology. While woodcock generally showed high fidelity to both diurnal and nocturnal locations (Figure 3.4), juveniles used larger diurnal and nocturnal home ranges (Figure 3.6.B and C), were more likely to commute further between diurnal and nocturnal locations (Figure 3.5.B), and displayed a greater degree of localised exploratory movement compared to adults (Table 3.4). Birds that experienced hunting activity had larger diurnal home ranges at the landscape-scale, with a carry-over effect of larger nocturnal home ranges (Figure 3.6.A), and were more

likely to commute greater distances (Figure 3.5), but did not use larger overall home ranges (Table 3.2). Hunting activity also disproportionately affected the commuting behaviour of adults, of which not hunted birds were significantly less likely to commute further than 100 metres than hunted adults, whilst both hunted and not hunted juveniles were equally more likely to commute further than 100 m than not hunted adults (Figure 3.5.B)

Chapter 4: The effects of hunting on habitat preferences of non-breeding Eurasian woodcock across a heterogenous landscape in Ireland

GPS devices were used to track 42 non-breeding woodcock at three hunted and three not-hunted sites in Ireland, with an average deployment duration of 64 days between December and early March from 2019 to 2022, largely coinciding with the open hunting season for this species (Figure 3.1, Table 3.1). GPS units recorded multiple diurnal and nocturnal locations per day, which were analysed using habitat-selection function logistic regression models. Diurnally, woodcock preferred roosting in broadleaved and mixed forest, followed by hedgerows and scrub, while coniferous forest was the least-favoured closed habitat type (Figure 4.5.A). Nocturnally, birds used a variety of available habitats but mostly favoured grassland habitats (Figure 4.5.B). Age of the birds had limited effect on habitat preference (Figure 4.6). At sites where hunting took place, birds tended to avoid more easily hunted habitats during the day, including hedgerows and scrub, in favour of safer broadleaved/mixed forests; not-hunted birds favoured each habitat equally (Figure 4.7.A). Although hunting occurs only during the day, birds at hunted sites showed a higher preference for open grassland habitats at night and were significantly less likely to use any closed habitats than were not-hunted birds (Figure 4.7.B). I suggest that heightened perceived predation risk from hunting is an important factor influencing habitat selection even at night-time when not hunted.

5.2 Contributions to knowledge and scope for further research

5.2.1 Breeding distribution and abundance

In Chapter 2, a two-step SDM method was used to estimate both the distribution and population size of breeding woodcock in Ireland, representing the first time that this

has been done for a bird species at a national scale, as far as I am aware. Based on this, I suggest that, where habitat allows, breeding woodcock are still widespread across and even locally common across parts of Ireland. They are likely to be present in some areas where they were unrecorded or only patchily recorded in the 2007-11 breeding bird atlas (Figure 1.4.B; Balmer et al., 2013; Figure 2.10), such as counties Roscommon, Westmeath, Longford, Laois, Kilkenny, north Tipperary, east and south county Galway, east county Mayo, north and east county Clare, and north and east Cork.

The existence of outlying records away from the estimated core range, such as those in counties Kerry, Donegal and Wexford (Figure 2.10), may represent relict breeding populations that remained in 'refuges' of suitable environmental conditions not reflected in our models as their range otherwise contracted. With respect to breeding woodcock found in the south-west of county Kerry and the Beara Peninsula, the first atlas from 1968-72 suggests that these have been isolated from the main breeding range in Ireland for some time (Figure 1.4.A; Sharrock, 1976). Why woodcock in these locations should have persisted until now given the general loss of woodcock from much the west of Ireland is unclear and warrants a focused study of this population.

Although observers for the 2007-11 atlas were encouraged to undertake crepuscular and nocturnal bird recording unlike for previous atlases (Balmer et al., 2013), it seems probable that this was insufficient to fully capture the true distribution of this species. One of the areas in Ireland where woodcock were particularly well-recorded for this atlas was county Waterford (Figure 1.4.B), where special effort was made by observers to record this species across as much of the county as possible (Walsh, 2024), an endeavour which was not replicated widely across Ireland as far as I am aware. This highlights how sampling bias and uneven distribution of effort can affect our understanding of species' distributions when using grid-based record mapping as was used in the atlases.

The methodology reported in Chapter 2, where quantitative occurrence data was generated through repeated surveys undertaken at a cohort of randomly-selected sites across Ireland and analysed using a two-step SDM, largely addressed the issue of sampling bias. However, some important land cover types, such as broadleaved forest, were under-represented by the cohort of survey sites (Figure A.1). To avoid this in the

future, the randomly-selected potential survey areas could be stratified by the land cover types they represent, and efforts made to ensure an adequate number of sites visited within each stratum. Additional surveys could be remotely undertaken using sound recording devices, which, although comparatively poor for measuring abundance, would increase the number and coverage of presence/absence records. Manual counts combined with sound recording allowing for the direct identification of individual males via vocal signatures (following (Hoodless et al., 2008; Bristow et al., 2023) would help to improve our understanding of the relationship between maximum roding registration count and male woodcock density. Further, detailed local-scale studies utilising methods such as GPS tracking of individual birds at different sites may provide important and relevant information about habitat choices and movement ecology of breeding woodcock to incorporate into SDMs.

As discussed in Chapter 2, the projected estimate of 27,434 breeding male woodcock in Ireland in 2017-2021 is feasible compared with recent estimates from the United Kingdom (55,241 in 2013, Heward et al., 2015; 50,750 in 2023, (Heward et al., 2024). However, this may be an overestimate due to the poor ability of the second model to predict zeros (Figure 2.8), and factors that negatively affect abundance which could not be reflected in the model, such as human disturbance. In reality, the true national population seems likely to lie between the projected estimate, and the lower 95% confidence limit of 16,947. The decision to collect data from three separate years was driven by the need to collate data from a sufficient sample of sites across Ireland. Although the year of survey was returned as a non-significant factor for explaining variation in abundance, the reality is that woodcock populations can be subject to a high degree of annual fluctuation (Fokin and Blokhin, 2013; Heward et al., 2015). If this was the case in Ireland between 2017 to 2021, it would have introduced some uncertainty into our results. In the future, if the same multi-year approach is required, the repetition of a cohort of sites in addition to increasing survey coverage by visiting new sites each year may help to address this source of uncertainty.

5.2.2 Climate, habitat and the future of breeding woodcock in Ireland

In Chapter 2, the modelled relationships between probability of presence and bioclimatic variables (Figure 2.5) indicate that climatic conditions significantly influence the distribution of breeding woodcock. This can be observed in other

populations on the south-western fringes of its European range, such as Switzerland, Northern Spain and the Azores, Canary Islands and Madeira, where it appears restricted to mountainous regions (Brüngger and Estoppey, 2008; Machado et al., 2008a; Braña et al., 2013) that likely experience cooler, moist conditions than at lower altitudes. Similarly, composition of landscape and habitat availability are important for determining the distribution and abundance of breeding woodcock (Figure 2.9; Figure 2.10; Heward et al., 2018).

Many bird species have shown and are expected to show range shift in response to climate change, which often takes the form of northward and/or altitudinal shift to higher elevations and may endanger some populations (Hitch and Leberg, 2007; Popy, Bordignon and Prodon, 2010; Ferrarini, Alatalo and Gustin, 2017; Rushing et al., 2020). However, such effects are influenced by each species' variable individual ecological traits, which can make the impacts of climate more difficult to predict (Reif and Flousek, 2012; Gillings, Balmer and Fuller, 2015). This seems likely to be the case for woodcock.

Whilst the complex combination of factors that influence the breeding distribution of woodcock and its potential ability to make forecasting difficult, I suggest that further range contraction may occur in Ireland in the future, particularly away from the west where conditions are warmest and wettest in winter. As the probability of breeding woodcock presence decreases where mean winter temperatures are higher than 5.5°C (Bio11, Figure 2.5), the predicted milder winter conditions (O'Brien and Nolan, 2023) may have a negative effect on resident breeding woodcock. This may be because more areas of Ireland become highly favourable to migratory woodcock which may compete for space and habitat resources with resident birds (intra-specific competition is further discussed below). On the other hand, with climate change creating warmer, more favourable winter conditions further to the east and north in Europe, new generations of migratory woodcock may respond by 'short-stopping', i.e. overwintering closer to their breeding grounds instead of journeying as far as Ireland. This climate-driven phenomenon has been observed in several waterfowl and wader species in Europe, driving relatively rapid shifts in their non-breeding ranges (Maclean et al., 2008; Lehikoinen et al., 2013; Nuijten et al., 2020). If it were to occur in migratory populations of woodcock across Europe, it may benefit the resident breeding population of Ireland through reduced competition in the winter, though these would

then be more susceptible to hunting pressure. Either way, predicted warmer and drier summers (O'Brien and Nolan, 2023) will likely prove challenging, given the possibility that chick mortality can be higher in seasons with dry conditions (Hirons, 1983).

The negative effects of climate change on breeding woodcock may be somewhat tempered by increasing afforestation with native broadleaved tree species (DAFM, 2023), given their preference for this habitat (Hoodless and Coulson, 1998; Heward et al., 2018). In particular, significant areas of wet woodlands that may regenerate over many industrially-mined peat bogs across the midland counties following rehabilitation (DECC, 2020; Crowley et al., 2021) may provide Irish resident woodcock with critically important breeding habitat into the future.

The results of the national survey of roding woodcock reported in Chapter 2 are intended to serve as a baseline reference against which future survey efforts may be compared to reliably monitor future population trends and range shifts. The establishment of a national breeding woodcock monitoring scheme in Ireland would require a repeat survey effort approximately every decade using the same cohort of sites where possible, comparable to the current monitoring project undertaken in the United Kingdom (Hoodless et al., 2009; Heward et al., 2015; 2024). Further, it would be useful to compare between the regional averaging analytical methods used to generate the United Kingdom population estimates and the two-step SDM method presented here (Chapter 2) to improve the comparability of the results.

5.2.3 Breeding woodcock in Northern Ireland

Unfortunately, Northern Ireland could not be included when estimating the distribution and abundance of breeding woodcock across Ireland, due to insufficient survey effort. However, its status in Northern Ireland is of interest given the differences in landcover and hunting open season dates between that region and Ireland. An improved understanding of the drivers behind the distribution of breeding woodcock on an all-Ireland basis could be informative in more precisely determining the pressures faced by this species.

The first breeding bird atlas of the UK and Ireland suggests that breeding woodcock were widespread across the six counties of Northern Ireland in 1968-72 (Figure 1.4.A;

Sharrock, 1976). However, the latest atlas from 2007-11 suggests that the species was then largely restricted to the south-west of the region in counties Fermanagh, Tyrone and north county Armagh, indicating a significant range contraction Figure 1.4.B; Balmer et al., 2013). The same caveat exists as for the apparent range contraction of >70% across Ireland discussed previously in this thesis: the atlases may not closely represent the true breeding distribution due to the species' elusive nature and non-species-specific methodology. Whilst I suggest that the range of breeding woodcock in Ireland may not have contracted as much as 70% since 1968-72 based on the findings reported in Chapter 2, there is evidence that the range contraction in Northern Ireland may be as severe as the atlases indicate.

Over the course of this project, efforts were made to collect records of woodcock displaying roding or breeding behaviour in Northern Ireland, through surveys or as casual records. Whilst a few records from county Fermanagh, south and west county Tyrone and north county Armagh were received, no credible records were received from counties Antrim, Derry or Down, with no presence recorded at the small number of survey sites undertaken across these counties. Further, in 2023 Northern Ireland was included for the first time as part of the decadal monitoring scheme of breeding woodcock in the UK, with thirty-eight randomly selected sites surveyed across the region using the same methodology as described in Chapter 2 (Heward et al., 2024). Of these, eight sites (21%) recorded presence of breeding woodcock, seven of which were in county Fermanagh or west county Tyrone. The eighth site which recorded presence was located in county Down, though the veracity of this record may be in doubt (Heward, 2024). This contrasts with the prevalence of occupied survey sites across Ireland reported in Chapter 2 (53%, n = 238; Figure 2.4). (Heward et al., 2024) estimated a breeding population size of 937 males in Northern Ireland in 2023.

The reason for this apparent severe range contraction of breeding woodcock in Northern Ireland is not clear, and may be down to a combination of factors. Whilst afforestation in recent decades has been slow compared to Ireland, and only 8.5% of its land area is covered by forest, the area of both coniferous and broadleaved forest types have increased (Cooper, McCann and Meharg, 2003; Kula, 2010). Wooded habitats remain in many areas such as the glens and uplands of Antrim, Armagh and Derry which once supported breeding woodcock but no longer appear to do so. It is possible that woodland management and structure has generally become unsuitable

for woodcock across much of its former range in these counties (Fuller et al., 2007). As climate is an important influence on the distribution of breeding woodcock and may have driven recent range shifts in Ireland (see Chapter 2), it is possible that this may also in part explain the observed range contraction in Northern Ireland. This may merit further work using hindcasting SDMs incorporating bioclimatic variables and an improved recent species occurrence dataset sampled from across Northern Ireland.

Finally, the start date for the legal open hunting season for woodcock differs between Ireland (1 November) and Northern Ireland (1 October), with both finishing on 31 January. This may be significant as migrant woodcock usually arrive in the UK and Ireland beginning from mid-October through to December, with a peak in November (Hoodless, Heward and Williams, 2020). Therefore, there is an elevated chance that any birds hunted in Northern Ireland during the month of October are from the resident breeding population. The effect that this would have on populations may be localised and dependent on hunting intensity, though little is known about numbers taken or the actual timing of woodcock hunting activity in Northern Ireland in recent decades. It is possible that when combined with other factors such as changes in habitat or climate, even low pressure from October hunting may have contributed to the apparent range contraction. Ultimately, it potentially serves as an intriguing contrast to the fortunes of breeding woodcock in Ireland given the difference in legal open hunting seasons, and warrants further research to understand how the vulnerability of resident breeding birds to the effects of hunting changes through the hunting open season in both regions.

5.2.4 Non-breeding habitat preferences

The results reported in Chapter 4 regarding general habitat preferences of woodcock in the non-breeding season (Figure 4.5) complement the findings of other habitat selection studies on this species (e.g. Duriez et al., 2005b; Powell, 2012), and together they demonstrate the importance of a varied habitat mosaic within a landscape for supporting overwintering populations.

Landscape-scale habitat composition in Ireland has changed significantly in recent decades, with expansion and intensification of agriculture in many areas, and changes in forestry practices. In some areas, hedgerows are the only semi-natural habitats remaining (Sullivan et al., 2013), yet hedgerow removal has occurred across Ireland at a rate of between 0.16% and 0.3% annually between 1995 and 2015 (Green et al.,

2021). Over a similar timeframe, from 1995 to 2022, afforestation has increased the total forest cover by half to 11.6% of the total land area (DAFM, 2023). This is dominated by non-native coniferous species (69.4%), which themselves may produce a relatively unimportant habitat for non-breeding woodcock, though such forests often support additional areas of important closed habitats. Whilst 33.1% of all new forest areas created between 2006 and 2022 formed by semi-natural regeneration dominated by broadleaved species, and an increasing proportion of planted forests are composed of broadleaved species (DAFM, 2023), annual loss of relatively rare older broadleaf forest continued annually between 2000 and 2012 within study areas comprising 28.9% of the total area of Ireland, with a higher rate of deforestation than coniferous plantation (Devaney, Redmond and O'Halloran, 2015). Changes to the extent of scrub cover have not recently been quantified nationally (DAFM, 2023).

I suggest that non-breeding woodcock will generally benefit from any increase in broadleaved forest cover with sufficient native shrub- and ground-level vegetation to enhance forest soil earthworm populations. Hedgerows are also important habitat features which should be created and maintained appropriately; tall, dense hedges with wide bases and thick shrub-level vegetation are most beneficial (Duriez et al., 2005b). Where present, other habitat types including scrub, heath and bog should also be retained and maintained in good quality to benefit woodcock as well as wider biodiversity.

5.2.5 Intra-specific interactions and local-scale distribution in winter

A common theme briefly discussed in Chapters 2 and 3, and earlier in this chapter, concerns interactions between individual woodcock in the non-breeding season, whether generally, or between residents and migrants, or juveniles and adults. Due to its elusive, nocturnal habits, little is known about intra-specific interactions in this species outside the breeding season and how these drive aspects of their ecology and distribution at different scales.

Individual woodcock have unique patterns of space use across a landscape (Figure 3.4). Aside from habitat and resource availability, what drives the spatial arrangement of woodcock within a landscape? Although home ranges often overlap, from these data it is difficult to ascertain whether these GPS tracked woodcock influenced the movement behaviour of each other. At night across open habitats such as grassland

pasture, woodcock are typically highly dispersed and mostly encountered singly; where multiple birds occur in the same field they can be widely spaced and apparently disassociated with each other (Figure 5.1). This contrasts with many other species inthe Scolopacidae such as red knot *Calidris canutus,* black-tailed *godwit Limosa limosa* or whimbrel *Numenius phaeopus*, which often show gregarious flocking behaviour in the non-breeding season. Flocking confers advantages such as increased likelihood of predator detection, reduced risk of predation for individuals, and allows birds, especially juveniles, learn from the experience of others in the group (Caraco, Martindale and Pulliam, 1980; Clark and Mangel, 1984). As a trade-off, there are also costs to individuals associated with being in a flock, such as increased energetic costs of maintaining cohesive flock movements, aggression and interference competition for the same food sources, and a greater risk of predator attraction (Beauchamp, 2005; 2010; Amano et al., 2006; Sansom et al., 2008). Given their unique habitat preferences coupled with a high degree of nocturnal activity, woodcock face pressure from a different host of predators compared to most other members of the family, such as mammals, owls and forest hawks (Hoodless and Coulson, 1998; Duriez et al., 2005a; Lourenço, 2006; Verdal, 2007). Therefore, reflecting their behaviour and anatomy, keen senses, crypsis and powerful bursts of evasive flight are probably more valuable defences for woodcock than flocking behaviour. Indeed, the benefits of flocking may be significantly outweighed by the costs in most situations for woodcock, explaining why woodcock remain largely solitary.

Figure 5.1. Map showing the distribution of woodcock (n = 48) across a winter study site (BL; Figure 3.1; Table 3.1) on the night of 1-2 December 2020 (21:00 – 02:00) prior to the commencement of capture and tagging undertaken later that month. All open habitats were comprehensively surveyed on foot, using a thermal imager and spot lamp to locate and identify woodcock whilst minimising disturbance. For each sighting the location and status as a single bird or a close pair was recorded and plotted.

What is the mechanism by which woodcock achieve this dispersed distribution across landscapes at night? It is possible that it arises by chance through the individual decisions of each bird, independent of the actions of other woodcock. However, as individual birds usually show strong fidelity to nocturnal locations within their home ranges through the course of a winter season (Chapter 3; Wilson, 1983; Duriez et al., 2005d; 2006; Powell, 2012), it is also possible that birds may hold these as 'territories' while they are occupied, perhaps resulting in intra-specific competition for space and resources. It is not known whether these locations may be actively defended, or if it is an aversion to other individuals that influences a bird's decision about where to settle each evening after commuting. Woodcock signal to each other using their highly reflective under-tail feather tips (Figure 1.1.B), as has been observed in the breeding season (Dunning et al., 2023 and references within) and in uncommon instances when woodcock have gathered in numbers together outside the breeding season such as at migration stop-over points (Ashton-Booth, 2020). It seems possible that birds may use this ability to signal in low light conditions, such as during twilight or under moonlight, to communicate their presence to others nearby in the non-breeding season. Dominance hierarchies have been demonstrated in male woodcock during the breeding season (Hirons, 1983) and the possibility of a social hierarchy in non-breeding woodcock has previously been suggested with respect to different strategies in space use displayed by individuals (Duriez et al., 2005d).

Conversely, whilst woodcock are usually solitary at night in the non-breeding season it is also not uncommon to encounter pairs, trios or, exceptionally, up to five or six birds associating with each other (Figure 5.1; personal observation). In addition, when commuting at dusk, two or more birds will sometimes follow or chase each other on tandem flights (personal observation), which may be a strategy to avoid aerial predators as woodcock have been observed to undertake similar tandem flights with other species during migration (Senzaki et al., 2023). I suggest that these observations indicate a degree of complexity regarding intra-specific interactions in this species and make it unlikely that the movements of individuals are not regularly influenced by other woodcock. Why these apparently social behaviours sometimes occur is unclear. It may be that juveniles sometimes associate with each other or adults to benefit from the experience of the other birds, as occurs in other bird species (Templeton et al., 2012). Other species in the Scolopacidae can demonstrate flexibility between adopting

territorial or flocking behaviour to variable degrees on non-breeding grounds depending on habitat quality, environmental conditions, bird sex, or risk of predation (Myers, 1980; Tripp and Collazo, 1997; Burton and Evans, 2001; Fernández and Lank, 2012). Alternatively, toward the onset of pre-breeding migration or the breeding season, males may instinctively begin to adopt courtship or mate-guarding behaviour toward females and agonistic behaviour toward other males, as is common in waterfowl (Hepp and Hair, 1983; Nakamura and Atsumi, 2000; Torres et al., 2002).

To explore the possibility of intra-specific interactions in non-breeding woodcock as discussed above, methods could incorporate technology and techniques which have only recently become available for common use. At night, birds may be observed without disturbance and their natural behaviour recorded using thermal imaging devices (Havens and Sharp, 2015). Tags which include GPS, VHF, and accelerometer components are now light enough to deploy on birds as small as woodcock, have the capability to detect the presence of other tagged individuals nearby and are able to transmit data remotely (Lotek, 2023).

5.2.6 Resident woodcock in winter

If indeed social hierarchies and intra-specific competition for space and resources occur in non-breeding woodcock, this could have important impacts on populations of resident breeding woodcock in Ireland. Large numbers of migratory woodcock overwintering in climatically favourable regions may impose competitive pressure on residents, and with warmer, wetter winters expected to occur into the 21st century under current projected climate scenarios (O'Brien and Nolan, 2023), the impacts of this may change into the future as discussed previously.

Amongst our cohort of GPS-tracked birds (Chapter 3), I suspected one juvenile was likely to be a resident bird among a predominantly migratory overwintering population. This bird routinely used the study site at night and commuted to its diurnal home range in an upland area approximately 7 km away where breeding activity has been recorded recently (Sliabh Beagh, county Tyrone/Monaghan, Figure 2.4), giving it by far the largest overall MCP home range (9.48 km^2) and mean and maximum commute distance (4,962 and 6,552 metres, respectively) of any bird in our study or indeed any previous study of non-breeding woodcock movement ecology to our knowledge (Wilson, 1983; Duriez et al., 2005d; Powell, 2012). It also remained within

its diurnal home range as late as mid-April. In addition, it had an exceptionally high body mass in both early and late winter (396-397g; cf. mean of all birds = 331.2 g), though it is unknown whether this was related to its migratory status. This singular case suggests that further study focusing on the year-round ecology of resident breeding woodcock is needed, given recent range contraction and current unfavourable conservation status in Ireland (Chapter 2; Gilbert, Stanbury and Lewis, 2021). Indeed, Powell (2012) found differences in the spatial ecology of resident and winter migrant woodcock using the same site in England with respect to habitat selection and commuting behaviour. More generally, as many bird species exhibit resident and migratory populations, which often share the same spaces, the differences in space use between resident and non-resident conspecifics, as well as how they interact, is likely to be an important area for further research.

5.2.7 Survival and hunting mortality

As discussed in Chapter 3, the monthly survival rate for non-breeding woodcock at these study sites was high in relation to the findings from comparable studies. As most of the tagged birds at our sites are likely to have been migratory, and woodcock show low migratory connectivity (Powell, 2012; Hoodless, Heward and Williams, 2020), the high survival rates we observed in the winter may be balanced by higher mortality rates during migration or in the breeding season, or indeed by much lower survival rates below levels required for stable populations reported in other parts of Europe (Tavecchia et al., 2002; Duriez, Eraud and Ferrand, 2006).

From a total of 168 tagged birds, three instances of natural mortality were recorded, the remains of which all occurred in forest habitats and were perpetrated twice by mammals and once by a sparrowhawk. While it is not possible to draw firm conclusions about the nature of natural mortality of woodcock in Ireland from such a low number of recorded deaths, this does contrast somewhat with the findings of Duriez et al. (2005a) who found that most predation events at a study site in northern France occurred in open habitats by mammals such as fox *Vulpes vulpes* and possibly martens *Martes* sp. and feral cats *Felis catus*, presumably at night. Foxes were present and common at all of my study sites, whilst feral cats and martens were seen at three and two sites, respectively. More work is certainly needed to establish the rates and causes of natural mortality in woodcock at a greater number of sites and under

different scenarios such as comparing winters with severe and mild weather conditions.

Hunting was the main cause of mortality of woodcock at these study sites. Nonetheless, the survival rate was high at both hunted and not hunted sites, though the possibility exists that hunters modified their behaviour with the knowledge that the birds on their hunting grounds were tagged. Indeed, one hunter described how he tried out of curiosity to see whether he could see a tag on each bird his dog flushed from cover, often forgetting or missing the opportunity to take a shot. Had hunters' behaviour not been influenced in this way, it is possible that mortality rates from hunting may have been higher. This is a difficult limitation of the study to address; even if hunters were not initially informed about the study, the first person to take a tagged bird would then have known and most likely spread the information to club members.

Although data was collected from three geographically disparate hunted sites, I can only speculate as to how representative they are in terms of hunting intensity. Woodcock hunting is undertaken widely across Ireland in the open season, though little is known about the distribution of hunting intensity, which is difficult to quantify (Rist et al., 2008). Methods of hunting can vary and some hunting that targets woodcock is offered on a more intensive commercial basis, where paying clients may expect to be given the opportunity to shoot relatively large numbers of birds. However, much hunting that takes place, including at our hunted study sites, is so-called 'rough hunting', undertaken as a pastime mainly by locals who usually use 'beating' dog breeds such as English springer spaniels to flush wildlife across large areas of suitable habitat. This differs from favoured methods in other regions of Europe, where the use of pointing dog breeds or driven hunting can be more prevalent (McKelvie, 1990; 1996). The intensity of rough hunting can vary based on hunter effort, but based on information provided by the hunters I consider the levels of hunting at our hunted study sites to be at relatively low to medium intensities and probably reasonably representative across much of the land hunted by local gun clubs. However, more work is needed to better quantify hunting intensities and understand the resulting impacts on terrestrial game birds.

Members of local gun clubs often express concern about the apparently more intensive hunting methods employed by commercial enterprises offering woodcock shooting to clients. I suggest that further research attempting to quantify hunting intensity and exploring in detail the survival rates and causes of mortality at a greater variety of sites should be conducted, particularly where hunting takes place at higher intensities. More generally, little is known about how many woodcock are hunted across Ireland annually, nor about the national distribution of woodcock hunting activity, as hunters are not obliged to submit this information to an authority. As sustainable harvest of a species depends on harvest rate not exceeding recruitment rate in the long-term, this information is fundamental for informing responsible and evidence-based hunting management practices (Hilborn, Walters and Ludwig, 1995; Lande, Engen and Saether, 1995; Ellis and Cameron, 2022). As a matter of priority, a system should be established for effectively gathering such data in Ireland as exists in a range of other European countries (Aubry et al., 2020).

5.2.8 Indirect effects of hunting

The results reported in Chapters 3 and 4 are important additions to the limited body of research regarding trait-mediated effects of hunting in birds. Like other quarry species, both aquatic and terrestrial (Cox and Afton, 1997; Béchet, Giroux and Gauthier, 2004; Whitaker et al., 2006; Casazza et al., 2012), for the first time it is shown that woodcock show significant behavioural responses to hunting pressure, including changes in space use, movement behaviour and habitat preferences. For waterfowl, an understanding of how such pressure affects habitat use can be used to inform measures to mitigate the indirect effects of hunting (Casazza et al., 2012) and I suggest the same can be done for woodcock. For example, given the increased preference for broadleaved forest by overwintering birds during the day where hunting occurs (Figure 4.7), it may be that landscapes with little forest cover may leave local woodcock populations more vulnerable to overexploitation by hunters. To address this, the creation and conservation of native forest habitat in such areas, as well as designated areas of sanctuary and the practice of restraint by hunters to daily or seasonal bag limits would be beneficial.

These results also highlight the importance of carry-over effects on non-breeding woodcock behaviour from low levels of hunting disturbance to night-time when

hunting does not take place (Figure 3.6; Figure 4.7). Whilst natural mortality rates and relative predation risk associated with each habitat type for this species are generally poorly understood, it is possible that by influencing birds to switch to open habitats more often at dusk and commuting greater distances, hunting activity may inadvertently increase natural predation risk as woodcock may be more vulnerable in open habitats and whilst commuting (Duriez et al., 2005a; Braña, Prieto and González-Quirós, 2010). To mitigate against this actions include restrained hunting practices, as well as the extensive creation and maintenance of suitable broadleaved forest and hedgerow habitats to provide cover for commuting birds or alternative, safer habitats for nocturnal activity.

5.3 Key messages

i) The breeding distribution and abundance of woodcock in Ireland is driven by climatic and landscape-scale habitat factors.

ii) Future trends and changes in breeding woodcock abundance and distribution are likely difficult to predict, but may be negatively affected by climate change.

iii) The establishment of a national breeding woodcock monitoring scheme repeated every decade and using the results reported in Chapter 2 as a baseline would be important for generating future trends.

iv) Survival of non-breeding woodcock was relatively high at our study sites and hunting was the main cause of mortality, though there were few instances of this.

v) A basic understanding of the extent and importance of woodcock hunting in Ireland is currently lacking, including simple statistics such as the annual number of birds harvested, and should be addressed. Care should be taken by hunters not to over-exploit this species.

vi) Diurnal hunting activity has significant indirect effects on both diurnal and nocturnal home range size and habitat preferences as well as on commute behaviour, indicating carry-over effects on woodcock spatial ecology.

vii) Heterogenous landscapes comprising mixed habitat types are beneficial for woodcock, with an emphasis on native broadleaved forest and hedgerows.

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Appendix

Table A.1. Index of the 19 bioclimatic variables for which global datasets are provided by WorldClim (https://www.worldclim.org; (Fick and Hijmans, 2017). A 'quarter' refers to a period of three months, or one quarter of a year. Detailed information on each variable can be found in O'Donnell and Ignazio (2012).

Variable	Description	Unit of measurement
Bio1	Annual mean temperature	Degrees Celsius (°C)
Bio2	Mean diurnal range (mean of monthly (max temp – min temp))	Degrees Celsius (°C)
Bio3	Isothermality ((BIO2/BIO7) × 100)	Percent (%)
Bio4	Temperature seasonality (standard deviation × 100)	Degrees Celsius (°C)
Bio5	Maximum temperature of warmest month	Degrees Celsius (°C)
Bio6	Minimum temperature of coldest month	Degrees Celsius (°C)
Bio7	Temperature annual range (BIO5-BIO6)	Degrees Celsius (°C)
Bio8	Mean temperature of wettest quarter	Degrees Celsius (°C)
Bio9	Mean temperature of driest quarter	Degrees Celsius (°C)
Bio10	Mean temperature of warmest quarter	Degrees Celsius (°C)
Bio11	Mean temperature of coldest quarter	Degrees Celsius (°C)
Bio12	Annual precipitation	Millimetres (mm)
Bio13	Precipitation of wettest month	Millimetres (mm)
Bio14	Precipitation of driest month	Millimetres (mm)
Bio15	Precipitation seasonality (coefficient of variation)	Percent (%)
Bio16	Precipitation of wettest quarter	Millimetres (mm)
Bio17	Precipitation of driest quarter	Millimetres (mm)
Bio18	Precipitation of warmest quarter	Millimetres (mm)
Bio19	Precipitation of coldest quarter	Millimetres (mm)

Table A.2. Correlation matrix for bioclimatic variables considered for Model 1 (n = 238)

	Bio1	Bio2	Bio3	Bio4	Bio5	Bio6	Bio7	Bio8	Bio9	Bio10	Bio11	Bio12	Bio13	Bio14	Bio15	Bio16	Bio17	Bio18	Bio19
Bio1	1.00																		
Bio2	0.04	1.00																	
Bio3	0.15	0.77	1.00																
Bio4	-0.09	0.76	0.19	1.00															
Bio5	0.55	0.81	0.55	0.69	1.00														
Bio6	0.75	-0.52	-0.12	-0.67	-0.04	1.00													
Bio7	-0.03	0.94	0.50	0.93	0.80	-0.63	1.00												
Bio8	0.55	0.02	0.19	-0.17	0.25	0.47	-0.09	1.00											
Bio9	0.30	-0.09	-0.11	-0.05	0.17	0.32	-0.06	-0.12	1.00										
Bio10	0.86	0.41	0.26	0.39	0.86	0.40	0.42	0.46	0.26	1.00									
Bio11	0.87	-0.29	0.08	-0.53	0.18	0.96	-0.44	0.57	0.29	0.57	1.00								
Bio12	-0.45	-0.58	-0.55	-0.32	-0.70	-0.10	-0.48	-0.37	-0.08	-0.60	-0.28	1.00							
Bio13	-0.38	-0.62	-0.53	-0.41	-0.70	0.01	-0.55	-0.38	0.03	-0.58	-0.19	0.98	1.00						
Bio14	-0.55	-0.41	-0.47	-0.14	-0.62	-0.29	-0.30	-0.39	-0.19	-0.61	-0.45	0.96	0.91	1.00					
Bio15	0.10	-0.65	-0.34	-0.70	-0.48	0.54	-0.69	-0.14	0.35	-0.23	0.38	0.46	0.60	0.23	1.00				
Bio16	-0.39	-0.62	-0.54	-0.41	-0.71	0.00	-0.55	-0.35	-0.01	-0.58	-0.19	0.99	1.00	0.92	0.58	1.00			
Bio17	-0.53	-0.43	-0.47	-0.18	-0.63	-0.26	-0.33	-0.38	-0.18	-0.61	-0.42	0.97	0.92	0.99	0.25	0.93	1.00		
Bio18	-0.45	-0.51	-0.54	-0.22	-0.65	-0.18	-0.40	-0.24	-0.27	-0.55	-0.33	0.92	0.85	0.93	0.20	0.87	0.94	1.00	
Bio19	-0.39	-0.60	-0.54	-0.38	-0.68	-0.01	-0.52	-0.41	0.07	-0.57	-0.21	0.98	0.99	0.90	0.60	0.99	0.91	0.83	1.00

Table A.3. Correlation matrix for bioclimatic variables considered for Model 2 (n = 133)

	Bio1	Bio2	Bio3	Bio4	Bio5	Bio6	Bio7	Bio8	Bio9	Bio10	Bio11	Bio12	Bio13	Bio14	Bio15	Bio16	Bio17	Bio18	Bio19
Bio1	1.00																		
Bio2	0.17	1.00																	
Bio3	0.29	0.81	1.00																
Bio4	-0.05	0.68	0.15	1.00															
Bio5	0.63	0.81	0.60	0.63	1.00														
Bio6	0.78	-0.37	-0.02	-0.59	0.10	1.00													
Bio7	0.06	0.92	0.53	0.90	0.79	-0.53	1.00												
Bio8	0.54	0.18	0.38	-0.17	0.34	0.47	0.01	1.00											
Bio9	0.08	-0.22	-0.27	-0.06	-0.05	0.16	-0.14	-0.21	1.00										
Bio10	0.89	0.45	0.36	0.35	0.87	0.52	0.42	0.47	0.03	1.00									
Bio11	0.89	-0.09	0.24	-0.44	0.35	0.95	-0.29	0.59	0.08	0.69	1.00								
Bio12	-0.40	-0.61	-0.53	-0.39	-0.66	-0.03	-0.55	-0.42	0.11	-0.53	-0.24	1.00							
Bio13	-0.34	-0.63	-0.52	-0.44	-0.65	0.04	-0.58	-0.42	0.17	-0.50	-0.17	0.99	1.00						
Bio14	-0.50	-0.53	-0.48	-0.30	-0.65	-0.16	-0.46	-0.44	0.03	-0.59	-0.36	0.97	0.95	1.00					
Bio15	0.01	-0.59	-0.39	-0.55	-0.44	0.37	-0.60	-0.26	0.28	-0.20	0.20	0.70	0.78	0.56	1.00				
Bio16	-0.34	-0.63	-0.51	-0.43	-0.65	0.04	-0.58	-0.41	0.14	-0.50	-0.17	0.99	1.00	0.95	0.77	1.00			
Bio17	-0.48	-0.55	-0.48	-0.34	-0.67	-0.13	-0.49	-0.42	0.05	-0.59	-0.33	0.98	0.95	0.99	0.57	0.95	1.00		
Bio18	-0.40	-0.58	-0.53	-0.32	-0.63	-0.07	-0.50	-0.33	-0.04	-0.50	-0.26	0.95	0.90	0.95	0.52	0.91	0.96	1.00	
Bio19	-0.36	-0.62	-0.53	-0.40	-0.64	0.01	-0.55	-0.46	0.20	-0.51	-0.20	0.99	0.99	0.95	0.76	0.99	0.95	0.89	1.00

Table A.4. Correlation matrix for land cover variables considered for Model 2 (n = 133). '**1 km**' and '**2 km**' refer to the measured parameter within buffers around the survey observation point of radius 1 km and 2 km, respectively (Figure 2.2). '**All forest**' = total area of forest cover as a percentage of total buffer area. '**Coniferous**' = area of coniferous forest as a percentage of total forest cover within buffer area. '**Broadleaved**' = area of broadleaved forest as a percentage of total forest cover within buffer area. '**Mature**' = area of mature, closed-canopy forest as a percentage of total forest cover within buffer area. '**Settlement**' = total area of urban settlement as a percentage of total buffer area. '**Settlement distance**' = distance from survey observation point to nearest urban settlement over 0.5 km^2.

	All forest 1 km	All forest 2 km	Coniferous 1 km	Coniferous 2 km	Broadleaved 1 km	Broadleaved 2 km	Mature 1 km	Mature 2 km	Settlement 1km	Settlement 2km	Settlement distance
All forest 1 km	1.00										
All forest 2 km	0.88	1.00									
Coniferous 1 km	0.29	0.31	1.00								
Coniferous 2 km	0.34	0.41	0.94	1.00							
Broadleaved 1 km	-0.29	-0.30	-0.86	-0.83	1.00						
Broadleaved 2 km	-0.32	-0.36	-0.82	-0.89	0.93	1.00					
Mature 1 km	-0.03	-0.10	-0.25	-0.28	0.29	0.30	1.00				
Mature 2 km	0.03	-0.06	-0.40	-0.42	0.39	0.43	0.77	1.00			
Settlement 1km	-0.20	-0.18	-0.27	-0.24	0.35	0.32	0.14	0.22	1.00		
Settlement 2km	-0.20	-0.20	-0.26	-0.25	0.34	0.33	0.15	0.23	0.96	1.00	
Settlement distance	0.34	0.39	0.15	0.20	-0.19	-0.20	-0.20	-0.22	-0.21	-0.29	1.00

Table A.5. Comparison of forest area and structure between the national forest estate within the Republic of Ireland, and the combined area within 2 km buffers from all survey sites (n = 238). This allows for an assessment of how well the combined survey sites represent the structure of the total Irish forest estate.

	Across Ireland		Within 2 km buffers from survey sites (n=238)		Percent of forest across Ireland included within 2km buffers from survey sites
	Total area (m^2)	% of all forest	Total area (m^2)	% of all forest	
All forest	6,659,005,124		580,654,800		8.72
Mature	4,598,652,535	69.06	426,841,700	73.51	9.28
Thicket	2,060,352,589	30.94	153,813,100	26.49	7.47
Coniferous	5,049,475,400	75.83	442,181,000	76.15	8.76
Broadleaved	1,181,533,063	17.74	96,669,500	16.65	8.18
Mixed	427,996,661	6.42	4,1804,300	7.20	9.77

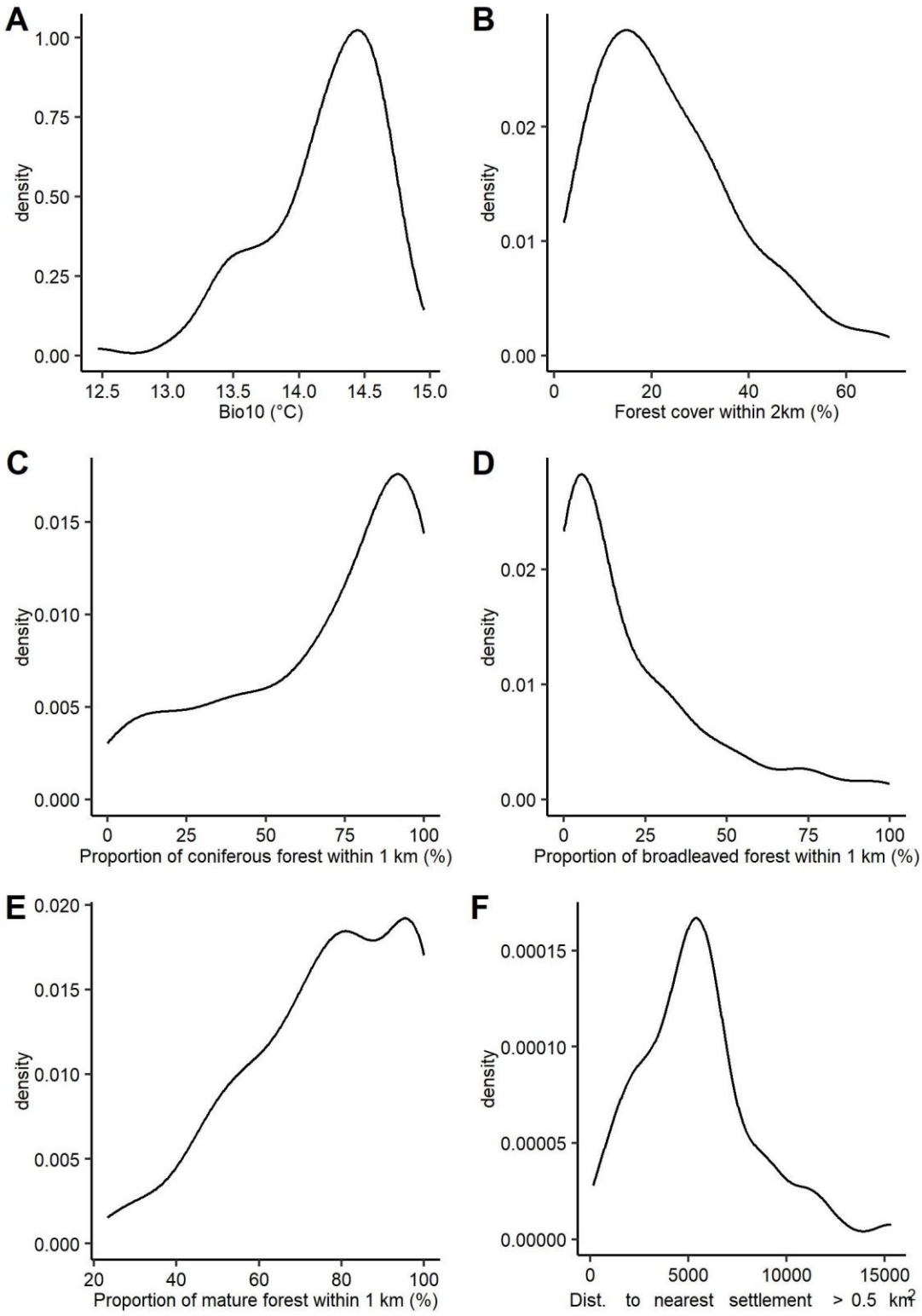

Figure A.1. Density plots showing the distribution of numeric data for bioclimatic and land cover variables considered or included in Model 2, including: **A**) Bio10 (mean temperature of warmest quarter); (**B**) Proportion of 2km radius buffer area comprising forest cover; (**C**) Proportion of all forest cover area as coniferous within 1km radius buffer; (**D**) Proportion of all forest cover area as broadleaved within 1km radius buffer; (**E**) Proportion of all forest cover as mature closed canopy (>20 years old) within 1km buffer; **F**) distance from survey observation point to nearest urban settlement over 0.5 km^2.

Table A.6. The number of days per month when minimum daily temperature fell below 0.0°C, recorded at the nearest weather stations to each study site in the respective year of study. Data source: Met Éireann, 2024; https://www.met.ie/climate/available-data/historical-data.

	Ballyhaise, Co. Cavan, 2019/20	Cork Airport, Co. Cork, 2020/21	Glengarriff, Co. Cork, 2021/22
December	3	1	0
January	2	9	2
February	3	1	0
March	4	0	7
Sum	12	11	9