ORIGINAL PAPER

Prey remains of brown skua is evidence of the long-term decline in burrow occupancy of blue petrels and thin-billed prions at Mayes Island, Kerguelen

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Abstract

Skuas are top predator and scavenger seabirds in marine and terrestrial ecosystems and monitoring their diet can provide valuable insights on the abundance and distribution of prey. The diet of the brown skua was studied at Mayes Island, Kerguelen archipelago, by collection of prey remains during their breeding cycle in 2013. We investigated a potential diet shift by comparing our results to those obtained two decades ago at the same colony. Our results confirmed the high specialisation of this skua colony in active predation of two burrowing petrels: the blue petrel and the thin-billed prion. We observed a shift in the diet of the brown skua with the importance of the thin-billed prion dropping significantly by 15%. Concomitantly, we observed a decreasing trend of burrow occupancy of the two main preys, with a more severe decline for the thin-billed prion. We suspected a dietary shift of brown skuas at Mayes Island related to a change in the relative abundance of blue petrels and thin-billed prions. Diet of brown skuas appears to be a valuable indicator of the relative abundance of burrowing petrels when they constitute the main food resource during breeding.

Keywords Procellariidae · Predation · Diet · *Catharacta lonnbergi* · *Halobaena caerulea* · *Pachyptila belcheri*

Introduction

Skuas are top predator and scavenger seabirds in marine and terrestrial ecosystems and monitoring their diet can provide valuable insights on the abundance and distribution of prey (Montevecchi and Myers 1995; Furness and

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Camphuysen 1997; Croxall et al. 1999; Furness and Tasker 2000; Dell'Arte et al. 2007). Skuas are dietary generalists and can display a wide range of foraging techniques according to the prey type (Carneiro et al. 2015), but they usually are highly specialised according to the local availability of prey, focusing on one or few main prey items (Mougeot et al. 1998; Reinhardt et al. 2000). Skuas actively deprecate small mammals (Andersson 1976; Votier et al. 2003) and other seabirds (Adams 1982; Fraser 1984; Zipan and Norman 1993; Mougeot et al. 1998), steal penguins' eggs and chicks (Jouventin and Guillotin 1979; Micol and Jouventin 2001), fish at the sea surface (Stahl and Mougin 1986; Young 1994), scavenge on dead animals, feed on seal placentae or are kleptoparasitic of other seabirds (Furness 1987; Spear et al. 1999; Reinhardt et al. 2000; Anderson et al. 2009). When there is a decrease in the availability of a prey, predators with a generalist diet may switch to alternative prey source (Garrott et al. 2007; Votier et al. 2004). However, very few studies have quantified the links between diet changes in skuas and changes in the abundance or distribution of their prey. The great skua *Catharacta skua* in Foula Island, Shetland, experienced a dietary shift from lesser sand eels *Ammodytes marinus* to bird prey (Hamer

et al. 1991; Ratcliffe et al. 1998), and these changes were correlated with the decline in lesser sandeel abundance since 1970 (Hamer et al. 1991; Ratcliffe et al. 1998; Wanless et al. 2004). On Marion Island (Prince Edward Islands, Southern Indian Ocean) where an invasive mammal (cat *Felis catus*) was eradicated, brown skua (*Catharacta lonnbergi* generic assignment following Carlos 2016) prey remains before and two decades after the eradication were used to assess a potential recovery in burrowing petrel populations (Cerfonteyn and Ryan 2016). The proportion of burrowing petrels in the diet of brown skuas changed slightly over the two decades and the authors suggested that there has been little recovery in the population of burrowing petrels since the eradication. This suggestion was confirmed by the comparison of burrow density estimation using quadrats before and after cat eradication (Dilley et al. 2017).

Here, we investigate whether the diet of the brown skua at the Kerguelen archipelago has shifted after two decades, and if changes could be related to a change in prey abundance. We assessed the diet of brown skuas by collecting prey remains in territories in 2013 and compared the results to those obtained in Mougeot et al. (1998) in 1992 at the same colony. We investigate the variation in prey abundance thanks to a long-term monitoring of burrow occupancy of its prey, two burrowing petrels: blue petrels *Halobaena caerulea* and thin-billed prions *Pachyptila belcheri*.

Material and methods

Study site and seabird species

The study was conducted in the valley "Val des Garrodias", Mayes Island (49°28′S, 69°57′E), Kerguelen archipelago (Fig. 1). Mayes is a volcanic island of nearly 3 km² culminating at 60 m. Its topography is shared by rocky plateaus and old glacial valleys covered on their slopes and bottom by a dense but short height vegetation growing in a peat soil (> 50% of the surface, Robin et al. 2011).

The brown skua breeds in isolated nests or colonies on subantarctic islands and the Antarctic continent (Furness 1987). Between 100 and 120 pairs breed annually on Mayes Island (2 000 to 4 000 on the Kerguelen archipelago), and 100 non-breeding individuals generally aggregate in two groups ("clubs") on the island (Weimerskirch et al. 1989; Mougeot et al. 1998). The number of brown skua breeding pairs remained constant during the last decades (Online Resource 1 Figure S1, Barbraud and Delord unpublished data). Pairs arrive on their breeding ground in September (Delord et al. 2018), and usually 2 eggs are laid at intervals of 2–4 days between October and December. Hatching of the eggs occurs in November–December and chicks fledge 50 days after (see Fig. 2 for breeding phenology of the brown skua, Hahn and Peter 2003). Diet studies of brown skuas during the breeding period (Mougeot et al. 1998; Reinhardt

Fig. 1 Map of the study site in Mayes Island (49°28′S, 69°57′E, Kerguelen archipelago) with the location of the area of burrow monitoring, the location of brown skua nests sampled in 1992 (Mougeot et al. 1998) and in 2013
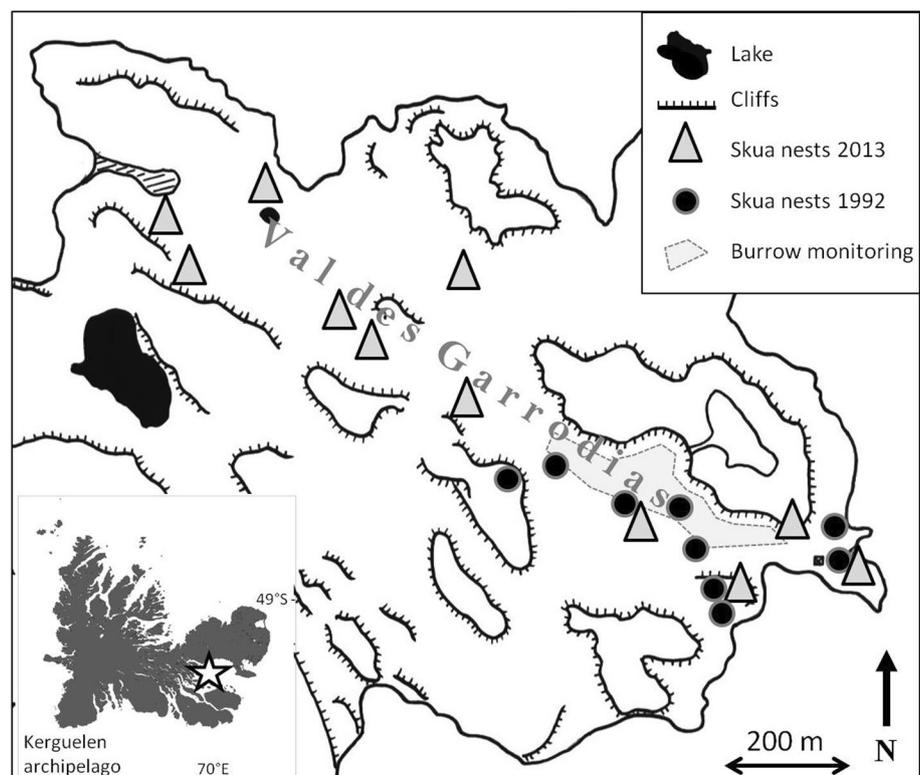
	Sept.	Oct.	Nov.	Dec.	Jan.	Feb	March
Brown skua							
Blue petrel							
Thin-billed prion							

Fig. 2 Breeding phenology of brown skuas and of its two main preys, blue petrels and thin-billed prions, at Mayes Island, Kerguelen archipelago (adapted from Mougeot et al. 1998). Grey colours, from very light to very dark, correspond, respectively, to the prelaying period, the incubation period and the chick rearing period

et al. 2000) have reported petrel species constitutes more than 90% of the diet in the majority of subantarctic populations studied, with often one main prey item representing more than half, and up to 96% on Prince Edward Island (Ryan et al. 2009), of the diet. Brown skuas predate burrowing petrels in flight at night (Sinclair 1980) and mostly when they are on the ground (Young 1978; Fraser 1984; Furness 1987; Mougeot et al. 1998). Petrels are particularly vulnerable and detectable during the courtship behaviour when vocalising at the entrance of burrows (Mougeot and Bretagnolle 2000a, b). On Mayes Island, brown skuas are highly specialised and feed predominantly, i.e. 92%, on two burrowing petrels: blue petrels and thin-billed prions (Mougeot et al. 1998). The two petrel species are nesting in sympatry in Kerguelen (Weimerskirch et al. 1989; see Fig. 2 for breeding phenology of the two petrels species adapted from Marchant and Higgins 1990; Mougeot et al. 1998, CEBC-CNRS unpublished data). Nevertheless, they differ in some habitat requirements: blue petrel burrows are exclusively in peat soil under a taller and denser vegetation cover than thin-billed prions, which are preferentially under a sparse vegetation cover in rocky soils (Genevois and Buffard 1994), although both species share sometimes the same burrow. Mouse *Mus musculus*, which is not currently known predating petrel eggs at Kerguelen, is the only terrestrial mammal introduced in Mayes Island. The number of blue petrels was estimated at ~ 142 000 breeding pairs (Barbraud and Delord 2006). There is no estimate of the number of breeding pairs of thin-billed prions on the island, but the species is probably 3–6 times less abundant than the blue petrel (Mougeot et al. 1998; Barbraud and Delord unpublished data).

Collection of prey remains

Brown skuas are highly territorial and defend their territory a few days after establishment and do not end till the breeding season is over. Adult brown skuas hunt on their territory (almost 10,000 m² here, Mougeot et al. 1998) and return their prey on the nest to feed their chick(s), leaving wings and pellets within approximately 10 m around the nest (Mougeot et al. 1998, see also Trivelpiece et al. 1980; Adams 1982). Fresh wings of blue petrels and thin-billed prions were collected on skua territories situated in the same southern part of the Val des Garrodias as Mougeot et al. (1998), and also on 700 m around where the topography and vegetation cover did not differ (Fig. 1). Wing collection was made once on 11 brown skua territories between the 29th January and the 5th February 2014 (referenced as year 2013, for the beginning of the breeding season), following the same protocol for collection as in Mougeot et al. (1998). The collecting period corresponded to the end of the chick rearing of brown skuas and before the fledging peak of blue petrels (10th February) and thin-billed prions (25th February). This collection was therefore assumed to cover the prey accumulation during the breeding season since September of the preceding year. Storms may have removed some wings in the most exposed nests nearest to the coast. However, if it likely affected the total number of wings collected, it did not affect the wing proportions between blue petrels and thin-billed prions. Petrel wings from previous years, recognisable with their heavily degraded feathers, were discarded (3–5%). Species identification between blue petrel and thin-billed prion was made on colour criterion (Shirihai and Kirwan 2008) and in some case on wing measurements (Mougeot and Bretagnolle 2000a). When wings were not connected to the sternum and clavicle (60% of cases), only left wings were counted to avoid double counting. Wings from common diving petrels *Pelecanoides urinatrix* and white-headed petrels *Pterodroma lessonii* were found occasionally (< 3% of the total number of wings counted) but not collected.

Testing for differences in diet between 1992 and 2013

We tested for the similarity in proportion of blue petrels (over thin-billed prions) in the prey remains found in the territories of brown skuas during the breeding season 1992 and during the breeding season 2013. For this purpose, we

used a non-parametric Wilcoxon Mann–Whitney test due to the small sample sizes (2×11 brown skua territories).

Modelling petrel burrow occupancy

We estimated temporal trends in burrow occupancy for the two petrel species, which was used as a proxy of prey abundance, based on a monitoring dataset. Monitoring started in 1985 for blue petrels and in 1986 for thin-billed prions (i.e. year of nest opening). An annual monitoring was performed on 221 ± 76 burrows of thin-billed prions and 251 ± 89 burrows of blue petrels per year (Online Resource 1 Figure S2). A total of 440 different burrows were monitored over 30 years, reaching 14,402 control events, where 219 burrows have a double-species occupation. Burrows were visited each year two to three times during the early breeding period (blue petrel: September, thin-billed prion: October, Fig. 2) and again two to three times at the beginning of the reproductive season (blue petrel: early November, thin-billed prion: late November, Fig. 2) (see Nevoux and Barbraud 2006; Barbraud and Weimerskirch 2003 for the monitoring procedure). The burrow was noted as occupied: "1", if at least an individual was found, and empty: "0" when no individual was found. The species occupying each burrow was also reported. The first monitoring of each burrow was systematically removed from the dataset (i.e. year 1985 for blue petrel and 1986 for thin-billed prion) to avoid bias in occupancy estimation due to the first occupation of a burrow being inevitably occupied. When several nests had the same burrow entrance, i.e. 48% of the burrows, we considered the burrow occupied when at least one nest was occupied. Consequently, an empty burrow corresponded to an absolute absence of breeders, while an occupied burrow may have corresponded to one or two (rarely more) pairs of breeders.

We performed a generalised linear mixed model (GLMM) with binomial distribution to investigate a linear trend in burrow occupancy over years and also the potential difference of the trend between species (package glmmTMB v0.2.2: Magnusson et al. 2017). Burrow occupancy was the response variable and we analysed the influence of year as a continuous fixed effect (standardised). The model accounted for repeated measurements in each burrow by adding burrow identity as a random effect, nested in a species effect. One model was run on the whole monitoring period (1986–2016) and another was run on the period between the two skua diet sampling years (1992–2013). We computed the explained variance based on Nakagawa et al. (2017) using the package sjstats v0.016 (Lüdecke 2018). We also provided a complementary analysis to ensure that the occupancy trends were not only driven by the time since burrow monitoring (Online resources 2).

Analyses were performed with the statistical software R V. 3.5.1 (RC Team 2018). The parameters were estimated based on maximum likelihood estimations. The parameter estimates were tested using a Wald z-test with a significance level of 0.05.

Results

On the 11 brown skua territories visited in 2013, 479 left wings were counted with a mean of 44.5 ± 35.2 wings per nest, ranging from 13 to 137 wings. The proportion of blue petrels compared to thin-billed prions in the brown skua diet increased significantly from $79.0 \pm 8.1\%$ in 1992 to $94.9 \pm 4.0\%$ in 2013 ($w = 2$, $p = 0.0001$, Fig. 3). The proportion of blue petrels in 2013 found around the brown skua nests located exactly in the same area ($n = 4$) between the two years was $93.1 \pm 1.7\%$.

Burrow occupancy strongly decreased over the whole monitoring period (Fig. 4; $\beta \pm SE = -1.13 \pm 0.08$, $z = -13.487$, p value < 0.0001) and over the period 1992–2013 ($\beta = -0.78 \pm 0.04$, $z = -19.496$, p value < 0.0001). The decline was more severe for thin-billed prions than for blue petrels (Fig. 4; $\beta_{1986-2016} = -0.36 \pm 0.05$, $z = -7.187$, p value < 0.0001; $\beta_{1992-2013} = -0.35 \pm 0.05$, $z = -6.495$, p value < 0.0001). In 1992, the predicted burrow occupancy was 0.57 [95% CI 0.52–0.61] for thin-billed prions and 0.43 [95% CI 0.39–0.47] for blue petrels, and in 2013, 0.10 [95% CI 0.08–0.11] and 0.13 [95% CI 0.12–0.15], respectively. No significant difference in average burrow occupancy between blue petrels and thin-billed prions was detected ($\beta_{1986-2016} = -0.06 \pm 0.11$, $z = -0.518$, p value $= 0.6$; $\beta_{1992-2013} = -0.06 \pm 0.13$, $z = -0.431$, p value $= 0.7$). The total variance explained by the model based on the whole monitoring period was 40% (conditional r squared), with 11% due to the fixed effects (marginal r squared).
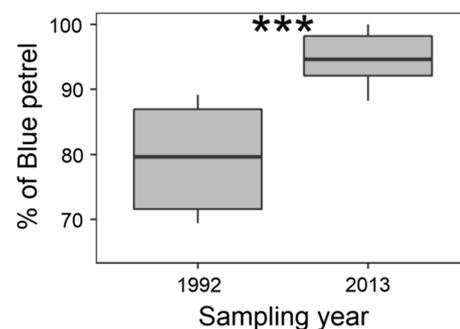
Fig. 3 Proportion of blue petrels compared to thin-billed prions in the diet of brown skuas in 1992 (Mougeot et al. 1998) and 2013 (present study)

Fig. 4 Trends in burrow occupancy (±95% CI, binomial regression) for blue petrels (black, 1986–2016) and thin-billed prions (grey, 1987–2016). Trends are decreasing at a significant different rate. Points represent the predicted values of occupancy per burrow and per species
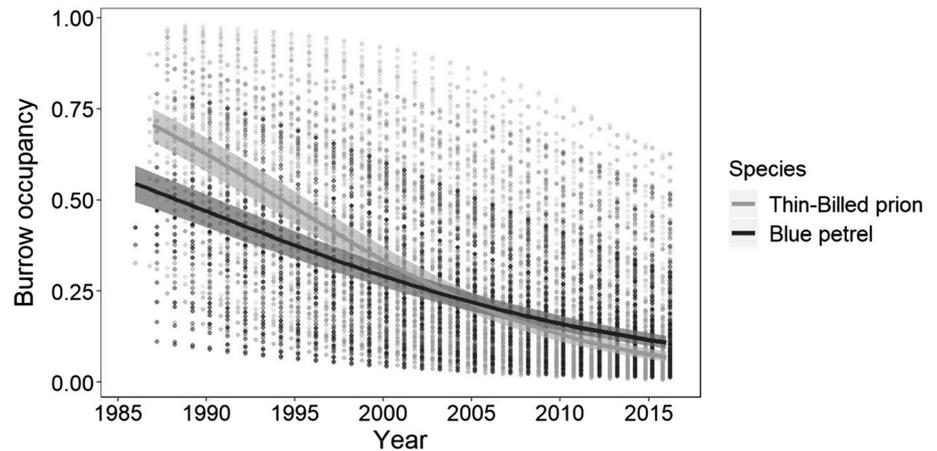
Discussion

This empirical study confirmed the blue petrel as the main component of brown skua diet at Mayes Island and clearly evidenced a difference in the ratio of blue petrels over thin-billed prions as prey remains between the years 1992 and 2013. Brown skuas seemed to rely around 15% more on blue petrels in 2013 than two decades ago. Both blue petrels and thin-billed prions showed a negative temporal trend in their burrow occupancy between 1992 and 2013, but the decline was around 2.5 times more severe for thin-billed prions. We suspect from our results a dietary shift of brown skuas at Mayes Island related to a change in the relative abundance of blue petrels and thin-billed prions, suggesting that the diet of brown skuas feeding on petrels provides a rapid assessment of the relative abundance of burrowing petrels.

Brown skua diet shift related to prey abundance

Our results suggested a dietary shift of brown skuas at Mayes Island twenty years apart. Fluctuation in relative prey abundance may induce a shift in dietary selection and thus in the ratio of species as prey items found in remains (Reif et al. 2004; Garrott et al. 2007; Marone et al. 2017). Between the two sampling years, i.e. 1992 and 2013, thin-billed prion burrow occupancy declined by on average 82% vs. 70% for the blue petrel. This 12% relative increase in the proportion of blue petrel abundance was coherent with the average increase by 15% of the blue petrel proportion in the prey remains. Blue petrel consisted in 2013 of almost all remains found in brown skuas' diet. The high degree of specialisation on blue petrels was consistent with other studies in Prince Edward Island (Adams 1982; Schramm 1983), in two other islands of the Kerguelen archipelago (Moncorps et al. 1998) and on the same site two decades ago (Mougeot et al. 1998).

The prey intake by brown skuas reflect the colony attendance patterns of thin-billed prions and blue petrels (Mougeot et al. 1998). Therefore, predation rates are high during laying and hatching, which coincide with periods of intense courtship by non-breeding individuals (probably both immatures and adults), but also during the fledging period when skuas predate mostly fledglings. Therefore, the relative number of skua preys (the burrowing petrels) reflects several demographic parameters of the prey such as productivity, breeding proportions or immigration, although the relative contribution of each parameter to the proportion of prey remains is unknown. It is thus difficult to infer what aspect of population change the proportions in skua diet may reflect. However, since all these demographic parameters affect the population growth rate, we can hypothesise that over long-time periods these proportions reflect the changes in the local population.

Methodological considerations

Remains could under-represent the contributions of soft-bodied prey (such as fish) and directly ingested food (when scavenging or feeding on seal placentae or little prey items). Brown skuas at Mayes Island appeared to feed mostly on burrowing petrels as indicated by isotopic data from feathers of brown skua chicks (Blévin et al. 2013; Delord et al. 2018). Few small prey items may also be consumed in situ, like dug up petrel chicks or mice, but it seemed to be anecdotal behaviour. In theory, the relative decrease in thin-billed prions in the brown skua diet in 2013 could be explained by three non-exclusive alternative hypotheses on breeding phenology: (i) an earlier breeding of the skuas, mismatching the activity peak of thin-billed prions, (ii) a later breeding of thin-billed prions, mismatching the peak of highest energy demand of brown skuas and (iii) a later breeding of the blue petrels, flooding the peak of highest energy demand for the skuas. We do not believe that these mechanisms were the main source of the diet shift as, in order to be influential, phenological shifts should have been tremendous, i.e. about 10 or 20 days (Mougeot et al. 1998) (Fig. 2). Brown skuas seemed to be flexible in their laying date and conversely to

the hypothesis (i); in 2013, the pairs holding sampled territories were relatively late breeders (mean date of laying: 51 days after 1st October) compared to the pairs studied by Mougeot et al. (1998) (28 days after 1st October). Thus, the proportion of thin-billed prions in remains should have instead been higher in 2013 due to their later attendance rate on breeding colonies than blue petrels (Fig. 2). Finally, a lower nest fidelity of thin-billed prions can decrease their observed burrow occupancy, but despite we do not have accurate information on the alternative burrow sites, the burrow fidelity is actually very high and very similar between thin-billed prions (87.5%) and blue petrels (88.3%) at Mayes Island, where we performed our study (Bried and Jouventin 2001).

Potential implication for conservation

Long-term seabird population monitoring is often challenging in subantarctic islands but the diet of brown skuas appears to be a valuable indicator of the relative abundance of burrowing petrels at a point in time as indicated by our study at Kerguelen and by Cerfonteyn and Ryan (2016) at Marion Island. Several burrowing petrel species have experienced rapid changes in abundance since the last decades in most of the subantarctic islands due to the negative effects of invasive predator species (Brooke et al. 2010), fisheries bycatch (Barbraud et al. 2008), climate change (Nevoux and Barbraud 2006) or to the positive effects of conservation measures at sea (Løkkeborg 2011) and on breeding islands (Lavers et al. 2010). Collection of prey remains over several years from breeding brown skuas could represent a simple and accessible method to evaluate variations in prey abundance when one prey abundance is known, and thus allowing to track the effectiveness of conservation measures, as it is done for raptors (Redpath et al. 2001; Sutherland et al. 2004).

Author contributions EG and NP had the original idea. EG, NP, KD and CB designed and coordinated the research. Data management and quality check were performed by KD, EG and NP. Analyses were performed by EG and NP with the support of CB. EG, NP, KD and CB wrote the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

Adams NJ (1982) Subantarctic Skua prey remains as an aid for rapidly assessing the status of burrowing petrels at Prince Edward Island. Mar Ornithol 10:97–102

Andersson M (1976) Population ecology of the long-tailed skua (*Stercorarius longicaudus* Vieill.). J Anim Ecol 45:537–559

Anderson ORJ, Phillips RA, Shore RF et al (2009) Diet, individual specialisation and breeding of brown skuas (*Catharacta antarctica lonnbergi*): an investigation using stable isotopes. Polar Biol 32:27–33

Barbraud C, Delord K (2006) Population census of blue petrels *Halobaena caerulea* at Mayes Island, Iles Kerguelen. Antarct Sci 18:199–204

Barbraud C, Weimerskirch H (2003) Climate and density shape population dynamics of a marine top predator. Proc R Soc Lond B Biol Sci 270:2111–2116

Barbraud C, Marteau C, Ridoux V et al (2008) Demographic response of a population of whit-chinned petrels *Procellaria aequinoctialis* to climate and longline fishery bycatch. J Appl Ecol 45:1460–1467

Blévin P, Carravieri A, Jaeger A et al (2013) Wide range of mercury contamination in chicks of Southern Ocean seabirds. PLoS ONE 8:e54508

Bried J, Jouventin P (2001) Site and mate choice in seabirds; an evolutionary approach. In: Schreiber EA, Burger J (eds) Biology of marine birds. CRC Press, Boca Raton, pp 263–305

Brooke MDL, O'Connell TC, Wingate D et al (2010) Potential for rat predation to cause decline of the globally threatened Henderson petrel *Pterodroma atrata*: evidence from the field, stable isotopes and population modelling. Endanger Species Res 11:47–59

Carlos CJ (2016) How many genera of Stercorariidae are there? Rev Bras Ornitol Braz J Ornithol 24:191–195

Carneiro AP, Manica A, Trivelpiece WZ, Phillips RA (2015) Flexibility in foraging strategies of Brown Skuas in response to local and seasonal dietary constraints. J Ornithol 156(3):625–633

Cerfonteyn M, Ryan PG (2016) Have burrowing petrels recovered on Marion Island two decades after cats were eradicated? Evidence from sub-Antarctic skua prey remains. Antarct Sci 28:51–57

Croxall JP, Reid K, Prince PA (1999) Diet, provisioning and productivity responses of marine predators to differences in availability of Antarctic krill. Mar Ecol Prog Ser 177:115–131

Dell'Arte GL, Laaksonen T, Norrdahl K, Korpimäki E (2007) Variation in the diet composition of a generalist predator, the red fox, in relation to season and density of main prey. Acta Oecol 31:276–281

Delord K, Cherel Y, Barbraud C et al (2018) High variability in migration and wintering strategies of brown skuas (*Catharacta antarctica lonnbergi*) in the Indian Ocean. Polar Biol 41:59–70

Dilley BJ, Schramm M, Ryan PG (2017) Modest increases in densities of burrow-nesting petrels following the removal of cats (*Felis catus*) from Marion Island. Polar Biol 40:625–637

Fraser MW (1984) Foods of subantarctic skuas on Inaccessible Island. Ostrich 55:192–195

Furness RW (1987) The Skuas. T. & A. D Poyser, Calton

Furness RW, Camphuysen K (1997) Seabirds as monitors of the marine environment. IceS J Mar Sci 54:726–737

Furness RW, Tasker ML (2000) Seabird-fishery interactions: quantifying the sensitivity of seabirds to reductions in sandeel abundance, and identification of key areas for sensitive seabirds in the North Sea. Mar Ecol Prog Ser 202:253–264

Garrott RA, Bruggeman JE, Becker MS et al (2007) Evaluating prey switching in wolf–ungulate systems. Ecol Appl 17:1588–1597

Genevois F, Buffard E (1994) Sites de nidification et caractéristiques des terriers chez deux espèces de pétrels sympatriques aux Iles Kerguelen: le pétrel bleu *Halobaena caerulea* et le prion de Belcher *Pachyptila belcheri*. Alauda 62:123–134

Hahn S, Peter H-U (2003) Feeding territoriality and the reproductive consequences in brown skuas *Catharacta antarctica lonnbergi*. Polar Biol 26:552–559. https://doi.org/10.1007/s00300-003-0522-z

Hamer KC, Furness RW, Caldow RWG (1991) The effects of changes in food availability on the breeding ecology of great skuas *Catharacta skua* in Shetland. J Zool 223:175–188

Jouventin P, Guillotin M (1979) Socio-écologie du skua Antarctique à Pointe Géologie. Société Nationale de Protection de la Nature et d'Acclimatation de France, Paris

Lavers JL, Wilcox C, Donlan CJ (2010) Bird demographic responses to predator removal programs. Biol Invasions 12:3839–3859

Løkkeborg S (2011) Best practices to mitigate seabird bycatch in longline, trawl and gillnet fisheries—efficiency and practical applicability. Mar Ecol Prog Ser 435:285–303

Lüdecke D (2018) Sjstats: statistical functions for regression models (Version 0.16.0). https://doi.org/10.5281/zenodo.1400701

Magnusson A, Skaug H, Nielsen A, et al (2017) Package 'glmmTMB'. R Package Version 0.2.2

Marchant S, Higgins PJ (1990) Handbook of Australian, New Zealand & Antarctic birds, vol 1: ratites to ducks. Oxford University Press, Melbourne

Marone L, Olmedo M, Valdés DY et al (2017) Diet switching of seed-eating birds wintering in grazed habitats of the central Monte Desert, Argentina. Condor 119:673–682

Micol T, Jouventin P (2001) Long-term population trends in seven Antarctic seabirds at Pointe Géologie (Terre Adélie). Polar Biol 24:175–185. https://doi.org/10.1007/s003000000193

Moncorps S, Chapuis J-L, Haubreux D, Bretagnolle V (1998) Diet of the brown skua *Catharacta skua lönnbergi* on the Kerguelen archipelago: comparisons between techniques and between islands. Polar Biol 19:9–16

Montevecchi WA, Myers RA (1995) Prey harvests of seabirds reflect pelagic fish and squid abundance on multiple spatial and temporal scales. Mar Ecol Prog Ser 117:1–9

Mougeot F, Bretagnolle V (2000a) Predation risk and moonlight avoidance in nocturnal seabirds. J Avian Biol 31:376–386

Mougeot F, Bretagnolle V (2000b) Predation as a cost of sexual communication in nocturnal seabirds: an experimental approach using acoustic signals. Anim Behav 60:647–656

Mougeot F, Genevois F, Bretagnolle V (1998) Predation on burrowing petrels by the brown skua (*Catharacta skua lönnbergi*) at Mayes Island, Kerguelen. J Zool 244:429–438

Nakagawa S, Johnson PC, Schielzeth H (2017) The coefficient of determination R2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. J R Soc Interface 14:20170213

Nevoux M, Barbraud C (2006) Relationships between sea ice concentration, sea surface temperature and demographic traits of thin-billed prions. Polar Biol 29:445–453

Ratcliffe N, Furness RW, Hamer KC (1998) The interactive effects of age and food supply on the breeding ecology of great skuas. J Anim Ecol 67:853–862

Redpath SM, Clarke R, Madders M, Thirgood SJ (2001) Assessing raptor diet: comparing pellets, prey remains, and observational data at hen harrier nests. Condor 103:184–188

Reif V, Jungell S, Korpimäki E et al (2004) Numerical response of common buzzards and predation rate of main and alternative prey under fluctuating food conditions. Ann Zool Fenn 41:599–607

Reinhardt K, Hahn S, Peter HU, Wemhoff H (2000) A review of the diets of Southern Hemisphere skuas. Mar Ornithol 28:7–19

Robin M, Chapuis J-L, Lebouvier M (2011) Remote sensing of vegetation cover change in islands of the Kerguelen archipelago. Polar Biol 34:1689

Ryan PG, Whittington PA, Crawford RJ (2009) A tale of two islands: contrasting fortunes for Subantarctic skuas at the Prince Edward Islands. Afr J Mar Sci 31:431–437

Schramm M (1983) Predation by subantarctic skuas *Catharacta antarctica* on burrowing petrels at Marion Island. Afr J Antarct Res 13:41–44

Shirihai H, Kirwan GM (2008) Complete guide to Antarctic wildlife. Princeton University Press, Princeton

Sinclair JC (1980) Subantarctic Skua *Catharacta antarctica* predation techniques on land and at sea. Cormorant 8:3–6

Spear LB, Howell SN, Oedekoven CS et al (1999) Kleptoparasitism by brown skuas on albatrosses and giant-petrels in the Indian Ocean. Auk 116:545–548

Stahl J-C, Mougin J-L (1986) La ségrégation alimentaire chez le Skua subantarctique *Stercorarius skua lönnbergi*. Oiseau Rev Francaise Ornithol 56:193–208

Sutherland WJ, Newton I, Green R (2004) Bird ecology and conservation: a handbook of techniques. Oxford University Press, Melbourne

Team RC (2018) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Austria, 2015. ISBN 3–900051–07–0. https://www.R-project.org

Trivelpiece W, Butler RG, Volkman NJ (1980) Feeding territories of brown skuas (*Catharacta lonnbergi*). Auk 97:669–676

Votier SC, Bearhop S, MacCormick A et al (2003) Assessing the diet of great skuas, *Catharacta skua*, using five different techniques. Polar Biol 26:20–26

Votier SC, Furness RW, Bearhop S, Crane JE, Caldow RWG, Catry P, Ensor K, Hamer KC, Hudson AV, Kalmbach E, Klomp NI, Pfeiffer S, Phillips RA, Prieto I, Thompson DR (2004) Changes in fisheries discard rates and seabird communities. Nature 427(6976):727–730

Wanless S, Wright PJ, Harris MP, Elston DA (2004) Evidence for decrease in size of lesser sandeels *Ammodytes marinus* in a North Sea aggregation over a 30-yr period. Mar Ecol Prog Ser 279:237–246

Weimerskirch H, Zotier R, Jouventin P (1989) The avifauna of the Kerguelen Islands. EMU 89:15–29

Young E (1994) Skua and penguin: predator and prey. Cambridge University Press, Cambridge

Young EC (1978) Behavioural ecology of lonnbergi skuas in relation to environment on the Chatham Islands, New Zealand. N Z J Zool 5:401–416

Zipan W, Norman FI (1993) Foods of the south polar skua *Catharacta maccormicki* in the eastern Larsemann Hills, Princess Elizabeth Land, East Antarctica. Polar Biol 13:255–262