

Diet specialization in an insular population of coastal Peregrine Falcons

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Individual diet specialization is known to occur in populations of generalist predators, where specific individuals develop specialist feeding strategies. Diet specialization has been reported in many raptor species and it may be an important driver of intraspecific population structure. Here, we quantify the diet of Peregrine Falcons *Falco peregrinus* from five breeding territories on an island determined from prey remains collected over four breeding seasons. Three prey species accounted for 69.8% of total prey frequency, with Manx Shearwater *Puffinus puffinus* being the primary prey accounting for 47.3% by frequency and 40.8% by biomass. European Herring Gull *Larus argentatus* was the second most important prey species by frequency (13.8%) and biomass (29.8%) followed by Feral Pigeon *Columba livia* (frequency: 8.7%, biomass: 7.0%). Prey frequency on specific prey groups varied substantially between breeding pairs and months. Two pairs specialized on Manx Shearwater, one pair specialized on Herring Gull and Manx Shearwater, with the remaining two pairs having a relatively generalist diet of Manx Shearwaters, Feral Pigeon and small passerines. Prey frequency on Manx Shearwaters increased throughout the breeding season with a peak in total diet frequency of 63.8% in July, with a concurrent decrease in Herring Gull prey frequency. Higher percentage of Manx Shearwater in the diet explained 87% of the variation in a narrower dietary breadth for the Peregrine pairs. Our results suggest individual diet specialization may be one of multiple factors important for understanding population density in insular raptor populations.

Key words: diet breadth, *Falco peregrinus*, individual diet specialization, Peregrine Falcon, raptor diet, resource partitioning

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Ecological specialization is a key concept in ecology and evolutionary biology (Bolnick *et al.* 2003, Araujo *et al.* 2011), with individual diet specialization a potential mechanism promoting coexistence between individuals through specialized use of food resources (Schoener 1974, Wiens 1984). Populations of diet generalist species are often comprised of a subset of diet specialized individuals (Pagani-Nunez *et al.* 2016). This may reduce resource-use overlap because specialized individuals utilize a narrower range of resources than conspecific competitors. Individual diet specialization is expected to be common amongst species occupying higher trophic levels, where intraspecific competition

for resources is expected to be high (Navarro-Lopez *et al.* 2014). Recently, studies of individual diet specialization have established that this behaviour may be common in raptors (e.g. Constantini *et al.* 2005, Whitfield *et al.* 2009, Navarro-Lopez *et al.* 2014, Terraube *et al.* 2014). Specialized individuals within raptor populations may have higher reproductive success than generalists (Dawson *et al.* 2011), though that assertion may not always apply (Whitfield *et al.* 2009). Therefore, understanding individual diet specialization is important because of its potential to regulate intraspecific population dynamics and breeding success (Bolnick *et al.* 2003, Ceia & Ramos 2015).

The Peregrine Falcon *Falco peregrinus* (hereafter Peregrine) is a widely distributed raptor with a global range and considered a diet generalist, feeding on a broad range of other bird species (White *et al.* 2013). Though individual diet specialization has been described in several Peregrine populations from North and South America (Beebe 1960, Verlade 1993, Castellanos *et al.* 2006, Garcia *et al.* 2014) and anecdotally from the British Isles (Ratcliffe 1993), quantitative data is lacking from much of the Peregrine's global range. In the British Isles, the Peregrine has a largely generalist diet (e.g. Dixon 2005, Sutton 2015a), with Feral Pigeon *Columba livia* the primary prey (Ratcliffe 1993, Dixon *et al.* 2018). The British Isles has many small offshore islands off its western seaboard, some of which have dense sub-populations of breeding Peregrines relative to their area (Ratcliffe 1993, Sutton 2015b, 2016). Ratcliffe (1993) suggested that the population density of these island Peregrines may be driven by seabird abundance, which are likely to comprise the main food source for insular Peregrine sub-populations.

Recent dietary assessments from Lundy, an island in the Bristol Channel between England and Wales, indi-

cate that seabirds, including Manx Shearwater *Puffinus puffinus* and European Herring Gull *Larus argentatus*, are the primary food source for the resident Peregrines (Sutton 2016, Sutton *et al.* 2017). Lundy was historically one of many important seabird colonies lying off the south west coast of the British Isles (Brown *et al.* 2011). Since the 1900's seabird populations on the island have declined due to predation from invasive predators and human over-harvesting. After the eradication of Black *Rattus rattus* and Brown Rats *R. norvegicus* on the island in 2006 and formal legal protection, there has been an increase in breeding seabirds, in particular Manx Shearwater (Booker & Price 2014). Lundy also has a high density of breeding Peregrines, with five territorial pairs resident from 2002 to the present (Sutton 2016). The factors influencing this high breeding density are complex and not fully understood. However, one contributory factor may be diet specialization, allowing reduced competition for food resources, possibly enabling more pairs to breed in close proximity. Here, we assess foraging behaviour and diet specialization in this insular Peregrine population during the breeding season between the years 2014 and 2017. We aim to (1) quantify diet composition and



Male Peregrine Falcon *Falco peregrinus* on hunting perch (photo LS, Lundy, Devon, 6 March 2016).

spatio-temporal patterns of predation and (2) determine the level of individual diet specialization amongst the five resident breeding pairs. Last, we discuss the potential implications this may have on breeding density and coexistence.

METHODS

Study area

Lundy (51°11'N, 4°40'W) is a small offshore island located in the Bristol Channel, England, 18 km from the nearest mainland point in the administrative county of Devon. The island is approximately 5 km long by 1 km wide, circled by 13 km of mainly granite sea cliffs (Figure 1). Elevation on the island plateau ranges from 80–143 m a.s.l., covering an area of approximately 445 ha. Two-thirds of the island plateau is comprised of unimproved grassland, moorland and maritime heath, dominated by Common Heather *Calluna vulgaris*. The southern third of the island supports a small tourist and farming community where the dominant land use is semi-improved and improved grassland.

Data collection

We collected prey samples on a monthly basis between April and August for the years of 2014–2017 from five breeding territories with resident adult unmarked Peregrines. We assumed prey from each territory was taken by the same pair over the four-year period. We followed a pre-determined circuit of the island recording food items from prey remains (including feathers, bones and carcasses) left after feeding (Marti *et al.* 2007). We conducted systematic transect searches within each territory, checking regular plucking areas along cliffs and slopes adjacent to nest cliffs. Prey remains were assigned to a territory if located within a 400-m radius of the nest cliff. This distance was determined as the minimum cross-over radius between territories to prevent recording outside of a known territory. We defined territories on cardinal points of the compass as: L1/NE (north-east), L2/E (east), L3/S (south), L4/SW (south-west), L5/W (west). Any remains found outside the 400-m radius from nest cliffs were assigned as random events and not used in the spatial analyses. Prey remains were removed for identification and the location recorded with a handheld GPS device to prevent double recording on subsequent visits. Remains observed on inaccessible feeding areas were recorded using a Digital Single Lens Reflex (DSLR) camera for later analysis and the location recorded indirectly using Google Earth (<https://earth.google.com/web/>) soft-

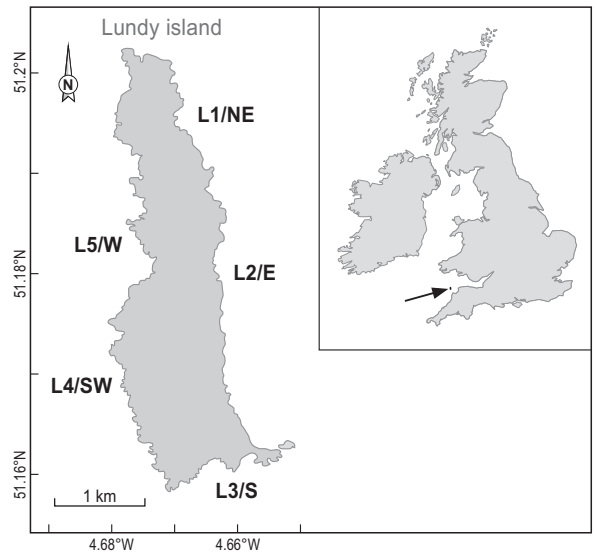


Figure 1. Map of Lundy island showing the spatial agreement for the five Peregrine Falcon territories. Precise nest locations have been omitted for confidentiality.

ware. We identified prey species from Brown *et al.* (2003) and previous experience (Sutton 2015a, 2016, Sutton *et al.* 2017). Avian prey remains from Peregrines are readily identified. On carcasses the breast is ruptured with distinct notches in the breastbone from the Peregrines' beak when feeding (Bang & Dahlstrom 2011). Plucked feathers will often be found concentrated in a pile surrounding the carcass indicating a kill, distinct from gull feeding remains (Corkhill 1973). Any raptor kills recorded during the breeding period were assumed to be from Peregrines as they are the only resident breeding raptor on Lundy (Davis & Jones 2007).

Statistical analysis

We divided prey items into nine prey groups (auks, corvids, ducks/waders, gulls, Lagomorphs, pigeons/doves, shearwaters, small passerines and other) and five weight classes (<50 g, 51–250 g, 251–500 g, 501–1000 g, >1000 g). Biomass was calculated following units of mass given by the British Trust for Ornithology (2016). We compared spatial (territories) and temporal (months) variation in total prey frequency using Fisher's Exact test. We calculated dietary niche breadth (B) on the sum total of all prey frequency items using the formula of Levins (Krebs 1999),

$$B = 1/\sum p_i^2 \quad (1)$$

where p_i represents the proportion of the diet contributed by the i th taxon. Niche breadth was then

standardized (B_A) for easier interpretation following Hurlbert (1978),

$$B_A = \frac{B-1}{n-1} \quad (2)$$

Values for this index range on a scale of 0 to 1 with lower values towards zero indicating narrower dietary breadth and higher values towards one indicating broader diet breadth. We used linear regression to model the relationship between prey weight and log-transformed frequency of predation, and to model the relationship between percentages of Manx Shearwater with total dietary breadth from each territorial pair. All statistical analyses were performed in R v. 3.5.1 (R Core Team 2018).

RESULTS

In total, we recorded 520 prey samples to a specific species or genus, with 36 prey species identified (Table S1), comprising 35 birds and one mammal, European Rabbit *Oryctolagus cuniculus*. Avian prey species ranged in size from Common Chiffchaff *Phylloscopus collybita* (8 g) up to Mallard *Anas platyrhynchos* (1210 g). Three prey species comprised 69.8% of the total diet by frequency. Manx Shearwaters were the most common prey species by frequency (47.3%) and biomass (40.8%), followed by Herring Gull (frequency: 13.8%, biomass: 29.8%) and Feral Pigeon (frequency: 8.7%, biomass: 7.0%). The most common prey group were shearwaters (comprised wholly of Manx Shearwater) by both frequency and biomass, followed by gulls (Table 1). Prey items in the 251–500 g weight class

Table 1. Prey groups by total frequency and biomass (%) predated by Peregrine Falcons breeding on Lundy from April–August 2014–2017.

Prey group	Frequency (%)	Biomass (%)
Auks	3.9	4.1
Corvids	1.0	1.0
Ducks/Waders	2.3	3.2
Gulls	17.5	34.1
Lagomorphs	3.1	6.9
Other	0.6	0.2
Pigeons/Doves	10.4	8.5
Shearwaters	47.3	40.8
Small passerines	13.9	1.2
Total	100.0	100.0

were most frequent (62.1%; Table 2), followed by the 501–1000 g weight class (18.9%). There was a positive relationship between prey mass and prey frequency with increased frequency on prey species with greater mass (Figure 2), explaining 16% of the variation in prey frequency ($F_{1,34} = 6.69$, $R^2 = 0.16$, $P = 0.014$).

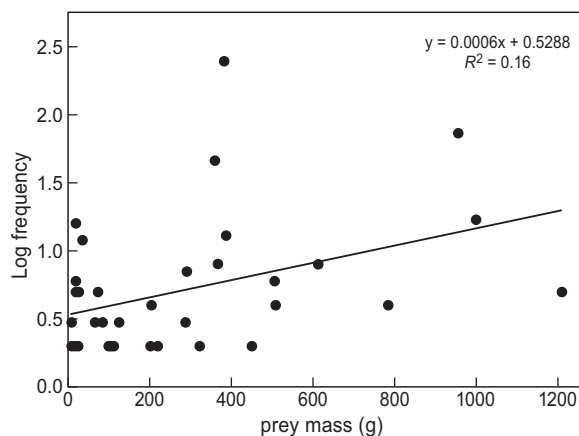


Figure 2. Predation frequency by mass of individual prey species taken by Peregrine Falcons breeding on Lundy from April–August 2014–2017. Unit mass (g) taken from BTO (2016).

Frequency of all prey groups varied substantially over the five-month (April–August) sampling period (Fisher's Exact: $P < 0.001$; Figure 3). Relatively equal numbers of gulls, shearwaters and small passerines were predated in April, with a steady increase in total frequency of shearwater predation from May onwards, peaking in July at 63.8%. Conversely, as frequency of shearwater prey group predation increased, gull prey group predation frequency dropped to a low of 6.3% by July, before a marked increase in August (26.3%). Prey group diet composition varied substantially between nest territories (Fisher's Exact: $P < 0.001$; Figure 4). Peregrine pairs in territories L1/NE and L4/SW had a high proportion of shearwaters indicating a specialized

Table 2. Frequency of predation by prey weight group

Prey weight group (g)	Frequency (%)
<50	11.5
51–250	3.7
251–500	62.1
501–1000	18.9
>1000	3.9
Total	100.0

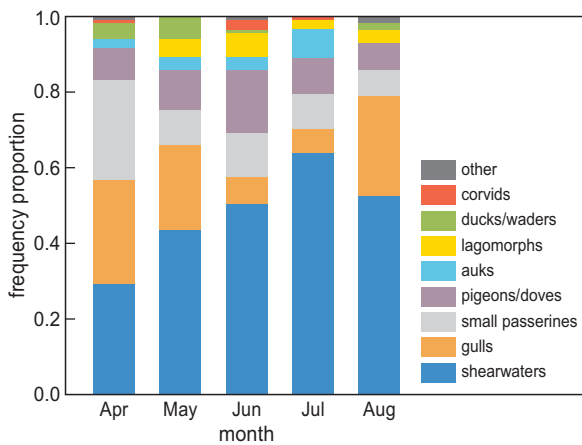


Figure 3. Temporal variation by month in frequency of prey groups predated by Peregrine Falcons breeding on Lundy from April–August 2014–2017. Sample sizes for each month: April: 120, May: 85, June: 113, July: 127, August: 57.

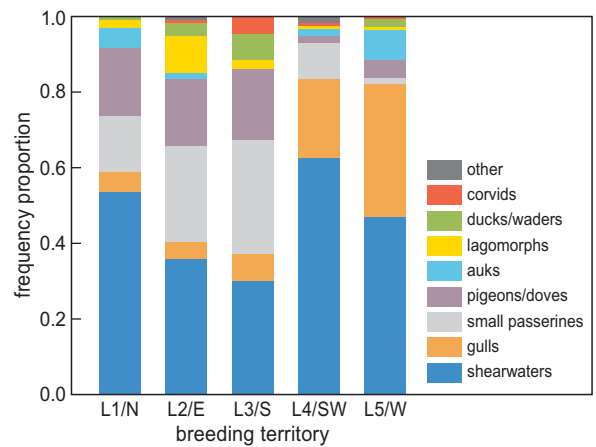


Figure 4. Spatial variation between nest territories in frequency of prey groups predated by Peregrine Falcons breeding on Lundy from April–August 2014–2017. Sample sizes for each territory: L1/NE: 95, L2/E: 114, L3/S: 43, L4/SW, L5/W: 140.

diet (L1/NE: 53.7%, L4/SW: 62.6%). Pairs in territories L2/E and L3/S showed a generalist diet of pigeons/doves, shearwaters and small passerines (Figure 4). The pair in territory L5/W were diet specialists of both shearwaters (47.1%) and gulls (35.0%), with the pair in territory L4/SW also regularly taking gulls, albeit less frequently (20.9%).

The pair in territory L4/SW had the narrowest diet breadth and were the most specialized in terms of diet ($B_A = 0.073$), followed by the pairs in territory L1/NE ($B_A = 0.116$) and L5/W ($B_A = 0.119$) both with similar narrow diet breadth. Pairs from the remaining territories had relatively broader niche breadth and a more generalist diet (L2/E: $B_A = 0.222$, L3/S: $B_A = 0.346$). There was a strong inverse relationship between narrow dietary breadth and high percentage of Manx Shearwater in the diet of the territorial pairs (Figure 5), with the percentage of Manx Shearwater in the diet explaining 87% of the variation in dietary breadth ($F_{1,3} = 20.2$, $R^2 = 0.87$, $P = 0.02$).

DISCUSSION

Our results demonstrate that specific breeding pairs of Peregrines on Lundy have a specialized diet, with Manx Shearwater the principal prey. This followed our general expectations given the marine location, though the finding that large prey such as Herring Gull and Rabbit were important food sources was unexpected. Prey mass was able to explain 16% of the variation in predation frequency, with prey between 251–500 g the most common prey group. There was noticeable varia-

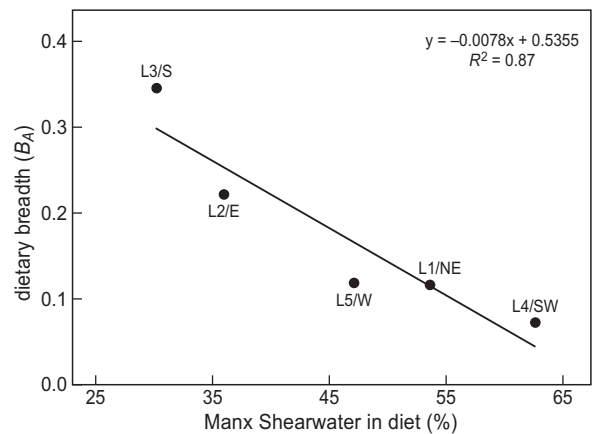


Figure 5. The relationship between Manx Shearwaters in total diet (%) and dietary breadth (B_A). Each black point represents a breeding pair of Peregrine Falcons.

tion in spatial and temporal prey frequency, with the number of Manx Shearwater predated increasing substantially during June and July at three specific nest territories. Even so, all breeding pairs had narrow dietary breadth, with just three prey species accounting for c. 70% of all prey taken. The trend of regular predation by Peregrines on specific prey types may have important implications for understanding individual diet specialization and its potential influence on the structure of insular raptor populations.

Our results show the importance of Manx Shearwater in the diet of Peregrines breeding on Lundy. They were the most common prey species and group by both frequency and biomass (Table S1). This finding is similar to other studies on insular Peregrine popula-

tions on offshore islands along the Pacific north west coast of North America. The resident Peregrine subspecies there, *F. p. pealei*, has adapted to local prey availability, specialising almost exclusively on Ancient Murrelets *Synthliboramphus antiquus* (Nelson 1990). Peregrine productivity and the number of breeding pairs fluctuates in accordance with seabird breeding density (Nelson & Myres 1976, Nelson 2004). Understanding whether Manx Shearwater abundance on Lundy directly affects Peregrine breeding success is a key question to be determined from future research. Our results show that Shearwater prey frequency increases during June and July when food demand is highest from nestlings. Though there is no evidence that Peregrine breeding density is linked to the increase in the Manx Shearwater population, this abundant food supply could facilitate an increase in productivity for certain pairs in this Peregrine sub-population.

The mechanisms driving the potential for individual diet specialization in this insular Peregrine population are still unclear. Peregrines are highly territorial; therefore individuals could be restricted by territoriality between nesting pairs, limiting access to certain food resources (Ratcliffe 1993). Patchy habitats could be a key driver by providing different prey types to specific individuals, which then increase their foraging success and handling time by specialization (Sargeant 2007, Terraube *et al.* 2014). However, with such a dense population of Peregrines in a small area, intense intra-specific competition between breeding pairs for territory space may be the strongest factor. Further research on home range size and foraging distances would be required to assess how Peregrines on Lundy defend territories and utilise habitats for these resources. The Peregrine pairs sited closer to the major Manx shearwater and gull colonies had the most specialized diets, though whether this is important for Peregrine population dynamics needs quantifying in future studies. Indeed, marking individual adults would enable further quantification of diet specialization amongst territories, both spatially and temporally.

Even though determining dietary habits from feeding remains is an established indirect method of assessing raptor diet (Marti *et al.* 2007), we recognise that indirect methods may over-represent large or brightly coloured prey species compared to small or darker prey remains that may go undetected (Ratcliffe 1993). Despite our thorough systematic sampling, we assume that some feeding areas were missed or inaccessible. Prey was observed being brought into nest ledges or feeding areas at territories L1/NE and L3/E that were inaccessible and out of sight. Thus, future

dietary assessments of breeding season diet would benefit from direct methods using stable isotope analysis from tissue sampling of nestlings (Denhard *et al.* 2016, Horswill *et al.* 2016). It follows that the results presented here are only representative of prey remains that were observed and accessible.

Density compensation theory postulates that island species tend towards a generalist foraging strategy once released from competition with other species (Wright 1980). However, in some species, such as the Peregrine, this may be reversed and individuals within a given population may become diet specialists. Establishing if any broad-scale patterns of diet specialization exist for insular Peregrine populations across the British Isles may help inform conservation management for offshore islands in the region. Many of these islands hold globally important populations of seabirds which are often the main prey of Peregrines (Ratcliffe 1993). Therefore, considered management of seabird populations could indirectly benefit the predators that utilise them as a food resource. Determining trophic relationships and relating those results to population dynamics in both predator and prey species is essential (Paine *et al.* 1990, Hipfner *et al.* 2011). This may establish how populations of avian apex predators are regulated on islands such as Lundy and how they interact in ecological community structures.

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SAMENVATTING

Het is bekend dat binnen vogelpopulaties van voedselgeneralisten individuele voedselspecialisatie kan voorkomen. Het verschijnsel komt ook bij veel roofvogelsoorten voor en kan een aanjager van een intraspecifieke populatiestructuur zijn. Wij hebben in 2014–2017 op het eiland Lundy voor de kust van Engeland op basis van prooiersten het menu van vijf paren Slechtvalken *Falco peregrinus* gekwantificeerd. Drie prooisoorten maakten 69,8% van het menu uit. De Noordse Pijlstormvogel *Puffinus puffinus* vormde de belangrijkste prooisoort (frequentie: 47,3%, biomassa: 40,8%), gevolgd door de Zilvermeeuw *Larus argentatus* (frequentie: 13,8%, biomassa: 29,8%) en tamme duiven *Columba livia* forma *domestica* (frequentie: 8,7%, biomassa: 7,0%). Er was een grote variatie in prooifrequentie van bepaalde soorten tussen broedparen en de maanden van het jaar. Twee paren waren gespecialiseerd in het vangen van Noordse Pijlstormvogels en één paar in dat van Zilvermeeuwen en Noordse Pijlstormvogels. Het menu van de overige twee paren bestond uit Noordse Pijlstormvogels, duiven en kleine zangvogels. Het aandeel Noordse Pijlstormvogels in het menu van de vijf paren nam in de loop van het broedseizoen toe tot 63,8% in juli. In dezelfde tijd nam het aandeel Zilvermeeuwen in het voedsel af. Het hoge aandeel Noordse Pijlstormvogels in het menu kon 87% van de smalle variatie in de menubreedte van de vijf paren verklaren. De resultaten van ons onderzoek suggereren dat voedselspecialisatie een van de vele factoren kan zijn voor het begrijpen van de populatiedichtheid in eilandpopulaties van roofvogels.

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SUPPLEMENTARY MATERIAL

Table S1. Frequency and biomass of all prey species taken by five breeding pairs of Peregrine Falcons on Lundy from April–August 2014–2017. Unit mass (g) taken from BTO (2016).

Prey species	Frequency	Unit mass	Total biomass
Mallard <i>Anas platyrhynchos</i>	4 (0.8)	1210	4840 (2.1)
Eurasian Teal <i>Anas crecca</i>	1 (0.2)	323	323 (0.1)
Manx Shearwater <i>Puffinus puffinus</i>	246 (47.3)	383	94,218 (40.8)
Common Kestrel <i>Falco tinnunculus</i>	1 (0.2)	220	220 (0.1)
Merlin <i>Falco columbarius</i>	1 (0.2)	202	202 (0.09)
Eurasian Woodcock <i>Scolopax rusticola</i>	6 (1.2)	291	1746 (0.8)
Common Snipe <i>Gallinago gallinago</i>	1 (0.2)	108	108 (0.05)
Eurasian Whimbrel <i>Numenius phaeopus</i>	1 (0.2)	451	451 (0.2)
Razorbill <i>Alca torda</i>	7 (1.4)	613	4291 (1.9)
Atlantic Puffin <i>Fratercula arctica</i>	12 (2.3)	387	4644 (2.0)
Black-headed Gull <i>Chroicocephalus ridibundus</i>	2 (0.4)	289	578 (0.3)
Lesser Black-backed Gull <i>Larus fuscus</i>	3 (0.6)	785	2355 (1.0)
European Herring Gull <i>Larus argentatus</i>	72 (13.8)	957	68,904 (29.8)
Black-legged Kittiwake <i>Rissa tridactyla</i>	7 (1.4)	368	2576 (1.1)
Feral Pigeon <i>Columba livia</i>	45 (8.7)	360	6200 (7.0)
Common Wood Pigeon <i>Columba palumbus</i>	5 (1.0)	507	2535 (1.1)
Eurasian Collared Dove <i>Streptopelia decaocto</i>	3 (0.6)	205	615 (0.3)
Common Cuckoo <i>Cuculus canorus</i>	1 (0.2)	114	114 (0.05)
Carrion Crow <i>Corvus corone</i>	3 (0.6)	509	1527 (0.7)
Eurasian Skylark <i>Alauda arvensis</i>	11 (2.1)	36	396 (0.2)
Barn Swallow <i>Hirundo rustica</i>	5 (1.0)	20	100 (0.04)
Long-tailed Tit <i>Aegithalos caudatus</i>	1 (0.2)	8	8 (0.01)
Common Starling <i>Sturnus vulgaris</i>	2 (0.4)	85	170 (0.07)
Common Blackbird <i>Turdus merula</i>	1 (0.2)	102	102 (0.04)
Song Thrush <i>Turdus philomelos</i>	4 (0.8)	75	300 (0.1)
Redwing <i>Turdus iliacus</i>	2 (0.4)	66	132 (0.06)
Mistle Thrush <i>Turdus viscivorus</i>	2 (0.4)	126	252 (0.1)
Common Chiffchaff <i>Phylloscopus collybita</i>	2 (0.4)	8	16 (0.01)
Willow Warbler <i>Phylloscopus trochilus</i>	1 (0.2)	9	9 (0.01)
European Robin <i>Erithacus rubecula</i>	1 (0.2)	19	19 (0.01)
Northern Wheatear <i>Oenanthe oenanthe</i>	4 (0.8)	28	112 (0.05)
House Sparrow <i>Passer domesticus</i>	1 (0.2)	27	27 (0.01)
Meadow Pipit <i>Anthus pratensis</i>	15 (2.9)	19	285 (0.1)
European Goldfinch <i>Carduelis carduelis</i>	1 (0.2)	16	16 (0.01)
Common Linnet <i>Carduelis cannabina</i>	4 (0.8)	19	76 (0.03)
<i>Alcidae</i> spp.	1 (0.2)	500	500 (0.2)
<i>Columbidae</i> spp.	1 (0.2)	357	357 (0.2)
<i>Corvidae</i> spp.	2 (0.4)	376	752 (0.3)
<i>Laridae</i> spp.	7 (1.4)	600	600 (0.3)
Unidentified Small Passerine	15 (2.9)	45	675 (0.3)
European Rabbit <i>Oryctolagus cuniculus</i>	16 (3.1)	1000	16,000 (6.9)
Total	520 (100)		230,951 (100)