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Landscape and temporal influences on the winter diet of a threatened diurnal raptor, the Hen Harrier *Circus cyaneus*

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ABSTRACT

Capsule: Habitat composition plays a key role in determining the winter diet of the Hen Harrier *Circus cyaneus*, which varies across the winter season and between years.

Aims: To determine the winter diet of the Hen Harrier and examine temporal and spatial variations in diet composition.

Methods: A total of 1117 Hen Harrier pellets were collected from 11 winter roosts between 2017 and 2021 in Ireland.

Results: Hen Harrier winter diet was dominated by avian prey (95.9% of pellets), with mammalian prey found in 12.0% of pellets. The 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 Common Snipe *Gallinago gallinago*) in the diet was positively associated with the proportion of bog and young conifer forests surrounding roost sites. Diet 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. The proportion of medium-sized birds in the diet changed across months, with that of small birds and small mammals remaining stable. There was also variation between winters in the proportion of small- and medium-sized birds in the diet.

Conclusions: 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 Harriers at a landscape scale.

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The diets of individual bird species 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 the observed dietary composition typically reflecting local prey abundance (Amar 2001, Clarke *et al.* 1997, de Boer *et al.* 2013, Nota *et al.* 2019, Redpath & Thirgood 1999).

Local prey availability has important consequences for Hen Harriers as it may impact on individual life histories and on population dynamics (Amar *et al.* 2003, Redpath & Thirgood 1999, Simmons *et al.* 1986). For example, food limitation has been suggested as an important driver of declining Hen Harrier populations in some parts of Scotland (Amar 2001, Amar *et al.* 2003, Redpath & Thirgood 1997). The distribution of prey communities can impact on the distribution of different ages and sexes of birds (Dobler 2021, Marquiss 1980), 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* (de Boer *et al.* 2013, New *et al.* 2011). Diet composition has also been linked with Hen Harrier breeding performance (Amar *et al.* 2003, Redpath *et al.* 2002a), with clutch size and fledging success shown to be positively associated with prey abundance (Redpath *et al.* 2002a, Schipper 1978, Simmons *et al.* 1986). Most dietary studies of Hen Harriers and other raptors have focussed on the breeding season, when the activity of birds is centred

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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 outcome (Amar *et al.* 2003, Redpath *et al.* 2002a). Outside of the spring and summer seasons, the 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, knowledge of the winter diet is valuable to understanding the ecological needs of this species.

Hen Harrier diet is typically dominated by birds and mammals (Clarke *et al.* 1993, Picozzi 1977, Watson 2017), though the species occasionally predates other taxonomic groups, including reptiles and amphibians (Bro *et al.* 2006, Marquiss 1980, Nota *et al.* 2019, Picozzi 1977). The diet has been shown to vary both spatially across the range, and temporally as prey abundance in the environment fluctuates (Clarke *et al.* 1997, Garcia & Arroyo 2004, Nota *et al.* 2019, Redpath & Thirgood 1999). Some differentiation between the diet of male and female Hen Harriers 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; different habitats host different prey communities (George & Johnson 2021) and the vegetation structure of habitats influences 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 twentieth 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 the winter diet in some areas (O'Donoghue 2010, Smiddy & Cullen 2017). More recently the Greater White-toothed Shrew *Crocidura russula* has been spreading across Ireland, following its introduction in the early 2000s (McDevitt *et al.* 2014, Tosh *et al.* 2008), and has been recorded in the diet of other small mammal predators, including the 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 the 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 Harriers in Ireland use the same wintering habitats as elsewhere in their range, including arable farmland, grasslands, and reedbeds (O'Donoghue 2020). 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 the species in Ireland (Buckley *et al.* 2021).

This study sets out to describe variation in Hen Harrier winter diet across its range in Ireland. In particular, we seek to investigate the influence of different regions and surrounding landscape-scale habitat on diet composition. We also explore 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.

Methods

Study area

Regurgitated pellets were collected from 11 Hen Harrier roost sites between November and March during 2019/20 and 2020/21 winters. 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 10 others were communal roosts, i.e. roosts where more than one bird was observed on at least one occasion (Figure 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

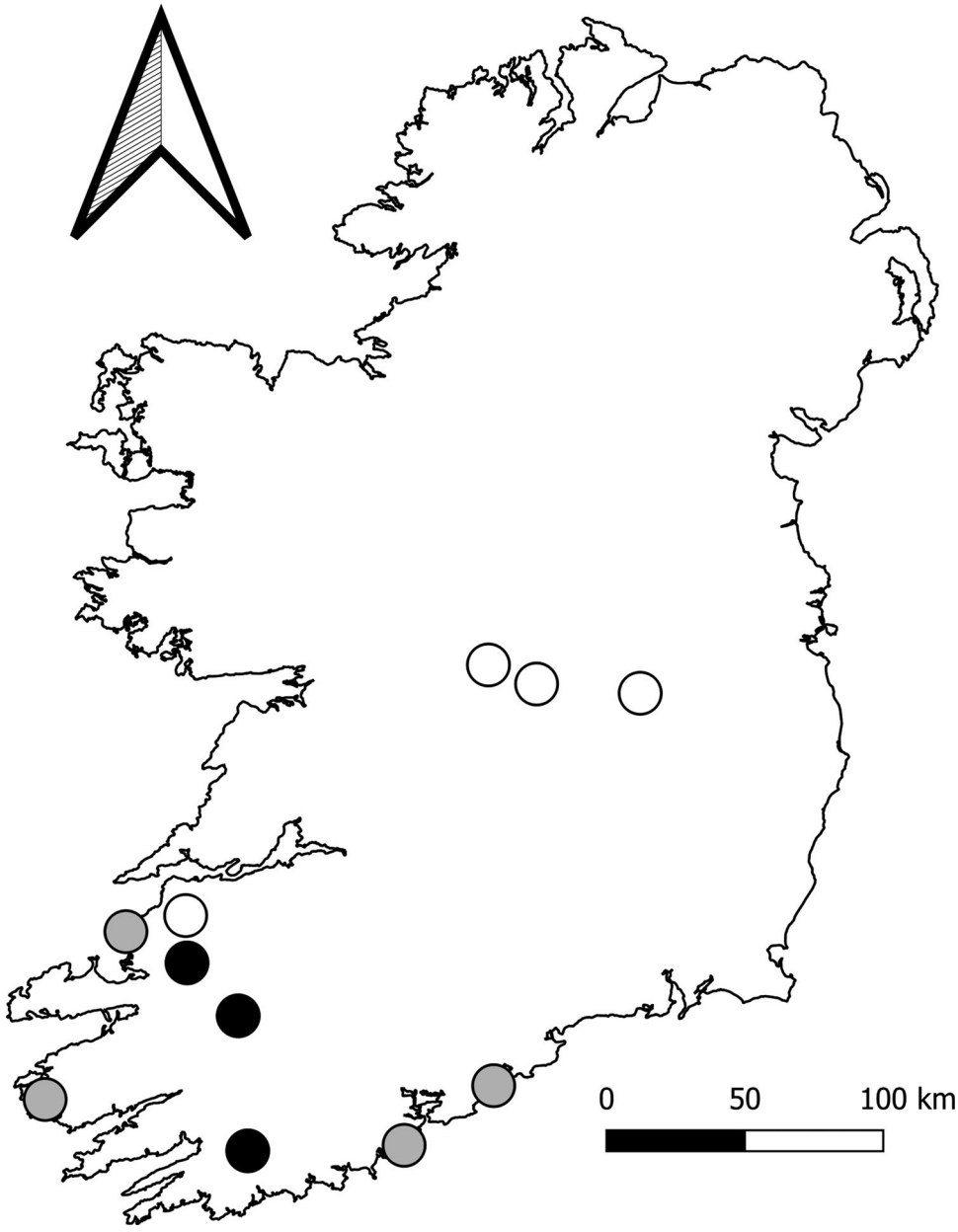

Figure 1. Locations of winter roosts in this study. Grey circles show lowland coastal roosts, white circles show lowland inland roosts and black circles show upland roosts. Note that circle size does not equal home range size.

proximity to the coast. The three regions were: (i) lowland coastal roosts (<150 m ASL; home range overlapped with coastline; $n = 4$); (ii) lowland inland roosts (<150 m ASL; home range did not overlap with coastline; $n = 4$); and (iii) upland roosts (>150 m 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 Harriers 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; McCarthy *et al.* in prep) and were, on average, 122 km apart (range of 15–260 km).

Pellet collection and dissection

Roost locations were mapped as accurately as possible during the monthly distant vantage point surveys, enabling the 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 one to two hours before dusk. Therefore, pellet searches were conducted between 1000 and 1500 h 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 faecal 'whitewash' and regurgitated pellets within the roost beds (Zagorski & Swihart 2020). The only other raptor species recorded roosting in proximity to the Hen Harrier roosts was the 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 3 m using handheld global positioning system (GPS) devices. Pellets were stored individually in labelled bags.

Pellets were frozen within six hours of collection at −20° C for 24–48 h to prevent degradation of the pellet contents. Pellets were then defrosted and left to air dry for 14–21 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 0.5 mm. Prey were identified to species level where possible based on bone, fur, and feather characteristics (Redpath *et al.* 2001, Teerink 1991). 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 60 g, such as finches and buntings. Medium-sized birds included species with an average body mass of 60–300 g, such as Common Snipe *Gallinago gallinago* and thrushes. Large birds included species with an average body mass greater than 300 g, 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 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 properties of a sequence differ 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 5–34 pellets (34 being the minimum available for a single site), without replacement, across 1000 iterations per sample size. Changepoint analysis was then applied to SD values using the power of the pruned exact linear time (PELT) method with a manual penalty of 2log(n) (Wambui *et al.* 2015) to identify the minimum maximum value at which preceding 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. 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 generalized 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). 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 0–1000 m) 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 a 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 Cover classes were 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 plantation forests), as this is the age of forests preferred by Hen Harriers for foraging (Wilson *et al.* 2009, 2012). These forest cover data were further divided into conifer (>50% cover of conifer species) and deciduous (>50% cover of deciduous species) young plantation 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.

We applied a principal component analysis (PCA) to the nine habitat variables. All variables were standardized, with mean = 0 and sd = 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

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

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 in 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 specializing in foraging on Greater White-toothed Shrews 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 mean ± 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 & Mundt 2020).

Results

Winter diet of Hen Harrier

We analysed 1117 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 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 in 8.2% of pellets and Bank Vole in 6.2% of pellets (Table 2).

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 (Figure 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%).

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

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
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
Common 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

positively associated with arable and low-intensity agriculture, but was negatively associated with wetlands (Table 3).

Habitat models showed that small birds occurred more frequently in the diet of Hen Harriers 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 mammal in the diet 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.

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 (Figure 3). The occurrence of small birds and small mammals did not

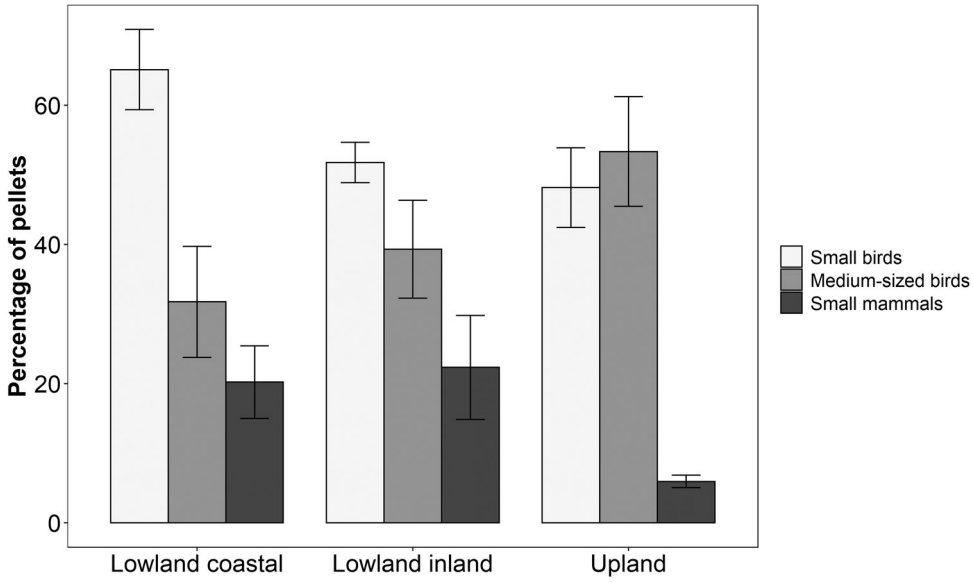

Figure 2. Mean (±se) percentage occurrence of each prey item in the winter diet of Hen Harriers across three regions.

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 Common 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 (Figure 4). Across these roosts, the frequency of small mammals remained relatively stable in the diet, whereas the occurrence of small birds and medium-sized birds in the diet varied between winters, although the observed differences were not statistically significant.

Discussion

Our results describe the winter diet of the Hen Harrier in the western-most part of its range and the variation in diet composition across regions, habitats, and over time. From lowland coastal roosts through lowland inland and upland roosts, there were contrasting patterns in the occurrence of prey groups in Hen Harrier pellets; medium-sized birds increased in occurrence along this gradation while small birds and small mammals decreased. These patterns appear to be driven by differing habitat compositions 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 and are 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 the 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 used in this study is a widely applied tool that provides an accurate overall assessment of diet composition (Smiddy & Cullen 2017, Redpath *et al.* 2001).

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.

	Principal components (variation explained)		
Habitat variable	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**

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) include the first levels of these categorical variables (lowland coastal roosts, November and 2019/20, respectively).

Model	*n*	Fixed effects	$\beta \pm$ se	*p*
(a) Small birds × 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 × 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 × 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 × 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 × 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 × 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 × 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 × 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 × 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 × winter	28	Intercept	0.39 ± 0.30	0.20
		2020/2021	−0.15 ± 0.21	0.47
(k) Medium-sized birds × winter	28	Intercept	−0.24 ± 0.37	0.51
		2020/2021	0.11 ± 0.23	0.64
(l) Small mammals × winter	28	Intercept	0.65 ± 0.45	0.15
		2020/2021	−0.31 ± 0.86	0.72

Winter diet of Hen Harriers

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 & 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 in 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 & 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 the diet in that study may reflect the influence of roost location, with small mammals found to occur 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 & Macdonald 1970, Clarke *et al.* 1997, Dickson 1994, Dobson *et al.* 2009).

Hen Harrier diet varies between different areas across Europe, being dominated by small birds in some areas and by small mammals in others, with some flexibility observed in response to local habitat and prey availability (Bro *et al.* 2006, Toffoli 1994, Vervoort & Klaassen 2016) and between sexes (Clarke *et al.* 1997, Marquiss 1980, van Manen 1996). In many parts of mainland Europe, small mammals are the most important component of Hen Harrier diet in winter (Bro *et al.* 2006, Toffoli 1994), with voles comprising more than 85% of the diet in some areas (de Boer *et al.* 2013, van Boekel & Berghuis 2014, van Manen 1996). 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 over-winter in larger numbers in these areas (Newton 2008). Higher winter temperatures are also likely to be favourable for small mammals, allowing higher over-

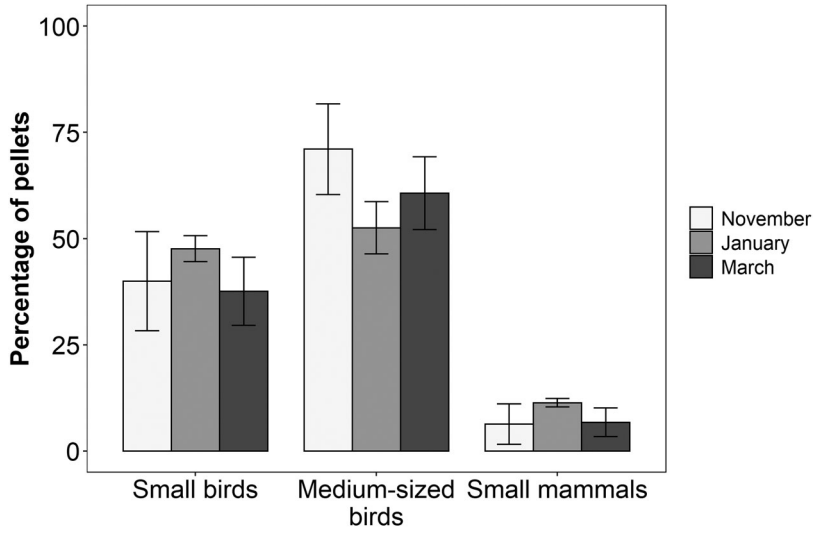

Figure 3. Mean (±se) percentage occurrence of each prey item in the winter diet of Hen Harriers across winter months.

winter 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 Common 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 Common 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 (Clarke *et al.* 1997, Marquiss 1980). 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 Common 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

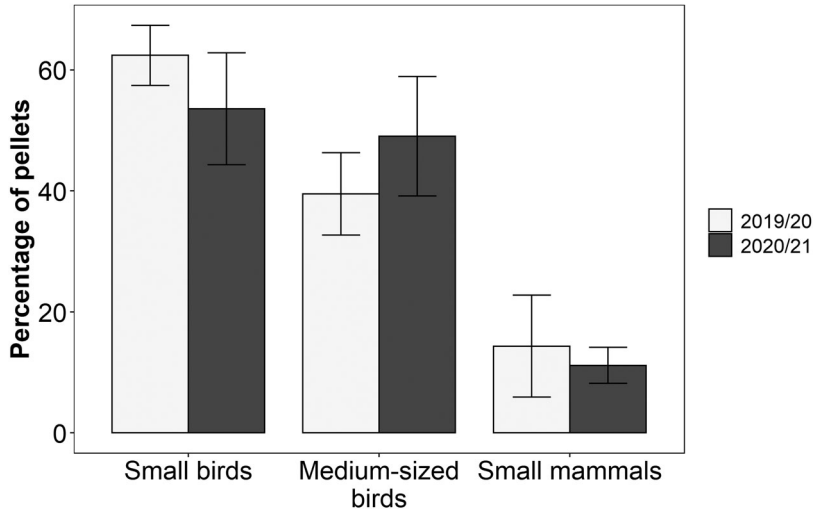

Figure 4. Mean (±se) percentage occurrence of each prey item in the winter diet of Hen Harriers between years.

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 the 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 Harriers, providing an abundance of prey, particularly in winter (Gillings *et al.* 2005). Over-winter stubble in arable areas provides small birds such as Linnet *Linaria cannabina*, Goldfinch *Carduelis carduelis*, Yellowhammer *Emberiza citrinella*, and Skylark with an abundance of food, thereby attracting large flocks of small birds (Henderson *et al.* 2004, Wilson *et al.* 1996). 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 Harriers 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: Common Snipe and, to a lesser extent, Redwing. Common Snipe is an open country species that occurs 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 & O'Halloran 2012). The prevalence of Common 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 & O'Halloran 2012). Interestingly, the prevalence of Common 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 & Cullen 2017).

Temporal variation in diet composition

We observed significant temporal variation in the 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 Common Snipe. Seasonal variation in the 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 from 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 fewer containing small birds in the second winter compared with the first. Such inter-annual variation in diet composition, particularly for medium-sized birds, may reflect annual fluctuations in the abundance of prey species such as Redwings, which only occur in Ireland during the autumn and winter (Balmer *et al.* 2013). Cold conditions on the Continent often cause large movements of birds, such as Redwings, 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 over-winter 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 the Hen Harrier diet perhaps suggests that some individuals, notably young Hen Harriers during their first winter, may particularly benefit from the temporal stability of these prey resources. 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 Harriers in Ireland. As Greater White-toothed Shrews 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. The Greater White-toothed Shrew will likely become an increasingly important prey item as the species spreads throughout the country, where it may have a disproportionate effect on Hen Harriers and other small mammal predators, particularly 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's range.

Conservation implications

Given the importance of the winter diet in the ecology and over-winter 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 underemphasize 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 Common Snipe, which was 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 Harriers, with knock-on impacts on survival and population dynamics. Although this study looked exclusively at the winter diet, such impacts could also extend into 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.

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