PHILOPATRY, MATE FIDELITY, AND NEST-SITE FIDELITY FOR SOUTH POLAR SKUAS *STERCORARIUS MACCORMICKI* AT THE VESTFOLD HILLS, EAST ANTARCTICA

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ABSTRACT

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Antarctica experiences continual spatial and temporal expansions in human activities, but information to understand how resident species may be impacted is usually inadequate. We analysed resights of South Polar Skuas *Stercorarius maccormicki* that were individually marked with leg rings during 1999–2004 to compare breeding behaviours such as philopatry, adult mate fidelity, and site fidelity in the Vestfold Hills population, East Antarctica, with other regions. Despite their impressive dispersal capabilities, philopatry for birds resighted in the study area was within 4 km of the natal nest, and adult nest-fidelity was within 1 km of a previous nest site. Such faithfulness to site, combined with a life expectancy of > 25 years, indicates that displacement of returning adults and offspring from established breeding habitat may be a slow process, perhaps at generational timescales. Mate fidelity for birds ringed as breeding pairs exceeded 10 years, with individuals of pairs who failed to return or skipped breeding for single or multiple seasons being readily replaced. Resights of marked individuals also showed the Vestfold Hills receives individual skuas from distant sources; hence, we can learn more about the role of this predatory, highly migratory species in the spread of disease across landscapes and between seabird species. This study extends our understanding of skua ecology and their high nest-site and mate fidelity. Findings suggesting that their capacity to relocate in response to human disturbance may be limited.

Key words: disease, dispersal, human activity, immigration, philopatry

INTRODUCTION

As a predator and a scavenger, the highly migratory South Polar Skua *Stercorarius maccormicki* (referred to herein as skuas) plays an important role in the Antarctic ecosystem, especially during the austral summer. During this period, their return from winter foraging grounds is synchronised with the locally abundant food resources required for raising young. Skua nesting territories are often adjacent to prey aggregations at ice-free areas, both along the coast and at some inland areas (Ainley *et al.* 1986, McGarry 1988, Mehlum *et al.* 1988, Young 1994). Eggs are laid from mid-November to early December, chicks hatch some 30 days later, and they are provisioned by parents until fledging in March (Young 1977, Pacoureau *et al.* 2019). Food is largely dependent on breeding location: some populations target the eggs and young of seabirds, others hunt exclusively fish or feed on carrion, and some have taken advantage of human garbage disposal sites (Reinhardt *et al.* 1998). Where skuas are associated with penguin colonies, their numbers increase with penguin colony size (Wilson *et al.* 2017). Skua numbers can exert top-down pressure on prey abundance, especially at small seabird colonies (Morrison *et al.* 2017), and like other seabird species, they are ecosystem engineers through their nutrient inputs and physical disturbance of soils at nesting sites (Smith *et al.* 2011).

In 1956, an international mark-recapture (leg-ringing) programme was initiated to quantify skua movement patterns and demography across 16 separate geographic regions (Eklund 1961). Longitudinal observations at the largest and best-studied skuary—Cape Crozier, Ross Sea—showed that individuals were long-lived (up to 50 years or more; D. Ainley pers. comm.); tended to have high fidelity to breeding, hatching sites, and mates; had low and variable nesting success; and had high survival rates for birds older than two years (Wood 1971, Ainley 1981, Ainley *et al.* 1990). Ringing and later satellite telemetry studies revealed that all age classes migrated northward following the summer breeding season, with some individuals travelling across the equator as far as Greenland and the Bering Sea (Weimerskirch *et al.* 1985, Kopp *et al.* 2011, Weimerskirch *et al.* 2015).

The Vestfold Hills (68°35′S, 077°58′E) on the coast of Princess Elizabeth Land, East Antarctica, is a 400 km^2 ice-free oasis within which is located Davis Research Station, an Australian Antarctic station that has been permanently occupied since 1969 (Fig. 1). The ice-free landscape provides skuas with the resources required for breeding, including locally abundant food resources in the form of Adelie Penguins *Pygoscelis adeliae*, fulmarine petrels, and Weddell Seals *Leptonychotes weddellii*. The size of the Vestfold Hills skua population has been estimated to be as few as 150 breeding pairs

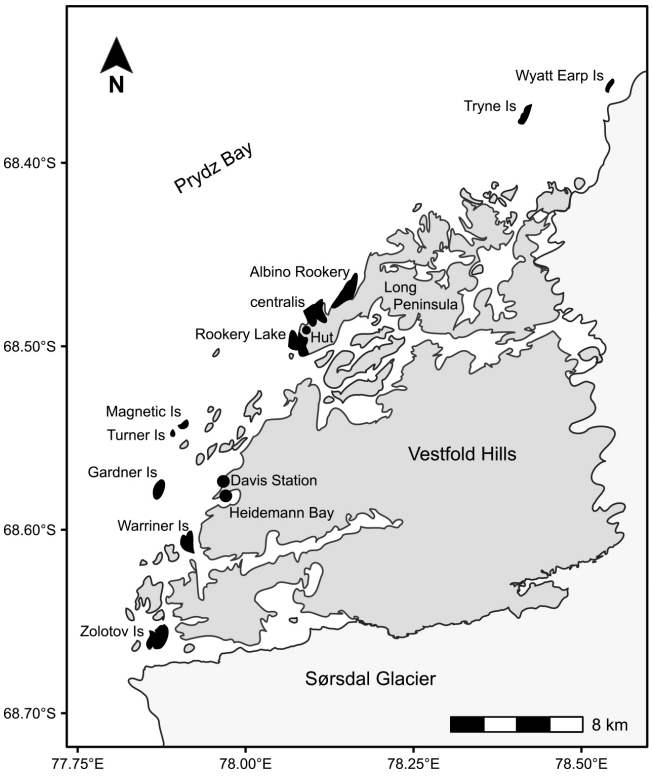

Fig. 1. Map of the Vestfold Hills showing areas where South Polar Skuas *Stercorarius maccormicki* were captured and individually marked with a leg ring. The ice-free land of Vestfold Hills is shaded black and light grey. The numbers of skuas (adults/nestlings) ringed within each area during 1999–2004 were: Wyatt Earp Island (4/0), Tryne Islands (3/1), Albino Rookery (17/22), Long Peninsula (32/0), centralis (37/20), Rookery Lake (81/36), Magnetic Island (19/10), Turner Island (11/6), Gardner Island (42/22), Davis Station (7/0), Heidemann Bay (28/0), Warriner Island (29/23), Zolotov Island (22/29), Hop Island (south of Zolotov Island, not shown on figure; 0/1).

(Woehler & Johnstone 1991), but as many as 204 active nests/pairs were observed in 2004 (GDM unpubl. data). While some focussed studies described the breeding chronology, breeding success, diet, and disease status of this population (e.g., Hull *et al.* 1994, Miller *et al.* 2008), there are aspects of the Vestfold Hills population that remain unclear.

Here we present results of skua leg-ring resights for birds marked as adults or nestlings between 1999 and 2004. The identity, related status, and behaviours of individuals were recorded in the Vestfold Hills and neighbouring areas during several consolidated resight periods over three decades. The collective data provide new information on breeding variables such as adult nest-site and mate fidelity, philopatry, and longevity. We compared those parameters with study results from South Polar Skua populations breeding elsewhere in Antarctica. This research is timely, given the expected and realised efforts for various national Antarctic programs, including Australia, to either establish, expand, and/or modernise their operations in Antarctica (Kennicutt *et al.* 2015, COMNAP 2020).

TABLE 1
Numbers of adult and nestling South Polar Skuas *Stercorarius maccormicki* ringed in the Vestfold Hills, East Antarctica, over three nesting seasons

Nesting season	Adults	Nestlings	Total
1999–2000	125	0	125
2001–2002	111	48	159
2003–2004	96	122	218
Total	332	170	502

METHODS

From November 1999 through January 2004, adult (n = 332) and nestling (n = 170) skuas were captured, leg-ringed, and released at their breeding and non-breeding sites within the Vestfold Hills (Table 1, Fig. 1). Most adult skuas (n = 294; 88.6%) were captured in association with Adelie Penguin colonies distributed from Wyatt Earp Island in the far north to Zolotov Island, south of Davis Station. One of the 170 skua nestlings was ringed on Hop Island, Rauer Group, south of the Sørsdal Glacier beyond the Vestfold Hills (Fig. 1). The rings applied were stainless-steel rings, all with the prefix number 1347, approved by the US Fish and Wildlife Service. Adult skuas were captured during egg-laying and incubation, and nestlings were ringed at their natal nest site when they weighed at least 800 g (~66% fledging weight; Hemmings 1984). As nesting seasons span the austral summer, each will be referred to by when eggs are laid, i.e. 2003/04 referred to as 2003 season.

Following the last ring application for the 2003 breeding season, there was a minimum three-year period when no effort was made to search for marked skuas. Then in January 2007, during a survey of Southern Elephant Seal *Mirounga leonina* haulout sites across the Vestfold Hills, a single ringed skua was seen on Zolotov Island and another four pairs were observed standing on rocks within the periphery of an Adelie Penguin colony in the Rookery Lake area (Figs. 1, 2). These sightings prompted further resighting efforts during 2011 and 2013. These efforts were not systematic, but they focussed along the coastal fringe and nearshore islands from the Sørsdal Glacier to the study site at centralis, near Rookery Lake (Fig. 1). The Rookery Lake, centralis, and bathing/club areas, which were designated separately during ringing, were amalgamated into

Fig. 2. From right to left, this pair of South Polar Skuas *Stercorarius maccormicki* were individually ringed #45237 and #45238 while breeding near Rookery Lake, Vestfold Hills, 29 December 2003. Seven years later (16 January 2011) they were resighted together within 1 km of the original ringing location (Photo: JvdH).

a broader "Rookery Lake" area for resighting. During 2013 and 2015–2019, the resight area was expanded to include Gardner Island, as well as Hop and Filla islands in the Rauer Group (Fig. 1). Overall, 38 confirmed sightings were made between January 2007 and 2019 for 27 of the 502 originally ringed skuas (Table 2). There were 11 sightings for which the ring numbers could not be fully deduced (e.g., 44?42), and all such sightings were discarded from further analysis.

When ringed skuas were seen, ring details were either collected directly using binoculars or deduced later from images captured using a digital camera (Fig. 2). Observation date, location, and the bird's ring number were recorded, and notes were made of the individuals' behaviour. Ringed adults seen within breeding territories and within 30 cm of another skua were considered to be a breeding pair. An adult in open sight of a nearby egg or nestling was assumed to be a parent and their status was assumed to be "breeding". A breeding-status category of "unknown" contained birds that were not assigned a status at resighting or that were bathing or roaming at the time of observation. If a ringed bird was categorised as "unknown" in a given season and was later observed and categorised as "breeding" within the same season, its status at the initial sighting was re-assigned to the "breeding" category.

Time elapsed between ringing and resighting was used to estimate minimum age and actual age for skuas ringed as adults and nestlings, respectively. Since the median age at first breeding in skuas is 6–7 years (Ainley *et al.* 1990), we added this range to the difference between the ringing date and the resight date for individuals first ringed as adults.

Over the course of this study there were different spatial scales at which skua nests were recorded. For the 1999 season, we recorded the general area of capture and whether the individual was territorial. During the 2001 and 2002 seasons, we marked and monitored verified nests, but in all later years, individual nests were not marked or monitored. Instead, we recorded the general area of resighting and the skua's breeding status at that time. Since areas such as Rookery Lake, centralis, and bathing/club areas were pooled during resights conducted from 2006 onward, we measure site fidelity at a scale of no less than 1 km.

We use the term philopatry to describe the return of nestlings to breed in the area (e.g., Rookery Lake area) where they hatched, and the term nest-site fidelity to describe breeding adults returning to the same nesting area in successive years (Coulson 2016). Although we often lack resight information over successive years, we have individual resights that were separated by just one nesting season.

RESULTS

1999–2004

Resights

Of the 125 adult skuas marked during the 1999 breeding season, 90 were known breeders and the remaining 35 were of unknown breeding status. Of these known breeders, both members of nine mated pairs were ringed (18 individuals) but the other 72 ringed adults were with unmarked mates. Of the 125 ringed adults, 59 (47.2%, including eight individuals who were of unknown breeding status in 1999) were seen again: 11 were seen nesting in both the 2001 and 2003 breeding seasons, nine were seen in 2001 only, and the remaining 39 were seen in 2003 only. Sixty-five (52%) of the ringed adults were not recorded again during the study period.

The 35 individuals of unknown breeding status mentioned above were captured away from nesting territories, either at Heidemann Bay (n = 28) or Davis Station (n = 7). These two sites are separated by about 500 m and can be considered the same as a site of origin. Seven birds (23%) were recorded breeding during one or both of the next breeding seasons at Gardner Island (n = 5), Warriner Island (n = 1), and Albino Rookery (n = 1). The Gardner and Warriner island sites are 3.5–4.0 km from the ringing sites, while Albino Rookery is ~15 km from the original ringing site. One adult of unknown status ringed in 1999 (ring #44926) was recorded at Davis Station during the 2001 breeding season without confirmed breeding status.

Of the 111 adults (representing 84 nests) ringed as breeders in the 2001 season, 69 (62%) returned to breed and were seen in the 2003 season; the remaining 42 (38%) were never recorded again during this study. Another 96 adults were ringed in 2003, with 93 of them representing 86 nests. The final three were of unknown breeding status.

Nest and mate fidelity

Of the 59 adult skuas ringed during the 1999 season that were observed in the next few seasons, 51 were resighted within their nesting territory and the other eight individuals were of unknown breeding status. All 51 breeding skuas were observed nesting within 1 km of their ringing site. Furthermore, 11 of the 59 marked individuals (including three that were of unknown breeding status in 1999) nested in both the 2001 and 2003 seasons with six of them using the same exact nest site in both years; the other five changed nest sites, but stayed within the same nest area (i.e., moved < 1 km). Of the 69 breeding skuas ringed in 2001 and who returned in 2003, 57 (82.6%) bred at the same nest site in both seasons, leaving 12 who changed nesting site.

In 1999, both individuals from ten breeding pairs were ringed. In three of those ten ringed pairs from 1999, neither individual was recorded again during this study. For another three of those pairs, both individuals returned for the 2001 and/or the 2003 study seasons: one pair from Rookery Lake (#45023 and #45024) were seen together using the same marked nest site in both seasons, while another pair ringed together on Turner Island in 1999 (#45917 and #45918) was not seen in 2001 but returned as a pair to Turner Island for the 2003 season. The pair ringed #45013 and #45014 were seen together at Rookery Lake in 1999 and again in 2003, but for the 2001 season, #45013 did not return to Rookery Lake; #45014 was joined by #45116 (ringed in 2001) within the Rookery Lake nesting area. (Thus, there were four instances when both individuals from those three pairs were present on the study area again, and they re-mated in all four occasions.) In each of the remaining four pairs ringed in 1999, only one bird in each those pairs was recorded again. In all four cases, the ringed individual that returned was seen only in the 2003 season and with a new mate in the same general nesting area as its 1999 nest; so, those four individuals changed mates, but the change was obligatory because the previous mates were unavailable. Of the four possible confirmed opportunities to change mates when both individuals were present, all four pairs chose their 1999 mate.

TABLE 2
Ring application and resight information for South Polar Skuas *Stercorarius maccormicki*[a]

Ring application details				Resight history				
Ring number[b] (mate ring number)	**Date**	**Place[c]**	**Status[d] (nest contents)**	**Date**	**Place[e]**	**Age[f] (y)**	**Status[g] (mate ring number)**	**Approximate distance from previous sighting (km)**
45165	05/02/2002	Gardner Island	N	24/12/2017	Davis Station	16	A	4
45173	13/02/2002	Turner Island	N	01/02/2018	Hawker Island	16	A	10
45180	17/02/2002	Zolotov Island	N	27/12/2013	Kazak Island	12	A	1
45310	23/01/2004	Rookery Lake	N	16/01/2019	Rookery Lake	15	BA (UM)	<1
45349	23/01/2004	Zolotov Island	N	17/12/2015	Hop Island	12	BA (Unk)	21
44750	26/01/2004	Gardner Island	N	10/01/2013	Rookery Lake	9	A	12
				16/01/2019	Rookery Lake	15	BA 1E (UM)	<1
44908 (UM)	19/11/1999	Gardner Island	A	22/11/2015	Gardner Island	22–23	A	<1
				11/02/2016	Zolotov Island	22–23	A	9
44950	05/12/1999	Heidemann Bay	A	23/11/2015	Gardner Island	22–23	A	4
				13/12/2015	Gardner Island	22–23	BA (Unk)	<1
				26/11/2017	Gardner Island	24–25	A	<1
45013 (45014)	22/12/1999	Rookery Island	BA	16/01/2019	Rookery Lake	25–26	BA 1N (UM)	<1
45038	11/12/2001	Gardner Island	BA	27/01/2017	Gardner Island	21–22	BA (UM)	<1
45083	29/12/2001	Rookery Lake	BA	16/01/2019	Rookery Lake	23–24	A	<1
45087 (45093)	31/01/2001	Rookery Lake	BA	10/01/2013	Rookery Lake	18–19	A	<1
45101 (45103)	12/01/2004	centralis	BA	31/01/2007	Rookery Lake	9–10	BA (UM)	<1
45102 (45133)	05/01/2002	Rookery Lake	BA	10/01/2013	Rookery Lake	17–18	BA 1C (45133)	<1
45133 (45102)	22/01/2002	Rookery Lake	BA	10/01/2013	Rookery Lake	17–18	BA 1C (45102)	<1
45201 (UM)	06/12/2003	Zolotov Island	BA	20/01/2007	Zolotov Island	9–10	A	0
45224	15/12/2003	Rookery Lake	BA	31/01/2007	Rookery Lake	9–10	BA (UM)	<1
				16/01/2011	Rookery Lake	13–14	A	<1
45237 (45238)	29/12/2003	centralis	BA (1E)	31/01/2007	Rookery Lake	9–10	BA (45238)	<1
				16/01/2011	Rookery Lake	13–14	BA (45238)	<1
45238 (45237)	29/12/2003	centralis	BA	31/01/2007	Rookery Lake	9–10	BA (45237)	<1
				16/01/2011	Rookery Lake	13–14	BA (45237)	<1
45239 (45255)	29/12/2003	centralis	BA	16/01/2011	Rookery Lake	13–14	BA (45253)	<1
				10/01/2013	Rookery Lake	15–16	A	<1
45253	06/01/2004	Rookery Lake	A	16/01/2011	Rookery Lake	13–14	BA (45239)	<1
				10/01/2013	Rookery Lake	15–16	BA (Unk)	<1
45240 (45241)	15/12/2003	Rookery Lake	BA (2E)	16/01/2011	Rookery Lake	14–15	A	<1
45241 (45240)	15/12/2003	Rookery Lake	BA (2E)	16/01/2011	Rookery Lake	14–15	BA (Unk)	<1
45244 (45015)	30/12/2003	Rookery Lake	BA (2C)	10/01/2013	Rookery Lake	15–16	A	<1
45252	06/01/2004	Rookery Lake	A	16/01/2011	Rookery Lake	14–15	A	<1
45255 (45223)	12/01/2004	Rookery Lake	BA (2E)	31/01/2007	Rookery Lake	9–10	BA (Unk)	<1
				16/01/2011	Rookery Lake	13–14	A	<1
				10/01/2013	Rookery Lake	15–16	A	<1
45276	14/01/2004	Rookery Lake	BA (1E)	16/01/2018	Zappert Point	20–21	A	<1
MOSKWA-DS014846	06/03/2015	Mirny Station	A	12/02/2017	Davis Station	8–9	A	695
				31/01/2018	Heidemann Bay	9–10	A	1

[a] A grey background indicates a breeding pair at original ringing and/or at resighting.
[b] All rings seen, excluding the MOSKWA ring, were prefixed 1347 and were applied at sites within the Vestfold Hills and Rauer Islands, East Antarctica, 1999–2004.
[c] Lower case place names denote an unofficial name.
[d] A = adult with unknown breeding status; BA = breeding adult; C = chick; E = egg; N = nestling
[e] The place name "Rookery Lake" in the resight history is a combination of Rookery Lake and centralis.
[f] Age provided for birds ringed as nestlings; estimated age range provided for skuas ringed as adults.
[g] UM = known to be an unmarked adult; Unk = mate not seen

The remaining 49 skuas previously ringed were all mated with unmarked individuals in 1999, so there is no way to confirm mate fidelity, nor was it possible to determine if any mate changes were by choice or by circumstance. Nevertheless, there were five confirmed cases of mate changes involving individuals ringed in 1999. Skuas #44920 and #44921 both had unmarked mates in 1999, missed 2001, and then paired with each other in 2003. Rings #44948 and #44949 were applied to skuas at Heidemann Bay in 1999, but their breeding status was unknown at the time. In 2001, the skua ringed #44948 paired with an unmarked skua on Gardner Island, then in 2003, skuas ringed #44948 and #44949 paired with each other on Gardner Island. Finally, the skuas ringed #44901 and #44984 both had unmarked mates in 1999, but then in 2003 paired with mates who had been ringed in 1999.

Of the 111 skuas ringed in 2001, 18 pairs (56%) were together again in 2003, with 14 pairs (44%) having confirmed mate changes over the same period. In nine of those mate changes, the mate from 2001 was not present in 2003, so choosing a new mate was obligatory. In another two mate changes, the 2001 mates were unmarked, but the 2003 mates were from the 2001 marked cohort; they were clearly present in that first season but were not seen in the latter season. The final three cases may have been mate changes by preference, but even those had special circumstances. In two instances, the 2003 mate had been ringed in 1999 but was not seen in 2001. In the final case, a skua ringed #45116 (marked in 2001) changed from a mate ringed #45014 in 1999 to a newly marked mate in 2003 (#45273). Meanwhile, the skua ringed #45014 returned to its 1999 mate who was not seen in 2001.

2007 onward

Nest and mate fidelity

Two pairs (rings #45102/#45133 and #45237/#45238) ringed as breeding adults in 2001 and 2003, respectively, were resighted together 9–11 years later within 1 km of their ringing sites (Table 2). Both individuals from another pair ringed in the 2003 season (#45240 and #45241) were seen within the same area again in 2011, but it was not confirmed whether these birds were a pair at resighting. One bird (#45239) of a known breeding pair (#45239 and #45255) was resighted seven years later, this time with a different ringed partner (#45253) that was not seen breeding when it was ringed in 2003. Skuas #45244 and #45087 were both breeding when ringed (with #45015 and #45093, respectively), but their breeding status was not reported when they were both resighted in 2013. Two skuas, #45013 and #45087, were paired (with #45014 and #45093, respectively) when ringed, but they were paired with different partners when resighted later.

All 17 of the resighted adults who were confirmed as breeding when ringed were seen again breeding within 1 km of their original nest site (Table 2). Three of the six ringed adults with unknown breeding status were also resighted within 1 km of their original ringing site. In contrast, three other skuas were resighted at some distance from their ringing sites. Skua #44950, ringed in 1999 as a 'roaming' individual, was seen breeding on Gardner Island (4 km from its ringing site) in November and December 2015; it was resighted again two years later at Gardner Island with unknown breeding status. Skua #44908, ringed at Gardner Island on 19 November 1999, was seen there in late 2015 with unknown breeding status; this same skua was then seen 9 km away from the 1999 sighting on Zolotov Island in early 2016, again with unknown breeding status.

Philopatry

Six (3.5%) of the 170 birds ringed as nestlings were later resighted as adults; three of these were from the 2001 cohort and three were from the 2003 cohort (Table 2). Three were observed paired with an unmarked partner and three were solitary. Of the birds observed with a partner, one skua, ringed #44750 at Gardner Island, was seen twice: the first time was when it was 9 years old at Rookery Lake, about 12 km from the original ringing location, and the second time was at Rookery Lake when it was 15 years old, this time with a nest containing a single egg (Table 2). Skua ringed #45310 was seen with an unmarked partner within its natal colony at Rookery Lake at 15 years of age. Skua #45349 was 12 years old when seen breeding at Hop Island, ~21 km from its natal location on Zolotov Island. Ringed nestlings that were later seen unpaired were 1–10 km from their natal locations (Table 2).

Immigration/emigration

No skuas ringed during this study were resighted beyond Hop Island in the Rauer Group, 21 km south of the Vestfold Hills. Over the course of this study, one bird bearing a ring inscribed MOSKWA-DS014846 was seen twice. The first time was following a storm in February 2017, when it was observed feeding on a mass of small bivalves that had washed up on the beach adjacent to Davis Station. The second time was a year later, less than 1 km from the first sighting, and its behavioural status was not recorded (Table 2). This bird was ringed as a non-breeding adult at Mirny Station (66°33′11″S, 093°00′35″E), Davis Sea, on 06 March 2015 (data source: Bird Ringing Centre of Russia) and had travelled a minimum of 695 km to reach the Vestfold Hills.

Longevity

The oldest estimated minimum age for skuas ringed as adults in the Vestfold Hills was 25 years for #45013. Three other skuas ringed as adults were between 20 and 24 years old when resighted. We were able to determine the precise ages of the six skuas ringed as nestlings, ranging from 9–15 years. The youngest known-age bird seen breeding was 12 years old.

DISCUSSION

The South Polar Skuas ringed in this study showed similar patterns of longevity, philopatry, and nest and mate fidelity reported for other Antarctic locations (e.g., Ross Island; Ainley *et al.* 1986, 1990). Our mark-recapture study provides evidence that individuals can be long-lived (up to 25 years) and are faithful to both nest location and mate, but fidelity can vary over decadal timescales. Results also showed nestlings returned to (or close to) sites where they were reared (philopatry), and most remained within 21 km from their natal sites. Despite those observations indicating that birds did not disperse widely, the degree of philopatry could not be accurately quantified from the limited number of resight histories available to us.

Although ring wear and loss can be an issue in avian studies, there was minimal loss of the stainless-steel rings used in this study (the same as those used on Ross Island; see Ainley *et al.* 1990). The rings seen on skuas in the Vestfold Hills were deployed as early as 1999, yet they were generally in good condition up to 20 years later. Most ring numbers were readily identifiable using binoculars

or could be deduced from multiple digital images (Fig. 2; van den Hoff 2017). We therefore assume that any unmarked skuas seen during this study had not been previously ringed. Moreover, skuas that were ringed within the study area should have been readily observable and individually identifiable at distant locations, as was the case for the skua we recorded that had been ringed some 700 km away.

Continuity in resighting effort is critical for gathering information on marked populations. During this study, there were breaks in resight continuity and variation in spatial coverage. Those temporal gaps in data collection combined with variable spatial coverage ultimately compromised our ability to quantify important demographic factors such as age-specific survivorship and fecundity. A similar scenario was reported for a population of Southern Giant Petrels *Macronectes giganteus* breeding at Hawker Island, Vestfold Hills (van den Hoff 2017). Nevertheless, the results from this study contribute to a baseline understanding of demographic behaviours and movements for South Polar Skuas in an area of proposed expansions in human activities.

Age at first reproduction is an important component of any population viability analysis (PVA) when attempting to estimate the extinction likelihood for disturbed versus undisturbed populations. Further, there is evidence that the frequency of immature birds attempting to breed for the first time is species-specific and density-dependent (Ferrer *et al.* 2003). For this study, the skuas ringed as nestlings were 9–16 years of age when first seen again, and the youngest bird seen breeding was 12 years old. These ages were dependent on our observation timings, which did not allow for individuals to be detected at an earlier age. By comparison, average age at first reproduction at the Cape Crozier skuary was 6–7 years for females and 8–9 years for males, but skuas as young as 4 years and older than 9 years were also observed laying for the first time (Ainley *et al.* 1990). Using age at first reproduction for Cape Crozier skuas may introduce inaccuracies into a PVA of skuas nesting within the Vestfold Hills.

Age-specific life tables for South Polar Skuas studied at Pointe Géologie and Cape Crozier indicate that mean maximum ages of 22 and 28 years, respectively, were possible (Ainley *et al.* 1990, Pacoureau *et al.* 2019), but birds of 50 years have since been seen at Cape Crozier (D. Ainley, pers. comm.). The estimated minimum age for adult skuas ringed in the Vestfold Hills fell within the range of 22–28 years (Table 2). Since this is a long-lived species, it will take many years to collect data related to demographic variables (e.g., age-specific mortality and recruitment), which inform sensitivity models and targeted conservation strategies (Finkelstein *et al.* 2010).

Young seabirds have been observed to visit several potential breeding colonies, including their natal colony, irrespective of where they may eventually breed. For example, European Herring Gull *Larus argentatus* nestlings that survived the first years of life visited their natal colony and, after having done so, some remained while some moved elsewhere to breed (references in Coulson 2016). The term natal philopatry describes the return of animals to breed in the area where they were reared, but in order to detect and quantify this behaviour, it is important to consistently survey within and beyond the immediate study area (Ainley *et al.* 1986, Coulson 2016). The skua nestlings resighted during this study were ringed for a study of blood parasites and viral antibodies (Jones *et al.* 2002, Miller *et al.* 2008), which was not principally a demographic or immigration/emigration study. Consequently, the spatial area across which ringed skuas were resighted in the later years did not include all ringing locations or known breeding locations within the Vestfold Hills and beyond. Nevertheless, except for Albino Rookery, Magnetic Island, and Turner Island (Fig. 1), we surveyed much of the original ringing area between Rookery Lake and Zolotov Island, close to the terminus of the Sørsdal Glacier (Fig. 1). Our very limited observations of three of 170 ringed nestlings indicated that a proportion of skuas that hatch in Vestfold Hills exhibit natal philopatry. Although that number of resights was very low and the resight effort was uneven between years, we were also able to show that ringed nestlings recruit outside their natal area to at least 21 km from the Vestfold Hills, at Hop Island (Table 2). Philopatry at Cape Crozier was very high compared with our study site—all but a few Cape Crozier skua nestlings were later seen breeding at Cape Crozier (Ainley *et al.* 1986). However, the skuas at nearby Cape Bird, Ross Island, were less faithful to their nesting areas (Ainley *et al.* 1990), a result indicating that the degree of philopatry for South Polar Skuas could depend on location/density, reiterating the point made above regarding the importance of collecting local data rather than using model parameters derived for other populations.

Results from this study confirm that skuas breed at the Vestfold Hills, and like breeding skuas elsewhere, the Vestfold Hills population shows varying levels of fidelity toward both mate and nest area. This is called nesting philopatry or fidelity. All 51 breeding adults ringed in 1999 who returned to the Vestfold Hills returned to their ringing site, and 57 (82.6%) of 69 returning breeders who were ringed in 2001 returned to the same nest in 2003. The remaining 12 individuals moved nest sites only short distances between seasons. No skuas ringed when breeding were resighted more than 1 km from the ringing site (Table 2), and nest area fidelity proved to be both high (> 80%) for this study and similar to Cape Crozier skuas (87%; Ainley *et al.* 1990). The individuals that changed mates in the short term were confirmed to have found another mate when their previous (ringed) partner was not detected (i.e., it failed to return to the nest site), and the same was true over the long term. Pairs in which one partner failed to return readily replaced lost partners (Table 2). Whether replacement of non-returnees was prompt, as it was at other breeding locations (Eklund 1961, Wood 1971, Ainley *et al.* 1990, Pietz & Parmelee 1994), could not be determined from our resight histories (Table 2). However, pairs for which both partners survived year to year appeared to remain faithful to one another for as long as 11 years. At Cape Crozier mate fidelity was 98.5% in two consecutive years (Wood 1971), and three pairs stayed together for 10 or more years (Ainley *et al.* 1990).

Individual skuas of various ages have been ringed across their Antarctic distribution, yet there are very few records of permanent long-range movements between breeding populations (see references in Eklund 1961, Wood 1971, Weimerskirch *et al.* 1985). Perhaps this is because the status of recaptured birds was rarely documented. For example, of the 971 skuas ringed at Pointe Géologie (some as adults and some as juveniles), nine were resighted outside the ringing location but their status was not reported, aside from one bird that had hatched there and was seen breeding on Possession Island, Indian Ocean, 5000 km away (Weimerskirch *et al.* 1985). Other skuas ringed at Pointe Géologie have been seen at Cape Royds and Cape Crozier, Ross Island, but it is unknown whether the birds were transients when ringed or held territories (D. Ainley,

pers. comm.). This is a curious result because, despite the apparent rarity of long-distance exchange between skua populations from the ringing studies, the short branches of this species' phylogenetic history indicate past rapid colonisation and widespread interactions among populations (Ritz *et al.* 2008).

Beyond the Vestfold Hills and Rauer Islands, South Polar Skuas are known to nest close to inhabited stations where ornithological research, including ringing studies, has been undertaken (e.g., Ross Island by Ainley *et al.* (1990), Larsemann Hills by Wang & Norman 1993, Haswell Islands by Golubev (2018)). During this study, we twice recorded a ringed South Polar Skua of unknown age and breeding status that had been ringed on 06 March 2015 at Mirny Station, Davis Sea, some 695 km away (Table 2). Since this bird was deemed to be an adult when ringed, it is impossible to be certain of its provenance, i.e. whether its sighting at the Vestfold Hills is an example of philopatry or immigration from the Haswell Archipelago. That is, it is impossible to determine whether this bird was returning to its natal colony or if it was searching for a new nesting location. Its appearance in our study area during two consecutive breeding seasons does however indicate the possibility of future breeding in that area.

Possible consequences of human disturbance

Natal and breeding philopatry can be thought of as collective knowledge, with inherent advantages and disadvantages. For example, persistence toward a specific nesting site attests to the site's suitability for breeding but it also places individuals/populations at risk of abrupt negative change (Coulson 2016), owing perhaps to the presence and activities of humans. Skua populations have been subjected to a range of impacts during the comparably short human occupation of Antarctica. Some human activities, such as the establishment of open refuse disposal sites and the slaughter of seals for dog food, have had positive impacts. The shooting of individual skuas, their capture for scientific purposes, and introductions of disease had clear negative outcomes, but the highest impacts on skuas were from construction-related habitat modifications and fisheries operations (Hemmings 1984). One suggested cause of short-range skua nest relocations in the Larsemann Hills was human activities associated with station construction and its operations (Wang *et al.* 1996 and references therein). Another seabird with apparently high site fidelity and disturbance potential, the Southern Giant Petrel, has been shown to respond similarly to human activities as did the skuas of the Larsemann Hills (Braun *et al.* 2018). Some individual Southern Giant Petrels shifted their nests to undisturbed sites while others returned to their original nest locations, a behaviour likely indicative of habituation, although habituated birds apparently very rarely raised a chick successfully (Braun *et al.* 2018). Clearly, without appropriate study design, negative outcomes can be veiled beneath apparently positive or neutral responses.

As human activities in Antarctica increase, potential mitigation and monitoring actions associated with those activities will need to consider how species and species complexes might respond in both the short term (e.g., reaction to stimuli) and the long term (e.g., distribution and demographics). Skua longevity, natal and breeding philopatry, and mate fidelity combine to ensure that the Vestfold Hills skuas nest almost continuously close to quality breeding locations, such as Adelie Penguin colonies at Rookery Lake (see Wilson *et al.* 2017 for skua-penguin nesting ratios) or Snow Petrel *Pagodroma nivea* aggregations further afield. It remains to be determined how future human activities within the Vestfold Hills might alter those relationships. However, it is clear that one of the main objectives of the Antarctic Treaty is to avoid detrimental changes in the distribution, abundance, or productivity of species or populations of species of fauna and flora (ATS 2021). The data presented herein provide a baseline against which particular skua responses can be quantified and mitigation measures assessed.

Finally, highly migratory predators in the upper trophic levels, such as South Polar Skuas, not only bioaccumulate toxins and bring them into Antarctica from afar (Bengston Nash *et al.* 2010), they are also potentially important vectors of disease over short and long distances (Weimerskirch *et al.* 1985, Daszak *et al.* 2000, Kopp *et al.* 2011, Weimerskirch *et al.* 2015, Smeele *et al.* 2018). Although Antarctica currently is reasonably isolated from the main pollutant sources (Bengston Nash *et al.* 2010), wildlife of the continent is particularly vulnerable to introductions of infectious diseases such as avian cholera (Gamble *et al.* 2020). Already the negative effects of avian cholera outbreaks have been felt across seabird species at Hope Bay, Antarctic Peninsula, where skua and Adelie Penguin carcasses were found together around ponds perhaps used as skua club bathing areas (Leotta *et al.* 2006). When sampled in the early 2000s, the skuas at the Vestfold Hills were free of viruses and ticks, but antibodies to infectious disease were present (Miller *et al.* 2008). Future increases in travel to ice-free Antarctica are more likely to include air transport, making the introduction, monitoring, and managing of exotic disease outbreaks an important consideration for Antarctic biosecurity (Barbosa *et al.* 2021).

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