Plate 247. White-tailed Eagle feeding young at a nest, Lewis, Outer Hebrides, 2019. © *Mark Hamblin*

The breeding season diet of White-tailed Eagles in Scotland

R. REID, J.R. GRANT, R.A. BROAD, D.N. CARSS & M. MARQUISS

The breeding season diet of White-tailed Eagles in Scotland was assessed from samples of food remains at nest sites, enabling spatial and temporal comparisons but likely underestimating smaller food items, soft-bodied items and fish. During the 20-year study, 293 samples from 92 different nest territories contained 11,375 food items, comprising 67% birds (70 species), 27% mammals (17 species) and 6% fish (at least 30 species). The types of foods in samples from individual territories were similar across years, even over the full length of the study.

At coastal territories most food remains were from seabirds and fish. In other territories, various dominant foods included wetland birds, rabbits, lambs, hares and gamebirds. Regional differences reflected this, with marine items most prevalent in the Outer Hebrides, north-west mainland, Skye, Islay and Jura. Large mammals were common food items in Mull, Lochaber and mainland Argyll, and waterfowl were important prey on the Uists, Islay, Jura, Mull, Lochaber and mainland Argyll. Hares and grouse were predominant at nests further inland towards the east of Scotland. Most lamb remains were recorded in those territories first occupied after reintroduction, with progressively fewer in territories established thereafter so that by 2017, lambs were frequent (30% or more of recorded items) in only five of the 58 territories sampled.

In retrospect, the previously widespread view that lambs are an important food for White-tailed Eagles has been superseded; the prevailing evidence now is that marine items (seabirds and fishes) are the most important breeding season food in Scotland. As elsewhere in their range, White-tailed Eagles in Scotland appear to be generalist foragers that take the most easily available local foods. Consequently, further dietary shifts might be expected as the population expands and more individuals settle in areas with greater access to the uplands or to rich freshwater habitats.

Introduction

The diet of White-tailed Eagles *Haliaeetus albicilla* is well-documented from studies across their geographical range. They are predators of a variety of fishes, large birds and medium-sized mammals, as well as scavenging carrion and stealing prey from other predators (review in Love 2013). The main foods of settled breeding pairs reflect what is locally prevalent, with fish predominating in areas offering rich freshwater wetlands and fish ponds (Fischer 1982, Helander 1983, Struwe-Juhl 2003, Sulkava *et al.* 1997), more terrestrial species of gamebirds and mammals taken in drier terrain (Dementavicius *et al.* 2020) and marine birds and fishes in coastal areas (Willgohs 1961, Wille & Kampp 1983). Diet varies seasonally with more birds taken in summer (Marquiss, Madders & Carss 2003a) and more terrestrial prey and carrion scavenged during the game shooting season and in winter when fish are less available (Nadjafzadeh *et al.* 2013). The recorded diet of sub-adult birds reflects their wider ranging behaviour which enables them to aggregate where food is superabundant, such as at large mammal carcasses, shooting discards or supplementary food provisioning sites (Halley & Gjershaug 1998). Studies of variation in the diversity of foods used suggest that the White-tailed Eagle is a 'generalist' foraging species, but that some individual pairs 'specialise' as they exploit local abundance, switching to alternatives as the preferred food becomes less available (Nadjafzadeh *et al.* 2016, Dementavicius *et al.* 2020).

The species was extinct in the UK by 1918 but was re-introduced to Rum on the west coast of Scotland from 1975, to Wester Ross from 1993 and to Fife in east Scotland from 2007 (Love 2003, 2013). From release onwards, there was interest in diet and most information accrued from the identification of food remains at roost perches and nests. An initial assessment involved two settled pairs and a few subadults (Watson, Leitch & Broad 1992) that fed variously on seabirds, hares, Rabbits, lambs, waterfowl and fish (Latin names of species are listed in Appendix). By the 1990s, more pairs had settled to breed on Mull where there was a perception amongst farmers that eagles were killing lambs. An intensive study from 1998 to 2002 showed that some lambs were killed, but most were scavenged with no economic damage to sheep farming on a broad scale, and little evidence for economic loss at individual holdings (Marquiss, Madders, Irvine & Carss 2003). In those years, the breeding season foods used by 15 pairs in western Scotland were principally seabirds, lamb, Rabbit, hare and fishes. There was substantial variation between pairs and little variation between years for any one pair (Marquiss, Madders & Carss 2003a). More lambs were taken to nests on Mull than elsewhere. Whitfield *et al.* (2013) used the same data together with some from Harris and Lewis to calculate the average proportions of various sorts of foods from 16 pairs, to compare with the diet of 18 pairs of neighbouring Golden Eagles.

Up until 2002, relatively few pairs had settled to breed, so although their foods were well documented, samples were small and mainly from the Inner Hebrides. From 2002 onwards, there was rapid population expansion and some settlement away from the west coast, inland and to the east. During the period 1998–2016, efforts were made to collect food remains from new territories in the first few years after establishment to characterise the diet of each pair in addition to making intermittent collections at some long-established territories. In 2017, when there were 122 known territorial pairs, an intensive effort collected food remains from 58 (85%) of the 68 nests that were known to hatch young that year (Challis *et al.* 2018). The present study used data from the full 20-year period (1998–2017) to assess patterns of variation in the breeding season foods of the Scottish White-tailed Eagle population over time and at a landscape scale.

Methods

The study area encompassed the entire White-tailed Eagle breeding range across Scotland which increased from a population of 18 pairs in 1998 (RSPB 1998) when the species breeding distribution was largely restricted to the Inner Hebrides, to a population of at least 122 pairs in 2017 when territories had established in most regions and island groups in northern and western

Scotland (Figure 1). During the period 1998–2013, the entire Scottish White-tailed Eagle population was monitored annually, largely by professional RSPB fieldworkers, to determine territory occupancy, breeding success and to search for and locate new establishing territories. From 2014 onwards, monitoring was done by Scottish Raptor Study Group volunteers across large areas of Scotland and coverage continued to be close to complete through to 2017.

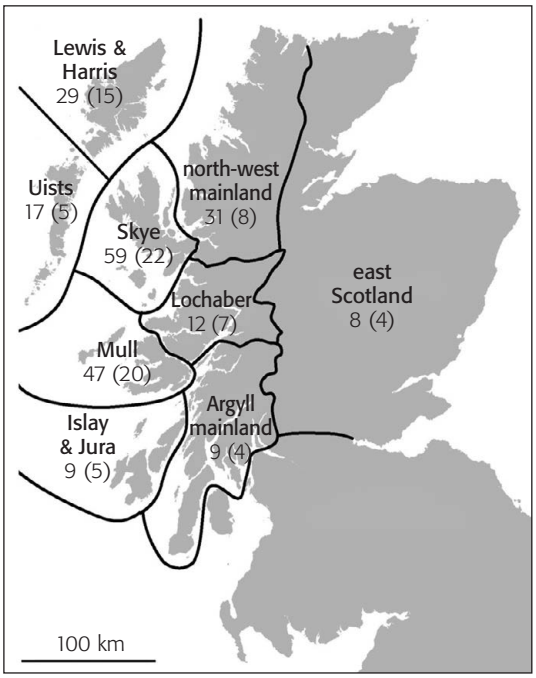

Figure 1. Geographical distribution of food samples collected from nine parts of Scotland. Number of post-fledge food samples with ten or more items collected from each area and in brackets number of territories from which samples were collected. *Contains Ordnance Survey data Crown copyright and database right 2020.*

The breeding season diet was sampled by recovering food remains from the recent years' occupation layers of nest material (Grant, Reid & Whitfield 2011), together with a few items gleaned from below the nest and nearby perches. Most were retrieved after the young had fledged and any remains removed at earlier visits during the nestling period were included. Adult eagles delivered food to nests from hatching until after fledging, so the sample included items consumed from April to August.

Food items were identified to the lowest taxon (most to species) using keys to the identification of hair (Teerink 1991), feather (Cieslak & Dul 2006, Brom 1986) and bone (Brown *et al.* 2002), supplemented with scrutiny of online imagery ('Featherbase') and our extensive reference material from Scotland. Most of the unidentified items were fish and juvenile birds. Within a sample, the count of individual items for each species was the minimum consistent with the numbers of the most frequent remains. There was bias towards the recovery of robust bone remains from large birds and mammals and against those of soft-tissue items that left few long lasting remains, or those with small bones that were wholly consumed and digested, so small birds and fish were under-represented (Wille & Kampp 1983, Mersmann *et al.* 1992, Marquiss, Madders & Carss 2003a).

Some samples included material from previous years' nest layers. This was not the case during the earlier study because nests were emptied of items annually, but for collections in later years it meant that counts of items sometimes reflected food deliveries to nests over several years. In 2017, when 60% of nests had previous years' layers, there were more items retrieved from those nests with more layers (Spearman rank correlation r_s= 0.368, df=56, p=0.005). One concern was that this may have affected estimates of the relative abundance of particularly resilient food remains, but there was no evidence for that because the proportion of large mammals amongst identified items was not at all correlated with the number of previous years' nest layers (r_s= 0.085, df=56, p=0.526). The consequence for our data analyses was that to assess the variation in the relative abundance of different sorts of food items, we used their proportions in samples rather than counts.

The high species diversity amongst food remains made statistical comparisons cumbersome. The majority of recorded species were infrequent, so foods were grouped into nine categories such that each comprised at least 3% of the overall recorded total but nevertheless seemed sensible in relation to eagle foraging. Most nest territories were coastal so Fulmars were combined with

Plate 248. White-tailed Eagle nest accessed to collect prey remains after young had fledged, Mull, Argyll, 2017. © *Robin Reid.*

Plate 249 (left). Fish remains identified from a nest in Sutherland, Highland, 2023. © *David Carss.* **Plate 250 (above).** Fish remains identified from a nest in Lochaber, Highland, 2023. © *David Carss*

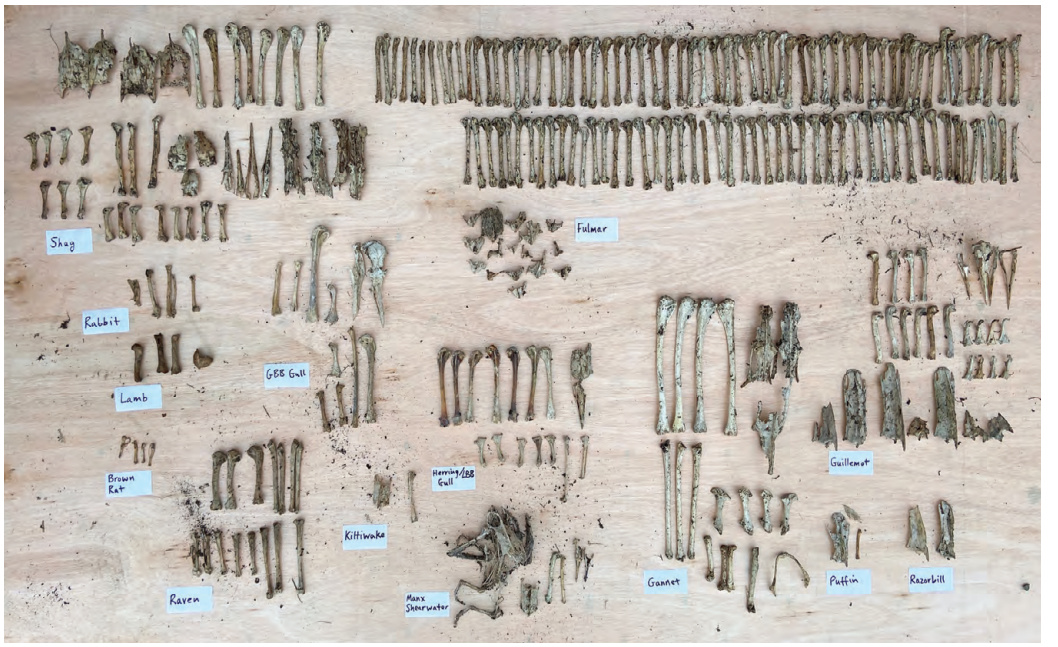

Plate 251. Bird and mammal bone remains identified from a nest on Lewis, Outer Hebrides, 2023. © *Robin Reid*

other colonial marine birds such as auks and Shag, to form a major category ('seabirds') of just over half of all items. Gulls and terns (4% of items) were grouped in a separate category because not all were marine. Wetland birds (7% of items) were mainly geese and ducks, but also included waders. Large mammals (14% of items) were predominantly lambs, but included numbers of deer calves, the occasional feral goat kid and the remains of sheep, deer and Common Seal taken as carrion. Other categories were Rabbit (10%), hares (4%), gamebirds (3%) and fish (5%). Most fish were marine species. All remaining species that did not fit within these categories were combined along with unidentified items as 'other' (4%). Grouping foods this way masked food diversity so we calculated 'Simpson's Index of Diversity' (Magurran 2004) for all items identified to species within each sample for each nest territory. Low values of this index indicated samples dominated by a single food species, whilst high values indicated those with an even spread of several species.

The basic unit used to test for differences in the composition of food categories associated with territory, year and region was a post-fledging collection with at least ten items. For data analyses, the proportions of food categories and values of the food diversity index were arcsine transformed prior to parametric statistical tests. We used nonparametric statistical tests where foods were so infrequent or the data so skewed that transformation was impractical and the assumptions required of parametric tests were invalid.

Results

Species composition within recorded food remains

In total, the remains of at least 11,375 food items comprising 121 species (Appendix) were recovered from 92 eagle territories during 20 years; 293 samples in all. Samples contained from one to 214 items and the smallest were from failed nests or the roost sites of non-breeding birds. The overall pooled total of items comprised 67% birds of at least 70 species, 25% mammals (17 species), 6% fishes (at least 30 species) and occasional individuals of Common Toad, Norway Lobster, Common Squid and Curled Octopus. Although many food species were identified, only six were frequent enough in post-fledging samples of at least ten or more items to estimate their average proportion per territory (Table 1). The most common was Fulmar (30% of items per territory); lamb remains were far less common (6%) as were those of Rabbit (4%), Guillemot (3%), Shag (2%) and Greylag Goose (1%). All other species were infrequent at 0.5 percent or less.

Table 1. The average proportions of items for the six commonest species identified in 221 post-fledging samples of ten or more food items, from nests at 90 territories in Scotland, 1998 to 2017.

Food species	Median proportion per territory	inter-quartile range	Proportion of territories where the species was recorded
Fulmar	0.299	0.068–0.502	0.944
Lamb	0.060	0.020–0.150	0.889
Rabbit	0.036	0.000–0.109	0.711
Guillemot	0.030	0.000–0.068	0.767
Shag	0.018	0.000–0.055	0.689
Greylag Goose	0.006	0.000–0.033	0.544

Variation within and between territories

This analysis examined the proportions of the nine food categories and tested whether the variation between territories was greater than the variation between years within a territory. The data comprised 179 samples from those 49 territories that had been sampled post-fledging in two or more different years. For the main food categories and for overall food species diversity, the difference between territories was substantially greater than the difference between years within a territory (F values and their probabilities in Table 2a).

Table 2. One-way Analysis of Variance F ratios and their associated probabilities for comparisons of the proportions of various food categories and an index of food species diversity, within and between (a) territories and (b) geographic regions.

	(a) territories		(b) regions	
Food category	F (df=48, 130)	p	F (df=8, 80)	p
Seabirds	13.07	<0.001	5.19	<0.001
Large mammals	7.97	<0.001	5.45	<0.001
Rabbit	5.59	<0.001	1.67	0.119
Wetland birds	5.88	<0.001	3.68	0.001
Fish	1.82	0.004	1.56	0.151
Gulls & terns	4.93	<0.001	0.87	0.548
Food species diversity index	4.98	<0.001	1.81	0.087

Data were arcsine transformed proportions of food categories within post-fledging samples of ten or more items from (a) 179 collections from the 49 territories with samples from two or more years and (b) 89 nest territories within nine geographic regions.

It was possible that the similarity between years in the composition of foods at individual territories was due to sampling over sequential years, when they were likely to have been tenanted by the same individual eagles. We therefore directly compared the composition of foods in those seven territories that had been sampled over the longest period; i.e. in both the earlier study (1998–2002) and in 2017. Within the seven territories, none of the food categories or the food diversity indices were significantly different between 2017 and the earlier period (paired t tests; t values all <1.4, df = 6, p>0.2), so, even over the long-term (15 to 19 years), the sorts of foods recorded at a nest territory were similar.

Variation between geographic regions of Scotland

The average composition of foods differed between regions (Figure 2), due to the significant variation in the proportions of the three main food categories: seabirds, large mammals and wetland birds (F values and their probabilities in Table 2b). Average values for 'seabirds' (predominantly Fulmars) were about half of items in nests on Lewis and Harris, the Uists, Skye, the north-west mainland and Islay & Jura. Large mammals (mainly lambs) were between a fifth and a third of items in Mull, Lochaber and nearby mainland Argyll. In contrast, they were scarce in nests in

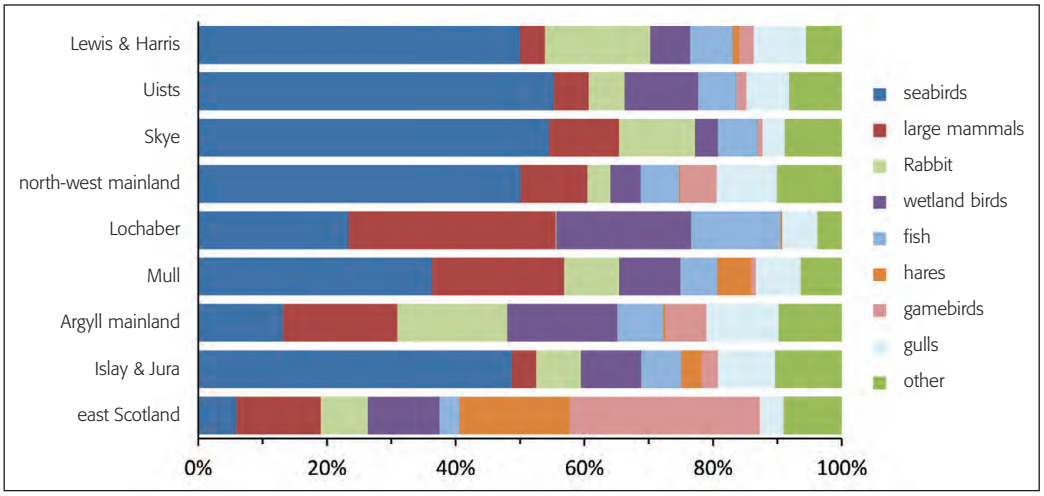

Figure 2. Average composition of food samples (post-fledging collections with ten or more items) from 89 territories in nine different parts of Scotland.

Lewis & Harris, the Uists and on Islay & Jura. The large mammal remains in east Scotland were from deer. Wetland birds (predominantly geese) were important in five of the nine regions, the Uists, Mull, Islay & Jura, Lochaber and mainland Argyll. There was no evidence of significant differences between regions for gulls & terns, Rabbit or fishes (Table 2b). Mountain Hares together with gamebirds (Red Grouse) were important at those few nests well away from lowland wetlands and far from the coast on higher ground in the north-west mainland and the east of Scotland.

Variation between nest territories associated with distance from the coast

The average proportion of particular food categories was calculated for each of the 89 territories for which there was at least one post-fledging sample of ten or more items. The variation between territories was dominated by the differences in the proportions of 'seabird' remains which occurred in all but four nest territories and outnumbered the remains of other items in 47% of territories. No other food category showed this sort of predominance. Large mammal items outnumbered others in only two territories, and Rabbit and wetland birds in only a single territory each.

It was unsurprising that seabirds were so common in almost all samples because many of the territories were close to the coast. Overall, the proportion of 'seabird' varied from zero to 0.890, with an average of 0.629 of items for 22 coastal territories in contrast to no 'seabird' remains recorded in the three furthest inland. The regression of proportion of 'seabird' on distance from the sea was highly significant ($F_{1, 86} = 38.1$, $p<0.001$) and explained almost a third of the overall variation ($r^2 = 0.299$).

We examined this further by grouping all the strictly marine species (11 birds, 26 fishes, Common Seal, Norway Lobster, Common Squid and Curled Octopus) and compared their combined proportion in samples against distance from the sea. At nests on the seacoast, on average there were about seventy percent of marine items amongst food remains, gradually decreasing for nests up to about six kilometres inland. More than half of items were marine at one nest 6.3 km from the coast, showing that eagles could regularly commute this sort of distance, but this was apparently not so for nests further inland (Figure 3).

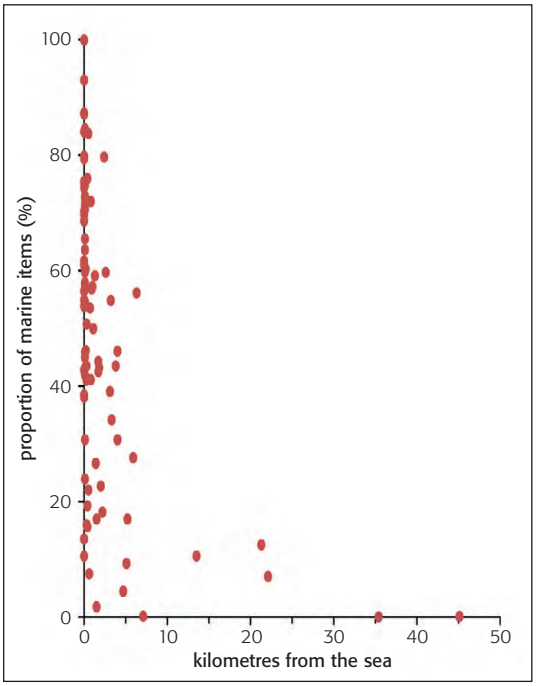

Figure 3. The median proportion of marine items in food remains (post-fledging collections with ten or more items) from 87 territories at various distances from the seacoast.

Variation in the relative abundance of lambs in eagle nests

There was information on the proportion of lambs amongst food remains in 219 post-fledge collections with ten or more items, from 89 territories within nine Scottish regions. The values were highly skewed with the majority of collections containing the remains of occasional lambs or none, and a few containing ten or more. Amongst those 49 territories that had been sampled more than once, the proportion of lambs varied much more between territories than within (Kruskal-Wallis test, $H = 133.7$, $df = 48$, $p<0.001$). We averaged proportions within territories and the resulting median values for 89 different territories were still extremely skewed. Half of all territories had values between zero and six percent of items; only seven territories had lambs as 30% or more of items, two in Lochaber and five on Mull.

Table 3. The average proportions of lambs amongst food remains in 219 post-fledging collections of ten or more items from 89 territories, in nine different parts of Scotland.

Region	Number of territories	Average proportion of lambs per territory		
		median	minimum	maximum
Lewis & Harris	15	0.020	0.000	0.166
Uists	5	0.021	0.000	0.130
Skye	21	0.077	0.000	0.271
north-west mainland	8	0.035	0.000	0.145
Lochaber	7	0.129	0.045	0.500
Mull	20	0.139	0.000	0.502
Argyll mainland	4	0.187	0.045	0.300
Islay & Jura	5	0.000	0.000	0.058
east Scotland	4	0.005	0.000	0.214

There were significant differences between different parts of Scotland. The median proportion of lambs varied much more between regions than within (Kruskal-Wallis test, H = 34.1, df = 8, p<0.001). The average values together with their ranges (Table 3) show that the significant variation between regions was attributable to a higher proportion of lambs in collections from nests at some territories on Mull and in nearby Lochaber and mainland Argyll.

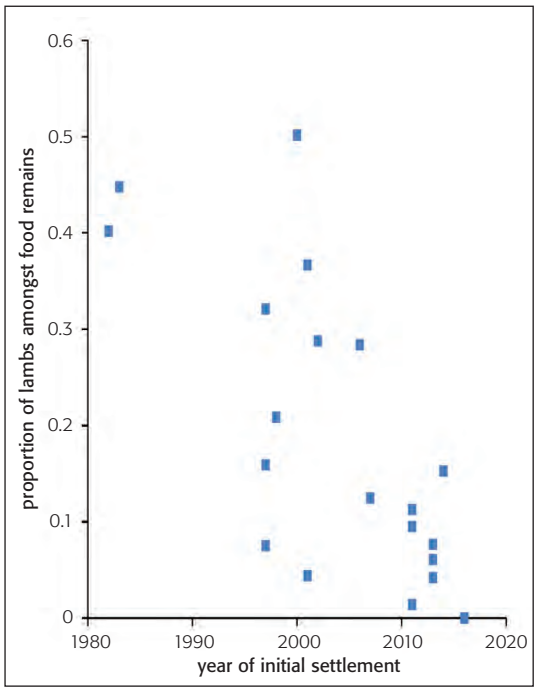

Figure 4. The median proportions of lambs in food remains from post-fledging collections at 20 territories on Mull. The initial two territories occupied in the 1980s had many lambs, whereas those first occupied from 2011 onwards had far fewer.

There was a strong association between the prevalence of lambs in nests and the order in which territories were settled during colonisation (Spearman rank correlation, r_s = -0.299, df=87, p=0.004). Collections of food remains from territories that were first occupied in the 1980s and 1990s had more lambs than did those newly occupied only recently. This was not simply because more lambs were recorded in the earlier years, as the relationship still held when the analysis used only the proportions of lambs in the most recent food data from the 58 territories sampled in 2017 (r_s = -0.321, df=56, p=0.014).

Moreover, the correlation was not because of a disproportionate number of recently established territories in those regions of Scotland with fewer lambs. Using information from Mull alone, data from 20 territories were strongly correlated (r_s = -0.669, df=19, p=0.001). The five territories which averaged more than thirty percent of lambs amongst food remains were those initially settled in 1982, 1983, 1997, 2000 and 2001, whereas those established from 2011 onwards averaged fifteen percent lambs or less (Figure 4).

Within the Scottish breeding population the proportion of territories with more than the occasional lamb has declined. In the earlier study (1998 to 2002), fifteen pairs of eagles were sampled and on average lambs were more than 30% of items in the nests of five of them (about a third). In 2017, only five of 58 pairs sampled (less than a tenth) had 30% or more lambs.

Foods and eagle productivity

Some territories regularly produced young but others much less frequently, and it was thought this might reflect the foods taken. We therefore used regression analysis to test for potential associations between the foods used at territories and the average productivity in the five most recent years (2013 to 2017) weighted (per territory) by the number of years for which there were breeding data. There was substantial variation between territories in productivity measurements but no significant association with food categories (all $F_{1,84}<2.6$; $p>0.111$) or with the food diversity index ($F_{1,84}=0.1$; $p=0.760$).

Plate 252. Adult White-tailed Eagle carrying prey, Mull, Argyll, 2004. © *Dom Morgan*

Evidence of dietary specialism from the food species diversity index

The average food species diversity index for 89 territories was high (median 0.78) and 90% of values lay between 0.61 and 0.97, showing that at most nests several food species were taken often. Nevertheless, the frequency distribution of index values was skewed (Anderson-Darling Normality Test, $A^2 = 1.690$, $p<0.001$), indicating specialisation on single foods at the nine territories with the lowest dietary diversity (0.28 to 0.60). Food remains at eight of these were dominated by Fulmar (60–83% of items) and the other by Rabbit (67% of items). No other food species predominated in samples to this extent.

Discussion

Previous assessments of the diet of White-tailed Eagles in Scotland had difficulties with small samples and bias. The present study examined much more material and overcame the previous potential bias towards pairs that consumed lambs by targeting all territories that produced young in 2017. The main strength of the method (clearing nests of food remains after young had fledged) was that samples were directly comparable between years, between territories and between regions of Scotland. This meant we could quantify the variation in recorded foods associated with location and over time. The main weakness of the method was that our samples of food remains could have overestimated the number of large mammals and birds in nests and certainly underrepresented fishes. In future, a specific study could address this by using carefully positioned nest cameras that can identify most items delivered including fish (Marquiss, Robinson & Tindal 2007).

Another potential weakness of the method was that our samples were almost all from nests that produced young. The lack of any association between foods used and average territory productivity suggested this might not result in major bias, but the issue could nevertheless be addressed in future studies by using tracking devices on eagles as part of a project specifically planned to monitor foraging behaviour and locate feeding perches to enable the identification of additional food remains. Importantly, this approach could be used to document foods taken by sub-adult eagles and by adults outside of the breeding season (Kenward 2006).

The main food remains retrieved from territories in Scotland in the 20 year study period were from seabirds, marine fishes, wetland birds, Rabbit, lambs, hares and gamebirds. There was substantial species diversity both within food remains samples and between, with little evidence of food specialisation, except perhaps where a single species predominated (Fulmar exceeded 80% of items at four territories and Rabbit at one). An important pattern across Scotland was that the

composition of foods at a territory varied little between years, even over the long term, and that the differences between territories were substantial. This is consistent with the idea that White-tailed Eagles are generalist foragers and their diet probably reflects whatever foods are locally available (Dementavicius *et al.* 2020). It is sufficient explanation for the variation in foods used from territory to territory and between regions.

Despite the overall similarity of foods at most territories, there were some changes over time at specific places. Rabbits in particular were taken in numbers in some years but not in others, as eagles switched temporarily to alternative foods when Rabbit numbers were apparently low, e.g. on Mull (Marquiss, Madders & Carss 2003b) and in Wester Ross (JG pers. obs.). Elsewhere there have been reports of a longer-term reduction in the remains of Fulmars at some nests perhaps because local seabird populations can be affected by eagle predation (Hipfner *et al.* 2012, Anker-Nilssen, Fayet, & Aarvak 2023). Future work might search for evidence of this by repeating the widespread sampling of 2017, targeting specific territories where change is predicted. Additionally, the extent of fish provisioning by eagle viewing tourist boats could be monitored to see how that influences the relative abundance of alternative foods such as seabirds in samples from nearby nests.

Fulmars stand out as being the most common food item at a large proportion of nests and a much more common food item than gulls which would have been similarly abundant in many coastal territories. This may reflect a particular susceptibility of Fulmars to White-tailed Eagle predation due to their predictable flight patterns or rigid flight compared to the more manoeuvrable flight of gull species. Almost all the Fulmar remains recovered were of full-grown individuals rather than nestlings, suggesting that Fulmars were most likely caught away from nesting areas. A high rate of predation on full grown or adult individuals of such a long-lived species with a low reproduction rate has the potential to affect local Fulmar populations and warrants further investigation.

Marine items occurred in most nests, and in just over half of the sampled territories they were the most important food, outnumbering all other items. This was not surprising because during the study period almost all White-tailed Eagles in Scotland bred within a few kilometres of the coast (Evans *et al.* 2010). The prevalence of marine items decreased gradually up to 6 km from the sea, falling off rapidly further inland. The foods predominating at the three upland territories distant from the sea were deer, hares and grouse. Closer to the coast, the foods at some nests with fewer seabirds included alternative foods such as wetland birds, Rabbits and lambs. The prevalence of local habitat that potentially provided an abundance of such foods was sufficient to explain some specific regional differences in diet such as the taking of hares on Mull, geese on the Uists, Islay and Mull, Rabbits on Skye and lambs on Mull and in Lochaber.

Another important aspect was that the foods used were associated with the historical order in which nest territories were settled by eagles. This was particularly clear in the pattern of lamb remains in nests, with most recorded in those territories that were initially settled during recolonization immediately following re-introduction. The earlier intensive study had shown that these territories were centred on areas with Sheep and lamb carrion. The lambs from these nests were mostly scavenged (Marquiss, Madders & Carss 2003b) and of those killed by eagles, more than half could have been particularly vulnerable as they were much smaller for their age than healthy live lambs (Marquiss, Madders, Irvine & Carss 2003). With this in mind, one potential explanation for the greater numbers of lambs in food remains from the earliest settled territories might be that during the initial settlement phase of recolonisation, following release some inexperienced young eagles were sustained by feeding on carrion. This tendency may well have predisposed some released immatures to settle in places where carrion was most available, which in some regions was where there were most dead or moribund sheep and lambs. Subsequent, later generations of wild bred recruits settled in areas where live prey (seabirds and increasing numbers of breeding geese) was more abundant and carrion became less important.

In retrospect, the previously widespread view that lambs are an important food for White-tailed Eagles has been superseded; the prevailing evidence now is that marine items (seabirds and fishes) are the most important breeding season food in Scotland. The implications for the future are that further foods might become important as eagles colonise other regions, settling in areas with greater access to Mountain Hares on upland terrain and to fishes in rich freshwater habitats.

Acknowledgements

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RSPB Scotland gave support with a four week sabbatical for Robin Reid to design the work in 2017, carry out physical prey collections and collate data. They also gave staff time to assist with prey collections. SNH (now NatureScot) also covered staff costs for a number of prey collections undertaken by contractors through the Sea Eagle Management Scheme. Forestry and Land Scotland assisted with access to some sites and staff time for prey collections.

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The late Mike Madders who knew much about eagles in Scotland, was an energetic and skilful colleague who collected food remains from nests in the years 1998 to 2002. The late Richard Evans meticulously recorded contextual data on nest territories up until 2012. The late Paul Haworth also enthusiastically supported the study, contributing to subsistence costs for prey collections in 2017. Alan Fielding drew the map for Figure 1, and the text was much improved following detailed comments by Phil Whitfield.

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Appendix

The total recorded number of items of specific foods and the frequency of their occurrence in 92 territories of White-tailed Eagle in Scotland, 1998–2017.

Foods	items (territories)	Foods	items (territories)
Hedgehog *Erinaceus europaeus*	29 (7)	Great Skua *Stercorarius skua*	1 (1)
Rabbit *Oryctolagus cuniculus*	1102 (62)	Guillemot *Uria aalge*	501 (66)
Brown Hare *Lepus europeaus*	42 (1)	Razorbill *Alca torda*	165 (46)
Mountain/Irish Hare *Lepus timidus*	353 (24)	Black Guillemot *Cepphus grylle*	26 (19)
Brown Rat *Rattus norvegicus*	18 (9)	Puffin *Fratercula arctica*	100 (36)
Red Fox *Vulpes vulpes*	13 (11)	Feral Pigeon/Rock Dove *Columba livia*	20 (16)
Stoat *Mustela erminea*	1 (1)	Woodpigeon *Columba palumbus*	16 (6)
Polecat/Ferret *Mustela* sp.	3 (2)	Collared Dove *Streptopelia decaocto*	2 (2)
American Mink *Neovison vison*	5 (3)	Cuckoo *Cuculus canorus*	6 (6)
Badger *Meles meles*	2 (1)	Barn Owl *Tyto alba*	7 (4)
Feral Cat *Felis catus* (domestic)	8 (4)	Tawny Owl *Strix aluco*	2 (1)
Common Seal *Phoca vitulina*	8 (5)	Long-eared Owl *Asio otus*	1 (1)
Red Deer *Cervus elaphus*	95 (33)	Short-eared Owl *Asio flammeus*	20 (10)
Fallow Deer *Dama dama*	1 (1)	Kestrel *Falco tinnunculus*	4 (4)
Roe Deer *Capreolus capreolus*	25 (9)	Peregrine *Falco peregrinus*	1 (1)
Feral Goat *Capra hircus* (domestic)	1 (1)	Jay *Garrulus glandarius*	2 (1)
Sheep *Ovis aries* (domestic)	1350 (76)	Jackdaw *Corvus monedula*	5 (2)
Unidentified mammals	6 (5)	Rook/Crow *Corvus* sp.	102 (33)
		Raven *Corvus corax*	63 (26)
Canada Goose *Branta canadensis*	15 (8)	Starling *Sturnus vulgaris*	3 (1)
Greylag Goose *Anser anser*	201 (48)	Blackbird *Turdus merula*	2 (1)
Shelduck *Tadorna tadorna*	23 (10)	Mistle Thrush *Turdus viscivorus*	3 (3)
Wigeon *Anas penelope*	1 (1)	Chaffinch *Fringilla coelebs*	1 (1)
Mallard *Anas platyrhynchus*	135 (33)	Unidentified birds	240 (59)

Domestic Duck *Anas* (domestic)	2 (2)
Teal *Anas crecca*	7 (5)
Eider *Somateria mollissima*	104 (32)
Common Scoter *Melanitta nigra*	1 (1)
Long-tailed Duck *Clangula hyemalis*	1 (1)
Red-breasted Merganser *Mergus serrator*	38 (18)
Black Grouse *Lyrurus tetrix*	2 (1)
Red Grouse *Lagopus lagopus scotica*	240 (32)
Red-legged Partridge *Alectoris rufa*	4 (3)
Pheasant *Phasianus colchicus*	85 (17)
Guinea Fowl *Numida meleagris*	2 (2)
Domestic Fowl *Gallus* (domestic)	3 (2)
Red-throated Diver *Gavia stellata*	7 (6)
Black-throated Diver *Gavia arctica*	3 (2)
Fulmar *Fulmarus glacialis*	4347 (81)
Manx Shearwater *Puffinus puffinus*	32 (19)
Grey Heron *Ardea cinerea*	107 (28)
Gannet *Morus bassanus*	31 (13)
Shag *Phalacrocorax aristotelis*	354 (61)
Cormorant *Phalacrocorax carbo*	20 (11)
Sparrowhawk *Accipiter nisus*	2 (2)
Hen Harrier *Circus cyaneus*	2 (2)
Common Buzzard *Buteo buteo*	2 (2)
Moorhen *Gallinula chloropus*	1 (1)
Oystercatcher *Haematopus ostralegus*	54 (30)
Lapwing *Vanellus vanellus*	17 (6)
Golden Plover *Pluvialis apricaria*	4 (2)
Curlew *Numenius arquata*	40 (18)
Turnstone *Arenaria interpres*	1 (1)
Dunlin *Calidris alpina*	1 (1)
Woodcock *Scolopax rusticola*	17 (13)
Common Snipe *Gallinago gallinago*	4 (3)
Common Sandpiper *Actitis hypoleucos*	3 (2)
Redshank *Tringa totanus*	3 (2)
Kittiwake *Rissa tridactyla*	43 (23)
Black-headed Gull *Chroicocephalus ridibundus*	12 (7)
Common Gull *Larus canis*	66 (23)
large gulls *Larus* sp.	70 (33)
Herring Gull *Larus argentatus*	146 (69)
Lesser Black-backed Gull *Larus fuscus*	13 (8)
Greater Black-backed Gull Larus marinus	70 (33)
Sandwich Tern *Sterna sandvicensis*	1 (1)
Common/Arctic Tern *Sterna* sp.	13 (6)
Common Toad *Bufo bufo*	2 (2)
Lesser-spotted Dogfish *Scyliorhinus canicula*	86 (31)
Thornback Ray *Raja clavata*	3 (2)
European Eel *Anguilla anguilla*	1 (1)
European Conger *Conger conger*	36 (23)
Herring *Clupea harengus*	2 (2)
Pilchard *Sardina pilchardus*	1 (1)
Atlantic Salmon *Salmo salar*	12 (8)
Trout *Salmo trutta*	11 (9)
Northern Pike *Esox lucius*	2 (1)
Anglerfish *Lophius piscatorius*	26 (10)
Cod *Gadus morhua*	35 (30)
Haddock *Melanogrammus aeglefinus*	14 (3)
Bib *Trisopterus luscus*	2 (2)
Trisopterus sp.	1 (1)
Saithe *Pollachius virens*	5 (2)
Ling *Molva molva*	21 (15)
Tadpole-fish *Raniceps raninus*	1 (1)
cod fishes sp. *Gadidae*	44 (29)
European Hake *Merluccius merluccius*	62 (4)
Garfish *Belone belone*	1 (1)
John Dory *Zeus faber*	17 (9)
Gurnard *Triglidae* sp.	2 (2)
Bullrout *Myoxocephalus scorpius*	14 (9)
Long-spined Sea scorpion *Taurulus bubalis*	1 (1)
Lumpsucker *Cyclopterus lumpus*	22 (8)
Scad *Trachurus trachurus*	3 (3)
Grey Mullet *Mugilidae* sp.	1 (1)
wrasses sp. *Labridae*	29 (20)
Mackerel *Scomber scombrus*	15 (10)
Turbot *Scophthalmus maximus*	1 (1)
Flounder *Platichthys flesus*	3 (1)
flatfish sp. Pleuronectiformes	20 (13)
Triggerfish *Balistes capriscus*	1 (1)
unidentified fish	165 (49)
Norway Lobster *Nephrops norvegicus*	3 (3)
Common Squid *Loligo vulgaris*	3 (2)
Curled Octopus *Eledone cirrhosa*	2 (2)