LONG-TERM CHANGES IN POPULATION SIZE, DISTRIBUTION AND PRODUCTIVITY OF SKUAS (*Stercorarius* spp.) AT SIGNY ISLAND, SOUTH ORKNEY ISLANDS

Ana P. B. Carneiro[1,2]*, Andrea Manica[1], Richard A. Phillips[2]

[1] Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, United Kingdom

[2] British Antarctic Survey, Natural Environment Research Council, Madingley Road, High Cross, Cambridge CB3 0ET, United Kingdom

* Corresponding author: ana.bertoldi.carneiro@gmail.com

Abstract

In this study, we investigate the numbers, productivity and territory distribution of the two species of skuas (brown *Stercorarius lonnbergi* and south polar *Stercorarius maccormicki*) breeding at Signy Island, South Orkneys, and compare the results with trends elsewhere. Comparison with previous counts indicates a biphasic increase in brown skuas at Signy Island; much faster from 1958/59 to 1982/83 (3.3% per annum), than in subsequent years (0.4% per annum from 1983/84 to 2013/14). Relative distribution of territories has changed little over time. The reduced rate of population growth in recent years was broadly coincident with a decrease in numbers of penguins (and therefore potential prey), which may also explain recent reductions in skua numbers at other Antarctic sites. As prey have become limiting, breeding success of brown skuas at Signy Island is now slightly lower than in the 1950s/early 1960s, but timing of breeding does not appear to have changed. Brown skuas at Signy Island may still have enough resources to start breeding, but as the season progresses and availability of resources declines, chick survival is reduced. South polar skuas have declined from 10 pairs in 1982/83 to one pair in 2013/14, and mixed-pairs have increased from one to three pairs. A review of the literature indicated that although population trend data are available for relatively few sites elsewhere in the subantarctic and Antarctic, numbers of brown skuas appear to be generally decreasing or stable, and of south polar skuas to be stable or increasing.

Keywords: Breeding success; Population trends; Seabird; *Stercorarius* spp.; Top predator

45 Introduction

46 Seabirds are top predators in marine ecosystems and often considered to be effective
47 monitors of the condition and health of aquatic systems (Furness and Camphuysen 1997).
48 Particularly in the Southern Ocean, there is increasing evidence that the population
49 dynamics of top predators have been subjected to the compounded effects of human
50 activities (including harvesting, pollution, introductions of alien species etc.) and global
51 climate change; the latter has led in some cases to changes in phenology across multiple
52 trophic levels and a mismatch between peak energy demands of predators and the
53 availability of their key prey (Jenouvrier et al. 2005; Österblom et al. 2006; Ainley and
54 Hyrenbach 2010; Péron et al. 2010; Péron et al. 2013). Accurate knowledge of the
55 distribution and abundance of marine predators can therefore provide insights into
56 ecosystem status, as well as essential information for management and conservation
57 (Creuwels et al. 2007; Chardine et al. 2013).

58 Skuas *Stercorarius* spp. are important top predators in Antarctic environments.
59 Together with giant petrels (*Macronectes* spp.), skuas are the only avian predators likely to
60 have a major impact on populations of other seabirds (Norman and Ward 1990). Brown
61 skuas (*S. lonnbergi*) breed on most sub-Antarctic islands and in the Chatham Islands, south
62 polar skuas (*S. maccormicki*) breed at high latitudes around the Antarctic continent, and the
63 two species overlap in the northern parts of the Antarctic peninsula (Furness 1987; Fig. 1).
64 Both species are regarded as opportunistic predators, scavengers and kleptoparasites,
65 which enables them to exploit a wide range of food resources (Moncorps et al. 1998;
66 Mougeot et al. 1998; Phillips et al. 2004; Malzof and Quintana 2008; Carneiro et al. 2014). In
67 southerly regions, brown skuas feed mainly on penguin and other seabird prey, as do south
68 polar skuas throughout most of their breeding range, but in areas of sympatry, the latter
69 species forages almost exclusively at sea (Trivelpiece et al. 1980; Pietz 1987; Reinhardt et
70 al. 2000).

Results from the few long-term studies of brown and south polar skuas indicate considerable variation in population trends among sites; mostly decreasing or stable for brown skuas, but stable or increasing for south polar skuas until the 1990s (Woehler et al. 2001; Phillips et al. 2004). The hybrid zone between the two species expanded with a northerly extension of the south polar skua range in the late 1970s (Ritz et al. 2006). At Signy Island, South Orkneys, the breeding population of brown skuas doubled between 1958/59 and 1982/83 (Burton 1968; Hemmings 1984; Rootes 1988), and a new population of south polar skuas was established in 1978/79 (Hemmings 1984).

Increases in skua numbers have been attributed to a rapid growth in penguin numbers (and therefore potential prey) since the 1950s, or availability of seal carrion (Rootes 1988; Phillips et al. 2004). In recent years, however, penguin populations at Signy Island have declined, considered to be a consequence of reduced prey biomass and increased competition for resources, associated with changes in the timing and extent of sea ice formation, and the recovery of seal and whale populations (Forcada et al. 2006). The aim of this study was to document possible responses of brown and south polar skuas breeding at Signy Island to changes in the availability of penguins (as prey) in the 30+ years since the last census. In addition, territory distribution, nesting density, and breeding parameters (timing, breeding success) are compared with previously published data from this site and elsewhere.

Materials and methods

Territories of breeding skuas (mostly brown skuas, but including a few pairs of south polar skuas and a mixed-species pair) were studied at Signy Island, South Orkney Islands (60°43' S, 45°36' W; Fig. 2), between late December (mid incubation) and early March (chick fledging) in the austral summer of 2013/14. All individuals were identified to species level by

plumage coloration, differences in body size and vocalisations. A full census of the island was carried out by visiting all ice-free areas and recording the position of nests with eggs, and defended territories without eggs, using a hand-held GPS logger. The majority of territories with eggs (~79%) were checked at 5-8 day intervals during the breeding season, and the remainder were visited at least twice (in incubation and late chick-rearing). Wing length (maximum flattened chord) and mass of the chicks were measured at each visit during chick-rearing. Hatching dates were observed directly or estimated using a logistic curve fitted to the relationship between wing length and age of chicks of known hatching date (Phillips et al. 2004) using the function nls in R. To ensure statistical independence, comparisons of hatching date were based on the first chick hatched in each clutch. Overall breeding success was calculated for each type of skua pair (brown, south polar, or mixed) as the number of chicks fledged per clutch laid. Chicks were assumed to have fledged if they survived to >50 days, or until the end of the study period, as the mortality rate of older chicks is low (Hahn and Peter 2003).

Population size, territory distribution and breeding parameters (timing, breeding success) in 2013/14 were compared with data from part or the whole island available for previous years in published papers and unpublished reports (Richards 1958; Pinder 1960; Jones and Pinder 1961; Topliffe 1962; Burton 1968; Hemmings 1982, 1984; Rootes 1988). Nesting density (pairs per km^2) was calculated according to: (1) the planar area of the entire island, and, (2) the planar area of suitable habitat, which excluded slopes above 150 m, and cliffs (Phillips et al. 2004). Minimum distances between neighbouring territories were also estimated from the GPS data.

Results

120 The number of skua pairs breeding at Signy Island has been counted sporadically since
121 1958/59 (Table 1). Although skua numbers have changed substantially over time, the
122 relative distribution of nests in 2013/14 is similar to that recorded in 1958/59, 1965/66 and
123 1982/83 (Fig. 2). Territories of brown skuas occur throughout the island, with the greatest
124 densities around the penguin colonies, and have always been scarce at higher elevations
125 (Fig. 2). The majority of nests of south polar skua and mixed-species pairs remain clustered
126 in the far south-east of Signy Island, which is the area where south polar skuas were
127 breeding in 1982/83 (Fig. 2). The skua nesting density in 2013/14 was nine pairs per km^2
128 over the entire island (18.9 km^2), and 15 pairs per km^2 over the area of suitable habitat (10.7
129 km^2). Minimum distance from each territory to its nearest neighbour ranged from 15.6 to
130 457.5 m (mean ± se, 103.6 ± 6.4 m). The majority of territories (60.6%) were <100 m apart,
131 and very few (3.0%) were >300 m from the nearest neighbour.

132 In total, 165 occupied territories (including five in which breeding was not confirmed)
133 were counted on Signy Island during 2013/14. Of these, 161 were defended by a pair of
134 brown skuas, one by a pair of south polar skuas, and three by mixed pairs (Table 1). Counts
135 of occupied territories were available for part or the entire island in previous seasons,
136 including most years from 1958/59 to 1965/66, and 1982/83 (Table 1). In seasons between
137 1958/59 to 1965/66 in which only part of the island was surveyed, the population size of
138 brown skuas for the whole island was estimated based on the proportion of territories in
139 these areas relative to those elsewhere on the island in 1960/61 (Pinder 1960; Hemmings
140 1982). The long-term trend in the breeding population of brown skuas appears to be
141 represented by two major phases; a relatively rapid increase from 1958/59 to 1982/83 (3.3%
142 per annum), and a much slower increase in subsequent years (0.4% per annum from
143 1982/83 to 2013/14), equivalent to a 1.7% increase per annum overall. The breeding
144 population of south polar skuas has declined from 10 pairs in 1982/83 to only one pair in
145 2013/14, and of mixed-pairs has increased from one to three pairs (Table 1).

The number of chicks fledged per pair of brown skua in the 2013/14 season was 0.97 (*N*= 150), and per mixed-pair was 1.33 (*N*= 3); the pair of south polar skuas failed to fledge any chick. The productivity of brown skuas in 2013/14 was slightly lower than in any of the seven years from 1958/59 to 1965/66 (range 1.06 to 1.42 chicks/pair) for which data are available (Table 1).

Discussion

The brown skua population at Signy Island increased by 3.3% per annum from the first survey in 1958/59 to 1982/83, and by 0.4% per annum in the subsequent 31 years to the present study (for references see Tables 1 and 2). This represents an overall annual increase of 1.7% per annum over the 55 years since the first count. In contrast, the population of south polar skuas increased after colonisation by two pairs in 1978/79 to 10 pairs in 1982/83, but had decreased to just one pair in our recent survey; over the same period, the number of mixed-species pairs has increased from one to three pairs (Tables 1 and 2). The decline in south polar skuas may have been driven by the increase in brown skuas, which are considerably larger and are better competitors on land, or it may reflect reduced abundance of the Antarctic silverfish (*Pleuragramma antarcticum*). This was the main component of the diet of south polar skuas in the early 1980s and may have facilitated their original expansion in range to Signy Island (Hemmings 1984). The south polar skuas in the mixed pairs probably represent the surviving members of these original colonists, or their offspring.

Skua population trend data are available for relatively few sites (Table 2, Fig. 1). Although these trends are highly variable and there are few data for recent years, numbers of brown skuas appear to be generally decreasing or stable, and of south polar skuas to be stable or increasing, although there are exceptions (Table 2). Brown skua breeding numbers

were stable at the Kerguelen and Chatham archipelagos, and Anvers Island; stable or declining (although with substantial annual fluctuations) at different sites on King George Island (South Shetlands), stable at Macquarie Island, and Marion Island (Prince Edward Islands), and increasing substantially at Bird Island (South Georgia), and at Prince Edward Island. Populations of south polar skuas were stable at different sites on Ross Island; increased at sites in King George Island (although recent counts indicate declines) and elsewhere in the South Shetlands, and at Adélie Land, and Anvers Island. The more limited data for mixed-species pairs indicate stable or increasing trends. See Table 2 for references and a more detailed comparison.

The biphasic increase in the population of brown skuas has occurred in parallel with changes in population sizes of pygoscelid penguins (chinstrap *Pygoscelis antarctica* and Adélie *P. adeliae)* at Signy Island over the same time period. Adélie and chinstrap numbers increased up to fivefold from the 1950s to the mid 1970s at breeding colonies in the Scotia Sea, attributed to competitive release following the cessation of commercial harvesting of whales and seals (Croxall et al. 1981; Trivelpiece et al. 2011). The subsequent decline is considered to have resulted from the reduction in prey biomass (Antarctic krill *Euphausia superba*) due to climate change (through reduction in winter sea-ice extent), and the recovery of seal and whale populations (Forcada et al. 2006; Hinke et al. 2007; Sander et al. 2007a,b; Carlini et al. 2009; Trivelpiece et al. 2011; Barbosa et al. 2012). One possible explanation for the slowing of skua population growth rate at Signy Island is that the availability of penguins as prey has become limiting. This is supported by the slightly lower breeding success in 2013/14 when compared with the late 1950s and early 1960s (Table 1). This seems to reflect the increased use of other resources in addition to penguin prey; regurgitates collected from brown skuas in 1981/82 and 1982/83 at Signy Island contained only avian material (Hemmings 1984), whereas the analysis of GPS tracking data collected during the breeding season of 2013/14 indicates that skuas now use three different foraging

197 strategies, exploiting penguin colonies, small petrels and marine resources (authors'
198 unpublished data).

199 Although diet seems to have diversified in response to declining resources, timing of
200 breeding on Signy Island does not appear to have changed since the 1950s/early 1960s;
201 mean hatching dates in 1963/64-1965/66, 1982/83 and 2013/14 were all in the first week of
202 January (Richards 1958; Burton 1968; Hemmings 1984; this study), and were similar to
203 those recorded for brown skuas at King George Island in 1983/84 to 2003/04, and at South
204 Georgia in 2000/01 and 2002/03 (Hahn and Peter 2003; Phillips et al. 2004; Hahn et al.
205 2007). Although some brown skuas at Signy Island occupy feeding territories in penguin
206 colonies, which can sustain skuas for much of the season (Hahn and Peter 2003; Hahn and
207 Bauer 2008), other birds at Signy Island feed in penguin colonies that are not defended
208 consistently by another pair of skuas, or elsewhere on small petrels and marine prey (see
209 above). It is possible that these non-territorial skuas have enough access to food, including
210 penguins, to start breeding, but as the season progresses and availability of resources
211 decreases, they may fledge fewer chicks because they have to rely on alternative and less
212 temporally and spatially predictable prey (Trivelpiece et al. 1980; Pietz 1986, 1987; Votier et
213 al. 2004). This would explain the slight decline in breeding success from the 1950s/early
214 1960s to the present. However, even if this somewhat reduced breeding success is the
215 result of density-dependent competition for resources, it is important to note that productivity
216 of brown skuas at Signy Island remains similar to levels reported for populations breeding
217 elsewhere (0.5-1.8 chicks fledged/pair) (Reinhardt 1997; Phillips et al. 2004; Hahn et al.
218 2007). There is no evidence of any substantive long-term change in breeding chronology of
219 penguins at Signy Island (Lishman 1985; British Antarctic Survey unpublished data).

220 Phillips et al. (2004) pointed out that habitat saturation (in terms of feeding or nesting
221 resource availability) can also restrict recruitment rates in skuas. It is difficult to make a direct
222 comparison of nesting densities at Signy Island with skuas breeding elsewhere because of

223 the considerable variation in prey availability and the variety of skua foraging strategies.
224 However, when comparing with sites where the main food resources on land are penguin
225 eggs and chicks, as on Signy Island, nesting densities are in general similar. The overall
226 density across Signy Island is 15 pairs per km^2, which is comparable with that at King
227 George Island, South Shetland Islands (15.3 pairs per km^2 in 2004/05; Carneiro et al. 2010).
228 Part of the skua population that usually breeds at King George Island, however, deferred
229 breeding in the last three consecutive seasons (Carneiro et al. 2015; Trivelpiece pers.
230 comm.), indicating that a nesting density of about 15 birds per km^2 may represent the
231 threshold that limits the establishment of new territories. It is possible that the skua
232 population at Signy Island reached close to the maximum sustainable at some point during
233 the 1980s, hence the subsequent reduction in growth rate and decreased breeding success.
234 In contrast, at Bird Island (South Georgia) where brown skuas feed mainly by scavenging
235 seal carrion and placentae on beaches, and to a lesser extent by predation of other
236 seabirds, the nesting density in the austral summer of 2003/04 was far higher, at 119 pairs
237 per km^2, and the minimum nest spacing just 44 m, on average (Phillips et al. 2004). Bird
238 Island is, however, by far the most densely populated colony of brown skuas in the world
239 with comparatively good feeding conditions related to the abundance of fur seal carrion
240 (Phillips et al. 2004; Anderson et al. 2009).

241 In conclusion, it seems unlikely that breeding numbers on Signy Island will increase
242 to any great extent in the future because of a combination of decreased penguin abundance
243 and habitat saturation. Future work should involve monitoring of skua numbers and breeding
244 success at Signy Island and elsewhere in order to assess the conservation status of these
245 species. Both the brown skua and south polar skua remain relatively uncommon seabirds in
246 global terms, with a worldwide population of just c. 7–9,000 and 8–10,000 breeding pairs,
247 respectively, of which an estimated 3-4% and <1% breed in the South Orkney Islands
248 (Furness 1987; Higgins and Davis 1996). Indeed, this study stresses the importance of long-
249 term population monitoring programs in general, especially for species that are subject to

strong annual fluctuations such as skuas, to detect trends more reliably and to identify their underlying causes.

Acknowledgements Fieldwork costs were supported by a Natural Environment Research Council (NERC) Collaborative Gearing Scheme (CGS-85) award. This study is part of the Ecosystems component of the British Antarctic Survey Polar Science for Planet Earth Programme, funded by The Natural Environment Research Council.

References

Ainley DG, Hyrenbach KD (2010) Top-down and bottom-up factors affecting seabird population trends in the California current system (1985–2006). Prog Oceanogr 84:242–254

Ainley DG, Morrell SH, Wood RC (1986) South polar skua breeding colonies in the Ross Sea region, Antarctica. Notornis 33:155–163

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

Barbosa A, Benzal J, León AD, Moreno J (2012) Population decline of chinstrap penguins (*Pygoscelis antarctica*) on Deception Island, South Shetlands, Antarctica. Polar Biol 35:1453–1457

271 Brodier S, Pisanu B, Villers A, Pettex E, Lioret M, Chapuis J-L, Bretagnolle V (2011)
272 Responses of seabirds to the rabbit eradication on Ile Verte, sub-Antarctic Kerguelen
273 Archipelago. Anim Conserv 14:459–465

274 Burton RW (1968) Breeding biology of the brown skua, *Catharacta skua lonnbergi*
275 (Mathews), at Signy Island, South Orkney Island. Brit Antarct Surv B 15:9–28

276 Carlini AR, Coria NR, Santos MM, Negrete J, Juares MA, Daneri GA (2009) Responses of
277 *Pygoscelis adeliae* and *P. papua* populations to environmental changes at Isla 25 de
278 Mayo (King George Island). Polar Biol 32:1427–1433

279 Carneiro APB, Polito MJ, Sander M, Trivelpiece WZ (2010) Abundance and spatial
280 distribution of sympatrically breeding *Catharacta* spp. (skuas) in Admiralty Bay, King
281 George Island, Antarctica. Polar Biol 33:673–682

282 Carneiro APB, Manica A, Phillips RA (2014) Foraging behaviour and habitat use by brown
283 skuas *Stercorarius lonnbergi* breeding at South Georgia. Mar Biol 161:1755–1764

284 Carneiro APB, Manica A, Trivelpiece WZ, Phillips RA (2015) Flexibility in foraging strategies
285 of brown skuas in response to local and seasonal dietary constraints. J Ornithol (in
286 press)

287 Chardine JW, Rail J-F, Wilhelm S (2013) Population dynamics of northern gannets in North
288 America, 1984–2009. J Field Ornithol 84:187–192

289 Creuwels JCS, Poncet S, Hodum PJ, Franeker JA van (2007) Distribution and abundance of
290 the southern fulmar *Fulmarus glacialoides*. Polar Biol 30:1083–1097

291 Croxall JP, Rootes DM, Price RA (1981) Increases in penguin populations at Signy Island,
292 South Orkney Islands. Brit Antarct Surv B 54:47–56

293 Forcada J, Trathan PN, Reid K, Murphy EJ, Croxall JP (2006) Contrasting population
294 changes in sympatric penguin species in association with climate warming. Glob
295 Change Biol 12:411–423

296 Furness RW (1987) The skuas. T and AD Poyser, Calton

297 Furness RW, Camphuysen CJ (1997) Seabirds as monitors of the marine environment.
298 ICES J Mar Sci J Cons 54:726–737

299 Garcia Esponda CM, Coria NR, Montalti D (2000) Breeding birds at Half-moon Island, South
300 Shetland Islands, Antarctica, 1995/96. Marine Ornithology 28:59–62

301 Gil-Delgado JA, González-Solís J, Barbosa A (2013) Populations of breeding birds in Byers
302 Peninsula, Livingston Island, South Shetland Islands. Antarct Sci 25:303–306

303 Graña Grilli MG (2014) Decline in numbers of Antarctic skuas breeding at Potter Peninsula,
304 King George Island, Antarctica. Marine Ornithology 42:161–162

305 Hahn S, Bauer S (2008) Dominance in feeding territories relates to foraging success and
306 offspring growth in brown skuas *Catharacta antarctica lonnbergi*. Behav Ecol
307 Sociobiol 62:1149–1157

308 Hahn S, Peter H-U (2003) Feeding territoriality and the reproductive consequences in brown
309 skuas *Catharacta antarctica lonnbergi*. Polar Biol 26:552–559

310 Hahn S, Peter H-U, Quillfeldt P, Reinhardt K (1998) The birds of the Potter Peninsula, King
311 George Island, South Shetland Islands, Antarctica, 1965-1998. Marine Ornithology
312 26:1–6

313 Hahn S, Ritz MS, Peter H-U (2003) Living in mixed pairs–better for fitness? A study in skuas.
314 In: Huiskes AHL, Gieskes WWC, Rozema J, Schorno RML, van der Vies SM, Wolff

315 WJ (eds) Antarctic biology in a global context. Bachhuys Publishers, Leiden, pp 229–
316 233

317 Hahn S, Reinhardt K, Ritz MS, Janicke T, Montalti D, Peter H-U (2007) Oceanographic and
318 climatic factors differentially affect reproduction performance of Antarctic skuas. Mar
319 Ecol Prog Ser 334:287–297

320 Hemmings AD (1982) A census of breeding pairs of brown skua (*Catharacta lonnbergi*) and
321 McCormick's skua (*C. maccormicki*), Signy Island. British Antarctic Survey Archives
322 No. AD6/2H/1982/Q3, Cambridge

323 Hemmings AD (1984) Aspects of the breeding biology of McCormick's skua *Catharacta*
324 *maccormicki* at Signy Island, South Orkney Islands. Brit Antarct Surv B 65:65–79

325 Higgins PJ, Davies SJJF (1996) Handbook of Australian, New Zealand and Antarctic birds,
326 vol 3. Snipe to pigeons. Oxford University Press, Melbourne

327 Hinke JT, Salwicka K, Trivelpiece SG, Watters GM, Trivelpiece WZ (2007) Divergent
328 responses of *Pygoscelis* penguins reveal a common environmental driver. Oecologia
329 153:845–855

330 Jenouvrier S, Barbraud C, Cazelles B, Weimerskirch H (2005) Modelling population
331 dynamics of seabirds: importance of the effects of climate fluctuations on breeding
332 proportions. Oikos 108:511–522

333 Jones NV, Pinder R (1961) Ornithological report, 1961. British Antarctic Survey Archives No.
334 AD6/2H/1961/Q, Cambridge

335 Lishman GS (1985) The comparative breeding biology of Adélie and chinstrap penguins
336 *Pygoscelis adeliae* and *P. antarctica* at Signy Island, South Orkney Islands. Ibis
337 127:84–99

338 Malzof SL, Quintana RD (2008) Diet of the south polar skua *Catharacta maccormicki* and the
339 brown skua *C. antarctica lonnbergi* at Cierva Point, Antarctic Peninsula. Polar Biol
340 31:827–835

341 Micol T, Jouventin P (2001) Long-term population trends in seven Antarctic seabirds at
342 Pointe Géologie (Terre Adélie): human impact compared with environmental change.
343 Polar Biol 24:175–185

344 Miller GD (1993) Reproductive success of south polar skuas at Cape Bird, Ross I. Antarctic
345 Journal of the United States 27:150–151

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

349 Mougeot F, Genevois F, Bretagnolle V (1998) Predation on burrowing petrels by the brown
350 skua (*Catharacta skua lonnbergi*) at Mayes Island, Kerguelen. J Zool Lond 244:429–
351 438

352 Norman FI, Ward SJ (1990) Foods of the south polar skua at Hop Island, Rauer Group, East
353 Antarctica. Polar Biol 10:489–493

354 Österblom H, Casini M, Olsson O, Bignert A (2006) Fish, seabirds and trophic cascades in
355 the Baltic Sea. Mar Ecol Prog Ser 323:233–238

356 Péron C, Authier M, Barbraud C, Delord K, Besson D, Weimerskirch H (2010) Interdecadal
357 changes in at-sea distribution and abundance of subantarctic seabirds along a
358 latitudinal gradient in the Southern Indian Ocean. Glob Change Biol 16:1895–1909

359 Péron C, Grémillet D, Prudor A, Pettex E, Saraux C, Soriano-Redondo A, Authier M, Fort J
360 (2013) Importance of coastal marine protected areas for the conservation of pelagic

seabirds: the case of vulnerable yelkouan shearwaters in the Mediterranean Sea. Biol Conserv 168:210–221

Peter H-U, Braun C, Janowski S, Nordt A, Nordt A, Stelter M (2013) The current environmental situation and proposals for the management of the Fildes Peninsula Region. Federal Environment Agency (Umweltbundesamt), Germany

Phillips R, Phalan B, Forster I (2004) Diet and long-term changes in population size and productivity of brown skuas *Catharacta antarctica lonnbergi* at Bird Island, South Georgia. Polar Biol 27:555–561

Pietz PJ (1986) Daily activity patterns of south polar and brown skuas near Palmer Station, Antarctica. Auk 103:726–736

Pietz PJ (1987) Feeding and nesting ecology of sympatric south polar and brown skuas. Auk 104:617–627

Pinder RW (1960) Ornithological report, 1960. British Antarctic Survey Archives No. AD6/2H/1960/Q2, Cambridge

Reinhardt K (1997) Breeding success of southern hemisphere skuas *Catharacta* spp.: the influence of latitude. Ardea 85:73–82

Reinhardt K, Hahn S, Peter H-U, Wemhoff H (2000) A review of the diets of southern hemisphere skuas. Marine Ornithology 28:7–19

Richards PA (1958) Ornithological report, 1958. British Antarctic Survey Archives No. AD6/2H/1958/Q2, Cambridge

Ritz MS, Hahn S, Janicke T, Peter H-U (2006) Hybridisation between south polar skua (*Catharacta maccormicki*) and brown skua (*C. antarctica lonnbergi*) in the Antarctic Peninsula region. Polar Biol 29:153–159

384 Rootes DM (1988) The status of birds at Signy Island, South Orkney Islands. Brit Antarct
385 Surv B 80:87–119

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

388 Sander M, Balbão TC, Costa ES, Santos CR, Petry MV (2007a) Decline of the breeding
389 population of *Pygoscelis antarctica* and *Pygoscelis adeliae* on Penguin Island, South
390 Shetland, Antarctica. Polar Biol 30:651–654

391 Sander M, Balbão TC, Polito MJ, Costa ES, Carneiro APB (2007b) Recent decrease in
392 chinstrap penguin (*Pygoscelis antarctica*) populations at two of Admiralty Bay's islets
393 on King George Island, South Shetland Islands, Antarctica. Polar Biol 30:659–661

394 Skira J (1984) Breeding distribution of the brown skua on Macquarie Island. Emu 84:248–
395 249

396 Topliffe F (1962). Ornithological report, 1962. British Antarctic Survey Archives No.
397 AD6/2H/1962/Q1, Cambridge

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

400 Trivelpiece WZ, Hinke JT, Miller AK, Reiss CS, Trivelpiece SG, Watters GM (2011)
401 Variability in krill biomass links harvesting and climate warming to penguin population
402 changes in Antarctica. Proc Natl Acad Sci 108:7625–7628

403 Votier S, Bearhop S, Ratcliffe N, Furness R (2004) Reproductive consequences for great
404 skuas specializing as seabird predators. Condor 106:275–287

405 Woehler EJ, Croxall JP (1997) The status and trends of Antarctic and sub-Antarctic
406 seabirds. Marine Ornithology 25: 43–66

Woehler EJ, Cooper J, Croxall JP, Fraser WR, Kooyman GL, Millar GD, Nel DC, Patterson DL, Peter H-U, Ribic CA, Salwicka K, Trivelpiece WZ, Weimerskirch H (2001) A statistical assessment of the status and trends of Antarctic and sub-Antarctic seabirds. SCAR, Cambridge

Wood RC (1971) Population dynamics of breeding south polar skuas of unknown age. Auk 88: 805–814

Young EC (1994) Is cooperative breeding in brown skua (*Catharacta skua lonnbergi*) on the Chatham Island habitat-forced? Notornis 41:143–163

Table 1: Long-term changes in population size and breeding success of brown skuas (*Stercorarius lonnbergi*), south polar skuas (*S. maccormicki*) and mixed-species pairs at Signy Island.

Season	Count of occupied territories			Brown skua productivity (chicks fledged/pair)	Reference
	Brown skua	South polar skua	Mixed pairs		
1958/59[a]	65	0	0	1.30	Richards (1958)
1960/61	71	0	0	1.30	Pinder (1960); Hemmings (1982)
1961/62	81	0	0	1.16	Jones and Pinder (1961)
1962/63	64	0	0	1.42	Topliffe (1962); Hemmings (1982)
1963/64[b]	79	0	0	1.32	Burton (1968)
1964/65[c]	99	0	0	1.10	Burton (1968)
1965/66[d]	96	0	0	1.06	Burton (1968)
1981/82	NA	9	3	NA	Hemmings (1984)
1982/83	143	10	1	NA	Hemmings (1984)
2013/14	161	1	3	0.97	This study

Estimate based on original part-island counts (of [a]59, [b]67, [c]84 and [d]81 pairs), corrected for the proportion of territories in surveyed and unsurveyed areas recorded in 1960/61.

437

438 Table 2: Trends in population sizes of brown skuas (*Stercorarius lonnbergi* - BS), south polar skuas (*S. maccormicki* - SPS) and mixed-species pairs (MS). [a]

439 Most recent count. See Fig. 1 for the location of study sites.

Site	Study period	Species	Occupied territories [a]	Trend	Reference
1. Chatham Islands					
Mangere Island	1980-1992	BS	19	Stable	Young (1994)
Rangatira Island	1979-1992	BS	43	Stable	Young (1994)
2. Prince Edward Islands					
Prince Edward Island	2001, 2008	BS	267	Increasing	Ryan et al. (2009)
Marion Island	1987, 1997, 2001, 2008	BS	282	-5%	Ryan et al. (2009)
3. Iles Kerguelen					
Ile Verte	1991-2006	BS	6 ± 1 (average)	Stable	Brodier et al. (2011)
4. South Georgia					
Bird Island	1958, 1976, 1980	BS	375	+3.6%	Phillips et al. (2004)
	1981-2003	BS	467	+0.9%	
5. Macquarie Island	1974, 1983	BS	206	Decreasing	Skira (1984)
6. South Orkney Islands					
Signy Island	1958, 1960-1965, 1982	BS	143	+3.3%	This study
	1983-2013	BS	161	+0.4%	

		MS	16	Stable
	2012, 2013	BS	14	Decreasing
		SPS	0	Decreasing
Livingston Island				
Byers Peninsula	1965, 2008	BS	15	Decreasing
Half-moon Island	1993, 1994, 1995	BS	3	Stable
	1993, 1994, 1995	SPS	103	Stable

446 Figure captions:

447

448 **Fig. 1** Breeding distribution of brown (*Stercorarius lonnbergi*) and south polar skuas (*S.*
449 *maccormicki*). Filled symbols represent sites with at least two years of count data (see Table
450 2); open symbols indicate that no trend was available. Site names (1-11: see Table 2, 12:
451 Iles Crozet, 13: Amsterdam and St Paul, 14: Heard and McDonald Islands, 15: New Zealand
452 and offshore islands, 16: The Snares, 17: Auckland Islands, 18: Campbell Islands, 19:
453 Antipodes Islands, 20: Bounty Islands, 21: South Sandwich Islands, 22: Bouvet Island, 23:
454 Peter I Island, 24: Antarctic coast and offshore islands)

455

456 **Fig. 2** Location and maps of the study site. (a) South Orkney Islands. Distribution of nests
457 and occupied territories of brown skuas (*Stercorarius lonnbergi*), south polar skuas (*S.*
458 *maccormicki*) and mixed-species pairs at Signy Island (South Orkneys) in (b) 1958/59
459 (redrawn from Richards 1958), (c) 1965/66 (redrawn from Burton 1968), (d) 1982/83
460 (redrawn from Rootes 1988), and (e) 2013/14

461

Fig. 1.

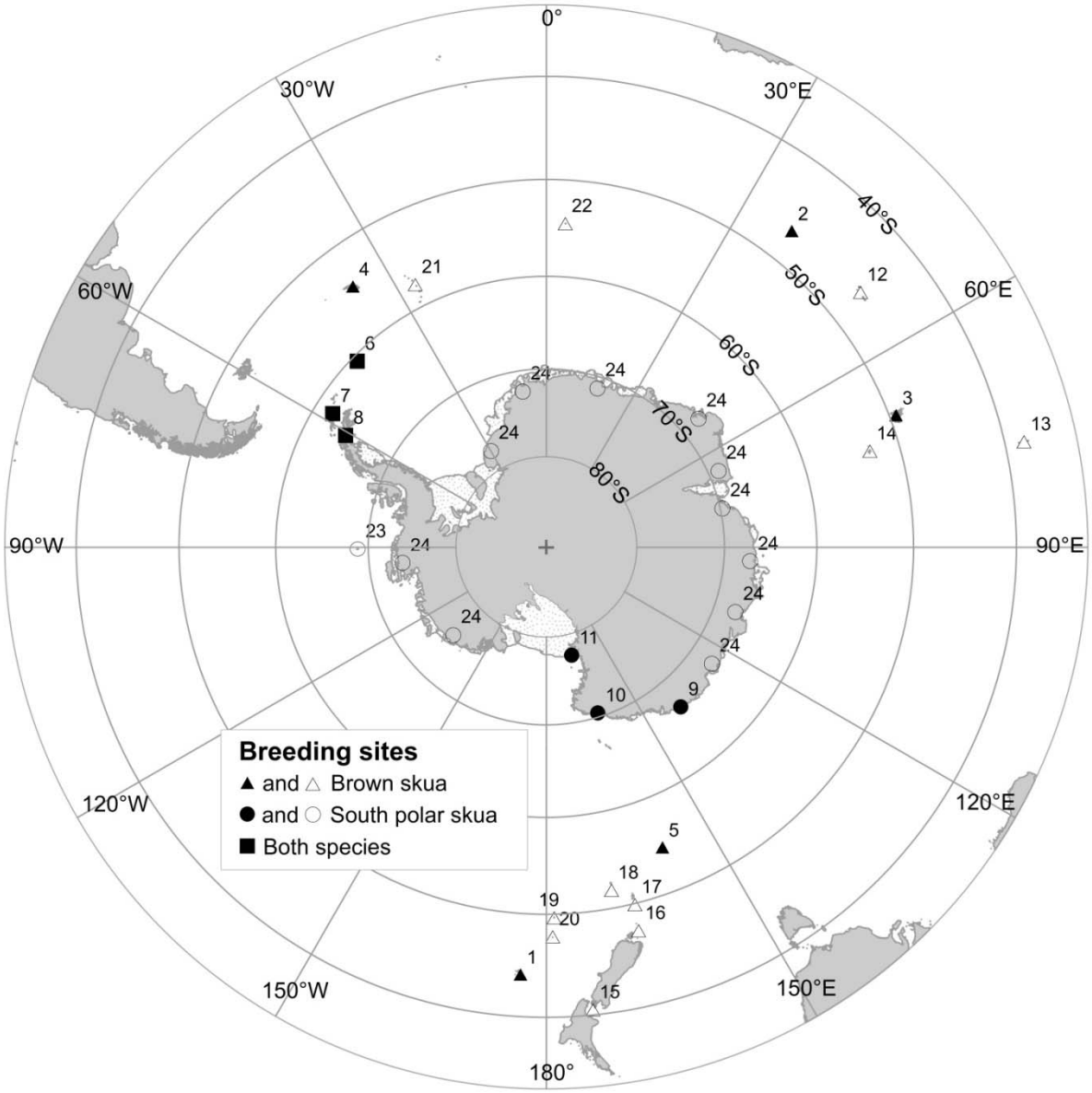
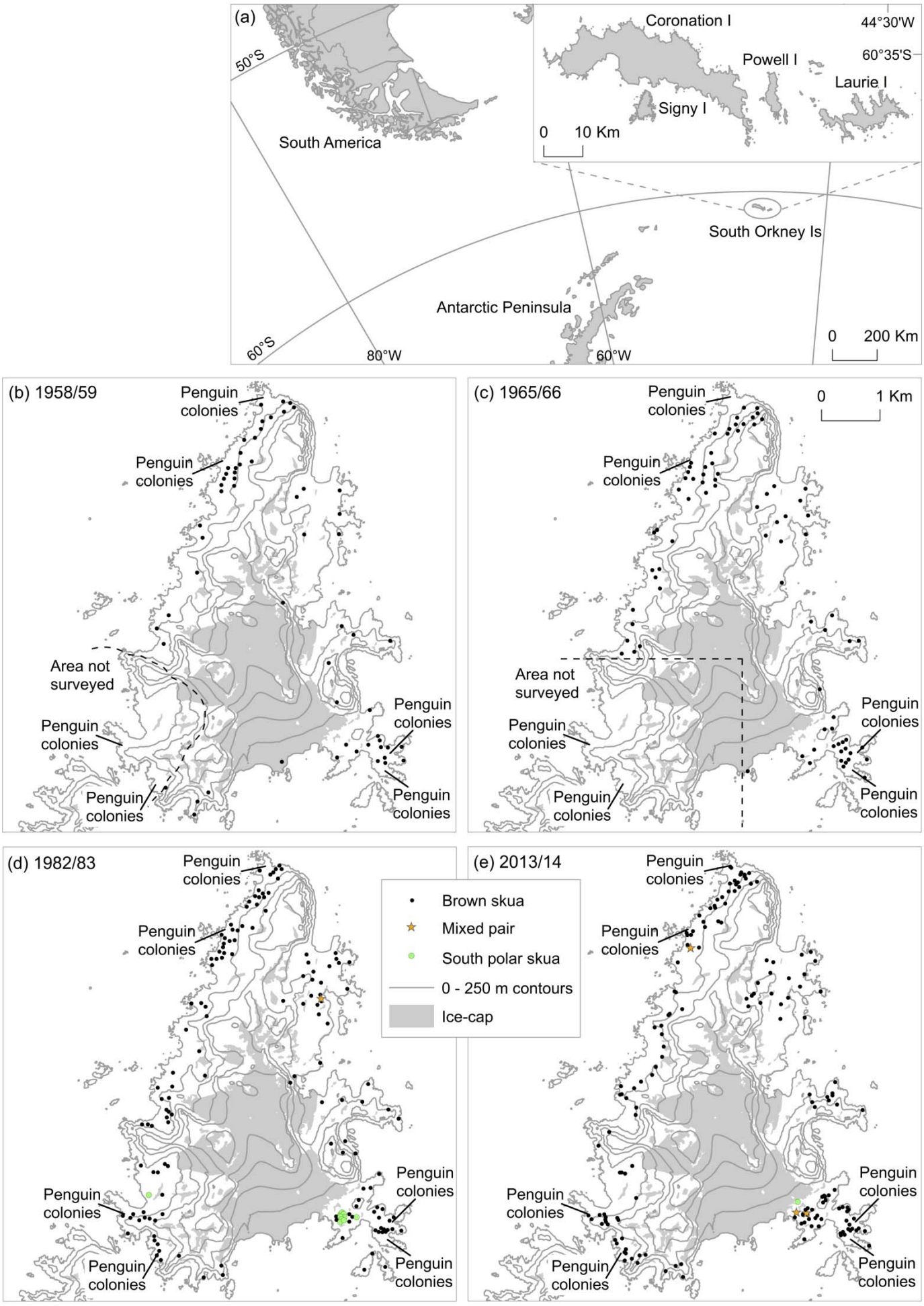

0°
30°W
30°E
60°W
60°E
90°W
90°E
120°W
120°E
150°W
150°E
180°
40°S
50°S
60°S
70°S
80°S
Breeding sites
▲ and △ Brown skua
● and ○ South polar skua
■ Both species

Fig. 2.


(a)
50°S
South America
Coronation I
44°30'W
Powell I
60°35'S
Laurie I
Signy I
0 10 Km
South Orkney Is
Antarctic Peninsula
60°S
80°W
60°W
0 200 Km
(b) 1958/59
Penguin colonies
Area not surveyed
(c) 1965/66
0 1 Km
(d) 1982/83
(e) 2013/14
Brown skua
Mixed pair
South polar skua
0 - 250 m contours
Ice-cap