Gull Predation on Leach's *Hydrobates leucorhous* and European Storm-petrels *H. pelagicus* on Elliðaey Island, Iceland

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Abstract
Studies of predator-prey interactions, and quantification of predation frequencies can be crucial to understanding prey population declines. We present a study of gull *Larus* spp. predation on Leach's Storm-petrels *Hydrobates leucorhous* and European Storm-petrels *H. pelagicus*, relative to other prey types. We studied a population of approximately 160 gulls in mixed colonies of Herring Gulls *L. argentatus* and Lesser Black-backed Gulls *L. fuscus*, on Elliðaey Island, Iceland. We dissected 191 pellets and found gulls fed mostly on avian prey, insects and molluscs. We estimate that the total consumption of Leach's Storm-petrels by all gulls in the colonies amounted to approximately two individuals per day, over the course of the study. European Storm-petrels were not preyed upon in high quantity during the study period, with a minimum of one individual depredated within a four-day study period, potentially reflecting the later breeding season of this species. We also provide a correction factor of pellets produced per storm-petrel consumed, which could be used to quantify the number of individual storm-petrels consumed from counts of pellets in future studies.

Introduction
Studies of trophic interactions are crucial to understanding how species respond to changes in prey availability, and changes to predator populations. Consideration of predator-prey dynamics is important where predator or prey species are of conservation concern, where predators are undergoing rapid population increases, where predators are breeding in areas they have recently colonised, and where prey availability is changing (Rodríguez *et al*. 2019; Church *et al*. 2018). For example, population dynamics of generalist avian top-predators can be relatively independent of availability of single prey types and this can lead to potential negative impacts on particular prey species, even if they comprise a small proportion of the total diet (Miles *et al*. 2013). Such predator species, including some large gulls and skuas *Stercorarius* spp., can switch prey or vary their foraging strategies to allow population resilience; in some populations, successful dietary switching and exploitation of abundant resources has led to locally-increased populations (e.g. Furness *et al*. 1992; Mitchell *et al*. 2004; Duhem *et al*. 2008). There is evidence that increased populations of generalist avian top-predators, and the development of individual dietary-specialisations within these populations, is

having negative impacts on other avian populations through predation (e.g. Phillips *et al*. 1999; Matias & Catry 2010). For example, Great Skua *S. skua* predation on seabirds has shown a general increasing trend since the 1970s, implicated to be a consequence of changing environmental and anthropogenic factors (Church *et al*. 2018). Large gulls have undergone similar local expansions in some areas (e.g. Duhem *et al*. 2008; Lisnizer *et al*. 2011), despite ongoing global population declines.

Leach's Storm-petrel (c. 45 g) and European Storm-petrel (c. 25 g) are highly pelagic petrel species (Snow & Perrins 1998). Generally, they come to land only to breed and activity at the colony is restricted to the hours of darkness. They breed in colonies between May and November, in burrows and crevices on islands free of invasive, non-native predators such as rodents. Their burrowing ecology and nocturnal behaviour are adaptations to predator avoidance (Watanuki 1986; Miles *et al*. 2013). However, Leach's and European Storm-petrels are still vulnerable to predation by avian predators such as gulls, skuas and owls (e.g. Williams & Frank 1979; Phillips *et al*. 1999; Stenhouse & Montevecchi 1999; Votier *et al*. 2006; Miles 2010; Pollet & Shutler 2019). The global population of Leach's Storm-petrel is estimated at approximately 7 million breeding pairs, though numbers are declining; the species is therefore listed as 'Vulnerable' by the International Union for Conservation of Nature (IUCN), having been upgraded from 'Least Concern' in 2016 (BirdLife International 2017a). A recent population study estimated that the local population of Elliðaey Island, in the archipelago of Vestmannaeyjar, south Iceland, has undergone a substantial decline since 1991 (Deakin *et al*. pers. comm.). Despite this, there is little understanding of the causes of population declines of Leach's Storm-petrels. European Storm-petrels are classified as 'Least Concern' by the IUCN, with an estimated global population of 430,000–519,999 breeding pairs, however their population trends are unknown (BirdLife International 2017b). The population size of Vestmannaeyjar is also unknown, but is thought to be relatively small (<20,000 pairs), so is therefore potentially vulnerable to population-level impacts of predation.

The interaction between generalist avian top-predators and storm-petrels at breeding colonies is relatively well studied. For example, Phillips *et al*. (1999) estimated that a population of just 229 breeding pairs of Great Skuas consumed 36,000 seabirds in the breeding season of 1996 on St Kilda, including almost 13,000 Leach's Storm-petrels and 6,500 European Storm-petrels. A more recent estimate by Miles (2010) found storm-petrels to be depredated in similarly high numbers by 175–229 breeding pairs of Great Skuas on St Kilda, with approximately 21,000 Leach's Storm-petrels depredated annually, as well as approximately 8,500 European Storm-petrels. Less research has focused on gulls as predators of Leach's Storm-petrels (but see Watanuki 1986). However, multiple studies have focused on Yellow-legged Gulls *L. michahellis* feeding on European Storm-petrels. Oro *et al*. (2005) found that a population of over 400 pairs of Yellow-legged Gulls consumed around 115 European Storm-petrels annually. Sanz-Aguilar *et al*. (2009) showed that the majority of predation upon storm-petrels was being carried out by specialist individuals within the gull population. Additionally, studies have found that Herring Gull predation on Leach's Storm-

petrels on Great Island, Newfoundland was high until Capelin *Mallotus villosus* arrival (Stenhouse & Montevecchi 1999; Stenhouse *et al*. 2000). Only storm-petrel-specialist gulls continued predation beyond that point, implying that alternative prey availability could be an important factor in predation rates upon storm-petrels. The results of Stenhouse *et al*. (2000) suggest that breeding bird-specialist Herring Gulls were capable of consuming more than five Leach's Storm-petrels per pair per day. Therefore, predation rates could be relatively unpredictable and prone to variation between populations dependent on relative proportions and absolute quantities of avian specialist predators.

Herring Gulls and Lesser Black-backed Gulls are large gulls (adults <1.4 kg and <1 kg, respectively). Both species have wide breeding ranges across Europe, breeding in colonies between April and July (Harris 1964; MacRoberts & MacRoberts 1972). Herring Gulls will breed in a range of habitats but show some preference for cliffs and rocky shores (Snow & Perrins 1998). Lesser Black-backed Gulls will also use a wide range of breeding habitats but show preference for short vegetation and level-ground. They exhibit a highly generalist diet at the population level, feeding on a wide range of marine and terrestrial prey, in addition to anthropogenic waste. Both gull species are listed as 'Least Concern' by the IUCN, though Herring Gull populations are decreasing (and Red-listed within Europe, BirdLife International 2015) whilst Lesser Black-backed Gulls are increasing (BirdLife International 2018a; 2018b). Within Iceland, population trends are unknown, but previous estimates have suggested 5,000–10,000 Herring Gull pairs in 1990 and 40,000–50,000 pairs of Lesser Black-backed Gulls in 2004 (Guðmundsson & Skarphéðinsson 2012). Both species are presumed to have colonised Elliðaey Island since 2008, when human presence on the island declined following a hiatus on Atlantic Puffin *Fratercula arctica* hunting, though the local gull population was not previously estimated.

The aim of this study was to assess the consumption of Leach's and European Storm-petrels relative to other prey types by Herring and Lesser Black-backed Gulls resident on Elliðaey Island from pellet analysis. We also provide an estimate of how many pellets are produced by *Larus* spp. for every Leach's and European Storm-petrel consumed, for use in future bioenergetics models to estimate rates of consumption of these species (e.g. Phillips *et al*. 1999; Deakin *et al*. 2018). No previous studies have been carried out into the diet of gulls, or their impact on storm-petrel populations, at the study site. Given the apparent decline of Leach's Storm-petrels on this island, and the importance of the Vestmannaeyjar archipelago to the local storm-petrel population, understanding the role of predation in these areas is crucial to storm-petrel conservation.

Methods

This study was carried out on Elliðaey Island (63°27'55"N 20°10'30"W), south Iceland, in June 2018. The island is approximately 0.45 km^2. Two mixed-species colonies of Herring Gulls and Lesser Black-backed Gulls were present; however, it was not possible to carry out a survey of the number of breeding pairs of each species due to time constraints and the inaccessible nature of sections of the

European Storm-petrel
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potential breeding areas. Snapshot counts of gulls in the vicinity of the colonies were used to provide a crude index of the local population size. This was done by counting the number of sitting birds and recording the species ratio, and applying the ratio to an estimate of the number of flying birds. It was not possible to directly identify the species of flying birds due to distance and weather conditions. It is unknown how many of these were breeding and non-breeding individuals, though at least five active nests at the incubation or early chick-rearing stages were present during the study in Colony 1, and at least one in Colony 2. Colony 1 was on an area of level ground covered with short vegetation, surrounded by sea stacks and rocky areas. Colony 2 was located on rocky cliff and rock platform habitat.

Pellets were collected by a team of one to four people walking transects, approximately two metres wide, through the length of each colony. The characteristics of Colony 2 meant not all areas were accessible, so pellet collection was restricted to accessible areas. All prey remains within the searched areas were removed, but only pellets which were entire (or where loose remains were obviously in association with a pellet) were retained for individual dissection in the field laboratory. Prey items were identified from hard part remains (e.g. diagnostic feathers, fur, feet, skulls and other bones, or gastropod and bivalve shells), and the Frequency of Occurrence (FO, %) was calculated for each prey type within the sample of pellets. For Leach's and European Storm-petrels, the key distinguishing features between remains of the two species were the larger size of Leach's Storm-petrels; linear measurements of Leach's Storm-petrels are around 1.3 times larger than European Storm-petrels. The first pellet collection took place on 25 and 27 June 2018 for Colony 1 and 2, respectively. A second pellet collection was carried out on the 29 June 2018 at both colonies. Pellets were dissected and identified in the same manner as previously, and in addition, the quantity of individual body parts (e.g. wings, legs, furculae, beak, feet) of Leach's and European Storm-petrel remains were recorded, to allow quantification of the minimum number of individual storm-petrels of each species represented in the sample of pellets. We then calculated the average number of pellets produced for each storm-petrel consumed, and the rate of consumption (individuals consumed per day) of each species for each gull colony.

Fisher's exact tests were used to assess whether there was a difference in diet composition between collections, which could be a consequence of either differing decay rates of prey, or dietary changes. This was done separately for each colony, where the first pellet collection, representing the 'standing crop' of pellets, accumulated over an unknown time period, was compared to the second collections which represented pellets deposited during the preceding days.

Results

The snapshot counts produced estimates of approximately 20 Herring Gulls and 130 Lesser Black-backed Gulls in Colony 1, and eight Herring Gulls and five Lesser Black-backed Gulls in Colony 2. A total of 191 pellets were collected: 147 from Colony 1, and 44 from Colony 2. Avian prey, molluscs, and insects were all important prey types across both gull colonies (Table 1).

Table 1. Frequency of Occurrence (FO, %) of prey types found in the pellets of Herring Gulls *Larus argentatus* and Lesser Black-backed Gulls *L. fuscus*. Pellets were collected from within a mixed species colony of approximately 150 gulls (Colony 1) and 13 gulls (Colony 2).

	Colony 1		Colony 2		Total
Prey Type	1st Collection (N = 78)	2nd Collection (N = 69)	1st Collection (N = 23)	2nd Collection (N = 21)	(N = 191)
Leach's Storm-petrel (*Hydrobates leucorous*)	12.8	11.6	34.8	14.3	15.2
European Storm-petrel (*Hydrobates pelagicus*)	2.6	4.3	13.0	0.0	4.2
Eider Duck (*Somateria mollissima*)	25.6	8.7	0.0	19.0	15.7
Gull (*Larus* spp.)	3.8	4.3	8.7	0.0	4.2
Meadow Pipit (*Anthus pratensis*)	3.8	0.0	0.0	0.0	1.6
Snipe (*Gallinago gallinago*)	9.0	0.0	0.0	0.0	3.7
Redshank (*Tringa totanus*)	1.3	0.0	0.0	0.0	0.5
Unidentified Bird spp.	9.0	17.4	30.4	47.6	18.8
Total Birds	67.9	46.4	87.0	81.0	63.9
Eggshell	5.1	7.2	21.7	9.5	8.4
Plant Matter	30.8	50.7	0.0	14.3	32.5
Insect	28.2	21.7	0.0	4.8	19.9
Mollusc	24.4	7.2	52.2	52.4	24.6
Plastic	1.3	2.9	4.3	0.0	2.1
Fish	6.4	7.2	0.0	0.0	5.2
Mammal	2.6	0.0	0.0	0.0	1.0
Crustacean	0.0	0.0	0.0	4.8	0.5
Unidentified	2.6	1.4	0.0	0.0	1.6

There were differences in the frequency of occurrence of prey types between the first and second collection for both gull colonies (Fisher's exact tests P = 0.001 and P = 0.026). For Colony 1, a smaller number of prey types were found in the second sample collection compared to the first, whereas the reverse was true for Colony 2. For both colonies, the differences in pellet composition between collection events occurred mostly within avian prey types, as well as plant matter and molluscs.

Approximately half of all pellets contained only one prey type (53% in Colony 1; 52% in Colony 2), and the maximum number of different prey types found in a pellet was 4 (3% of pellets). 75% of pellets containing Leach's Storm-petrel and 89% containing European Storm-petrel contained no other prey types. Some pellets contained the remains of unidentified bird species, however these were not thought to be remains of storm-petrels, given the multiple distinguishing features of storm-petrels in pellets (odour, size, colour of feathers). Only one ringed bird was found in a pellet: a Leach's Storm-petrel ringed as an adult in 2015. European Storm-petrels formed only a small fraction of the diet at Colony 1, and formed a large proportion of the first collection for Colony 2 but were not found in the second collection. All passerine and wader species found in the diet of birds at Colony 1 were not identified in the pellets analysed from Colony 2, but may be represented as unidentified birds.

Across both colonies, quantification of Leach's Storm-petrel remains in the second collection period showed that at least 6 individuals were represented in 11 pellets, giving an approximation of 1.8 pellets produced per individual consumed. Only one pellet was found to contain evidence of more than one individual, containing two complete beaks. At the population level, gulls at Colony 1 consumed at least 1.1 Leach's Storm-petrels per day, over the four-day study period, and at Colony 2 consumed at least 0.8 Leach's Storm-petrels per day, over the two-day study period. For European Storm-petrels, a minimum of one individual was represented across three pellets, giving an approximation of 0.33 European Storm-petrels per pellet, or three pellets produced per European Storm-petrel consumed. No European Storm-petrels were found in the second collection from Colony 2, so this estimate is based on a very small sample of pellets from Colony 1 only. Therefore, Colony 1 consumed at least one European Storm-petrel over the four-day study period.

Discussion

In this study, we found storm-petrels present in just under 20% of gull pellets, making them one of the most frequent prey types found. The colony of approximately 160 gulls depredated at least two Leach's Storm-petrels per day over our study period. European Storm-petrels were found in the diet of gulls at a much lower frequency, with a minimum of one European Storm-petrel depredated over a four-day study period. This may be a consequence of the slightly later breeding season of European relative to Leach's Storm-petrels. The lower occurrence rate means our estimation of three pellets produced per European Storm-petrel is likely an overestimation, especially when considered alongside our estimate of 1.8 pellets per Leach's Storm-petrel consumed, and given the size differences between the species.

As well as storm-petrels, gulls in our study fed on a range of prey types, mainly other bird species, insects and molluscs. This is consistent with previous research, as large gulls are known to have a generalist diet, that varies with age, local prey availability and individuals (Cramp and Simmons 1998). Our results also align with studies of gulls foraging in similar habitat; Elliðaey Island consists of rocky cliff habitat and intertidal rock shore, as well as grassy vegetated areas. The island is small (<0.5 km^2), and studies have shown Herring Gulls may travel 5–10 km away from the colony to forage (Enners *et al*. 2018), and Lesser Black-backed Gulls may travel more than 90 km (Juvaste *et al*. 2017; Isaksson *et al*. 2016; Thaxter *et al*. 2012). Therefore, it is unlikely that proximity to the breeding areas of both storm-petrel species on the island limits predation rate. Pierotti and Annett (1991) found Herring Gulls on Great Island (Newfoundland), fed more on intertidal molluscs in rocky shore habitat, and those in meadow habitat (such as that surrounding Colonies 1 and 2) fed more on Leach's Storm-petrels. The high occurrence of insects in the diet of Colony 1 is an indication of the gulls feeding in vegetated areas. Plant matter also occurred at high frequency in Colony 1, but is assumed to be accidental ingestion whilst feeding on terrestrial prey, as opposed to deliberate ingestion (Pedro *et al*. 2013). Matias and Catry (2010) report that Yellow-legged Gulls on Selvagem Grande (Portuguese Madeira archipelago), an island similarly of mixed vegetated and sea-cliff habitat, had a similar diet to gulls in our study,

consisting primarily of birds including storm-petrels, and very little fish relative to other dietary studies of gulls. The low occurrence of fish in the gulls' diet could be a result of low fisheries waste production by Icelandic fisheries (Popescu & Poulsen 2012), which is the primary fish source of gulls from other populations (e.g. Votier *et al*. 2004 and references therein). It is also possible that any fish consumed was as discarded offal and did not show in pellets due to lack of hard parts. Similarly, other anthropogenic food sources (e.g. refuse) are relatively absent in our study. Nearby Heimaey Island is the only inhabited island in the Vestmannaeyjar archipelago, so could provide a source of anthropogenic food, though we found little to no evidence that gulls were foraging on such food sources. The only exception to this was a small proportion (2%) of pellets containing plastic, which may be directly from feeding on anthropogenic waste.

Avian pellet analysis can result in bias towards less digestible prey. Votier *et al*. (2003) found that analysis of Great Skua pellets tends to overestimate the amount of avian prey consumed, compared to other dietary analysis methods. Votier *et al*. (2001) also found that pellets present a bias towards avian prey compared to fish. Additionally, bias can be created by the way in which avian prey is consumed (whole vs. plucked apart), as this may affect how many pellets are produced per bird consumed. Therefore, we have calculated predation frequency accounting for the quantity of pellets produced per storm-petrel consumed, thus reducing overestimation of this particular prey type.

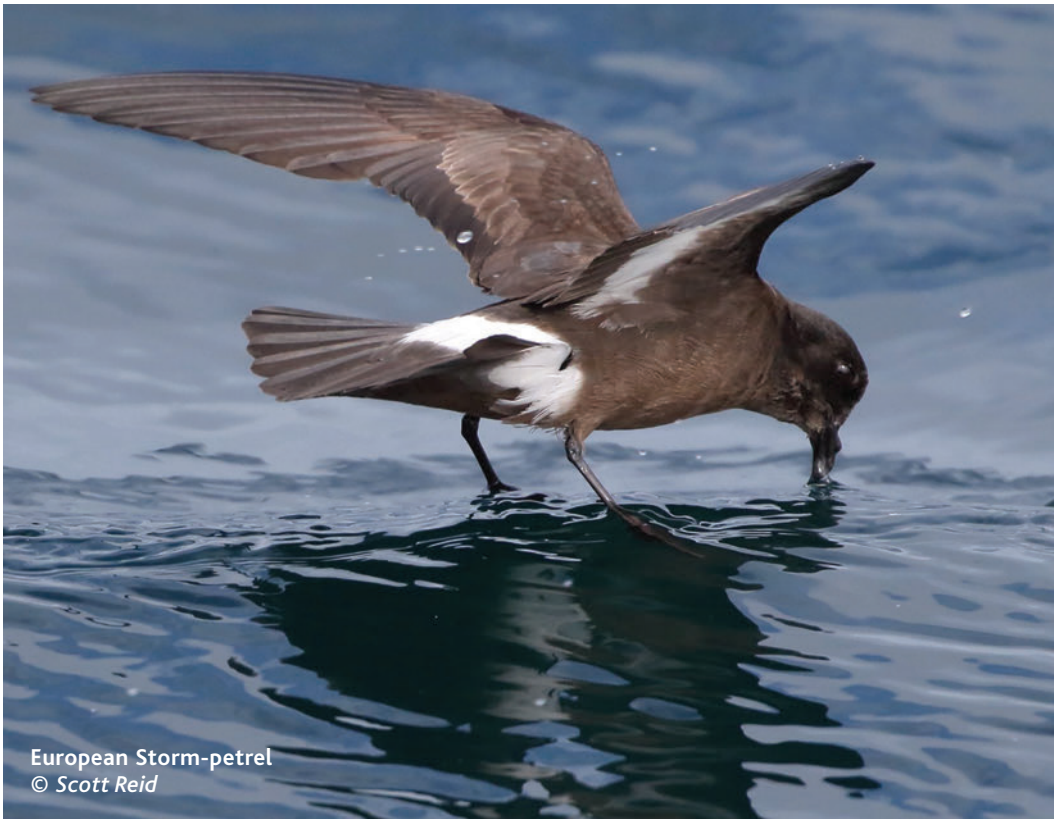
The remains found in pellets have unknown rates of decay, and the diet represented by the 'standing crop' collection (first collection) is likely biased towards prey with longer decay times. A significant difference in occurrence of each prey type between the first and second collections (calculated separately for each colony) could be as a result of differing decay rates, or temporal variation in prey availability. For example, Eider *Somateria mollissima* decreased in occurrence between the two collections at Colony 1. A number of depredated nests were noted around the colony, leaving only a small number of nests available for depredation between collections, all of which were destroyed by the second collection. On the other hand, the high frequency of mollusc remains, most marked in the first collection at Colony 1, could be a result of the relatively long degradation times of hard-shell parts relative to other, faster degrading items.

At the population level, gulls across both colonies consumed Leach's Storm-petrels at a similar, low, daily frequency, despite a large difference in the colony sizes, suggesting that petrel predation may be practised by a small number of specialist gulls at each colony, rather than being widespread across each colony. This is supported by the high number of pellets containing Leach's Storm-petrel remains that contained no other prey types (75%). The impacts on storm-petrel populations could therefore vary depending on the level of specialisation that arises in gull populations, and breeding localities. For example, results from Fife *et al*. (2015) suggest that Leach's Storm-petrel survival was lower for birds breeding in close proximity to Herring Gull territories; however, it is unknown whether this was a

direct result of predation. Sanz-Aguilar *et al*. (2009) found that selective culling of only 16 individual Yellow-legged Gulls, from a population averaging more than 500 breeding pairs that were either known storm-petrel specialists or breeding in close proximity to European Storm-petrels on Benidorm Island, reduced the number of pellets containing petrels by 65%. In the absence of culling, storm-petrel survival and breeding success was reduced by gull predation. The findings of these studies suggest that gull populations do not need to be large to have significant impacts upon breeding storm-petrel populations. Oro *et al*. (2005) found that the rate of gull predation upon European Storm-petrels was not affected by size of gull colony nor alternative food, as mainly specialist gulls were depredating storm-petrels.

Matias and Catry (2010) estimated that 12 breeding pairs of Yellow-legged Gulls consumed more than 4,500 adult seabirds over the breeding season, demonstrating that predator populations do not need to be large to depredate high numbers of seabird prey. Across a three-and-a-half-month storm-petrel breeding season, with a presumed rate of c. two Leach's Storm-petrel individuals/day, the gull population on Elliðaey Island could depredate over 200 individual storm-petrels. In species such as storm-petrels with slow life histories and high adult survival (estimated 79–93%, Schreiber & Burger 2001; Sanz-Aguilar *et al*. 2012), this predation rate would be significant; in such species, the survival of adult individuals is the key demographic parameter affecting population dynamics (Prévot-Julliard *et al*. 1998; Lebreton & Clobert 1991). Therefore, the population-level impacts of predation may depend on the age structure of depredated storm-petrels. Storm-petrels spend around two to four years prospecting for breeding sites (Okill & Bolton 2005). Studies have suggested that population-level impact is reduced as these non-breeding, prospecting storm-petrels are more vulnerable to avian predation, as these individuals will spend longer out of burrows over land, searching for suitable breeding locations (Stenhouse *et al*. 2000; Miles 2010). Breeding storm-petrel pairs, on the other hand, exchange incubation duties every three to four days on average (Watanuki 1986; Hedd *et al*. 2018), limiting their activity over land and therefore predation opportunities. Nonetheless, our study occurred in mid to late June, before the majority of prospecting immature birds are likely to have arrived (Stenhouse & Montevecchi 1999; Stenhouse *et al*. 2000), showing that, at least for this period, predation upon breeders could be occurring, supported by our finding of one Leach's Storm-petrel ringed as an adult three years previously, which is therefore a presumed breeder. Further, Oro *et al*. (2005) found that 11–14% of European Storm-petrels killed by Yellow-legged Gulls were known breeders, though in reality this value could be higher as it only accounts for known, ringed birds.

This study only covered a very small period within the breeding season, and therefore it must be considered that the results found may not represent predation behaviour throughout the entirety of the storm-petrel or gull breeding season. Watanuki (1986) found that Slaty-backed Gulls *L. schistisagus* consumed the most storm-petrels in May to July, when energy requirements are highest, therefore the gulls of Elliðaey Island may be following a similar pattern, and predation could fall



European Storm-petrel
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after this point; additionally, gulls may move away from the colony after breeding. Conversely, as more prospecting Leach's Storm-petrels arrive and their activity increases, we could expect predation of petrels to increase. We could also expect a prey switch towards the behaviourally similar European Storm-petrel as their incubating and chick-rearing season begins.

The impacts of high predation pressure could also be ameliorated by immigration from other storm-petrel populations (Bicknell *et al.* 2014; Fife *et al.* 2015). Indeed it has been shown that there is gene flow between Icelandic and Scottish colonies of Leach's Storm-petrels (Bicknell *et al.* 2012). However, storm-petrels breeding on other Icelandic islands also remain unstudied, and both Icelandic and Scottish storm-petrels are subject to predation at varying levels, therefore the ability of storm-petrel populations to be maintained in these areas requires further investigation.

Over a short study period, we have shown that a small population of gulls can consume storm-petrels at a relatively modest frequency (c. two individuals per day). If this rate was maintained over the duration of the gull and storm-petrel breeding season, or indeed, were higher later in the season when greater numbers of immature storm-petrels attend the colony, then the total number consumed could be significant. Herring and Lesser Black-backed Gulls are thought to have only bred on

Elliðaey Island since 2008, when Puffin hunting ceased on the islands and therefore persecution of gulls on the island also diminished. Therefore, we could expect the gull population to continue to rise in the future. Given the importance of Elliðaey Island and surrounding islets for storm-petrels breeding in the North-East Atlantic, long-term monitoring is necessary to determine if there are population-level effects of gull predation. For example, ringing storm-petrels of known breeding status would provide more insight into preferences of gulls for breeding or non-breeding storm-petrels. It is also necessary to consider the storm-petrel populations of nearby islands, to assess whether these are large enough to supplement the populations of Elliðaey Island and elsewhere. This study population provides opportunity for long-term monitoring of predation impacts, and our estimate of pellets produced per Leach's Storm-petrel consumed has potential to improve the accuracy of similar studies in the future.

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