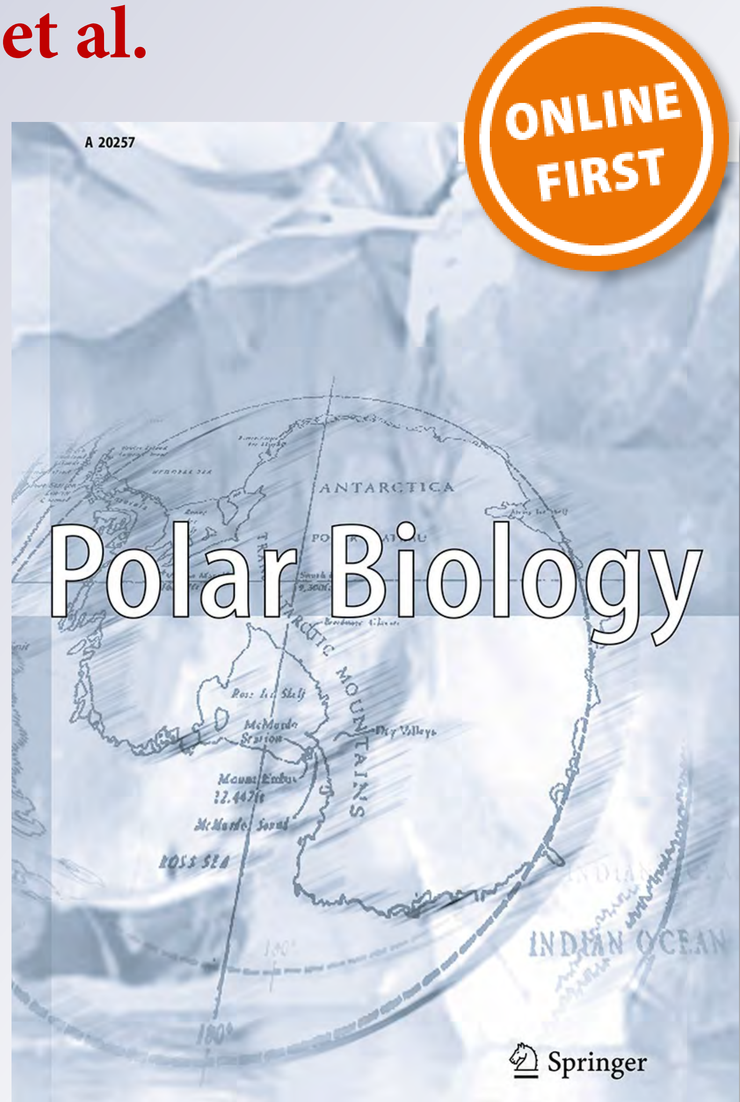
South Polar Skua breeding populations in the Ross Sea assessed from demonstrated relationship with Adélie Penguin numbers

Deborah J. Wilson, Philip O'B. Lyver, Terry C. Greene, Amy L. Whitehead, Katie M. Dugger, Brian J. Karl, James R. F. Barringer, et al.

Polar Biology

ISSN 0722-4060

Polar Biol
DOI 10.1007/s00300-016-1980-4



Springer

Polar Biol
DOI 10.1007/s00300-016-1980-4

ORIGINAL PAPER

South Polar Skua breeding populations in the Ross Sea assessed from demonstrated relationship with Adélie Penguin numbers

Deborah J. Wilson[1] · Philip O'B. Lyver[2] · Terry C. Greene[3] · Amy L. Whitehead[4] · Katie M. Dugger[5] · Brian J. Karl[2] · James R. F. Barringer[2] · Roger McGarry[6] · Annie M. Pollard[7] · David G. Ainley[8]

Received: 20 October 2015 / Revised: 25 April 2016 / Accepted: 25 May 2016

Abstract In the Ross Sea region, most South Polar Skuas (*Stercorarius maccormicki*) nest near Adélie Penguin (*Pygoscelis adeliae*) colonies, preying and scavenging on fish, penguins, and other carrion. To derive a relationship to predict skua numbers from better-quantified penguin numbers, we used distance sampling to estimate breeding skua numbers within 1000 m of 5 penguin nesting locations (Cape Crozier, Cape Royds, and 3 Cape Bird locations) on Ross Island in 3 consecutive years. Estimated numbers of skua breeding pairs were highest at Cape Crozier (270,000 penguin pairs; 1099 and 1347 skua pairs in 2 respective years) and lowest at Cape Royds (3000 penguin pairs; 45 skua pairs). The log–log linear relationship ($R^2 = 0.98$) between pairs of skuas and penguins was highly significant, and most historical estimates of skua and penguin numbers in the Ross Sea were within 95 % prediction intervals of the regression. Applying our regression model to current Adélie Penguin colony sizes at 23 western Ross Sea locations predicted that 4635 pairs of skuas now breed within 1000 m of penguin colonies in the Ross Island metapopulation (including Beaufort Island) and northern Victoria Land. We estimate, using published skua estimates for elsewhere in Antarctica, that the Ross Sea South Polar Skua population comprises $\sim$50 % of the world total, although this may be an overestimate because of incomplete data elsewhere. To improve predictions and enable measurement of future skua population change, we recommend additional South Polar Skua surveys using consistent distance-sampling methods at penguin colonies of a range of sizes.

Electronic supplementary material The online version of this article (doi:10.1007/s00300-016-1980-4) contains supplementary material, which is available to authorized users.

✉ Deborah J. Wilson
wilsond@landcareresearch.co.nz

1 Landcare Research, Private Bag 1930, Dunedin 9054, New Zealand

2 Landcare Research, PO Box 69040, Lincoln 7640, New Zealand

3 Department of Conservation, Private Bag 4715, Christchurch 8140, New Zealand

4 National Institute of Water and Atmospheric Research, 10 Kyle Street, Riccarton, Christchurch 8011, New Zealand

5 U.S. Geological Survey, Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331, USA

6 PO Box 57-021, Owairaka, Auckland 1025, New Zealand

7 247 South 2nd Street, Coos Bay, OR 97420, USA

8 H. T. Harvey and Associates Ecological Consultants, Los Gatos, CA 95032, USA

Keywords Distance sampling · Environmental change · *Pygoscelis adeliae* · Seabirds · South Polar Skua · *Stercorarius maccormicki*

Introduction

The underlying factors most likely to limit the abundance of breeding seabirds in the Antarctic are prey availability and access to nesting space (Ainley et al. 1995). Among these seabird species, South Polar Skuas (*Stercorarius maccormicki*; referred to herein as skuas) and Adélie Penguins (*Pygoscelis adeliae*) have been of great interest since the first European expeditions to Antarctica, mostly because of their interspecific interactions and colonial nesting on relatively level, coastal terrain also favored by humans to build logistic facilities. The nesting biology and behavior of both species have been well studied (reviews in Young 1994; Ainley 2002). The population sizes of Adélie Penguins have been repeatedly assessed (e.g., Micol and Jouventin 2001; Croxall et al. 2002; Lyver et al. 2014; Southwell et al. 2015), and the species is one of those monitored by CCAMLR's (Commission for the Conservation of Antarctic Marine Living Resources) Ecosystem Monitoring Program (CEMP), as indicators of environmental change (CCAMLR 2014). In contrast, skua numbers are estimated infrequently (cf. Micol and Jouventin 2001) in most locations (Woehler et al. 2001; Wilson et al. 2015).

Much of the research on South Polar Skuas has been conducted in the western Ross Sea, where Adélie Penguins and South Polar Skuas are the dominant avian species. It has been suggested that 80 % of skuas nest in association with Adélie Penguins (Harper 1984; Ainley et al. 1986; Young 1994), on the basis of extensive surveys of the Ross Sea continental coast (Ainley et al. 1986, 1990). This interspecific association may occur primarily because both birds require nesting areas that are free of ice and snow and close to abundant marine food (Ainley et al. 1986; Young 1994). Studies in the southern Ross Sea show that skuas feed primarily on fish (particularly Antarctic silverfish *Pleuragramma antarctica*) (Young 1963, 1994; Ainley et al. 1984), but they also prey on and scavenge Adélie Penguin eggs, chicks, and adults as well as other food sources when available (e.g., seals, other seabirds including skuas; Young 1963, 1994; and see Reinhardt et al. 2000). As a result, skua diet varies in relation to the penguin breeding season and degree of association with penguins, and also between individuals with access to penguins and those without (Young 1994; Young and Millar 1999; Grilli et al. 2011). The territorial behavior of skuas at penguin colonies affects which individuals can access penguins as food, and penguin colonies of different sizes differ in the degree to which they are divided into skua nesting or feeding territories (Young 1994; Young and Millar 1999).

Skua populations in the Ross Sea region (the type locality of this species; McCormick 1841; surgeon on James Clark Ross's Antarctic expeditions) have fluctuated in recent decades, sometimes apparently as the result of anthropogenic activities, including changes in the availability of food from refuse dumps at research stations, and sometimes in relation to unknown environmental factors (Harper 1984; Ainley et al. 1986; Pinkerton et al. 2010a, b). Concurrent population declines of skuas and Adélie Penguins were observed at Cape Hallett during the 1960s, owing perhaps in part to effects of a former research station (Johnston 1971; Pascoe 1984; Ainley et al. 1986). Elsewhere in Antarctica, the relationship between numbers of South Polar Skuas and Adélie Penguins may differ (Wilson et al. 2015). Much of the Antarctic coast is at lower latitudes than the Ross Sea, and South Polar Skuas compete with larger avian predators and scavengers. Southern Giant Petrels (*Macronectes giganteus*; breeding distribution in Patterson et al. 2008) and, on the Antarctic Peninsula, also Brown Skuas (*Stercorarious lonbergii*) (Trivelpiece and Volkman 1982; Pietz 1987; Reinhardt et al. 2000) and the smaller Kelp Gulls (*Larus dominicanus*) and Snowy Sheathbills (*Chionis alba*) all subtract some portion of the foraging niche exhibited by South Polar Skuas in the Ross Sea (e.g., Burger 1981 describes partitioning of scavenging/predatory foraging in a sub-Antarctic avian community). Also on the Antarctic Peninsula, large populations of the 2 other pygoscelid Adélie Penguin congeners (Gentoo Penguin *Pygoscelis papua*, Chinstrap Penguin *P. antarctica*; Lynch et al. 2012) supply alternative prey and carrion. Despite this additional complexity, concurrent population changes in South Polar Skuas and Adélie Penguins have occasionally been documented in other Antarctic regions. In Adélie Land, East Antarctica, increases in skua numbers in the 1990s corresponded to increasing numbers of Adélie Penguins during the same period (Micol and Jouventin 2001), whereas breeding skua numbers in Commonwealth Bay, East Antarctica, have changed little in the last 100 years (Wilson et al. 2015). In some Antarctic Peninsula locations, both Adélie Penguins and South Polar Skuas have recently declined (cf. Lynch et al. 2012; Grilli 2014).

In this study, we quantify the relationship between skua numbers and the better-quantified penguin numbers (Lyver et al. 2014) at 5 locations within the Ross Sea region, to then predict population sizes of skuas associated with other Ross Sea penguin colonies. First, we estimate the breeding population sizes of skuas at 3 Adélie Penguin colonies on Ross Island in 2 consecutive years and at one colony in a third year. Colonies are divided into 5 disjunct penguin breeding locations, and distance sampling (Buckland et al. 2001; Barbraud et al. 2014) is used to adjust the numbers of breeding birds actually seen, taking into account imperfect detection. Next, we model a relationship between our estimates and the Adélie Penguin breeding population sizes measured at these 5 locations in the same 3 years (from the data set used by Lyver et al. 2014). We then use this relationship to predict the number of skuas breeding in association with Adélie Penguin colonies elsewhere in the western Ross Sea (also Lyver et al. 2014), where skuas have been relatively sparsely counted (Ainley et al. 1986). We tabulate published and unpublished skua population estimates elsewhere in Antarctica, and calculate the approximate proportion of the world population breeding in the Ross Sea region.

Methods

Study species and sites

Skuas arrive in McMurdo Sound between 18 October and 14 November each year, coinciding with the arrival of Adélie Penguins (Spellerberg 1971). On Ross Island, skuas lay eggs during late November and early December (Ainley et al. 1990). Chicks hatch around mid-December to early January and begin to fledge in early February (Wang and Norman 1993). The last birds do not leave the colonies until early April (Spellerberg 1971).

We surveyed skuas at 3 Adélie Penguin colonies (Cape Bird, Cape Crozier and Cape Royds) on Ross Island (Fig. 1). Cape Crozier is thought to be the largest skua colony globally, with ~1000 pairs estimated to have been breeding there in the 1960s to 1980s (Wood 1971; Ainley et al. 1986). The Cape Crozier colony is anomalous in size, as the next largest ones in Victoria Land and on Ross Island are much smaller (Possession and Sven Foyn Islands and Cape Bird, with 474, 397 and 399 breeding pairs, respectively; 1980s estimates, Ainley et al. 1986), on par with colonies elsewhere (e.g., Micol and Jouventin 2001; Grilli 2014; Wilson et al. 2015).

To maximize our sample size and simplify our sample design, the Cape Bird penguin colony was subdivided into smaller units, called 'breeding locations,' on the basis of obvious spatial separation of the penguin subcolony clusters (1.3 km between Cape Bird North and Middle, and 2 km between Cape Bird Middle and South; see Ainley 2002 for definition of colony and subcolony). The corresponding shortest distances between transects (see below) where we surveyed skuas at Cape Bird were 845 and 730 m, as the colonies were more spatially extensive than the penguin breeding locations. We did not subdivide Cape Crozier (consistent with Ainley 2002), because, although it has 2 discrete locations of Adélie Penguins (East and West), some skuas nest between them (Ainley et al. 1990). Skua surveys were completed therefore at each of the resulting 5 locations: Cape Bird (North, Middle and South), Cape Crozier and Cape Royds (Fig. 1).

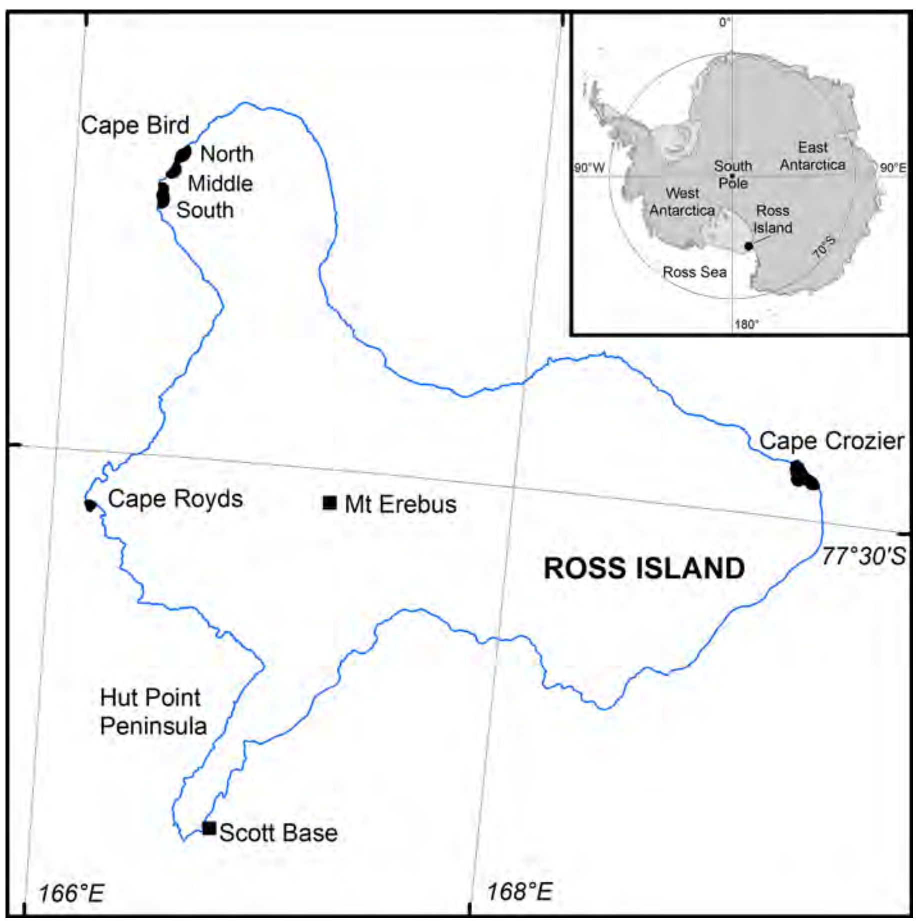


Fig. 1 Map of Ross Island showing locations of Adélie Penguin colonies where South Polar Skua populations were surveyed. *Black shading* shows the area within 1000 m of penguin subcolonies at each location (details in Fig. 2)

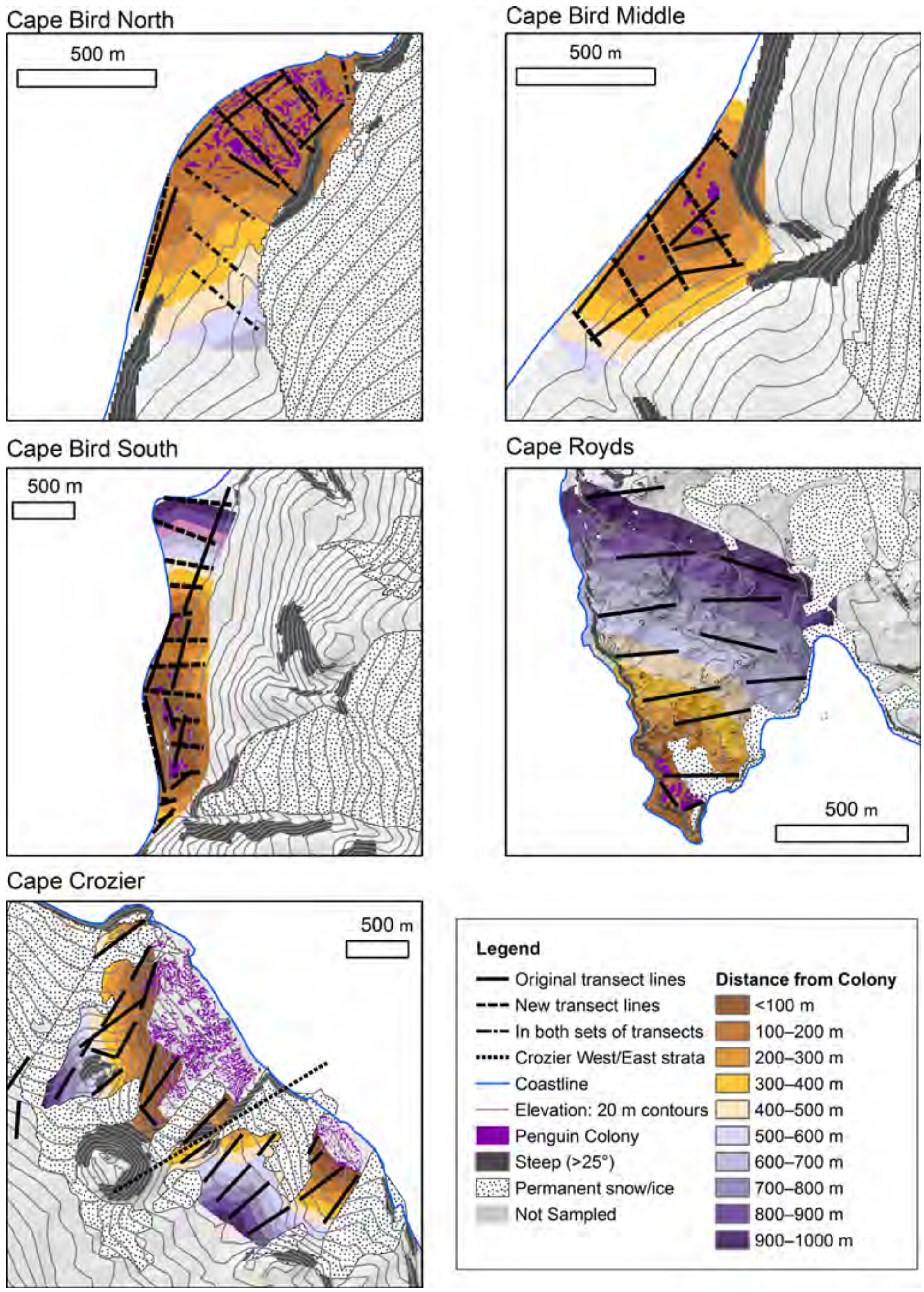


Fig. 2 Maps of Adélie Penguin colonies, with Cape Bird separated into 3 breeding locations, showing a gradient of distance up to 1000 m (see Legend) from penguin subcolonies (groups of penguin territories within a colony; see Ainley 2002). At Cape Bird, new sets of transect lines were established for the second survey in 2012–2013 and used again in 2013–2014 (with the most northerly line and the 3 most southerly lines at Cape Bird North used in both surveys). Cape Crozier was stratified into Crozier West and Crozier East at the dashed line for distance analysis. Maps are drawn to different scales

Skua surveys

Distance sampling (Buckland et al. 2001; Thomas et al. 2010) was used to estimate the skua breeding population size (i.e., the number of breeding pairs with nests) at each of the 5 locations. A set of transects was established (see below), from which an observer measured the perpendicular distance from the line to each skua nest detected. Density was estimated using a detection function fitted to these distance measurements, assuming that all skua nests on the transect line were detected and that distances to nests were measured accurately (Buckland et al. 2001). This method was chosen instead of complete counts of breeding birds in order to avoid bias resulting from expected variation in detectability of birds due to differences in survey effort and between observers, and effects of weather, topography, and temporal changes in bird behavior (Buckland et al. 2001, 2004). Whereas intensive complete count methods (e.g., by mapping all nests or breeding territories, or banding all or most individuals) can ensure that all or most breeding pairs are detected (e.g., Wood 1971), distance sampling is relatively quick and provides an estimate of detection probability and hence of the number of nests that were not observed (Bibby et al. 2000; Buckland et al. 2001; Barbraud et al. 2014).

Surveys were completed at each of the 5 locations in late November or in December of 2 consecutive breeding seasons (2011–2012 and 2012–2013), with a third season (2013–2014) at Cape Bird only (Online resource 1). We defined sampling areas (measured in hectares) at each location where we expected to find breeding skuas, based on observations in previous years, and placed sufficient transects to thoroughly cover each sampling area. At each location, 5–26 transects (1220–8340 m total transect length per location) were placed in walkable ice-free terrain within and around the penguin colony (Fig. 2). At Cape Crozier, we did not place transects within the high-density penguin colony, where few skuas nest (Ainley et al. 1990; Young 1994), so as not to disturb breeding penguins. At Cape Royds, transects were surveyed twice in each year, within one or two days. At Cape Bird a second survey was done in 2012–2013, with the transect set redesigned to reduce between-transect variation in skua sightings, by aligning most transects perpendicular to the coast so that each was likely to traverse a similar gradient of skua density (Fig. 2). The new transect set replaced the original Cape Bird transects and was used again in the 2013–2014 survey. At Cape Bird Middle, this change also reduced the degree of overlap between areas sampled by different transects from 32 to 9 % (after right truncation during data analysis; see "Distance analysis" section). At other locations, the areas sampled by different transects overlapped by 1–12 %, but some overlap is not a serious problem in distance sampling if surveying one line does not affect the distribution of animals on nearby lines (Buckland et al. 2001).

The spatial distribution of breeding skuas may be affected by topography in addition to penguin numbers (Young 1994). At Cape Bird and Cape Crozier, potential skua nesting habitat is thought to be limited by the presence of steep slopes and permanent ice and snow (Fig. 2). At these locations, most skua nests and therefore most transects were within 1000 m of penguin subcolonies. Two transects at Cape Crozier were placed 1000–1300 m from penguin subcolonies, but only 2 nests were detected on these transects in 2011 and 2012. At Cape Royds, in contrast, skuas nest at low density on a relatively flat, ice-free peninsula with penguin subcolonies concentrated at its southern tip. Eight transects were placed 1000–3000 m from the penguin subcolonies at Cape Royds, but only 1 or 2 nests were detected on these transects in 2011 and 2012, 1000–1400 m from the subcolonies. We decided to limit our sampling areas to include only skua nests within 1000 m of penguin subcolonies, because so few nests were found further away at all of the locations we studied. Setting the same restriction in future studies would confer the advantages of limiting sampling effort and making skua breeding population estimates comparable among locations. Therefore, we excluded transects placed >1000 m from penguin subcolonies at Cape Crozier and Cape Royds from analyses.

To survey breeding skuas, 2 observers walked together slowly along each transect, using a GPS and compass to maintain a straight line between pre-defined start and end points, looking and listening for skuas. When one or more skuas were seen, the presence of a nest was determined by sight or inferred from the behavior of nesting birds. The perpendicular distance from the line to each nest was measured with a digital laser range-finder (Leupold RX–IV, 8 × 28 mm, accurate to ±1 m; Leupold and Stevens, Beaverton, Oregon, USA). Distances <6 m from the survey transects were too short to measure with the range-finder, and were estimated by eye or by pacing. Surveys were done when visibility was good (≥120 m; usually unlimited). Wind speed (km h^{-1}, measured with a La Crosse Technology EA-3010U handheld anemometer; La Crosse Technology, La Crosse, Wisconsin, USA) and temperature (°C) were measured as additional covariates (Buckland et al. 2004; Marques et al. 2007), but they were not included in our analysis because exploration of the data showed that they were not consistently related to detection distances.

Distance analysis: fitting detection functions and model selection

Skua nest observations from each location were analyzed separately with program Distance version 6.2 (Thomas et al. 2010). We fitted detection functions to the data from each location, based on half-normal and hazard rate key functions (which define a basic curve shape), with and without an adjustment term based on a cosine series (which makes the shape more flexible; Buckland et al. 2001). Detection functions were accepted or rejected on the basis of model fit (Cramer von Mises and Kolmogorov–Smirnov tests) and visual examination (including quantile–quantile plots), after right truncation (i.e., deleting observations at distances beyond which estimated detection probability was below ~0.15; Buckland et al. 2001). These explorations showed that different truncation distances were suitable for transects associated with the penguin nesting locations at Cape Crozier East and West. We therefore analyzed these data as 2 separate strata and then calculated a combined Cape Crozier population estimate for each year, weighted by the area of each stratum (Buckland et al. 2001). Different truncation distances also suited surveys

Table 1 Areas used at each location for calculation of South Polar Skua breeding population sizes. Sampling area is the region at each location where we expected to find breeding skuas. Transect area is the total area surveyed from all transects at each location, after right truncation of distant observations during analysis (see Distance analysis section in "Methods")

Location	Sampling area (ha)	Transect area (ha)		Transect area as % of sampling area	
		2011–2012	2012–2013[a]	2011–2012 (%)	2012–2013[a] (%)
Cape Bird North	42.6	24.6	32.8	58	77
Cape Bird Middle	32.9	22.5	22.9	68	70
Cape Bird South	112.0	52.5	74.5	47	67
Cape Crozier West	81.8	47.5	47.5	58	58
Cape Crozier East	79.4	41.8	41.8	53	53
Cape Royds	82.8	31.9	31.9	39	39

[a] For Cape Bird in 2012–2013, areas are given only for the new set of transects. This new transect set was repeated in 2013–2014

using the original and new sets of transects, at both Cape Bird North and Cape Bird South, and therefore we analyzed these transect sets separately.

For each set of analyses (Cape Royds, Cape Crozier East and West, Cape Bird Middle, and original and new transect sets at Cape Bird North and South) we compared detection models (1) with years combined, (2) with a year covariate, and (3) stratified by year, on the basis of Akaike's Information Criterion adjusted for small sample size (AIC_c; Burnham and Anderson 2002). In (2), the same detection function was fitted to all of the data, with additional parameter(s) (one less than the number of years in the model) to vary its scale for each year. In (3), separate models were fitted for each year, each with the same key function and number of adjustment terms. For Cape Bird Middle, where surveys with original and new sets of transects were analyzed together, we also compared models with (4) a covariate reflecting individual surveys. Repeated surveys of the same transect within a year at Cape Royds were analyzed by doubling the transect length (i.e., the survey effort) and were not considered replicates (Buckland et al. 2010).

Estimates of skua nest density and breeding population size

Skua nest density estimates at each location were calculated for each year, or for each survey within year, using Distance's stratification capabilities. The corresponding skua breeding population sizes (i.e., numbers of nests or numbers of breeding pairs) were calculated as the product of density and area sampled. Sampling areas at each location (within 1000 m of the periphery of penguin subcolonies; see above and Fig. 2) excluded permanent ice and slopes >25°, which were not skua habitat, and were adjusted to account for slope on the basis of 20-m contours (LINZ Data Service 2015), using GIS. At each location, the area surveyed by transects (after right truncation as described above) was a large fraction (39–77 %) of the total area occupied by skuas (Table 1). We therefore used finite population corrections (Buckland et al. 2001) in calculating variances of density and abundance estimates.

Final density and abundance estimates and their CVs were then calculated by model-averaging (Burnham and Anderson 2002). When adding one parameter to an otherwise identical model increased AIC_c by up to 2 units (i.e., model log-likelihood increased by <2, which was insufficient to compensate for the AIC_c penalty imposed by the additional parameter), the parameter was considered uninformative (Arnold 2010) and the more highly parameterized model was excluded from model-averaging.

Count of skua nests at Cape Bird North

For comparison with the estimated number of breeding pairs at Cape Bird North only, we systematically searched known skua nesting areas on foot, and recorded the position of every nest found (i.e., mapped nests), during 20–25 December 2012. The entire region surveyed by transects was searched, except for the area around one transect that traversed the Antarctic Specially Protected Area (ASPA) No. 116 New College Valley and where few skuas previously had been recorded. This count was done by 2 observers (different from those who did the distance sampling) working in separate skua nesting areas.

Adélie Penguin colony sizes

The number of breeding pairs of Adélie Penguins at each location were estimated on a date close to 1 December in 2011, 2012, and 2013, from aerial photos taken with a digital camera (Canon EOS 1DS Mark III; see McNeill et al. (2011) and Lyver et al. (2014) for survey procedures). Emperor Penguins (*Aptenodytes forsteri*) breeding at Cape Crozier (e.g., Barber-Meyer et al. 2008) were not included in these estimates.

Table 2 Historic Adélie Penguin and South Polar Skua breeding pair counts in the Ross Island metapopulation (Beaufort Island and the Ross Island colonies in the present study) and along the Victoria Land coast

Location	Penguin counts		Skua counts		
	Year	Breeding pairs	Dates counted	Breeding pairs	Method
Cape Adare	1960–1961	289,400	15 and 25 Jan 1961	306	Territory map and estimated nest failures
Possession Island	1983–1984	110,818	9 Jan 1982	474	Ground count 2–6 h
Coulman Island—Middle	1983–1984	3989	11 Jan 1982	55	Ground count 2–6 h
Inexpressible Island	1984–1985	24,864	12 Jan 1982	60	Ground count 2–6 h
Beaufort Island	1981–1982	34,644	15 Jan 1982	209	Ground count 2–6 h
Cape Royds	1983–1984	2579	24 Dec 1981	76	Ground count 1–2 days
Cape Bird North	1982–1983	22,727	16–18 Dec 1981	167	Ground count 1–2 days
Cape Crozier (East and West)	1985–1986	167,666	Dec 1980	1000	Rebanding birds from extensive 1960s study, 14 days
Cape Hallett	1982–1983	42,931	17–20 Jan 1983	84	Territory maps
Beaufort Island	1996–1997	21,147	27 Jan 1997	53	Ground count 5 h
Edmonson Point (Wood Bay)	1996–1997	1481	Dec 1998–Feb 1999	101	Territory map
Cape Royds	2002–2003	2239	Dec 2002	29	Ground count 4 h
Cape Hallett	2013–2014	47,169[a]	Nov–Dec 2009	37	Ground count 5–6 days

Skua data from most locations are from Ainley et al. (1986), in addition to data from Edmonson Point (Pezzo et al. 2001), Beaufort Island in 1996–1997 and Cape Royds in 2002–2003 (D. G. Ainley personal communication), and Cape Hallett in 1983 (Pascoe 1984) and 2009–2010 (ATCM 2010; C. M. Harris personal communication). Methods for counting skua breeding pairs are noted, with effort (h or days) for ground counts. Penguin counts were made from aerial photos (Lyver et al. 2014 includes only 2012 counts and 1981–2012 means; P. O'B. Lyver, personal communication) or by extrapolation from partial ground counts (Cape Adare in January 1961; Reid 1962)

[a] Penguin breeding pairs at Cape Hallett were estimated at 64,041 in ATCM (2010)

Testing for a relationship between breeding pairs of skuas and Adélie Penguins

We fitted a linear mixed-effects model to our 3 years (2011–2012, 2012–2013, and 2013–2014) of estimated skua numbers at 5 locations on Ross Island (response variable) and corresponding Adélie Penguin breeding population sizes (Lyver et al. 2014; P. O'B. Lyver personal communication) (predictor variable fitted as fixed effect). Both variables were $\log_e$-transformed prior to analysis to achieve linearity and limit the leverage of outlying estimates. Both year and location were included as random effects, because the same locations were remeasured in 2 or 3 different years, and we wanted to account for between-year variation in skua numbers without testing for effects of particular years. With this model, we estimated different random intercepts for each year and each location; we did not attempt to estimate different random slopes because the dataset was sparse and unlikely to be able to support the additional parameters ($n = 12$ skua breeding pair estimates). For Cape Bird in December 2012, we used skua population estimates from the new set of transects (which were based on an improved design; see Skua Surveys above), and discarded estimates from the original transect set. Statistical significance of the fixed effect at probability level P was determined when the corresponding confidence interval (e.g., 99 % CI for $P = 0.01$) of its coefficient excluded zero. We estimated the 95 % CI for the regression line by bootstrapping from the fitted model (10,000 iterations) to incorporate random effects and residual variation. Analyses were done with functions lmer, bootMer and predict.merMod (lme4 package in program R; R Core Team 2015). We also estimated a 95 % prediction interval (95 % PI) for new skua population estimates at penguin breeding locations and years not represented in our data (Gelman and Hill 2007), by simulating new data and bootstrapping from the fitted model (10,000 simulations with functions bootMer and simulate.merMod).

Validating our model with historic skua and Adélie Penguin counts in the western Ross Sea

We tested whether past estimates of breeding skua numbers at Adélie Penguin colonies were also predicted by the regression model that we had fitted to the 2011–2012, 2012–2013, and 2013–2014 data from Ross Island (above).

We assembled published data of ground counts of skua territories and nests at 10 Adélie Penguin colonies in the Ross Island metapopulation (the 5 Ross Island locations in the present study, and Beaufort Island) and along the northern Victoria Land coast, and unpublished penguin counts from aerial photos done in the same year or within a few years of the skua counts (Table 2). Most of the published skua ground counts were done in the early 1980s by 2 people walking through each nesting area and counting, with effort per location varying from 2–6 h to 1–2 days, depending on the area needing to be covered (Table 2; Ainley et al. 1986; D. G. Ainley personal communication). At Cape Crozier, the skua breeding population was estimated during the 1960s, on the basis that ~80 % of the birds were banded (Wood 1971), and almost all nests were marked (D. G. Ainley personal communication). When known birds were identified and re-banded during 14 days in each of 1980–1983, the extent and density of the skua breeding area, and hence the breeding population size, were judged to be unchanged (Ainley et al. 1986, 1990). We also included results of ground counts at Beaufort Island in 1996–1997 and Cape Royds in 2002–2003 (D. G. Ainley personal observation), Cape Hallett in 2009–2010 (ATCM 2010) and territory mapping at Cape Adare in 1961 (with penguin counts based on partial ground counts; Reid 1962), Cape Hallett in 1983 (Pascoe 1984), and Edmonson Point in 1998–1999 (Pezzo et al. 2001) (Table 2). We plotted the historical data onto the graph showing our regression relationship, for comparison to the fitted line.

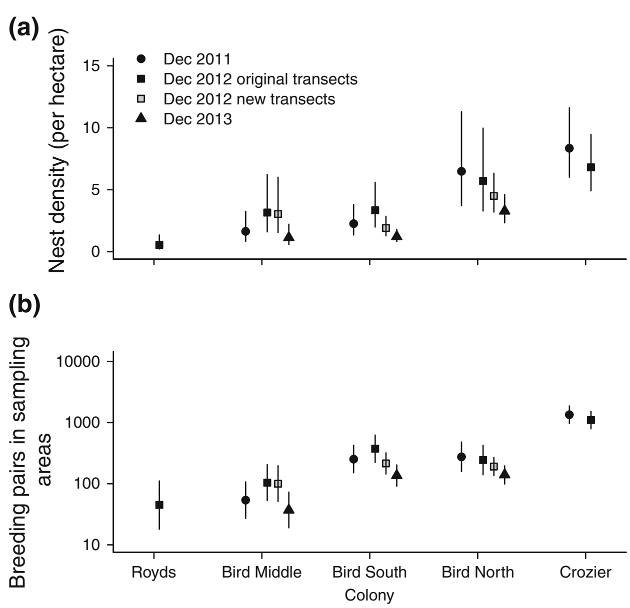


Fig. 3 Estimated **a** nest densities and **b** number of breeding pairs of South Polar Skuas in sampled areas within 1000 m of 5 Adélie Penguin breeding locations in summer 2011–2012 and 2012–2013, and at 3 locations in 2013–2014, with 95 % CIs. The horizontal axis is ordered by estimated numbers of penguins at each location. The vertical axis in (**b**) is plotted on a logarithmic scale. Estimates were not calculated for Cape Royds in 2011–2012, because no nests were found within 1000 m of the penguin colony

Estimating a modeled skua population size for the western Ross Sea

We used our regression model (Eq. 1 in "Results") to predict the average number of skua breeding pairs that should be associated with Adélie Penguin colonies in the western Ross Sea (the Ross Island metapopulation and along the northern Victoria Land coast), by applying it to mean counts (1981–2012) of penguin breeding pairs at each of 23 locations (Lyver et al. 2014). For each location, error in the prediction is given by the 95 % PI described above.

South Polar Skua numbers elsewhere in Antarctica

We reviewed published and unpublished skua population estimates to estimate the total number of South Polar Skuas in Antarctica, and hence the proportion of that total present in the Ross Sea. For the Antarctic Peninsula we supplemented estimates in Harris et al. (2015) with unpublished estimates for the central-southern Antarctic Peninsula in the Palmer Long-Term Ecological Research (LTER) database (W. R. Fraser personal communication). For East Antarctica, we compared estimates in Harris et al. (2015) and Wilson et al. (2015), and unpublished estimates from E. Woehler (personal communication). The Weddell Sea coast probably has few or no skuas, as it lacks ice-free land. For Marie Byrd and Ellsworth Lands, Harris et al. (2015) list only 2 locations where skuas breed, with no numbers available. We considered that our modeled relationship (Eq. 1 in "Results") may apply to Adélie Penguin colonies in these coastal regions, which are at similar latitudes to the northern Victoria Land populations, and also lack other large predatory and scavenging birds (notably Southern Giant Petrels and Brown Skuas) and other pygoscelid penguins. We therefore estimated skua numbers in Marie Byrd and Ellsworth Lands by applying the model to penguin breeding population estimates given in Lynch and LaRue (2014, supplementary material).

When reporting results below, we use figures and tables to show 95 % CIs and sample sizes for estimated nest densities and skua breeding population sizes. For regression results, we use a figure to illustrate the 95 % CI for the fitted line and the 95 % PI for breeding skua numbers at new locations and years, and we present standard errors (SEs) for random model coefficients in a table.

Table 3 Detection function models chosen for South Polar Skua nests at each of 5 Adélie Penguin breeding locations, and the number of observations (n) of nests before and after observations at distances greater than the truncation point were removed for analysis

Location	Transect set	Survey years	Key function	Number of cosine adjustment terms	Covariates	Truncation (m)	n total	n after truncation	% truncated
Cape Bird North	Original	2011–2012, 2012–2013	Half-normal	1	–	60	187	174	7
Cape Bird North	New	2012–2013, 2013–2014	Half-normal	0	–	90	199	192	4
Cape Bird Middle	Original and New	2011–2012, 2012–2013, 2013–2014	Half-normal	0	Survey	110	188	161	14
Cape Bird South	Original	2011–2012, 2012–2013	Half-normal	0	–	80	207	188	9
Cape Bird South	New	2012–2013, 2013–2014	Half-normal	0	–	90	183	165	10
Cape Crozier West	Original	2011–2012, 2012–2013	Hazard rate	0	–	55	639	554	13
Cape Crozier East	Original	2011–2012, 2012–2013	Half-normal	0	–	90	277	267	4
Cape Royds	Original	2012–2013	Half-normal	0	–	50	23	18	22

At Cape Bird, a new set of transects was used in the second survey in 2012–2013 and in 2013–2014. At Cape Crozier, the sampling area was stratified into Cape Crozier West and East for analysis. No estimates were possible at Cape Royds in 2011–2012, where no nests were found within 1000 m of the penguin colony

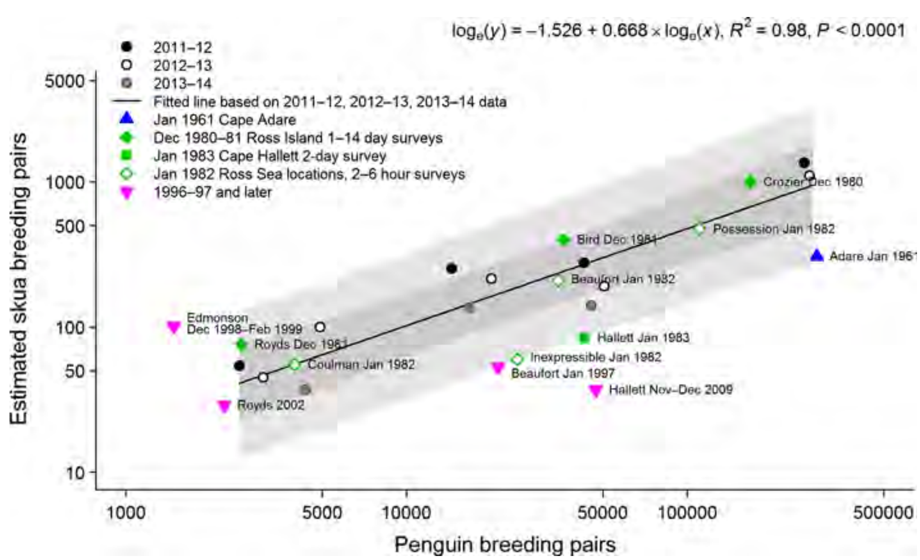


Fig. 4 Regression model relating numbers of breeding pairs of South Polar Skuas and Adélie Penguins in 2011–2012, 2012–2013, and 2013–2014, for skua breeding pairs estimated within 1000 m of penguin breeding locations at Cape Bird, Cape Crozier, and Cape Royds. *Darker shading* shows the 95 % CI for the regression; *lighter shading* shows the 95 % PI (prediction interval) for locations and years not included in the data to which the regression was fitted. Historical skua and penguin population estimates (*colored points*; Table 2) are shown for comparison but were not included in the regression. Both axes are plotted on a logarithmic scale

Table 4 Estimated random intercepts and SEs for the random effects Breeding location and Year in the linear mixed-effects model relating numbers of breeding pairs of South Polar Skuas and Adélie Penguins

Random effect	Level	Intercept (SE)
Breeding location	Cape Bird North	−0.33 (0.14)
	Cape Bird Middle	0.08 (0.14)
	Cape Bird South	0.25 (0.14)
	Cape Crozier	0.08 (0.15)
	Cape Royds	−0.08 (0.18)
Year	2011–2012	0.30 (0.14)
	2012–2013	0.08 (0.13)
	2013–2014	−0.37 (0.15)

Results

Estimates of breeding skua abundance

Skua nest density, based on model-averaging, was highest at Cape Crozier and lowest at Cape Royds (Fig. 3a). At Cape Bird, all estimates based on the new sets of transects were lower than estimates based on the original transect sets, and more or similarly precise. Precision was reasonable (CV 14–29 %) for 10 of 15 nest density estimates, and was <40 % for all estimates except at Cape Royds in 2012–2013 (CV 49 %). Only 23 nests were observed at Cape Royds in 2012–2013 (including all observations on transects repeated twice), much lower than the minimum sample size of 60–80 suggested by Buckland et al. (2001). We did not estimate nest density at Cape Royds in 2011–2012, when no nests were observed within 1000 m of the penguin colony (although mating birds were seen, egg-laying may not have commenced). The covariate 'survey' was included in one best nest-detection model, but none of the best models was stratified by year or survey (Table 3, Online resources 2, 3).

The number of breeding skuas, calculated from nest densities, ranged from 45 pairs at Cape Royds (estimated in 2012–2013 only) to 1099 and 1347 pairs at Cape Crozier in 2011–2012 and 2012–2013, respectively (Fig. 3b, Online resource 4). The total estimated number of breeding pairs of skuas in all sampling areas combined was 1930 in 2011–2012 (excluding Cape Royds) and 1866 and 1650 in 2012–2013, based on the old and new transect sets, respectively, at Cape Bird (Fig. 3b, Online resource 4).

We found 157 skua nests in systematic searching at Cape Bird North from 20 to 25 December 2012. This count was less than the corresponding breeding population size estimate (191 pairs) from distance sampling on the new transects done 2 weeks earlier (12 December 2012), but well within its 95 % CI (136–269; Fig. 3b, Online resource 4).

Table 5 Published and unpublished numbers of South Polar Skua pairs in Antarctic regions

Region	South Polar Skua pairs
Antarctic Peninsula/Scotia Sea	1979[a]
East Antarctica	480[b]
Victoria Land	4635[c]
Marie Byrd and Ellsworth Lands	1435[d]
Total	8529

[a] Estimate from Harris et al. (2015), except that for the central west coast, we replaced the Litchfield Island estimate with an estimate for the Palmer Long-Term Ecological Research study area (LTER; W. B. Fraser personal communication)

[b] Estimate from Harris et al. (2015), confirmed by Wilson et al. (2015); E. J. Woehler (personal communication) estimated 600–700 pairs including localities away from penguin colonies

[c] This study

[d] This study, i.e., we used our regression model to predict skua numbers at Adélie Penguin pairs in this region (226,584 total penguin pairs; Lynch and LaRue 2014 supplementary material for CCAMLR statistical subareas 88.2 and 88.3). Harris et al. (2015) list only two skua breeding locations, with unknown numbers

Estimating a modeled skua population size for the western Ross Sea

Skua numbers were strongly related to Adélie Penguin breeding populations at the Ross Island locations we studied in 2011–2012, 2012–2013, and 2013–2014 ($\log_e$–$\log_e$ scale; $n = 12$; 99.9 % CI of slope coefficient 0.28–1.12; $P < 0.0001$; $R^2 = 0.98$; Fig. 4, Online resource 5). Absolute values of random intercepts for the breeding locations Cape Bird North, Cape Bird South, and the years 2011–2012 and 2013–2014 were large relative to their SEs (Table 4), indicating that there was some important variation among breeding locations and years in estimated numbers of breeding skuas relative to numbers of breeding penguins.

The fitted regression equation for an average breeding location and year, i.e., considering only the fixed effect (Adélie Penguin breeding population size) is:

$$\log_e(\text{Skua breeding pairs}) = -1.526 + 0.668 \times \log_e(\text{Penguin breeding pairs}) \quad (1)$$

or

$$\text{Skua breeding pairs} = 0.218 \times \text{Penguin breeding pairs}^{0.668}, \quad (2)$$

which predicts that for every tenfold increase in penguin breeding pairs, skua breeding pairs will increase more than 4.5-fold on average (i.e., $10^{0.668} = 4.658$).

When historic skua and Adélie Penguin counts in the western Ross Sea were compared with this modeled relationship, most observations fell within its 95 % PI (Fig. 4). Most skua counts done early in the breeding season (December) and with greater degrees of effort (territory maps, 1- to 2-day surveys, and the banding study at Cape Crozier) were above the line, whereas counts done in January (after some nests may have failed) or with less effort (2–6-h surveys) were on or below the line. Cape Royds in December 2002 and Cape Hallett in November–December 2009, both based on multi-day surveys, were exceptions to this finding, as both points fell below the line.

Based on mean penguin breeding populations (1981–2012) in Lyver et al. (2014), thus including penguin colonies with and without historic or recent skua information, this regression model predicts that, on average, 4635 skua pairs breed within 1000 m of Adélie Penguin colonies in the western Ross Sea. Of this total (which excludes skua colonies not associated with penguins), ~1208 skua pairs are estimated to breed in the Ross Island metapopulation, which includes the 5 Ross Island locations in the present study and Beaufort Island, and ~3427 skua pairs are estimated to breed at the 19 penguin colonies along the northern Victoria Land coast.

Comparing the western Ross Sea skua population with populations elsewhere in Antarctica

On the basis of our estimated 4635 skua breeding pairs in the western Ross Sea (above) and published and unpublished skua population estimates elsewhere in Antarctica, it appears that ~50 % of the world South Polar Skua population may nest in the western Ross Sea (Table 5). This percentage is approximate, as it compares modeled predictions based on distance sampling with estimates (some quite old) based mostly on complete ground counts (references in Harris et al. 2015).

Discussion

Number of breeding skuas at Adélie Penguin colonies on Ross Island

The number of skuas on Ross Island has been estimated in the past at ~1500 breeding pairs (Young 1981; Ainley et al. 1986) and our estimates of the total number of skuas breeding at the 3 Adélie Penguin colonies on Ross Island (1650 and 1930 breeding pairs in 2 different years at Capes Bird, Crozier and Royds combined) are of a similar order of magnitude. All 3 estimates are dominated by the large skua population at Cape Crozier, where 1000 breeding pairs were estimated in the 1960s (Wood 1971), and the number present in 1981 was thought to be equivalent based on spread and density of the colony (Ainley et al. 1986, 1990). These historical estimates at Cape Crozier are within the 95 % CIs of our recent estimates of 1099 and 1347 breeding pairs. Differences may be the consequence of imperfect detection in earlier estimates, possible bias in our estimates, annual variation in skua breeding propensity, or long-term changes in skua numbers or distribution.

The survey method we used (i.e., distance sampling along line transects) allows counts of breeding birds to be corrected for the proportion not observed, by estimating probabilities of detection (Buckland et al. 2001). There is, however, some potential for bias in our distance-sampling estimates, for 3 reasons. First, because estimates of skua breeding pairs were the product of estimated population density and the area occupied by nesting skuas at each location, they could be affected by inaccuracies in the boundaries of these sampled areas, which were approximated based on previous observations and experience. Second, because transects were placed non-randomly owing to constraints posed by terrain and permanent ice at each location, estimated skua densities could be unrepresentative (Buckland et al. 2001) of mean densities across each sampling area. Third, errors could have been made in inferring the presence or absence of nests, which for distant birds was judged on the basis of their behavior. For example, the lower count of skua nests at Cape Bird North compared with our distance-sampling estimate in December 2012 could result from one or more factors: underestimation by the complete count method, upward bias in the distance-sampling estimate, and likely nest failures during the 2-week period between the 2 surveys. Probably only a few nests were missed by omitting the area sampled by one transect (in the ASPA) from the systematic search at Cape Bird, because only 1 or 2 nests and 2 or 3 individual skuas were recorded on that transect in each of the 2 distance-sampling surveys done in December 2012.

Relationship between breeding pairs of skuas and Adélie Penguins

We found a strong log–log linear relationship between numbers of skuas and Adélie Penguins breeding at 5 locations on Ross Island. The close coupling of these species may be driven by the combination of their predator/scavenger–prey linkage (Young 1994; Mund and Miller 1995) and mutual requirements for nesting habitat and access to marine resources (Young 1963; LaRue et al. 2013). As noted by Young (1994), while most skuas forage principally on fish caught at sea, access to penguins provides insurance when at-sea conditions inhibit foraging; in those circumstances, skuas that are able to forage in a penguin colony have a better chance of successful chick rearing. Therefore, while the number of skuas breeding may not be determined directly by the number of breeding penguins present, the increased availability of penguins as prey or otherwise a food resource at Adélie Penguin colonies of greater size augments the capacity for the site to support a greater number of skuas. For example, skuas at Edmonson Point with less access to penguins as a food source had lower breeding success compared with pairs whose territories included Adélie Penguin subcolonies (Pezzo et al. 2001), whereas skuas at Cape Crozier fed entirely within the penguin colony in January (Young and Millar 1999).

The number of breeding skuas associated with a given number of penguins is likely to vary among both locations and years, as indicated by the random intercepts in the model; for annual variation this has been shown also at Pointe Géologie (Micol and Jouventin 2001). The spatial structure of skua territories that allows them to defend and access penguins as food differs between small and large Adélie Penguin breeding locations (Young 1994), and depending on penguin colony size may or may not allow for more skuas to be resident. For example, the small penguin colony at Cape Royds (~3000 pairs) lies entirely within territories of breeding skuas that largely prevent other skuas from foraging in the colony (Young 1963). The larger Cape Bird North penguin breeding location is also within peripheral skua territories, but additional skua breeding and/or feeding territories lie between the penguin subcolonies (Young 1994). In contrast, in central parts of the largest penguin colony, at Cape Crozier (~270,000 pairs), skua breeding and feeding territories occur mainly around the outer edge, and therefore hundreds of skuas without feeding territories can forage in the central area of the colony (Müller-Schwarze and Müller-Schwarze 1973; Young and Millar 1999). Owing to this spatial structuring and to differences in foraging patterns among skuas, the relative reliance of skuas on penguins vs. marine prey varies not only among individual skuas but also within and between penguin breeding locations (Young 1994). Nesting locations also differ in the availability of alternative prey types, which we did not measure or attempt to model. For example, Emperor Penguins breed at Cape Crozier (average ~800 pairs in 2011–2013; G. Ballard et al. unpublished data) but not at the other locations we studied, and Weddell seals (*Leptonychotes weddellii*; a source of carrion) are more abundant at Cape Royds than at the other Ross Island penguin colonies (D. G. Ainley personal observation). On the other hand, the skua–penguin ratio may be restricted at locations that lack much extra space for skua breeding territories, e.g., on Beaufort Island where the penguin colony is hemmed in by glaciers (LaRue et al. 2013).

Some annual variation in numbers of breeders is expected to result from extreme weather and from large changes in the extent of sea ice cover, which affects the availability of marine prey (Young 1981; Ballerini et al. 2009; Dugger et al. 2014). For example, in 2013–2014 skua breeding propensity and productivity may have been affected by factors that also lowered Adélie Penguin productivity, which was only about half of its 20-year mean in that same 2013–2014 season (P. J. Kappes personal communication).

Extrapolating our model to the western Ross Sea

Despite the different methods used in past studies to census skua breeding pairs at Adélie Penguin breeding locations in the western Ross Sea, most of the historical estimates fell within the prediction interval of our regression model (Fig. 4). The position of each count relative to the regression line is likely to be influenced by both the census method used and the stage of the breeding season when the census was done. The expectation that greater survey effort means fewer birds are missed is consistent with the positions above the regression line of most historical skua counts based on territory maps or multi-day surveys, and the positions on or below the line of those based on brief surveys. Variation in the stages of the breeding season when populations were surveyed may compound these differences, as many of the higher-effort surveys were done early in the breeding season (November and December) and many of the lower-effort surveys were done in January after some nests had probably failed.

Known colony-specific or year-specific factors may help to explain why some historical estimates, although based on territory maps or intensive ground counts, nevertheless appear far from the regression line. The Cape Hallett ground count estimate in 2009 (27 November–2 December, done by 2 people working in separate areas; C. M. Harris personal communication) is considerably below the regression line and outside of its prediction interval. It is possible that many skuas had not yet commenced nesting when the survey was done, as in our Cape Royds survey in 2011 (3–6 December). In addition, populations of both skuas and Adélie Penguins declined during the establishment and operation of the Cape Hallett research station from 1956 to 1973, and remediation and cleanup after the station closed were not completed until 2010. Skua breeding pairs declined from 181 in 1960–1961, with fewer than 100 counted in the 4 surveys since 1968–1969 (ATCM 2010). Although penguin numbers have largely recovered (ATCM 2010; Lyver et al. 2014), these results suggest that the breeding skua population has not done so.

Data from Edmonson Point in 1998–1999 and Cape Royds in 2002 are not ideal tests of our regression model because these penguin colonies (~1500 and 2240 breeding pairs, respectively) were smaller than the smallest colony on which the model was based (∼3000 pairs at Cape Royds during our study). The Edmonson Point datum is well above the line, with an unusually high ratio of skua pairs to penguin pairs (Pezzo et al. 2001). Skuas at this location may benefit from the world's largest Emperor Penguin colony, at Cape Washington (Fretwell et al. 2012), and the presence of Weddell seals. However, breeding skuas were highly dependent on penguins for food, at least during the 1998–1999 breeding season when their diet was investigated (Pezzo et al. 2001). The Cape Royds ground count estimate from December 2002 is below the regression line but within its prediction interval. At this small penguin colony, skua numbers are likely limited by the ceiling imparted by skua territoriality, as discussed above.

Estimating a modeled skua abundance for the western Ross Sea

Some relatively small groups of skuas, suggested to be ∼20 % of the Ross Sea population, breed away from Adélie Penguin colonies (Ainley et al. 1986). In addition, although ∼80 % of the skuas at nesting colonies are breeders, only 70 % of the total population may breed in any given year, with most birds younger than 3 years remaining at sea and not visiting nesting areas (Ainley et al. 1984, 1986, 1990). Adding these 2 groups of skuas, those breeding away from penguins and those not breeding, to our modeled skua breeding population size for the western Ross Sea (4635 breeding pairs within 1000 m of Adélie Penguin colonies) results in ∼8277 pairs or 16,554 individual skuas. This total is 10 % higher than the 15,000 skuas estimated for the Ross Sea in the 1980s (Ainley et al. 1984, 1986), and does not include skuas nesting in Marie Byrd Land in the eastern Ross Sea. Therefore, the suggestion that since refuse dumps were closed in the 1990s (Mund and Miller 1995) the Ross Sea skua population may have declined to ∼11,000 birds (Pinkerton et al. 2010a, b) may be pessimistic. While decreasing near research bases, skua numbers may well have risen elsewhere, particularly in relation to strongly increasing Ross Sea Adélie Penguin populations during the current decade (Lyver et al. 2014) and the expansion of ice-free terrain (LaRue et al. 2013). On the other hand, the difference between our calculated 16,554 skuas and this lower estimate may be mitigated if the proportion of the skua population breeding at locations distant from Adélie Penguin colonies has declined, which could considerably lower our estimate. At 4 such locations, Capes Barne and Evans and Pram Point on Ross Island, and the Dailey Islands in southern McMurdo Sound, skua numbers declined between 1981 and 2002 (e.g., 88 and 41 breeding pairs in 1981 at Capes Evans and Barne, respectively, but 16 and 5 in 2002; Ainley et al. 1986; D. G. Ainley personal observation). These locations were an easy skua flight from the now closed refuse dumps at McMurdo Station and Scott Base, and the molting Weddell seals in that vicinity (now much reduced in number, Ainley et al. 2015).

South Polar Skua breeding population in the Ross Sea relative to the Antarctic population

The Ross Sea breeding South Polar Skua population includes not only skuas nesting on the coast and islands in the western Ross Sea, but also birds nesting away from penguins and at a few unsurveyed locations in the eastern Ross Sea on King Edward VII Peninsula, Marie Byrd Land. Our estimate that the western Ross Sea population may account for ∼50 % of Antarctica's breeding South Polar Skuas may be high because the relatively low search effort in much of Antarctica (Harris et al. 2015; Wilson et al. 2015) is likely to have led to population underestimates in other regions. Still, the Ross Sea breeding population appears to comprise a significant fraction of the world total (see also Wilson et al. 2015), and the smaller number of South Polar Skuas at lower latitudes is consistent with the greater competition from other avian scavengers and predators mentioned above. For perspective, 35 and 25 %, respectively, of the world's Adélie Penguin and Emperor Penguin breeding populations nest in the Ross Sea, further emphasizing the biological importance of this region (Ballard et al. 2012, with slightly modified penguin numbers in Fretwell et al. 2012; Lynch and LaRue 2014). Our calculations demonstrate the relevance of conducting surveys to better quantify the South Polar Skua population throughout the Ross Sea region, as well as elsewhere.

Conclusions and recommendations

Although most of the historic skua counts were consistent with our regression model, it was based on skua breeding population estimates from only 3 Adélie Penguin colonies, at 5 breeding locations measured over either 2 or 3 years on Ross Island. A model based on additional penguin colonies in additional years may well provide more reliable estimates of the uncertainty associated with its predictions. Ideally, we would like to survey skuas using distance sampling at multiple representative Adélie Penguin colonies of a range of sizes in the western Ross Sea. Results of any other recent counts based on skua territory mapping should have a high degree of accuracy and could also be included in the model. Revising the model by extending it beyond the Ross Island Adélie Penguin colonies will make it possible to obtain robust estimates of total skua numbers in the western Ross Sea. In addition, resurveying locations where skuas breed in the absence of penguins, especially at

Blue Glacier, the fourth largest Victoria Land colony in the 1980s (Ainley et al. 1986), would complement current model predictions. Perhaps most importantly, surveys and resurveys based on a consistent methodology will allow us to better test the change in skua numbers in accord with Adélie Penguin population changes such as those documented in the southern Ross Sea during 1981–2012 (Lyver et al. 2014) and at Pointe Géologie 1985–1999 (Micol and Jouventin 2001).

We therefore propose that a consistent, standardized distance-sampling approach be used for sampling skuas at the other locations, to minimize bias in distance-sampling estimates and permit comparison of estimated skua numbers between colonies and years. At each new colony we suggest that the following be considered during the study design:

1. Surveying during the incubation period of South Polar Skuas, so that counts can be compared between studies;
2. Conducting a preliminary survey to identify skua nesting areas within 1000 m of penguin colonies;
3. Delineating the survey area on a map and laying out transects within that area using an appropriate sampling design;
4. Accounting for the shape of Adélie Penguin colonies and topography in determining areas to be surveyed and allocation of survey effort. For example, skua distribution is likely to differ between a peninsula (like Cape Royds), a beach below cliffs or glacier (like Cape Bird), and a patchy nesting area with regions of permanent ice or steep bluffs (like Cape Crozier);
5. Stratifying according to either distance from the penguin colony (e.g., 0–500 and 500–1000 m away), identifiable sections within the nesting area, or habitat types (e.g., beaches, ridges, and slopes) before laying out transects; and
6. Where the terrain permits, choosing at random the position of at least the first transect, or the first transect within each stratum or discrete subsampling area (Buckland et al. 2001). Other transects can then be placed systematically relative to the initial transect.

In future surveys, it might also be possible to further refine estimates by using density surface modeling (Hedley and Buckland 2004) to generate a model-based abundance estimate that did not assume constant skua nest density across each sampling area. This approach would require that both the distance along the transect and the distance from the transect be recorded for each nest detected. Variation in nest density could then be modeled in relation to spatial variables (e.g., elevation, distance from the penguin colony, or distance from the coast) along the transect.

Acknowledgments We thank G. Barclay, J. Whitehead, Q. Barr-Glintborg and R. Hunter for assistance in the field, K. Drew for data compilation, Antarctica New Zealand and the U.S. Antarctic Program for logistical support, and the New Zealand Ministry for Primary Industries' Antarctic Fisheries Working Group for discussions. We are grateful to W. Fraser and E. Woehler for insights into skuas and penguins in the Antarctic Peninsula and East Antarctic regions, respectively; W. Fraser of the Palmer LTER also provided unpublished data on skua numbers in the middle portion of the Antarctic Peninsula. Similarly, we thank C. Harris for access to the Important Bird Areas data base to check on our gleaning of the literature for skua numbers in the Antarctic Peninsula. We thank reviewers and editors for their valuable comments on previous versions of this paper. This research was conducted in compliance with New Zealand Ministry of Foreign Affairs and Trade Preliminary Environmental Evaluation Notification/Permits (K121-1112; K121-1213 and K122-1415-A). It was supported by contestable Grants (C01X1226 and C01X1001) and core funding for Crown Research Institutes from the New Zealand Ministry of Business, Innovation and Employment's Science and Innovation Group, by the New Zealand Ministry for Primary Industries (MPI17238-S01-LC), by the New Zealand Department of Conservation (Science and Capability), and by Grant ANT-0944411 from the U.S. National Science Foundation. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US government.

Compliance with ethical standards

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

Human and animal rights All applicable international, national, and institutional guidelines for the care and use of animals were followed.

References

Ainley DG (2002) The Adélie Penguin: bellwether of climate change. Columbia University Press, New York

Ainley DG, O'Connor EF, Boekelheide RJ (1984) The marine ecology of birds in the Ross Sea, Antarctica. Ornithological Monographs 32. American Ornithologists' Union, Washington, DC

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

Ainley DG, Ribic CA, Wood RC (1990) A demographic study of the South Polar Skua *Catharacta maccormicki* at Cape Crozier. J Anim Ecol 59:1–20

Ainley DG, Nur N, Woehler EJ (1995) Factors affecting the distribution and size of pygoscelid penguin colonies in the Antarctic. Auk 112:171–182

Ainley DG, LaRue MA, Stirling I, Stammerjohn S, Siniff DB (2015) An apparent population decrease, or change in distribution, of Weddell seals along the Victoria Land coast. Mar Mam Sci 31:1338–1361. doi:10.1111/mms.12220

Arnold TW (2010) Uninformative parameters and model selection using Akaike's information criterion. J Wildl Manag 74:1175–1178

ATCM (2010) Final report of the thirty-third Antarctic Treaty Consultative Meeting. Punta del Este, Uruguay, 3–14 May 2010. Buenos Aires: Secretariat of the Antarctic Treaty, 2010. Measure 5 Annex. Management Plan for Antarctic Specially Protected Area (ASPA) No. 106 Cape Hallett, Northern Victoria Land,

Ross Sea (170°14′E, 72°19′S). http://www.ats.aq/documents/recatt/Att443_e.pdf. Accessed 11 Aug 2015
Ballard G, Jongsomjit D, Veloz SD, Ainley DG (2012) Coexistence of mesopredators in an intact polar ocean ecosystem: the basis for defining a Ross Sea marine protected area. Biol Conserv 156:72–82
Ballerini T, Tavecchia G, Olmastroni S, Pezzo F, Focardi S (2009) Nonlinear effects of winter sea ice on the survival probabilities of Adélie penguins. Oecologia 161:253–265
Barber-Meyer SM, Kooyman GL, Ponganis PJ (2008) Trends in western Ross Sea emperor penguin chick abundances and their relationships to climate. Antarct Sci 20:3–11
Barbraud C, Fortin M, Charbonnier Y, Delord K, Gadennne H, Thiebot J-B, Gelinaud G (2014) A comparison of direct and distance sampling methods to estimate abundance of nesting gulls. Ardeola 61:367–377
Bibby CJ, Burgess ND, Hill DA, Mustoe SH (2000) Bird census techniques. Academic Press, London
Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2001) Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, Oxford
Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2004) Advanced distance sampling: estimating abundance of biological populations. Oxford University Press, Oxford
Buckland ST, Plumptre AJ, Thomas L, Rexstad EA (2010) Design and analysis of line transect surveys for primates. Int J Primatol 31:833–847
Burger AE (1981) Food and foraging behaviour of lesser sheathbills at Marion Island. Ardea 69:167–180
Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information theoretic approach. Springer, New York
CCAMLR (2014) CCAMLR ecosystem monitoring program—standard methods. CCAMLR, Hobart, Australia. https://www.ccamlr.org/en/document/publications/ccamlr-ecosystem-monitoring-program-standard-methods. Accessed 11 Apr 2016
Croxall JP, Trathan PN, Murphy EJ (2002) Environmental change and Antarctic seabird populations. Science 297:1510–1514
Dugger KM, Ballard G, Ainley DG, Lyver POB, Schine C (2014) Adélie penguins coping with environmental change: results from a natural experiment at the edge of their breeding range. Front Ecol Evol 2:68. doi:10.3389/fevo.2014.00068
Fretwell PT, LaRue MA, Morin P, Kooyman GL, Wienecke B, Ratcliffe N, Fox AJ, Fleming AH, Porter C, Trathan PN (2012) An emperor penguin population estimate: the first global, synoptic survey of a species from space. PLoS One 7:e33751
Gelman A, Hill J (2007) Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, New York
Grilli MG (2014) Decline in numbers of Antarctic Skuas breeding at Potter Peninsula, King George Island, Antarctica. Mar Ornithol 42:161–162
Grilli MG, Libertelli M, Montalti D (2011) Diet of South Polar Skua chicks in two areas of sympatry with Brown Skua. Waterbirds 34:495–498
Harper PC (1984) The status and conservation of birds in the Ross Sea sector of Antarctica. In: Croxall JP, Evans PGH, Schreiber RW (eds) Status and conservation of the world's seabirds. International Council for Bird Preservation Technical Publication, vol 2, pp 593–608
Harris CM, Lorenz K, Fishpool LDC, Lascelles B, Cooper J, Coria NR, Croxall JP, Emmerson LM, Fraser WR, Fijn RC, Jouventin P, LaRue MA, Le Maho Y, Lynch HJ, Naveen R, Patterson-Fraser DL, Peter H-U, Poncet S, Phillips RA, Southwell CJ, van Franeker JA, Weimerskirch H, Wienecke B, Woehler EJ (2015) Important bird areas in Antarctica 2015. BirdLife International and Environmental Research & Assessment Ltd., Cambridge
Hedley SL, Buckland ST (2004) Spatial models for line transect sampling. J Agric Biol Environ Stat 9:181–199
Johnston BR (1971) Skua numbers and conservation problems at Cape Hallett, Antarctica. Nature 231:468
LaRue MA, Ainley DG, Swanson M, Dugger KM, Lyver PO, Barton K, Ballard G (2013) Climate change winners: receding ice fields facilitate colony expansion and altered dynamics in an Adélie penguin metapopulation. PLoS One 8:e60568
LINZ Data Service (2015) Land Information New Zealand. https://data.linz.govt.nz/layer/1155-nz-ross-dependency-contours-ant-150k/. Accessed 20 Oct 2015
Lynch HJ, LaRue ML (2014) First global census of the Adélie Penguin. Auk 131:457–466
Lynch HJ, Naveen R, Trathan PN, Fagan WF (2012) Spatially integrated assessment reveals widespread changes in penguin populations on the Antarctic Peninsula. Ecology 93:1367–1377
Lyver POB, Barron M, Barton KJ, Ainley DG, Pollard A, Gordon S, McNeill S, Ballard G, Wilson PR (2014) Trends in the breeding population of Adélie penguins in the Ross Sea, 1981–2012: a coincidence of climate and resource extraction effects. PLoS One 9:e91188
Marques TA, Thomas L, Fancy SG, Buckland ST (2007) Improving estimates of bird density using multiple-covariate distance sampling. Auk 124:1229–1243
McNeill SJ, Barton K, Lyver P, Pairman D (2011) Semi-automated penguin counting from digital aerial photographs. In: Proceedings of the IEEE international geoscience and remote sensing symposium 2011 (IGARSS-2011), pp 4312–4315
Micol T, Jouventin P (2001) Long-term population trends in seven Antarctic seabirds at Pointe Géologie (Terre Adélie): human impact compared with environmental change. Polar Biol 24:175–185
Müller-Schwarze D, Müller-Schwarze C (1973) Differential predation by South Polar Skuas in an Adélie penguin rookery. Condor 75:127–131
Mund MJ, Miller GD (1995) Diet of the South Polar Skua *Catharacta maccormicki* at Cape Bird, Ross Island, Antarctica. Polar Biol 15:453–455
Pascoe JG (1984) A census of the South Polar Skua at Cape Hallett, Antarctica. Notornis 31:312–319
Patterson DL, Woehler EJ, Croxall JP, Cooper J, Poncet S, Peter H-U, Hunter S, Fraser WR (2008) Breeding distribution and population status of the Northern Giant Petrel *Macronectes halli* and the Southern Giant Petrel *M. giganteus*. Mar Ornithol 36:115–124
Pezzo F, Olmastroni S, Corsolini S, Focardi S (2001) Factors affecting the breeding success of the South Polar Skua *Catharacta maccormicki* at Edmonson Point, Victoria Land, Antarctica. Polar Biol 24:389–393
Pietz PJ (1987) Feeding and nesting ecology of sympatric South Polar and Brown skuas. Auk 104:617–627
Pinkerton MH, Bradford-Grieve JM, Sanchet SM (2010a) A balanced model of the food web of the Ross Sea, Antarctica. CCAMLR Sci 17:1–31
Pinkerton MH, Bradford-Grieve J, Wilson P, Thompson D (2010b) Birds: trophic modelling of the Ross Sea. http://www.niwa.co.nz/sites/default/files/02_birds_ccamlr_final.pdf. Accessed 11 Aug 2015
R Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/. Accessed 11 Aug 2015

Reid B (1962) An assessment of the size of the Cape Adare Adélie penguin rookery and skuary—with notes on petrels. Notornis 10:98–111

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

Southwell C, Emmerson L, McKinlay J, Newbery K, Takahashi A, Kato A, Barbraud C, DeLord K, Weimerskirch H (2015) Spatially extensive standardized surveys reveal widespread, multi-decadal increase in East Antarctic Adélie penguin populations. PLoS One 10:e0139877. doi:10.1371/journal.pone.0139877

Spellerberg IF (1971) Arrival and departure of birds at McMurdo Sound, Antarctica. Emu 71:167–171

Thomas L, Buckland ST, Rexstad EA, Laake JL, Strindberg S, Hedley SL, Bishop JRB, Marques TA, Burnham KP (2010) Distance software: design and analysis of distance sampling surveys for estimating population size. J Appl Ecol 47:5–14

Trivelpiece W, Volkman NJ (1982) Feeding strategies of sympatric South Polar *Catharacta maccormicki* and Brown skuas *C. lönnbergi*. Ibis 124:50–54

Wang Z, Norman FI (1993) Timing of breeding, breeding success and chick growth in South Polar Skuas (*Catharacta maccormicki*) in the eastern Larsemann Hills, Princess Elizabeth Land, East Antarctica. Notornis 40:189–203

Wilson K-J, Turney C, Fogwill C, Hunter J (2015) Low numbers and apparent long term stability of South Polar Skuas *Stercorarius maccormicki* at Commonwealth Bay, Antarctica. Mar Ornithol 43:103–106

Woehler EJ, Cooper J, Croxall JP, Fraser WR, Kooyman GL, Miller GD, Nel DC, Patterson DL, Peter HU, Ribic CA, Salwicka K, Trivenliece WZ, Weimerskirch H (2001) A statistical assessment of the status and trends of Antarctic and Subantarctic seabirds. Workshop on southern ocean seabird populations. SCAR Breeding Bird Subgroup, Cambridge. http://www.scar.org/scar_media/documents/publications/Woehler_etal_Status_of_Seabirds_2001.pdf. Accessed 11 Apr 2016

Wood RC (1971) Population dynamics of breeding South Polar Skuas of unknown age. Auk 88:805–814

Young EC (1963) Feeding habits of the South Polar Skua *Catharacta maccormicki*. Ibis 105:301–318

Young EC (1981) The ornithology of the Ross Sea. J R Soc New Zeal 11:287–315

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

Young EC, Millar CD (1999) Skua (*Catharacta* sp.) foraging behaviour at the Cape Crozier Adélie penguin (*Pygoscelis adeliae*) colony, Ross Island, Antarctica, and implications for breeding. Notornis 46:287–297