Assessment of Great Skua *Stercorarius skua* pellet composition to inform estimates of storm petrel consumption from bioenergetics models

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Abstract

Generalist predators may exert levels of predation on particular prey that result in, or contribute to, decline of that prey species. Bioenergetics models have been used to estimate the rates of consumption of Leach's Storm Petrels *Oceanodroma leucorhoa* (45 g) and European Storm Petrels *Hydrobates pelagicus* (25 g) by Great Skuas *Stercorarius skua* on St Kilda (Western Isles, UK) and Hermaness (Shetland, UK). The models require estimates of the number of indigestible pellets produced from each individual storm petrel consumed, which have previously been determined by captive feeding trials or examination of pellets cast by free-living birds, but which have not discriminated between the two storm petrel species. Here we use information from dissection of 427 Great Skua pellets collected on Hirta (St Kilda, UK) and Mousa (Shetland, UK) to provide empirical estimates of the pellet:prey ratios for Leach's and European Storm Petrels separately. We found that pellet:prey ratios were similar for collections of the 'standing crop' of pellets accumulated over the entire breeding season and samples of pellets cast within the preceding five days. However, pellet:prey ratios of both Leach's and European Storm Petrel were considerably lower than reported previously. Furthermore, we found the pellet:prey ratio for European Storm Petrels consumed on St Kilda was 80% higher than the value for the same species on Mousa. Our study suggests that the use of a single generic value for the pellet:prey ratio for both species and all locations may lead to inaccuracies in estimation of consumption rates, and we recommend further work to understand the causes of such variation.

Introduction

Bioenergetics models have been widely used for many years in seabird ecology to estimate rates of prey consumption at scales ranging from individual colonies to ocean basins (e.g. Guinet *et al*. 1996; Barrett *et al*. 2006). Such models can shed light on a range of processes from large-scale patterns of energy flux across ecosystems (Hunt *et al.* 2005) to the extent of competitive interactions between particular toppredator species and fishery activity (Bunce 2001). Here we focus on the application of bioenergetics models to assess rates of predation by seabirds on other seabird species. Quantifying rates of predation on specific prey types is important for understanding population dynamics, particularly where changes in predator or prey numbers are apparent or where conservation management may be required.

Numbers of Great Skuas *Stercorarius skua* have rapidly increased in Scotland during the last century, likely due to reduced persecution, increased availability of food from fishery discards and prey-switching, including direct predation of other seabirds (Mitchell *et al*. 2004; Votier *et al*. 2004a). Great Skuas are generalist predators and their diet includes fish, birds and invertebrates (Bayes *et al*. 1964; Furness 1987). Many of the seabird species that Great Skuas prey upon are declining in the UK (JNCC 2016) and the implementation of the Common Fisheries Policy discard ban is predicted to result in an increase in predation on seabirds as the availability of discarded fish decreases (Reeves & Furness 2002; Votier *et al*. 2004a; Bicknell *et al*. 2013).

Storm petrels (Hydrobatidae) are vulnerable to predation due to their small size and relative immobility on land. The breeding ecology of storm petrels is strongly influenced by predation risk: nest sites are located in crevices and burrows on islands free from introduced mammalian predators and adult birds are active at the colony only at night. Despite these adaptations, storm petrels remain vulnerable to avian predators such as gulls (Laridae) and skuas (Stercorariidae) (Watanuki 1986; Stenhouse & Montevecchi 1999; Stenhouse *et al*. 2000; Oro *et al*. 2005; Votier *et al*. 2006).

Traditionally, a range of methods have been used to study seabird diet, including identification of prey from feeding observations, pellets, prey remains, spontaneous regurgitates and stomach flushing (Votier *et al*. 2003). These techniques give broadly similar results, but there are biases associated with each (Votier *et al*. 2003). More recent advances include the extraction and identification of prey DNA from predator faeces or regurgitates (Bowser 2013) which may reduce bias, but are costly and time-consuming to implement at a large scale. In contrast, pellets of regurgitated, indigestible prey remains are easy to collect and can provide large sample sizes to determine the proportions of different prey types consumed (Votier *et al*. 2003). However, pellet analysis tends to overestimate indigestible material and any pellets produced away from the colony are not available for analysis, leading to uncertainty regarding the absolute quantities of prey consumed (Votier *et al*. 2003).

Pellet analysis can be combined with bioenergetics modelling to quantify consumption rates of different prey types without the need to estimate rates of pellet production. Such models have been used to calculate levels of storm petrel predation by Great Skuas at two large colonies in the UK (Phillips *et al*. 1999; Votier *et al*. 2004b; Miles 2010). The models firstly estimate the total energy requirement of the entire breeding and non-breeding population over the breeding season, then use the proportion, energy content and assimilation efficiency of each prey type to estimate its relative contribution to the total energy budget. The proportion of each prey type may be assessed by pellet analysis. Typically, each pellet comprises a single prey type, and the model requires for each prey type: (i) an estimate of the size (in prey mass or number of individuals) of an average 'meal' (i.e. the quantity of food present in a bird's proventriculus on its return from a foraging trip, Phillips *et al*. 1999), and (ii) the number of pellets that are produced from a single meal. From these two quantities the number of pellets produced from each prey individual consumed (i.e. the pellet:prey ratio) is calculated, which is used as a so-called "correction factor" (Phillips *et al*. 1999) in the model. Although European *Hydrobates pelagicus* and Leach's *Oceanodroma leucorhoa* Storm Petrels differ considerably in size (25 g and 45 g respectively), Phillips *et al*. (1999) considered that a single storm petrel of either species constituted a single meal, and "*on the evidence of groups of pellets found together on breeding territories clearly consisting of combinations of wings, whole legs or body feathers, it was estimated that at least three pellets result from a meal of a single individual*" of either species. Phillips *et al*. (1999) therefore used a correction factor of 3.0 pellets produced per storm petrel consumed, and concluded that in 1996 Great Skuas on St Kilda consumed 7,450 European Storm Petrels and 14,850 Leach's Storm Petrels. Votier *et al*. (2004b) used a similar bioenergetics model to estimate the number of European Storm Petrels consumed annually by Great Skuas at Hermaness, Shetland, using a pellet:prey ratio of 2.5 pellets per European Storm Petrel consumed, as estimated by Votier *et al*. (2001). The ratio was obtained by feeding 11 storm petrel carcasses, as six separate meals, to captive, full-grown Great Skua fledglings (Votier *et al*. 2001, Tables 2 & 3, though note the methods section of that study incorrectly states that eight storm petrels were fed to the captive skuas). Since carcasses of European Storm Petrels were not available, a variety of larger-bodied storm petrel species from the austral Oceanitidae family were used (S. Votier pers. comm.). A total of 28 pellets were cast from the 11 storm petrels consumed, giving a pellet:prey ratio of 2.5 (Votier *et al*. 2001, Table 3). Pellets produced by Great Skuas held in captivity or produced from the consumption of large austral storm petrel species may not be entirely representative of pellets of European and Leach's Storm Petrels produced by free-living Great Skuas. Votier *et al*. (2004b) concluded that Great Skuas at Hermaness consumed 215 European Storm Petrels in 2001.

Here we use dissection of Great Skua pellets collected at two colonies and containing remains of both European and Leach's Storm Petrels to quantify the pellet:prey ratios for each prey species. For each sample of pellets, we calculated the minimum number of storm petrels consumed from the number of the most frequently occurring body part. For example, since each storm petrel has only one furcula, a sample of pellets that contains five storm petrel furculae represents the remains of a minimum of five storm petrels. We calculated pellet:prey ratios by dividing the number of pellets in a sample by the minimum number of storm petrels represented in that sample. For example, a sample of ten pellets that contained a total of five storm petrel furculae would give a pellet:prey ratio of 2:1, and a correction factor of two in a bioenergetics model. Specifically, we compare the pellet:prey ratios (i) for Leach's and European Storm Petrels; (ii) for European Storm Petrels at two different colonies and (iii) for samples collected as the 'standing crop' of pellets accumulated over an extensive (and unknown) period of time with those collected from an area cleared of pellets five days previously.

Methods

Sampling for comparison of pellet:prey ratios for Leach's and European Storm Petrels: Archived Great Skua pellets from Hirta, St Kilda, UK (57°49'N, 08°35'W) were analysed to compare pellet:prey ratios for European and Leach's Storm Petrels. The St Kilda archipelago supports 94% of the British and Irish population of Leach's Storm Petrels, with 45,433 apparently occupied sites (AOS) in the Seabird 2000 census, as well as an estimated 1,121 European Storm Petrel AOS (Mitchell *et al.* 2004). Pellets were collected from a Great Skua club site in August 2015, 2016 and 2017. Club sites are areas where non-breeders congregate and are rarely, if ever, attended by breeding skuas (Klomp & Furness 1992). All pellets at the site were collected during a single visit each year, so represent the standing crop of pellets deposited by predominantly non-breeding Great Skuas over an unknown period of time. Each year's standing crop is unlikely to include intact pellets from the previous breeding season, however, because winter storms cause pellets to disintegrate. In addition, pellets collected in 2016 and 2017 could not be more than one year old as all pellets had been removed from the site in the previous August.

Sampling for comparison of pellet:prey ratios for European Storm Petrels at two colonies: To compare pellet:prey ratios for European Storm Petrels between colonies, Great Skua pellets were also collected on Mousa, Shetland, UK (60°00'N, 01°11'W) in August 2018. Mousa supports an estimated 10,778 breeding pairs of European Storm Petrels (Bolton *et al.* 2017), the largest colony in the UK, but is not known to support breeding Leach's Storm Petrels. To maximise the sample size of pellets containing storm petrel remains, we focussed search effort in areas where storm petrel predation had been noted previously (M. Bolton, pers. obs.). Table 1 summarises the areas searched and the number of pellets found in each area. All pellets were collected and dissected to identify their contents.

Sampling for comparison of pellet:prey ratios for standing crop and freshly deposited pellets: Pellets containing only feathers may disintegrate faster than pellets containing hard parts. Such differential pellet degradation would reduce the estimate of the number of pellets produced per storm petrel consumed. To assess this potential bias, area A was sampled twice, five days apart, to test for differences in the composition of the standing crop and freshly cast pellets. Although some pellets may have been overlooked on the first visit, pellets collected on the second visit to area A largely represent those deposited in the previous five days.

Pellet analysis: Storm petrel remains were easily identifiable from feathers and bone morphology (Votier *et al.* 2006). Prey remains were compared with reference material and pellets were classified as containing storm petrel remains if we found

Table 1. Summary of the remains of European Storm Petrels *Hydrobates pelagicus* found in Great Skua *Stercorarius skua* pellets collected at five sites on Mousa, Shetland, UK in August 2018. Estimates of the number of pellets produced per European Storm Petrel consumed are calculated by dividing the number of pellets containing the species by the minimum number of individuals in those pellets (i.e. the highest count of either furculae, left humeri or right humeri). For samples from all sites, the most frequently occurring body part was the right humeri, so this was used to represent the minimum number of individuals. Area A was sampled twice to test for differences between the 'standing crop' and freshly cast pellets.

Area	Date searched	No. of pellets collected	No. of pellets containing storm petrel remains	Furculae	Left humeri	Right humeri	Pellets per storm petrel
A	1 Aug	55	53	65	62	65	0.82
A	6 Aug	32	32	40	34	41	0.78
B	6 Aug	18	13	14	14	17	0.76
C	14 Aug	20	19	31	32	32	0.59
D	9 Aug	42	28	26	26	29	0.97
E	14 Aug	4	0	0	0	0	-
Total		**171**	**145**	**176**	**168**	**184**	**0.79**

Table 2. Summary of the remains of European Storm Petrels *Hydrobates pelagicus* (ESP) and Leach's Storm Petrels *Oceanodroma leucorhoa* (LSP) found in Great Skua *Stercorarius skua* pellets collected at a club site on Hirta, St Kilda, UK in 2015, 2016 and 2017. For each species, estimates of the number of pellets produced per storm petrel consumed are calculated by dividing the number of pellets containing the species by the minimum number of individuals in those pellets (i.e. the highest count of either furculae, left humeri or right humeri).

Year	No. of pellets collected	No. of pellets containing storm petrel remains
2015	71	6[a]
2016	84	9[b]
2017	101	11
Total	**256**	**26**

European Storm Petrel (ESP)

Year	No. of pellets	Furculae	Left humeri	Right humeri	Pellets per ESP
2015	5	3	3	2	1.67
2016	6	5	5	4	1.20
2017	6	3	4	4	1.50
Total	**17**	**11**	**12**	**10**	**1.42**

Leach's Storm Petrel (LSP)

Year	No. of pellets	Furculae	Left humeri	Right humeri	Pellets per LSP
2015	0	0	0	0	-
2016	4	2	2	1	2.00
2017	5	3	2	2	1.67
Total	**9**	**5**	**4**	**3**	**1.80**

[a] 1 pellet from 2015 contained storm petrel feathers that were not identified to species level.
[b] 1 pellet from 2016 contained remains of both ESP and LSP.

any of the following diagnostic features: skull, keel, humerus, pelvis, furcula, bill, legs, feet, remiges or retrices, or any fully diagnostic contour feather (such as a tail covert). Remains of European and Leach's Storm Petrels were distinguished from each other based on size, with the above diagnostic features of Leach's Storm Petrels being obviously larger than those of European Storm Petrels. Pellets from St Kilda that comprised dark contour feathers but none of the above diagnostic features often contained bones of other avian prey, such as auks (Alcidae), and so were considered not to contain storm petrel remains.

For the initial sample of 55 pellets from area A on Mousa, we retained and counted multiple easily-identifiable body parts (furcula, humeri, keel, skull, synsacrum, feet and wings) to determine which were found at the highest frequency and were therefore most representative of the total number of storm petrels consumed. The most frequently occurring body parts in this initial sample were then counted in the full sample of pellets from both Mousa and St Kilda.

Data analysis: Below we compare the pellet:prey values obtained from our dissection of pellets collected on St Kilda with those from Mousa and also with values used in earlier studies of skua consumption of storm petrels. Since pellet:prey ratios are incorporated into bioenergetics models as a correction factor, to account for non-parity between the number of individuals consumed and pellets produced, their effect on model estimates of prey consumption depends on their absolute magnitude. We therefore focus our analysis on the *magnitude* of the differences in estimates of the ratio, rather than on any statistical significance of differences.

Results

A total of 256 pellets were collected on St Kilda: 71 in 2015, 84 in 2016 and 101 in 2017. Within the entire sample, we identified storm petrel remains in 26 pellets (Table 2). Seventeen of these pellets contained European Storm Petrel remains and nine contained Leach's Storm Petrel remains. A single pellet (from 2016) contained storm petrel remains that could not be identified to species level. Nine pellets containing storm petrel remains (five of European, three of Leach's and one of unknown storm petrel species) each contained one additional food item: fish (n = 2), auk (Alcidae sp.; n = 1), unidentified bird species (n = 2), mammal (n = 1), goose barnacle *Lepus* sp. (n = 2) and unidentified mollusc (n = 1). A further three pellets containing storm petrel remains (one of European and two of Leach's Storm Petrel remains) contained two additional food items: fish + goose barnacle (n = 1), auk + mollusc (n = 1), mammal + vegetation (n = 1).

On Mousa, we collected a total of 171 pellets, of which 145 contained European Storm Petrel remains (Table 1). Of these, six pellets contained one additional item: fish (n = 3), Common Starling *Sturnus vulgaris* (n = 1), seaweed (n = 1) and grass (n = 1). One additional pellet contained both fish and auk remains, alongside European Storm Petrel remains. No remains of Leach's Storm Petrel were found.

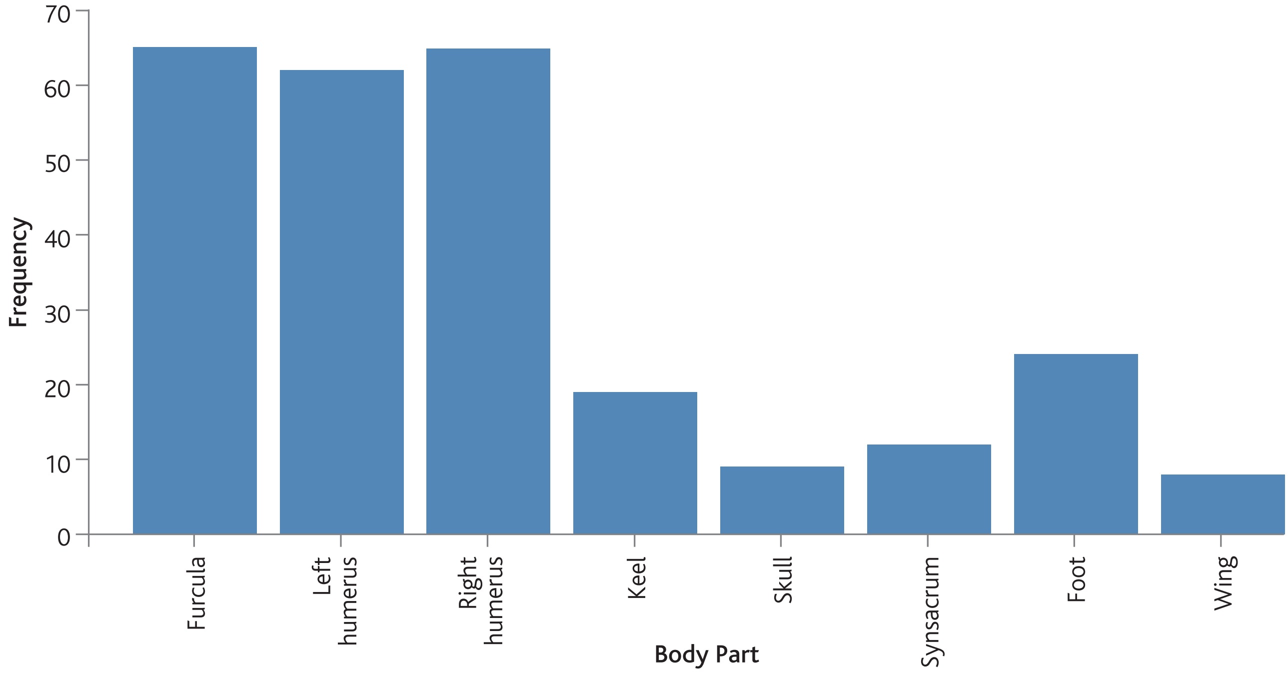

Figure 1. Frequency of occurrence of European Storm Petrel *Hydrobates pelagicus* body parts in 55 Great Skua *Stercorarius skua* pellets found on Mousa, Shetland.

In the initial sample of 55 pellets from area A on Mousa, furculae (n = 65), left humeri (n = 62) and right humeri (n = 65) were the most frequently found body parts (Figure 1). Since these three bones were found at similar frequencies in the first sample of pellets examined, we counted all three in the full sample of pellets from both colonies.

Comparison of pellet:prey ratios for Leach's and European Storm petrels on St Kilda: In the full sample of pellets from St Kilda we found 11 furculae, 12 left humeri and 10 right humeri from European Storm Petrels and five furculae, four left humeri and three right humeri from Leach's Storm Petrels (Table 2). The majority of pellets from St Kilda containing storm petrel remains included parts from just one storm petrel of either species (i.e. no more than one furcula, left humerus or right humerus). Two pellets (one from 2016 and one from 2017) contained body parts of a minimum of two European Storm Petrels. A single pellet from 2016 contained body parts from a minimum of two European Storm Petrels and one Leach's Storm Petrel. The mean number of pellets produced per European Storm Petrel ingested was 1.42. For Leach's Storm Petrel this value was 27% higher, at 1.80.

Comparison of pellet:prey ratios for European Storm petrels at two colonies: In the combined sample of 171 pellets from Mousa, we found 173 furculae, 168 left humeri and 184 right humeri, giving a minimum estimate of 184 European Storm Petrels (Table 1). The number of each of these body parts found in a single pellet ranged from zero to five. The right humerus was the most commonly found body part in the samples from each area. Within the sample of pellets that contained storm petrel remains (n = 145), the mean number of right humeri per pellet was 1.27. This value equates to 0.79 pellets produced per storm petrel consumed, compared with 1.42 pellets per European Storm Petrel from the St Kilda sample. The pellet:prey ratio for European Storm Petrels on St Kilda was therefore 80% higher than that for Mousa.

Comparison of pellet:prey ratios for standing crop and freshly deposited pellets: In the initial sample (standing crop) from area A on Mousa we found 65 right humeri in 53 pellets containing storm petrel remains, giving an estimate of 0.82 pellets per storm petrel (Table 1). In the second sample (freshly cast pellets), 41 right humeri were found in 32 pellets containing storm petrel remains, giving an estimate of 0.78 pellets per storm petrel. The standing crop estimate was therefore just 5% higher than that for the freshly cast pellets.

Discussion

Bioenergetics models offer a means of quantifying prey consumption and require estimates of multiple parameters, such as prey energy content and ratios of pellets:prey. Here, we aimed to improve the accuracy of one of the input parameters for future Great Skua bioenergetics models by determining pellet:prey ratios for European and Leach's Storm Petrels consumed by wild-living skuas.

Our analysis of Great Skua pellets collected in Shetland and St Kilda shows that field estimates of pellet:prey ratios may be somewhat variable. Our estimates of the ratios for European Storm Petrels from different sampling areas on Mousa ranged from 0.59 to 0.97, and the estimate for European Storm Petrels consumed on St Kilda (1.42) was 80% greater than the estimate from the combined samples from Mousa (0.79). The reason for this difference is unclear but could be related to the rate of storm petrel consumption by individual skuas, and the extent to which storm petrels were inter-mixed with other prey types. If a skua feeds exclusively on multiple storm petrels in a night, it is likely to produce pellets containing remains of multiple individuals. However, if storm petrels are taken only occasionally, there is little opportunity for multiple birds to be contained within a single pellet. Additional food items were found alongside storm petrel remains in a greater proportion of pellets from St Kilda (0.46) than from Mousa (0.05), which may reflect differences in the temporal pattern of storm petrel ingestion, alongside other prey, at the two colonies. In addition, pellets from St Kilda were collected from primarily non-breeding skuas over three years, while pellets from Mousa were from breeding territories and were collected in only one year. Skua breeding status and inter-annual differences may have contributed to the differences in pellet: prey ratios that we found.

On St Kilda, the estimate of the pellet:prey ratio for Leach's Storm Petrels (1.80) was 27% greater than that for European Storm Petrels (1.42). Previously, a common correction factor was used for both species (Phillips *et al*. 1999), despite Leach's Storm Petrels being approximately 80% larger than European Storm Petrels. Our results suggest that a single correction factor is unlikely to be appropriate for all studies of Great Skua predation on European and Leach's Storm Petrels.

Figure 2. A Great Skua *Stercorarius skua* on St Kilda, Western Isles, UK. © *Mark Bolton*

Previous estimates of generic storm petrel pellet:prey ratios (Phillips *et al.* 1999; Votier *et al.* 2001) are 76–280% higher than our field-based estimates for European Storm Petrels and 39–67% higher than our estimates for Leach's Storm Petrels. Phillips *et al.* (1999) based their pellet:prey ratio on the presence of wings, legs and body feathers found in groups of pellets, and this may explain their higher estimate. In the sample of pellets from Mousa where all body parts were counted, we found 24 feet/legs and eight wings in 53 pellets containing storm petrel remains (Figure 1). Based on these body parts, we would have estimated a minimum of 12 storm petrels in 53 pellets, giving a pellet:prey ratio of 4.42. This is considerably higher than the ratio of 0.82 estimated using the number of furculae or right humeri (n = 65 for both body parts) found in this sample. We are unable to quantify the effects of our lower pellet:prey ratios on Great Skua bioenergetics models since previous sensitivity analyses do not state the effects of changes to this correction factor (Phillips *et al.* 1999; Miles 2010). Given the size of the differences between our estimates and those used previously, it is likely that our values would have a large impact on the estimated numbers of storm petrels consumed.

There was only a 5% difference between the pellet:prey ratios for the samples from the initial and repeat visits to area A on Mousa, suggesting that sampling pellets from the standing crop does not bias estimates of the number of pellets produced per storm petrel consumed. However, standing crop samples could not be used to determine the proportion of diet that consists of storm petrels since pellets containing different prey types disintegrate at different rates (Furness & Hislop 1981). Fish would generally be under-represented in the standing crop since pellets of fish bones may begin to disintegrate within two days, while pellets containing feathers can remain intact for ten days or more (Furness & Hislop 1981).

From this study it is not possible to assess the level of predation of storm petrels by Great Skuas on Mousa, since pellets were not collected systematically and known predation hotspots were targeted. In addition, pellets were collected during what may be the peak period for storm petrel predation, since Great Skuas were feeding large chicks and large numbers of non-breeding storm petrels were prospecting for nest sites, making them vulnerable to predation as they spend more time above ground. However, ring recovery data suggests breeding storm petrels were also consumed. Twenty-six European Storm Petrel rings were recovered from the Great Skua pellets collected on Mousa during this study, of which 11 rings were from birds greater than three years old, including nine from birds greater than four years old. Since European Storm Petrels begin breeding at age three or four (Okill & Bolton 2005), these birds are likely to have been breeders. Given the large number of individual storm petrels found in pellets after modest search-effort, there is a need for quantification of predation levels at this colony. The European Storm Petrel population on Mousa more than doubled between surveys conducted in 1996 and 2008 (Bolton *et al.* 2010) but growth had ceased by the most recent survey in 2015 (Bolton *et al.* 2017). Great Skua numbers on Mousa increased from 20–24 pairs between 2001 and 2005 to 30–40 pairs between 2008 and 2015; an average annual increase of around 4% (RSPB, unpubl. data). There is scope for further work to identify the extent of storm petrel predation by Great Skuas on Mousa so that any population-level impacts can be determined.

While we have identified considerable differences in pellet:prey ratios for storm petrels consumed by Great Skuas, the causes of those differences are unclear. The sample sizes of pellets containing storm petrels remains from St Kilda are small and the breeding status and stage of the skuas that produced the pellet samples are unknown. We encourage further extensive sampling of Great Skua pellets across sites, years and breeding stages, and also consideration of co-occurrence of other prey types, in order to establish the causes of variation in pellet:prey ratios. Improved understanding of variation in pellet:prey ratios will enable more accurate estimation of this input parameter for bioenergetics models, and therefore more reliable estimates of prey consumption in future studies.

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