Ollscoil na hÉireann, Corcaigh

National University of Ireland, Cork

University College Cork, Ireland
Coláiste na hOllscoile Corcaigh

Seasonal Ecology and the Conservation of Hen Harriers (*Circus cyaneus*) in Ireland

Thesis presented by

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for the degree of

Doctor of Philosophy

University College Cork

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March 2022

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Declaration

This is to certify that the work I am submitting is my own 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.

Alan McCarthy

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Alan McCarthy

Abstract

The Hen Harrier (*Circus cyaneus*) is an Annex-I listed species under the EU Birds Directive (Directive 2009/147/EC) whose breeding populations have declined in recent decades across its Western European range. The species is of conservation concern in Ireland, where it is on the Amber list of Birds of Conservation Concern. The population of the Republic of Ireland was most recently surveyed in 2015 and 108-157 breeding pairs were recorded, representing a 15.6% decline over the preceding five-year period. Previous research and conservation efforts have primarily focussed on their breeding ecology, where they experience clear human-induced pressures on the breeding grounds. However, we have a poor understanding of Hen Harrier ecology and the pressures that they face outside of the breeding season. A year-round understanding of their ecology is crucial to develop effective conservation strategies for Hen Harriers. By gathering new information on the movement, survival, and habitat use of birds throughout the annual cycle, we can better understand the pressures they face and whether their ecological requirements are being met. The aim of this PhD was to address knowledge gaps in both the breeding and non-breeding ecology of Hen Harriers in Ireland, and to develop a suite of conservation recommendations to inform the development of appropriate future conservation management actions. This PhD research was conducted in Ireland between October 2017 and March 2022 using a range of methods, including satellite tracking, vantage point roost watches, pellet analysis, camera trapping, bird point counts and small mammal trapping.

Analysis of Hen Harrier satellite tracking data revealed new insights into the juvenile dispersal period, during which they experienced high levels of mortality. Juvenile dispersal typically involved a sudden, long-distance (>25km) initial movement away from the natal area, followed by exploratory movements around Temporary Settlement Areas (TSAs). Arable and lowland bogs were important habitats for juveniles at that time. The use of protected areas throughout the juvenile dispersal period and into winter was low as birds dispersed away from the breeding Special Protection Area (SPA) network. This shows that the current network of protected areas for Hen Harriers are insufficient for their year-round protection.

Winter roosts represent an important focal point of Hen Harrier distribution and behaviour during the non-breeding season. The habitat of landscapes surrounding these roosts has an important influence on the number (size) and age/sex (composition) of Hen Harriers using the roosts. Variation in the size and composition of winter roosts is driven by several factors, including habitat/prey associations in the surrounding landscape and Hen Harrier sexual dimorphism. Winter roosts are at high risk from destruction or degradation as they occur mostly outside of protected areas. Conservation measures are therefore required to provide protection for roost sites and surrounding foraging areas.

This thesis includes the first detailed analysis of Hen Harrier winter diet in Ireland. During the winter months, the Hen Harrier's diet is dominated by small birds, though the importance of small birds, medium-sized birds and small mammals in the diet varies across habitats, regions, and time. Specifically, small birds are more abundant in the diet in lowland coastal and arable areas, while medium-sized birds are more abundant in the diet in upland and peat bog areas. This variation in diet has important implications for Hen Harrier winter distribution and the identification of appropriate targeted conservation measures in their wintering grounds. In some areas, non-native small mammals can constitute a significant proportion of the winter diet, and their continued spread may have an important influence on Hen Harrier ecology into the future.

On the breeding grounds, in landscapes now dominated by conifer plantations, many Hen Harriers nest in young conifer forests. Although these habitats are used by Hen Harriers for nesting and foraging, our remote camera study identified a diverse predator community in young plantation forests which may be contributing to the high failure rates through predation of nests in Ireland. In addition, prey groups in pre-thicket forests and open moorland were markedly different, with highest bird densities in moorlands and highest small mammal abundances in young forests. As Hen Harriers' preferred breeding season prey is small birds, this suggests young conifer forest is a suboptimal foraging habitat for Hen Harriers compared with traditional open habitats.

Changes to policy focus and conservation strategies that address the pressures experienced by Hen Harriers across the full annual cycle must be implemented urgently in order to halt the continued decline of the species in Ireland. The findings of this thesis provide evidence-based information for policy makers and practitioners to further the development of appropriate Hen Harrier conservation management plans. Twenty-five recommendations for year-round management of Hen Harriers in Ireland were identified and refined during an external stakeholder review, encompassing habitat management, further research, and conservation policy.

Effective conservation measures are required to fulfil the habitat requirements of Hen Harriers at their nesting, winter roosting and foraging sites. The future for Hen Harrier populations depends on the actions taken now, and filling research and conservation priority gaps has important implications for Hen Harriers in Ireland and beyond. While this study provides a detailed understanding of their ecology across the full annual cycle allowing us to better understand the pressures they face and improve conservation actions, further research is required on their responses to human activities and habitat loss, to inform conservation management and policy development. Continuous assessment of the effectiveness of Hen Harrier conservation measures should form part of ongoing conservation efforts, including the measures proposed in this study.

Acknowledgements

I would not have been able to complete this PhD were it not for the encouragement and support of my supervisors, friends, and family, together with a large group of fieldworkers who assisted with data collection.

Firstly, I'd like to extend unending thanks to my outstanding supervisory team; John O'Halloran, Anthony Caravaggi and Fidelma Butler. John, thank you for having my back every step of the way and for giving me everything I needed to succeed. Your advice and encouragement always gave me a boost when things slowed down. Crab Lane has done well to produce two doctors of ornithology! Sandra Irwin, you gave me so much of your time, effort, and advice over the last four and a bit years, and you always gave me a good laugh too with the email banter! I can not thank you enough for your help, guidance, and especially all the fantastic feedback you gave on so many drafts! Anthony, thank you for your tolerance in the early days when I would call/shout across the office to you looking for help, and also when this migrated to WhatsApp chats on your return to Wales. Thank you for all the help you gave me, especially with my least favourite aspects; statistics and R! With all the outstanding support from my supervisors, my PhD experience was as smooth sailing as it could be for which I am so grateful.

Darío Fernández-Bellon, you always showed fantastic willingness to offer advice whenever I needed, for which I am very grateful. All our chats in the corridor provided me with much food for thought, and some ideas in this PhD originated from your words of wisdom. You were the best devil's advocate during my PhD!

Tony Nagle, the man, the myth! During our many days belting around the uplands of Munster in your little Nissan Note, and then your slightly more respectable Qashqai, many thoughts and ideas were formed that contributed to this research. You have always given me incredible encouragement, knowledge, and of course many words of wisdom, most of which I wouldn't dare put on paper. The craic with you has always been mighty and often served as a well needed distraction. Thank you so much for all your time and the knowledge that you have shared with me. I hope this thesis meets with your approval!

Allan Mee, I am so very grateful for all the help and advice you have given me over the last few years. Many of the satellite tagged harriers would not have sported their tags without your trojan work! Thank you so much for your many contributions to this research. John Lusby, you've always been and continue to be some man for one man for good advice and enlightening insights. Thanks a million too for giving me the opportunity to spend my spare time in the summer months working on Barn Owls. I am very much looking forward to working with you more in the near future. Also, my sincere thanks to many others who provided me with excellent advice and assistance along the way, including Pat Smiddy, Paul Moore, Donal Sheehan, and Mark Wilson.

I want to extend my sincere thanks to a long list of National Parks and Wildlife Service (NPWS) staff for their incredible help with fieldwork over the last few years. This includes David Rees, Colm Malone, Sarah Stapleton, Robert Edge, Noel Bugler, Eileen Canny, Elaine Keegan, Tony Murray, Kathryn Freeman, Hazel Doyle, Jimi Conroy, Áine Lynch, Jay Cornish, Jason Monaghan, Leonard Floyd, Irene O'Brien, Clare Heardman, Emma Glanville, Helen Carty, Ciara Powell, Daniel Buckley, Stefan Jones, Danny O'Keefe, Brian Duffy, Cyril Saich, Dominic Berridge, Damian Clarke, Tim Roderick, Gemma Weir, Sean Breen, Robert Wheeldon, Sam Birch, and Declan O'Donnell. I also want to extend my sincere thanks to Sinéad Cummins, David Tierney, and Alyn Walsh for all their help and advice over the past few years, and for trusting me to deliver this body of research.

Beyond NPWS, I would like to thank several individuals who put in huge efforts to collect data for this PhD thesis. This includes Michael O'Clery, Irene Sullivan, Sam Bayley, Tom Siekaniec, Alex Copland, Jack Kennedy, Chris Nelms, Conor O'Keefe, Davey Farrar, and Tony Kenneally. Also, my thanks to Paul O'Donoghue, John Murphy, John Deasy, Pat McDaid, Val Swann, David Cooke and Gyr Penn for their additional assistance. To all those who helped with data collection, thank you for all your hard work, effort, and time. Without your help, this PhD would be very thin on data!

Many thanks to Lorcán O'Toole and the Golden Eagle Trust for granting permission for me to use satellite tracking data from one of the first Hen Harrier tagging projects in Ireland. Thanks to Neil Reid of Queen's University Belfast for providing access to spatial data from two Hen Harriers that were fitted with satellite transmitters by Marc Ruddock, supported by the Natural Heritage Research Partnership (NHRP) between Quercus and the Northern Ireland Environment Agency (NIEA), and to Fiona Leckie, supported by Natural Research Ltd. Also, thanks to the Hen Harrier Project's Fergal Monaghan, Marc Ruddock, and Shane O'Neill for providing sightings of one of our satellite tagged Hen Harriers. Sincere thanks to the team at IRD Duhallow, James O'Keefe Institute, for working with us at UCC and NPWS on the most recent satellite tracking project, and to NPWS for providing data from the first joint IRD Duhallow/NPWS Hen Harrier satellite tracking project. Satellite tracking was greatly assisted by Stephen Murphy from Natural England who provided guidance in 2016 for the most recent satellite tracking project. Sincere thanks too to Cathleen Thomas and Steve Ewing from the Royal Society for the Protection of Birds (RSPB) for providing satellite tracking data from two of their Hen Harriers that overwintered in Ireland.

Additionally, I would like to thank Nuala Riordan, Darren Reidy, Ilse Corkery and John Ballinger for their work on this research. Sincere thanks to Chris Cullen and Mark McCorry in Bord Na Móna for their assistance and advice, and for providing excellent spatial data for this research. Thanks also to Ryan Wilson-Parr for his contributions to my earlier research and for inviting me to present at the 2022 Irish Raptor Study Group Conference. Big thanks to Pat Neville and Kevin Collins for their help during the days of the 'SHINE' project, and to all Coillte establishment officers who provided information that guided study site selection during this project.

Sincere thanks to the funders of this research; National Parks and Wildlife Service together with the Department of Agriculture, Food and the Marine. Also, my sincere thanks to the James O'Keefe institute, IRD Duhallow, who, through the EU LIFE+ funded Raptor LIFE project funded many of the satellite trackers used in this research.

To the G16 and Cooperage crew, past and present. Jenny, Sammy, Jamie, Camille, Shane, Sara, and James, it has been a pleasure sharing this PhD experience with you all. Thanks so much for all the help you gave, rants listened to and craic that was had both inside and outside the office. Also big thanks to Luke Harman and Allen

Whitaker for helping whenever I needed field equipment and copious amounts of sample tubes.

To my non-PhD friends, Shane, Cian, Zack, Eric and Dylan, thanks lads for being a very welcomed distraction from the PhD life and for listening to the odd rant and grumble here and there! And of course, to Cliona (and Labrador Ted!), thanks for the many walks over the last four years which helped me to get away from this laptop!

Finally, thank you to my family and especially my incredibly supportive and caring parents. You have always done everything you can to support me through my (now very drawn out!) education. Thank you for always being there and for everything you have done and continue to do for me. I am so happy to make you proud by becoming a Dr!

Chapter One

General Introduction

Adult male Hen Harrier
Photograph: Darío Fernández-Bellon

Overview

Hen Harriers (*Circus cyaneus*) are medium-sized diurnal raptors found from Western Europe through to Eastern Russia (Fig. 1). Hen Harriers only occur in the breeding season (April to August) throughout Northern Scandinavia, Eastern Europe, Russia, and Northern Asia. They migrate south to North Africa, Southern Europe, Southern Asia, and Japan during the non-breeding season (September to March). They occur in Western Europe all year round, though even here they are partial migrants (Watson 1977, Etheridge and Summers 2006, Murphy 2019, Agostini 2021).

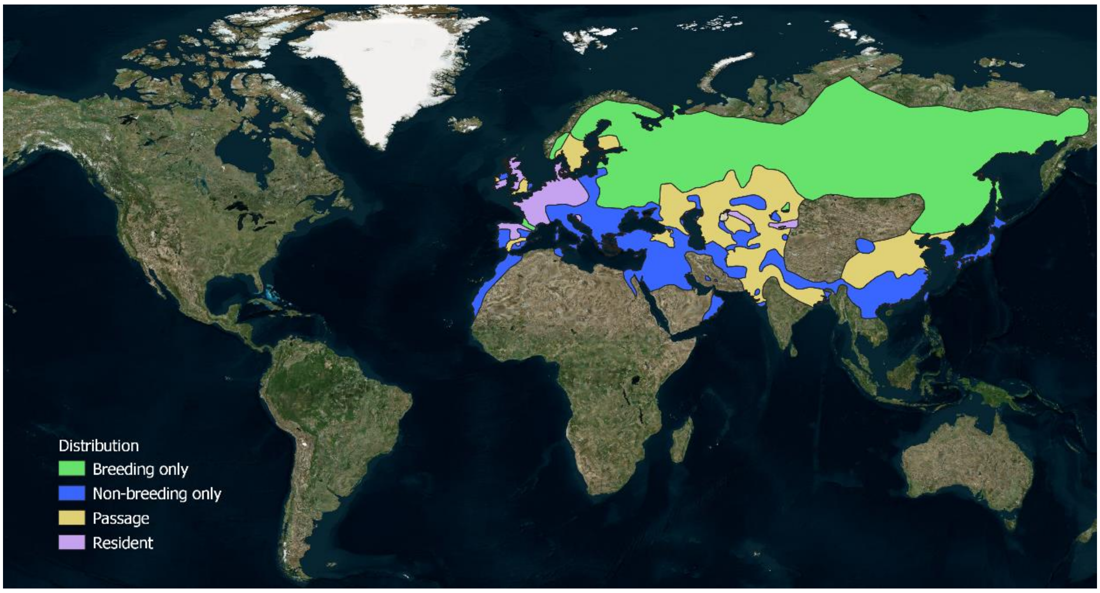

Figure 1. Global distribution of Hen Harriers (after Birdlife International 2021).

Hen Harriers are an open country species and use a variety of habitats including peat bogs, moorland, natural and unimproved grasslands, wetlands including reedbeds and marshes, and young conifer forests (Watson 1977, Redpath et al. 1998, Sim et al. 2001, Norriss et al. 2002, Wilson et al. 2006). Hen Harriers nest and roost on the ground in tall vegetation which provides shelter from weather and predators (Watson and Dickson 1972, Watson 1977, Picozzi and Cuthbert 1982). They have occasionally been recorded nesting and roosting in trees (Scott et al. 1991, Scott 1994, Bělka and Bělková 2019).

Like many raptor species, Hen Harriers display sexual dimorphism, with females (wing length of 358-392mm) being larger than males (wing length of 323-362mm; Demongin 2016). Colouration is also notably different between the sexes, with adult males being grey and white with black primary wing tips, whereas females are brown with speckled white on the breast and underwing (Plates 1 and 2). As juveniles, both sexes are brown in colour, making visual differentiation between juveniles of less than one year and adult females in the field difficult (Watson 1977).

Plates 1 and 2. Adult female (left) and adult male (right) Hen Harrier.

Status and trends

With an estimated global population of between 330,000 and 512,000, Hen Harriers are listed as 'Least Concern' across their range in the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (Birdlife International 2021). This evaluation comes, despite suspected decreasing population trends, because of their large range and current population size, neither of which approach the thresholds for the IUCN's 'Vulnerable' classification (Birdlife International 2021). Hen Harrier populations fluctuate locally and, in Europe, where their range has contracted in recent decades (Keller et al. 2020), they are classified as a species of conservation concern in 20 of 33 countries due to ongoing declines in local populations (Staneva and Burfield 2017, Fernández-Bellon et al. 2021). As a result of these declines, Hen Harriers are listed as an Annex-I species in the EU Birds Directive (2009/147/EC), which affords the species added protections through the requirement for European member states to regularly monitor local populations and to designate protected areas for the species to ensure their survival and reproduction in their area of distribution. Declining trends are seen in many local Hen Harrier populations of Western Europe. In Spain, for example, a decline of 36-45% was recorded in their breeding populations between 2006 and 2017 (Arroyo 2019), while in the UK and the Isle of Man a 24% decline in the breeding population was reported between 2004 and 2016 (Wotton et al. 2018).

The Hen Harrier population of Ireland has shown long-term fluctuations (O'Flynn 1983, Ruddock et al. 2016). Hen Harriers in Ireland were almost driven to extinction by widespread persecution between the late 19th century and the first half of the 20th century. They were reported breeding in only two areas during this time, the Slieve Bloom Mountains and along the Co. Waterford/ Co. Tipperary border (Usher and Warren 1900, Kennedy et al. 1954, Watson 1977, O'Flynn 1983). A recovery in the Hen Harrier population began in the 1950s, with some estimating that the population increased to as many as 300 pairs by the 1970s (Sharrock 1976, O'Flynn 1983). Towards the end of the 1970s, however, the population began to decline once again, and this decline continued through the 1980s (O'Flynn 1983, Balmer et al. 2013). Since 1998 there have been four national surveys of the Hen Harrier breeding population in Ireland, coordinated by the National Parks and Wildlife Service (NPWS). Between 1998 and 2015 the recorded Hen Harrier population remained relatively stable, despite large increases in survey effort (Norriss et al. 2002, Barton et al. 2006, Ruddock et al. 2012, 2016). Despite a small increase in recorded numbers up to 2010, the latest survey in 2015 revealed the population had declined by 15.6% since 2010 to an estimated 108-157 breeding pairs (Ruddock et al. 2016). Due to their long-term population declines, Hen Harriers are on the Amber list of Bird Species of Conservation Concern in Ireland (Gilbert et al. 2021).

Drivers of population declines

The decline in Hen Harrier populations across their range has been driven by anthropogenic pressures, which differ between local populations. Many of these relate to land use change, particularly agricultural intensification and habitat loss which are the main anthropogenic pressures experienced by Hen Harriers in Europe (Fernández-Bellon et al. 2021). In France, Spain, and the Czech Republic, accidental nest destruction during crop harvesting is a significant pressure (Millon et al. 2002, Fernández-Bellon et al. 2021), while agricultural intensification is the main pressure in the Netherlands (Fernández-Bellon et al. 2021). Persecution is an important driver of Hen Harrier declines in central and eastern Europe, and particularly in Great Britain (Tucker and Heath 1994, Whitfield and Fielding 2009, Murgatroyd et al. 2019, Newton 2021). In Great Britain, vast areas of upland Hen Harrier breeding habitat are managed for Red Grouse (*Lagopus lagopus*) shooting (Newton 2021). Hen Harriers are persecuted by game keepers as they predate grouse chicks and can limit grouse populations (Thirgood et al. 2000, Murgatroyd et al. 2019, Newton 2021), which severely constrains the population size and distribution of Hen Harriers in these areas (Etheridge et al. 1997, Potts 2008, Anderson et al. 2009). In England, for example, persecution pressure is so severe that only 31 breeding attempts were made by Hen Harriers in 2021 despite there being sufficient habitat to support an estimated 300 nesting pairs (Fielding et al. 2011, Slater 2021). In Orkney, where there is no persecution pressure, increases in sheep numbers between the 1970s and 1990s led to a reduction in rough grassland which resulted in lower Hen Harrier prey abundance, causing a 73% reduction in the Hen Harrier population over this period (Meek et al. 1998, Amar et al. 2011, Amar 2019). The Orkney Hen Harrier population has since recovered following a reduction in sheep numbers and an associated increase in rough grasslands (Amar et al. 2011, Amar 2019). Climatic influences, particularly spring rainfall, also have an impact on Hen Harrier productivity (Whitfield and Fielding 2009, Amar 2019, Arroyo 2019, Caravaggi et al. 2019), with future climate change posing an additional risk to Hen Harrier populations (Fernández-Bellon et al. 2021).

In Ireland, widespread planting of commercial conifer forests is the greatest pressure on Hen Harrier populations (Caravaggi et al. 2020a, b). Since the 1920s, plantation forest cover in Ireland has increased from 1% to 11% (Cross 1987, DAFM 2018), with most of this afforestation using non-native Sitka spruce (*Picea sitchensis*) (DAFM 2018). The drive for this afforestation has arisen through policies aimed at mitigating Ireland’s carbon dioxide emissions and through a need for landowners in marginal areas to generate an income from agriculturally unproductive land (Upton et al. 2014). Much of the afforestation in Ireland has taken place in areas inhabited by birds of conservation concern, including the Hen Harrier, and today over 50% of some Hen Harrier breeding areas are afforested (Moran and Wilson-Parr 2015, Corkery et al. 2020). Although Hen Harriers are known to use young commercial conifer forests (between 3 and 12 years post-planting) for nesting and foraging in the absence of more suitable traditional open habitats (Wilson et al. 2009a), the overall impacts are negative. Hen Harriers can only use conifer forests during the early stages of the forest growth cycle before the canopy closes over, with widespread planting also removing large areas of previously open habitat (O'Flynn 1983, Moran and Wilson-Parr 2015, Corkery et al. 2020). Where Hen Harriers do use young conifer forests, their breeding success may be compromised (Wilson et al. 2012). The negative effects of commercial afforestation on Hen Harrier breeding populations may be mediated by effects on prey and predator populations (Thirgood et al. 2003, Amar et al. 2003). Conifer forests may provide suitable habitat for predators that would otherwise be absent, or occur in lower numbers, in open upland areas (Piña et al. 2019), with edge effects in commercial conifer forests being associated with increases in nest failure rates (Sheridan et al. 2020). The latest national Hen Harrier survey in Ireland in 2015 reported that 65% of Hen Harrier nests occurred in young conifer forests (Ruddock et al. 2016).

Balancing the expansion of commercial forest cover and Hen Harrier conservation is a significant challenge (Bonsu et al. 2019, Caravaggi et al. 2020a). Current legislation in Ireland requires that forests cannot be removed once planted, which impedes large-scale habitat restoration efforts. In addition, landowners in marginal areas need sufficient support to farm and manage marginal, low productivity land in a way which benefits Hen Harriers, but is also economically viable (Moran and Wilson-Parr 2015, McLoughlin et al. 2020). There is also distrust between stakeholders relating to forest development and decision making that may create additional obstacles to effective Hen Harrier conservation (Bonsu et al. 2019a).

In addition to afforestation, the development of wind farms has also increased in the uplands of Ireland in recent times in response to the growing demand for renewable energy, with large overlap between areas suitable for wind energy production and Hen Harrier breeding distribution (McGuinness et al. 2015, Wilson et al. 2017). Although collision risk for Hen Harriers is lower than for other raptors (Fernández-Bellon 2020) and displacement effects of wind farms is limited (Madden and Porter 2007, Haworth and Fielding 2012), they are vulnerable to direct and indirect displacement effects associated with wind farm construction. Access tracks to wind turbines may increase accessibility of nests for ground predators (Gómez-Catasús et al. 2021), while turbines also displace small bird prey (Fernández-Bellon et al. 2019). These changes to habitat around wind farms may be linked to reductions in Hen Harrier presence (Pearce-Higgins et al. 2009) and nest success in areas close to turbines (Fernández-Bellon et al. 2015). The marginal lands surrounding commercial forests and wind farms in Hen Harrier breeding areas have also experienced anthropogenic pressures in recent years through land reclamation, further reducing availability of suitable habitat for Hen Harriers (Wilson et al. 2009a).

Little information is available on the pressures faced by Hen Harriers during the non-breeding season. Low survival during this period has been suggested as a possible driver of population declines in the German Wadden Sea. There, the breeding population has declined in recent years despite stable reproductive performance, including clutch sizes, numbers of chicks hatched, and numbers of chicks fledged per breeding attempt (Knipping et al. 2019). Low survival during the non-breeding season has also been suggested as a contributing factor in the decline of the Hen Harrier population in Ireland (Irwin et al. 2011, Ruddock et al. 2016). In addition, the loss of winter roosts and foraging grounds through afforestation and other land-use changes has been reported in Ireland (O'Donoghue 2021).

Many pressures affecting Hen Harriers are a direct result of land uses that, in their current form, conflict with Hen Harriers' ecological requirements. Conservation measures must therefore be developed and implemented that protect Hen Harriers and their habitats, but also address stakeholder concerns and land use demands (Redpath et al. 2010, Bonsu et al. 2019a, St John et al. 2019).

Breeding ecology

Hen Harriers nest on the ground in vegetation that is typically less than a meter in height (Redpath et al. 1998). They have one brood per season, with nests typically containing between 3 and 7 eggs which are laid between mid-April and late-May (Cramp and Simmons 1980, Hardey et al. 2013). Incubation lasts for between 29 and 31 days and the young remain in the nest for a further 28 to 39 days after hatching

(Cramp and Simmons 1980). A mean of 2.4 and 3.0 young typically fledge from successful Hen Harrier nesting attempts, with some variability recorded between different breeding areas (Fielding et al. 2011, Irwin et al. 2011, Hardey et al. 2013). Polygyny, where a single adult male pairs with more than one breeding female, has been reported in some populations (Balfour and Cadbury 1979, Picozzi 1984, Amar et al. 2005).

Hen Harriers are generalist predators, preying primarily on birds, small mammals, and lagomorphs, with other taxa such as reptiles and amphibians accounting for just a small proportion of the diet (Watson 1977). The breeding diet of Hen Harriers in continental Europe and Great Britain is largely dominated by small mammals, particularly *Microtus* voles (Millon et al. 2002, Redpath et al. 2002). Studies of Hen Harriers' diet during the breeding season have been conducted using a range of techniques including pellet analysis which is the most often used method (Redpath et al. 2001, Ludwig et al. 2018), and also observational studies (Redpath et al. 2001, Ludwig et al. 2018) and genetic analysis (Nota et al. 2019). Diet and prey availability play important roles in breeding success and condition (Amar et al. 2003), with population cycles of *Microtus* voles being reflected in Hen Harrier productivity across multiple years (Redpath et al. 2002).

Non-breeding season

Hen Harrier distribution during the non-breeding season differs from their breeding season distribution, both across their range and locally. In some areas, such as Scandinavia, they are migratory and only occur in the breeding season, while in others, such as Western Europe, they occur all year round and are locally migrant (Agostini 2021). In regions where Hen Harriers occur year-round, the range of habitats and areas they use increases during the non-breeding season (Watson 1977, Balmer et al. 2013).

In Ireland, Hen Harriers occur in upland areas during the breeding season, and during the rest of the year they disperse throughout the uplands and lowlands (Balmer et al. 2013, O'Donoghue 2021). Differences in the winter movements and distribution of different Hen Harrier cohorts has also been observed. For example, the winter population of Hen Harriers in Orkney consists mostly of ringtails (juveniles of less than one year old and adult females), while adult males that breed in Orkney are reported to overwinter in mainland Great Britain (Mead 1973, Watson 1977, Picozzi and Cuthbert 1982). In England and mainland Scotland, similar differentiation in local distribution of sexes is seen with females remaining in upland areas during the winter while males move to lowland areas (Murphy 2019). These differences in local distribution may be influenced by factors such as competition (Dobler 2021) and variation in prey preferences driven by sexual dimorphism (Picozzi and Cuthbert 1982, Clarke and Watson 1990), though our understanding of this aspect of Hen Harrier non-breeding ecology is currently poor. Limited information is available on the fine-scale movements of Hen Harriers during the non-breeding season, with most records of movements during this time arising from wing tagging projects and ringing recoveries that only provide broad-scale information, including the movement of some Hen Harriers between Ireland, Great Britain, and continental Europe (Etheridge and Summers 2006, O'Donoghue 2010, Agostini 2021). An early GPS (Global Positioning System) tracking study by Wilson et al. (2009b) revealed the fine-scale movements of three adult Hen Harriers during the breeding season for the first time, however this study was constrained by difficulties with tag deployment and retrieval. Klaassen et al. (2014) provided the first insights into fine-scale winter movements and habitat use of Hen Harriers using GPS tracking technology. One male in this study migrated from its breeding grounds in the Netherlands to Southern Spain during the winter, while two other GPS tagged Hen Harriers remained near their breeding areas in the Netherlands over winter.

Winter roosts are the focal point of Hen Harrier distribution and ecology during the winter months (Watson 1977). Winter roosts are areas of habitat where Hen Harriers settle to rest at night on the ground during the winter (Clarke and Watson 1990). Hen Harrier winter roosts can be solitary or communal and can occur in a wide range of habitats including reedbed, peat bog, marshlands, scrub, crops, and grasslands (Clarke and Watson 1990, O'Donoghue 2021). During the day, Hen Harriers forage in the surrounding landscapes. Winter foraging grounds are typically prey rich habitats, including grasslands, set-aside, and arable stubble (Klaassen et al. 2014, Bělka and Bělková 2019, Klaassen 2019, Vincheuski 2019, Dobler 2021). Social interactions between Hen Harriers often take place on the winter foraging grounds, where adult females typically dominate due to their larger size (Dobler 2021).

Hen Harrier winter diet varies across their range. In Japan, on the eastern edge of the species range, small birds dominate (Hirano et al. 2005), while small mammals comprise the bulk of their winter diet in many parts of continental Europe (van Manen 1996, de Boer et al. 2013, van Boekel and Berghuis 2014, Klaassen et al. 2019). Ireland is on the western edge of the species range and lacks the small mammal species that account for a large proportion of the Hen Harrier diet elsewhere, particularly Field Vole (*Microtus agrestis*) and Common Vole (*Microtus arvalis*) (Lysaght and Marnell 2016). Hen Harrier diet may also differ between sexes due to their sexual dimorphism (Schipper et al. 1975, Picozzi and Cuthbert 1982). Males are capable of capturing highly agile prey, whereas females, due to their larger size, are less agile but are capable of predating lagomorphs and large birds such as ducks (Nieboer 1973, Vincheuski 2019).

Hen Harrier conservation

The pressures that Hen Harriers experience during the breeding season highlight the conflict that exists between their conservation and ongoing land use change, including afforestation, agricultural intensification, grouse moor management, or other practices. Many conservation measures have been implemented across their range in an effort to mitigate against the negative effects of changing land use, with some proving to be more effective than others (Fernández-Bellon et al. 2021). The most widely used conservation measure is the designation of protected areas. This has been implemented across Europe through the designation of Special Protection Areas (SPAs) for Hen Harriers within the Natura 2000 network (Fernández-Bellon et al. 2021). In response to local pressures, other conservation measures that have been implemented include both ecological measures relating directly to Hen Harriers (e.g. brood management) and their predators (e.g. nest fencing, predator control), habitat management (e.g. provision of foraging habitats) and policy/legislative measures. In Great Britain, brood management, where the chicks from wild Hen Harrier nests are removed, reared in captivity, and then released into other suitable areas, has recently been trialled in an attempt to reduce persecution pressures and conflict with grouse moor management. However, this is seen as a controversial conservation management strategy by many (St John et al. 2019) and may only be effective as a temporary measure while persecution pressures on grouse moors are reduced (Watson and Thirgood 2001). Reintroductions of Hen Harriers to areas where they historically bred have also been suggested where the original drivers of population extinction are no longer present (Lee 2019). Supplementary feeding during the breeding season has been trialled in Scotland, with some success, in an attempt to minimise the level of Hen Harrier predation on Red Grouse chicks, and thus reduce conflict between grouse moor management and Hen Harriers (Redpath et al. 2001). More recently in Scotland, the Heads Up for Harriers project, which ran from 2015 to 2020, monitored 52 Hen Harrier nests across 26 estates, with trail cameras deployed at 37 nests. As well as monitoring nests, this project increased public awareness of Hen Harriers online and through media outlets (Etheridge 2020). In the Netherlands, in order to counteract the effects of declining prey abundance and availability, a bespoke habitat measure was developed, called ‘bird fields’ (a combination of lucerne and set-aside). This measure has successfully increased year-round small mammal and small bird abundance and availability which has benefitted Hen Harriers (Wiersma and Bos 2019). In Germany, regular monitoring is used to identify the locations of Hen Harrier nests in crop fields, and farmers are then paid to leave an unharvested area around these nests (European Commission 2022). While most conservation actions aim to provide protection during the breeding season, one project that used year-round conservation measures was the Hen Harrier LIFE project (2014 – 2019) led by the Royal Society for the Protection of Birds (RSPB 2020). This project provided protection for 150 winter roost sites in Northern England and Southern Scotland, primarily against illegal persecution (Thomas 2019).

Although successful in their local areas, each of these conservation measures was implemented in response to local pressures on Hen Harrier populations, and as a result, these may not be directly transferrable to their conservation in Ireland (Fernández-Bellon et al. 2021). The selection of appropriate conservation measures for Hen Harriers in Ireland requires further local scientific research to inform decision making.

In Ireland, Hen Harrier conservation efforts to date have only focussed on the pressures experienced on the breeding grounds, and the designation of protected areas has been the primary conservation tool. In 2007, six Special Protection Areas (SPAs) covering 1,671km^2 of upland Hen Harrier breeding habitat were designated as a requirement of the EU Birds Directive (Directive 2009/147/EC) for the conservation of the species (Fig. 2). A moratorium on new forest planting, wind energy developments and certain agricultural practices was put in place on lands within the SPA network in an attempt to halt the pressures experienced by Hen Harriers in these areas. In 2013 the Irish government initiated the drafting of the Hen Harrier Threat Response Plan (HHTRP). The aim of the HHTRP is to "*synthesise the key scientific evidence for the Hen Harrier population decline, to outline the views and concerns presented by the relevant sectors, and then to lay out a set of actions that address the identified issues along with the aim of improving the long-term prospects for the species*". The HHTRP considers forestry (NPWS 2015), agriculture and wind energy developments as the most significant threats to breeding Hen Harriers in Ireland at present. As of March 2022, the HHTRP has yet to be published.

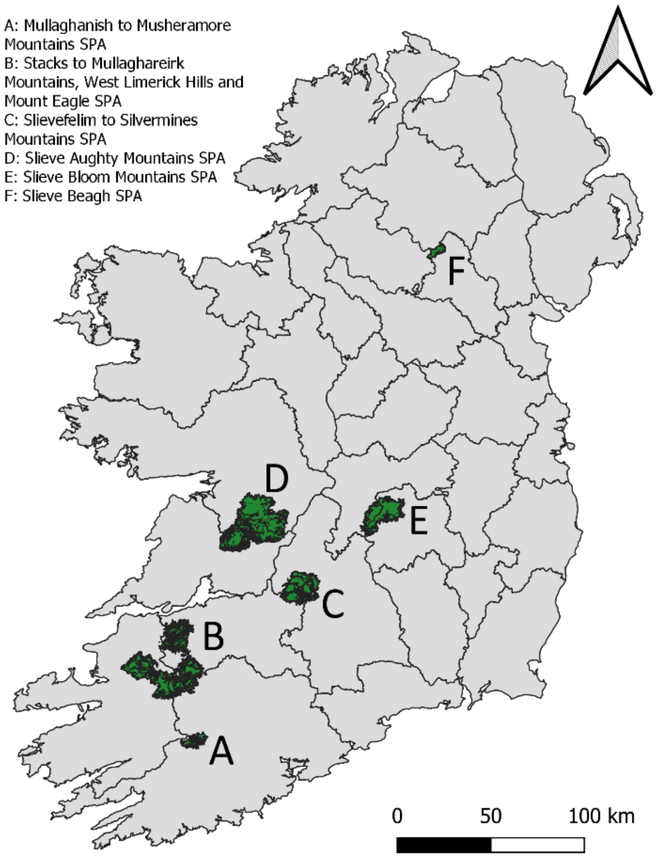

Figure 2. Hen Harrier Special Protection Areas (SPAs) in Ireland.

In late 2017, the largest European Innovation Partnership (EIP) in Ireland, the 'Hen Harrier Project', was initiated (Hen Harrier Project 2018). This EIP aims to promote sustainable management of farmland within the Irish Hen Harrier SPA network through the development and implementation of habitat improvement measures. The project is a results-based scheme, where farmers receive higher payments for better quality habitats and for the implementation of conservation measures (McLoughlin et al. 2020). Smaller scale conservation measures for Hen Harriers have also been implemented through the Green, Low-Carbon, Agri-Environment Scheme (GLAS) and the NPWS Farm Plan Scheme. The Duhallow Raptor LIFE project (2015-2019), initiated by IRD Duhallow and funded through the EU+ LIFE Programme, encouraged farmers in part of the Stack's to Mullagharierk Mountains, West Limerick Hills and Mount Eagle SPA to provide suitable Hen Harrier habitat. This project incorporated regular monitoring of several Hen Harrier breeding sites and one winter roost, as well as a coordinated satellite tagging project in collaboration with NPWS, which is also part of the current PhD research. The focus of Hen Harrier conservation efforts in Ireland on the breeding season is largely due to the lack of knowledge and data on Hen Harrier ecology across the rest of the year and of the pressures and threats they face outside of their breeding grounds.

Knowledge gaps

An understanding of year-round ecology is crucial to the conservation of declining species (Fryxell et al. 2014, Marra et al. 2015, O'Connor and Cooke 2015). Despite considerable research efforts aimed at informing decision making in the face of declining populations, many gaps remain in our knowledge of the year-round ecology of Hen Harriers (Ruddock et al. 2016, Bos et al. 2019). Further research is therefore needed to address these gaps and to determine whether the current conservation measures, such as those currently being implemented within the SPA network, might be appropriate for their year-round conservation.

Our current understanding of Hen Harrier ecology is strongly biased towards the breeding season and is notably limited beyond the juvenile post-fledging dependence period. The juvenile dispersal characteristics of Hen Harriers, including timing, distance, direction, and habitat use, remain poorly understood, with current knowledge limited to ringing and wing tagging studies (Etheridge and Summers 2006, O'Donoghue 2010, Irwin et al. 2011). Juvenile dispersal is a challenging life cycle stage for raptors, and there is an urgent need for information on pressures that Hen Harriers face during this time which could ultimately reduce survival and compromise population viability (Ruddock et al. 2016, Bos et al. 2019, Knipping et al. 2019). While we suspect that recruitment to the breeding population is low in Ireland, we have no reliable estimates of Hen Harrier survival across their life cycle, and our understanding of natal dispersal, survival, and recruitment of birds into the breeding population is poor (Irwin et al. 2011, Ruddock et al. 2016). Information on breeding habitat forms the basis of current conservation measures (Fernández-Bellon et al. 2021) but the lack of information on habitats used during juvenile dispersal and distribution outside of the breeding season is an obstacle to the development of effective and targeted conservation measures.

Current conservation measures for Hen Harriers also take no account of the differences in distribution between sex and age class of birds. Variation in the distribution of different ages and sexes of Hen Harriers has been reported across their range, but the drivers behind this variation remain unclear. This gap in our understanding of the areas used by different cohorts of Hen Harrier, and the reasons behind this, requires attention to inform the development of suitable conservation actions. Further, we lack a detailed knowledge of Hen Harrier diet during the winter months, and how this varies across habitats and time. It is crucial that this knowledge gap is filled given the importance of winter diet for winter distribution, survival, and subsequent breeding success of Hen Harriers. This information will enable the identification of targeted conservation actions to promote Hen Harrier prey populations across the annual cycle. We know that Hen Harriers use young, planted forests in the absence of their preferred open heather and bog habitats, but the capacity of commercial forests to provide a suitable prey source is a particularly important knowledge gap. Vulnerability to predation in young commercial forest habitats in areas of extensive land use change and increased fragmentation, negatively impacts Hen Harrier breeding success (Sheridan et al. 2020) and is a conservation issue requiring further investigation (O’Donoghue 2010, Irwin et al. 2012, Fernández-Bellon et al. 2018, Caravaggi et al. 2020b).

Despite their widespread implementation as a conservation measure for Hen Harriers across their range (Fernández-Bellon et al. 2021), we currently lack direct evidence of the extent to which they use protected areas, or whether these are sufficient to provide benefits beyond the breeding season. We also know very little about fine-scale individual Hen Harrier movement and behaviour across their annual cycle that may play a key role in survival, distribution, and breeding success. Addressing these gaps in existing knowledge will inform the continued conservation management of Hen Harriers and their habitats in Ireland.

Thesis aims and chapter outlines

The aim of my PhD research project was to address knowledge gaps in the year-round ecology of Hen Harriers in Ireland, and to develop a suite of conservation recommendations based on the findings to inform future conservation management actions. Based on identified knowledge gaps, the specific aims of this thesis were to:

1. Describe juvenile Hen Harrier dispersal strategies, investigate causes of mortality and survival rates and habitat use across the life cycle, and examine the extent of the use of designated protected areas by Hen Harriers.
2. Explore the characteristics of Hen Harrier winter roosts and describe regional variation and the influence of habitat on roost size (number of birds) and composition (adult male and ringtail), and examine the protection status of roost locations.
3. Describe temporal variation in the winter diet of Hen Harriers across their range in Ireland and investigate regional variation and the impact of surrounding landscape on diet composition.
4. Use satellite telemetry to document the movement of individual female Hen Harriers in Ireland across the full annual cycle over multiple years.
5. Assess the composition and abundance of bird and small mammal prey of Hen Harriers in upland second rotation pre-thicket conifer forests compared with open upland moorland.
6. Describe the composition of predator communities in young conifer forests and assess the effect of habitat structure and proximity to interior forest edge on predator occurrence.
7. Develop a suite of conservation recommendations that draw on the full annual life-cycle requirements of Hen Harriers in Ireland.

This thesis is set out as a series of self-contained data chapters, some of which are published and others that are currently under review for publication. While chapters are presented as individual studies, they constitute a coherent body of research for this PhD. In the final chapter, I draw together the results of these studies and set out a series of recommendations for conservation measures and identify priority areas for further research.

In **Chapter Two**, I investigated aspects of Hen Harrier annual ecology that are relevant to their conservation management using remote tracking. I described the timing, direction, and distance of juvenile Hen Harrier dispersal in Ireland, and examined the habitats used during dispersal and their impact on survival through this life-cycle stage. I also examined habitat use, survival and causes of mortality. I addressed these research questions using satellite tracking data from 31 Hen Harriers that were tagged in Ireland between 2009 and 2019, along with data from two Scottish tagged Hen Harriers that overwintered in Ireland. This included data from 22 Hen Harriers that were tagged specifically for this PhD Research Project.

In **Chapter Three**, I investigated the influence of surrounding habitat on the size (number of birds) and composition (adult male compared with juvenile and adult female) of Hen Harrier winter roosts. I also estimated the degree of protection that the current network of protected areas provides to roosts and the surrounding foraging grounds. I used data collected during a two-year winter roost survey, supplemented with archived data, to address these research questions. I identified 101 roosts, with 413 roost watch surveys taking place at 53 of these roosts.

In **Chapter Four**, I investigated Hen Harrier winter diet, and the influence of surrounding habitat and time on diet composition, by analysing 1,117 pellets collected from 11 winter roosts over two winters. This research has been accepted for publication in *Bird Study*[1].

In **Chapter Five** I provided an in-depth look at the individual life histories of two satellite tagged female Hen Harriers, describing their lifetime movements and behaviours, and highlighting the importance of considering individuality in conservation efforts.

In **Chapter Six**, I explored the small bird and small mammal prey communities in young, planted conifer forests and compared these with prey communities in open habitats traditionally used by Hen Harriers, and investigated their importance for predators such as Hen Harriers. This study was published in the *European Journal of Wildlife Research*[2].

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[1] McCarthy et al. 2022. Landscape and temporal influences on the winter diet of a threatened diurnal raptor, the Hen Harrier *Circus cyaneus*. Accepted for publication in *Bird Study*.

[2] McCarthy et al. 2021. Bird and small mammal community composition and abundance in upland open habitats and early conifer forests. *European Journal of Wildlife Research*, 67(26).

In **Chapter Seven**, I described the predator communities of young, planted conifer forests using data collected from baited camera trap stations, and investigated their importance for ground nesting Hen Harriers. This chapter is under review by the *Journal of Wildlife Management*[3].

In **Chapter Eight**, I brought together the main findings from this PhD research project and identified a suite of recommendations for the year-round conservation management of Hen Harriers in Ireland that were developed in consultation with a range of stakeholders.

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[3] McCarthy et al. in review. Predator community composition in young forest plantations in Ireland: implications for Hen Harrier conservation. In review with the *Journal of Wildlife Management*.

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Chapter Two

Patterns of Hen Harrier juvenile dispersal, survival, breeding population recruitment, natal dispersal and habitat use as revealed by satellite tracking

Satellite tagged nestling Hen Harrier

Abstract

Hen Harriers (*Circus cyaneus*) are an Annex-I listed species that have experienced declines in breeding populations across their Western European range over the last number of decades. Research and conservation efforts have primarily focussed on their breeding ecology, while our understanding of their ecology and requirements across the rest of the year is poor. In this study, we analysed tracking data from 31 Hen Harriers that were satellite tagged in Ireland between 2009 and 2019, in addition to two Scottish satellite tagged Hen Harriers that overwintered in Ireland during this time, to gain an understanding of their year-round movement, survival and habitat use. These data comprised 3,581 transmission days with 15,261 individual high quality location fixes. Juvenile dispersal typically involved a sudden, long-distance (>25km) initial movement away from the natal area, followed by shorter exploratory movements and the use of Temporary Settlement Areas (TSAs). Hen Harrier survival was lowest during the first three months of life, with over half of the satellite tagged birds dying during this period. First year survival was estimated as 17.7 ± 7.5%. Starvation was the most common cause of mortality (n = 7), where the cause of mortality was known. Other causes of mortality included predation (n = 1), entanglement (n = 1), persecution (n = 1) and trauma (n = 1). Two of the Irish tagged Hen Harriers were recruited into the Irish breeding population, though neither successfully produced young, with these two birds showing considerable variation in natal dispersal. The use of protected areas was lowest during juvenile dispersal (14.8% of fixes) and was higher during the breeding season compared with the non-breeding season. Habitat use varied throughout the year, and between years, for individual birds, with some evidence that juvenile survival rates are higher for those birds that use arable areas during juvenile dispersal. The findings of this research will inform specific conservation management strategies and policies to improve habitat suitability and thus population trends for Hen Harriers in Ireland and throughout their range.

Introduction

Hen Harrier (*Circus cyaneus*) populations have declined in recent decades across Europe due to habitat loss, persecution, agricultural intensification, nest predation, forestry activities and wind energy development (Wilson et al. 2017, Murgatroyd et al. 2019, Caravaggi et al. 2020, Fernández-Bellon et al. 2021). These pressures can impact negatively on breeding success and present challenges for Hen Harrier conservation given the extensive land use change encountered across their range (Wilson et al. 2012, Fernández-Bellon et al. 2015, Caravaggi et al. 2019, Murgatroyd et al. 2019, Fernández-Bellon et al. 2021). As a result, Hen Harriers are of conservation concern and are listed in Annex I of the EU Birds Directive (Directive 2009/147/EC). Conservation measures aimed at preserving and reinforcing Hen Harrier populations across Europe include the designation of protected areas, habitat management and predator control (Fernández-Bellon et al. 2021). Hen Harriers are Amber-listed in Ireland (Gilbert et al. 2021) where the number of breeding pairs declined by 15.6% between 2010 and 2015 (Ruddock et al. 2016). Much of the research to date in Ireland has focussed on landscape and anthropogenic factors affecting nesting habitat selection, breeding success and population distribution (Wilson et al. 2009, 2012, Ruddock et al. 2016). An understanding of juvenile dispersal, survival, movement patterns and habitat use are important in identifying conservation needs and informing conservation measures to support post-fledging survival. These aspects of Hen Harrier ecology have remained unexplored until now due mainly to difficulties in gathering the relevant data.

Juvenile dispersal is a crucial yet poorly understood demographic process in raptor ecology (Morrison and Wood 2009, Moliner et al. 2015). Knowledge of individual species dispersal strategies, including distance, direction, timing, and habitat use, is critical to understanding how conservation efforts can be targeted to improve survival during dispersal (Paradis et al. 1998, Soutullo et al. 2006, Moliner et al. 2015). Dispersal strategies vary among raptor species (Moliner et al. 2015), with some species, such as Golden Eagle (*Aquila chrysaetos*), undertaking slow, gradual dispersal (Weston et al. 2013, Murphy et al. 2017), while others, such as Bonelli's Eagle (*Aquila fasciata*), undertake sudden and clearly defined dispersal (Cadahía et al. 2010). Research on Hen Harrier juvenile dispersal has thus far been limited to ringing and wing-tagging studies that provide limited spatial and temporal information, particularly regarding fine-scale movements of individuals (Etheridge et al. 1997, Etheridge and Summers 2006, Whitfield and Fielding 2009, O'Donoghue 2010). Gaining an in-depth understanding of Hen Harrier juvenile dispersal will aid in identifying additional pressures that may be affecting Hen Harrier population viability.

Juvenile survival is an important component of population viability and stability. Although low juvenile survival has been suggested as a potential driver of population decline of Hen Harriers in Ireland and some populations in Europe (Irwin et al. 2012, Ruddock et al. 2016, Knipping et al. 2019), there remains a lack of knowledge regarding this period of the Hen Harriers' life cycle, and the factors that may be driving low survival (Bos et al. 2019). The initial phase of juvenile dispersal is often the most challenging time for raptors, during which they must find and catch their own food, often in landscapes that have limited hunting opportunities or where good foraging areas are sparsely distributed (Newton 1979). Many juvenile raptors establish Temporary Settlement Areas (hereafter TSAs) during dispersal (Morrison and Wood 2009, Moliner et al. 2015). TSAs are typically areas of good quality foraging habitat with an abundance of prey and are normally located away from the natal area and breeding territories (Cadahía et al. 2010, Weston 2014, Moliner et al. 2015). Identifying the locations and habitat characteristics of these TSAs helps with devising conservation measures aimed at improving the quality and extent of suitable habitats that could be used by juveniles during dispersal (Balbontín 2005).

Beyond the juvenile dispersal period, habitat use is a central aspect of Hen Harrier ecology and determines survival, breeding condition, breeding productivity and distribution (Newton 1979, Amar and Redpath 2005, Amar et al. 2008, Wilson et al. 2009, Sarasola et al. 2018). Understanding what habitats are used by different cohorts of Hen Harriers, and when they are used, is crucial to protecting existing suitable habitat and increasing the availability of suitable habitat. For Hen Harriers, little is known about their year-round habitat use, and particularly how habitat use differs across ages, sexes and seasons with current knowledge based primarily on observational studies and small-scale tracking studies (Amar and Redpath 2005, Klaassen et al. 2014b, Bělka and Bělková 2019). It is therefore important to broaden our knowledge of general habitat use of Hen Harriers.

Natal dispersal is the movement between the natal site and the site of first breeding (Howard 1960, Greenwood and Harvey 1982). It is an important consideration in population ecology and in the designation of protected areas. Some species, such as Sparrowhawks (*Accipiter nisus*), show low natal dispersal (Newton 1979), whereas others, such as Rough-legged Buzzards (*Buteo lagopus*) show extensive dispersal from natal areas (Galushin 1972). Hen Harriers appear to have variable natal dispersal (Whitfield and Fielding 2009), however this aspect of their ecology, together with levels of recruitment into the breeding population, have received little research attention to date. It is therefore unknown, for example, the extent to which juveniles from protected areas return to breed themselves within the protected area network.

The designation of protected areas is a widely used tool in conservation management for species under threat (McClure et al. 2018, Fernández-Bellon et al. 2021). Under the EU Birds Directive (Directive 2009/147/EC), member states are required to designate Special Protection Areas (SPAs) for Hen Harriers. In 2007, six breeding areas covering 1,671km^2 were designated as SPAs for Hen Harriers in Ireland. However, the effectiveness of this conservation strategy is unclear, with designation of areas perceived to have little meaningful influence on Hen Harrier conservation status (Fernández-Bellon et al. 2021). In Ireland, the Hen Harrier population within the SPA network has continued to decline despite the implementation of a number of conservation projects, with a 25% decline in the number of breeding pairs recorded within SPAs between 2007 and 2021 (Ruddock et al. 2016, Hen Harrier Project 2021). In addition, only Hen Harrier breeding areas have been designated as SPAs, thereby raising questions regarding the suitability and effectiveness of the current SPA network for the year-round protection of Hen Harriers in Ireland.

The aim of this research was to describe juvenile Hen Harrier dispersal strategies in Ireland, using satellite tracking devices deployed on individual birds to inform conservation planning. We also examined survival rates, along with habitat use within and across years for individual birds. We explored differential habitat use of juveniles based on survival and described the causes of mortality of Hen Harriers. Finally, we investigated the extent of overlap between designated protected areas and areas used by Hen Harriers.

Methods

Satellite tagging and data collection

Between 2009 and 2019, satellite transmitters were fitted to 31 Hen Harrier nestlings from nests across seven breeding areas on the island of Ireland (Table 1; Fig. 1). In addition to the 31 Irish tagged Hen Harriers, data from two Hen Harriers that were tagged in Scotland by the Royal Society for the Protection of Birds (RSPB) that overwintered in Ireland between 2018 and 2021 were also obtained. Hen Harrier nests were located by experienced fieldworkers who found and monitored nests from distant (> 500m) vantage points to determine breeding success and approximate age of broods. Satellite transmitters were fitted, under licence, to nestling Hen Harriers between 24 and 34 days after hatching (i.e. while young were well feathered but not yet capable of flying). No specific criteria were used to select between siblings for tagging in nests between 2009 and 2016. This approach was subsequently revised and first order (eldest) nestlings, which typically have higher survival than lower order (younger) nestlings (Newton 1979), were selected for tagging on all but one occasion where a second order bird was chosen. All satellite transmitters deployed on Hen Harrier nestlings were solar-powered Argos Platform Transmitter Terminals (hereafter PTTs; produced by Microwave Telemetry Inc., Columbia, MD, USA; Plate 1).

Figure 1. Breeding areas where Hen Harriers were satellite tagged in Ireland between 2009 and 2019.

Plate 1. Platform Transmitter Terminal (satellite transmitter) and harness (neck loop and chest strap) used in the current study.

Table 1. Details of each satellite tagged Hen Harrier included in this study.

PTT ID	Sex	Natal Area	Year tagged	Brood size	Brood order	PTT weight (g)	Cycle	Source
NA (1)	F	Antrim Hills	2009	2	-	12	1	A
95134	M	Galtees	2009	4	1	9.5	2	B
95135	F	Knockmealdowns	2009	3	3	12	2	B
NA (2)	M	Antrim Hills	2010	2	-	12	1	A
118197	M	Mullaghareirks	2012	3	3	9.5	2	C
118198	F	Mullaghareirks	2012	3	2	9.5	2	C
118198	M	Mullaghareirks	2013	3	3	-	2	C
118199	F	Mullaghareirks	2013	2	1	-	2	C
118200	F	Mullaghareirks	2013	2	2	-	2	C
159138	F	Slieve Blooms	2016	3	1	9.5	2	D
159139	F	Ballyhouras	2016	3	2	9.5	2	D
159140	F	Ballyhouras	2016	3	3	9.5	2	D
159141	M	Ballyhouras	2016	3	2	9.5	2	D
159142	M	Slieve Blooms	2016	2	2	9.5	2	D
159143	M	Knockmealdowns	2016	4	3	9.5	2	D
160248	F	Boggeraghs	2016	4	3	9.5	2	D
160249	M	Mullaghareirks	2016	2	2	9.5	2	D
160250	M	Ballyhouras	2016	3	3	9.5	2	D
160251	F	Mullaghareirks	2016	2	1	9.5	2	D
159139	F	Slieve Blooms	2017	3	1	9.5	3	D
159142	F	Slieve Blooms	2017	3	1	9.5	3	D
160250	F	Knockmealdowns	2017	5	1	9.5	3	D
170132	F	Mullaghareirks	2017	4	1	9.5	3	D
170498	M	Ballyhouras	2017	3	1	5	3	D
170499	M	Mullaghareirks	2017	3	1	5	3	D
53304	M	Scotland	2018	-	-	-	3	E
54222	M	Knockmealdowns	2018	5	1	9.5	3	D
160251	M	Ballyhouras	2018	4	1	9.5	3	D
170004	M	Scotland	2018	-	-	-	3	E
170133	F	Mullaghareirks	2018	5	2	9.5	3	D
54070	F	Mullaghareirks	2019	2	1	9.5	3	D
54224	F	Knockmealdowns	2019	2	1	9.5	3	D
54225	F	Slieve Blooms	2019	5	1	9.5	3	D

Cycle: (1) 6 on/ 30 off; (2) 10 on/48 off; (3) 4 on/19 off.

Source: (A) Queens University Belfast and the Northern Ireland Environment Agency; (B) Golden Eagle Trust; (C) National Parks and Wildlife Service and IRD Duhallow 2012/13; (D) National Parks and Wildlife Service and IRD Duhallow 2016-2019; and (E) Royal Society for the Protection of Birds.

Nestlings were also fitted with British Trust for Ornithology (BTO) metal leg rings at the time of tagging, were sexed, and tarsus width (to nearest 0.1mm), wing length (maximum cord to nearest 1mm) and body mass (to nearest 1g) were recorded. Nestlings were sexed based on eye colour and tarsus width, while wing length was used to estimate age in days (Balfour 1970, Hardey et al. 2013, Demongin 2016). All ringing, tagging and nest visits were conducted under licence from the National Parks and Wildlife Service and the BTO. PTTs weighed 5g (n = 2), 9.5g (n = 24) or 12g (n = 5), or 2% (range of 1.1 to 2.6%, n = 21) of the body weight of tagged Hen Harriers, which is less than the recommended upper limit of 3% for tagging of birds (Kenward 2001). All PTTs, except those weighing 5g, had built-in UHF transmitters that transmitted a radio signal when movement of the PTT ceased for eight hours, thereby enabling the location of the PTT when the birds died. The PTTs were fitted to nestlings using a backpack-style harness (Kenward 2004; Plate 1) specially designed and adapted for Hen Harriers and previously used successfully to tag Hen Harriers in England and Scotland (Murgatroyd et al. 2019) using 6mm wide Teflon ribbon (Bally Ribbon Mills, PA, USA).

The PTTs were programmed to three different transmission cycles: (i) 4 hours on and 19 hours off (n = 12; 2017-19); (ii) 10 hours on and 48 hours off (n = 17; 2009, 2012-13); and (iii) 6 hours on and 30 hours off (n = 2; 2009-10). Transmission cycles were selected by trial and error, with the aim of optimising both the frequency of location data (i.e. fixes) and battery life. It was not possible to change transmission cycles once the PTTs were deployed. As the PTTs were solar powered, the number of fixes obtained during each transmission period, and the reliability of on-time transmissions, varied depending on season, weather conditions and bird behaviour. The PTTs estimate the location of the unit using Doppler shift, and tracking data were downloaded using the Argos satellite system (see Argos 2016 for details). An accuracy estimate, termed location class (LC), was provided for each location. Only the highest accuracy location class fixes (3, 2, and 1) were retained (68th percentile accuracy of 0.4, 1.0 and 2.5km, respectively (Douglas et al. 2012)). Low accuracy location estimates (0, A, B, and Z) were not retained for analyses (68th percentile accuracy of 10.4, 8.1, 30.5 and 30.3, respectively).

Juvenile dispersal

Juvenile dispersal was recorded when a juvenile made a defined journey a minimum of 5km away from the nest with no return to within 5km of the nest within seven days of original departure (Cadahía et al. 2007, O'Donoghue 2010). If the bird died within the first seven days of travelling further than 5km of the nest, this was still recorded as onset of dispersal due to the clear, defined movement of the bird up to the point of mortality. Where there were gaps in transmission of less than seven days during which time dispersal started, the mid-point of the transmission gap was taken as the date of dispersal. A date of dispersal was not estimated where gaps between transmissions at the time dispersal started were greater than seven days (Johnson et al. 2017).

Survival

The majority of PTTs (n = 27) transmitted additional sensor data that provided an indication of PTT movement, temperature, and battery level, as well as the location data. It was possible to use these additional sensor data, together with location data, to determine the fate of each bird. Methods described by Klaassen et al. (2014a) were used to determine the likely fate of each bird as follows: Alive (A) - bird was known to be still alive based on transmission data; Dead (D) - bird was known to be dead by the recovery of the PTT and carcass; Presumed Dead (PD) - bird was presumed to be dead based on location and sensor data, but the PTT and carcass were not recovered; and Transmitter Failure (TF) - PTT suspected to have failed with no subsequent sightings of the tagged bird.

When sensor data indicated that a possible mortality event had occurred, attempts were made by fieldworkers to locate the bird and PTT as quickly as possible in order to determine a cause of mortality. Searches for suspected dead birds were conducted either as "cold searches" (walking around the area of last known transmission), using a radio receiver to detect the UHF mortality signal, or using a goniometer (RXG134, CLS). If found, the location of the carcass was recorded using a GPS unit to an accuracy of 3m and photographed before being sent for post-mortem.

Habitat use

When examining habitat use across the different life stages, seasons, and sexes, we retained the highest accuracy daytime location fixes (class 3) and applied a 400m buffer around each location (Douglas et al. 2012). In order to investigate potential foraging habitat use rather than roosting habitat use, we retained only daytime fixes. Daytime was defined as the time between the midpoint of dawn/sunrise and the midpoint of sunset/dusk as calculated at each location fix. We then calculated the proportion of each habitat category within these 400m buffers. For birds tagged between 2009 and 2013, we used CORINE 2012 landcover data, supplemented with Coillte, Forest Service and Northern Ireland Forest Service Forest data for the relevant time period. The supplementary forest data were categorised into conifer, mixed and deciduous forest, as determined by the dominant planted species, and were combined with the relevant CORINE land classes. We repeated this process for birds tagged between 2016 and 2019, though with CORINE 2018 landcover data. Some CORINE land classes were merged, with full details provided in Table 2.

Table 2. Habitat variables included in the main habitat groups.

Variable	Manipulation	Source
Arable	Composite data	CORINE (2.1.1. Non-irrigated arable land; 2.4.2. Complex cultivation patterns)
Bog	Composite data	CORINE (4.1.2. Peat bogs; 3.2.2. Moors and heathland; 3.3.3. Sparsely vegetated areas)
Conifer	Composite data	CORINE (3.1.2. Coniferous forest), Coillte, Forest Service, Forest Service Northern Ireland
Pasture	Raw data	CORINE (2.3.1. Pasture)

Data analysis

We used general linear models to explore factors affecting Hen Harrier dispersal and dispersal timing. The response variable for global models was either dispersed (yes/no; binomial family, “logit” link function) or age in days at dispersal (Gaussian family, “identity” link function). We included sex, brood order, breeding area, year, and an interaction between sex and brood order, as fixed effects. We repeated this model structure for survival where the response variable was survival (yes/no; i.e. birds that did or did not survive dispersal) with a loglogistic distribution (distribution family selected by lowest model Akaike’s Information Criteria [AIC] value). These were treated as global models, with an information-theoretic approach used in combination with model averaging to generate models that had the greatest support (Grueber et al. 2011). Models with ΔAIC <2 were retained within the top subset of models. We assessed the Variance Inflation Factors (VIF) of fixed effects in each global model to ensure there was no multicollinearity between fixed effects (VIF <10; Quinn and Keogh 2002).

We examined habitat use across several cohorts and time frames. This included examining: (i) habitat use by juvenile Hen Harriers between dispersal onset and the end of their first October (i.e. the period during which all dispersal mortalities occurred), grouped by dispersal survival; (ii) habitat use across the first and second year autumn and winter periods, grouped by sex; (iii) habitat use between first and second autumn for four satellite tagged female Hen Harriers, grouped by first and second year; and (iv) habitat use across the first year of life, grouped by meteorological season. All habitat use data here exclude fixes that occurred prior to dispersal from the natal area. We used Mann-Whitney U Tests (i, ii, iii) and Kruskal-Wallis Tests (iv) to compare groups.

The use of protected areas by satellite tagged Hen Harriers was assessed by overlaying all location fixes (classes 3, 2 and 1) with protected area polygons (Limiñana et al. 2012). This analysis was only conducted for location fixes that occurred in the Republic of Ireland and included proposed Natural Heritage Areas (pNHAs), Natural Heritage Areas (NHAs), Special Areas of Conservation (SACs) and Special Protection Areas (SPAs). We looked at three time periods: (i) juvenile dispersal, which was the time between dispersal onset and the end of the birds first October; (ii) non-breeding season, which was September to March, inclusive; and (iii) breeding season, which was April to August for birds in their second calendar year and older, inclusive.

Results are presented as x̄ ± Standard Error, unless otherwise stated. Data were processed and analysed using QGIS version 3.12.3 (QGIS.org 2021) and R version 4.0.2 (R Core Team 2020) including packages *ggplot2* (Wickham 2016), *lme4* (Bates et al. 2015), *survival* (Therneau 2021) and *MuMIn* (Barton 2020).

Results

Juvenile dispersal

Of the 31 Irish satellite tagged Hen Harriers, 18 were female and 13 were male, while both Scottish tagged Hen Harriers were male. In total, we received 15,261 high quality location fixes across 3,581 transmission days. Of the Irish tagged Hen Harriers, 24 (77.4%) successfully dispersed from their natal areas, with the remaining seven (22.6%) dying before leaving the natal area (Table 3). Lower order (youngest of the brood) birds were less likely to disperse than higher order (eldest in the brood) birds. Of the seven nestlings that failed to disperse, four (57.1%) were the lowest order of the brood. Of the 15 first order birds tagged, only one (6.7% of first order birds tagged), an individual with a leg injury, failed to disperse from the natal area. The average model showed that the most important determinant of successful dispersal was brood order, followed by sex and then year. In addition, there was an interaction between brood order and sex. Brood order had a positive affect whereby higher order birds were more likely to successfully disperse (0.98 ± 0.82; Table 4). Males were less likely to successfully disperse than females (-1.51 ± 1.83; Table 4).

The mean age of Hen Harriers at the onset of dispersal was 60.1 days old (± SD of 5.1 days; range of 52 to 75 days). The mean date of onset of dispersal was the 8th of August (range of 19th July to 21st August). It was not possible to calculate the timing of onset of dispersal for four of the birds due to low PTT transmission frequencies. Breeding range was the most important factor influencing dispersal timing, followed by year, sex, and then order. The timing of onset of dispersal differed across breeding areas. The timing of onset of dispersal was similar between males (60.0 ± SD of 2.3 days old; n = 8) and females (60.1 ± SD of 5.8 days old; n = 16), and across years (0.46 ± 0.44) and brood order (0.36 ± 1.19; Table 4).

Table 3. Dispersal, survival, and mortality of Irish satellite tagged Hen Harriers. PD- presumed dead; TF- tag failure; D- confirmed dead; A- alive.

PTT ID	Hatched	Age at last live transmission	Dispersed	Fate	Cause of death
95134	12/06/2009	63	Y	PD	Unknown
NA (1)	21/06/2009	Unknown	Y	TF	NA
95135	21/06/2009	102	Y	PD	Unknown
NA (2)	17/06/2010	Unknown	Y	TF	NA
118198	06/06/2012	60	Y	D	Starvation
118197	26/06/2012	42	N	D	Unknown
118199	10/06/2013	74	Y	PD	Unknown
118198	13/06/2013	35	N	D	Starvation
118200	13/06/2013	565	Y	D	Persecution
160248	28/05/2016	54	Y	PD	Unknown
159142	01/06/2016	144	Y	D	Starvation
159140	02/06/2016	46	N	D	Unknown
159138	05/06/2016	106	Y	PD	Unknown
159141	06/06/2016	41	N	PD	Unknown
160249	06/06/2016	44	N	PD	Unknown
160250	10/06/2016	104	Y	D	Starvation
159143	11/06/2016	102	Y	PD	Unknown
159139	12/06/2016	48	N	D	Unknown
160251	17/06/2016	93	Y	D	Other*
170499	28/05/2017	124	Y	TF	NA
170498	06/06/2017	31	Y	D	Unknown
159139	08/06/2017	1,735**	Y	A	NA
160250	09/06/2017	57	Y	PD	Unknown
159142	13/06/2017	56	Y	PD	Unknown
170132	18/06/2017	527	Y	D	Predation
170133	07/06/2018	269	Y	D	Entanglement
54222	08/06/2018	78	N	D	Trauma
160251	10/06/2018	58	Y	D	Starvation
54224	02/06/2019	64	Y	D	Unknown
54070	04/06/2019	534	Y	D	Starvation
54225	10/06/2019	62	Y	D	Starvation

* A possible cause of mortality was collision with a wind turbine, however it was not possible to conclude this with certainty.

** Bird still alive at time of writing, March 2022.

Table 4. Model average outputs. P-values in **bold** are statistically significant.

Model	n	Fixed effects	β ± SE	p	Importance
(a) dispersed yes/no	29	Intercept	28.31 ± 173.91	0.88	
		Order	-0.98 ± 0.82	0.25	0.83
		Sex (male)	-1.51 ± 1.83	0.43	0.76
		Order*Sex	0.15 ± 0.63	0.82	0.15
		Year tagged	-0.01 ± 0.09	0.89	0.13
(b) dispersal timing	20	Intercept	-883.37 ± 897.76	0.36	
		Range - Boggeraghs	-2.24 ± 6.19	0.74	1
		Range - Galtees	8.58 ± 6.42	0.22	1
		Range - Knockmealdowns	3.68 ± 4.23	0.43	1
		Range - Mullagharierks	11.02 ± 4.52	**0.03**	1
		Range - Slieve Blooms	3.12 ± 4.18	0.5	1
		Year tagged	0.46 ± 0.44	0.33	0.8
		Sex (male)	3.16 ± 3.46	0.39	0.69
		Order	0.36 ± 1.19	0.78	0.29
(c) survival	31	Intercept	-15.64 ± 67.74	0.82	
		Log (scale)	-0.68 ± 0.17	**< 0.001**	
		Sex (male)	-0.10 ± 0.31	0.51	0.47
		Order	-0.05 ± 0.12	0.71	0.27
		Year tagged	0.01 ± 0.03	0.3	0.24

The Euclidean distance of juveniles from natal areas increased up to 12 weeks post-onset of dispersal (Figs. 2, 3 & 4), from 66.9 ± 14.5km on day 1, to 102.3 ± 20.8km in week four, and 142.2 ± 20.5km in week 12. The furthest any Irish tagged Hen Harrier travelled from their natal area during juvenile dispersal in this study was a straight-line distance of 337km. During juvenile dispersal, Hen Harriers moved across the island, spending time at Temporary Settlement Areas (TSAs) from where they occasionally made longer distance exploratory movements. The mean settlement time at the wintering grounds for juvenile Hen Harriers that survived the dispersal period was 60 days post-dispersal (range of 21st September [37 days post-dispersal] to 15th November [97 days post-dispersal], mean 13th October). Once settled, most juveniles used fewer than three roosts during the winter period.

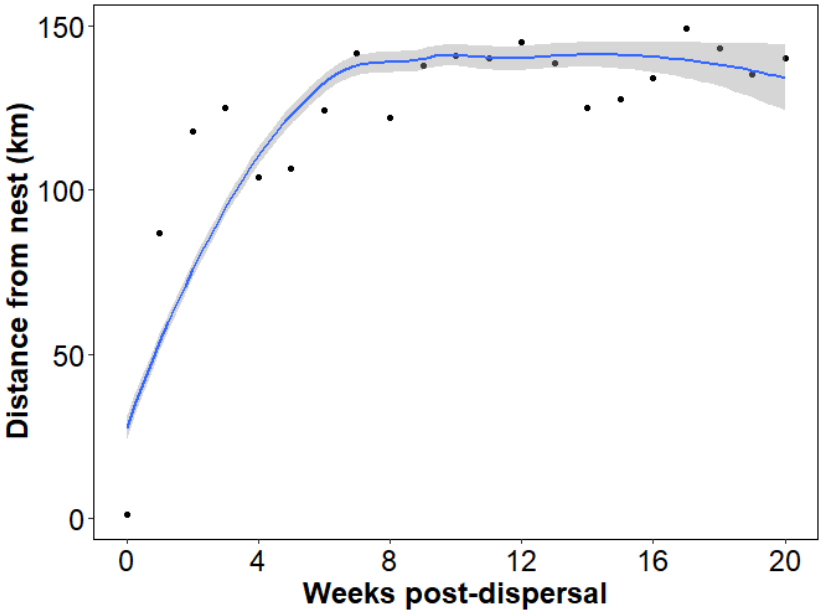

Figure 2. Weekly mean straight-line distance from nest after onset of juvenile dispersal, with least sum of squares smoothened line. Grey areas show 95% confidence interval around line of best fit. n = 20 at week 0, and n = 5 at week 20.

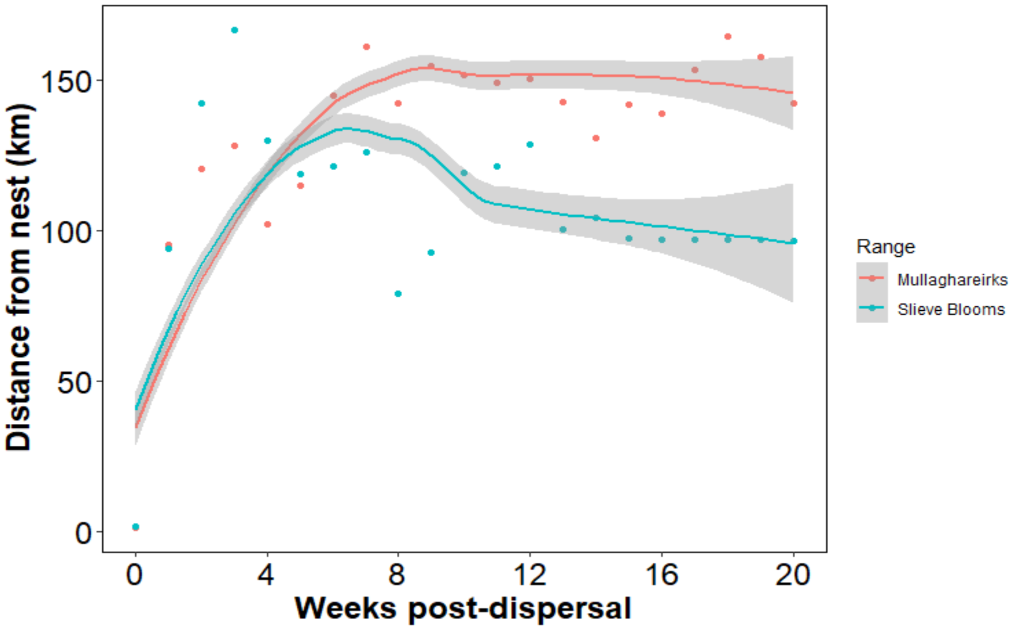

Figure 3. Weekly mean straight-line distance from nest after onset of juvenile dispersal, with least sum of squares smoothened line, in the two breeding areas from which juveniles survived the dispersal period. Grey areas show 95% confidence interval around line of best fit. n = 12 at week 0, and n = 5 at week 20.

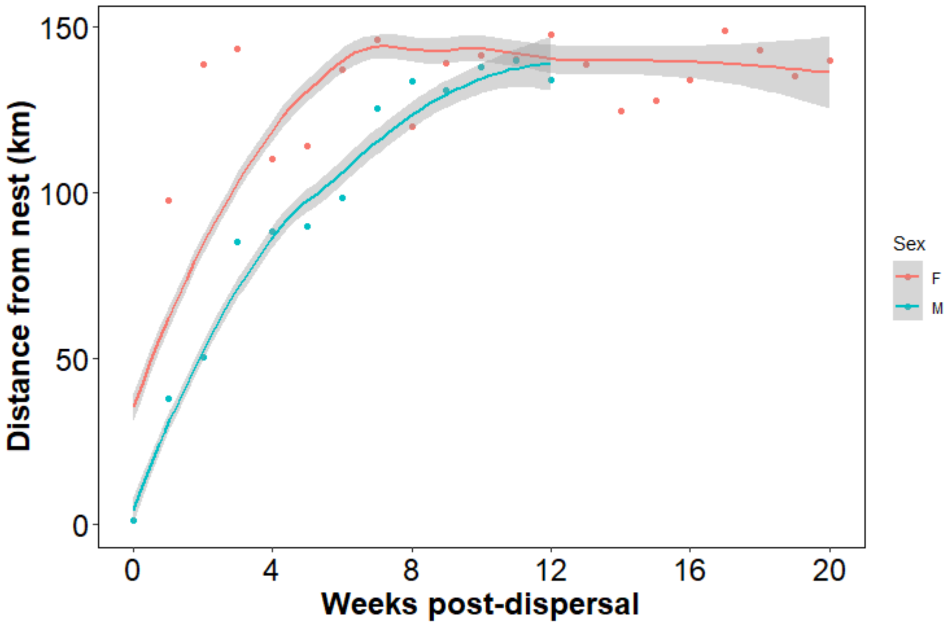

Figure 4. Weekly mean straight-line distance from nest after onset of juvenile dispersal, with least sum of squares smoothened line, for males and females. Note that no juvenile males survived beyond 12 weeks post-dispersal. Grey areas show 95% confidence interval around line of best fit. n = 20 at week 0, and n = 5 at week 20.

Overall dispersal direction followed a north-easterly pattern, however dispersal direction differed across breeding areas (Fig. 5). Hen Harrier nestlings from the Mullagharierks generally followed a north-easterly dispersal pattern, particularly after 28 days post-dispersal. Those from the Knockmealdowns followed a north-westerly to north-easterly dispersal direction, while those from the Slieve Blooms initially followed a north-easterly dispersal direction, though this changed after 28 days after onset of dispersal. It was not possible to reliably decipher an overall trend in dispersal direction for the Ballyhouras, Boggeraghs or Galtees due to low sample sizes of birds tagged. The majority (87%) of juveniles moved from the upland breeding areas to lowland areas, both inland and coastal, during dispersal (Fig. 6).

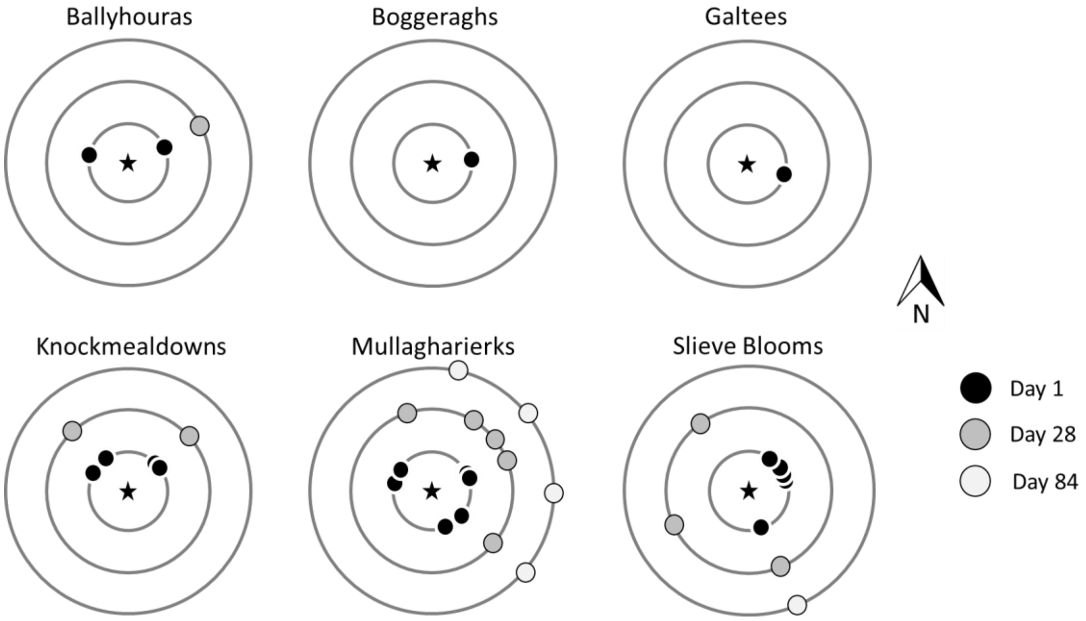

Figure 5. Orientation of direction of travel for each bird after one (inner circle), 28 (centre circle) and 84 days (outer circle) post-onset of dispersal in relation to their natal area across six breeding areas.

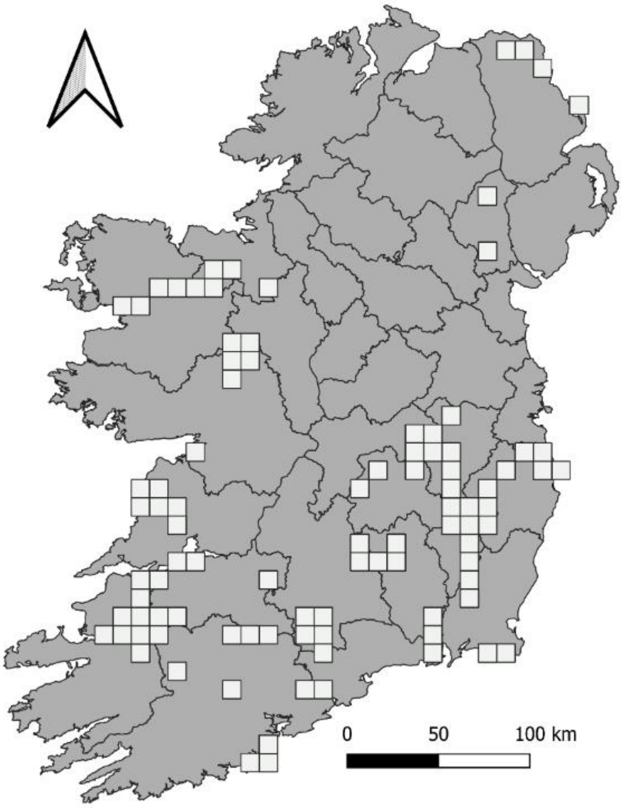

Figure 6. 10km squares used during juvenile dispersal by satellite tagged Hen Harriers in Ireland between 2009 and 2019 (i.e. the time between leaving the natal nest and the end of their first October). Only squares with class 3 locations are shown.

Survival

Survival analysis of the Irish tagged Hen Harriers showed that most mortality occurred in the first three months of life, with just 45.2 ± 8.9% of birds surviving beyond this stage. This decreased to 17.7 ± 7.5% at one year (first year daily mortality of 0.0047; Fig. 7). By contrast, survival of first order birds after one year was higher at 26.7 ± 11.4%. First year survival for females was 25.0 ± 10.6%. It was not possible to calculate overall first year survival for males due to PTT failures, however no males with functioning PTTs survived to their first year. Of the 28 birds whose tags remained functional during the study, just one survived to two years of age. This bird is still alive at the time of writing (9th March 2022, now 1,735 days old). Sex was the most important determinant of survival, with males having lower survival probability than females (-0.10 ± 0.31), followed by brood order, with lower orders having lower survival (-0.05 ± 0.12) and year (0.01 ± 0.03; Table 4). Of the birds that died during dispersal, five died of starvation, one died of trauma and ten had an unknown cause of mortality as carcasses were not recoverable or were too decomposed for post-mortem upon discovery (Table 2).

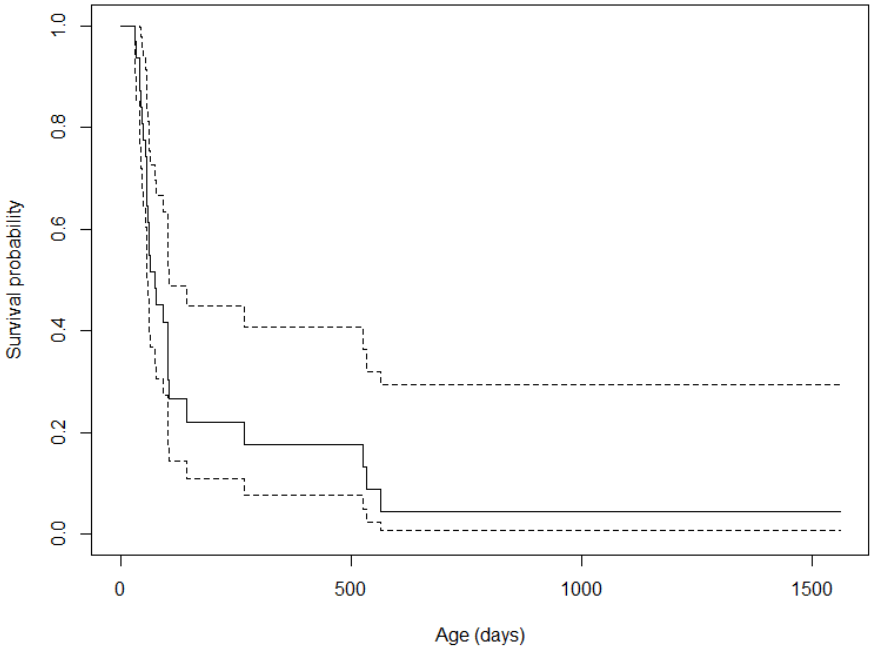

Figure 7. Survival curve of Irish satellite tagged Hen Harriers. Dashed lines show 95% confidence intervals.

Habitat use

There was a higher proportion of arable land around location fixes for juvenile Hen Harriers that survived dispersal (28.7 ± 2.0%) compared with those that died during dispersal (10.24 ± 1.30%; $p < 0.001$). Differences in the other three habitats were less pronounced (Fig. 8). The use of each habitat differed between sexes during the autumn and winter, with females using more arable (17.99 ± 1.25%; $p < 0.001$) and pasture areas (39.29 ± 1.60%; $p < 0.001$) compared with males who used more conifer forest (10.22 ± 1.17%; $p = 0.001$) and peat bog habitats (49.79 ± 2.56%; $p < 0.001$; Fig. 9). Female Hen Harriers in their first autumn used more arable (33.05 ± 2.57) and pasture habitats (42.47 ± 2.52) compared with their second autumn (17.03 ± 2.40%; $p < 0.001$; and 25.00 ± 2.64%, $p < 0.001$, respectively), at which time they used more peat bog habitats (10.52 ± 1.80% compared with 29.77 ± 2.91%; $p < 0.001$; Fig. 10). Habitat use also differed across seasons during the first year of life for Hen Harriers, with a peak in the use of arable areas occurring in autumn (18.44 ± 1.64%), and a peak in the use of peat bog (33.35 ± 2.05%) and conifer forest (22.02 ± 1.60%) in the spring (Fig. 11).

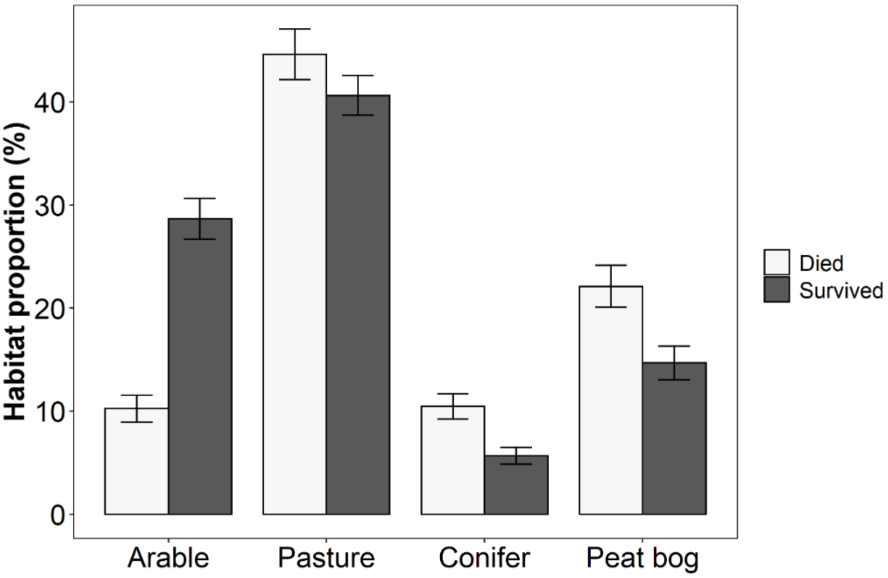

Figure 8. Mean (± SE) proportion of each main habitat within 400m of high-quality satellite tracking locations (n = 601) during juvenile dispersal (dispersal onset to end of first October), grouped by dispersal survival. This includes data from 19 Hen Harriers.

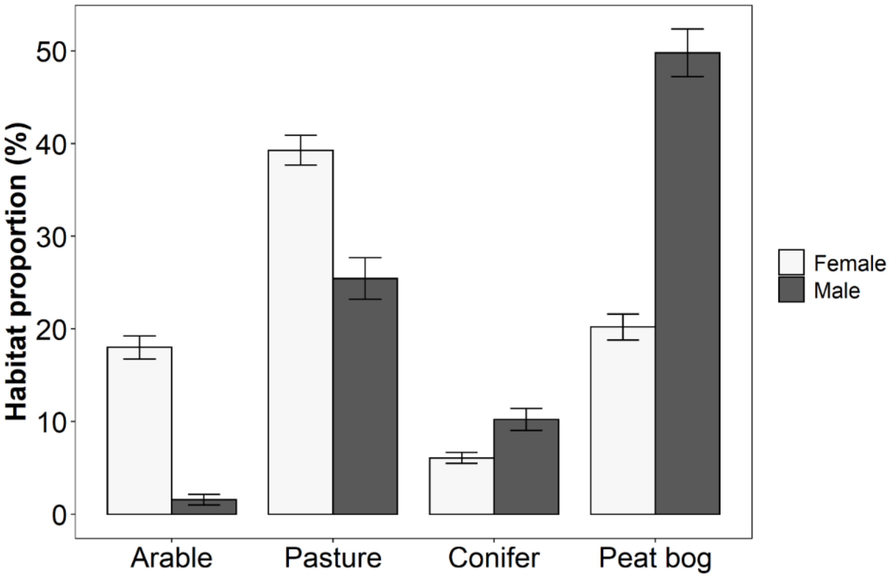

Figure 9. Mean (± SE) proportion of each main habitat within 400m of high-quality satellite tracking locations (n = 784) during first and second-year autumn and winter, grouped by sex. This includes data from 13 Hen Harriers.

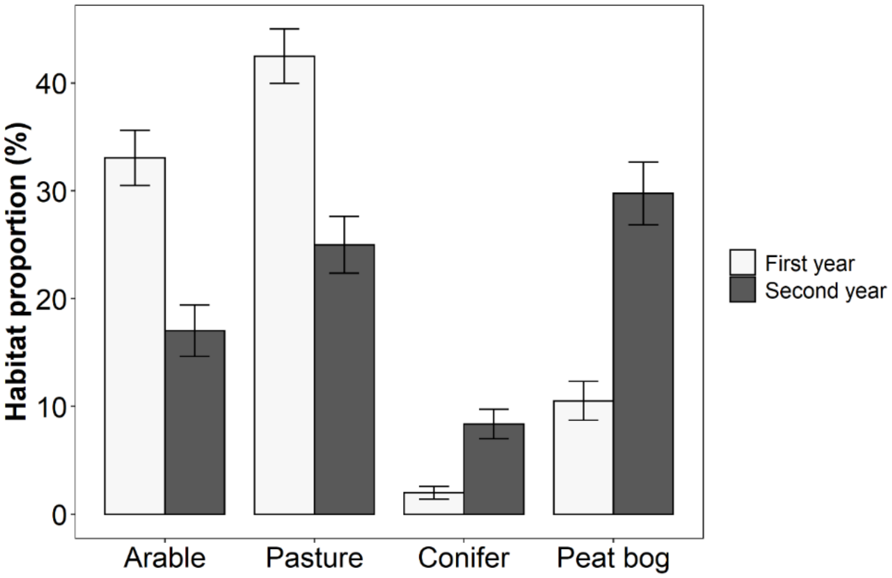

Figure 10. Mean (± SE) proportion of each main habitat within 400m of high-quality satellite tracking locations (n = 337), grouped by first and second-year autumn periods. This includes data from four female Hen Harriers.

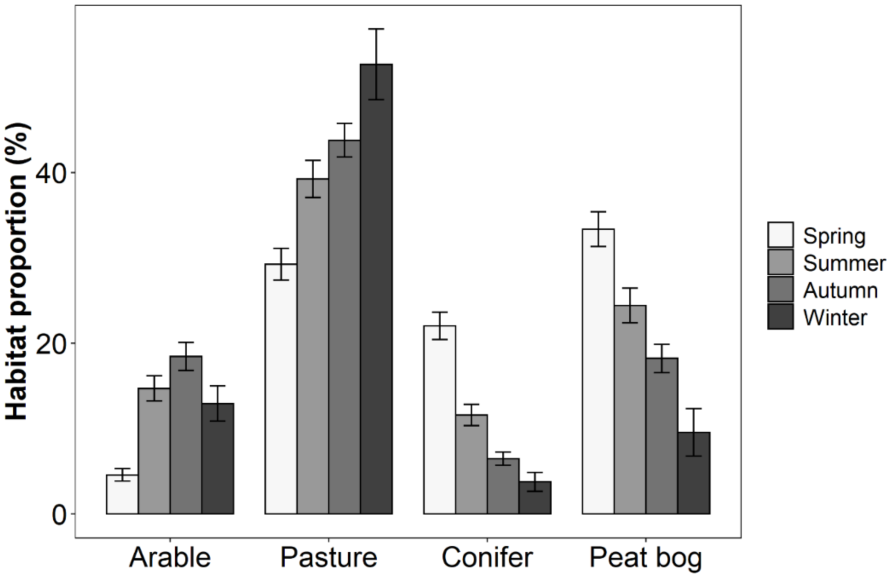

Figure 11. Mean (± SE) proportion of each main habitat within 400m of high-quality satellite tracking locations (n = 1,171), grouped by seasons within birds' first year. This includes data from 19 Hen Harriers.

Use of protected areas by Hen Harriers

The period with the lowest use of protected areas was juvenile dispersal, with only 14.8% of 2,541 location fixes from 21 birds during the juvenile dispersal period occurring in protected areas, while only 4.8% occurred within the Hen Harrier SPA network. Hen Harriers used protected areas more during the breeding season (mean of 34.1%) compared with the non-breeding season (mean of 22.6%), with this pattern also holding true for the use of the Hen Harrier SPA network (breeding season mean of 19.4% and non-breeding season mean of 3.7%; Table 5).

Table 5. Percentage of satellite tagged Hen Harrier locations (class 3, 2 and 1) that occurred within all protected areas and within the Hen Harrier SPA network (HH SPA) in the Republic of Ireland during this study. The number of satellite tagged Hen Harriers included in each timeframe along with the total number of location fixes within each time frame is also shown. Breeding season includes data from birds of breeding age only.

Timeframe	Birds	Fixes	% Protected (all)	% Protected (HH SPA)
Juvenile dispersal	21	2541	14.80	4.76
Non-breeding season	15	6725	22.62	3.74
Breeding season	6	4453	34.07	19.35

Natal dispersal and recruitment to the breeding population

Of the 28 birds whose fate is known, four (14.3%) survived to one year old (all four birds were female). Of these four birds, one bred in her first year (second calendar year), 17km south-west of her natal area, before dying at the end of her second calendar year. The other female that bred, who was the only Irish satellite tagged Hen Harrier in this study to survive beyond two years old, nested every year for three breeding seasons from her second year/third calendar year (2019-21). Her breeding sites were 109km, 14km and 9km from her natal area, respectively. This female’s breeding dispersal distances were 98km and 5km. Both of these females failed to successfully fledge young from their nesting attempts. The remaining two females that survived to breeding age did not breed in their first years, with both birds dying before reaching their second years.

Discussion

This study is the first to use satellite telemetry to provide insights into the movements of Hen Harriers in Ireland, on the western fringes of their range, to inform conservation measures for this vulnerable raptor species. It describes the characteristics of juvenile Hen Harrier dispersal, details low survival rates and causes of mortality of Hen Harriers, describes the habitat use of Hen Harriers across their lifecycle and highlights mismatches between designated protected areas and the areas used by Hen Harriers.

Juvenile dispersal

All Hen Harriers in this study undertook an initial sudden juvenile dispersal movement. For most juveniles, this was a long-distance movement (>25km; Etheridge and Summers 2006, Reid et al. 2011). For those birds that undertook an initial short-distance dispersal movement, poor condition at dispersal onset, reflected in their low survival, may have limited their dispersal abilities. Only one short-distance disperser survived to their first winter, with this bird undertaking a sudden long-distance movement five weeks after the initial short-distance movement. Birds that undertook sudden, long-distance dispersal tended to remain between 100km and 200km away from the natal area up to and during their first winter. This is similar to the juvenile dispersal distance of 175km reported for Hen Harriers in Scotland between the months of August and October of their first year, based on observations of wing tagged birds (Etheridge and Summers 2006).

The maximum juvenile dispersal distance recorded for an Irish tagged Hen Harrier in the current study was for a female who travelled 337km from her natal area. This is considerably shorter than the 1,047km maximum straight-line juvenile dispersal distance recorded for one male in a study of Hen Harriers in Scotland (Etheridge and Summers 2006). The shorter maximum dispersal distance of Irish tagged Hen Harriers reflects the fact that all birds remained in Ireland, with no outward migration. Dispersal outside of Ireland is a behaviour rarely recorded in the Irish Hen Harrier population. Movements of British-hatched Hen Harriers to Ireland, as demonstrated by the current study, may be more common (Mead 1973, Etheridge and Summers 2006). Male Hen Harriers demonstrated a similar dispersal distance to females in the current study, however it took longer for males to achieve this distance compared with females. This contrasts with previous research suggesting that males undertake a longer distance dispersal than females, thought to be driven by males taking advantage of distant lowland small bird prey bases (Clarke and Watson 1990, Etheridge and Summers 2006, Murphy 2019). However, male dispersal in the current study may have been limited by their condition and shorter survival than females, with no male satellite tagged Hen Harriers known to survive to their first winter.

Dispersal direction varied across breeding areas and appeared to be influenced by local geography and the proximity of the breeding area to the coast. For example, birds from south-western breeding areas travelled north-east away from the coast, whereas birds from the centre of Ireland dispersed in all directions. Landscape geography rather than any innate behaviour or prevailing wind direction has previously been suggested as the driver behind Hen Harrier dispersal direction (Etheridge and Summers 2006, Whitfield and Fielding 2009, O'Donoghue 2010), for which the current study provides further evidence. Although the timing of dispersal was similar across sexes and brood orders, the apparent difference across breeding areas may have been a consequence of limited sample size.

The sudden, long-distance dispersal strategy of Hen Harriers may be a response to poor availability of suitable prey in upland breeding areas outside of the summer months (Etheridge and Summers 2006). Juvenile Hen Harriers disperse to avail of the greater abundance of prey in distant lowland areas towards the end of summer and beginning of autumn (Clarke and Watson 1990, Etheridge and Summers 2006). Juveniles often established TSAs in prey-rich lowland habitats, such as arable areas (Wilson et al. 1996, Moorcroft et al. 2002, Vickery et al. 2009), during dispersal, occasionally making brief outward exploratory movements from their TSAs. Some birds also used their dispersal TSAs as their wintering grounds, while others moved to new areas for the winter. Stepped dispersal behaviour using TSAs may be the result of physiological constraints associated with being a medium-sized raptor (Moliner et al. 2015). Similar dispersal behaviour is seen in the closely related Northern Harrier in the United States where juveniles use TSAs during dispersal for days or weeks before exploring new areas (Beske 1982). If the availability of suitable TSAs, which Hen Harriers must travel long distances to find, is limited, this may compromise their survival probability.

Survival

Survival of juvenile Hen Harriers in this study (first year survival of 17.7 ± 7.5% for all birds, 26.7 ± 11.4% for first order birds) was comparable to, or lower than, previously reported Hen Harrier survival rates (Picozzi 1977, 1984, Whitfield and Fielding 2009, O'Donoghue 2010, Murgatroyd et al. 2019). Survival during the post-fledging independence period was 77.4% which is lower than reported for other harrier species (Kitowski 2002). Female Hen Harriers had higher survival rates (25.0 ± 10.6% first year survival) than males, with only females surviving past 6 months (5 of 28 birds, 17 of which were female) and recruiting to the breeding population in this study. This is lower than the 36.1% first year survival rate of females reported by Etheridge et al. (1997) for Hen Harriers in Scotland. A previous wing-tagging study in Ireland reported survival rates of Hen Harriers and found differential survival between sexes, with 34.4% first year survival reported for females and just 9.0% for males (O'Donoghue 2010). Similar differential survival between sexes has also been demonstrated for other Hen Harrier populations, with 29% of females surviving to one year old and just 7% of males surviving to two years old in Wales (Whitfield and Fielding 2009), while 29% of females compared with 14% of males survived to two years of age in a study in Orkney (Picozzi 1984). Differential survival between sexes may be due to different habitat use and prey capture capabilities, particularly during juvenile dispersal (Picozzi 1984). Indeed, differential habitat use between sexes was observed in this study and in Chapter 3 during the winter period. In addition, survival appeared to be lower for lower order birds. For Hen Harriers and other raptors, older, first hatched young may grow faster, have better body condition and outcompete younger siblings for food in the nest (Wiebe and Bortolotti 1994). First-hatched chicks may have further competitive advantage over their siblings once they fledge as they may be able to intercept prey deliveries from the adults.

The most common known cause of Hen Harrier mortality in this study was starvation, with most mortalities taking place soon after juvenile dispersal. This reflects the vulnerability of juveniles during the early days and weeks of independence due to their lack of hunting experience which may be exacerbated in landscapes with low abundance of suitable prey. Other causes of mortality recorded included a nine-month-old female who died towards the end of her first winter when she became trapped in twine that was being used as a pigeon/corvid deterrent on a wild bird cover crop. Another Hen Harrier was found dead close to a wind farm and had suffered wing and leg fractures, with traces of rodenticides found in its system. It was not possible to determine a definite cause of mortality, however collision with a wind turbine could not be ruled out. Although generally not considered a significant collision risk, there have been several cases of Hen Harriers being struck by wind turbines (Fernández-Bellon 2020). An 18-month-old female Hen Harrier who had attempted to breed in her first year, died on her wintering grounds in this study when she was predated by another raptor, most likely a Peregrine Falcon (*Falco peregrinus*). The mortalities recorded in the current study highlight the random nature of Hen Harrier mortalities and their vulnerability across their lifecycle. Given the small population, atypical mortalities such as these may have a disproportionate effect on the population, particularly when birds of breeding age are affected.

It is unlikely that the low observed survival rates of Hen Harriers in this study were the result of the PTTs or harnesses as the same methods are used elsewhere where birds do not experience the same natural mortality rates during the first few months of life (Murgatroyd et al. 2019). Post-mortems revealed no injuries to the birds caused by the harnesses, and the PTTs and harnesses always weighed less than the recommended 3% of the birds' body weight at tagging (Kenward 2001). Rather, we suggest poor quality habitat, particularly in the areas into which juveniles disperse, as the driving influence behind the low survival rates of juvenile Hen Harriers in Ireland.

Natal dispersal and recruitment to the breeding population

Limited information on natal dispersal was available from the current study as, of the four females that survived to breeding age (one year old), only two attempted to breed, one 17km from her natal site in her first year and the other 109km from her natal site in her second year. The results from these two female Hen Harriers demonstrate that, although individual Hen Harriers are commonly reported to nest within 20km of their natal area, individuals can sometimes breed in distant areas and different habitats to their natal site (Picozzi 1977, Etheridge et al. 1997, Whitfield and Fielding 2009, Aebischer 2019). The subsequent breeding dispersal movements of the female that first bred in her second year demonstrates the potential for individual Hen Harriers to use different breeding grounds and territories across years, and the lack of site fidelity of certain individuals. This breeding dispersal may have resulted from the failure of the previous nesting attempts (Newton 1979, Tapia and Zuberogoitia 2018).

Habitat use

The habitats used by Hen Harriers that survived juvenile dispersal were different to the habitats used by birds that died during dispersal. The main difference seen was in their use of arable habitats. Juvenile Hen Harriers that survived dispersal used arable areas three times as much as those that died during dispersal. Arable habitats are prey rich areas that host large flocks of small birds and small mammal prey in autumn and winter (Wilson et al. 1996, Moorcroft et al. 2002, Vickery et al. 2009), often in landscapes of sparsely distributed prey-rich foraging grounds. These habitats provide juvenile Hen Harriers with an opportunity to hone their hunting abilities before poorer winter weather conditions arrive. For juveniles that disperse into areas that lack such prey-rich habitats, foraging opportunities are more limited, making it more difficult to catch enough prey to survive. Furthermore, the loss of arable farmland through changes in agricultural practices, such as the conversion of arable land to dairy pasture, may have negative consequences for juvenile Hen Harriers and their survival probability. This suggests that conservation measures targeting the provision and maintenance of good quality habitats, such as arable farmland, could potentially play an important role in increasing juvenile survival rates.

During their first two autumns and winters, male Hen Harriers were found to rely more on peatland landscapes and less on arable landscapes, compared with females. Sex differences in autumn and winter habitat use have been reported previously, with some research suggesting that females remain in upland areas during the winter with males moving to lowlands to avail of small bird flocks (Picozzi 1984, Clarke and Watson 1990, Etheridge and Summers 2006, Murphy 2019). However, other studies have suggested that males mostly remain in upland areas during the winter (O'Donoghue 2010). As discussed in Chapter 3, the greater use of peatlands by males may be the result of differences in hunting capabilities, with males capable of catching more agile prey, such as snipe, due to their smaller size and increased agility, compared with females (Nieboer 1973, Schipper et al. 1975, Vincheuski 2019). In addition, competition on prime foraging grounds may also play a role, as females often outcompete males in prey-rich areas (Dobler 2021).

Autumn habitat use by juvenile Hen Harriers during their first year differed to autumn habitat use when they were in their second year. Juveniles in their first autumn used landscapes with more arable and pasture habitats compared with their second year, when they used landscapes with more peat bog and conifer forest. Age related differences in habitat use may be driven by factors including hunting experience and energy requirements (Newton 1979). Hen Harriers that use arable areas typically consume small birds and small mammals that are likely easier to catch compared with medium-sized birds, while Hen Harriers that use wetter peat bog habitats consume more medium-sized birds that may be more difficult to catch but more energetically cost-effective for experienced birds (Nieboer 1973, Schipper et al. 1975, Vincheuski 2019, Chapter 4).

Habitat use differed across the seasons for Hen Harriers in their first year, reflecting their annual movement patterns. In the late summer, autumn and through to winter, first year Hen Harriers in this study typically moved from their upland natal areas to lowland areas where they utilised arable and lowland cutover bog habitats. By the following spring and summer, first year Hen Harriers moved away from lowland arable and cutover bog habitats to upland breeding areas that, in Ireland, are often dominated by commercial conifer forest and peatland (Moran and Wilson-Parr 2015, Ruddock et al. 2016, Corkery et al. 2020). Non-breeding first year Hen Harriers in this study often remained in upland or lowland peatland habitats over the course of the summer. Therefore, although peatlands are used throughout the year, the type of peatland used differs over time.

Hen Harrier use of protected areas

The results of the current study considerably expand our knowledge of the use of protected areas by Hen Harriers and demonstrate that the current network of protected areas is insufficient for Hen Harrier conservation throughout their annual cycle. Currently, the only protected area designated specifically for Hen Harriers in Ireland is the Hen Harrier SPA network, which is based on their known breeding areas up to 2005, two years prior to SPA designation. Data from more recent national breeding surveys have shown that the majority of the Hen Harrier breeding population now occurs outside of this SPA network (53-56% of breeding pairs; Ruddock et al. 2016). The finding of the current study that Hen Harriers are afforded little protection during juvenile dispersal, one of the most challenging periods of their life cycle, highlights a further significant gap in current conservation measures. Low use of protected areas was also observed throughout both the breeding and non-breeding season in the current study. These findings point to the need for protection and conservation of important Hen Harrier areas not only in the breeding grounds, but also in dispersal areas and wintering grounds. Similar mismatches between the designation of protected areas and their subsequent use are seen in other harrier species, including Montagu's Harrier (*Circus pygargus*) in their African wintering grounds (Limiñana et al. 2012). In addition, for the two female Hen Harriers that were recruited to the breeding population, although both birds' natal areas were within the Hen Harrier SPA network, only two of their four breeding attempts were within the SPA network.

Despite being one of the most widely applied conservation strategies for Hen Harriers in Europe, the designation of conservation areas is not perceived to be a sufficient conservation approach (Fernández-Bellon et al. 2021). The current study confirms that the designation of SPAs for Hen Harriers does not confer sufficient protection to subsequent generations and provides further evidence of the urgent need for more effective conservation measures. The implementation of specific conservation measures is regarded as a more effective conservation strategy (Fernández-Bellon et al. 2021) and should be more widely applied to future conservation strategies.

Conservation implications

The new information presented here on Hen Harrier ecology across the full annual cycle will inform future conservation planning. Hen Harrier conservation measures in Ireland to date have focussed on the pressures they face during the breeding season, particularly in the Hen Harrier SPA network where a European Innovation Partnership (EIP) is currently working to improve habitat quality and increase breeding success (Hen Harrier Project 2021). No conservation efforts have targeted the juvenile dispersal or over-wintering areas of Hen Harriers. High mortality rates during juvenile dispersal demonstrate a clear need for conservation actions aimed at increasing survival during this period. Due to the long-distance and variable juvenile dispersal movements, conservation measures targeting increased juvenile survival rates should involve landscape-scale measures. This could include initiatives such as upscaling agri-environmental schemes and/or the development of new EIPs. Landscape scale habitat suitability modelling may aid in the selection of these areas by identifying gaps in suitable habitat that may compromise the survival of dispersing juvenile Hen Harriers (Balbontín 2005). Given that 22.6% of juveniles died before dispersing, there is additional need to improve habitat quality around nest sites during the breeding season to enhance survival to the point of dispersal, and possibly scope to explore additional conservation measures such as supplementary feeding.

The timing of the onset of dispersal has important implications for upland management practices that aim to enhance Hen Harrier protection. Our results indicate that forestry operations, and other land management activities, within potential disturbance distance of Hen Harrier territories should not take place before the end of August to prevent negative impacts on young Hen Harriers prior to dispersal.

The variability of natal dispersal demonstrated by two Hen Harriers in the current study highlights oversights in the current approach to the designation of protected areas. We show that Hen Harriers originating from the SPA network do not necessarily return to the SPA network to breed. Agricultural and forestry conservation measures similar to those implemented within the SPA network therefore need to be used in breeding areas that are outside of the current SPA network as non-SPA breeding areas may act as population sinks. Further, the mismatch between areas protected for Hen Harriers and areas that they were seen to use, particularly during the juvenile dispersal and winter period, highlights the need to either expand and more frequently review the designation of protected areas, and/or apply existing and new conservation measures to these areas.

Ethics statement

Nest monitoring, nest visits, ringing and satellite tagging were carried out by trained professionals under licence from the National Parks and Wildlife Service, Northern Irish Environment Agency, and the British Trust for Ornithology. Health Products Regulatory Authority (HPRA) licence was not required for this study.

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Chapter Three

Landscape and temporal influences on the size and composition of Hen Harrier winter roosts in Ireland

Hen Harrier winter roost

Photograph: Michael O'Clery

Abstract

Winter roosts represent an important focal point of Hen Harrier (*Circus cyaneus*) distribution and behaviour during the non-breeding season. The breeding biology and breeding season conservation requirements of Hen Harriers have been the focus of much previous research, but little is known about their non-breeding ecology, particularly their winter roosting requirements, which is an essential aspect of their year-round conservation. The purpose of this study was to examine the impact of surrounding habitat on the number of Hen Harriers using roosts (size) and the ratio of adult males to adult females and juveniles (composition) at winter roosts in Ireland. We also examined short and long-term temporal trends in roost size and composition and described the protected status of lands used for roosting and foraging by Hen Harriers in winter. We undertook Hen Harrier winter roost surveys across the winters of 2019/20 and 2020/21, completing 413 roost watches at 56 roosts. Our results showed the importance of surrounding habitat as a factor influencing the size and composition of Hen Harrier winter roosts, with adult male dominated roosts occurring in upland and peatland areas, while ringtail (juveniles of less than one year old and adult females) dominated roosts occurred in lowland and wetland, scrub, and arable areas. We also demonstrated temporal variation in the number of Hen Harriers attending roosts and the long-term temporal stability of roost composition. We found that 53% of roosts occurred in areas with statutory protection, however only 9% of roosts occurred within the European Natura 2000 Hen Harrier Special Protection Area (SPA) Network. Foraging grounds around winter roosts may be particularly vulnerable to anthropogenic land-use change due to lack of protection. Our results demonstrate that the current network of protected areas does not provide adequate protection for wintering Hen Harriers in Ireland.

Introduction

Wintering ecology is a critical yet poorly understood period of the annual cycle of many raptors (Newton 1979, Sarasola et al. 2018). Until recently, research and conservation efforts for raptors were focussed on the breeding season due to its clear importance in population dynamics and relative ease of study (Newton 1979, Sarasola et al. 2018). This is the case for the Annex I listed Hen Harrier (*Circus cyaneus*) where research priorities have been set in response to declining populations and a growing need for information to support conservation priorities in areas that are experiencing ever-increasing anthropogenic land-use changes and associated pressures (Caravaggi et al. 2019, Fernández-Bellon et al. 2021). These breeding season pressures include afforestation of upland habitats (Wilson et al. 2009, 2012, Caravaggi et al. 2019, 2020, Sheridan et al. 2020), wind-energy development (Fernández-Bellon et al. 2015, Wilson et al. 2017, Fernández-Bellon 2020), climate change (Caravaggi et al. 2019), persecution (Etheridge et al. 1997, Murgatroyd et al. 2019), and other anthropogenic impacts (Caravaggi et al. 2020). Conservation strategies aimed at facilitating population recovery, including the designation of Special Protection Areas (SPAs), have been implemented in core breeding ranges (Fernández-Bellon et al. 2021), informed by relevant breeding season research.

In contrast to the breeding season, the winter ecology of the Hen Harrier is much less well understood. Despite advances in our knowledge of roost locations (Clarke and Watson 1990, O'Donoghue 2021) and fine-scale roost characteristics (Watson and Dickson 1972, Picozzi and Cuthbert 1982), there remains a considerable knowledge gap regarding the factors that influence the number of Hen Harriers using roosts (hereafter referred to as size), the ratio of adult males to adult females and juveniles at roosts (hereafter referred to as composition), and the potential vulnerability of roosts and surrounding foraging areas to anthropogenic land-use change. Hen Harrier winter roosts are afforded no legal protection from human disturbance, unlike their nest sites and the nest sites of all other wild birds in Ireland which are protected under the Wildlife Act 1976. Some Hen Harrier roosts occur on lands within the breeding Hen Harrier SPA network and lands that are protected for other species or habitats (O'Donoghue 2021). However, the extent of foraging areas surrounding winter roosts that are protected is unknown. An understanding of these factors is central to the conservation of wintering Hen Harrier populations. It is also important to understand the potential links and possible carryover effects that might occur between wintering sites and breeding sites.

Hen Harriers use winter roosts between late September and March, with peak numbers of birds typically occurring at roosts in mid-winter (Watson 1977, Picozzi and Cuthbert 1982, Clarke and Watson 1990, Noga 2013). Some winter roosts are also used during the breeding season as nest sites (O'Donoghue 2021). Hen Harrier winter roosts occur in a range of habitats, including reedbed, bog, salt marsh, scrub, crops, and young planted conifer forest, and can be solitary or communal, and regularly or irregularly used (Clarke and Watson 1990, Noga 2013, O'Donoghue 2021). Most are solely used by Hen Harriers for roosting, though some roosts can also host other birds of prey including Short-eared Owls (*Asio flammeus*), Marsh Harriers (*Circus aeruginosus*) and Merlins (*Falco columbarius*) (Watson and Dickson 1972, Watson 1977, O'Donoghue 2010, Noga 2013). Hen Harriers roost on the ground in flattened areas of vegetation up to one square metre in size (roost beds), typically in tall, dense vegetation and often in areas where the ground is saturated or where there is standing water under the roost bed (Watson and Dickson 1972, Picozzi and Cuthbert 1982). Occasional use of trees for roosting has also been reported (Scott 1994, Bělka and Bělková 2019). Roost beds on the ground may be naturally flattened areas of vegetation, or flattened areas created by the birds themselves, or the tracks of other animals (Watson 1977, Noga 2013), and are typically surrounded by taller vegetation that provides shelter from wind and rain (Watson and Dickson 1972). Roost beds can be used for several nights, either by the same or different birds, as evidenced by the collection of multiple pellets at some roost beds (O'Donoghue 2010, Noga 2013, Chapter 4). However, moving between roost beds likely reduces the risk of predation (Picozzi and Cuthbert 1982). Communal roosting is a widespread and well documented behaviour of many bird species. For harriers (*Circus* spp.), communal roosting likely takes place for a combination of reasons (Picozzi and Cuthbert 1982), including protection against predators (Watson and Dickson 1972, Watson 1977, Kitowski 2005), information transfer regarding daytime foraging areas (Ward and Zahavi 1973, Watson 1977, Kitowski 2005) and pair bonding (Gurr 1968). Regardless of the drivers of roosting behaviours, it is clear that Hen Harrier winter roosts are central points of safety and resting in proximity to suitable winter foraging grounds (Watson 1977, Picozzi and Cuthbert 1982).

Within their Western Europe range, geographic differences are apparent in the winter distribution of adult male Hen Harriers compared with juveniles of less than one year old or adult females (hereafter referred to as ringtails), both of which share similar plumage. In Great Britain, adult males are typically found in the south-west in winter, whereas ringtails typically remain in upland and northern areas (Marquiss 1980, Picozzi and Cuthbert 1982, Clarke and Watson 1990, Murphy 2019). O'Donoghue (2010) observed a similar geographic cline in Ireland whereby adult males occurred most often in western regions, compared with ringtails in the south and east. Several factors may be responsible for the observed variation in distribution, such as differences in hunting agility between sexes that may lead to diet separation (Nieboer 1973, Schipper et al. 1975, Marquiss 1980, Vincheuski 2019), as well as competition, with adult females displacing adult males from prey-rich winter foraging grounds (Dobler 2021). No research has investigated the impact of surrounding habitat on the composition of Hen Harrier winter roosts.

In this study, we explore the characteristics of Hen Harrier winter roosts across Ireland. We describe the influence of habitat and region on the size and composition of Hen Harrier roosts and investigate temporal variation in roost size. We also examine the protection status of lands where Hen Harrier winter roosts are located and the protection status of the surrounding landscapes.

Methodology

Study area

Hen Harrier winter roosts (hereafter referred to as 'roosts') in this study are defined as discrete areas of land where Hen Harriers roost on the ground at night, either singularly or communally, between the months of October and March, inclusive. We identified Hen Harrier roost locations across Ireland by contacting local birdwatchers, researchers, National Parks and Wildlife Service conservation rangers, and through examination of Environmental Impact Statements conducted for wind energy and other developments. We also identified roost locations by examining Hen Harrier satellite tracking data collected for Chapter 2. Roosts were grouped by region based on altitude above sea level (ASL) (Perrin et al. 2014) and proximity to the coast. The three regions were: (i) lowland coastal roosts (<150m ASL; home range overlapped with coastline); (ii) lowland inland roosts (< 150m ASL; home range did not overlap with coastline); and (iii) upland roosts (> 150m ASL; home range did not overlap with coastline).

Roost watches

Roost watches were conducted at each roost, where possible, once per month between October and March, inclusive, during the winters of 2019/20 and 2020/21. Roost watches were conducted from distant vantage points located at least 250m from the roost and commenced at least 30 minutes before sunset and lasted until the fieldworker could no longer effectively observe the roost due to fading light. Roost watches were not conducted in persistent rain or heavy fog. A minimum of two weeks separated roost watches at individual roosts. Our capacity to conduct monthly roost watches over both winters at each roost was determined by fieldworker availability, travel time to roosts and weather conditions.

During each roost watch, for all Hen Harriers observed, we recorded whether it was an adult male or a ringtail. It was not possible to identify with certainty the age and sex of every ringtail that was observed. In addition, we noted sighting time, direction of arrival to the roost, behaviour, settling time to roost, settling habitat, and settling location. We also noted the number and species of any other raptors that were observed during the roost watch. Finally, we determined the main habitat type of the roost and grouped them according to Chapter 4 and O'Donoghue (2021) (heath/bog, reedbed, scrub, saltmarsh, conifer forest and grassland/fen).

Long-term trends

We obtained roost watch data collected in the years prior to the current study, between 2007/08 and 2018/19, from observers of three roosts. One of these, an upland roost, is the largest known communal Hen Harrier roost in Ireland. The other two roosts are lowland coastal communal roosts. These data were collected using the same methods as the current survey, however the timing between watches varied as it was not possible to conduct watches at all roosts every month, while more than one watch was conducted per month at some roosts on some occasions.

Priority mapping

We identified priority wintering areas for the implementation of Hen Harrier conservation measures. We defined four categories: (i) high priority roosts (communal roosts); (ii) medium priority roosts (those that held one Hen Harrier on a minimum of one occasion); (iii) low priority (prior knowledge of roost use by Hen Harriers though none were observed during roost watches); and (iv) insufficient data (roost present, but no data on its use by Hen Harriers). We selected the high and medium priority roosts (i.e. those where Hen Harriers were observed during roost watches) and created two buffers around each roost, one equal to the mean Hen Harrier home range radius (5.40km; Chapter 4, Appendix 1) and one equal to the maximum foraging distance (12.35km; Chapter 4, Appendix 1). Then, using a 10km square grid, we identified those squares that included land covered by the mean and maximum home range buffers.

Protection status

We assessed the protection status of the land on which each roost was located by mapping roost locations over the four categories of conservation areas in Ireland (NPWS 2022). These were proposed Natural Heritage Areas (pNHA), Natural Heritage Areas (NHA), Special Areas of Conservation (SAC) and Special Protection Areas (SPAs). We also calculated the proportion of protected areas within the mean home range of 25 roosts that were included in the habitat and region models (details below).

Data analysis

We explored the influence of surrounding habitat on the size and composition of roosts using data from the 25 roosts where watches were conducted in 11 months of the two-winter survey (October 2019 excluded) (Fig. 1). This gave a total of 275 roost watches. This subset of data ensured that each roost included in these models had equal survey effort and the maximum number of monthly watches. We calculated the area of 15 habitat categories within the mean home range of each of these roosts (91.75km^2; Chapter 2). We used CORINE 2018 land cover as the base spatial layer (European Environment Agency 2018), supplemented by forest cover data provided by Coillte and the Forest Service. We subdivided the forest cover data into conifer (>50% cover of conifer species) and deciduous (>50% cover of deciduous species), with conifer further subdivided based on time in years since planting: early (0 to 2 years post-planting); young (3 to 12 years post-planting); and closed canopy (13+ years post planting; Wilson et al. 2009, 2012). Bord Na Móna, the semi-state body that owns large areas of cutover raised bog habitats in Ireland, provided detailed habitat data for land on their properties. We also included data from the Green Low-carbon Agri-environment Scheme (hereafter referred to as GLAS) provided by the Department of Agriculture, Food and the Marine (DAFM). The GLAS measures used were wild bird cover, Hen Harrier measures, and Grey Partridge (*Perdix perdix*) measures. We obtained an index of scrub and hedgerow cover from the Copernicus Small Woody Features layer (European Environment Agency 2015). We clipped each spatial data layer to ensure there were no overlapping layers. A full description of the spatial data used in this study is provided in Table 1.

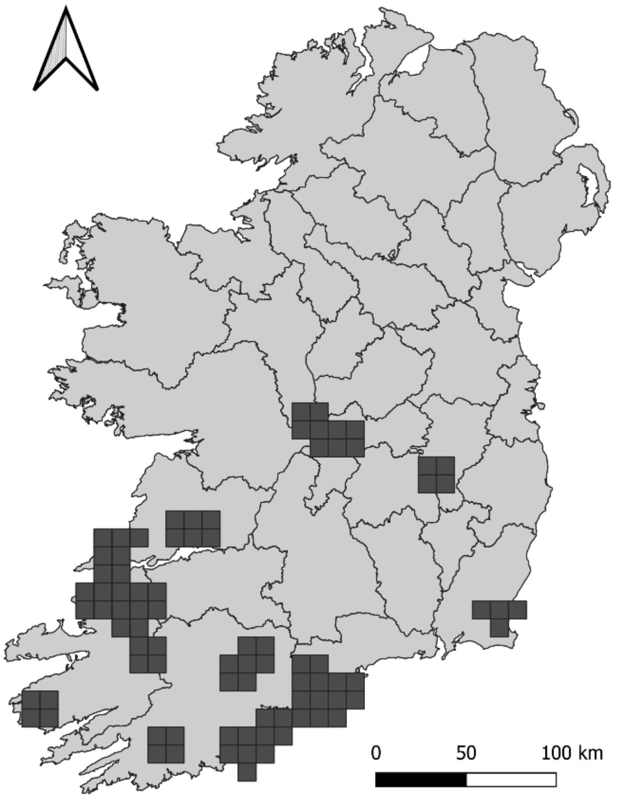

Figure 1. 10km squares that included the home ranges of Hen Harrier roosts used in the habitat models.

Table 1. Habitat variables included in models.

Variable	Manipulation	Source
Arable	Composite data	CORINE (2.1.1. Non-irrigated arable land; 2.4.2. Complex cultivation patterns), DAFM (Grey Partridge GLAS measures)
Bare peat	Raw data	Bord Na Móna (gravel subsoil, bare peat)
Bog	Composite data	CORINE (4.1.2. Peat bogs; 3.2.2. Moors and heathland), Bord Na Móna (bog, cutover bog, heath, heath & scrub, pioneer open cutaway habitats)
Broadleaf	Raw data	Coillte, Forest Service, CORINE (3.1.1. Broad-leaved forest; 3.1.3. Mixed forest)
Built areas	Composite data	CORINE (1.1.1. Continuous urban fabric; 1.1.2. Discontinuous urban fabric; 1.2.1. Industrial or commercial units; 1.2.2. Road and rail networks and associated land; 1.2.3. Port areas; 1.3.2. Mineral extraction sites; 1.4.2. Sport and leisure facilities), Bord Na Móna (built)
Coastal	Raw data	CORINE (3.3.1. Beaches, dunes, sands; 4.2.3. Intertidal flats; 5.2.1. Coastal lagoons; 5.2.2. Estuaries; 5.2.3. Sea and ocean)
Early forest	Composite data	Coillte, Forest Service
Closed-canopy forest	Composite data	Coillte, Forest Service, Bord Na Móna
Low intensity agriculture	Composite data	CORINE (2.4.3. Land principally occupied by agriculture, with significant areas of natural vegetation; 3.2.1. Natural grasslands)
Pasture	Composite data	CORINE (2.3.1. Pasture), Bord Na Móna (grassland or agriculture)
Young forest		Coillte, Forest Service
Scrub & hedgerows	Raw data	Copernicus (Small woody features- Linear structures of trees, hedges, bushes, and scrub; patchy structures of trees, hedges, bushes, and scrub), DAFM (Hen Harrier GLAS measure), Bord Na Móna (scrub & grassland, scrub & pioneer open cutaway habitats, scrub)
Water bodies	Composite data	CORINE (5.1.1. Water courses; 5.1.2. Water bodies), Bord Na Móna (open water)
Wild bird cover	Raw data	DAFM (Wild bird cover GLAS measure, Hen Harrier GLAS measure, Grey Partridge Glas measure)
Wetlands	Composite data	CORINE (4.1.1. Inland marshes; 4.2.1. Salt marshes), Bord Na Móna (fen; riparian; temporary flooded areas; wetlands; wetlands & scrub)

We applied a Principal Component Analysis (PCA) to the 15 habitat variables. All variables were standardised, with $\overline{x} = 0$ and $\sigma = 1$. We constructed three models to examine the influence of habitat on the size and composition of roosts. The first model was a general linear mixed effects model (GLMM) with a Poisson family. The response variable was set as the number of Hen Harriers recorded during each roost watch with a Poisson family distribution. Habitat Principal Components (PCs) were set as fixed effects, with a combined year/month variable, roost, and fieldworker name included as random effects. The other two models were zero-inflated negative binomial linear mixed effects models with the response variable set as: (i) a binary variable of whether more adult males (coded as 1) were recorded during the roost watch than ringtails, or not (coded as 0); and (ii) a binary variable of whether more ringtails (coded as 1) were recorded during the roost watch than adult males, or not (coded as 0). We used the same fixed and random effects as above. We assessed the Variance Inflation Factors (VIF) of fixed effects in each model to ensure there was no collinearity between fixed effects (VIF <10; Quinn and Keogh 2002). For each model, we tested for spatial autocorrelation between model residuals by calculating Moran's *I* statistic based on residual distances.

We used GLMMs with the same model structure as above to compare the numbers of Hen Harriers using roosts across regions. However, in this case, we instead set region as the fixed effect. For the adult male model, it was only possible to include roost and fieldworker name as random effects due to non-convergence of the model with year/month included as a random effect.

When examining temporal variation in the number of Hen Harriers using roosts, we only included roosts where watches were conducted during each of the 12 months of the two-winter survey (n=20) to ensure that each roost had equal survey effort across both years and data for every month of the winter period. For this, we used a GLMM with a Poisson distribution. The number of Hen Harriers using the roost was set as the response variable, with month, winter and the interaction between month and winter set as the fixed effects. We included roost and fieldworker name as random effects.

When examining settling times of birds to roost, we included data from all roost watches conducted at all roosts across both winters. We compared settling times of adult males with females using an unpaired two-sample Wilcoxon test. Results are presented as mean (x̄) ± standard error (SE), unless otherwise stated. Data were processed and analysed using QGIS version 3.12.3 (QGIS.org 2021) and R version 4.0.2 (R Core Team 2020) including packages *ggplot2* (Wickham 2016), *lme4* (Bates et al. 2015), *glmmTMB* (Brooks et al. 2017), *DHARMa* (Hartig 2020), and *factoextra* (Kassambara and Mundt 2020).

Results

Hen Harrier roost survey

We identified 101 Hen Harrier roosts across Ireland and conducted 413 roost watches at 56 of these roosts where we had sufficient fieldworker availability (Fig. 2). The mean number of Hen Harriers recorded during roost watches was 1.36 ± 0.12 (0.74 ± 0.06 ringtails per roost watch and 0.65 ± 0.07 adult males per roost watch).

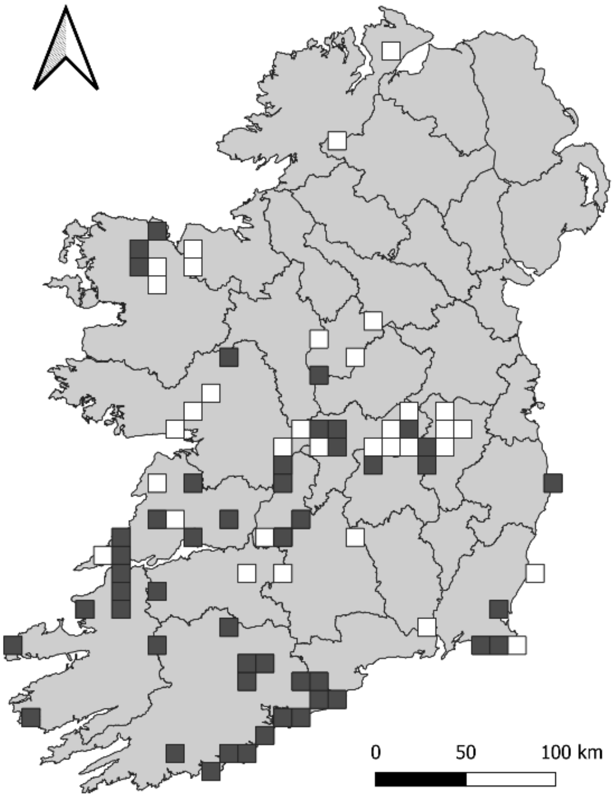

Figure 2. 10km squares where the 101 Hen Harrier roosts identified during this study were located. Squares containing the 56 roosts that were surveyed are shown in dark grey, squares containing only those identified but not surveyed are shown in white.

The highest count of Hen Harriers using a roost on a single occasion was 18. Twenty-eight of the 56 roosts (50%) that were surveyed were communal. Fifty priority roosts were identified, from which 150 10km squares were highlighted as priority wintering areas for Hen Harriers in Ireland when accounting for mean home range, with 302 10km squares covered by maximum home range (Fig. 3).

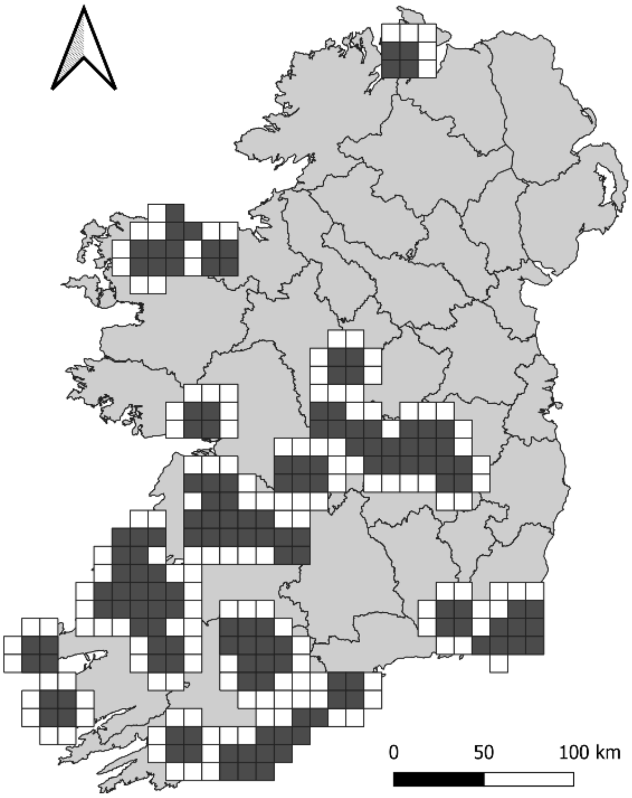

Figure 3. Priority 10km squares in Ireland, based on mean home range (dark grey) and maximum home range (dark grey and white) around high and medium priority Hen Harrier roosts.

The median settling time at roosts was 4.4 minutes after sunset. Ringtails (median of 2.0 minutes after sunset) settled to roost before adult males (median of 7.0 minutes after sunset, $p = 0.03$).

We recorded ten other raptor species during roost watches. The most commonly recorded raptor was Buzzard (*Buteo buteo*; observed during 53 of 413 roost watches), followed by Kestrel (*Falco tinnunculus*; 41 watches), Sparrowhawk

(*Accipiter nisus*; 21 watches), Merlin (18 watches), Peregrine Falcon (*Falco peregrinus*; 12 watches), Short-eared Owl (11 watches) and Marsh Harrier (7 watches), with Long-eared Owl (*Asio otus*), Northern Harrier (*Circus hudsonius*) and White-tailed Eagle (*Haliaeetus albicilla*) each observed during one roost watch.

The habitat of the winter roosts surveyed included heath/bog (37.5% of roosts), reedbed (32.1%), scrub (14.3%), saltmarsh (7.1%), conifer forest (5.3%) and grassland/fen (3.6%).

Influence of habitat on roost attendance

We retained three PCs, which together accounted for 66.7% of variation in landscape scale habitat around winter roosts, in the habitat models (Table 2). The overall number of Hen Harriers at winter roosts was positively associated with PC1 (0.37 ± 0.15, $p = 0.01$) and PC2 (0.37 ± 0.18, $p = 0.04$). Roosts that held more adult males than ringtails were positively associated with PC1 (0.42 ± 0.14, $p = 0.002$). Roosts that held more ringtails than adult males were positively associated with PC2 (0.39 ± 0.14, $p = 0.005$) and negatively associated with PC3 (-0.39 ± 0.17, $p = 0.03$; Table 3). Upland roosts were positively associated with PC1 and negatively associated with PC2, lowland coastal roosts were negatively associated with PC1, while lowland inland roosts were positively associated with PC2 (Fig. 4).

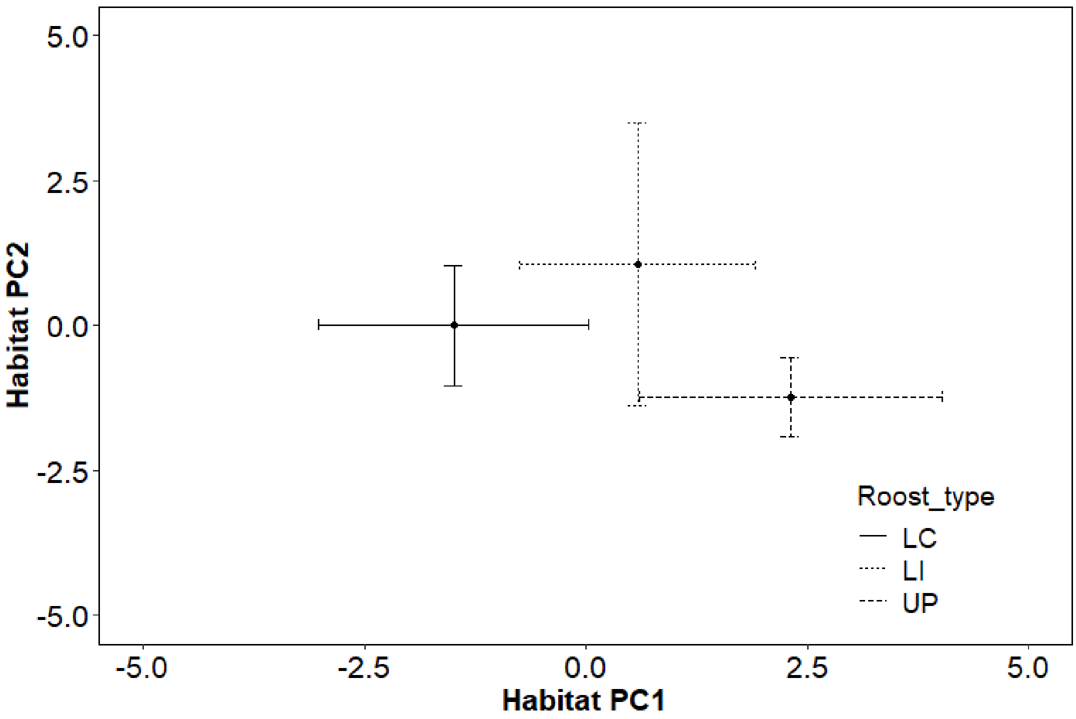

Figure 4. Principal Component (PC) score (±SD) biplot for landscape-scale habitat. LC- lowland coastal; LI- lowland inland; UP- upland.

Table 2. Principal Component (PC) axes loadings capturing habitat variation around Hen Harrier winter roosts. Values in **bold** show the habitat variables that most describe each PC.

Habitat variable	Principal Components (variation explained) PC1 (32.98%)	PC2 (20.53%)	PC3 (13.17%)
Arable	**-0.686**	-0.193	0.405
Bare peat	0.199	**0.787**	0.099
Bog	**0.711**	0.266	-0.227
Broadleaf	-0.090	0.024	**0.760**
Built areas	-0.506	0.265	0.293
Coastal	**-0.787**	-0.120	-0.246
Early forest	**0.755**	**-0.497**	0.287
Closed-canopy forest	**0.830**	**-0.394**	0.274
Low-intensity agriculture	0.485	-0.003	-0.396
Pasture	-0.487	-0.259	**-0.575**
Young forest	**0.862**	-0.342	0.220
Scrub & hedgerows	0.247	**0.623**	0.278
Water bodies	0.291	**0.804**	-0.069
Wild bird cover	**-0.646**	0.051	0.501
Wetlands	0.103	**0.801**	-0.040

Table 3. Full model outputs for habitat (a-c), region (d-f) and temporal (g) models. n = number of roost watches. Statistically significant results are shown in **bold**. Intercept values for region and temporal models include the first level of these categorical variables (lowland coastal roosts, October, and 2019/20, respectively).

Model	n	Fixed effects	β ± SE	P
(a) All x habitat	275	Intercept	-0.81 ± 0.36	**0.03**
		PC1	0.37 ± 0.15	**0.01**
		PC2	0.37 ± 0.18	**0.04**
		PC3	-0.44 ± 0.24	0.07
(b) More adult males x habitat	275	Intercept	-2.62 ± 0.39	**< 0.001**
		PC1	0.42 ± 0.14	**0.002**
		PC2	0.10 ± 0.15	0.49
		PC3	-0.03 ± 0.23	0.89
(c) More ringtails x habitat	275	Intercept	-1.95 ± 0.28	**< 0.001**
		PC1	-0.15 ± 0.13	0.24
		PC2	0.39 ± 0.14	**0.005**
		PC3	-0.39 ± 0.17	**0.03**
(d) All x region	275	Intercept	-1.11 ± 0.61	0.07
		Lowland inland roosts	0.40 ± 0.97	0.68
		Upland roosts	0.67 ± 1.02	0.51
(e) More adult males x region	275	Intercept	-3.57 ± 0.60	**< 0.001**
		Lowland inland roosts	1.39 ± 0.73	0.06
		Upland roosts	2.30 ± 0.72	**0.001**
(f) More ringtails x region	275	Intercept	-1.56 ± 0.37	**< 0.001**
		Lowland inland roosts	-0.09 ± 0.57	0.87
		Upland roosts	-1.24 ± 0.70	0.07
(g) All x time	240	Intercept	-1.55 ± 0.58	**0.007**
		November	0.70 ± 0.29	**0.02**
		December	0.62 ± 0.30	**0.04**
		January	0.73 ± 0.29	**0.01**
		February	0.40 ± 0.33	0.22
		March	0.27 ± 0.33	0.4
		2020/21	0.62 ± 0.33	0.06
		November:2020/21	-0.16 ± 0.36	0.66
		December:2020/21	-0.09 ± 0.38	0.82
		January:2020/21	-0.63 ± 0.38	0.1
		February:2020/21	-0.39 ± 0.44	0.37
		March:2020/21	-0.97 ± 0.45	**0.03**

Influence of region on roost attendance

Roost attendance by Hen Harriers differed across regions. For all Hen Harriers combined, mean roost size counts were highest in upland regions (2.80 ± 0.48), followed by lowland inland (1.45 ± 0.23) and lowland coastal regions (1.14 ± 0.17).

The mean attendance of adult males at roosts was highest in upland regions (1.89 ± 0.33), and lowest in lowland coastal regions (0.33 ± 0.08). For ringtails, mean attendance at roosts was similar across upland (0.95 ± 0.20), lowland inland (0.84 ± 0.15) and lowland coastal regions (0.83 ± 0.12; Fig. 5). Upland regions (2.30 ± 0.72, p = 0.001) had more male dominated roosts with the same pattern persisting for lowland inland regions, albeit non-significantly (1.39 ± 0.73, p = 0.06), compared with lowland coastal regions. For ringtails, the difference between lowland coastal regions and upland regions approached significance, whereby roosts in lowland coastal regions had a higher likelihood of being dominated by ringtails (1.24 ± 0.70, p = 0.07; Table 3).

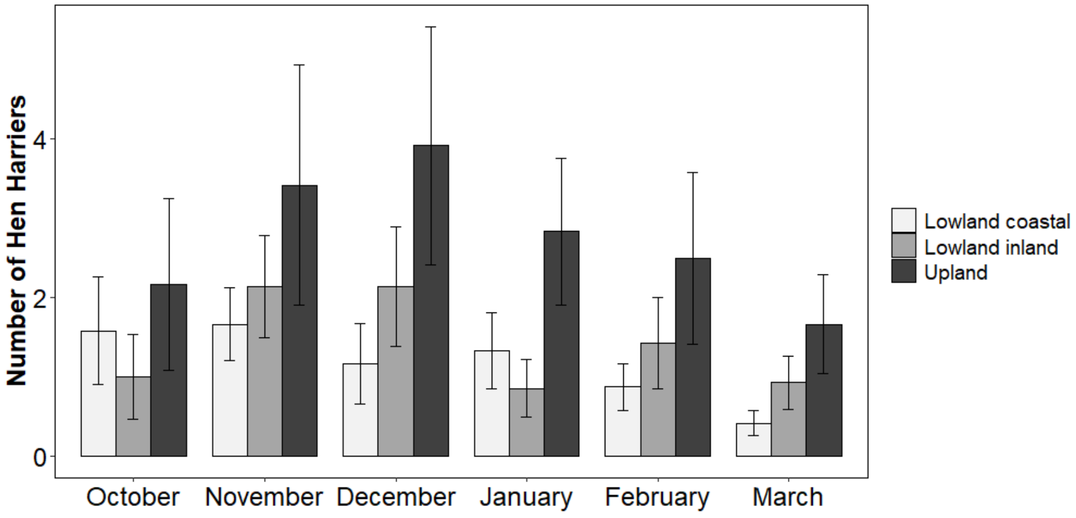

Figure 5. Mean (± SE) number of Hen Harriers recorded during monthly roost watches across regions. Data shown here are from the 25 roosts where watches were conducted in 11 months of the two-winter survey (October 2019 excluded).

Temporal variation in roost attendance

The numbers of Hen Harriers using roosts varied across months and between years (Fig. 6). For all Hen Harriers, peak counts at roosts typically occurred in November (2.28 ± 0.54 Hen Harriers per watch), with the lowest counts typically recorded in March (0.98 ± 0.24). Mean roost attendance was significantly higher in November (0.70 ± 0.29, p = 0.02), December (0.62 ± 0.30, p = 0.04) and January (0.73 ± 0.29, p = 0.01) compared with the beginning of the winter period in October. The highest number of Hen Harriers (n=18) recorded during one roost watch was at an upland roost in November 2020. Differences between winters were also observed, with mean roost attendance in the second winter (1.89 ± 0.29) being higher than the first winter (1.44 ± 0.19; Table 3), although the observed difference was not statistically significant (0.62 ± 0.33; p = 0.06).

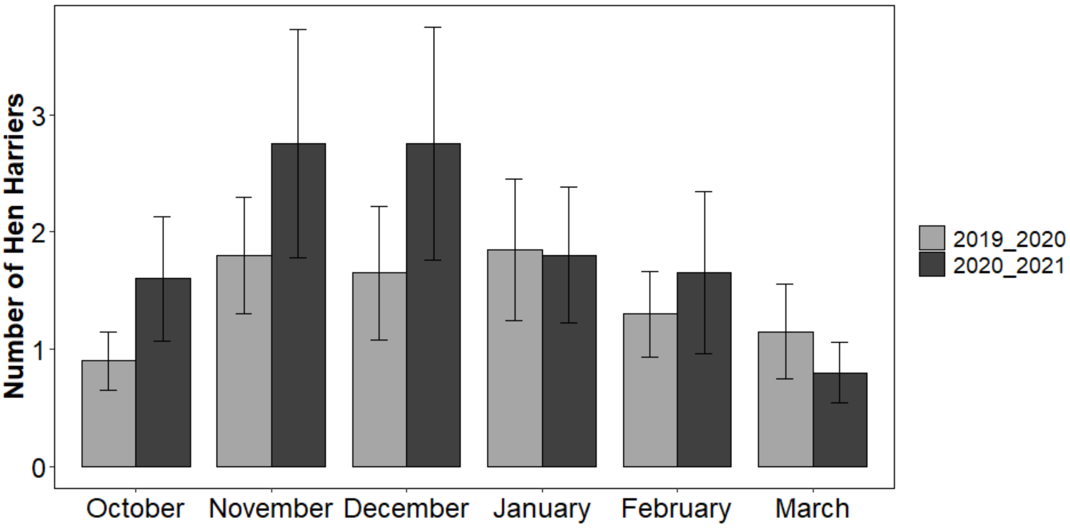

Figure 6. Mean (± SE) number of Hen Harriers recorded during monthly roost watches between both years of the winter roost survey. Data shown here are from the 20 roosts where watches were conducted in 12 months of the two-winter survey.

Long-term trends

Long-term data show stability in roost composition, with the largest roost in Ireland, an upland roost, having more adult males than ringtails during 78.7% of 75 watches over five winters. The second roost included in this long-term study, a lowland coastal roost, also showed long-term consistency of composition with more ringtails than adult males recorded during 89.3% of 28 watches over seven winters. The third roost, a lowland coastal roost, was again consistent in its composition with 86.96% of 23 watches over three winters having more ringtails than adult males.

Protection status of roosts

Of the 101 winter roosts identified in this study, 53 (52.5%) were within a protected area (9% were located within the existing Hen Harrier SPA network). Eighteen of 34 (53%) high priority roosts, eight of 16 (50%) medium priority roosts, and four of nine (44%) low-priority roosts occurred in protected areas, while five high priority, one medium priority and one low priority roost occurred within the Hen Harrier SPA network. The largest known roost in Ireland, with a maximum monthly count of 18 Hen Harriers, was not located in a protected area.

Of the 25 roosts that were included in habitat and region models, nine (36%) were in protected areas. One of these roosts occurred within the Hen Harrier SPA network and had 91.4% of its home range within a protected area. Excluding this outlier site, the mean percentage of the home range that occurred within designated protected areas was 6.6 ± 1.5%. Only three of the 25 roosts had home ranges that overlapped with the Hen Harrier SPA network. The mean proportion of roost home range that occurred within the Hen Harrier SPA Network for these 25 roosts was 5.3 ± 3.8% (1.7 ± 1.2%, excluding the outlier site mentioned above).

Discussion

Our results describe habitat and regional influences on Hen Harrier roost size and composition on the western edge of the species distribution. The habitat of the surrounding landscape was an important determinant of roost size and composition, with composition also differing across regions. The number of Hen Harriers using roosts also differed across months both within winters and between winters, however roost composition remained stable over long time periods at the three roosts used in the long-term study. We describe the priority wintering areas for Hen Harriers in Ireland and highlight the lack of overlap between protected areas and the locations of Hen Harrier winter roosts and associated foraging grounds. Roosts in the current study were generally comparable in size to those surveyed in Great Britain (Clarke and Watson 1990). However, the maximum count of 18 Hen Harriers at one roost in the current study is much lower than maximum counts recorded at roosts elsewhere, including the Isle of Man (83; Cullen 1991), Scotland (31; Clarke and Watson 1990), England (28; Clarke and Watson 1990), Slovakia (27; Noga 2013) and Germany (216, Helbig et al. 1992). This may be reflective of a smaller wintering population and/or patchier availability of large and contiguous habitats that could support large numbers of roosting Hen Harriers in Ireland.

Influence of habitat on roost attendance

The results of this study demonstrate the importance of surrounding habitat in determining the size and composition of Hen Harrier roosts. Larger, adult male dominated roosts occurred most often in peatland areas, whereas smaller, ringtail dominated roosts tended to occur in wetland, scrub, and arable areas. The mechanism by which surrounding habitat influences the size and composition of Hen Harrier roosts is most likely related to prey availability (Picozzi and Cuthbert 1982). Prey communities vary across habitats, with habitat-prey associations reflected in the diet of harriers (Collopy and Bildstein 1987, Chapter 4). In Ireland, arable areas are associated with the occurrence of small birds and small mammals in Hen Harriers' winter diet, whereas peatland habitats are strongly associated with medium-sized birds in the diet, primarily Snipe (*Gallinago gallinago*) and Redwing (*Turdus iliacus*; Chapter 4). The association between the higher numbers of Hen Harriers recorded at roosts in peatland landscapes, and the increased occurrence of adult-male dominated roosts in these areas, is likely related to availability and abundance of prey favoured by adult males in these habitats. Due to their greater hunting agility, colouration and hunting techniques, adult male Hen Harriers are more proficient hunters of agile and fast reacting prey, such as Snipe, compared with females (Nieboer 1973, Schipper et al. 1975, Vincheuski 2019). Therefore, adult males have an advantage over females when hunting in areas that hold higher numbers of these prey.

The habitat associations of ringtail dominated roosts also reflects their prey preferences. Ringtails predate small mammals more so than adult males, due to the larger size and lower agility of females and the relative ease with which small mammals can be captured by inexperienced juveniles (Marquiss 1980, Picozzi and Cuthbert 1982, Clarke et al. 1993, 1997, Vincheuski 2019). The positive association between wetland habitats and ringtail dominated roosts may be related to adult female Hen Harriers' ability to target larger prey items, including waterfowl (Marquiss 1980, Clarke et al. 1993). This association may also relate to finer-scale, site-specific conditions. Wetland areas in this study typically occurred in lowland inland regions, and specifically around and within the raised bogs of Co. Offaly. A Grey Partridge conservation programme is ongoing in this area, with supplementary feeding for the partridges attracting large numbers of small mammals and small birds, which in turn attracts Hen Harriers (Buckley et al. 2021), particularly ringtails. Intraspecific competition between males and females may also play an important role in the distribution of Hen Harrier cohorts in winter months. Dobler (2021) reported that females displaced adult males from prey-rich winter foraging grounds to suboptimal areas, whereas juvenile males were less prone to displacement by females. Such interactions may further drive differentiation in winter habitat associations between adult males and ringtails.

Influence of region on roost attendance

Region influenced the composition more so than the size of Hen Harrier roosts. Our results show that large Hen Harrier roosts are not restricted to upland areas, in contrast to an earlier study by Clarke and Watson (1990) which found that only one lowland roost out of 202 included in their study had similar peak counts to roosts in upland breeding areas. In the current study, large Hen Harrier roosts occurred across all regions, from upland areas to lowland coastal areas, with overall numbers of Hen Harriers at roosts driven primarily by local habitat composition. Roosts dominated by adult male Hen Harriers occurred most frequently in upland areas, while roosts dominated by ringtails occurred most often in lowland coastal areas. This pattern is in stark contrast to neighbouring Hen Harrier populations in Scotland and England, where females typically remain in upland breeding areas during the winter, while adult males move to lowland areas (Marquiss 1980, Picozzi and Cuthbert 1982, Clarke and Watson 1990, Murphy 2019). These contrasting patterns in regional winter distribution between neighbouring populations may be explained by local prey communities. Upland areas in Great Britain hold high numbers of small mammals, particularly Field Voles (*Microtus agrestis*), which enables ringtail Hen Harriers to remain in these areas over winter (Marquiss 1980, Picozzi and Cuthbert 1982). As Field Voles are absent from Ireland, there is lower abundance of suitable prey in upland areas for ringtails and therefore fewer overwinter in these areas. This highlights the importance of prey communities and diet differentiation between sexes in determining the winter distribution of Hen Harriers (Marquiss 1980, Picozzi and Cuthbert 1982, Clarke and Watson 1990).

The regional differences in roost composition are reflective of the local habitats. Ringtails dominate in lowland coastal areas due to the higher abundance of small mammals and small birds that are found in the arable lands of lowland coastal areas (Wilson et al. 1996, Moorcroft et al. 2002, Chapter 4). For ringtails, and particularly inexperienced juveniles, targeting smaller but potentially easier to catch prey in low complexity vegetation, such as arable stubble fields that were most often recorded in lowland coastal areas, may be more beneficial than targeting higher energy prey, such as medium-sized birds, that are more difficult to catch, both due to prey agility and increased vegetation structure complexity in peatland habitats (Schipper et al. 1975). Vegetation structure plays an important role in prey capture success for harriers (Klaassen et al. 2019), with the simple vegetation structure of arable stubble perhaps aiding the capture of small birds, a prey group that would typically be assumed to be difficult to capture (Collopy and Bildstein 1987), as well as small mammals.

Temporal influences on roost attendance

We observed variation in the number of Hen Harriers using roosts, both across months and between winters. The highest mean number of Hen Harriers using roosts was recorded in November, with the lowest mean number recorded in March. Similar temporal patterns have previously been described for roosting Hen Harriers (Watson and Dickson 1972, Picozzi and Cuthbert 1982, Clarke and Watson 1990, O'Donoghue 2010). The variation in overall numbers of Hen Harriers at roosts across the winter reflects movements from neighbouring populations and movement of individuals between roost sites on their wintering grounds (Watson and Dickson 1972, Dobson et al. 2012). Chapter 5 describes how individual Hen Harriers can use several winter roosts within their wintering grounds, with one bird using five different roosts over the course of her first winter. Weather may also play an important role in determining roost attendance across the winter (Watson and Dickson 1972), along with survival, as more juveniles would be expected to occur at roosts in the early winter period compared with the late winter period due to winter mortality.

Variation in the number of Hen Harriers at roosts also occurred between winters, with roost watches during the first winter having more Hen Harriers than the second winter, although the observed difference was not statistically significant. Between winter variation in roost attendance is likely the result of several factors. Breeding productivity of the Irish population would influence the number of overwintering Hen Harriers in Ireland, with productive breeding seasons leading to more juveniles at winter roosts. In addition, migration from neighbouring populations may also have an important effect. Between 15 and 175 Hen Harriers hatched in Great Britain are estimated to overwinter in Ireland each winter (Dobson et al. 2012). Fluctuations in the numbers of Hen Harriers migrating between Great Britain and Ireland would lead to fluctuations in the numbers recorded at roosts in Ireland. Such variation may be caused by breeding productivity where greater numbers of juvenile Hen Harriers may disperse into Ireland following a productive breeding season in Great Britain. Additionally, individual behaviour may play an important role in the recorded fluctuations between winters, with Hen Harriers observed using different roosts in their first winter compared with subsequent winters (Chapter 5).

Long-term roost watch data from 2007 to 2021 showed that roost composition remained relatively stable across several winters. This suggests that the factors influencing roost composition, such as habitat and intraspecific competition, remained stable over time (Picozzi and Cuthbert 1982), while factors that affect roost size fluctuated, such as the prior breeding productivity (in Ireland and in neighbouring populations), survival and migration.

The time that birds settle to roost is often closely linked to light levels, which can be influenced by weather conditions (Kitowski 2005, Smiddy et al. 2007). For Hen Harriers, settling time may be further influenced by foraging success during the day, with individuals that have had a successful day of foraging typically going to roost earlier (Kitowski 2005). The observed difference in settling time between adult males and ringtails, with adult males settling to roost later than ringtails, may reflect observer bias as adult males are easier to see in fading light compared with ringtails. However, there may also be underlying ecological influences of age, sex, intraspecific interactions at roosts and distance to foraging grounds on settling time.

Protection status of roosts

Almost half of the roosts in the current study were in areas that did not have statutory protection, with just 9% occurring within the Hen Harrier SPA network, making them vulnerable to anthropogenic disturbance and land use change. Hen Harrier winter roosts in Ireland have seen a high rate of abandonment in recent years. Some 31% of roosts monitored during a 16-year long winter roost survey were no longer active at the conclusion of the study as a result of anthropogenic pressures in the absence of targeted protective measures (O'Donoghue 2021), despite regular monitoring. Given the critical role that roosts play in Hen Harrier winter ecology and survival, further loss or degradation of these sites may have significant negative consequences for Hen Harriers in Ireland and, therefore, their conservation and protection should be prioritised.

To date, no research has been undertaken on foraging grounds associated with Hen Harrier winter roosts in Ireland. Our results demonstrate that the overall protection of the surrounding landscapes at roosts is minimal at present, with a clear mismatch between Hen Harrier wintering areas and the areas selected for protection. There is a widespread risk of loss and degradation of the winter foraging grounds around these winter roosts through land use pressures including agricultural intensification, changes in agricultural practices, afforestation, and wind energy development. For example, the continued decline of arable farmland in Ireland through conversion to pasture for dairy farming may be a significant pressure on wintering Hen Harriers, particularly juveniles and females. Since the 1980s, there has been a 42% decline in arable farmland in Ireland, with these declines ongoing (Wallace 2020). Further loss of important wintering grounds, such as arable land, would likely lead to increased competition in dwindling suitable foraging areas, lower overwinter survival and negative carry-over effects for those birds that survive to the breeding season, potentially compromising their breeding productivity (Harrison et al. 2011, Tapia and Zuberogoitia 2018). Protecting and enhancing roost sites without simultaneously providing protection for the surrounding landscape, which serves to attract Hen Harriers to these areas, would be an oversight in conservation policy.

Priority Hen Harrier wintering areas

Through our research on Hen Harrier winter roost distribution, we have identified priority Hen Harrier wintering areas in Ireland. These cover a larger geographical area than the breeding grounds and are reflective of the winter distributions previously suggested by Balmer et al. (2013) and O'Donoghue (2021). These priority areas include a range of habitats, topographical, soil and climatic conditions. Given the larger geographical distribution of the Irish Hen Harrier population in winter compared with the breeding season, current Hen Harrier conservation strategies based solely on breeding season distributions, notably the designation of protected areas, are not appropriate for the winter period. A broader-scale approach, with measures implemented through schemes such as the new Common Agricultural Policy (CAP), together with smaller scale designation of protected areas, may be a more effective conservation strategy (Fernández-Bellon et al. 2021).

Conservation implications

Special Protection Areas (SPAs) are designated in six core Hen Harrier breeding areas in Ireland in an effort to reduce the pressures experienced by Hen Harriers during the breeding season. Many of these pressures are similar to those experienced by Hen Harriers during the winter months (O'Donoghue 2021), however we found little overlap between existing SPAs and Hen Harrier winter distribution. More conservation attention should be focussed on the human disturbance threat to wintering populations. Furthermore, the perception by Hen Harrier conservationists in Europe is that the designation of protected areas is a less effective conservation tool compared with habitat management strategies as, although designation can prevent habitat loss through land-use changes such as afforestation and agricultural intensification, it does not ensure that habitat improvement measures will take place (Fernández-Bellon et al. 2021). Therefore, rather than simply designating winter roosts and associated foraging grounds as protected areas, future conservation efforts should instead prioritise the implementation of habitat improvement measures. Such habitat improvement measures should focus on increasing the quantity and quality of winter foraging habitats in priority Hen Harrier wintering areas, while roost sites themselves should be directly protected from human induced habitat degradation, destruction, and disturbance.

The inclusion of consideration of temporal variation during the monitoring and locating of Hen Harrier winter roosts as part of ecological assessments, particularly for large-scale developments or similar activities that may have a detrimental impact on roosts or surrounding landscapes to roosts, would enhance the effectiveness of this process. In addition, coordinated roost watches should be considered for roost complexes when trying to gain an understanding of Hen Harrier winter habitat use, as individuals occasionally move between nearby roosts over the course of a winter, as described in Chapter 5. Furthermore, the average foraging distance from winter roosts (5.4km) should be considered when designing bird surveys as part of ecological assessments for large-scale developments, such as wind farms, in Hen Harrier wintering areas.

Ethics statement

No licences were required for the fieldwork that was undertaken during this study. Roost watches were conducted from distant vantage points to prevent disturbance to Hen Harriers using the roosts.

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Chapter Four

Landscape and temporal influences on the winter diet of a threatened diurnal raptor, the Hen Harrier (*Circus cyaneus*)[4]

Hen Harrier pellet

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[4] McCarthy, A., P. Smiddy, T. Nagle, A. Mee, S. Irwin, A. Caravaggi and J. O'Halloran. *In press*. Landscape and temporal influences on the winter diet of a threatened diurnal raptor, the Hen Harrier *Circus cyaneus*. Bird Study

Abstract

The aim of this study was to determine Hen Harrier (*Circus cyaneus*) winter diet and examine temporal and spatial variations in diet composition. A total of 1,117 Hen Harrier pellets were collected from 11 winter roosts between 2017 and 2021 in Ireland. Hen Harrier winter diet was dominated by avian prey (95.9% of pellets), with mammalian prey found in 12.0% of pellets. Occurrence of small birds and small mammals in the diet was positively associated with the proportion of arable, wild bird cover and low-intensity agriculture around the roost sites. The frequency of medium-sized birds (primarily Redwing [*Turdus iliacus*] and Snipe [*Gallinago gallinago*]) in the diet was positively associated with the proportion of bog and young conifer forests surrounding roost sites. Diet also varied across regions, with pellets from roosts in lowland coastal areas having a greater prevalence of small birds and small mammals, and pellets from roosts in upland areas having a greater prevalence of medium-sized birds. Investigation of temporal changes revealed that the proportion of medium-sized birds in the diet changed across months, with that of small birds and small mammals remaining stable. Variation in the proportion of small birds and medium-sized birds in Hen Harrier diet was also observed between winters. The results of this study suggest that habitat, along with region and time, are important drivers of variation in Hen Harrier diet. Our findings highlight the opportunity for the enhancement of Hen Harrier habitat through land management and can be used to inform effective conservation strategies for wintering Hen Harrier on the landscape scale.

Introduction

Individual bird species' diets can vary considerably in response to local variations in prey communities and availability, driven in part by landscape composition and habitat (Civantos et al. 2018). This is particularly true for generalist raptors such as the Hen Harrier (*Circus cyaneus*) with geographic differences in observed dietary composition typically reflecting local prey abundance (Clarke et al. 1997, Redpath and Thirgood 1999, Amar 2001, de Boer et al. 2013, Nota et al. 2019).

Local prey availability has important consequences for Hen Harriers as it may impact on individual life histories and on population dynamics (Simmons et al. 1986, Redpath and Thirgood 1999, Amar et al. 2003). For example, food limitation has been suggested as an important driver of declining Hen Harrier populations in some parts of Scotland (Redpath and Thirgood 1997, Amar 2001, Amar et al. 2003). The distribution of prey communities can impact on the distribution of different ages and sexes of birds (Marquiss 1980, Dobler 2021), with the recruitment of young Hen Harriers to certain areas being linked to the availability of prey such as voles and Meadow Pipits (*Anthus pratensis*) (New et al. 2011, de Boer et al. 2013). Diet composition has also been linked with Hen Harrier breeding performance (Redpath et al. 2002a, Amar et al. 2003), with clutch size and fledging success shown to be positively associated with prey abundance (Schipper 1978, Simmons et al. 1986, Redpath et al. 2002a). Most dietary studies of Hen Harrier and other raptors have focussed on the breeding season, when the activity of birds is centred around nests, facilitating the collection of pellets and observational data (Redpath et al. 2001). However, the composition of the diet during the pre-breeding period may play an important role in subsequent breeding attempts and their success (Redpath et al. 2002a, Amar et al. 2003). Outside of the spring and summer seasons, winter diet can also exert an influence on the subsequent breeding success and population dynamics of some bird species (Martin 1987). Winter diet and prey availability are important determinants of over-winter survival, which has been identified as a potential limiting factor for some Hen Harrier populations (Ruddock et al. 2016). Therefore, winter diet is key to understanding this species' ecological needs.

Hen Harrier diet is typically dominated by birds and mammals (Picozzi 1977, Clarke et al. 1993, Watson 2017), though they occasionally predate other taxonomic groups including reptiles and amphibians (Picozzi 1977, Marquiss 1980, Bro et al. 2006, Nota et al. 2019). Their diet varies both spatially across their range and temporally as prey abundance in the environment fluctuates (Clarke et al. 1997, Redpath and Thirgood 1999, Garcia and Arroyo 2004, Nota et al. 2019). Some differentiation between the diet of male and female Hen Harrier is also reported with males taking smaller and more agile prey than females (Marquiss 1980, Picozzi 1980). Although broad geographic differences in Hen Harrier diet have been reported across several studies, few studies have examined finer geographic variation (Clarke et al. 1997) or explored the influence of landscape composition. Habitat can significantly influence the diet of predator species as different habitats host different prey communities (St. George and Johnson 2021), with vegetation structure of habitats influencing prey availability (Redpath et al. 2002b). Understanding the influence of habitat on diet is therefore crucial to inform the development of effective conservation strategies and the implementation of appropriate conservation measures.

The island of Ireland is at the western edge of the Hen Harrier's range and lacks many of the prey species that are an important feature of Hen Harrier diet elsewhere in their range, most notably the Field Vole (*Microtus agrestis*) and Common Vole (*Microtus arvalis*). However, recent introductions of non-native small mammal species could increase prey availability for Hen Harriers and other raptors in some parts of Ireland. The Bank Vole (*Myodes glareolus*) was introduced into Ireland in the early 20th century (Stuart et al. 2007). It is now an established component of Hen Harrier diet in the south-west of the country, accounting for up to 13% of winter diet in some areas (O'Donoghue 2010, Smiddy and Cullen 2017). More recently, the Greater White-toothed Shrew (*Crocidura russula*) has been spreading across the island of Ireland since its introduction in the early 2000s (Tosh et al. 2008, McDevitt et al. 2014), and has been recorded in the diet of other small mammal predators such as Barn Owl (*Tyto alba*; Smiddy 2018). The low number of native small mammal species combined with the patchy presence of introduced non-native species provides a good opportunity to study the effects of variation in availability of different prey species on Hen Harrier diet. The landscape of Ireland also offers an excellent opportunity to explore the influence of habitat on diet. Hen Harrier in Ireland utilise the same wintering habitats as elsewhere in their range, including arable farmland, grasslands and reedbeds (O’Donoghue 2021). However, there are also vast areas of cutover lowland raised bogs, an uncommon habitat elsewhere within the Hen Harrier’s range, which appears to be an important wintering habitat for Hen Harrier in Ireland (Buckley et al. 2021).

This study set out to describe variation in Hen Harrier winter diet across their range in Ireland. In particular, we sought to investigate the influence of different regions and surrounding landscape-scale habitat on diet composition. We also explored temporal variation in diet both across winter months and between years. This research will increase our knowledge of Hen Harrier winter diet, allowing us to better understand the threats to this vulnerable species and to develop conservation management actions across the winter period.

Materials and methods

Study area

Hen Harrier pellets were collected from 11 roost sites between November and March during 2019/20 and 2020/21. These roost sites were located and monitored monthly between October and March using distant vantage point watches as part of a separate study of Hen Harrier winter roost characteristics (McCarthy et al. in prep). One roost site held a single bird while ten were communal roosts, i.e. roosts where more than one bird was observed on at least one occasion (Fig. 1). Pellet collections also took place at one of these roosts over the earlier winters of 2017/18 and 2018/19. Roosts were grouped into three regions based on altitude above sea level (ASL) (Perrin et al. 2014) and proximity to the coast. The three regions were: (i) lowland coastal roosts (<150m ASL; home range overlapped with coastline; n=4); (ii) lowland inland roosts (< 150m ASL; home range did not overlap with coastline; n=4); and (iii) upland roosts (> 150m ASL; home range did not overlap with coastline; n=3). Roosts were distributed across a range of habitats that are typically used by wintering Hen Harrier in Ireland and Great Britain: two roosts were in reedbeds, two were in scrub vegetation, two were on upland cutover bogs, one was on degraded lowland raised bog, three were on lowland cutover bog, and one was on lowland grassland/fen. All roosts were spatially independent of each other (based on average winter home range size; Appendix 1) and were on average 122km apart (range of 15km to 260km).

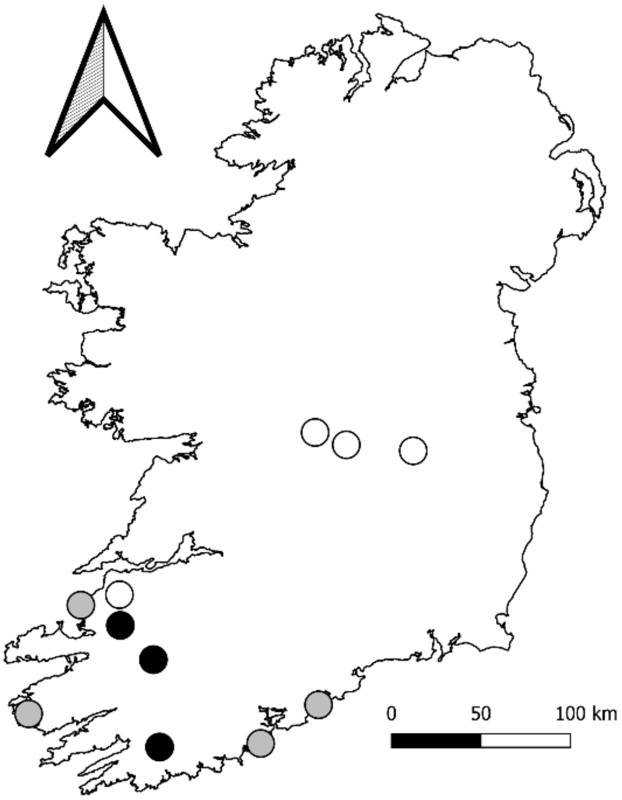

Figure 1. Locations of winter roosts in this study. Grey circles show lowland coastal roosts, white circles show lowland inland roosts and black circles show upland roosts. Note that circle size does not equal home range size.

Pellet collection and dissection

Roost locations were mapped as accurately as possible during the monthly distant vantage point surveys, enabling location of roosting beds during pellet collections. The frequency of pellet collections was dependent on the timing of bird attendance at roosts and on local weather conditions, and collections were made once per month where conditions allowed.

Hen Harriers typically leave roosts to forage soon after dawn and return to roosts 1-2 hours before dusk. Therefore, pellet searches were conducted between 1000hrs and 1500hrs to avoid disturbance to birds leaving or returning to the roost. Hen Harrier night-time roosts (hereafter ‘roost beds’) were easily identifiable in the field and were typically flattened areas of grasses and sedges surrounded by higher vegetation, with whitewash and pellets within the roost beds (Zagorski and Swihart 2020). The only other raptor species recorded roosting in proximity to the Hen Harrier roosts was Short-eared Owl (*Asio flammeus*). Short-eared Owl pellets are clearly distinguishable from Hen Harrier pellets based on pellet size and consistency (Holt et al. 1987, Smiddy 2013). Pellets were also collected from frequently used perches such as fence posts within the roosts. The location of each pellet collected was recorded to an accuracy of three metres using handheld GPS devices. Pellets were placed in individual labelled bags.

Pellets were frozen within six hours of collection at -20°C for 24 to 48 hours to prevent degradation of the pellet contents. Pellets were then defrosted and left to air dry for 14 to 21 days. Once dry, two researchers each analysed all of the pellets to ensure accurate identification of prey remains. Before dissection, the maximum length and width of intact pellets were measured to the nearest 0.5mm. Prey were identified to species level where possible based on bone, fur, and feather characteristics (Teerink 1991, Redpath et al. 2001). It is often not possible to identify prey remains within Hen Harrier pellets to species level. Therefore, prey remains were identified to the lowest possible taxonomic level and grouped into six categories: 1) small mammals; 2) medium-sized mammals; 3) small birds; 4) medium-sized birds; 5) large birds; and 6) lizards. Small mammals included Wood Mouse (*Apodemus sylvaticus*), House Mouse (*Mus domesticus*), Bank Vole, Pygmy Shrew (*Sorex minutus*), Greater White-toothed Shrew and Brown Rat (*Rattus norvegicus*). Medium-sized mammals included European Rabbit (*Oryctolagus cuniculus*) and Irish Hare (*Lepus timidus hibernicus*). Small birds included species with an average body mass of less than 60g, such as finches and buntings. Medium-sized birds included species with an average body mass of 60-300g, such as Common Snipe (*Gallinago gallinago*) and thrushes. Large birds included species with an average body mass greater than 300g, such as Woodcock (*Scolopax rusticola*) and ducks (Demongin 2016).

Data analysis

As it was often not possible to determine with confidence how many individual prey items were represented in a single pellet, we calculated diet composition by recording the presence/absence of prey species/groups within each pellet rather than the number of individual prey items (Redpath et al. 2001). As this method may potentially overestimate the occurrence of individual large prey items, it was not possible to assess the importance of prey species/groups based on biomass. The minimum number of pellets required to support modelling was determined via power analysis and supplementary changepoint analysis, where power was given precedence. These analyses revealed that a minimum of 19 pellets were required to give an accurate representation of the diet (see Appendix two). The minimum number of pellets collected at any one winter roost overall was 34.

Differences in diet across regions (lowland coastal; lowland inland; upland) were assessed using generalised linear mixed effects models with binomial family distribution for small birds and medium-sized birds, and a negative binomial linear mixed effects model for small mammals due to zero-inflation of the response variable. For the small bird and medium-sized bird models, the response variable was the number of pellets containing the relevant prey group for each collection divided by the total number of pellets in each collection, with the explanatory variable set as region. To account for any temporal variation in diet both within and between winters, we created a combined winter/month variable which was included as a random effect. We also included the number of Hen Harriers using the roost site in each respective month as a random effect. Both small bird and medium-sized bird models were weighted according to the total number of pellets in each respective pellet collection. For the small mammal model, we included the number of pellets containing small mammal remains as the response variable, with month/year, number of Hen Harriers using the roost site and total number of pellets in the collection as random effects.

To examine the influence of habitat on wintering diet, we first calculated home ranges around winter roosts as part of a separate satellite tracking study (McCarthy et al. in prep; Appendix 1). We used tracking data from five satellite tagged Hen Harriers that overwintered in Ireland across seven roosts over four winters. We calculated an average 95% Minimum Convex Polygon (MCP) home range from this satellite tracking data. Only roosts with a minimum of 30 high quality (accuracy of 0-2500m) daytime location fixes within a given winter (November to March, inclusive) were included in this analysis. Where roosts included in the current study were also used by satellite tagged Hen Harriers, MCPs were applied directly to each respective roost. Where there was insufficient or no satellite tracking data available for roosts used in the current study, an average home range size was calculated, and a buffer of given area was applied to these roost sites. For coastal roosts, average home range size was applied only to the land around the roosts, with open water of the sea not included in the home range buffer as the Hen Harrier is a terrestrial species.

We then calculated the area of several habitats relevant to Hen Harrier feeding ecology within the home range of each roost site (Watson 2017). Corine land-class data was used as a base layer, with forest cover data provided by Coillte and the Forest Service. These forest cover data were filtered to include forests aged between 3 and 12 years post-planting (hereafter referred to as young, planted forests), as this is the age of forests preferred by Hen Harrier for foraging (Wilson et al. 2009, 2012). This forest cover data was further divided into conifer (>50% cover of conifer species) and deciduous (>50% cover of deciduous species) young, planted forests. Bord Na Móna, the semi-state body that owns large areas of cutover raised bog habitats in Ireland, provided detailed habitat maps for their properties. Spatial data from the Green Low-carbon Agri-environment Scheme (hereafter referred to as GLAS), including wild bird cover, Hen Harrier, and Grey Partridge (*Perdix perdix*) habitat measures were provided by the Department of Agriculture, Food and the Marine (DAFM). An index of scrub and hedgerow cover was obtained from the Copernicus small woody features layer. A full description of spatial data included in this study is provided in Table 1.

Table 1. Habitat variables included in diet models.

Variable	Manipulation	Source
Arable	Composite data	CORINE (2.1.1. Non-irrigated arable land; 2.4.2. Complex cultivation patterns), DAFM (Grey Partridge GLAS measures)
Bog	Composite data	CORINE (4.1.2. Peat bogs; 3.2.2. Moors and heathland; 3.3.3. Sparsely vegetated areas), Bord Na Móna (bog, blanket bog, cutover bog, degraded blanket bog, heath, heath & scrub)
Broadleaf	Raw data	Coillte, Forest Service
Conifer	Raw data	Coillte, Forest Service
Low intensity agriculture	Composite data	CORINE (2.4.3. Land principally occupied by agriculture, with significant areas of natural vegetation; 3.2.1. Natural grasslands), DAFM (Grey Partridge GLAS measures; Hen Harrier GLAS measures)
Pasture	Composite data	CORINE (2.3.1. Pasture), Bord Na Móna (grassland or agriculture), DAFM (Grey Partridge GLAS measures; Hen Harrier GLAS measures)
Scrub & hedgerows	Raw data	Copernicus (Small woody features- Linear structures of trees, hedges, bushes, and scrub; patchy structures of trees, hedges, bushes, and scrub)
Wetlands	Composite data	CORINE (4.1.1. Inland marshes; 4.2.1. Salt marshes; 4.2.3. Intertidal flats), Bord Na Móna (fen; riparian; temporary flooded areas; wetlands; wetlands & scrub)
Wild bird cover	Raw data	DAFM

We applied a Principal Component Analysis (PCA) to the nine habitat variables. All variables were standardised, with $\bar{x} = 0$ and $\sigma = 1$. The same model structures as above were applied for small birds, medium-sized birds and small mammals, however, Principal Components (PCs) were included as explanatory variables in place of region.

We compared diet across two temporal scales: months within an individual winter and months across two winters. To compare diet across months, we filtered pellet collections from roosts where a minimum of 19 pellets were collected in each of November, January, and March (early, mid, and late winter). To model these data for small birds and medium-sized birds, the response variable used was the number of pellets containing the relevant prey group for each collection divided by the total number of pellets in each collection, with month included as the explanatory variable. The number of Hen Harriers using the roost site in each respective month was included as a random effect. Both small bird and medium-sized bird models were weighted according to the total number of pellets in each respective pellet collection. For the small mammal model, we used a zero-inflated negative binomial linear mixed effects model. We included the number of pellets containing small mammal remains as the response variable, month was set as the explanatory variable and the number of Hen Harriers using the roost site and total number of pellets in the collection were included as random effects. Roost site was not included as a random effect in these cross-month comparison models due to insufficient factor levels.

The same approach described for monthly diet comparisons was applied to cross-winter comparisons, except data were filtered to roosts where a minimum of 19 pellets were collected from each roost site in each winter (2019/20 and 2020/21). The same model structure was applied above, however in this case, roost site was also included as a random effect in all three models.

One lowland inland winter roost was an outlier in the data several ways. The pellets from this winter roost had a prevalence of small mammals (occurring in 70.2% of pellets), driven by a large number of pellets containing Greater White-toothed Shrew (61.7% of pellets). Small birds occurred in 40.4% of pellets, whereas medium-sized birds and medium-sized mammals each occurred in 6.4% of pellets. Greater White-toothed Shrew was found in pellets at only one other roost site located in an area where the species has been established for several years (National Biodiversity Data Centre 2021), however, at this roost site it only occurred in 2.9% of pellets. Furthermore, the roost site where most pellets contained Greater White-toothed Shrew was occupied by one individual Hen Harrier (a first-year female) and was the only single-bird roost site in this study. This female was specialising on Greater White-toothed Shrew and given the diet of birds using all other roost sites, both where this species does and does not occur, it is clear this female did not have a “typical” diet. Therefore, we excluded this site from the general Hen Harrier diet description, region, habitat, and temporal models.

Results are presented as x̄ ± standard error, unless otherwise stated. Data were processed and analysed using QGIS version 3.12.3 (QGIS.org 2021) and R version 4.0.2 (R Core Team 2020) including packages *ggplot2* (Wickham 2016), *lme4* (Bates et al. 2015), *glmmTMB* (Brooks et al. 2017) and *factoextra* (Kassambara and Mundt 2020).

Results

Winter diet of Hen Harrier

We analysed 1,117 Hen Harrier pellets during this study, 242 from four lowland coastal roosts, 268 from four lowland inland roosts and 607 from three upland roosts. Pellets had an average maximum length and width of 30.3 ± 0.3 mm and 15.8 ± 0.1 mm, respectively (n=678). Avian prey occurred in 95.9% of pellets while mammalian prey occurred in 12.0% of pellets. Small birds were the most frequently recorded prey group in the diet, occurring in 52.8% of pellets, followed by medium-sized birds in 46.1% of pellets and small mammals in 11.8% of pellets. A single prey group was found in 89.0% of pellets, 10.9% of pellets contained two prey groups, and 0.1% of pellets contained three prey groups. Thirty prey species were identified, including 12 small bird species, eight medium-sized bird species, one large bird species, six small mammal species, two medium-sized mammal species and one reptile species. Of those prey remains identified to species level, Common Snipe was the most frequent and occurred in 31.0% of pellets, followed by Redwing (*Turdus iliacus*) in 8.2% of pellets and Bank Vole in 6.2% of pellets (Table 2).

Table 2. Percentage of Hen Harrier pellets within which each prey group/species occurred across each roost site. The total number of Hen Harrier pellets analysed from each roost site is also included.

	Roost Site											
	Lowland Coastal				Lowland Inland				Upland			
Prey group/species	A	B	C	D	E	F	G	H	I	J	K	Total
All												
Small birds	58.0	80.3	54.5	67.6	50.9	47.2	57.1	40.4	58.5	47.3	38.7	52.3
Medium-sized birds	43.2	18.4	47.7	17.6	49.1	43.1	25.7	12.8	40.4	52.0	67.6	44.7
Large birds	0.0	0.0	2.3	0.0	0.0	1.4	0.0	0.0	0.0	0.0	0.0	0.2
Small mammals	11.4	31.6	11.4	26.5	13.2	16.7	37.1	70.2	6.4	7.1	4.2	14.2
Medium-sized mammals	1.1	0.0	0.0	2.9	0.0	0.0	2.9	6.4	0.0	0.0	0.0	0.5
Unknown species												
Small birds	44.3	68.4	31.8	32.4	47.4	41.7	54.3	36.2	51.5	37.4	31.7	42.9
Medium-sized birds	12.5	10.5	4.5	2.9	4.4	4.2	14.3	6.4	3.5	5.4	3.5	5.8
Small mammals	1.1	0.0	2.3	0.0	0.0	1.4	2.9	0.0	0.0	0.7	0.0	0.5
Mouse	1.1	0.0	0.0	0.0	0.0	0.0	5.7	0.0	0.0	0.3	0.0	0.4
Shrew	1.1	0.0	0.0	0.0	0.0	0.0	2.9	0.0	0.0	0.0	0.0	0.2
Small mammals												
Bank Vole	2.3	14.5	9.1	23.5	9.6	6.9	20.0	10.6	3.5	3.4	1.4	6.4
Brown Rat	0.0	1.3	0.0	2.9	0.0	0.0	0.0	0.0	0.6	0.3	0.7	0.4
Greater White-toothed Shrew	0.0	0.0	0.0	0.0	0.0	0.0	2.9	61.7	0.0	0.0	0.0	2.7
House Mouse	5.7	17.1	0.0	2.9	0.0	2.8	2.9	6.4	0.6	0.0	0.0	2.3
Pygmy Shrew	0.0	0.0	0.0	0.0	2.6	0.0	0.0	0.0	0.6	1.4	0.7	0.8
Wood Mouse	1.1	0.0	0.0	0.0	0.9	6.9	5.7	2.1	1.2	1.0	1.4	1.5
Medium-sized mammals												
Irish Hare (leveret)	0.0	0.0	0.0	2.9	0.0	0.0	0.0	6.4	0.0	0.0	0.0	0.4
European Rabbit	1.1	0.0	0.0	0.0	0.0	0.0	2.9	0.0	0.0	0.0	0.0	0.2
Small birds												
Blue Tit	1.1	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.3
Bullfinch	2.3	2.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	1.4	0.7
Chaffinch	0.0	0.0	0.0	0.0	0.0	1.4	0.0	0.0	0.0	0.7	0.0	0.3
Dunnock	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.1
Goldcrest	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.4	1.4	0.5
House Sparrow	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.1
Long-tailed Tit	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.1
Meadow Pipit	0.0	0.0	9.1	32.4	3.5	0.0	0.0	0.0	2.9	4.1	1.4	3.4
Reed Bunting	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.3
Robin	0.0	2.6	0.0	0.0	0.0	0.0	0.0	0.0	1.2	0.3	1.4	0.6
Wren	11.4	3.9	15.9	5.9	0.9	4.2	2.9	4.3	1.8	3.4	1.4	3.9

	Roost Site											
	Lowland Coastal				Lowland Inland				Upland			
Prey group/species	A	B	C	D	E	F	G	H	I	J	K	Total
Yellowhammer	1.1	3.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4
Medium-sized birds												
Blackbird	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.1	0.0	0.7	0.0	0.3
Fieldfare	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.1
Redwing	2.3	3.9	2.3	8.8	14.0	0.0	0.0	0.0	4.1	12.6	13.4	7.9
Snipe	28.4	1.3	38.6	5.9	30.7	37.5	11.4	4.3	32.7	32.0	50.0	29.9
Song Thrush	0.0	2.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.7	0.4
Starling	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.7	0.3
Water Rail	0.0	0.0	2.3	0.0	0.0	1.4	0.0	0.0	0.0	0.0	0.0	0.2
Large birds												
Pintail	0.0	0.0	0.0	0.0	0.0	1.4	0.0	0.0	0.0	0.0	0.0	0.1
Woodcock	0.0	0.0	2.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1
Other												
Lizard	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	2.1	0.4
Number of pellets	88	76	44	34	114	72	35	47	171	142	294	1117

Variation in diet composition across regions

Small birds were the prey group recorded most frequently in the diet of Hen Harrier at both lowland coastal (65.1 ± 5.8%) and lowland inland roosts (51.7 ± 2.9%), while medium-sized birds were the most frequently recorded prey group in the diet at upland roosts (53.3 ± 7.9%). There were significant differences in the occurrence of each main prey group in the diet of Hen Harrier across the three regions (Fig. 2). Lowland coastal roosts had significantly higher levels of occurrence of small birds in the diet (65.1 ± 5.8%) compared with both lowland inland roosts (51.7 ± 2.9%; $P = 0.02$) and upland roosts (48.16 ± 5.72%; $P < 0.001$). Medium-sized birds occurred significantly more frequently in the diet at upland roosts (53.3 ± 7.9%) compared with lowland coastal roosts (31.7 ± 8.0%; $P < 0.001$), but not when compared with lowland inland roosts (39.3 ± 7.0%). Small mammals occurred significantly more frequently in the diet at lowland coastal roosts (20.2 ± 5.2%) when compared with upland roosts (5.9 ± 0.9%; $P = 0.005$), but not when compared with lowland inland roosts (22.3 ± 7.5%).

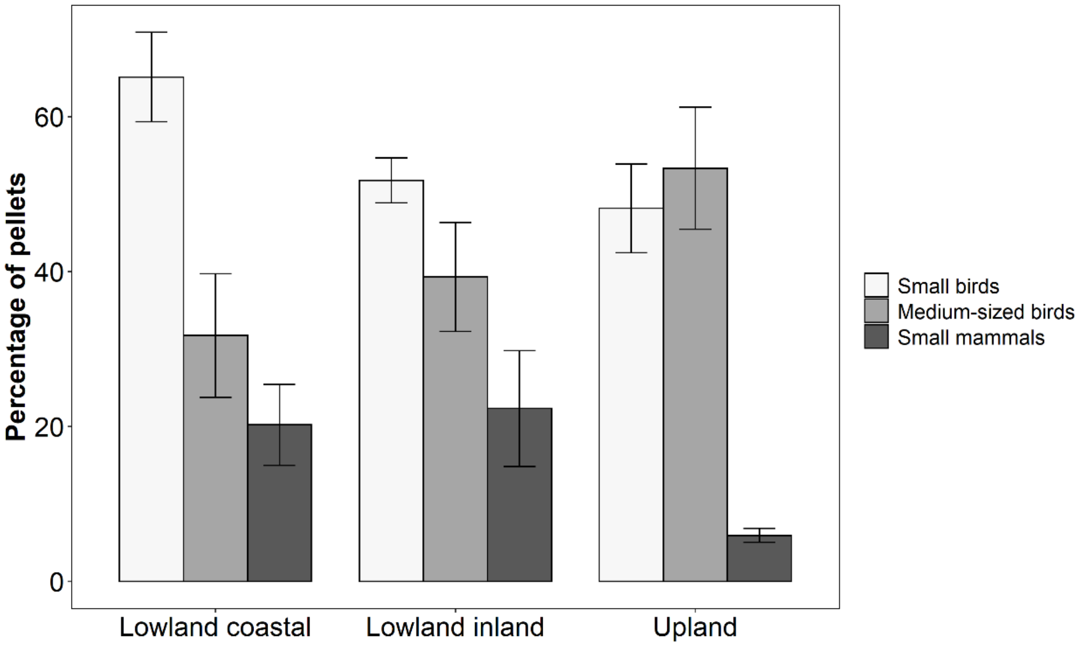

Figure 2. Mean (± SE) percentage occurrence of each prey item in the winter diet of Hen Harrier across three regions.

Effect of habitat on diet composition

Three PCs, which together explained 73.6% of habitat variance, were retained for inclusion in the habitat models. PC1 was positively associated with both arable land and wild bird cover, whereas it was negatively associated with bog and young conifer forest. PC2 was positively associated with pasture, and negatively associated with young broadleaf forests, low intensity agriculture and scrub and hedgerows. PC3 was positively associated with arable and low intensity agriculture but was negatively associated with wetlands (Table 3).

Table 3. Principal component (PC) axes loadings capturing habitat variation around winter roosts. Values in **bold** show the habitat variables that most describe each PC. This analysis excludes the outlier roost.

Habitat variable	Principal components (variation explained)		
	PC1 (30.46%)	PC2 (28.08%)	PC3 (15.06%)
Arable	**0.539**	0.398	**0.540**
Bog	**-0.690**	-0.439	-0.019
Broadleaf	-0.156	**-0.745**	0.327
Conifer	**-0.814**	0.041	-0.017
Low intensity agriculture	-0.400	**-0.648**	**0.539**
Pasture	-0.541	**0.738**	-0.216
Scrub & hedgerows	0.291	**-0.636**	-0.388
Wild bird cover	**0.741**	-0.072	0.298
Wetlands	0.449	-0.493	**-0.616**

Habitat models showed that small birds occurred more frequently in the diet of Hen Harrier in areas with a higher proportion of arable crops, wild bird cover and low intensity agriculture, and less frequently in areas of bog, young conifer forest and wetlands. Medium-sized birds occurred more frequently in the diet in areas with a higher proportion of bog and young conifer forest, whereas they occurred less frequently in the diet in areas of arable and wild bird cover. Small mammals had a positive association with arable areas, wild bird cover and wetlands, and negative association with bog, young conifer forest and low intensity agriculture. Full model outputs are shown in Table 4.

Table 4. Full model outputs for region (a-c), habitat (d-f), month (g-i) and winter (j-l) models. *n* = number of pellet collections. Statistically significant results are highlighted in **bold**. These models exclude the outlier roost. Intercept values for region (a-c), month (g-i) and winter models (j-l) includes the first levels of these categorical variables (lowland coastal roosts, November and 2019/20, respectively).

Model	n	Fixed effects	β ± SE	p
(a) small birds x region	40	Intercept	0.64 ± 0.19	**< 0.001**
		Lowland inland roosts	-0.61 ± 0.25	**0.02**
		Upland roosts	-0.71 ± 0.20	**< 0.001**
(b) medium-sized birds x region	40	Intercept	-0.59 ± 0.22	**< 0.009**
		Lowland inland roosts	0.24 ± 0.28	0.39
		Upland roosts	0.69 ± 0.22	**< 0.002**
(c) small mammals x region	40	Intercept	1.35 ± 0.32	**< 0.001**
		Lowland inland roosts	0.78 ± 0.41	0.06
		Upland roosts	-0.98 ± 0.34	**0.005**
(d) small birds x habitat	40	Intercept	0.17 ± 0.11	0.13
		PC1	0.19 ± 0.05	**< 0.001**
		PC2	0.10 ± 0.06	0.08
		PC3	0.20 ± 0.08	**0.02**
(e) medium-sized birds x habitat	40	Intercept	-0.41 ± 0.16	**0.01**
		PC1	-0.32 ± 0.06	**< 0.001**
		PC2	-0.08 ± 0.08	0.30
		PC3	-0.15 ± 0.09	0.10
(f) small mammals x habitat	40	Intercept	1.17 ± 0.22	**< 0.001**
		PC1	0.46 ± 0.10	**< 0.001**
		PC2	-0.002 ± 0.13	0.98
		PC3	-0.29 ± 0.14	**0.04**
(g) small birds x month	9	Intercept	-0.46 ± 0.25	0.07
		January	0.34 ± 0.32	0.30
		March	0.05 ± 0.33	0.87
(h) medium-sized birds x month	9	Intercept	0.89 ± 0.26	**< 0.001**
		January	-0.76 ± 0.34	**0.02**
		March	-0.55 ± 0.34	0.10
(i) small mammals x month	9	Intercept	0.52 ± 0.60	0.38
		January	0.89 ± 0.74	0.23
		March	0.34 ± 0.72	0.64
(j) small birds x winter	28	Intercept	0.39 ± 0.30	0.20
		2020/2021	-0.15 ± 0.21	0.47
(k) medium-sized birds x winter	28	Intercept	-0.24 ± 0.37	0.51
		2020/2021	0.11 ± 0.23	0.64
(l) small mammals x winter	28	Intercept	0.65 ± 0.45	0.15
		2020/2021	-0.31 ± 0.86	0.72

Temporal variation in diet composition

We compared diet across November, January, and March during the winter of 2020/21 for three roosts: two upland roosts and one lowland inland roost (Fig. 3). The occurrence of small birds and small mammals did not change significantly in the diet across these months. There was a significant decline in the occurrence of medium-sized birds in the diet between November (71.0 ± 10.7%) and January (52.5 ± 6.2%, *P* = 0.02). This was primarily driven by declines in the occurrence of Snipe in the diet over this period. Five roosts were included in a cross-winter comparison of diet: three upland roosts and two lowland coastal roosts (Fig. 4). Across these roosts, small mammals remained relatively stable in the diet, whereas the occurrence of small birds and medium-sized birds in Hen Harrier diet varied between winters, although the observed differences were not statistically significant.

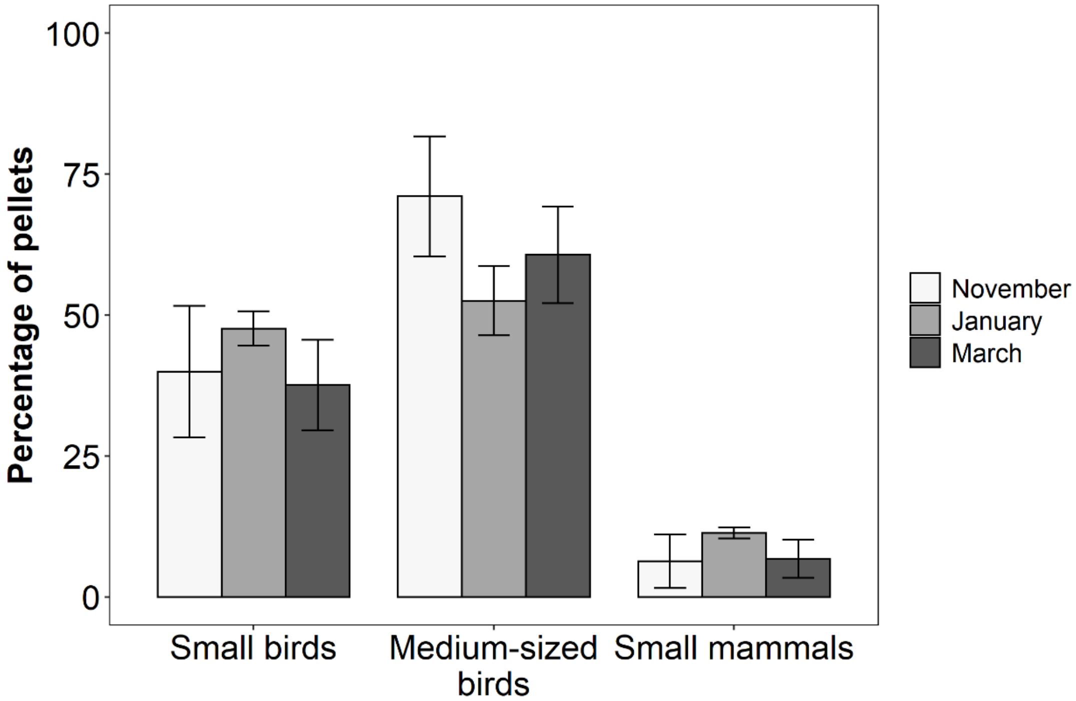

Figure 3. Mean (± SE) percentage occurrence of each prey item in the winter diet of Hen Harrier across winter months.

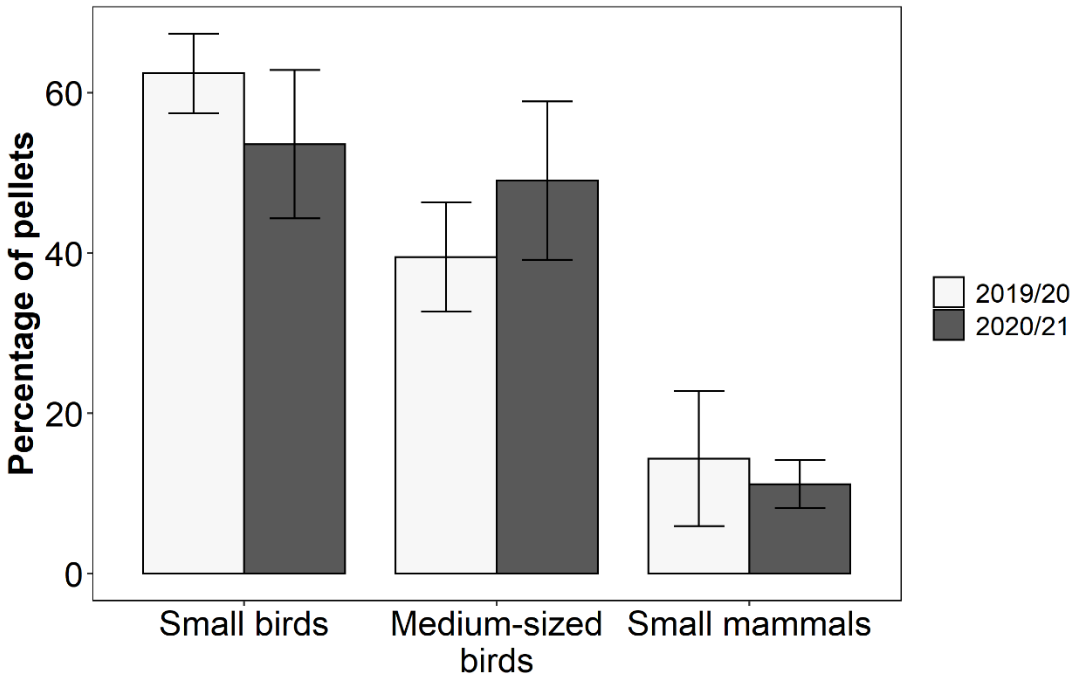

Figure 4. Mean (± SE) percentage occurrence of each prey item in the winter diet of Hen Harrier between years.

Discussion

Our results describe the winter diet of Hen Harrier in the western-most part of their range and the variation in diet composition across regions, habitats and over time. From lowland coastal roosts through lowland inland and upland roosts, there are contrasting patterns in the occurrence of prey groups in Hen Harrier pellets; medium-sized birds increase in occurrence along this gradation while small birds and small mammals decrease. These patterns appear to be driven by differing habitat composition across these areas. Arable areas typically found around lowland coastal roosts, together with wild bird cover and low-intensity agriculture, were associated with a prevalence of small birds and small mammals in Hen Harrier diet. In contrast, bogs, and young conifer plantation forests, which are more typically a feature of upland areas, where most large-scale commercial forestry is located in Ireland, were associated with a prevalence of medium-sized birds in the diet. Significant temporal variation in diet composition was observed across months and was most pronounced for medium-sized birds, whereas non-significant variation in the proportion of small birds and medium-sized birds in Hen Harrier diet was observed between winters. Our results also highlight the contribution that non-native small mammals can make to Hen Harrier diet. While direct observation of foraging birds is assumed to give the most accurate measure of diet composition (Redpath et al. 2001), these data are difficult and time consuming to collect, particularly during the winter as captured prey are consumed at or near the point of capture and not brought back to one location (such as a nest) to be consumed. The pellet frequency method we employed in this study is a widely used tool that provides an accurate overall assessment of diet composition (Redpath et al. 2001, Smiddy and Cullen, 2017).

Winter diet of Hen Harrier

This is one of the most comprehensive studies of Hen Harrier winter diet to date, with much of the previous research focussing on smaller numbers of winter roosts and/or pellets (Marquiss 1980, Smiddy and Cullen 2017, Watson 2017). Overall, Hen Harrier winter diet in this study was dominated by small birds (occurring in 52.8% of pellets), followed by medium-sized birds (46.1% of pellets) and small mammals (11.8% of pellets). Lizards, medium-sized mammals, and large birds occurred at much lower numbers (0.5%, 0.3% and 0.2% of pellets, respectively). These results show some differences from other studies in Ireland, Great Britain, and elsewhere within the Hen Harrier's range. Smiddy and Cullen (2017) analysed 163 pellets from lowland, coastal winter roosts along the south coast of Ireland and found avian prey in 77.2% of pellets and mammalian prey in 39.9% of pellets. The high proportion of mammals in Hen Harrier diet that study may reflect the influence of roost location, with small mammals occurring at relatively high levels in the diet of Hen Harriers using lowland coastal roosts in our study. In Great Britain, as in the current study, small birds often dominate the diet, particularly species such as Skylark (*Alauda arvensis*; Balfour and Macdonald 1970, Dickson 1994, Clarke et al. 1997, Dobson et al. 2009). Hen Harrier diet varies between different areas across Europe, being dominated by small birds in some areas and by mammals in others, with some flexibility observed in response to local habitat and prey availability (Toffoli 1994, Bro et al. 2006, Vervoort and Klaassen 2016) and between sexes (Marquiss 1980, van Manen 1996, Clarke et al. 1997). In many parts of mainland Europe, small mammals are the most important component of Hen Harrier diet in winter (Toffoli 1994, Bro et al. 2006) with voles comprising more than 85% of the diet in some areas (van Manen 1996, de Boer et al. 2013, van Boekel and Berghuis 2014). A shift in diet composition has been reported across the winter with the importance of small birds decreasing as that of small mammals increases through the early winter, with both declining in response to increasing lagomorph consumption in early spring (Clarke et al. 1993, 1997). The current study further demonstrates temporal and geographic variation in Hen Harrier diet in a region where the availability of small mammals is more limited and patchily distributed than in most other parts of the species' range.

Variation in diet across regions

There were pronounced differences in Hen Harrier diet across regions in the current study. The greater prevalence of small birds and small mammals in the diet at lowland coastal roosts likely reflects their availability in the surrounding environment. Lowland coastal areas experience higher temperatures and generally less severe weather in winter compared with inland or upland areas. As a result, small birds overwinter in larger numbers in these areas (Newton 2008). Higher winter temperatures are also likely to be favourable for small mammals, allowing higher overwinter survival of populations in lowland versus upland areas. Variation in prey availability may also be a contributing factor, with small mammals and small birds perhaps being easier to catch in the winter stubble of arable fields that most often occurred around lowland coastal roosts, compared to habitats with more complex vegetation structures in other regions. Lowland inland areas serve as a mid-point in the transition in prey communities between lowland coastal areas and upland areas. Here, a small decrease was observed in the number of small birds in Hen Harrier diet, with a corresponding increase in the number of medium-sized birds, primarily Snipe and thrushes, including Redwing. The more extreme weather conditions in upland areas are likely unfavourable to small mammals and small birds, and this is reflected in their comparatively lower levels of occurrence in Hen Harrier diet. Larger and more resilient medium-sized birds, such as Snipe and Redwing, are more capable of persisting in such areas over winter. The sex and age of Hen Harriers may also have an influence on observed variation in diet composition across regions (Marquiss 1980, Clarke et al. 1997). More agile, experienced adult males, that typically occur more frequently at upland roosts (McCarthy et al. in prep), may be more capable of catching species such as Snipe, whereas less experienced immature Hen Harriers, more often recorded in lowland and coastal areas, may target easier to catch small birds and small mammals. These results highlight the importance of considering local variations in diet composition when devising conservation strategies for Hen Harriers across their range. Gaining a more thorough understanding of the drivers of these regional variations in diet will require further research.

Effect of habitat on diet composition

Another important driver of observed differences in diet between areas is the influence of surrounding habitat. There was a significant positive association between the occurrence of small birds and small mammals in the diet with the proportion of arable crops, wild bird cover and low-intensity agriculture in the surrounding landscape. These are important foraging habitats for Hen Harrier, providing an abundance of prey, particularly in winter (Gillings et al. 2005). Over-winter stubble in arable areas provides small birds such as Linnet (*Carduelis cannabina*), Goldfinch (*Carduelis carduelis*), Yellowhammer (*Emberiza citronella*) and Skylark with an abundance of food, thereby attracting large flocks of small birds (Wilson et al. 1996, Henderson et al. 2004). The abundance of small mammals in these areas can also be attributed to the availability of food sources such as unharvested grain. The results from our study suggest that the conservation and provision of prey-rich habitats, such as wild bird cover and over-winter stubble, benefit Hen Harrier through the provision of small bird and small mammal prey.

The positive association of medium-sized birds in Hen Harrier diet with bog and young conifer forest habitats was primarily driven by two species: Snipe and, to a lesser extent, Redwing. Snipe is an open country species that occur widely throughout Ireland during the winter months. It can be found from lowland coastal areas to the uplands in a variety of habitats, including marsh, bog, and wet grassland (Nairn and O’Halloran 2012). The prevalence of Snipe in the diet in areas with bog and young conifer forest reflects their association with wetter areas where these habitats are most common (Nairn and O’Halloran 2012). Interestingly, the prevalence of Snipe in Hen Harrier winter diet in the current study (31.0% of all pellets, 36.4% of upland pellets) is far greater than previously reported by other studies in Ireland and elsewhere within their range (Clarke et al. 1997, O'Donoghue 2010, Smiddy and Cullen 2017).

Temporal variation in diet composition

We observed significant temporal variation of Hen Harrier diet in this study across winter months, with some evidence of between winter variation in diet. The occurrence of small birds and small mammals in the diet did not vary significantly across months. Medium-sized birds on the other hand occurred significantly less frequently in the diet as the winter progressed, a pattern likely driven by a decline in the number of pellets containing Snipe. Seasonal variation in diet has also been reported by other studies of Hen Harrier winter ecology. In the Netherlands, Hen Harrier diet shifted from passerines to small mammals to young lagomorphs through November to March in response to changes in the availability of prey (Clarke et al. 1993). The observed trend in the current study may reflect a similar shift in the abundance of medium-sized bird prey in the landscape as the winter progresses. It may also reflect an increase in the predator avoidance abilities of these prey as young birds become more experienced in avoiding capture. Although not statistically significant, there was some evidence of between winter variation in Hen Harrier diet, with more pellets containing medium-sized birds and less small birds in the second winter compared with the first winter. Such inter-annual variation in diet composition, particularly for medium-sized birds, may reflect annual fluctuations in the abundance of prey species such as Redwing. Redwing only occur in Ireland during the autumn and winter (Balmer et al. 2013). Cold conditions on the continent often cause a large movement of these birds to the western fringes of Europe where winter conditions are more favourable. Fluctuations in the abundance of certain prey groups may have knock-on effects for those Hen Harriers that rely more heavily upon these groups. When the availability of these prey species is low, this may lead to increased competition for prey resources and feeding areas, which could cause Hen Harriers to move wintering grounds, possibly impacting on overwinter survival. A similar dynamic has been observed in areas where cyclical population fluctuations of voles occur over several years, with Hen Harrier diet and productivity responding to this temporal variation in prey abundance (Redpath et al. 2002a). The greater temporal stability of small mammals in Hen Harrier diet may suggest that individuals that are more reliant on these prey may benefit from the greater temporal stability of these prey resources, particularly young Hen Harriers during their first winter. However, further research is needed to understand the ecological processes that influence temporal variation in diet.

Impact of non-native species on diet

This study provides the first evidence of Greater White-toothed Shrew being predated by Hen Harrier in Ireland, further demonstrating the adaptability of this raptor to variation in the availability of different prey species. The prevalence of Greater White-toothed Shrew in the diet of one individual Hen Harrier using a lowland inland roost, occurring in 61.7% of pellets, highlights the potential for significant contributions of non-native prey species to the diet of Hen Harrier in Ireland. As Greater White-toothed Shrew are highly vocal (Siemers et al. 2009), the ease with which they can be detected may in part explain their prevalence in the diet of this individual Hen Harrier in this study. Greater White-toothed Shrew will likely become an increasingly important prey item as they spread throughout the country and may have a disproportionate effect on Hen Harriers and other small mammal predators here, given the depauperate native small mammal community. Given the ongoing spread of non-native prey species across Ireland (McDevitt et al. 2014), such impacts will likely be replicated elsewhere within the Hen Harrier range.

Conservation implications

Given the importance of winter diet in the ecology and overwinter survival of the Hen Harrier, the findings from this study have relevance for the design of effective conservation strategies. However, it should be borne in mind that these findings relate to the influence of current landscape composition and associated agricultural practices for Hen Harrier ecology. As such, it may underemphasise Hen Harrier prey items that were traditionally important, but which have already been negatively impacted by anthropogenic practices and land use change.

The practice of leaving arable fields in stubble over winter, as well as the provision of wild bird cover crops, should be encouraged in important Hen Harrier wintering areas to provide stable sources of small bird and small mammal prey. The protection and retention of wet, open habitats would maintain habitat suitability for species such as Snipe, which were an important component of Hen Harrier diet in lowland inland and upland areas. This study also provides the first evidence of the potential for the non-native Greater White-toothed Shrew to contribute to Hen Harrier diet. Future increases in the abundance and range of this and other non-native small mammal species could have profound effects on the feeding ecology of Irish Hen Harrier, with knock-on impacts on survival and population dynamics. Although this study looked exclusively at winter diet, such impacts could also extend to the breeding season to affect productivity and survival of fledged young. Understanding these impacts and their consequences for Hen Harrier populations in Ireland will require further research over the coming years as the Greater White-toothed Shrew expands its range across the country.

Ethics statement

No licences were required for the fieldwork that was undertaken during this study. Pellets were collected from roosts in the middle of the day to ensure no disturbance was caused to roosting Hen Harriers.

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Chapter Five

Individual life histories and movement of satellite tagged Hen Harriers in Ireland

Satellite tagged female Hen Harrier- Female A

Photograph: Paul Kelly

Abstract

Two female Hen Harrier (*Circus cyaneus*) nestlings were fitted with satellite tracking devices in July 2017 (at ages 29 and 34 days) at their nests in the south-west and midlands of Ireland. One bird (Female A) was tracked until her death in November 2018 and the other (Female B) until the end of this study on 30th September 2021, providing the first descriptions of the movement of female Hen Harriers in Ireland across the full annual cycle. Both females occupied post-fledging dependence areas within 2km of their natal nest for three weeks prior to the onset of sudden, long-distance (>25km) juvenile dispersal at 58 and 62 days old. Both birds used temporary settlement areas (TSAs) in arable croplands during juvenile dispersal, from where they undertook brief exploratory movements before settling on their first-year wintering grounds during October 2017. Female A used the same primary wintering area on the Co. Wexford coast during both of her winters. Female B used a primary wintering area in Co. Kilkenny during her first winter, and a different primary wintering area in Co. Offaly during her three subsequent winters. Both female Hen Harriers departed their first-year wintering grounds at the end of March 2018. Female A made an unsuccessful nesting attempt during her first and only breeding season in 2018, with a natal dispersal of 17km. Female B made her first breeding attempt during her second breeding season in 2019, which was also unsuccessful, with a natal dispersal of 109km. After her first two full years, Female B largely remained in the midlands of Ireland, using lowland cutover regenerating bogs during the non-breeding season, and nesting twice more in 2020 and 2021 in the Slieve Bloom Mountains where she was hatched in 2017. This study provides the first description of the movement of individual female Hen Harriers that were recruited into the Irish breeding population across the full annual cycle, and across multiple years. Movement patterns of individual Hen Harriers can determine survival and reproductive success, and their investigation is critical to informing conservation actions.

Introduction

Studying the individual life histories of satellite tracked birds provides a unique insight into behaviours that would otherwise go unrecorded and that may have a significant influence on survival and population dynamics (Moliner et al. 2015). Individual patterns of movement and space use are key factors in survival, with individual behaviours being an important consideration in conservation management, particularly for small and declining populations (Merrick and Koprowski 2017). Individual behaviours can be influenced by a range of factors, including age (Daunt et al. 2007), sex (Lewis et al. 2002), and cognitive abilities (Morand-Ferron et al. 2015).

Advances in remote tracking technology, particularly in relation to reductions in the size of transmitters and the cost of data collection, have led to advances in our understanding of raptor behaviour, ecology, and conservation (López-López et al. 2014, Moliner et al. 2015, Sarasola et al. 2018). Hen Harriers (*Circus cyaneus*) are experiencing widespread declines across much of their range (Fernández-Bellon et al. 2021), and although research has explored the anthropogenic pressures that are driving these declines (Wilson et al. 2009a, 2012, Fernández-Bellon et al. 2015, Caravaggi et al. 2019, 2020), gaps remain in our understanding of many aspects of their year-round ecology. In recent years, we have begun to see the benefits of the use of remote tracking technology which has provided new insights into Hen Harrier ecology and conservation, including studies of habitat use (Wilson et al. 2009b, Klaassen et al. 2014, Bělka and Bělková 2019, Klaassen 2019), juvenile dispersal (Murphy 2019), and illegal persecution (Murgatroyd et al. 2019).

We used satellite telemetry to document the movement of two female Hen Harriers in Ireland across the full annual cycle over multiple years. Prior to this study, no published studies were available on the fine-scale movements of individual Hen Harriers in Ireland and information was confined to occasional observations in the field. Satellite tracking technology provides a unique insight into the life-histories of Hen Harriers, revealing new behaviours and movements that were previously unknown and that have important implications for their ecology and conservation management.

Methods

The tagging procedure we used in this study employed light-weight, 9.5g satellite tracking devices (known as Platform Terminal Transmitters; hereafter PTTs) fitted to nestlings using a backpack-style harness and is described in detail in Chapter 2. The PTTs were on a 4 hour on/19 hour off transmission cycle. As the PTTs were solar powered, transmissions did not always occur during every cycle, particularly in the middle of winter and during the nest incubation period. We tagged the two female Hen Harriers in July 2017 and one of these birds, Female A, survived until 30th November 2018, providing 454 days of high-quality location data. The second bird, Female B, is still alive at the time of writing (9th March 2022) and provided 1,027 days of high-quality location data from this individual for use in this study (until 30th September 2021). High quality location data are location classes 3, 2 and 1, which correspond to an accuracy of 0.4, 1.0 and 2.5km, respectively (Douglas et al. 2012). We calculated home ranges using 95% Minimum Convex Polygon (MCP), unless otherwise stated, with high quality daytime location fixes. Both daytime and night-time location fixes were used to assess movements and dispersal. Mapping was carried out using QGIS version 3.12.3 (QGIS.org 2021) and R version 4.0.2 (R Core Team 2020) including package *adehabitatHR* (Calenge 2006).

Results and Discussion

Female A

Tagging and post-fledging dependence period

On 17th July 2017, we fitted a 29-day old female Hen Harrier nestling (Female A) with a satellite tracking device (PTT) (Plate 1). She weighed 505g at the time of tagging, and the PTT and harness used weighed 2% of her body weight at tagging, which is within the limit of 3% suggested by Kenward (2001) as being the maximum recommended weight of a tracking device for a bird of prey. This female was the oldest of four chicks, two males and two females, in a nest located in the Stacks to Mullaghariek Mountains, West Limerick Hills and Mount Eagle Special Protection Area (SPA) on the border between Co. Cork and Co. Kerry, in a valley dominated by gorse (*Ulex* sp.) and heather (*Calluna* sp.). The nest was situated approximately 15m from mature conifer forest bordering the top of the valley (Plate 2). Mature conifer forest dominated the immediate area (within 1km) around the nest site.

Plate 1. Female A fitted with her Platform Terminal Transmitter (PTT), July 2017. The PTT and antenna can be seen on her back.

Plate 2. Female A nest valley habitat, July 2017.

The post-fledging dependence period is the time between fledging and the onset of dispersal and is a crucial stage in the life history of birds (Weathers and Sullivan 1989). For young raptors, this is when they develop their flying (Watson

1977, Bustamante and Hiraldo 1989, Kitowski 2002) and hunting skills (Watson 1977, Bustamante 1993, Kitowski 2004), learning to survive independently of their parents, sometimes through social learning (Kitowski 2009). However, this period is poorly understood for many raptor species (McIntyre and Collopy 2006), and particularly Hen Harriers (Watson 1977). The post-fledging dependence period for Female A lasted approximately three weeks, which is typical for Hen Harriers (Watson 1977, O'Donoghue 2010) and for the closely related Northern Harriers (*Circus hudsonius*) (Beske 1982). The post-fledging dependence period shows some inter-individual variability for Hen Harriers, with some juveniles recorded close to their nest site as much as five weeks after fledging (Hardey et al. 2013, Chapter 2). During this time, juvenile Hen Harriers, like other harrier species, are provisioned by one or both adults (Kitowski 2002, 2005, 2009, O'Donoghue 2010). Female A had a home range of 4.0km^2 (2.0km^2 85% MCP) during the post-fledging dependence period and travelled up to 2km from the nest in the days immediately prior to dispersal, a movement behaviour often seen in birds of prey (Delgado et al. 2009).

Juvenile dispersal

Between 17th and 19th August 2017 (60 to 62 days old), Female A began juvenile dispersal, undertaking a journey of 170km in a north-west direction (Fig. 1). Her first location after dispersal was on 19th August when she roosted in an arable field in Co. Laois. For the following ten days, she roosted in at least four different arable fields within 5km of each other in this area. Roosting in arable fields has seldom been reported for Hen Harriers in Ireland or Great Britain. In a study of 203 winter roosts in Ireland, only two were recorded in crops (O'Donoghue 2021). Similarly, in a study by Clarke and Watson (1990), just four of 202 roosts studied across Britain and Ireland were in crops, with one of these holding up to seven Hen Harriers before being destroyed by crop harvesting. As most Hen Harrier roost monitoring takes place during and after the annual harvesting of many crops, it is possible that the importance of arable fields for roosting by Hen Harriers in Ireland has been underestimated by previous studies.

Figure 1. Juvenile dispersal movement direction and distance of Female A, 17th to 19th August 2017.

By 30th August (73 days old), Female A had travelled 14km further east. She remained in this area for 49 days until 17th October (121 days old), establishing a juvenile temporary settlement area (TSA) that covered 128km^2 across Co. Laois and Co. Carlow (Fig. 1). The dominant land use within the TSA was arable fields, with daytime and night-time location fixes suggesting she was both foraging and roosting in arable fields. Between 30th August and 17th October, she left the TSA on four occasions on brief exploratory movements, the furthest of which was to another arable area 62km to the north. Similar dispersal behaviour has been reported for Northern Harriers in North America, where juveniles also undertake short exploratory movements outside of TSAs (Beske 1982). Exploratory movements such as these are common behaviour of young raptors (Newton 1979, Soutullo et al. 2006, McCaslin et al. 2020), which is driven by a search for food, while also enabling them to build a picture of the surrounding landscape, and to find new areas that they may utilise in the future. Landscapes dominated by arable fields are likely attractive for dispersing juvenile Hen Harriers due to the relative abundance of prey these area provide, primarily small mammals and small birds (Wilson et al. 1996, Moorcroft et al. 2002, Gillings et al. 2005, Chapter 4). They also provide suitable roosting sites, meaning that the use of foraging grounds is not restricted by proximity to suitable roosting habitat, and juveniles do not need to expend energy travelling between separate foraging and roosting sites. However, once the crops are harvested, these areas are no longer suitable as roosting sites for Hen Harriers if there are no other alternative roosting habitats in the area (van Gasteren 2018). For Female A, it is possible that she was displaced from this TSA due to decreasing availability of suitable roosting habitat following crop harvesting.

On 18th October (122 days old), she began a southward movement away from her TSA (Fig. 2). She continued to use arable areas, including an area where another satellite tagged Hen Harrier, Female B, was overwintering the same year (details on this bird below), with both birds recorded at the same salt marsh during the daytime on 21st October. This highlights the individuality of Hen Harrier settling behaviour, as an area that one Hen Harrier selected for overwintering was only used in passing by another Hen Harrier of similar age and same sex. On 22nd October (126 days old), Female A arrived on the south Co. Wexford coast, 181km to the east of her natal nest and 72km to the south of her dispersal TSA (Fig. 2). This is where she settled for the winter of 2017/18. This juvenile dispersal distance is comparable to that reported for juvenile female Hen Harriers in Great Britain (Etheridge and Summers 2006). These insights into dispersal characteristics are crucial for the design of effective conservation strategies (Paradis et al. 1998, Soutullo et al. 2006).

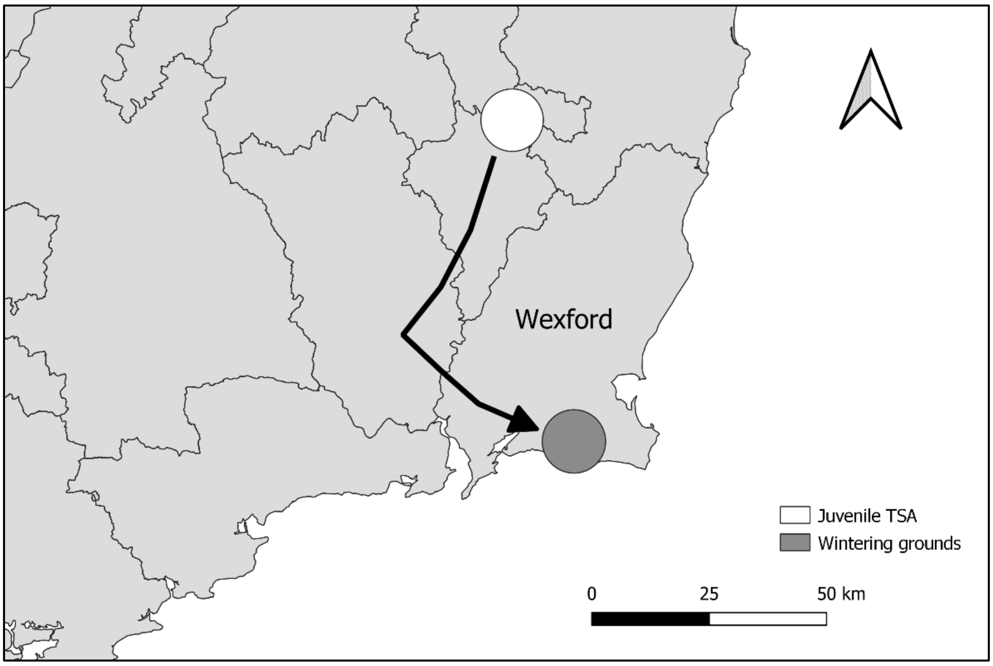

Figure 2. Movement of Female A from her juvenile temporary settlement area (TSA) to her wintering grounds, 18th to 22nd October 2017.

First winter

Between 22nd October 2017 and early March 2018, Female A used five separate roost areas within her winter home range on the south Co. Wexford coast. One of these was her primary roost, which she was recorded using for 80 nights (out of 136 nights) during this time. She was recorded using the four other roosts on 15 nights or less, and all were located within 8km of her primary roost. Her primary winter roost was an island reedbed which was occasionally also used by two other Hen Harriers (an adult male and a ringtail). Her second-most frequently used roost (15 nights) was a larger reedbed that was primarily used by ringtails (one to six). Her third-most used roost (five nights) was an overgrown rush/gorse field that was within 200m of wild bird cover and arable fields. The remaining two roosts (one night each) were in salt marshes. It was not possible to establish whether the three least used roosts were also used by other Hen Harriers. Her winter home range over this period was 127km^2. Female A continued to use her primary roost site until 7th March 2018 (262 days old). After this and until 22nd March, her movements and behaviour changed as she began to move frequently between new roost areas within her home range that she had not used during the previous months.

First breeding season

On 23rd March (278 days old), Female A departed her wintering grounds and travelled north to the dispersal TSA that she had used between August and October the previous autumn (Fig. 3). Here, she used the same arable field that she had foraged and roosted in on 1st October 2017 (105 days old). It is unclear what vegetation she roosted in as arable crops would unlikely be tall enough for roosting given the time of year. She may have roosted in a cover crop, or it is also possible that she roosted in a tree, a behaviour that has occasionally been reported for Hen Harriers (Clarke and Watson 1990, Scott 1994, Bělka and Bělková 2019), and has been observed for Montagu's Harriers (*Circus pygargus*) following the loss of roosting habitat to crop harvesting (van Gasteren 2018). By the next day, she had travelled 105km south-west to an upland area of Co. Waterford, and between 25th March and 15th April, she foraged and roosted along the Co. Cork coast, using four known Hen Harrier marshland and reedbed coastal roosts. Between the 16th and 19th of April, she roosted in various locations in west Co. Waterford.

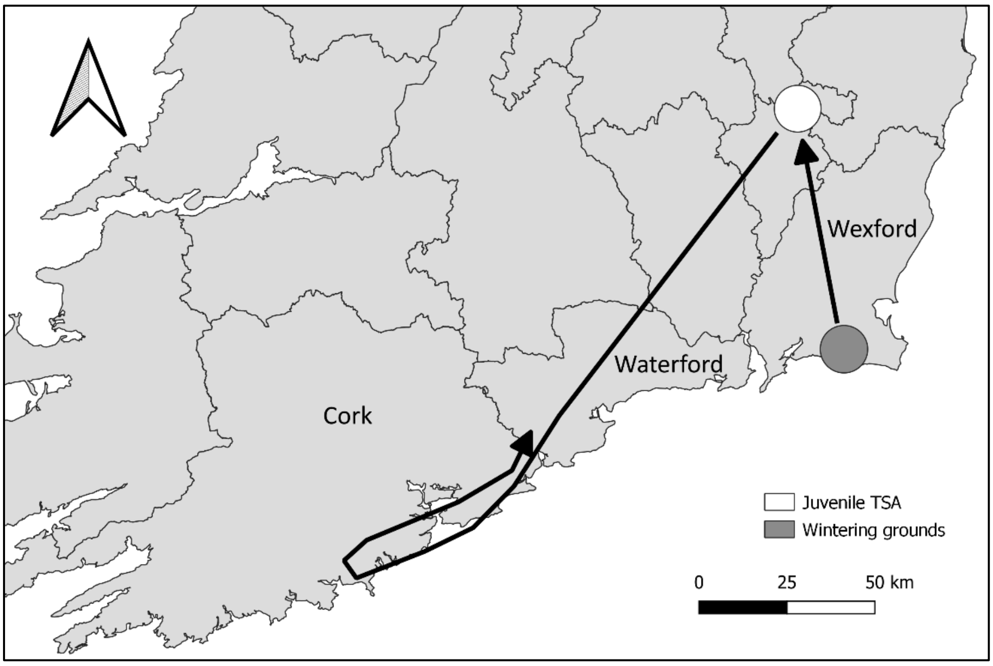

Figure 3. Movement of Female A between 23rd March and 19th April 2018.

On 20th April (306 days old), she moved inland to a known Hen Harrier breeding territory in the Boggeragh Mountains in Co. Cork (Fig. 4). She remained at this breeding territory until the morning of 24th April when she travelled 21km south-east to marshland on the outskirts of Cork city. She roosted at this marsh for two nights before moving 49km to the north-west. Between then and the 29th of April, she travelled north-west through Co. Cork and into Co. Kerry (Fig. 4).

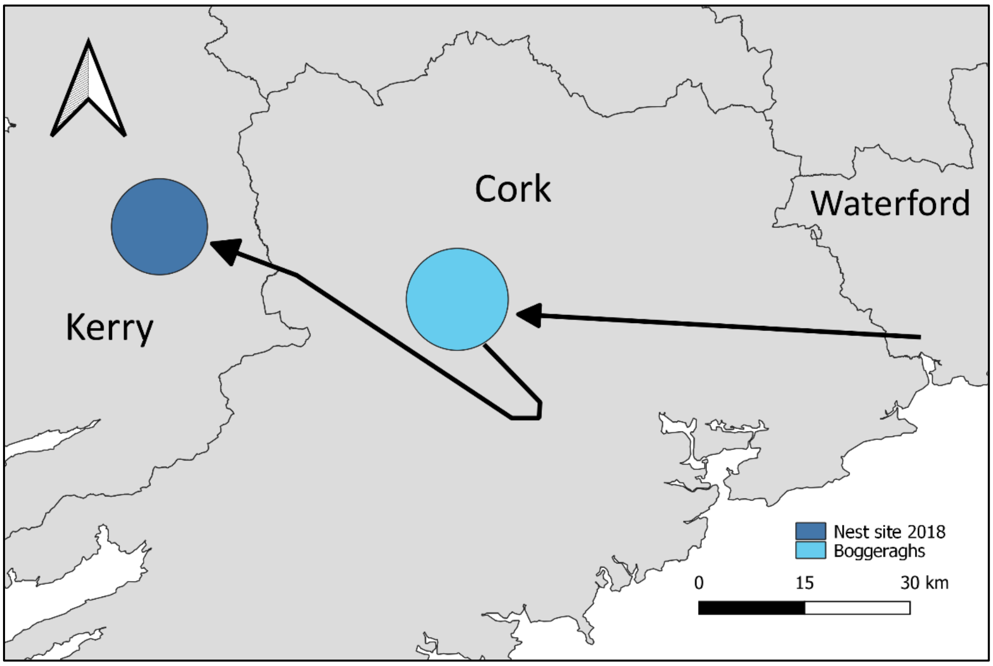

Figure 4. Movement of Female A between 19th and 29th April 2018.

The movement of Hen Harriers between their wintering and breeding grounds has not previously been described in detail in Ireland, which has limited our knowledge of this aspect of Hen Harrier ecology. The number of Hen Harriers using winter roosts has previously been reported to decline through March (Clarke and Watson 1990, Chapter 3). However, Hen Harriers do not appear in the breeding grounds in large numbers until April, with nest building typically observed from April through to early May (Watson 1977, Irwin et al. 2008, Hardey et al. 2013). Hen Harrier movements and behaviour in the interval between leaving the wintering grounds and arriving at the breeding grounds is a significant knowledge gap. The movements of Female A in this study demonstrate that some juveniles in their first year may spend time exploring lowland areas before moving to upland breeding areas. As Hen Harriers often vacate the breeding grounds in the winter, the timing of their return to the breeding grounds may influence where they settle to breed as some territories may already be occupied if their return to the breeding grounds is late (Newton 1979). This also has implications for monitoring as it demonstrates that some pairs may not appear on territory until early May. This may explain why Female A did not settle at the first breeding territory that she visited. In addition, the habitats used in the time between leaving the wintering grounds and settling to breed are an important determinant of breeding productivity, as females must maintain good body condition during this time (Newton 1979). The use of poor-quality habitats in this interval may lead to negative carry-over effects such as low reproductive output during the subsequent breeding season.

On 29th April 2018 Female A visited a large area of upland cutover bog in Co. Kerry, and after 1st May (317 days old) she remained in this location. Observations on 14th May (330 days old) from a distant vantage point confirmed that she had paired up with an adult male and, based on her behaviour, was likely incubating a clutch of eggs, just two weeks after first arriving in the area. Their nest was located in a bracken, heather and *Molinia* dominated valley, surrounded by cutover bog where peat was harvested annually, and the bog was occasionally burned. Only a fraction of the bog remained intact. As is the case in in other Hen Harrier populations, such as in Wales (Whitfield and Fielding 2009), this demonstrates that female Hen Harriers can breed in their second calendar year. Female A's natal dispersal distance (straight line distance from her natal nest to where she first bred) was 17km, which is consistent with female natal dispersal described previously (Etheridge et al. 1997, Whitfield and Fielding 2009, O'Donoghue 2010). Unlike her natal nest, her breeding nest was not located within the Hen Harrier SPA network. This highlights the importance of accounting for natal dispersal of offspring beyond protected areas when designating and establishing conservation objectives for these areas. It also highlights the importance of applying conservation measures beyond the current SPA network. Between 1st May and 12th July, her home range was 13.8km^2 (85% MCP home range of 4km^2). This compares with suggested home range sizes of between 0.1 and 5.4km^2 for females (Schipper 1977). Tracking data suggested that she did not travel further than 2km from her nest site, which is shorter than previously reported in Ireland (7.5km from the nest for an adult female Hen Harrier; Irwin et al. 2012), but similar to that reported in Scotland (Arroyo et al. 2014). Variation in foraging distance of breeding females may be related to hunting proficiency of the male, immediate surrounding habitat, and individual behaviours (Newton 1979).

The oldest chick in Female A's nest was selected for satellite tagging, with a pre-tagging nest visit confirming a brood of 4 chicks on 12th July 2018. A nest visit carried out on 13th July with the aim of tagging the oldest chick revealed that the nest had been predated. A dead, intact chick found 2m from the nest had puncture wounds on the neck indicating predation by a mammalian predator, likely a Red Fox (*Vulpes vulpes*). Predation is one of the most commonly suspected causes of Hen Harrier nest failure in Ireland, with high predation rates likely driven by land-use changes in upland areas (Sheridan et al. 2020, Chapter 7). For example, all of the ten Hen Harrier nesting attempts in the Slieve Blooms SPA failed as a result of suspected nest predation in 2021 (Hen Harrier Project 2021). Two days after this event, on 15th July (392 days old), Female A was again observed at her nest site and satellite tracking data revealed that she travelled 115km east-northeast to an arable area in south Tipperary later that day.

Second non-breeding season

Prior to this satellite tracking project, very little was known about the movements of breeding Hen Harriers in the days and weeks after a failed breeding attempt as it had not been possible to collect detailed information on this aspect of Hen Harrier behaviour using traditional monitoring methods such as vantage point watches and wing tagging (Etheridge and Summers 2006, Whitfield and Fielding 2009). Our results show that Female A did not immediately return to her wintering grounds (Fig. 5). Instead, between 15th July and 10th August, she travelled widely across the south of Ireland, visiting two well-known Hen Harrier breeding areas, the Ballyhoura Mountains and the Mullagharierk Mountains during this time.

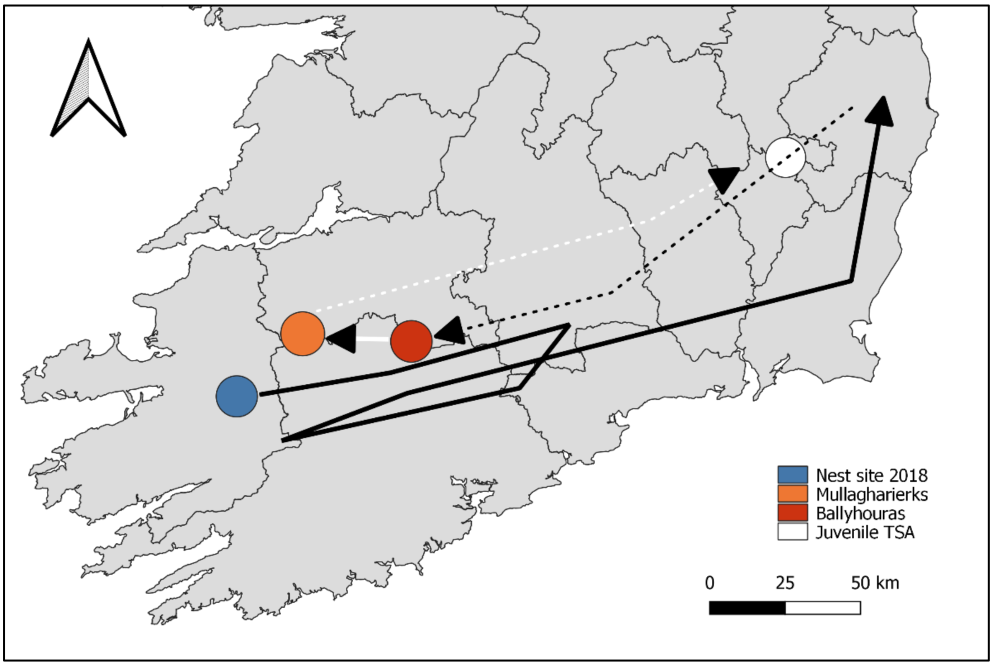

Figure 5. Movement of Female A between 15th July and 10th August 2018. Chronological sequence is: (i) solid black line; (ii) dashed black line; (iii) solid white line; and (iv) dashed white line.

On 10th August 2018 (418 days old) she returned to the same arable fields that she used as her main TSA the previous year. She remained here, foraging and roosting in arable fields for 38 days, until 17th September. Her home range during this time covered 46km^2. This compared with the much larger home range of 128km^2 she used as a TSA the previous year in the same area. The smaller home range in her second year may reflect her improved foraging abilities and efficiency, and knowledge of optimal foraging areas, with home ranges of raptors reported to decrease after their first year (Cadahía et al. 2009). Between 18th and 24th September, she made exploratory movements north and east, travelling up to 33km from her TSA.

On 24th September 2018 (463 days old), Female A returned to the same wintering grounds that she used the previous winter in Co. Wexford. She used the same primary roost, as well as two roosts that she again used only occasionally. Hen Harriers are known to be site faithful during the breeding season (Balfour and Cadbury 1979, Etheridge et al. 1997, Watson and Thirgood 2001, Whitfield and Fielding 2009, Geary et al. 2018), with site fidelity thought to extend to the non-breeding season, based on the limited available information (O'Donoghue 2010). Female A displayed strong site fidelity, both during the autumn period and early winter. Based on temperature and activity data from her PTT, she died on 30th November 2018 in pasture fields 5km to the east of her primary roost, and 3km to the west of her secondary roost, aged 530 days old. We recovered her carcass and tag on 3rd December 2018 (Plate 3). The most likely cause of death was predation by another bird of prey, possibly a Peregrine Falcon (*Falco peregrinus*) or a Common Buzzard (*Buteo buteo*), due to the lack of chewed feathers and marks on the sternum of the carcass. Predation of harriers by other birds of prey is thought to be a rare occurrence, though Peregrine Falcons have been recorded predating Montagu's Harriers (*Circus pygargus*) and Hen Harriers in Spain (Zuberogoitia et al. 2012). Predation of adult Hen Harriers by other raptors has not been observed in Ireland previously. Between 24th September and the time of her death, she used an area of 31.7km^2. Over the course of her life, she used a total area of 17,446km^2 (Fig. 6).

Plate 3. Carcass and tag of Female A, December 2018.

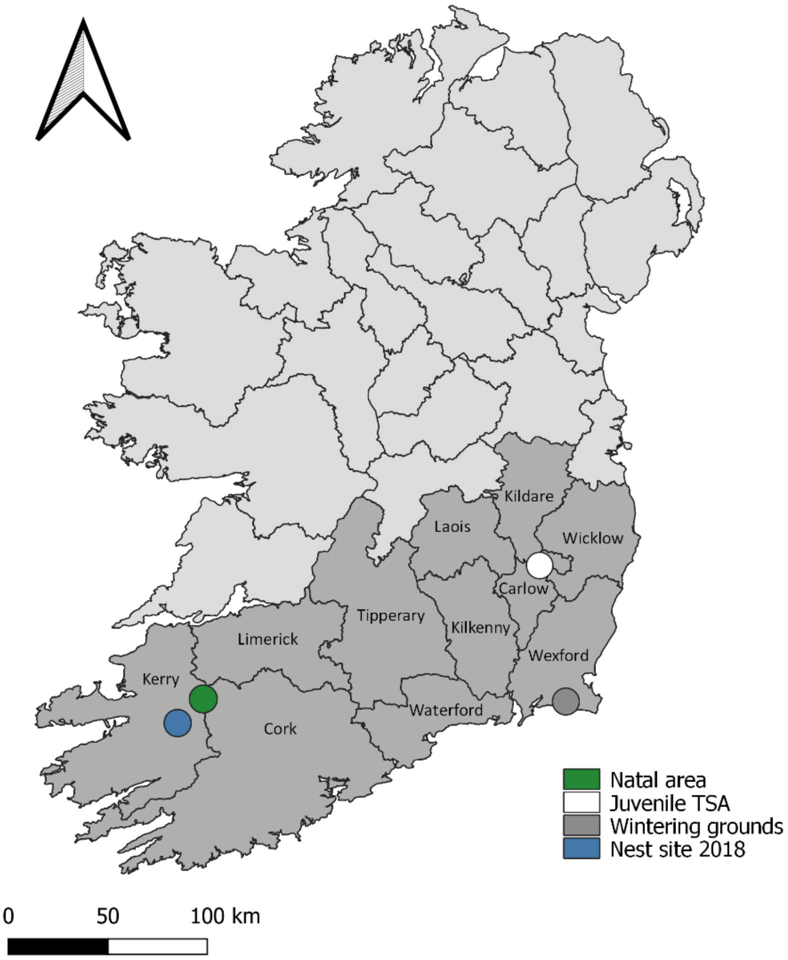

Figure 6. Main areas used by Female A during her lifetime. Counties coloured dark grey are those she visited.

Female B

Tagging and post-fledging dependence period

On 12th July 2017, we fitted a 34-day old female Hen Harrier nestling with a PTT at a nest in the northern area of the Slieve Blooms Mountains SPA in Co. Laois. She weighed 530g, with the PTT and harness weighing 2% of her body weight at tagging, within recommended limits (Kenward 2001). This Hen Harrier (Female B) was the oldest of a brood of three chicks. Her nest was located in open heather moorland which dominated the area (within 1km) around the nest site. At 22 days, the post-fledging dependence period for Female B was approximately 4 days shorter than Female A. Her home range during the post-fledging dependence period was 6.4km^2 (2.1km^2 85% MCP), which is comparable to the 4.0km^2 (2.0km^2 85% MCP) home range recorded for Female A, and she remained within 2km of her nest prior to dispersal. This is the first empirical information on the length of the post-fledging dependence period and on the movement of juvenile Hen Harriers between fledging and dispersal in Ireland. It highlights the requirement for protection from disturbance around the natal area in the weeks after fledging.

Juvenile dispersal

Female B remained on her natal territory until 4th August (57 days old), before undertaking a sudden long-distance dispersal which brought her 111km south-east to an arable area on the east Co. Waterford coast the following day (Fig. 7). She remained here for ten days, using two arable areas 5km apart. On 14th August (67 days old), she made a brief exploratory movement 55km to the west, before returning east the following day to an arable area just 13km north of where she had originally settled immediately after dispersal on 5th August. She remained here for a further 32 days until 16th September (100 days old), using this as her primary dispersal TSA. This is also where she eventually settled for the 2017/18 winter period. Similar to the behaviour of Female A during juvenile dispersal, Female B roosted and foraged in arable fields. Between 5th August and 16th September, she used an area of 108.9km^2. However, she used this large area only for the first 10 days and between 15th August and 16th September she used just 25.7km^2. This is considerably smaller than the 128km^2 dispersal TSA used by Female A. Conservation efforts for Hen Harriers currently ignore the potential for birds in their first year to spend considerable amounts of time in TSAs away from known breeding and wintering grounds. The similarity in use of dispersal TSAs with stable home ranges by both birds in this study, coupled with the typically low survival of Hen Harriers in their first year (Chapter 2), suggests that TSAs may represent crucial areas of conservation interest (Balbontín 2005, Moliner et al. 2015, Sarasola et al. 2018).

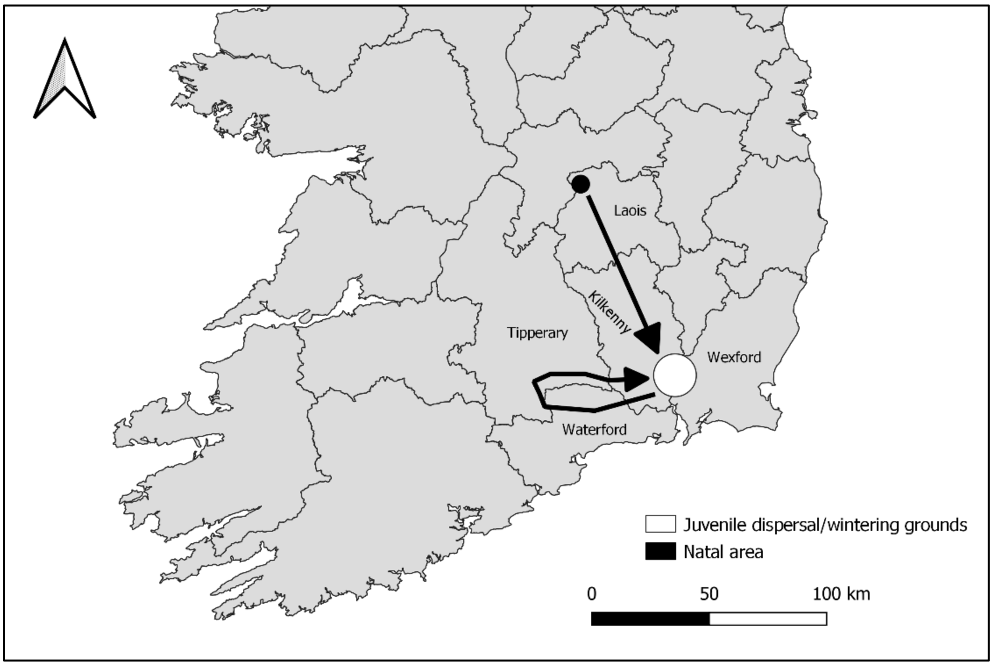

Figure 7. Movements of Female B from her natal site to her juvenile temporary settlement area (TSA) and exploration between 4th August to 16th September 2017.

Between 17th and 20th September (101 to 104 days old), Female B travelled west from her dispersal TSA to visit several known upland Hen Harrier breeding areas including the Ballyhouras (106km west of her TSA), Boggeragh Mountains (133km west of her TSA) and Knockmealdown Mountains (67km west of her TSA; Fig. 8). She returned to her dispersal TSA by 21st September and remained here until 25th September before exploring parts of the midlands until 2nd October. During this time, she visited a known communal Hen Harrier winter roost, and a regenerating cutover bog that she would come to use frequently in the coming years (Area 1). Such exploratory movements of juvenile Hen Harriers during juvenile dispersal may be a common behaviour, as Female A also undertook similar, though less extensive, exploratory movements. Detailed information on dispersal characteristics of raptors is difficult to obtain and this study makes an important contribution to the literature in this area providing basic information required to understand pressures and conservation priorities (Cadahía et al. 2010, Serrano 2018).

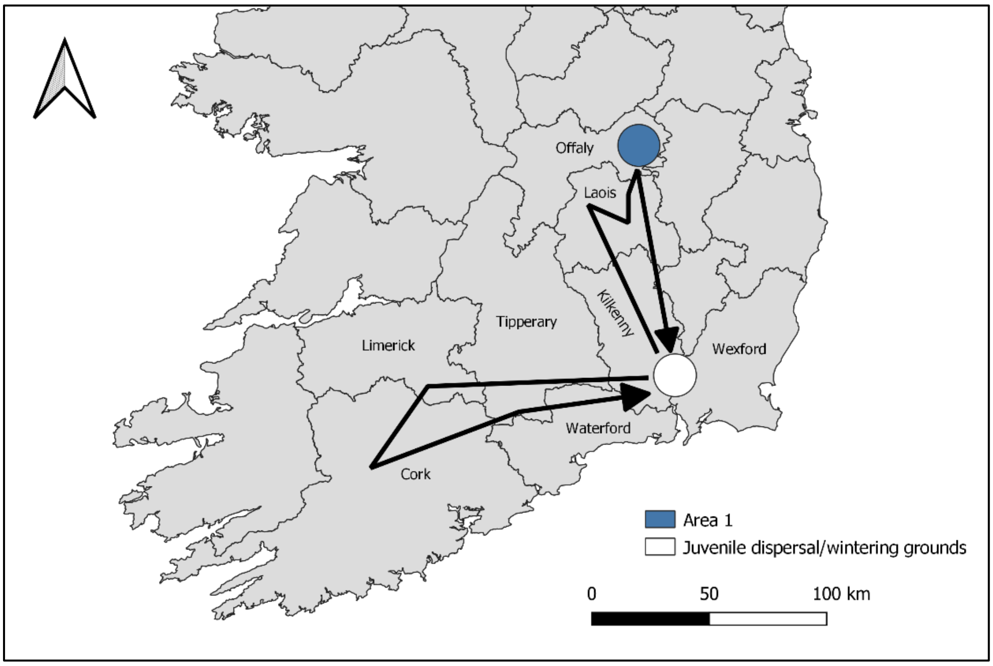

Figure 8. Movements of Female B between 17th September and 3rd October 2017.

First winter

By the morning of 3rd October (117 days old) she had returned to her dispersal TSA in south-east Co. Kilkenny and was roosting on a salt marsh, rather than in arable fields as she had done when using the area as a dispersal TSA. As with Female A, this change of roosting habitat may have been driven by decreasing availability of arable crops suitable for roosting due to harvesting. She settled here for the winter and remained until 25th March 2018 (290 days old). Her primary roost during the winter period was a salt marsh on the River Barrow. Her winter home range was 67.2km^2. This compares with 127km^2 for Female A during her overwinter period. During her first winter, Female B was recorded undertaking one exploratory movement, travelling 34km from her primary winter roost along the Waterford coast on 10th November (155 days old). She was recorded roosting away from her primary roost on only one occasion, 4th February 2018 (241 days old), when she roosted in an area of heath and grassland 4km to the north-east of her primary winter roost. This strong roost site fidelity contrasts with the behaviour shown by Female A who used four sub-roosts to her primary roost, and used a larger home range, while on her wintering grounds. This may be due to a limited availability of other potential roost sites, individual behaviour, competition, or other factors, such as disturbance. It highlights the vulnerability of some Hen Harrier wintering areas as if this primary roost site becomes unsuitable through anthropogenic land-use change, this may have led to the abandonment of the wintering area due to limited suitable alternative roost sites, as perhaps was the case for Female A at her juvenile TSA.

First breeding season

On 25th March 2018 (290 days old), two days after Female A left her wintering grounds (23rd March, 278 days old), Female B also left her wintering grounds in south-east Co. Kilkenny and travelled 104km north to a cutover bog in east Co. Offaly (Area 1). Between 26th March and 15th May, she travelled widely, visiting bogland in counties Offaly, Roscommon, and Longford (Areas 2 to 5). This included brief trips to upland breeding areas of the Slieve Aughties and West Co. Clare (Nest 2019 area in Fig. 9) on the same date (20th April 2018) that Female A first travelled to an upland breeding area. On several occasions during this time, Female B travelled as much as 120km between areas in a single day, in stark contrast to the sedentary behaviour she displayed during her first winter. On 15th May (341 days old), she travelled to West Co. Clare (Nest 2019), to an area just 1.2km from where she would subsequently nest the following summer (2019). She remained in this area of West Co. Clare until 5th June (362 days old), in an area dominated by planted conifer forest. Between 15th May and 5th June she used an area of 7.4km^2. Although she was in a Hen Harrier breeding area, she did not settle down to nest during this time. This contrasts with Female A who bred during her first year, as has previously been reported for Hen Harriers (Whitfield and Fielding 2009).

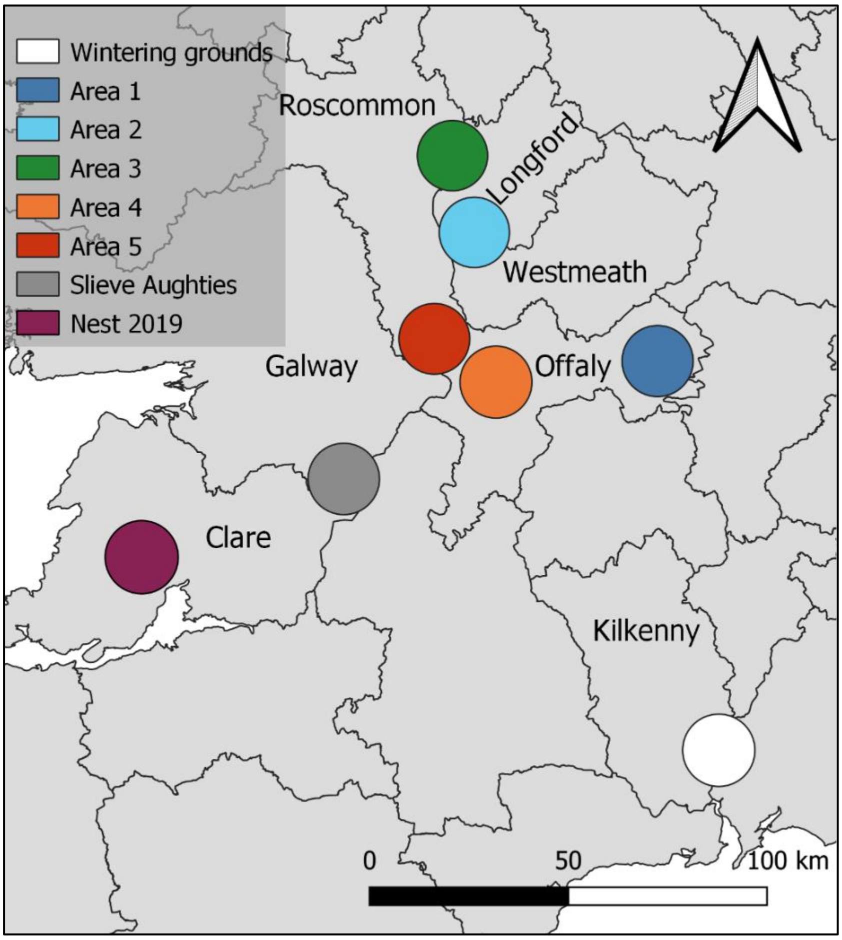

Figure 9. Areas used regularly by Female B between 25th March and 15th June 2018. Movements were so frequent that it is not possible to plot direction of travel arrows.

By 8th June (365 days old), she had returned north to the regenerating bogland of Area 5 where she remained until 5th July (392 days old), at which point she travelled 52km east to Area 1, remaining here until the 10th August (428 days old; Fig. 10). Location fixes during late July and early August showed that she was foraging within a windfarm over multiple days. While individual birds may fly close to turbines, there is evidence for displacement effects of Hen Harriers and other harrier species (Wilson et al. 2015, Fernández-Bellon 2020). Although collision risk for Hen Harriers is lower compared with other raptor species, incidences of Hen Harrier turbine collisions have been documented (Fernández-Bellon 2020).

The tracking data from Female B during this time provided a unique insight into the behaviour of non-breeding first year Hen Harriers during the breeding season. These data demonstrate that lowland regenerating cutover bogs are crucial areas for Hen Harriers even during the breeding season.

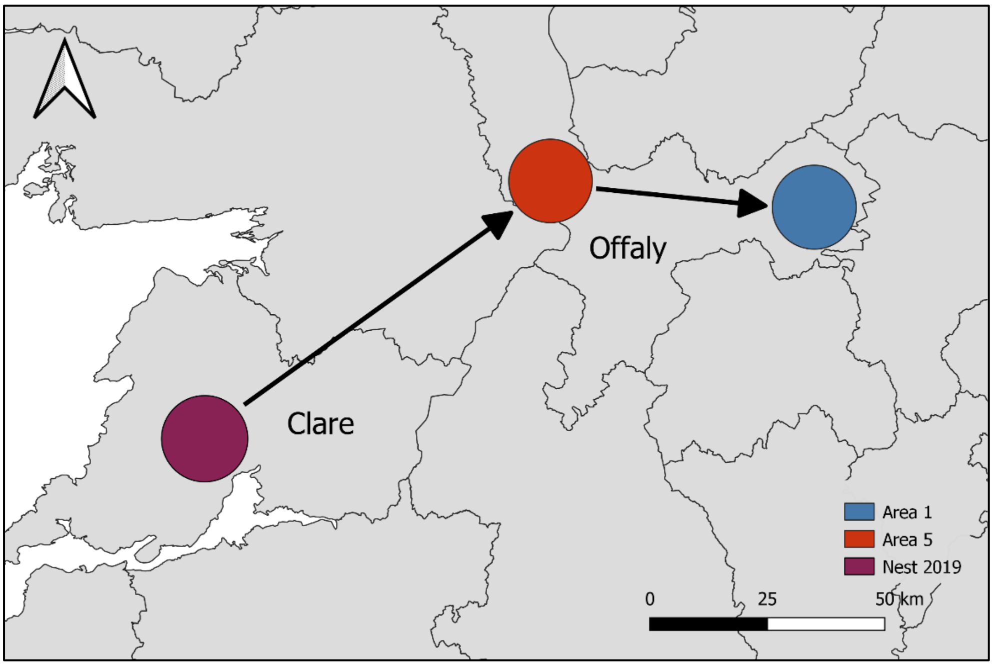

Figure 10. Movements of Female B between 5th June and 10th August 2018.

Second non-breeding season

On 11th August 2018 (429 days old), Female B moved from Area 1 to the north-east corner of Area 4 (hereafter NE Area 4). For the two months between 11th August (429 days old) and 5th October, she remained on the cutover regenerating bogs in Areas 4 and 5, using each for a few days or a few weeks at a time (Fig. 11). On 6th October 2018 (485 days old), she returned to her first-year wintering grounds in south-east Co. Kilkenny where she remained for two days before travelling back north to the midlands. She spent most of October in NE Area 4, apart from brief trips to Areas 2, 3 and 5. She returned to her south-east Kilkenny wintering grounds from 29th October to 18th November (508 to 528 days old), however on this occasion she moved roost site to a smaller saltmarsh 1km south of the primary saltmarsh roost she had used the previous winter. The reason for this change of roost site is unclear. Transmission on 18th November showed her return movement north to the midlands and she was recorded travelling 31km in 46 minutes (equivalent of 40.4km/hr straight line speed). The following day, 19th November (529 days old), she was back at NE Area 4.

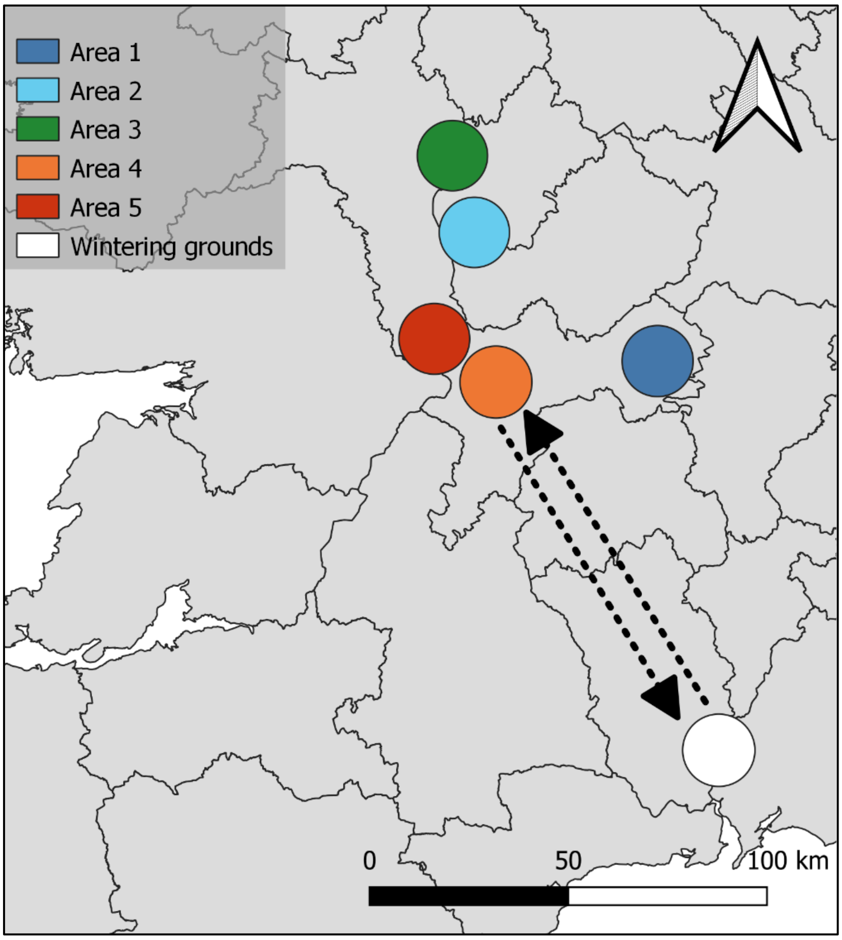

Figure 11. Movements of Female B between 11th August and 19th November. Dashed lines represent two return trips from Area 4 to her first-year wintering grounds.

Between 19th November 2018 and 25th March 2019 (655 days old), she remained at Areas 4 and 5 (Fig. 12). A cutover regenerating bog in the centre of Area 4 (hereafter centre Area 4) was her primary roost and Area 5 was her secondary roost. Her home range around Area 4 was 80km^2. It was not possible to calculate her home range around Area 5 during this period due to the low number of high-quality daytime location fixes. She occasionally travelled to Area 2 for brief periods. Throughout March, long-distance movements (>25km) became more frequent, and she travelled south to near the Slieve Aughties and Area 1 between 25th to 31st March (655 to 661 days old).

Figure 12. Areas used and movements of Female B between 19th November 2018 and 31st March 2019. Most of her time during this period was spent in Areas 4 and 5.

Second breeding season

Female B was first recorded at the breeding grounds of West Co. Clare on 1st April 2019 (662 days old) having travelled there from her non-breeding grounds in Co. Offaly. Between 1st and 10th April (671 days old), she travelled 21km north on two occasions from where she had settled in West Co. Clare. Movements such as this may be driven by low prey availability and specific nutritional requirements, such as high calcium demands, ahead of breeding that can not be satisfied by the surrounding habitat of the breeding area that early in the breeding season (Newton 1979). After 10th April (671 days old), she remained within 4km of her suspected nest site. Sensor data from the PTT suggested that she settled down to nest during the end of April, and we confirmed this on 4th May 2019 (695 days old) during a distant vantage point watch when we recorded a food pass with an adult male. Her nest site was located in a firebreak between a mature planted conifer forest and a recently clear-felled conifer forest block. Her natal dispersal distance was 109km, much further than the natal dispersal distance of just 17km recorded for Female A. Although little is known about the complex natal dispersal strategies of Hen Harriers, owing to difficulties generating relevant data, Female B's natal dispersal distance is considerably larger than that typically recorded for Hen Harriers (Etheridge et al. 1997, Whitfield and Fielding 2009, O'Donoghue 2010), except for one female Hen Harrier from Wales that had a natal dispersal of 180km (Whitfield and Fielding 2009). As with Female A, the first nesting site of Female B was also outside of the Hen Harrier SPA network. Between 1st May and 18th June (692 to 740 days old) she remained on her breeding territory and had an 85% MCP home range of 5.8km^2 (95% MCP home range of 15km^2). We suspect that the nest failed around 18th June, as on the morning of 19th June 2019 (693 days old), she was 95km to the north-east of her breeding territory at Area 5. Subsequent distant vantage point watches at her breeding territory confirmed no further activity there. It was not possible to determine a definite cause of nest failure.

Third non-breeding season

Following the failed breeding attempt, Female B travelled widely from 19th June to 3rd July 2019 (741 and 755 days old), between Areas 1, 4 and 5, with her most notable movement being a visit to her first-year wintering grounds from 29th June to 1st July (Fig. 13). On 3rd July (755 days old), she returned to Area 5, where she remained until 30th July (782 days old), using the same primary roost that she had used the previous winter, and foraging on cutover regenerating bog. Through August and September 2019, she mostly remained in NE Area 4 before later moving to CE Area 4 and the west side of Area 4 (hereafter W Area 4), roosting and foraging on cutover regenerating bog. From 27th September to 3rd October, she returned again, for the third year in a row, to her first-year wintering grounds in south-east Co. Kilkenny, 112km to the south-east of Area 4. By 6th October (850 days old) she had returned to Area 5, 128km to the north-west of her first-year wintering grounds. After this, and until the end of February 2020, she primarily used Area 5 and CE Area

4, moving the 17km between these bogs on multiple occasions throughout the winter.

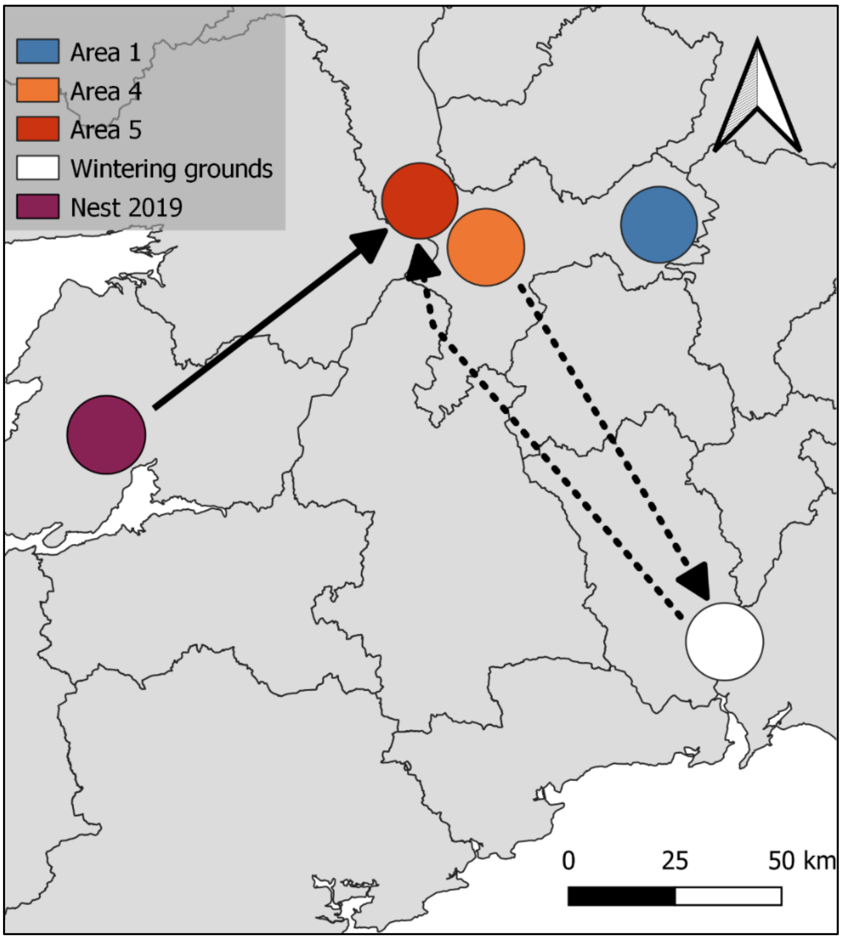

Figure 13. Movements of Female B between 18th June 2019 and 28th February 2020. The majority of her third winter was spent in Areas 4 and 5.

Third breeding season

Between 1st and 25th March 2020 (997 to 1,021 days old), as she had done the previous March, Female B began using additional areas, including Areas 1, 2 and 3, as well as Area 5 and CE Area 4 (Fig. 14). Her first movement to breeding grounds this year was on 26th March 2020 (1,022 days old) when she travelled to the Slieve Bloom Mountains. She returned to the lowlands (Area 1 and CE Area 4) on the 27th and 28th, before returning on 29th March to an upland area in the Slieve Blooms where she subsequently nested, 14km to the southwest of her natal nest area and 98.3km to the east-northeast of where she had nested the previous year. She did not return to her 2019 nest site in West Co. Clare. If the original breeding site is suitable, returning there to breed in subsequent years would be advantageous as breeding adults would be most successful in areas they are familiar with (Newton 1979). Therefore, moving nest site is likely a response to poor quality habitat and/or the previous nest failure, with Northern Harriers also less likely to return to a breeding territory if the breeding attempt failed the previous year (Newton 1979).

Throughout April and early May 2020, Female B made regular trips between her upland breeding territory in the Slieve Blooms and her lowland wintering grounds of CE Area 4, between 19 and 23km to the north. On some occasions, transmission coincided with these movements between non-breeding lowland areas and breeding areas. For example, on 9th May at 15:22, Female B was at her non-breeding grounds in W Area 4, but by 16:57 she was 19km to the south at her breeding territory. Similar behaviour was observed the previous year when she travelled a similar distance to North Co. Clare during April 2019 from her West Co. Clare breeding territory. No previous study has documented an adult Hen Harrier moving rapidly and frequently between their breeding and non-breeding grounds during the breeding season. This has important implications for not only the conservation of Hen Harriers, but also for their monitoring during the breeding season. Sightings in non-breeding areas during the breeding season would typically be assumed to be non-breeders, however these results show that this is not necessarily the case. In addition, this result highlights the importance of non-breeding areas for breeding Hen Harriers, and in particular females as they may use these areas to achieve good body condition ahead of breeding (Newton 1979). Therefore, loss or degradation of these habitats could have negative carry-over effects into the breeding season for breeding female harriers. Observations by the Hen Harrier Project confirmed that Female B attempted to nest in the Slieve Blooms, however the nesting attempt failed at an early stage, possibly around 14th May (1,071 days old). The cause of this nesting attempt failing is not known. Movements between the lowland non-breeding areas and her breeding territory continued through to the end of May.

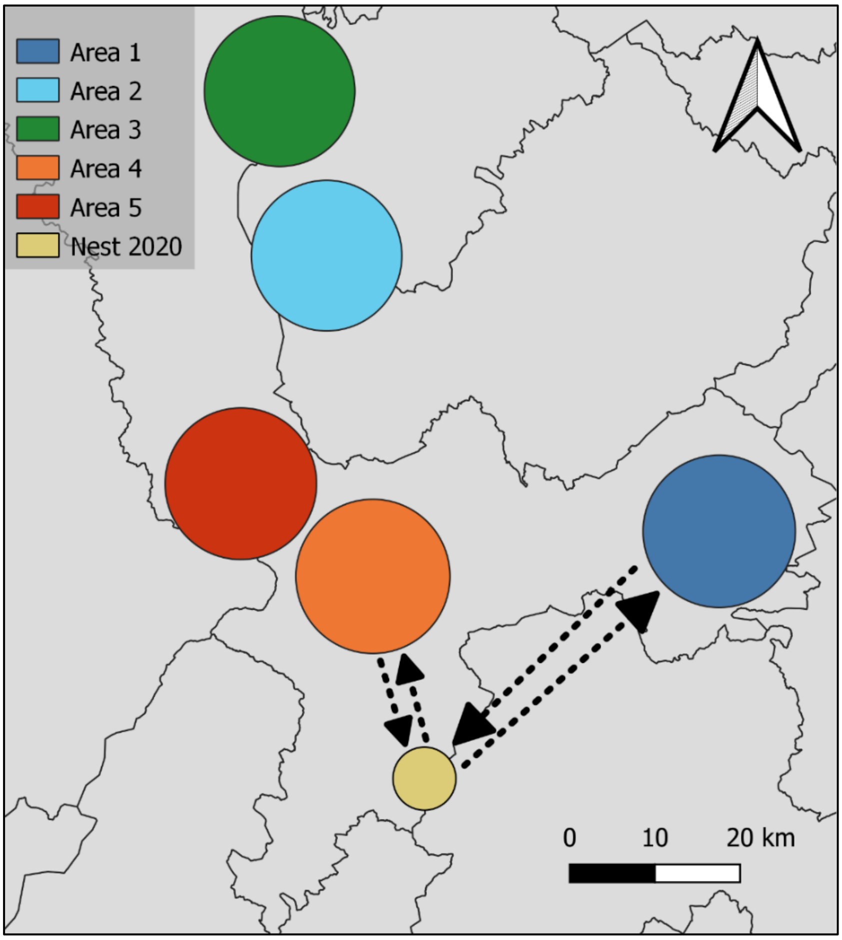

Figure 14. Movements and areas used by Female B between 1st March and 14th May 2020. Dashed lines show her repeated back-and-forth movements from her breeding site to her lowland non-breeding grounds.

Fourth non-breeding season

After her failed nesting attempt, between 28th May and 15th July (1,085 to 1,133 days old), Female B remained at Area 5 and used her primary roost that she had also used during the winter while she foraged on the cutover regenerating bog, as well as the nearby wet grasslands (Fig. 15). Her home range during this time was 30km^2 (85% MCP 14km^2). She then moved between here and CE Area 4, before settling at Area 1 between 22nd July (1,140 days old) to 2nd August (1,151 days old). Unlike during previous visits, she was not recorded foraging within the windfarm in Area 1 during this visit. Throughout September and October, she mostly used CE and W Area 4, while occasionally also using NE Area 4, Areas 2 and 5 for brief periods. Through November and December 2020, her activity was concentrated on CE Area 4, while she also used Area 5 to a lesser extent. From 4th to 9th January 2021 (1,306 to 1,311 days old), she returned to her first-year wintering grounds in south-east Co. Kilkenny, before returning 100km north-west on 10th January (1,312 days old) to a known roost on the edge of Area 1 that she had used just once before, on 1st and 2nd October 2017 (115 and 116 days old). For the remainder of January and February 2021, she travelled between Areas 1 and 5. Although it was assumed that the site fidelity displayed by Hen Harriers in the summer months extended to the wintering period (O'Donoghue 2010), little information on this aspect of their ecology was available. Female B displayed variable site fidelity. While she was loyal to one area in her first winter, she established a different primary wintering area over 100km away in subsequent winters. This is in contrast with Female A, who, until her death, displayed strong site fidelity across her first and second winters. However, outside of the breeding season, Female B generally only used areas that she had visited within her first year of life, and she was rarely recorded using new areas after her first year.

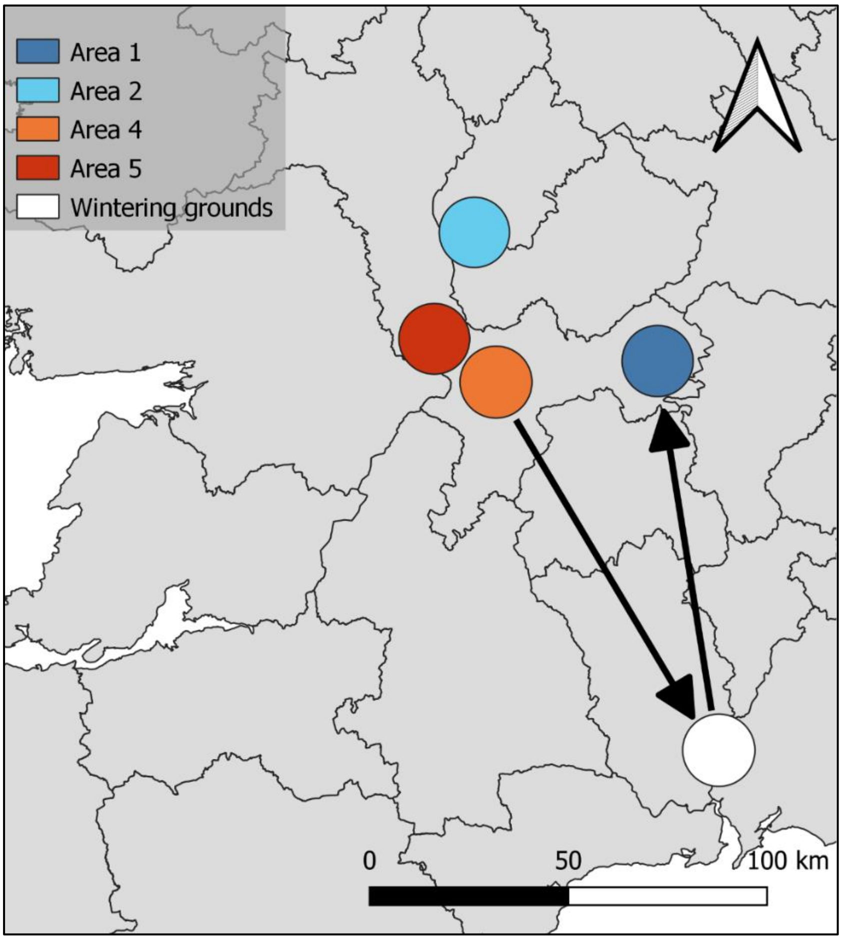

Figure 15. Movements and areas used by Female B between 28th May 2020 and March 6th 2021.

Fourth breeding season

On 7th March 2021 (1,368 days old), Female B travelled to the upland breeding grounds for the first time in 2021, earlier than in previous years: 26th March in 2020; 1st April in 2019; and 20th April in 2018 (Fig. 16). She spent 7th and 8th March at her breeding territory from the previous year before returning to the lowlands (Area 1 and W Area 4) between 12th and 23rd March (1,373 to 1,384 days old). Between 24th March and 6th April (1,385 to 1,398 days old), she continued moving back and forth between her 2020 breeding territory and her lowland wintering grounds (Areas 4 and 5), as she had done in previous breeding seasons. On 7th April 2021 (1,399 days old) she visited a new area in the centre of the Slieve Blooms, 5km from her previous year's territory and 9km from her natal territory. This is where she subsequently nested in 2021. Between 7th April and 2nd May (1,424 days old), she continued to make frequent trips between this new territory and the lowlands (CE Area 4 and Area 5). From 4th May (1,426 days old), she remained within 4km of her breeding territory. Tracking and PTT sensor data suggest that she settled to nest around 10th May (1,432 days old). We conducted a vantage point watch on 13th May (1,435 days old) and confirmed that Female B was incubating at a nest. Her PTT sensor and location data suggested that she became more active on 20th June (1,473 days old), when the chicks would have been approximately a week old.

Early in the morning of 1st July (1,484 days old) at 06:17, she was back in the lowlands (CE Area 4), however by 07:34 the same morning she had returned 19km south to her breeding territory. The following day, 2nd July, she was again in the lowlands (CE Area 4). On the 3rd and 4th, she had returned to her breeding territory. A vantage point watch on the afternoon of 5th July (1,488 days old) confirmed the nest was still active, with the adult male making two prey deliveries directly to the nest during an hour and a half long vantage point watch. We also had a brief sighting of an adult female, though it was not possible to identify her as Female B as she was too distant. Female B's PTT did not transmit a location on this day. On 6th July (1,489 days old), she transmitted roosting locations from the Slieve Blooms, 5.7km to the north-east of her nest site. A vantage point watch by National Parks & Wildlife Service (NPWS) and the Hen Harrier Project fieldworkers on 8th July resulted in no Hen Harrier sightings. A nest visit conducted by NPWS on 12th July confirmed that the nest, with at least two chicks, had been predated. Given the prey deliveries observed on 5th July, it might be assumed the nest had not yet failed at this point. However, an adult male Hen Harrier has previously been observed delivering prey to a nest after chicks had died due to inclement weather (Irwin et al. 2008) and it is possible that adult males might respond similarly after nest predation.

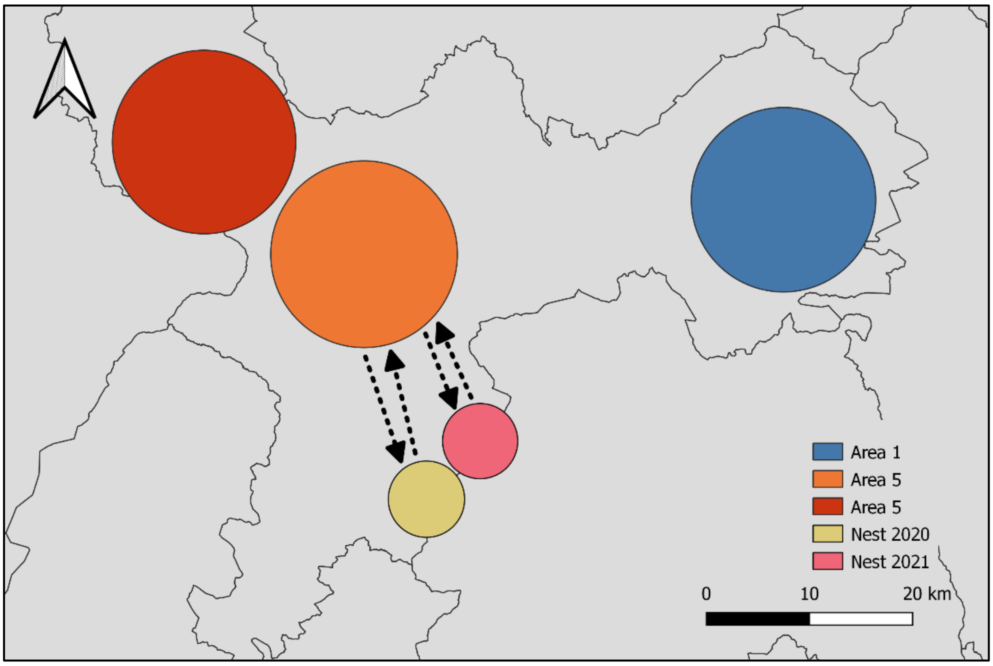

Figure 16. Movements and areas used by Female B between 12th March and 6th July 2021. Dashed lines represent frequently repeated journeys.

Fifth non-breeding season

Between 7th and 18th July 2021 (1,490 to 1,501 days old), Female B remained in the lowlands at Area 1, CE Area 4, and Area 5. However, between 19th and 25th July (1,502 to 1,508 days old), she returned to her breeding territory. Between 26th to 31st July, she was at Area 1 before travelling to CE and W Area 4 and Area 5, where she remained throughout August and September 2021, with most of her activity focussed in W Area 4 where she roosted and foraged in a 3km^2 area of cutover regenerating bog. This chapter includes data collected until 30th September 2021 (1,575 days old). However, location data continues to be transmitted from Female B's PTT. As of 9th March 2022, she remains at her non-breeding grounds in Co. Offaly, at 1,735 days old. Between her date of tagging and 31st September 2021, Female B used an area of 20,761km^2 across 15 counties and provided the longest dataset of the movements of an individual Hen Harrier in Ireland on record (Fig. 17).

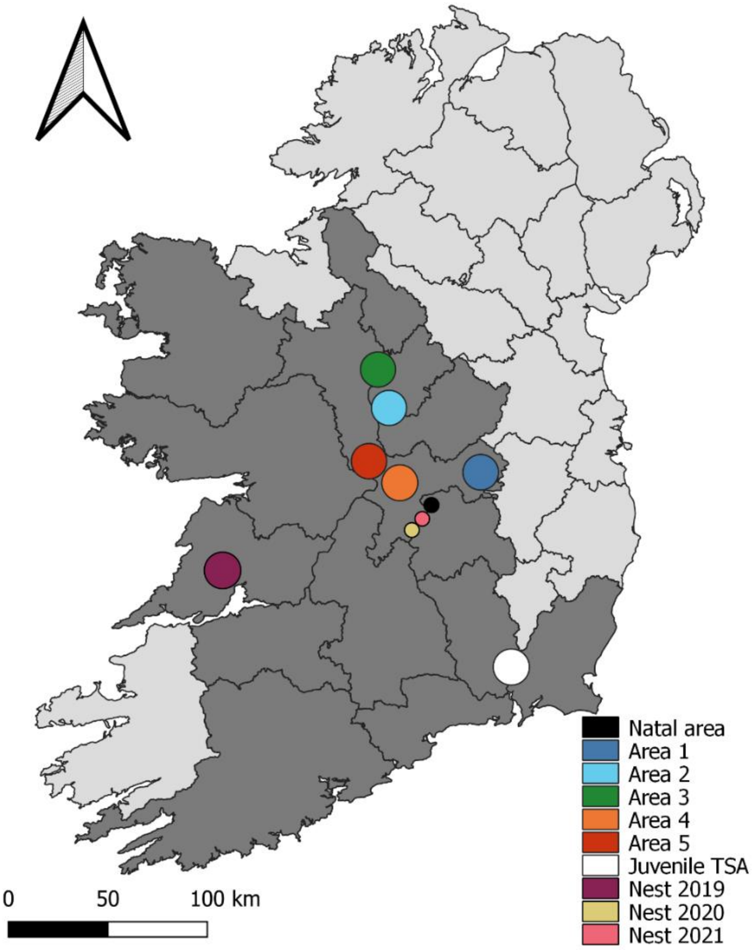

Figure 17. Main areas used by Female B during her lifetime. Counties coloured dark grey are those she visited.

Ethics statement

Nest monitoring, nest visits, ringing and satellite tagging were carried out by trained professionals under licence from the National Parks and Wildlife Service and the British Trust for Ornithology. Health Products Regulatory Authority (HPRA) licence was not required for this study.

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Chapter Six

Bird and small mammal community composition and abundance in upland open habitats and early conifer forests[5]

Early conifer forest

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[5] McCarthy, A. A. Caravaggi, D. Fernández-Bellon, S. Irwin, J. Lusby, and J. O'Halloran (2021). Bird and small mammal community composition and abundance in upland open habitats and early conifer forests. European Journal of Wildlife Research 67(26).

Abstract

Anthropogenic land-use change, such as commercial afforestation, is a significant driver of shifts in ecological communities and species abundance. In this study, the consequences of afforestation of upland habitats for two distinct animal groups, birds and small mammals, were examined by comparing open moorland, early pre-thicket conifer forests (2-4 years post-replanting) and late pre-thicket conifer forests (6-8 years post-replanting) across 24 upland study sites in Ireland. Field data were collected using bird point counts, live trapping of small mammals and detailed vegetation surveys. A total of 17 bird species and four small mammal species were detected. Both groups showed contrasting patterns of abundance between moorland and pre-thicket forests, with bird density being higher in moorland, while small mammal abundance was higher in pre-thicket forests. Bird diversity was lowest in moorland and highest in late pre-thicket forests while small mammal diversity was highest in moorland and lowest in late pre-thicket forests. Our study shows that afforestation can alter the abundance and community composition of bird and small mammal populations, and that the consequences of land-use change associated with afforestation in upland areas vary across different taxa. Our findings have important implications for forest management practices and conservation of upland habitats and species.

Introduction

Land-use change is an important driver of shifts in species composition and abundance (Sala et al. 2000, Jetz et al. 2007). As much as 60% of land-use change occurs as a direct result of human activities (Song et al. 2018), and manifests through a range of mechanisms having positive, neutral, or negative impacts on biodiversity. Understanding the impacts of land-use change and the creation of new habitats, such as urban areas (Ortega-Álvarez and MacGregor-Fors 2009, Reis et al. 2012), agricultural lands (Reidsma et al. 2006) and commercial forests (Graham et al. 2013) on biodiversity and ecosystems is crucial to inform conservation efforts.

As in many parts of Europe, anthropogenic land-use change has reshaped the landscape of Ireland for millennia. Widespread deforestation occurred since the

Mesolithic period (Preece et al. 1986), with forest cover falling to less than 1% by the turn of the 20th century (Cross 1987). Total forest cover has since increased to its current level of 11% in the Republic of Ireland (DAFM 2018), driven by government policy and commercial afforestation, with a target of 18% forest cover by 2046 (DAFM 2014). Much of this afforestation has occurred on land unsuitable for intensive agriculture in upland areas, with 39% of forests planted on peatlands (DAFM 2018) comprising mostly of monospecific, even-aged plantations (Forest Service 2017). The replacement of natural and semi-natural open habitats with forests impacts significantly on species whose ecology is closely linked to the preceding open habitats, particularly species of conservation concern (Thompson et al. 1988, Stillman and Brown 1994, Douglas et al. 2014). The transition from semi-natural habitat to commercial forest reduces the availability of key resources for foraging, nesting and predator avoidance which may ultimately result in population decline. For example, non-native Sitka spruce (*Picea sitchensis*) forests in Ireland have significantly fewer species and lower densities of birds of conservation concern than peatland habitats, highlighting the potential for commercial afforestation to significantly affect bird communities in upland areas (Armstrong and van Hensbergen 1995, Graham et al. 2017). An understanding of the impact of this new habitat on the ecology of upland communities is required to underpin conservation ecology and sustainable forest management.

Birds are an important component of forest ecosystems and are useful indicators of biodiversity due to the ease with which they can be surveyed and their responsiveness to environmental change (Furness et al. 1993, Venier and Pearce 2004, Fraixedas et al. 2020). The change in land-use from open to forested habitats can have varied effects on bird communities and is largely dependent on the specific vegetative composition of the preceding habitat (Graham et al. 2017, Castano-Villa et al. 2019). Where open habitats are converted to forest, there is a transition from open habitat specialists to scrub specialists and then generalist forest bird species (Sweeney et al. 2010). Previous research on the impact of afforestation on birds has looked at the influence of prior land-use (Graham et al. 2017), forest age (Sweeney et al. 2010) and tree composition (Irwin et al. 2014). However, there remains a gap in our knowledge of bird community composition and density during the open pre-thicket planted forest stage when compared with preceding open habitats such as moorland. As young upland forest accounts for nearly 18% of forest cover in Ireland (DAFM 2018), with afforestation due to increase further in the coming decades, gaining an understanding of the changes to bird density and community composition in the initial stages of afforestation is a crucial first step to identify conservation priorities and potential wider ecosystem effects.

Small mammals are also integral components of forest ecosystems, being important herbivores and omnivores, as well as a key prey resource for mammalian and avian predators (Olofsson et al. 2004, Twining et al. 2019). It is therefore important to understand the influence of forest planting on small mammal communities. However, much of the previous research in this field has taken place in North America (Sullivan and Sullivan 1982, Fisher and Wilkinson 2005, Craig et al. 2006, Sullivan and Sullivan 2012), and this remains a largely unexplored topic in a European, and particularly in an Irish, context. Consequently, there is a requirement for a greater understanding of small mammal communities of young, upland conifer forests, and how they differ from those of preceding open habitats.

Together, bird and small mammal communities in upland areas provide an important food resource for many apex predators, including birds of prey (Redpath 1991, Fernández-Bellon and Lusby 2011, Nota et al. 2019). Thus, understanding the capacity for forest habitats to provide prey resources is crucial for the development of appropriate conservation and management decisions aimed at supporting birds of prey. Certainly, commercial forests harbour potential prey species and offer foraging opportunities, particularly during the early growth stages prior to canopy closure. For example, Hen Harrier (*Circus cyaneus*) and Merlin (*Falco columbarius*), species typically associated with open upland landscapes, often occupy planted upland areas where there is an absence of more suitable habitat (Petty 1996, Wilson et al. 2009, Lusby et al. 2017). However, the capacity for these habitats to support suitable prey populations is not yet fully understood and may be critical to the long-term persistence of these vulnerable upland birds of prey.

The turnover of bird and small mammal communities associated with the conversion of open upland areas to forest habitats is related to changes in structural habitat features that provide food and shelter (Ecke et al. 2001, Wilson et al. 2010, Gasperini et al. 2016). Furthermore, there is evidence that bird and small mammal communities change in response to further structural habitat changes that occur as forests age (Staines et al. 1987, Sullivan et al. 2000, Sweeney et al. 2010). Typically, conifer forests are harvested by clear-felling and then replanted shortly thereafter. The post clear-felling woody debris (brash) that remains in replanted areas during the early stages of the second and subsequent forest cycles enhances structural complexity and can provide habitat for birds and small mammals (Kirkland 1990, Sweeney et al. 2010). Despite the strong relationship between bird and small mammal abundance and structural complexity, few studies have investigated the potential role of woody debris in providing habitat for birds and small mammals during the early growth stages of commercial forests (Seibold et al. 2015).

This study set out to assess the composition and abundance of birds and small mammals in early upland second rotation pre-thicket conifer forests compared with open upland moorland. Particular focus was given to the conservation implications for the predators that rely upon these animals as prey.

Methods

The abundance of birds and small mammals was investigated in three different upland habitats in the Republic of Ireland between April and July 2018: i) heather/grass moorland (hereafter referred to as ‘moorland’); ii) early second rotation pre-thicket conifer forests (aged 2-4 years post-replanting; hereafter referred to as ‘early pre-thicket forests’); and iii) late second rotation pre-thicket conifer forests (aged 6-8 years post-replanting; hereafter referred to as ‘late pre-thicket forests’). Moorland sites were dominated by heather (*Calluna* and *Erica* spp.) and grasses (primarily *Molinia*). Forest sites were largely comprised of Sitka spruce, with lodgepole pine (*Pinus contorta*) and larch (*Larix* spp.) at lower densities. The age classes of forests were calculated based on time-since-planting, relative to 2018, as defined in a database of forest planting provided by the Irish commercial forestry operator, Coillte.

Eight study areas were selected, based on the availability of focal habitats and brash management strategy (windrowing, i.e. lines of discarded material, heaped in rows by harvesting machinery) within forest patches. Each study area contained three study sites (one of each habitat), giving a total of 24 sites (Fig. 1). Study areas were separated by an average of 71.5 ± 43.1km. Study sites averaged 12.6 ± 3.1ha in size, were separated by an average of 1.30 ± 0.63km within study areas, and were located on average 350 ± 62m above sea level.

Figure 1. Location of eight study areas in Ireland.

Bird Surveys

Non-raptorial bird species (i.e. putative prey) abundance was quantified at each site using point counts (Bibby et al. 2000). Three points with a detection radius of 100m were randomly generated at each study site, avoiding overlap. Two count surveys were carried out at each point, the first count period from mid-April to mid-May 2018 (early-mid breeding season; n=72), and the second count period from mid-May to late June 2018 (mid-late breeding season; n=72) (see Dettmers et al. 1999, Drapeau et al. 1999). Surveys were carried out between one hour after dawn and 12:00 and lasted ten minutes, following a one-minute settlement period. The survey schedule for areas, sites and points was randomised with the stipulation that all three sites within a study area were surveyed on the same morning. All bird surveys were conducted in suitable weather conditions, with no persistent rain, good visibility, and calm winds (< Beaufort scale 4). Birds were detected both visually and by sound (song, calling, alarming). The same observer undertook all bird surveys. The distance from the observer to detected bird(s) was measured using an Eyoyo® Rangefinder and the species, number of individuals, behaviour, and the direction of the detection relative to North were recorded. Only those birds deemed to be actively using the site (i.e. foraging, nesting, or perching) were included in the analyses. Flocks greater than five individuals were excluded from analyses to minimise over-inflation of densities arising from transient flocks (Sweeney et al. 2010).

Small Mammal Surveys

Small mammals were surveyed at each site using live trapping (Gurnell and Flowerdew 2006) in June and July 2018. Two parallel, linear transects, each a minimum of 10m from the edge of the site (i.e. boundary of forest coup / where moorland meets other land-use), measuring 90m and separated from each other by approximately 50m, were established in each study site. Transects in moorland were established perpendicular to the site edge. Transects in forest sites were established in direct proximity to windrows. Each transect consisted of 10 trapping stations spaced approximately 10m apart (± 1m). Each trapping station consisted of two live-capture small mammal traps: one Heslinga trap and one Longworth trap (Chitty and Kempson 1949), giving a total of 40 traps per study site. Paired traps at each station were placed within 1m of each other and orientated in opposite directions along the transect. The alignment of specific trap models was randomised across all stations. Traps were angled downward to enable drainage of any moisture and were covered with vegetation to prevent overheating from direct sunlight. Traps were baited with peanuts, apple and dried mealworms and straw was provided as bedding. Trap chambers were fitted with shrew holes (11mm diameter) to prevent retention of the protected Pygmy Shrew (*Sorex minutus*).

All sites in each study area were surveyed simultaneously. Traps were deployed without pre-baiting on the evening of day one, checked at approximately 08:00 and 20:00 on days two and three, and checked and removed at 08:00 on day four, giving five 12-hour trap events for every site (Sullivan et al. 2017). Fresh bait was added to traps each evening while bedding was replaced after periods of rainfall. Both bedding and bait were replaced in traps where a small mammal had been caught. Captured animals were identified to species, aged (adult/juvenile), sexed (male/female), weighed (to the nearest 0.1g using a digital scales), their breeding condition recorded (breeding/non-breeding), and photographed. Previously uncaptured individuals were given a unique combination of fur clips to facilitate subsequent identification. For recaptured individuals, the unique fur clip pattern was noted along with age, sex, breeding condition and weight (Gurnell and Flowerdew 2006).

The area in which this study was undertaken covered the distribution of two invasive small mammal species in Ireland: the Bank Vole (*Myodes glareolus*) and the Greater White-toothed Shrew (*Crocidura russula*). The native Wood Mouse (*Apodemus sylvaticus*) and Pygmy Shrew also occur in this area (McDevitt et al. 2014).

Small Mammal Vegetation Surveys

Vegetation surveys were undertaken at each site on the morning of days two and three of small mammal surveys. These surveys were carried out at trap stations three and eight on each transect (20% of trap stations) to account for possible variation in vegetation characteristics along the length of the transect (Fig. 2). Vegetation cover was visually estimated for each plant species/group, to the nearest 5% (Hoffmann et al. 2010) in each of three 1m^2 quadrats. Vegetation was subsequently grouped according to structural similarities: bare ground and moss; gorse and bramble; grasses and forbs; heather and bilberry; rushes and woodrush; and ferns. Maximum vegetation height was recorded within a 5cm radius of the corner of each quadrat. Visual Obstruction Readings (VORs) were taken to obtain an index of vegetation density by placing a Robel pole (Robel et al. 1970) in the centre of the middle quadrat. The lowest number visible on the Robel pole was recorded at three observation heights (0.5m, 0.8m, 1m) at each of three distances (2m, 3m, 4m) away from the

Robel pole, along a straight line (adapted from Evrard and Bacon 1998). The direction that VOR measurements were taken followed the line of least slope, as determined in the field, to mitigate impacts of slope on VOR measurements.

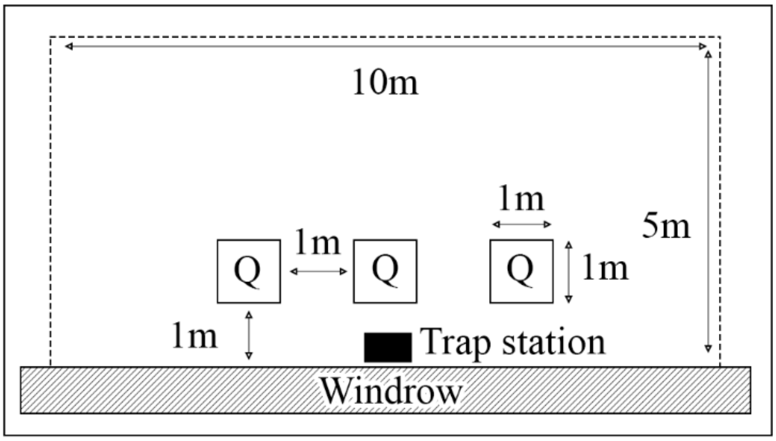

Figure 2. Vegetation survey plots within study sites.

The distance from the trap station to the five nearest trees was recorded to the nearest centimetre (Happold and Happold 1987). The heights of these trees were visually estimated and categorised within half-metre categories, and the tree species was also recorded. A 5x10m plot was marked out with the innermost edge parallel to the windrow and with the trap station at the centre. The number of planted trees (i.e. tree density), tree stumps (>50cm diameter), and upturned tree root masses and logs (>50cm diameter) were counted within these larger plots (Carey and Harrington 2001, Fuller et al. 2004). Total coarse woody debris (CWD) was calculated as the sum of logs + stumps + root masses (Fuller et al. 2004).

Brash structure was assessed by measuring brash pile width and height at the point of the trap station, thus allowing an estimation of brash volume (Hardy 1996).

Data analysis

Bird observations were grouped into four distance bands (0-40m, 41-60m, 61-80m and 81-100m) to facilitate the fitting of distance functions and, hence, the calculation of density estimates. A minimum of 60 detections are required to produce a reliable detection function, and so it was not possible to construct individual detection functions for each species/habitat combination (Buckland et al. 2001). Therefore, bird species were grouped into three categories based on typical species-specific habitat associations: all bird species; open-country species; and scrub species (Nairn and O'Halloran 2012) (Table 1).

Table 1. Bird species included in analyses with associated Irish conservation status (Colhoun and Cummins 2013), habitats within which they were detected (M = moorland, E = early pre-thicket forest, L = late pre-thicket forest) and habitat group (Nairn and O'Halloran 2012). Six species were generalists and therefore were not grouped into either open or scrub habitat categories.

Common name	Latin name	Conservation status	Habitats detected	Habitat Group
Meadow Pipit	*Anthus pratensis*	Red-listed	M/E/L	Open
Skylark	*Alauda arvensis*	Amber-listed	M	Open
Red Grouse	*Lagopus lagopus*	Red-listed	M	Open
Blackbird	*Turdus merula*	Green-listed	L	Scrub
Blackcap	*Sylvia atricapilla*	Green-listed	L	Scrub
Dunnock	*Prunella modularis*	Green-listed	E/L	Scrub
Common Whitethroat	*Sylvia communis*	Green-listed	E/L	Scrub
Reed Bunting	*Emberiza schoeniclus*	Green-listed	E	Scrub
Robin	*Erithacus rubecula*	Amber-listed	E/L	Scrub
Willow Warbler	*Phylloscopus trochilus*	Green-listed	M/E/L	Scrub
Wren	*Troglodytes troglodytes*	Green-listed	M/E/L	Scrub
Blue Tit	*Cyanistes caeruleus*	Green-listed	L	NA
Chaffinch	*Fringilla coelebs*	Green-listed	M/E/L	NA
Coal Tit	*Periparus ater*	Green-listed	L	NA
Goldcrest	*Regulus regulus*	Amber-listed	L	NA
Lesser Redpoll	*Acanthis cabaret*	Green-listed	L	NA
Ring-necked Pheasant	*Phasianus colchicus*	Green-listed	E/L	NA

As information on the detectability of individual species is scarce, birds with similar ecologies were assumed to have similar detection rates. Densities were calculated for all species in each habitat, for open-country species in moorland and early pre-thicket forests, and for scrub species in early and late pre-thicket forests. It was not possible to calculate densities of open-country species in late pre-thicket forests nor scrub species in moorland due to insufficient numbers of bird detections.

Six species were not assigned to a group as five of these species are typically associated with post-thicket forests, while one species, the Ring-necked Pheasant (*Phasianus colchicus*), is associated with both open and scrub habitats. Akaike's Information Criteria (AIC) was used to select the best fitting detection function between five models: Half-normal/Cosine, Hazard-rate/Cosine, Uniform/Cosine, Uniform/Polynomial and Half-normal/Hermite (Sweeney et al. 2010, Broekema and Overdyck 2012). Densities were calculated at each point for each count period and the maximum of these two values was taken as the density at that point. Differences in bird densities between habitats and species groups were investigated using general linear mixed effects models (GLMMs), with bird density as the response variable, habitat as the fixed factor and site as the random factor.

The minimum number of individual small mammals alive (MNA) within each site was used as an index of small mammal abundance (Gurnell and Flowerdew 2006) as too few small mammals were captured to support population estimation via more complex capture-recapture methods.

Zero-inflated negative binomial mixed effects models were constructed to explore differences between habitats. A discrete model was not constructed for Greater White-toothed Shrew due to the low number of captures across all habitats (*n* = 27). A suite of models were constructed including MNA of (i) all species, (ii) Bank Vole, and (iii) Wood Mouse as the response variables, with habitat as the fixed factor, and habitat nested within study area and surveyor (*n* = 5) as random factors. Models were compared to their null alternatives (i.e. with no explanatory variables) using Akaike's Information Criterion (AIC); the model with the lowest AIC value was considered to be the best performing model. Two discrete Principal Component Analysis (PCA) processes were applied to habitat data; one captured all ground vegetation data while the other was comprised of tree data. All variables were standardised, with $\bar{x} = 0$ and $\sigma = 1$. It was not possible to incorporate habitat components in more complex models, primarily due to over-specification (i.e. non-Hessian matrix) errors in models with ≥2 variables and issues with model convergence. Thus, PCAs were only used to describe the vegetative composition of each habitat in the context of the simpler model, above.

Species diversity of both birds and small mammals was assessed using the inverse of the Simpson's Diversity index. This index is suitable for assessing species diversity where sample sizes are small and indicates the probability that two individuals drawn randomly from a sample belong to the same species (Magurran 2004). In addition, Simpson's Diversity index accounts for both species richness and abundance. Simpson's diversity was calculated separately for each bird survey period (first and second).

Data were processed and analysed using ArcGIS 10.4.1 (ESRI 2011), Distance (Thomas et al. 2010) and R version 3.5.1 (R Core Team 2018), including packages *caret* (Kuhn 2018), *ggplot2* (Wickham 2016), *glmmTMB* (Brooks et al. 2017), *lme4* (Bates et al. 2015) and *vegan* (Oksanen et al. 2018). The datasets generated and analysed during the current study are available at https://bit.ly/3tKi3j1.

Results

Bird communities

Thirty-five bird species were recorded during this study. Seventeen species were included in the analyses as these were deemed to be utilising the habitat in which they were recorded. Of these 17 bird species, six were detected in moorland, nine were detected in early pre-thicket forests and 14 were detected in late pre-thicket forests. Moorland held the highest proportion of species of conservation concern, with one of the six species being Amber-listed and two being Red-listed (Table 1). Just one Red-listed species and two Amber-listed species were recorded in pre-thicket forest habitats.

There were significant differences in bird densities across the three habitats when considering all bird species together. Bird density was significantly higher in moorland (8.23 ± 0.43 birds/ha^{-1}) than in either early pre-thicket forests (3.41 ± 0.42 birds/ha^{-1}; $P < 0.01$) or late pre-thicket forests (6.49 ± 0.41 birds/ha^{-1}; $P < 0.05$). Early pre-thicket forests had significantly lower bird densities than late pre-thicket forests ($P < 0.01$). Densities of open-country birds were significantly higher in moorland (8.15 ± 0.45 birds/ha^{-1}) compared with early pre-thicket forests (2.74 ± 0.39 birds/ha^{-1}; $P < 0.01$). Densities of scrub species were significantly lower in early pre-thicket forests

(0.88 ± 0.20 birds/ha^{-1}) than in late pre-thicket forests (5.23 ± 0.45 birds/ha^{-1}; $P < 0.01$; Fig. 3). Full model outputs are shown in Table 2.

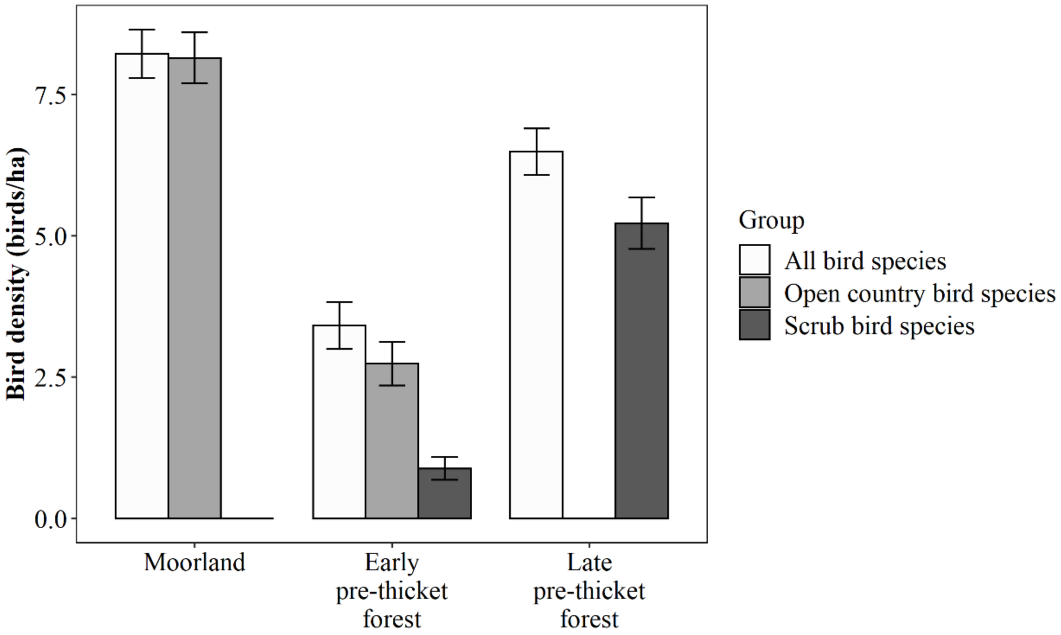

Figure 3. Mean (±SE) density for three groups of bird species, grouped according to typical habitat associations (see Table 1), in moorland, early pre-thicket forests and late pre-thicket forests.

Table 2. Top models for avian-focussed GLMMs (a- c; n = number of density estimates) and mammal-focussed zero-inflated negative binomial mixed effects models (d - f; n = number of site capture site totals). Parameter coefficients (*β)* with standard errors and probability (*p*) values are given.

Model	*n*	Fixed effects	*β* ± SE	*p*
(a) all bird species density	71	early pre-thicket forests	-4.82 ± 0.59	<0.001
		late pre-thicket forests	-1.74 ± 0.59	<0.05
(b) open bird species density	47	early pre-thicket forests	-5.36 ± 0.54	<0.001
(c) scrub bird species density	48	early pre-thicket forests	-4.34 ± 0.40	<0.001
(d) all small mammal habitat model	72	early pre-thicket	2.33 ± 0.71	<0.01
		late pre-thicket	0.90 ± 0.54	0.09
(e) Bank Vole habitat model	24	early pre-thicket	2.03 ± 0.56	<0.001
		late pre-thicket	0.69 ± 0.46	0.14
(f) Wood Mouse habitat model	24	early pre-thicket	3.06 ± 1.20	<0.05
		late pre-thicket	2.54 ± 0.97	<0.01

Across both count periods (i.e. early and late), moorland held the lowest bird diversity (*I* = 0.23 ± 0.07 and *I* = 0.08 ± 0.03, respectively), followed by early pre-thicket forests (*I* = 0.43 ± 0.12 and *I* = 0.37 ± 0.09, respectively) and late pre-thicket forests (*I* = 0.69 ± 0.03 and *I* = 0.62 ± 0.05).

Small mammal communities

Two hundred and thirty-seven individual small mammals of three species were recorded from 351 captures, including 114 recaptures, across 4,760 12-hour trap events. The Bank Vole was the most frequently recorded species, with 152 individuals captured (64.1%). Fifty-eight individual Wood Mice (24.5%) and 27 Greater White-toothed Shrews (11.4%) were also captured (Table 3). Small mammal diversity was highest in moorland (0.42 ± 0.14), followed by early pre-thicket forests (0.41 ± 0.09) and late pre-thicket forests (0.20 ± 0.08).

Table 3. Total number of captures of three small mammal species recorded across three habitats. Letters denote significant differences ($p < 0.05$) where UPPER > lower. The number of individuals re-trapped are shown in parentheses. The number of captures per trap event (excluding false triggers) is also shown to ease comparison between studies.

	Habitat		
	Moorland	Early pre-thicket forest	Late pre-thicket forest
Bank Vole	21 (14) ^{a}	95 (21) $^{A, B}$	36 (18) ^{b}
Wood Mouse	2 (0) $^{c, d}$	30 (6) ^{C}	26 (10) ^{D}
Greater White-toothed Shrew	7 (2)	18 (6)	2 (0)
Captures per trap event	0.04	0.14	0.08
Total	30 (16) ^{e}	143 (33) $^{E, F}$	64 (28) ^{f}

Ground vegetation PC1 had positive associations with gorse and bramble and taller and denser vegetation, as seen in late pre-thicket forests, with a negative association with bare ground and moss that characterised moorland sites (Table 4; Fig. 4a). Ground vegetation PC2 showed a positive association with heather and bilberry cover (i.e. late pre-thicket forests and moorland) and a negative association with grasses and forbs (i.e. early pre-thicket forests; Table 4, Fig. 4a). Tree vegetation PC1 had a positive association with the number of trees, tree height and brash volume, and a negative association with greater distance between trees, describing early and late pre-thicket forest sites (Table 5; Fig. 4b). Tree PC2 had positive associations with canopy cover, and a negative association with course woody debris, separating late and early pre-thicket forest (Table 5; Fig. 4b).

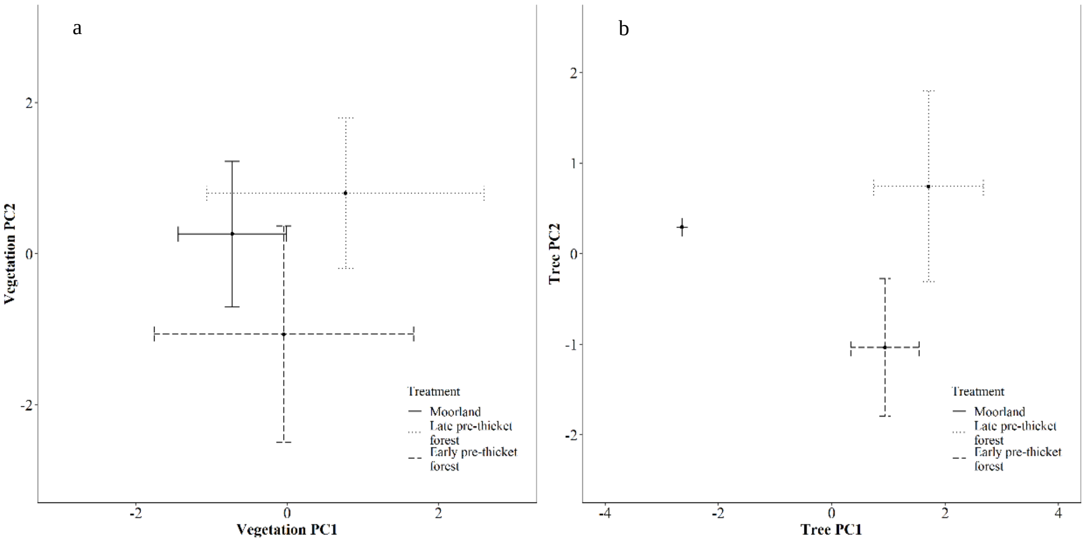

Figure 4. Principal Component (PC) score (±SD) biplots for (a) ground vegetation and (b) tree vegetation.

Table 4. Principal Component (PC) Axes loadings capturing ground vegetation variation at small mammal survey sites. Those loadings that explain the greatest proportion of variation within each of the retained PCs are in **bold** and the percentage variation explained by each PC is given. Vegetation variables are listed alphabetically.

Vegetation variable	Principal Components (variation explained)	
	PC1 (33.3%)	PC2 (24.5%)
Bare ground and moss	**-0.567**	-0.146
Ferns	0.446	-0.116
Gorse and brambles	**0.747**	0.067
Grasses and forbs	0.006	**-0.873**
Heather and bilberry	-0.153	**0.943**
Rushes and woodrush	0.075	-0.515
Vegetation height	**0.948**	0.054
Visual obstruction reading	**0.811**	0.068

Table 5. Principal Component (PC) Axes loadings capturing tree vegetation variation at small mammal survey sites. Those loadings that explain the greatest proportion of variation within each of the retained PCs are in **bold** and the percentage variation explained by each PC is given. Tree variables are listed alphabetically.

Tree variable	Principal Components (variation explained)	
	PC1 (69.6%)	PC2 (19.3%)
Brash volume	**0.866**	-0.094
Canopy cover	0.688	**0.669**
Course woody debris	0.602	**-0.760**
Distance to nearest tree	**-0.935**	0.199
Number of trees	**0.934**	-0.001
Tree height	**0.919**	0.289

Habitat models showed that total small mammal abundance was significantly higher in early pre-thicket forests compared with both moorland (2.33 ± 0.71; $P < 0.01$) and late pre-thicket forests (1.42 ± 0.67; $P < 0.05$; Table 2). There was no significant difference between total small mammal abundance in moorland and late pre-thicket forests ($P > 0.05$). Bank vole abundance was significantly higher in early pre-thicket forests compared with both moorland (2.03 ± 0.56; $P < 0.001$) and late pre-thicket forests (1.34 ± 0.56; $P < 0.05$). There was no significant difference in Bank Vole abundance between moorland and late pre-thicket forests ($P > 0.05$). Wood Mouse abundance was significantly higher in both early pre-thicket forests (3.06 ± 1.20; $P < 0.05$) and late pre-thicket forests (2.54 ± 0.97; $P < 0.01$) than in moorland. There was no difference between early and late pre-thicket forests ($P > 0.05$). Full model outputs are shown in Table 2.

Discussion

Our results showed contrasting patterns in the abundances of birds and small mammals between moorland, early pre-thicket forests and late pre-thicket forests. Our findings suggest that the transition from moorland to pre-thicket habitats increased shrub vegetation complexity, altering the suitability of these areas for different bird groups. Specifically, the change from moorland to pre-thicket forests resulted in a reduction of open-country bird species and an increase in scrub-dwelling bird species. The observed differences are mediated by the increase in the complexity of shrub vegetation as moorlands are displaced by commercial forests (Sweeney et al. 2010, Graham et al. 2017, Burton et al. 2018). By contrast, small mammal species diversity was lowest in pre-thicket forests, but overall abundance was highest, primarily driven by Bank Voles. The increased cover, vegetation density and complexity afforded by windrowed pre-thicket second rotation forests appears to be beneficial in supporting higher densities of small mammals.

Bird communities in open moorland and young forests

Although the effect of afforestation on bird communities has been a focus of research attention in recent years (Graham et al. 2017, Burton et al. 2018, Castano-Villa et al. 2019), this is the first fine-scale study to compare bird communities across different ages of the pre-thicket stage of second rotation upland forests with moorland. Although Meadow Pipits, a Red-listed species in Ireland (Colhoun and Cummins 2013), were recorded in pre-thicket forests, they occurred at much lower densities than in moorland. Skylark and Red Grouse (*Lagopus lagopus*) are also of high conservation priority (Colhoun and Cummins 2013), and were both only recorded in moorland (Table 1). Open moorland therefore supports a greater abundance of birds of conservation priority, with afforestation leading to the replacement of these threatened open habitat bird species with lower densities of a wider variety of species that are currently of less conservation priority. These results have considerable implications for current forest management and future afforestation, with new forests continually replacing the habitat of threatened species, further contributing to their ongoing declines.

Similar effects of afforestation on open habitat bird communities have been reported in other parts of northern Europe where a greater abundance of common generalist species is found in young forest habitats, replacing the open-habitat bird assemblage of less common and more specialist bird species (Moss et al. 1979, Thompson et al. 1988, Calladine et al. 2013). The lower abundance, and in some cases absence, of open habitat specialists recorded in young forests in this study reflects the specific habitat requirements of these species during the breeding season (Vanhinsberg and Chamberlain 2001). Though these species may persist for short periods in first rotation pre-thicket forests due to the retention of suitable habitat features (Wilson et al. 2006), this is not the case with subsequent rotations. Second rotation pre-thicket forests therefore appear to be sub-optimal habitats for several open-country bird species of conservation concern.

Within young forest sites, there was a shift in bird communities from open to scrub species with increasing forest age, related to the increase in the complexity of shrub vegetation layers over time (Wilson et al. 2006, Sweeney et al. 2010). Similar patterns have been observed in commercial forests in other parts northern Europe (Patterson et al. 1995). Bird density and diversity also increased from early to late pre-thicket forests, likely driven by increased habitat suitability for a wider variety of generalist scrub habitat bird species (Quine et al. 2007).

Results from the current study suggest that the presence of woody debris (brash) may benefit scrub bird species, particularly during the initial growth stages post planting (early pre-thicket forest stage). Brash adds structural complexity necessary for these bird species to a habitat otherwise bereft of such complexity (Kirkland 1990, Sweeney et al. 2010). The higher abundance of scrub species in the later pre-thicket stage is likely the result of increased shrub vegetation complexity as the forests develop (Wilson et al. 2010, Calladine et al. 2013). In a study of bird species richness in pre-thicket plantation forests and open moorland in Scotland, Calladine et al. (2013) reported lower bird species richness in pre-thicket Sitka spruce forests compared with adjacent open moorland. The observed difference was found to be mediated by differences in the extent of shrub cover, demonstrating the importance of vegetation complexity in providing resources for bird communities (Wilson et al. 2010, Calladine et al. 2013), further evidence of which is provided by the current study.

Small mammal communities in open moorland and young forests

In contrast to the negative impact observed on open-country bird species, land-use change from open habitat to pre-thicket forest appears to benefit small mammals. More small mammals were captured in early pre-thicket forests than in either of the other habitats. The abundance of grasses and forbs in young forest sites appears to be particularly suitable for bank voles, in clear contrast to the denser, taller and gorse- and bramble-dominated old forest sites where bank voles were less abundant. The trend seen in this study whereby small mammals reach higher densities soon after clearcutting, followed by a decrease in abundance, has also been demonstrated in other studies where vegetation community and structural changes caused by clearcutting resulted in enhanced habitat quality for small mammal species (Kirkland 1990, Fisher and Wilkinson 2005, Gasperini et al. 2016). The lower abundance of small mammals in moorland compared with pre-thicket forests observed in this study reflects the lower suitability of moorland as a habitat for those small mammals in Ireland. Within young forest sites, brash in the form of windrows, provides small mammals with suitable runways and cover (Carter 1993, Fisher and Wilkinson 2005) and is associated with increased small mammal abundance (Fauteux et al. 2012, Gasperini et al. 2016). Small mammals showed a positive association with both the presence of brash and brash volume in the current study, likely due to the provision of food resources (Gunderson 1959, Bowman et al. 2000, Kaminski et al. 2007). The most frequently captured small mammal species across all sites in this study was the Bank Vole, making up 64% of all individuals captured. Although bank voles were captured in moorland in this study, their numbers were significantly lower than in pre-thicket forests, likely due to the absence of dense vegetation cover in moorland (Mazurkiewicz 1994, Hayden and Harrington 2000). Pre-thicket forest is known to be an important habitat for the species in Ireland (Smiddy and Sleeman 1994) and elsewhere in their range (Savola et al. 2013).

While the abundance of bank voles was significantly higher in early pre-thicket compared with late pre-thicket forests, the numbers of wood mice did not differ between pre-thicket forests of different ages. The differing effects of increasing forest age on Bank Voles and wood mice can be explained by vegetation differences between forest ages and comparative habitat requirements of both species. As forests age, dense herbaceous ground cover of grasses and forbs, important for both species, decreases, while shrub cover, important for wood mice, increases (Loy and Boitani 1984, Dickman and Doncaster 1987). Therefore, while the vegetation remains suitable for wood mice throughout this period, it becomes less suitable for bank voles.

Greater White-toothed Shrews were also captured during this study. This species was unintentionally introduced into Ireland around 2004 and their range is predicted to expand to cover the whole of Ireland by 2050 (Tosh et al. 2008, McDevitt et al. 2014). Greater White-toothed Shrews displace native pygmy shrews from the invaded range, with habitats such as peatlands and woodlands thought to be the only possible refugia for the Pygmy Shrews (McDevitt et al. 2014). The current study revealed that greater white-toothed shrews have spread further west in south Limerick than had been previously recorded (National Biodiversity Data Centre 2019) and that they are capable of inhabiting upland moorlands (400m asl). This suggests that peatlands may not be effective refugia habitat for the native pygmy shrew as they were previously thought to be. However, a number of Pygmy Shrews were temporarily captured in one late pre-thicket forest within the core range of the Greater White-toothed Shrew. This is the first evidence that pygmy shrews are able to persist within the core range of the invasive Greater White-toothed Shrew (in this case, Greater White-toothed Shrews have been present for at least six years (McDevitt et al. 2014)). These findings warrant further research as the identification of potential refugia habitats for the Pygmy Shrew and the potential coexistence of both species in relatively close proximity have important implications for Pygmy Shrew conservation in Ireland.

Implications for predators

Studying prey communities enables a deeper understanding of the underlying mechanisms of observed impacts of land-use change on predators. The bird and small mammal species that are the focus of this study are prey for a wide range of upland predators, including some of conservation concern. The results from this study indicate that the shift in land-use from moorland to forest habitat leads to lower prey abundance for those predators that rely primarily on birds, such as Hen Harrier and Merlin (Fernández-Bellon and Lusby 2011, Irwin et al. 2012). For example, decreased prey abundance and accessibility in pre-thicket forests has been suggested as a contributing factor to lower breeding outputs of Hen Harriers nesting in landscapes with a high proportion of pre-thicket forests (Wilson et al. 2012).

Conversely the shift from open to forested habitats may increase the abundance of preferred small mammal prey of predators such as the Short-eared Owl (*Asio flammeus*) and Pine Marten (*Martes martes*) (Glue 1977, Lynch and McCann 2007, Twining et al. 2019). However, this increased prey abundance may only be temporary as bird and small mammal abundances change with increasing forest age beyond the pre-thicket stage (Sweeney et al. 2010, Savola et al. 2013). Such shifts in prey abundances could have additional important ecological consequences. For example, increases in small mammals in upland forests may lead to increased abundance of mammalian predators, such as Pine Marten, potentially leading to increased rates of predation on the nests of declining ground-nesting birds, such as the Hen Harrier.

Conclusions

An understanding of the bird and small mammal communities in upland open moorland and commercial conifer forests has important applications in forest management, policy development and conservation science. The results of our study show how the bird and small mammal populations of open habitats and young forests in the uplands differ, and that the consequences of land-use change associated with afforestation are taxa specific. This study demonstrates the important ecological benefits of retained brash to provide essential cover for small mammals and nest sites for scrub bird species. Where planting follows clear-felling, the retention of brash can enhance the suitability of young forests for birds and small mammals by providing appropriate habitat and is an important tool in the management of forests as habitats for wildlife.

The results further demonstrate that open habitats, such as moorland, hold higher densities of bird prey, and therefore conservation management strategies should focus on the preservation and restoration of these habitats. Strategic deforestation, selective clear-felling to promote age-diversity, and habitat restoration could support increased numbers of open habitat birds, which are important prey species for threatened predators such as Hen Harrier and Merlin. Our findings demonstrate the importance of preserving remaining open natural and semi-natural habitats in order to protect the specialist open habitat bird species that rely upon them. In addition to leaving sites of conservation value unplanted, efforts should also be made to remove self-seeded conifer trees from open areas that originate in nearby plantations in order to preserve the suitability of these habitats for open habitat species. In addition, open habitats of high biodiversity value require identification and mapping in order to inform afforestation policies in these habitats, thereby protecting vulnerable and threatened open habitat specialists. Additional research will expand our understanding of bird and small mammal ecology in response to land-use change and the wider ecosystem consequences of further forest expansion. Of particular importance in this regard will be long-term studies of prey abundance under different forest management strategies in tandem with habitat restoration studies and the knock-on effects on foraging success of key predator species.

Ethics statement

All applicable international, national, and institutional guidelines for the care and use of animals were followed. All small mammal trapping was in accordance with the ethical standards of University College Cork’s Animal Experimentation Ethics Committee, where the study was conducted.

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Chapter Seven

Predator community composition in young forest plantations in Ireland: implications for Hen Harrier conservation[6]

Red Fox at a bait station

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[6] Submitted for review to the Journal of Wildlife Management

Abstract

Afforestation, particularly the large-scale planting of conifer forest stands, has important consequences for a wide range of biodiversity and ecological processes, including predation. Predators are key components of habitats and ecosystems, and predator communities can change in response to anthropogenic land-use changes, such as afforestation. Increased predation plays a role in population declines of birds across Europe, and ongoing forest expansion poses risks to vulnerable species that are inhabiting increasingly fragmented habitats. We examined predator communities in young upland conifer forests in Ireland using baited camera traps and assessed the influence of distance to interior forest edge (the boundary between forest blocks and tracks/roads) and habitat characteristics on predator occurrence and activity in the context of ground nesting birds, particularly ground-nesting Hen Harrier *(Circus cyaneus*) that are vulnerable to predation. Nine predator species were detected, including avian and mammalian predators. Red Fox (*Vulpes vulpes*), Hooded Crow (*Corvus cornix*) and Pine Marten (*Martes martes*), all of which are known predators of Hen Harrier nests, were the most frequently recorded species. Interior forest edge was positively, albeit non-significantly, associated with higher predator detection rates, while daily bait station survival (time to first detection) for mammalian predators and all predators combined was lower, albeit non-significantly, closest to interior forest edge. Fine-scale habitat characteristics were an important determinant of predator detections and daily bait station survival. This study demonstrates that young conifer forests host a wide variety of predator species with potential implications for ground nesting birds, which we discuss in the context of forest management and conservation processes, including the need for targeted deforestation and upland habitat restoration.

Introduction

Commercial afforestation - the large-scale planting of trees, primarily non-native conifers, in areas of suboptimal conditions for other land-uses - represents a significant land-use change globally (Grebner et al. 2013, FAO and UNEP 2020). Vast areas across the northern hemisphere, including North America and Western Europe, have undergone significant afforestation in recent times. In Europe, and particularly Ireland and Britain, timber production and the mitigation of increases in anthropogenic carbon dioxide emissions have been important drivers of the expansion of the forest estate (Zanchi et al. 2007, van der Gaast et al. 2018).

Forest expansion on previously unplanted land has occurred across upland areas in Ireland where extensive planting of commercial forests since the early 20th century has increased forest cover from 1% to 11% of the total land area (DAFM 2020). Here, commercial afforestation represents a significant transformation of often semi-natural open habitats into monotypic plantations of non-native tree species, with considerable potential for negative impacts on ecosystems, biodiversity, and ecosystem service provision (Sweeney et al. 2010, Horák et al. 2019). Expansion of the forest estate in Ireland has predominantly occurred on open peatlands, with 39% of state forests planted on this habitat (DAFM 2018). Although the planting of state forests in Ireland is decreasing, planting of small forest stands by private landowners is set to continue, with a national target to reach 18% forest cover in Ireland by 2046 (DAFM 2014). Balancing the multiple objectives of increasing forest cover and biodiversity conservation is critical to the sustainable development of land-use change in Ireland and across the globe.

Forest expansion in Ireland and other countries has impacted on vulnerable ground nesting bird species (Douglas et al. 2014, Veldman et al. 2015) including Hen Harrier (*Circus cyaneus*; Bonsu et al. 2019a, b). Once widespread in open upland habitats across Ireland (O'Flynn 1983), Hen Harriers are now scarce in the Irish landscape where conifer forest has replaced much of their preferred open habitat with widespread degradation of remaining open habitats through agricultural intensification, peat extraction and wind energy developments (Wilson et al. 2006). Despite extensive conservation efforts, including the designation of Special Protection Areas (SPAs) in important Hen Harrier breeding areas, the national population continues to decline (Ruddock et al. 2016). Although Hen Harriers are known to nest in pre-thicket forest plantations (3 to 12 years post-planting, hereafter referred to as young conifer forest; Wilson et al. 2009, Ruddock et al. 2016, Caravaggi et al. 2019), nesting within this habitat may impact negatively on their breeding success (Wilson et al. 2009, 2012). A large proportion of Hen Harrier nest failures in certain areas are attributed to nest predation (Whitfield and Fielding 2009, Ludwig et al. 2020), with some forest nesting populations even driven to extinction, in part due to high predation pressures (McMillan 2014). Higher nest predation associated with afforestation has been identified as a likely factor in the reduced breeding success associated with their use of young conifer forest (Wilson et al. 2012). Ground-nesting birds breeding in these new forest and adjacent habitats may experience increased predation pressure as a result of increased predator numbers, as well as increased ease with which their nests can be detected by predators due to changes in vegetation structure (Paton 1994, Lahti 2001, Thompson et al. 1988, Wilson et al. 2012). For example, Red-backed Shrikes (*Lanius collurio*) nesting in young conifer forests in Belgium experience higher nest predation risk due, in part, to decreased nest concealment compared with their preferred farmland habitat (Hollander et al. 2015). Similar processes may occur for Hen Harriers in young conifer forests (Wilson et al. 2012, Sheridan et al. 2020). Afforestation can lead to an increase in the numbers of forest-dwelling medium-sized mammalian and avian predators (Piña et al. 2019) through provision of habitat edges (Chalfoun et al. 2002), as well as suitable cover and increased prey availability (Jenkins 1986, Ratcliffe 1986). Further, the combination of high levels of afforestation (typically resulting in uneven-aged mosaics of forest) and the creation of new forest road and track networks (DAFM 2020) in previously open upland landscapes, in Ireland and other countries, has created extensive areas of new interior forest edge habitats. The influence of forest edges on predator communities and predator-prey dynamics may represent a mechanism contributing to the negative relationship between forest edges and Hen Harrier breeding success and productivity (Sheridan et al. 2020).

Understanding the distribution, composition, and potential impacts of predator communities in these new forest habitats is of key importance both in terms of species conservation and land management (Ripple et al. 2001, Terborgh 2001). Effective conservation of Hen Harriers in recently afforested landscapes relies on an understanding of the modified ecological processes that result from this land-use change which may contribute to species declines. However, most studies to date that have examined forest edge impact on predation have focussed on the transition between forest and open habitat (Paton 1994, Lahti 2001, Pfeifer et al. 2017). In contrast, information on the effects of interior forest edge at roads and tracks on predator communities, and of the potential influence of habitat structure on predation risk, is scarce.

The mammalian predator community in Irish forests comprises medium-sized species from the Canidae and Mustelidae families (Hayden et al. 2000), including Red Fox (*Vulpes vulpes*), Pine Marten (*Martes martes*), Stoat (*Mustela ermine*), and Badger (*Meles meles*). These species have benefitted from the large-scale afforestation of recent decades (Hayden et al. 2000, O'Mahony et al. 2012). The abundance of avian predators, including Raven (*Corvus corax*), Hooded Crow (*Corvus cornix*) and Common Buzzard (*Buteo buteo*), has also increased in Ireland in recent times (Balmer et al. 2013). Ireland has a limited predator community compared with continental Europe (Hayden et al. 2000, Shirihai and Svensson 2018), allowing us to explore variation in predation risk by focussing on just a few, key species.

This study aims to describe the composition of predator communities in young conifer forests in Ireland using baited camera traps. It also assesses whether proximity to interior forest edge associated with tracks and roads affects predator occurrence in this habitat, as well as the influence of habitat structure on predator occurrence. As this study was undertaken as part of a larger project on the effects of afforestation on Hen Harrier, we also considered the findings in terms of the potential ecological consequences of predator abundance and activity for prey species, particularly for ground-nesting Hen Harrier.

Study area

The study area comprised four separate upland areas with breeding Hen Harrier in the south-west of Ireland and was undertaken between May and August 2018. These were the Nagle Mountains, Boggeragh Mountains, Ballyhoura Mountains and Mullagharierk Mountains (covering approximately 274km^2 in total). The study area experiences a cool, temperate, and humid climate with long-term average annual rainfall of 1228.0mm and long-term average air temperature of 9.8°C (Met Éireann 2021). Land use in these areas is dominated by commercial conifer plantations, wind-energy developments, and low-intensity agriculture.

Twelve study sites were selected in young conifer forests, ranging from three to eight years post-planting ($\bar{x} = 5.2 \pm 1.5$ [standard deviation; SD] years) (Fig. 1). Sites were selected such that forest blocks were on average 12.1ha in size (± 4.3ha). Sites were selected, *a-priori*, using ArcGIS 10.4.1 (ESRI 2011) and forest cover data provided by Coillte, the Irish semi-state forestry body. The age profile of forests selected for use in this study is within the range used by Hen Harrier (Wilson et al. 2009, 2012). In addition, all study sites were selected such that they were located between one and five kilometres from confirmed Hen Harrier territories, based on data from the 2015 National Survey of Breeding Hen Harrier in Ireland (Ruddock et al. 2016). We selected sites that were dominated by Sitka spruce (*Picea sitchensis*), with lodgepole pine (*Pinus contorta*) and larch (*Larix* spp.) also planted at lower densities. The edge density, defined as edge (in metres) to area (in square metres) ratio, was calculated for each forest study site.

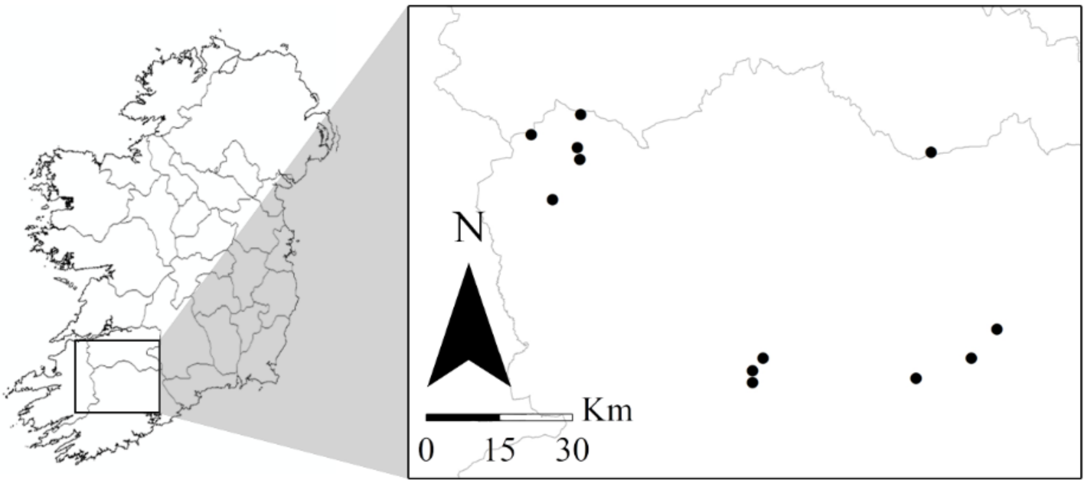

Figure 1. Location of study sites in four Hen Harrier breeding grounds in Ireland (May to August 2018).

Methods

Camera Trapping

We used remote-sensing camera traps to conduct predator surveys at the 12 study sites between mid-May and mid-August 2018, covering much of the breeding season for Hen Harrier and other upland bird species. We set up three bait stations at each study site, giving a total of 36 bait stations, located at 10m, 50m and 100m from the edge of the forest stands at the interface with forest tracks and roads. The small size of forest blocks in the selected study areas, typical of forest block size across Ireland, limited the maximum distance from interior forest edge that was possible to use. The edge of forest stands in this study is defined as the intersection between a forest block and a forest track/road, with conifer forest on the opposite side of the track/road (i.e. an interior edge). Each bait station comprised a Bushnell® Trophy Cam HD camera trap (model 119676), bait within a cage and a scent lure. We fixed cameras on wooden posts at a height of 1m and at a distance of 3m from the bait cage. Cameras were set to take five-megapixel photographs with a sensitivity set to 'normal' and the inter-trigger frequency interval set to five seconds. We placed bait (0.5kg of fresh, raw chicken) in a 0.01m metal mesh cage measuring 0.3x0.3x0.2m that was fixed in place with a 0.5m steel bar staked into the ground. We applied four 0.04m long lines of Premium Lockmittel Hagpour® commercial Pine Marten scent lure to two opposing sides of a 0.04x0.04x0.5m high wooden post driven into the ground next to each bait cage to maximise detection of focal species (Burki et al. 2010). We situated the bait cage and the wooden scent lure stick in the centre of the camera's field of view, which we determined *in-situ*. We trimmed loose vegetation immediately around the bait station to minimise the number of false detections resulting from moving vegetation. We deployed bait stations for two consecutive weeks and refreshed the scent lure one week after deployment. Detections were treated as separate events when separated by 30 minutes or more (Kelly and Holub 2008). No licences or permits were required to conduct this study.

Habitat Surveys

We conducted habitat surveys at every bait station within one week of the end of the camera deployment period in order to examine fine-scale habitat influences on predator detections. We set up four 10m transects around each bait station, each transect starting at the station and orientated in a cardinal direction (Fig. 2). We established sampling points at 1.5m, 5.0m and 10.0m along each transect. At each sampling point, we deployed a 1m^2 quadrat. We visually estimated the percentage vegetation cover within each quadrat (to the nearest 5%) for each of 9 taxonomic/structural groupings (bare ground and mosses; conifer trees; dead wood;

ferns; gorse (*Ulex* spp.) and brambles (*Rubus* spp.); grasses and forbs; heather (*Calluna vulgaris* and *Erica* spp.) and bilberry (*Vaccinium myrtillus*); rush (*Juncus* spp.) and wood rush (*Lusula* spp.); and willows (*Salix* spp.). We recorded maximum ground/shrub vegetation height within a 0.05m radius of the four corner points of each 1m^2 quadrat. We took four additional vegetation height measurements at the centre point of each quadrat edge at the 1.5m sampling points. We also recorded the distance from the centre of the bait cage to the nearest five trees and recorded their heights (within half-metre categories), their diameters at breast height (1.3m) (DBH) and the species.

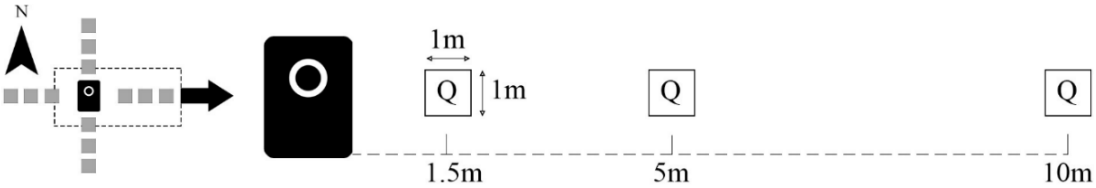

Figure 2. The distribution of quadrats (Q) used in habitat surveys, relative to camera trap bait stations at each study site in Ireland (May to August 2018). The east arm of the quadrat array is shown.

We estimated the openness of the vegetation around each camera for each cardinal direction by recording the minimum distance at which the top surface of the bait cage was no longer visible by an observer (from a height of 1.5m above the ground (adapted from Simmons and Smith 1985)) walking away from the cage in that direction. We also determined vegetation density using visual obstruction measurements (Robel et al. 1970). Once the bait cage had been removed, we took Visual Obstruction Readings (VORs) from the centre of where the cage had been positioned using a Robel pole. We recorded the lowest number visible on the Robel pole at three observation heights (0.5m, 0.8m and 1.0m) and at three distances (2m, 3m and 4m) away from the Robel pole along each of the four transects.

We calculated habitat composition within a 2km radius of each study site. We extracted the percentage cover of the main CORINE land class categories within this radius from the CORINE 2012 dataset (European Environment Agency 2016). We supplemented this with forest cover data sourced from Coillte and the Forest Service that supported the designation of forest age classes. Age-classes corresponded to previously published information on Hen Harrier nest site selection preferences (Wilson et al. 2009, 2012; Caravaggi et al. 2019): (i) early (0-2 years, post-planting); (ii) young conifer forest (3-12 years, post-planting); and (iii) closed canopy (≥ 13 years, post-planting).

Data analysis

One observer (Alan McCarthy) examined all camera trap photographs manually. A second observer (Anthony Caravaggi) assessed a random sample of photographs (10%) to confirm species identification. We recorded details of all photographs containing predators, including site, distance from interior forest edge, date and time of photograph, and species of predator observed.

We applied two discrete Principal Component Analyses (PCAs) to the fine-scale and landscape-scale habitat data. We included 14 habitat variables in the fine-scale habitat PCA and eight variables in the landscape-scale PCA. We standardised all variables with $\bar{x} = 0$ and $\sigma = 1$. Where model convergence allowed, we retained Principal Components (PCs) that accounted for at least 70% of variation for inclusion in the models.

We applied two sets of models to the camera trap data. The first examined the number of predator detections at each distance from interior forest edge (10m, 50m and 100m). Exploratory analyses showed that the data were zero-inflated, therefore we used zero-inflated negative binomial mixed effects models. We constructed five models, where the response variable was set as the number of: (i) all predator detections; (ii) avian predator detections; (iii) mammalian predator detections; (iv) Red Fox detections; and (v) Pine Marten detections. Within each of these five models, we set distance from interior forest edge, the top four fine-scale habitat PCs, and the top two landscape-scale habitat PCs as the fixed effects, with site and date as random effects. As well as the number of predation detections, daily survival also provides a useful measure of predation risk of nests. High daily survival indicates a nest is less likely to be detected by a predator before the chicks fledge from the nest, whereas low daily survival indicates a nest is more likely to be predated before fledging takes place. We used the second set of models to examine the daily station survival (hereafter referred to as DSS; i.e. time to detection of each station by a predator) at each distance from interior forest edge (Mayfield 1975). We constructed five further models where the response variable was set as DSS for: (i) all predators; (ii) avian predators; (iii) mammalian predators; (iv) Red Foxes; and (v) Pine Marten. Within each of these models, we set distance from interior forest edge, the top two landscape-scale and top two fine-scale PCs as fixed effects. We also included both site and date in the 'all predators' and 'mammalian predators' models as singular fit and convergence issues prevented inclusion of these fixed effects in the Red Fox and Pine Marten models. We were able to include date, but not site, in the 'avian predators' model. Akaike's Information Criterion (AIC) was used to rank all possible model permutations in each instance. All models within ΔAIC<2 (i.e. the top subset) were considered a reasonable approximation to reality. The model with the lowest AIC weight was considered the best approximating or 'top', model (Burnham & Anderson, 2002). Where there was more than one top model in the top subset, we applied model averaging to extract appropriate coefficients and measures of variable importance. We calculated the distribution of predator detections across 24 hours of the day for avian and mammalian predators by summing the number of detections of each predator group that occurred during each hourly interval.

We processed and analysed data using R version 3.5.1 (R Core Team 2020), including packages *glmmTMB* (Brooks et al. 2017), *ggplot2* (Wickham 2016), *MuMIn* (Barton 2020) and *lme4* (Bates et al. 2015). Results are presented as x̄ ± standard error, unless otherwise stated. Data and code used in this study are available at https://github.com/arcaravaggi/McCarthy_predators.

Results

We collected a total of 602 photographs of predators across 10,080 hours of camera deployment. There was 100% agreement on detected species identities between the two independent observers. We excluded two sites from the data analyses due to camera failure at a single bait station in each site, thus avoiding relative inflation of detections at distances unaffected by camera malfunctions. We recorded 79 separate predator detections at 23 of the 30 bait stations with 35 detections at 10m, 19 detections at 50m and 25 detections at 100m from interior forest edge. In most cases, we captured several photographs during individual detections. Mammals accounted for 67.1% of all predator detections and birds for 32.9% of detections and this pattern was consistent across all three distances from interior forest edge (65.7%, 34.3% respectively at 10m; 73.7%, 26.3% at 50m; 64.0%, 36.0% at 100m). We detected three avian and six mammalian predator species. The most frequently detected avian predator was Hooded Crow (30.4% of all predator detections) while the most frequently detected mammalian predator was Red Fox (26.6% of all predator detections), closely followed by Pine Marten (25.3%). Other predators that we recorded included Stoat (6.3%), Badger (6.3%) and Jay (*Garrulus glandarius*; 1.4%) (Table 1).

Table 1. Number of detections of each predator species at three distances from interior forest edge at study sites in Ireland (May to August 2018). Numbers in parentheses are relative to the total number of detections at each distance.

Species	10m	50m	100m	Total
Birds				
Hooded Crow (*Corvus cornix*)	11 (31.4%)	5 (26.3%)	8 (32.0%)	24
Eurasian Jay (*Garrulus glandarius*)	1 (2.9%)	0 (0%)	0 (0%)	1
Magpie (*Pica pica*)	0 (0%)	0 (0%)	1 (4.0%)	1
Mammals				
Red Fox (*Vulpes vulpes*)	11 (31.4%)	3 (15.8%)	7 (28.0%)	21
Pine Marten (*Martes martes*)	9 (25.7%)	8 (42.1%)	3 (12.0%)	20
Badger (*Meles meles*)	1 (2.9%)	0 (0%)	4 (16.0%)	5
Stoat (*Mustela erminea*)	1 (2.9%)	2 (10.5%)	2 (8.0%)	5
American Mink (*Neovison vison*)	0 (0%)	1 (5.3%)	0 (0%)	1
Domestic Dog (*Canis lupus familiaris*)	1 (2.9%)	0 (0%)	0 (0%)	1
Total	35	19	25	79

Landscape-scale habitat PC1 showed a positive association with moorland, heath, early forest and closed canopy forest and a negative association with pasture. PC2 showed a positive association with bog, and a negative association with broadleaf and young conifer forest (Table 2). Fine-scale habitat PC1 had a positive association with aerial visibility (openness) and a negative association with visual obstruction reading and ground vegetation height. PC2 had a positive association with heather and bilberry, and a negative association with grasses and forbs. PC3 showed a positive association with bare ground and moss, and a negative association with willow. PC4 showed a positive association with conifer trees and a negative association with ferns (Table 3).

Table 2. Principal component (PC) axes loadings capturing landscape-scale habitat variation around study sites (May to August 2018). Those values highlighted in **bold** show those that best describe each PC.

Landscape-scale habitat variable	Principal components (variation explained)	
	PC1 (44.66%)	PC2 (24.05%)
Agriculture	0.057	0.068
Moorland & heath	**0.867**	-0.250
Bog	-0.074	**0.911**
Pasture	**-0.963**	-0.192
Early forest	**0.943**	-0.009
Closed-canopy forest	**0.767**	0.591
Pre-thicket forest	0.638	**-0.523**
Broadleaf	0.026	**-0.607**

Table 3. Principal component (PC) axes loadings capturing fine-scale habitat variation around bait stations (May to August 2018). Those values highlighted in **bold** show those that best describe each PC.

Fine-scale habitat variable	Principal components (variation explained)			
	PC1 (31.08%)	PC2 (18.44%)	PC3 (12.32%)	PC4 (8.96%)
Dead wood	0.375	-0.283	-0.084	0.335
Ferns	-0.574	-0.529	0.061	**-0.421**
Willow	0.026	0.365	**-0.564**	-0.256
Grasses & forbs	0.568	**-0.693**	-0.248	0.130
Bare ground & moss	0.251	0.276	**0.784**	-0.166
Heather & bilberry	-0.215	**0.896**	-0.228	-0.069
Gorse & bramble	-0.666	-0.584	-0.127	-0.243
Rushes & woodrush	0.426	-0.318	0.533	-0.072
Conifer trees	-0.302	-0.069	-0.037	**0.773**
Ground vegetation height	**-0.910**	-0.216	-0.175	0.002
Tree height	-0.730	0.229	0.373	0.237
Visual obstruction reading (VOR)	**-0.754**	0.001	0.266	-0.020
Aerial visibility (openness)	**0.702**	0.009	-0.045	-0.206

We recorded higher detection rates of both avian (1.2 ± 0.7 detections per station) and mammalian (2.3 ± 0.9 detections per station) predators at bait stations situated 10m from interior forest edge, compared with 50m (0.5 ± 0.3 and 1.4 ± 0.6 detections per station, respectively) and 100m bait stations (0.9 ± 0.5 and 1.6 ± 0.6 detections per station, respectively). We recorded a higher number of Red Fox detections at 10m (1.1 ± 0.7 detections per station) compared to 50m (0.3 ± 0.2) and 100m (0.7 ± 0.3), however this result was not statistically significant. We detected Pine Martens most frequently closest to interior forest edge (0.9 ± 0.6 detections per station) and least frequently furthest from interior forest edge (0.3 ± 0.2 detections per station), though the observed difference was not statistically significant (Fig. 3a). Habitat and distance from interior forest edge had no statistically significant effect on the overall number of predator detections nor mammalian predator detections only. For all predators and mammalian predators, fine-scale habitat PC1 was the most descriptive fixed effect for explaining the number of predator detections. Furthermore, for Pine Marten, fine-scale habitat PC1 was also the fixed effect that best described detections with a near-significant effect (p = 0.061). For avian predators and Red Foxes, the null model was the best fitting model, therefore no fixed effects accurately described the number of predator detections for either group (Table 4).

We recorded the lowest DSS of the three distances at bait stations situated 10m from interior forest edge for mammalian predators (0.60 ± 0.13), including Red Foxes (0.84 ± 0.09) and Pine Marten (0.81 ± 0.11). This pattern was not observed for avian predators, with the lowest DSS at the furthest distance from interior forest edge (0.71 ± 0.12) (Fig. 3b). The most important determinant of DSS for mammalian predators was fine-scale habitat PC2 and date. For Red Foxes alone, there was one top model which included fine-scale habitat PC1 and PC2. No fixed effects accurately described DSS for all predators combined, avian predators nor Pine Marten. Across all DSS models, no fixed effect had a statistically significant effect (Table 4).

Table 4. Model average results for zero-inflated negative binomial linear mixed effects models for detections data (a to e) and general linear models for daily station survival data (GLMs; f to j). The top two most important variables are shown for each model, along with importance values (proportion of top models that included each variable), β ± SE, z-values, and p-values (May to August 2018).

Model	Variable	n	Importance	β ± se	z-value	p-value
(a) detections (overall)	Intercept			0.994 ± 0.212	4.503	< 0.001
	Fine-scale PC1	30	0.67	-0.087 ± 0.094	0.904	0.366
	Distance from interior edge	30	0.22	-0.001 ± 0.003	0.340	0.734
(b) detections (mammalian)	Intercept			0.430 ± 0.275	1.494	0.135
	Fine-scale PC1	30	0.92	0.227 ± 0.139	1.573	0.116
	Fine-scale PC2	30	0.5	-0.130 ± 0.180	0.702	0.482
(c) detections (avian)	Intercept			-2.200 ± 1.523	1.376	0.169
	Fine-scale PC4	30	0.17	-0.113 ± 0.346	0.317	0.751
	Fine-scale PC3	30	0.12	-0.031 ± 0.147	0.202	0.840
(d) detections (Red Fox)	Intercept			-1.248 ± 0.680	1.753	0.080
	Fine-scale PC2	30	0.58	-0.285 ± 0.321	0.872	0.383
	Fine-scale PC1	30	0.35	0.100 ± 0.188	0.521	0.602
(e) detections (Pine Marten)	Intercept			-1.671 ± 1.068	1.489	0.137
	Fine-scale PC1	30	1	0.909 ± 0.463	1.876	0.061
	Distance from interior edge	30	0.48	0.342 ± 0.541	0.615	0.539
(f) daily station survival (overall)	Intercept			72.616 ± 212.143	0.333	0.739
	Fine-scale PC4	30	0.43	0.057 ± 0.222	0.246	0.806
	Landscape PC2	30	0.32	-0.083 ± 0.218	0.365	0.715
(g) daily station survival (mammalian)	Intercept			422.300 ± 352.600	1.142	0.253
	Fine-scale PC2	30	1	0.575 ± 0.337	1.630	0.103
	Date	30	1	-0.024 ± 0.020	1.140	0.254
(h) daily station survival (avian)	Intercept			1.427 ± 0.543	2.517	0.012
	Fine-scale PC2	30	0.55	-0.332 ± 0.444	0.731	0.465
	Landscape PC1	30	0.27	0.063 ± 0.186	0.327	0.743
(i) daily station survival (Red Fox)	Intercept			2.331 ± 0.742	3.143	0.002
	Fine-scale PC1	30	NA	-0.365 ± 0.306	-1.192	0.233
	Fine-scale PC2	30	NA	0.607 ± 0.443	1.369	0.171
(j) daily station survival (Pine Marten)	Intercept			2.007 ± 0.887	2.173	0.030
	Fine-scale PC1	30	0.61	-0.389 ± 0.535	0.708	0.479
	Fine-scale PC2	30	0.39	-0.303 ± 0.567	0.522	0.602

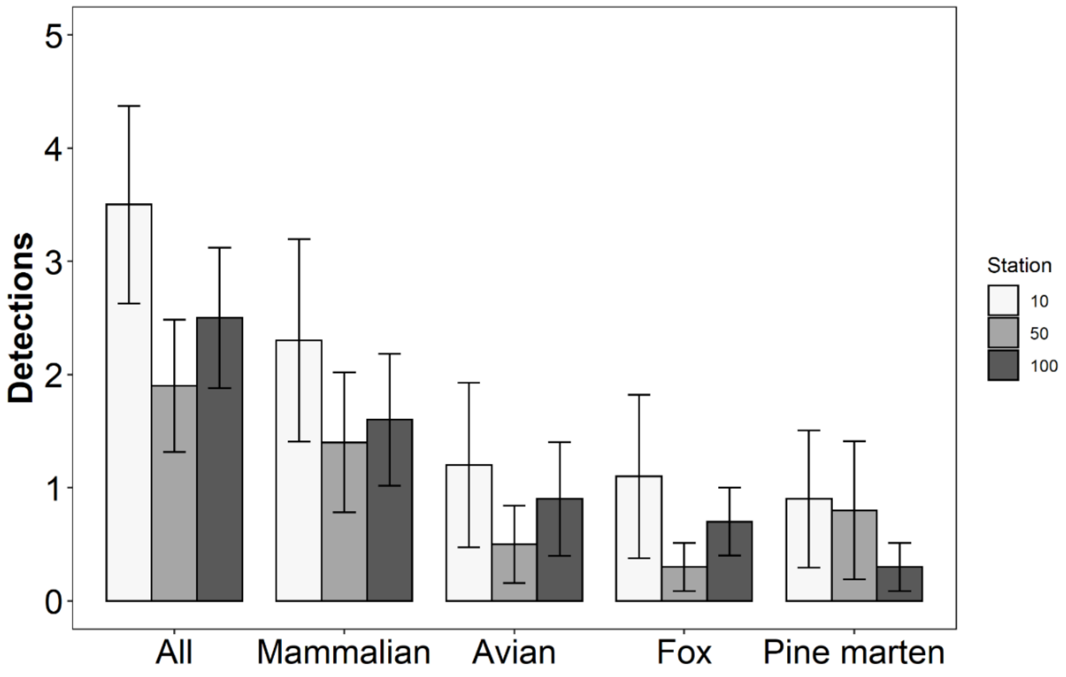

Figure 3a. Mean (±SE) number of avian and mammalian predator detections per station at each distance from interior forest edge at study sites in Ireland (May to August 2018).

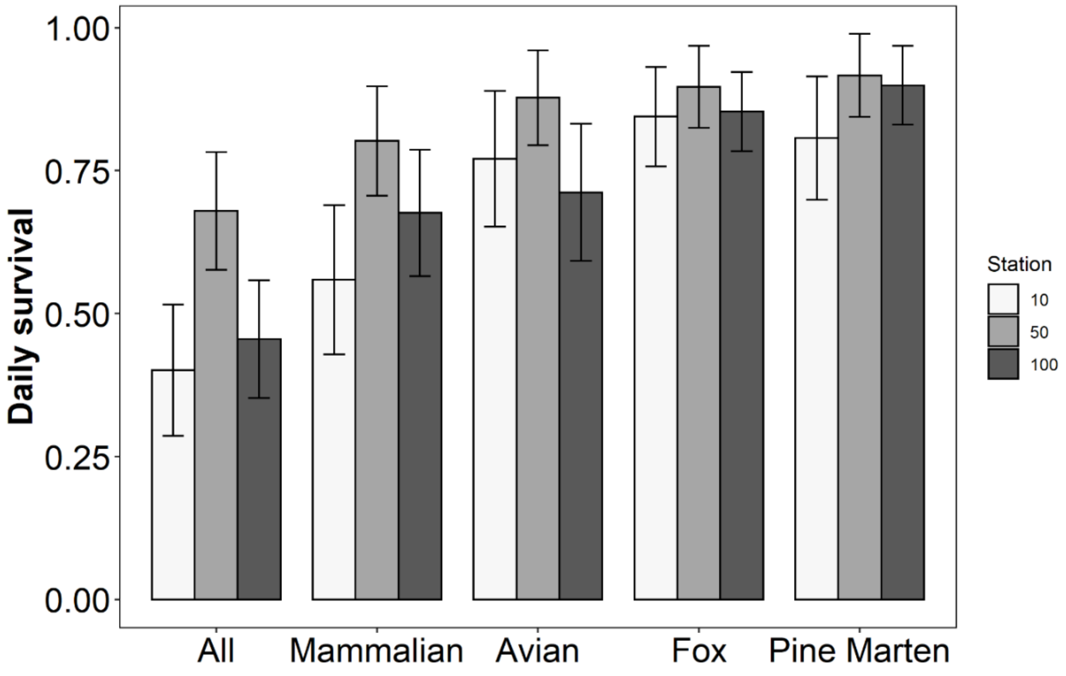

Figure 3b. Mean (±SE) Daily survival of bait stations (DSS) of avian and mammalian predators per station at each distance from interior forest edge at study sites in Ireland (May to August 2018).

There was a difference in the circadian patterns in detections between avian and mammalian predators (Fig. 4). All detections of avian predators were recorded during hours of daylight (0600 to 1900 hours) and were unimodal, with a peak between 1200 hours and 1400 hours. In contrast, we detected mammals across the full 24-hour period, with some evidence of a bimodal signature, with peaks at dawn (0400 to 0500 hours) and dusk (2100 to 2200 hours).

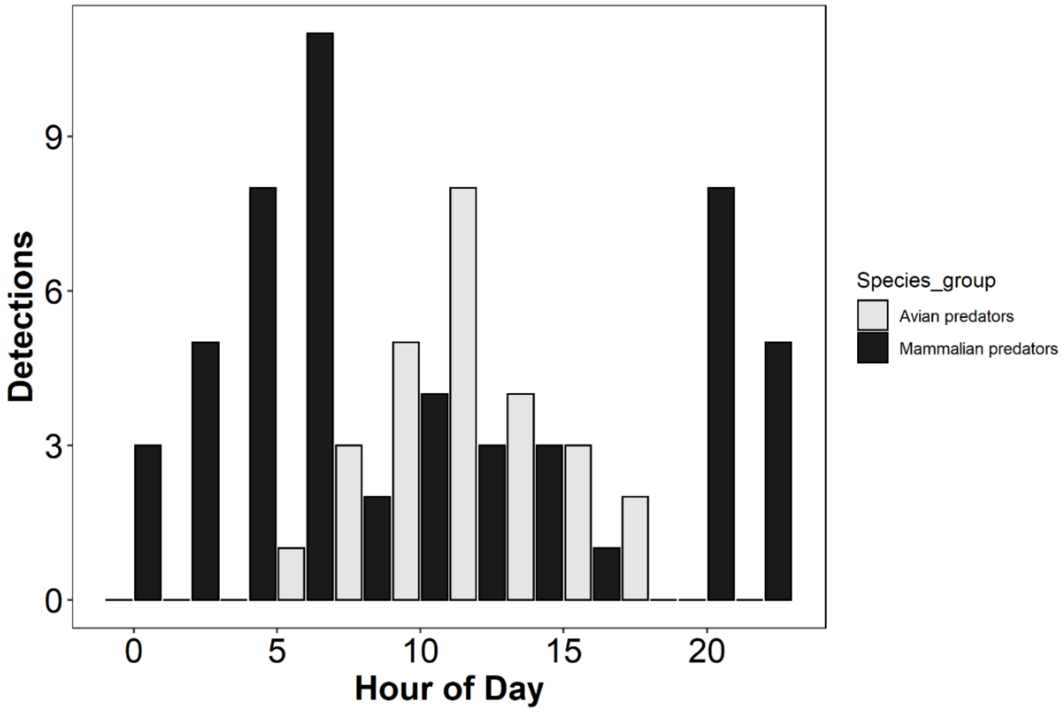

Figure 4. Distribution of avian and mammalian detections over 24 hours at study sites in Ireland (May to August 2018). Data are grouped into two-hour intervals.

The dominant landscape habitats recorded within 2km of study sites were pasture (29.0 ± 5.5%), closed canopy forest (23.9 ± 2.6%), moorland and heath (17.5 ± 1.8%) and young conifer forest (13.4 ± 1.8%). Combined, conifer forest habitats accounted for an average of 41.6 ± 4.2% of surrounding habitat (Appendix 3).

Discussion

A varied mammalian and avian predator community was associated with young conifer forest at all three distances from interior forest edge (10m, 50m and 100m) in this study. Although not statistically significant, more predators were detected close to interior forest edge at all study sites, while bait stations close to interior forest edge had the lowest DSS (daily station survival), except for avian predators.

Overall, fine-scale habitat had the greatest influence on predator detections and DSS. Predators were more likely to be detected, and to be detected faster, in areas with short and more open vegetation structure. While such habitat features afford ground-nesting birds a view of approaching predators, the converse is also true, where brooding adults and chicks in the nest may be more readily detectable and more easily accessible to predators. Previous research has highlighted the importance of such fine-scale habitat influences on the vulnerability of nests to predation (Hollander et al. 2015). Further, habitat composition, density and structure have an influence on the diversity and abundance of small mammals, an important prey group for mammalian predators. Recent research has highlighted the positive association between small mammal abundance and the cover of grasses and forbs in young conifer forests (McCarthy et al. 2021). The positive association between mammalian predator encounters and this vegetation type, particularly Red Foxes, in this study may be the result of these predators utilising these areas for hunting small mammals, as well as the openness of the vegetation structure. Traditional open upland habitats, such as heather moorland, are less suitable for small mammals in Ireland (McCarthy et al. 2021), and therefore are perhaps less likely to attract associated mammalian predators.

The frequency with which Pine Marten and Red Fox were detected in this study suggests that both species occur regularly in young conifer forests. Extensive afforestation in Ireland over the last half century has contributed to range expansion and increase in Pine Marten (O'Mahony et al. 2012) and Red Fox populations (Hayden et al. 2000, Fisher and Wilkinson 2005). Both species have been implicated in Hen Harrier nest failures (Ruddock et al. 2016). For example, Red Fox predate adult Hen Harrier, particularly incubating females (McMillan 2014), and Hen Harrier chicks, either when they are left unattended by foraging parents, or by flushing adults from the nest (Ruddock et al. 2016, Fernández-Bellon et al. 2018, Ludwig et al. 2020). In addition to the small mammal prey base that young conifer forest supports, which likely attracts predators (Pereboom et al. 2008, Horák et al. 2019, McCarthy et al. 2021), these forests also provide windrows (decaying brash and pine needles left on the ground after felling) and dead wood which are used by mammalian predators as den sites (Sullivan et al. 2017) and access routes between mature forest stands (Buskirk et al. 1989, Moriarty et al. 2015, Sullivan et al. 2017). The structure and composition of young conifer forests may therefore help to support mammalian predator populations in upland areas.

Badger, American Mink (*Neovison vison*) and Domestic Dog (*Canis lupus familiaris*) are potential nest predators and were detected in young conifer forests during this study. Badgers are often associated with forest habitats (Hayden et al. 2000, Chiatante et al. 2017). American Mink, however, are strongly associated with aquatic habitats (Harrington et al. 2010). In this specific case, there was no significant water body, river, or stream within the forest block where the bait station was located. It is likely, therefore, that the detection was of an individual transiting between two river systems, rather than specifically using the study habitat. The single detection of a domestic dog which occurred in the nearest distance category to interior forest edge highlights the potential effects of human disturbance to nesting Hen Harrier via recreational activities (Caravaggi et al. 2020).

Hooded Crow was the most frequently detected avian predator in the current study. Hooded Crow are common and widespread corvids in Ireland that nest in mature forest plantations (Kelly 2008, Nairn and O'Halloran 2012). They are an opportunistic, generalist predator and often predate eggs in nests (Zduniak 2006) as well as young Hen Harrier chicks (Whitfield and Fielding 2009, McMillan 2014). In Orkney, for example, Hooded Crow are the main egg predator of Hen Harrier nests and an increase in crow numbers has been identified as a possible factor in reduced Hen Harrier breeding productivity there (Amar and Burthe 2001). Jay and Magpie (*Pica pica*), both of which consume eggs and chicks (Holyoak 1968), also utilise planted forests for nesting (Nairn and O'Halloran 2012). The results of this study highlight the wide range of predators utilising young conifer forests, many of which are common predators of the ground-nesting Hen Harrier, and the potential for predation events. These findings can be used to inform management plans, including, but not limited to, long-term landscape planning and habitat management, as well as short-term and targeted predator control, including exclusion, to limit predation loss and protect vulnerable species.

Bait stations closest to interior forest edge detected the highest number of both avian and mammalian predators in this study and had lower DSS for all predator species/groups, with the exception of avian predators, than stations further from interior forest edge. The higher number of detections and lower DSS of bait stations for mammalian predators 10m from interior forest edge may be due the presence of forest tracks that bordered all stands in this study. Such linear features in matrix landscapes often facilitate the movement of mammals (Kuefler et al. 2010, Wysong et al. 2020). While predators were detected at each of the three distances from interior forest edge, demonstrating the capacity of predators to move and detect bait stations independently of linear features, the higher (though not statistically significant) number of detections at 10m could have important ecological implications. Sheridan et al. (2020) demonstrated that Hen Harrier preferentially nest in areas of high edge/area ratio, but that subsequent breeding success and productivity are negatively impacted by habitat fragmentation and edge. Taken together, the number of detections and DSS observed in the present study suggest that predator activity is higher in these areas. This may lead to increased predation pressure along interior forest edge, with knock-on effects for ground-nesting birds that select breeding sites close to interior forest edge. Although not all of the observed trends in the current study were statistically significant, the ecological relevance of the observed patterns merits further investigation to inform conservation policy and practice.

The circadian distribution of predator detections differed between avian and mammalian predators, with avian predators only detected during daylight hours, peaking in the middle of the day, while mammalian predators were detected across the 24 hours of the day, with peaks in the hours around both dawn and dusk. Hence, ground-nesting birds breeding in sub-optimal habitat may find their nests threatened more regularly during the 24-hour period than conspecifics that nest in more suitable habitat. Hen Harrier are diurnal and so adults may have greater capacity to defend their nests against diurnal avian predation (Simmons and Smith 1985). However, where food is limited, adults may be required to forage at greater distances from the nest, leaving eggs and chicks more vulnerable (Amar and Burthe 2001, Fernández-Bellon et al. 2017). Furthermore, the ocular capabilities of exclusively diurnal species are compromised during the hours of twilight and darkness (Schmitz and Motani 2010). Thus, diurnal, ground-nesting species may be most vulnerable to predation by crepuscular and nocturnal mammalian predators in young conifer forests, including adults as they incubate eggs and young chicks at night. These findings have important implications for assessing relative predation risk of and conservation implications for ground-nesting birds such as Hen Harrier in afforested landscapes, particularly those comprised of small land parcels where nests may frequently be located close to interior forest edge.

While predation levels have been identified as a primary pressure on Hen Harrier in Ireland and other parts of the Hen Harrier's range (McMillan 2014, Caravaggi et al. 2020, Fernández-Bellon et al. 2021**),** data on predation rates and predator densities is scarce. This study represents the first exploration of predator community composition in young forests used by Hen Harrier. The only similar previously published study of predator occurrence in Irish landscapes was conducted by McGowan et al. (2019). They used camera trapping across a wide range of habitats, representative of the Irish landscape as a whole, as part of an Irish Hare (*Lepus timidus hibernicus*) survey. That study found 0.004 Red Fox detections per hour (0.002 in the current study; lower), 0.002 Badger detections per hour (0.0005; lower), and 0.00003 detections of Pine Marten per hour (0.002; higher). However, both studies used different thresholds to define independent detections; 1 minute in McGowan et al. (2019) versus 30 minutes in young conifer forests in the current study; therefore, a direct comparison of detection rates is not possible.

The findings of this study have important implications for the conservation of the Annex 1 listed Hen Harrier in Ireland and throughout its range. Predation of Hen Harrier nests can have a significant impact on breeding populations and has been identified as a contributing factor in the extinction of forest-breeding Hen Harrier populations (McMillan 2014). A recent European-wide study of Hen Harrier conservation found that predator control was considered one of the most effective conservation strategies (Fernández-Bellon et al. 2021). At a population level, nest success rates have a greater effect on population trends than the number of chicks produced per nest (Etheridge et al. 1997, Whitfield and Fielding 2009). Therefore, predation, which typically results in full broods being lost (Skutch 1985, Yanes and

Suarez 1996, Fernández-Bellon et al. 2018), is of particular importance at the population level for Hen Harrier (Wilson et al. 2012). Prior to the current study, no published data were available on the predator communities in the young conifer forests in Ireland that are now utilised for nesting by some 60% of breeding Hen Harrier (Ruddock et al. 2016). Thus, the findings of this study provide an important insight into the potential for forest management practices to impact on Hen Harrier breeding success.

The current study will inform landscape and forest management to reduce predation risk associated effects on sensitive ground nesting bird populations, including Hen Harrier. Further knowledge gaps are highlighted regarding predation risk of ground-nesting birds in young, planted forests in Ireland, and the need for further research to identify specific factors that could be managed to benefit the conservation of ground-nesting birds.

Management implications

Our findings highlight the importance of landscape composition for the conservation management of upland landscapes and the conservation of ground-nesting bird species, including Hen Harriers, that may be threatened by increased predation pressures associated with fragmentation by forest roads and tracks. Young conifer forests in this study were home to a wide range of predators, meaning that forest expansion, such as that proposed across Europe, could be associated with the provision of new areas of suitable habitat for predators of Hen Harrier and other ground nesting birds. Furthermore, the fragmentation of forest stands by forest roads and tracks may provide new areas of interior forest edge where predator activity is increased and where there is a simultaneous decrease in daily survival of nests. Forest management practices that are cognisant of the potential impact they may have on predator populations and that seek to minimise predation risk may lessen the negative impact of afforestation on Hen Harrier and other ground nesting birds. This may include the avoidance of afforestation in Hen Harrier strongholds because of the potential associated predation risk. Large-scale, targeted deforestation and upland habitat restoration should also be considered as a future conservation measure. Management of existing forests in Hen Harrier areas should focus on optimising the habitat to minimise predation risk and could include practices such as removal of brash from clear-fell sites to decrease small mammal prey abundance and den site availability, as well as management of ground vegetation to increase nest concealment. Predator control, including exclusion, may also be beneficial to vulnerable bird species in the short-term, while long-term and sustainable landscape and forest management practices are implemented. The incorporation of information on predator communities in the development of management plans would be a useful tool to mitigate against the effects of afforestation on predator communities and associated ecological processes.

Ethics statement

No licences were required for this study. All study sites were located a minimum of 1km from the nearest active Hen Harrier nest.

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Chapter Eight

Concluding synthesis and recommendations

Adult female Hen Harrier

Photograph: Richard T. Mills

Overview

An understanding of year-round ecology is crucial to developing effective conservation strategies for species of conservation concern (Fryxell et al. 2014, Marra et al. 2015). By collecting scientific information on the movement, survival, and habitat use of birds throughout the annual cycle, we can better understand the pressures they face and determine whether their ecological requirements are being met. Systematic research and conservation efforts for Hen Harriers (*Circus cyaneus*) have been largely focussed on the breeding season and centred on habitat use, diet composition and pressures faced in the breeding grounds, while many aspects of their non-breeding ecology remain poorly understood. This approach to conservation ignores the seasonality of resource use and the potential for distribution, habitat use and diet to change across the year. By focussing research and conservation efforts exclusively on a single period of the year there is a risk that important pressures beyond this will not be identified or mitigated against. Although the breeding and non-breeding periods of Hen Harriers' annual cycle are temporally and, in many cases, geographically separate, they remain inextricably linked through carry-over effects, such as the influence of pre-breeding habitat quality and diet on the subsequent breeding condition of females (Redpath et al. 2002, Harrison et al. 2011, Marra et al. 2015). The lack of conservation attention and research on potential negative carry-over effects from the non-breeding season compromises the current conservation strategy for Hen Harriers in Ireland (O'Connor and Cooke 2015). Like many bird species, Hen Harriers are at risk from future climate change which poses an additional, largely unexplored threat in the context of future conservation pressure on Hen Harrier populations (Caravaggi et al. 2019).

Juvenile dispersal

Juvenile dispersal is an important determinant of raptor population dynamics. Therefore, understanding the causes and consequences of dispersal patterns is crucial for managing threatened species and predicting responses of populations in changing landscapes (Sarasola et al. 2018). However, juvenile dispersal is often poorly understood due to challenges in studying raptor movement. Only broad-scale data describing approximate dispersal distance and direction was available for Hen Harriers prior to the current research (Etheridge and Summers 2006, O'Donoghue 2010). Greater availability and affordability of remote tracking technologies has provided the opportunity to gather detailed information on the movements of Hen Harriers during juvenile dispersal. Chapter 2 provides the first comprehensive understanding of this crucial demographic process for Hen Harriers in Ireland, including distance, direction, timing, habitat use and survival, using satellite tracking technology. Hen Harrier juveniles undertake an initial sudden, and typically long-distance (>25km), dispersal movement at approximately two months of age. Survival is low during this period, with 76% of juveniles that initiated dispersal, and whose fate was known, dying before settling on wintering grounds, with an overall first year survival of just 17.7 ± 7.5%. This survival rate was consistent with that reported in an area of high persecution pressure (Murgatroyd et al. 2019), but lower than the 36% of stable/declining populations (Etheridge et al. 1997, Whitfield and Fielding 2009), and much lower than the 50% reported for an expanding population (Redpath and Thirgood 1997). The low survival rate in the current study, together with low breeding outputs and anthropogenic pressures across the annual cycle, compromises the stability of the Irish Hen Harrier population (Ruddock et al. 2016). Our results suggest that low survival during juvenile dispersal is primarily driven by the use of poor-quality habitats during this period, with juveniles that utilise prey rich habitats during dispersal having higher survival probability than those who use less suitable habitats. Additional factors also contribute to low survival, such as sex (lower survival of males) and brood order (lower survival of lower order birds). Developing conservation measures that improve habitat quality for dispersing juveniles would improve the conservation outlook for Hen Harriers in Ireland. The random and long-distance nature of Hen Harrier juvenile dispersal presents a challenge for developing targeted conservation strategies to increase their survival due to the lack of focus on specific geographic areas. In this regard, identifying large gaps in suitable habitat around breeding areas may be the best approach to selecting areas where conservation measures, such as the provision of prey rich habitats, would be most needed. To a large extent, the land used by Hen Harriers during juvenile dispersal was outside of areas protected for biodiversity conservation, which further highlights the vulnerability of the species during this lifecycle stage. The findings of this study lay the foundation for future research on Hen Harrier juvenile dispersal in Ireland.

Non-breeding season

The non-breeding season distribution of Hen Harriers covers a larger area than their breeding season distribution and includes a wider range of habitats. The areas used by Hen Harriers in Ireland during the non-breeding season are currently afforded little statutory protection. Winter roost sites and the surrounding foraging grounds that attract Hen Harriers are vulnerable to disturbance and habitat loss or degradation through agricultural practices, commercial afforestation, and wind energy developments. These pressures are already known to negatively impact on Hen Harriers in their breeding grounds (Wilson et al. 2012, 2017, Fernández-Bellon et al. 2021). The continued conversion of arable lands to pasture is an additional land-use change pressure experienced by Hen Harriers during the non-breeding season. Fixed protected areas designated according to breeding season distribution, as is the case for Hen Harriers in Ireland at present, do not fully accommodate their needs across the annual cycle. The location of breeding birds commonly forms the basis for the designation of protected areas, but dynamic conservation strategies that include regular post-designation reviews and consideration of long-term spatial and temporal variation are needed to adequately provide for their protection (Limiñana et al. 2012).

Variation in the winter distribution between cohorts of Hen Harriers has previously been described (Picozzi and Cuthbert 1982, Clarke and Watson 1990, O'Donoghue 2010, Murphy 2019). This study provides new insights into this variation in winter distribution and identifies habitat related differences in diet as an influencing factor. Chapters 3 and 4 reveal that adult male dominated winter roosts were most likely to occur in areas of upland peatland habitats where medium-sized birds, primarily Snipe (*Gallinago gallinago*), occur in highest numbers in the diet, while ringtail dominated roosts most often occur in lowland and arable areas where small birds and small mammals occur at highest levels in the diet. Differing hunting strategies are likely to play an important role in diet differentiation (Nieboer 1973, Schipper et al. 1975, Vincheuski 2019). As well as being possibly driven by diet, variation in winter distribution may also be influenced by competition on winter foraging grounds (Dobler 2021). Advances in understanding the drivers of seasonal variation in distribution and diet of Hen Harriers is an important step towards developing conservation actions tailored to each cohort, such as the creation and enhancement of habitats that promote certain prey communities.

In this study a map of important Hen Harrier wintering areas was created which identifies where the protection of roost sites and foraging grounds should be prioritised. A mean home range size of 92km^2 around winter roosts was calculated using satellite tracking technology. Prior to this, the only available information on foraging distances around winter roosts was from occasional sightings of uniquely identifiable individuals and small-scale GPS tracking (Watson 1977, Bělka and Bělková 2019). Given the shortcomings of protected areas alone as a conservation measure for Hen Harriers across Europe (Fernández-Bellon et al. 2021), future non-breeding season conservation actions may be best implemented through broad-scale schemes, such as the new Common Agricultural Policy (CAP) and European Innovation Partnerships (EIPs), together with the designation of smaller and specific areas where necessary. Information on the locations of Hen Harrier winter roosts recorded during this study provides an opportunity to begin an open consultation process with semi-state bodies that own large areas of Hen Harrier habitat towards the careful planning of developments and activities to reduce negative effects on Hen Harrier winter roosts.

Breeding season

Research during the breeding season has provided us with a good understanding of Hen Harriers' breeding biology (Watson 1977, Hardey et al. 2013) and of the impacts of human induced pressures during the breeding season, such as afforestation and wind energy developments (Wilson et al. 2009, 2012, 2015, Fernández-Bellon et al. 2015, Caravaggi et al. 2020). In addition, recent studies using detailed analysis of nest camera images have provided new insights into Hen Harrier behaviour at nest sites (Fernández-Bellon et al. 2017, 2018; Etheridge 2020). The satellite tracking study described in Chapter 5 provided additional insights into breeding season behaviours of two female Hen Harriers in Ireland. These included the movement of an adult female between upland breeding territories and lowland non-breeding areas during the nesting period, and the use of both upland and lowland areas throughout the breeding season by non-breeders, thus highlighting the year-round use of some areas that were typically associated with Hen Harriers in the winter months. We also demonstrated individual variation in natal dispersal and intraindividual variation in subsequent breeding dispersal. These findings again highlight the risks associated with the exclusive use of fixed protected areas, which may not adequately provide for birds that subsequently breed outside of protected areas.

Commercial conifer forests now cover large areas of traditional Hen Harrier breeding grounds in Ireland (Moran and Wilson-Parr 2015, Corkery et al. 2020). Although Hen Harriers have adapted to nesting and foraging in young commercial conifer forests where their traditional open upland habitats are absent (Wilson et al. 2009, Caravaggi et al. 2019), these forests may represent an ecological trap for the species, ultimately leading to poor breeding success (Wilson et al. 2012, Sheridan et al. 2020). Given the importance of complex predator-prey dynamics in population ecology and the potential impact these may have on Hen Harrier breeding outcomes in young conifer forests, an understanding of Hen Harrier predators and prey in young forests is essential. Chapters 6 and 7 describe a lower abundance of preferred Hen Harrier prey in young conifer forests compared with traditional open habitat, and an increased abundance of small mammal prey related to the provision of windrows and suitable ground vegetation in forest sites (McCarthy et al. 2021). This abundant small mammal prey base may, in part, promote the diverse predator community, particularly mammalian predators, that was also recorded in young conifer forests. It is this predator community which is now causing widespread failures of Hen Harriers’ nests in the Irish uplands every year (Ruddock et al. 2016, Sheridan et al. 2020, Hen Harrier Project 2021). Our study provides evidence of the potential drivers (low prey abundance and diverse predator community) of the observed lower success and productivity of Hen Harrier nests in young conifer forests (Wilson et al. 2012, Sheridan et al. 2020). This study highlights the need to implement habitat restoration and forest management practices targeting increased Hen Harrier prey abundance and reduced predator occurrence in forested Hen Harrier breeding areas.

Conclusions

This research has broadened our knowledge of key aspects of the year-round ecology of Hen Harriers, from the juvenile dispersal period through to recruitment to the breeding population. Juvenile dispersal is a challenging period for Hen Harriers, with many not reaching breeding age. Outside of the breeding season, Hen Harriers disperse to use a much larger area and a greater diversity of habitats compared with the breeding season. The distribution of Hen Harriers differs between cohorts in the winter, influenced by variation in diet across different habitats, with ringtails occurring in lowland, arable areas where they predate small birds and small mammals in higher numbers compared with adult males who occur mostly in upland areas where the diet is dominated by medium-sized birds, primarily snipe. This research has identified a mismatch between areas designated for the protection of Hen Harriers in Ireland and the areas that they use during juvenile dispersal and the non-breeding period. Therefore, the current conservation measures that are focussed in these designated areas are inadequate for the year-round protection of the species. We also now have a better understanding of the mechanisms by which young upland conifer forests may be having a negative impact on breeding Hen Harriers.

Recent conservation efforts for Hen Harriers in other parts of Europe have produced some positive results, most notably in England where 84 chicks fledged from 31 nesting attempts in 2021, the highest number of chicks to fledge from nests in England since 2002 (Slater 2021). Monitoring by the Hen Harrier Project in Ireland since 2017 suggests continued declines in breeding populations within the SPA network here, except for 2021 where breeding numbers returned to 2017 levels, however productivity of breeding pairs dropped to the lowest level since the beginning of the project (Hen Harrier Project 2018, 2021). This follows a 27% decline in the Hen Harrier population within the SPA Network between 2005 and 2015 (Ruddock et al. 2016). The upcoming national Hen Harrier survey in Ireland in the spring and summer of 2022 will provide a much-needed update on the status of the breeding population.

The improved understanding of Hen Harriers' year-round ecology gained from this study will inform and improve future conservation actions and research recommendations. An overarching shift in policy focus and conservation strategy is required for Hen Harriers in Ireland to address the pressures faced throughout the annual cycle and account for temporal variation in distribution and resource use of the species. Given the continued decline of the Hen Harrier population in Ireland, we owe it to future generations to implement these changes urgently if we wish to retain this iconic raptor of the Irish countryside.

Recommendations

We used the findings of this PhD research in conjunction with existing knowledge to develop a suite of recommendations for the year-round conservation management of Hen Harriers in Ireland. The 25 recommendations are divided into the categories: Habitat Management; Further Research; and Conservation Policy. These recommendations were subject to review by external stakeholders through an open consultation process. Forty-three individuals were consulted, including forest practitioners, policy makers, conservation scientists, academics, and semi-state bodies in ownership of large areas of Hen Harrier breeding and wintering habitat. There was a response rate of just 23% to this consultation process.

Feedback received during the open consultation process revealed a disconnect between knowledge of Hen Harrier winter roost locations held by third parties, the National Parks and Wildlife Service, and the semi-state bodies that own large areas of Hen Harrier roosting habitat. In many cases, semi-state bodies were requesting information on Hen Harrier roost locations to inform the future sustainable development of their properties, however this information was not available for this purpose. This is at odds with conservation efforts applied during the breeding season where forestry operations are increasingly informed by up-to-date monitoring of breeding Hen Harrier locations, thereby preventing disturbance. In a similar way, Hen Harrier winter roost locations should be made available, under strict conditions of confidentiality and use, to semi-state bodies in ownership of large areas of Hen Harrier wintering habitat to ensure that developments and activities can be adequately informed and mitigated.

An option for the implementation of the measures proposed in these recommendations may be through current or future Agri-Environment Schemes (AESs), where farmers are rewarded financially for providing for Hen Harrier conservation through, for example, provision of foraging habitat for wintering Hen Harriers and the protection of roost sites from agricultural intensification, similar to what is being implemented through the Hen Harrier Project EIP.

More research is needed on the impacts of human activities on Hen Harriers to inform their conservation management and policy development, particularly around the long-term impacts of habitat loss and degradation. Periodic assessments of the effectiveness of Hen Harrier conservation measures should form part of ongoing conservation efforts, which should include the measures proposed in this study.

The findings of the current research provide further evidence to support the Hen Harrier Threat Response Plan (HHTRP), which is currently in development, and which aims to restore Hen Harrier populations and the habitats on which they depend. Given the wide distribution of the species and the pressures it faces across the annual cycle, a landscape-scale, year-round, approach to their conservation will be essential to their successful protection and conservation. The recommendations are aimed at improving Hen Harrier conservation status so that the Irish Hen Harrier population is self-supporting over time.

Definitions

- The definition of ‘development’ in these recommendations follows that used in the Planning and Development Act 2000-2021, Section 3(1), where "*’development’ means, except where the context otherwise requires, the carrying out of any works on, in, over, or under land or the making of any material change in the use of any structures or other land*". The primary developments applicable to Hen Harrier conservation include, but are not restricted to, wind energy, solar energy, road, housing developments, and associated works.

- ‘Activities’ in these recommendations refers to those that are not typically considered ‘developments’ under planning legislation but have reasonable potential to cause disturbance to Hen Harriers at their winter roost, foraging grounds and/or nest sites. An example of a relevant activity would be game bird hunting within or close to a winter roost. A precautionary approach should be taken when assessing what may constitute a development or an activity that has potential for negative impacts on Hen Harriers.
- The broad habitat categories used in the recommendations follow the Fossitt habitat classification (Fossitt 2000).
- ‘*Hen Harrier breeding areas*’ includes the Hen Harrier Special Protection Area (SPA) network and areas outside the SPA network where Hen Harriers are known to breed, based on most recent available information (e.g. national breeding survey data, red zone survey data).

Table 1. Recommendations for the future conservation management of Hen Harriers in Ireland.

Recommendation	Objective	Thesis chapter
Habitat Management		
Future management of existing conifer forests in Hen Harrier breeding areas should include strategic deforestation; selective clear-felling (creating a semi-structured age mosaic within the forest which ensures a consistent cover of pre-thicket forest while minimising edge to area ratio); forest removal (increasing connectivity of suitable open foraging and nesting habitat); and the restoration and management of high-quality upland heath, bog, and scrub habitats. In addition, failed/poor growth conifer forest should be removed and the original open habitat restored.	Increase habitat suitability and connectivity for Hen Harriers, reduce nest predation risk and increase prey availability.	6, 7
Avoid forest planting on existing natural and semi-natural open habitats suitable for Hen Harrier foraging and breeding, including heath, bog, and semi-natural grasslands (particularly High Nature Value grasslands), in Hen Harrier breeding areas.	Prevent deterioration or loss of suitable habitats and their associated prey communities.	6
Remove self-seeded conifer trees that are growing outside planted forests and encroaching and spreading on to natural and semi-natural open habitats.	Prevent deterioration or loss of existing suitable habitats and their associated prey communities.	6
Remove brash and corvid perches during clear-felling of conifer forests in proximity to Hen Harrier nests.	Reduce habitat suitability for Hen Harrier nest predators.	7
Increase the cover of arable crops in priority Hen Harrier wintering areas where climate, topography and soil conditions permit*.	Ensure long-term suitability of Hen Harrier wintering areas by enhancing prey abundance through the winter period.	2, 3, 4
Leave arable fields in stubble over winter in priority Hen Harrier wintering areas*.	Increase the abundance and maximise the period of availability of small bird and small mammal prey over winter.	4

Recommendation	Objective	Thesis chapter
Increase the provision of wild bird cover crops in priority Hen Harrier wintering areas*. Crop species should be tailored to local soil conditions.	Increase the abundance of small bird and small mammal winter prey.	4
Protect and restore semi-natural grasslands, peatlands, heath, and freshwater marshes in priority Hen Harrier wintering areas*.	Increase the abundance of important winter prey species.	4
Further Research		
Assess the effectiveness of predator control in Hen Harrier breeding areas and predator fences around Hen Harrier nests.	Reduce nest predation.	7
Initiate a long-term study of prey abundance in open habitats suitable for Hen Harriers, including, but not limited to, rehabilitated cutover bogs, arable stubble, peatlands, semi-natural grasslands, and in areas of existing forest under different management strategies.	Identify the highest quality open habitats for Hen Harriers. Explore foraging value of differently managed forest habitats.	2, 4, 6
Assess the effects of non-native small mammal species on Hen Harrier diet and breeding productivity.	Determine future impacts of non-native small mammal species on Hen Harrier populations.	4
Assess the value and feasibility of habitat restoration and rehabilitation measures on upland bogs that have been afforested and lowland cutover bogs.	Inform habitat and landscape management strategies.	2, 4, 6
Assess the foraging success of Hen Harriers in different breeding and wintering habitats.	Inform habitat management strategies.	2, 4, 6
Investigate home range ecology and foraging habitat selection of breeding adults during the breeding season.	Inform habitat management strategies.	2, 6
Explore the potential for results-based agri-environment schemes in important Hen Harrier dispersal and wintering areas.	Improve juvenile and overwinter survival, and provide a mechanism by which habitat and other conservation measures can be implemented.	2, 3

Recommendation	Objective	Thesis chapter
Undertake habitat suitability modelling to identify gaps in suitable foraging habitat around breeding areas into which juvenile Hen Harriers disperse.	Identify priority areas for habitat improvement measures to increase connectivity of suitable habitats and increase juvenile survival.	2
Conservation Policy		
Protect existing natural and semi-natural habitats suitable for Hen Harrier foraging and breeding from afforestation, development, and agricultural improvement (such as, but not limited to, drainage, clearance of scrub and/or hedgerows, and/or re-seeding of semi-natural grasslands) within Hen Harrier breeding areas.	Prevent deterioration or loss of existing suitable habitats.	6, 7
Remove legislation that requires replanting of conifer forests after felling in Hen Harrier breeding areas.	Enable restoration of open habitats.	6, 7
Preserve, restore, and manage heath, bog, scrub, and semi-natural grassland habitats in Hen Harrier breeding areas.	Enhance habitat suitability.	6, 7
Forestry operations and land management activities within potential disturbance distance of active Hen Harrier nests should not take place before the end of August.	Prevent disturbance and premature dispersal of juveniles.	2
Include Hen Harrier winter roost surveys in, for example, the Environmental Impact Assessment (EIA) process, for all proposed developments and activities in areas of suitable roosting habitat, within 5km of the development/activity, that may adversely impact Hen Harriers. EIA report scoping should include consultation with the Birds Unit of NPWS to establish the requirement for any appraisal of likely significant effects on wintering Hen Harriers.	Prevent deterioration or loss of Hen Harrier winter roosts.	3
All potential Hen Harrier winter roosts discovered during EIAs or similar, together with all associated sensitive Hen Harrier survey data, should be reported to the National Parks and Wildlife Service Birds Unit upon discovery.	Increase knowledge of Hen Harrier winter roost distribution and provide for their protection.	3

Recommendation	Objective	Thesis chapter
The National Parks and Wildlife Service Birds Unit should compile and maintain an up-to-date database of Hen Harrier roosts, with annual winter roost surveys conducted using standardised methods at priority winter roosts**.	Ensure the future protection of winter roosts.	3
Priority Hen Harrier wintering areas should be the focus of specific and targeted Hen Harrier conservation measures*. These could be implemented, for example, through new European Innovation Partnership (EIP) projects.	Increase habitat suitability, prey availability and survival of Hen Harriers over winter.	2, 3, 4
Proposed developments, along with afforestation, land reclamation and other activities within or immediately adjacent to Hen Harrier winter roosts, should be prohibited. All Hen Harrier winter roosts should be afforded protections similar to those afforded to nest sites of wild birds under the Wildlife Act (1976).	Prevent deterioration or loss of Hen Harrier winter roosts.	3

* Priority Hen Harrier wintering areas are the 10km Irish grid squares that include land that is within the maximum foraging range (5.4km) of Hen Harriers of known roost sites, as determined by satellite tracking data (2017-2021). Priority Hen Harrier winter areas should be updated as new survey data is gathered.

** Priority Hen Harrier winter roosts are those where Hen Harriers were recorded roosting during the 2019/20 and/or 2020/21 wintering season (October – March). Priority Hen Harrier winter roost data base should be updated as new survey data is gathered.

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Appendix 1

Chapters 3 & 4 - Winter roost home range calculation

We calculated the home range of Hen Harriers at winter roosts where there were more than 30 high quality (classes 3, 2 and 1) daytime location fixes around a given winter roost in a single winter. For these roosts, we retained daytime location fixes that were clearly associated with a roost (e.g. when a bird was settled at a roost over winter with infrequent movements away from that roost). We excluded location fixes that were associated with exploratory movements, and those associated with movements between different wintering areas.

Based on these criteria, we calculated home ranges for seven roosts using tracking data from five satellite tagged Hen Harriers across four winters. Although we set the minimum umber of location fixes for calculating home range around any one winter roost as 30 fixes, we used a mean of 109 fixes for each winter roost per winter (range of 38 to 160). For one roost, there was a sufficient number of location fixes to calculate a home range for each of three winters, from which we then obtained a mean. Six other roosts had home ranges calculated for single winters. Mean winter roost home range around the seven roosts was 91.75 ± 24.28km^2 (± SD). The mean maximum daytime location fix from winter roosts was 12.35 ± 1.69km (±SD). Home ranges were calculated using 95% Minimum Convex Polygon (MCP) area.

Appendix 2

Chapter 4 - Procedure for determining minimum pellet sample size for models

The minimum number of pellets required to support modelling was determined via power analysis and supplementary changepoint analysis, where power is given precedence. Power analysis suggested that a minimum of 19 pellets would be sufficient to detect a difference at P = 0.05. Changepoint analysis identifies locations where the statistical property of a sequence differs along its length. The mean number of prey categories present in a pellet and associated variance (standard deviation [SD]) were calculated for each site, using sample sizes of 5-32 pellets (32 being the minimum available for a single site), without replacement, across 1,000 iterations per sample size. Changepoint analysis was then applied to SD values using Power of the Pruned Exact Linear Time (PELT) method with a manual penalty of 2×log(n) (Wambui et al., 2015) to identify the minimum maximum value at which pre- and succeeding values significantly differed (Killick & Eckley, 2014; Killick et al., 2016). Changepoint analysis suggested that a minimum of 15 pellets would be sufficient. Following our requirement that power is given precedence, sample size was fixed at 19 pellets for modelling purposes.

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Killick, R., and I. A. Eckley (2014). changepoint: An R Package for Changepoint Analysis. Journal of Statistical Software 58: 1-19.

Killick, R., K. Haynes, and I. A. Eckley (2016). changepoint: An R package for changepoint analysis. R package version 2.2.2.

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Appendix 3

Chapter Seven- Landscape-scale habitat data

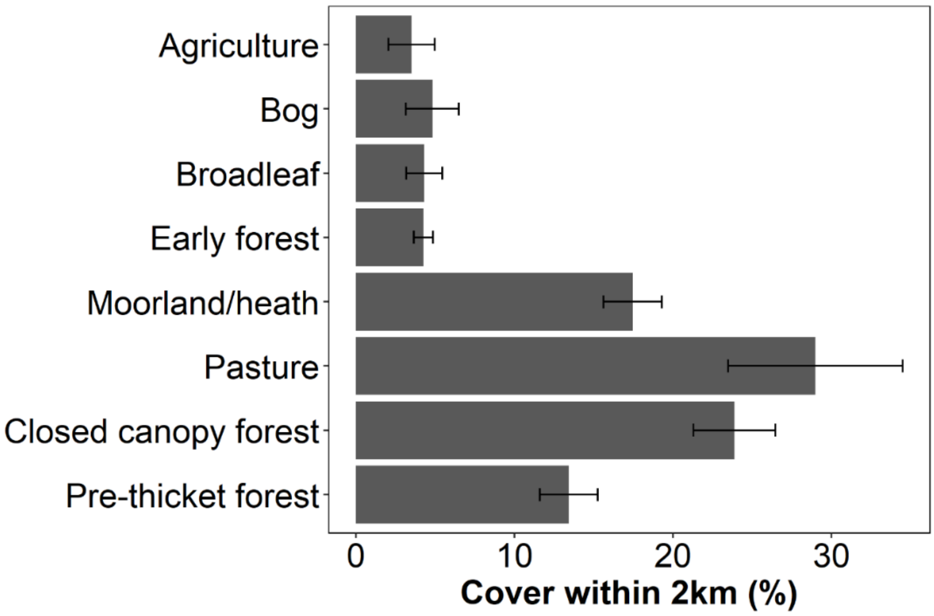

Figure S1. Mean (+/- SE) cover of main habitats within a two-kilometre radius of the study sites.