

THE ANNUAL CYCLE OF SOUTHERN GIANT PETRELS *MACRONECTES GIGANTEUS* IN EAST ANTARCTICA

SASA OTOVIC¹, MADALYN RILEY¹, IAN HAY², JOHN MCKINLAY², JOHN VAN DEN HOFF² & BARBARA WIENECKE²

¹IMAS, 20 Castray Esplanade, Battery Point 7001, Tasmania, Australia

²Australian Antarctic Division, 203 Channel Highway, Kingston, Tasmania 7050, Australia
(barbara.wienecke@aad.gov.au)

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SUMMARY

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We report the first results from a 3-year study of the annual cycle of Southern Giant Petrels *Macronectes giganteus* in two colonies in East Antarctica. We tested the utility of a system of automated cameras that monitored and recorded events in the colonies year-round. Based on the collected images, we determined a detailed phenology of breeding events and activities throughout winter. The timing of some portions of the annual cycle (e.g., laying dates) were similar, whereas other aspects of the annual cycle differed between locations (e.g., pair formation and length of the non-brooding guard phase). Comparisons with other breeding locations throughout the species' range showed that lay dates vary with latitude but are synchronous at each site.

Key words: Southern Giant Petrels, *Macronectes giganteus*, phenology, automated cameras, East Antarctica

INTRODUCTION

The annual breeding cycle of seabirds reflects the seasonality of their environments (Visser & Both 2005). High latitude seabirds breed primarily during the relatively short austral summer, and some species migrate to warmer climates to escape challenging winter conditions. In Antarctica, there are distinct advantages to breeding during the summer. Reduced sea ice coverage increases access to foraging grounds when food is abundant, ambient temperatures are comparatively mild (near or above freezing), and blizzards are relatively infrequent. Furthermore, in the high Antarctic, surface nesting flying seabirds need snow-free areas to construct their nests, and pebbles are generally the only nest building material available.

Because species respond differently to climate change drivers, long-term data sets are needed to evaluate a species' ability to respond and adapt to new environmental conditions. Such information could be useful in conservation and management. Collecting suitable data can be challenging when dealing with populations at the extremes of their range, where site access is often difficult; when populations are small, individuals can be easily disturbed. In East Antarctica, Southern Giant Petrels *Macronectes giganteus* (hereafter SGP) are at the southernmost extent of their breeding range; currently there are only four known colonies ranging in size from 2–4 to about 200 pairs (Wienecke *et al.* 2009). In the past, visits to some colonies occurred sporadically and at different times of the season, mainly to band chicks. Thus, a good understanding of the annual cycle of these birds is lacking (Wienecke *et al.* 2009).

Breeding colonies of SGPs extend from Gough Island (40.5°S) at the northern extreme to the East Antarctic coastline at 68°S in the south (Patterson *et al.* 2008). However, much of the knowledge of SGP breeding activities and phenology is based on a few studies at colonies in the mid-latitudes of their range, such as Îles Crozet (Voisin 1988), Signy Island (Conroy 1972), Marion Island (Cooper *et al.* 2001), and South Georgia (Hunter 1984).

Given SGPs' susceptibility to human disturbances (Cooper *et al.* 2001), new and preferably non-invasive technologies might well be preferred to examine their phenology (Wienecke *et al.* 2009) and to document, in detail, changes in environmental parameters and possible shifts in phenology, breeding success, and other variables. In this study, we tested the usefulness of automated nest cameras developed for the study of Adélie Penguins *Pygoscelis adeliae* (Newbery & Southwell 2009) to gather data on the annual cycle of SGPs in East Antarctica at two sites. Automated cameras can be used in existing monitoring programs to deliver more detailed, year-round data, and are also valuable as the sole source of information at sites

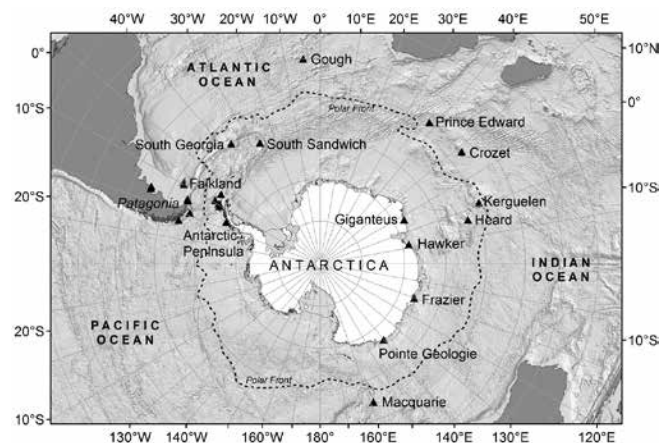


Fig. 1. Map showing the circumpolar breeding locations of the Southern Giant Petrel *M. giganteus*. Not all locations are shown. For further detail see Patterson *et al.* (2008). The average position of the Antarctic Polar Front is shown as a dotted line (Orsi *et al.* 1995).

that are visited infrequently. The SGP populations occupying the two small islands in our study, Hawker and Nelly (Fig. 1), have been visited intermittently since the early 1960s, but information about the phenology of SGP has been collected only on an *ad hoc* basis (Creuwels *et al.* 2005, Wienecke *et al.* 2009 and references therein).

The aims of the study were: 1) to evaluate the effectiveness of an automated camera system for long-term monitoring in a challenging environment; and 2) to document the little-known breeding cycle of SGPs in East Antarctica and to compare the phenology of key activities in the annual cycle of SGPs at two study sites. Finally, we briefly compared the results from this study with published data from other breeding locations.

METHODS

Study sites

This study was undertaken at two of the southern-most breeding localities of SGPs, Hawker and Nelly islands (see Patterson *et al.* 2008), located in East Antarctica. Both study sites are designated as an Antarctic Specially Protected Area (ASPA). Accordingly, Australian Antarctic Treaty (Environmental Protection) Act 1980 permit number ATEP 10-11-3154 was issued by the Australian

Government Department of Sustainability, Water, Population and Communities to carry out this research in the protected areas.

Site One was Hawker Island (68°35'S, 77°50'E, ASPA 167, Fig. 1), a 2.2 km² island situated on the coastal fringe of the Vestfold Hills, Prydz Bay. From 1972 to 2007, 20 ± 6 (range 10–31) eggs were laid at the single SGP colony located at the northern end of the island (Wienecke *et al.* 2002 and references therein; Australian Antarctic Division, unpubl. data). Potential food resources near the SGP colony include breeding colonies of Adélie Penguins and Cape Petrels *Daption capense*. Weddell Seals *Leptonychotes weddellii*, another potential food source (e.g., placenta), breed on the sea-ice in the nearby fjords of the Vestfold Hills and along the coast line. Mean monthly temperatures range from 3.2 °C (January) to -20.8 °C (August). On average, <1 sunshine hour per day is experienced over the period May to July, inclusive (<http://www.bom.gov.au/climate/data/>; accessed 23 June 2017). On 8 October 2009, three cameras were positioned at the periphery of the single SGP colony. For the purposes of this study, only data that were concurrent with those collected at Nelly Island were analysed.

Site Two was Nelly Island (66°14'S, 110°10'E, ASPA 160, Fig. 1), the largest (0.4 km²) of the three Frazier Islands, positioned approximately 13 km offshore where SGPs breed in several

TABLE 1
Descriptions of key events and event periods in the annual cycle of Southern Giant Petrels *M. giganteus*

Event/Activity	Description	Comments/Observations
First Adult On Nest	First adult observed sitting within a known nest area	Nest-specific event (date recorded); may be indicative of future breeding attempt
Pair Formation	Two adults sitting on or near known nest	Nest-specific event (date recorded); pairs form and copulations may be observed; not all will continue to laying
Prelay Period*	Period from first adult on nest to pair formation. Either or both adults intermittently occupy nest	Various behaviours can be observed, including courtship, nest building, copulation
Egg Laying	Eggs not visible but from a certain day onward nest continuously occupied by at least one sitting adult	First day of a period during which nest is continuously occupied
Incubation Period*	Period from laying to hatching; nest continuously occupied by at least one sitting adult	Hatching date minus laying date
Hatching	Sitting adult changes body attitude; wings separate, tail exposed and body appears to flatten	Egg shell fragments ejected from nest; distinct change in body attitude of parent bird: adult fluffs feathers, spreads out wings and flattens body
Brooding	Period from hatching to the day until chick attains homeothermy. Occurs in two phases: Brooding = Parent's body covers chick entirely	Chick not yet homeothermic; chick becomes more visible with age
Guard	Guard: Parent still present but chick no longer covered by parent and clearly visible next to adult	Chick can regulate its body temperature but at least one parent still present usually next to the nest
Guard Period*	Period during which both chick and at least one parent are present	Nest-specific event, period ends when adults absent from nest for at least 24 hours. Chick has no contact with adult body in 9 consecutive images (~ 1 full day)
Last Adult on Nest	Last time breeding adult is observed sitting on nest	Adult may be outside the field of view. Important for images that are near the edge of the field of view
Last Chick Seen	Last chick/fledgling observed	Fledglings are very mobile and may move off the nest and out of view of the camera for several days before leaving
Chick Rearing Period*	Time from hatching to the chick leaving (last seen) the colony	Rough estimate due to caveats described above

* Duration of periods derived from recorded dates of observed events/activities

sub-colonies (e.g., Crewels *et al.* 2005). A local Adélie Penguin colony offers potential food resources, as do various breeding sites of Weddell seals. Incidental observations off Nelly Islands confirmed that SGPs also use marine resources and hunt for fish (JVDH, pers. obs.). The cameras were deployed at Nelly Island on 12 December 2011 during incubation; the four monitored sub-colonies collectively comprised approximately 80 birds on nests. Mean monthly temperatures range from 2.3 °C in January to -18.8 °C in August. Similar to Hawker Island, there is <1 sunshine hour per day from May to July, inclusive (<http://www.bom.gov.au/climate/data/>, accessed 23 June 2017).

Data Collection

Seven automated nest cameras, three on Hawker Island and four on Nelly Island, recorded the activities of SGPs over three consecutive breeding seasons (2012/13 to 2014/15). Each camera system included a DSLR camera placed inside a weatherproof housing fitted with an optical window and an external movable protective shutter (Newbery & Southwell 2009). The system was mounted on a surveyor's tripod and anchored to the ground using matting weighed down by rocks. Solar panels provided energy throughout the summer, and charged the external batteries that kept the cameras operational during winter. Nest cameras were pre-programmed through an automated shutter controller (Newbery & Southwell

2009) to take images at pre-set local times (Davis = UTC + 7; Casey = UTC + 8), accommodating annual changes in day length and light levels. For example, one image per day was taken at solar midday on every day of the year. During the winter darkness from 1 June to 30 August, this was the only image per day. As day length increased, the number of images taken per day increased to six from 1 September to 30 October, nine from 1 November to 30 March, and was reduced to seven from 1 April to 30 May.

Cameras were positioned to minimise snow accumulation and, at Hawker Island, to capture the maximal number of nests while minimising image overlap. Each camera was numbered; the memory cards had sufficient memory capacity to store images until the cards/cameras could be retrieved. At Hawker Island, the cameras were serviced annually and the memory cards were retrieved and replaced. At Nelly Island, the four cameras remained in the field un-serviced for the duration of their deployment. To minimise human disturbance to SGPs, all camera servicing and card retrievals occurred at Hawker Island outside the breeding season in May/June. However, at Nelly Island, the camera systems were deployed and retrieved during December and January, respectively, due to logistical necessity.

One objective of this study was to examine the usefulness of cameras in determining phenology; we did not conduct population counts. At Hawker Island, approximately 90% of all nests were visible in the images; in contrast, the cameras at Nelly Island only partially covered the total SGP breeding area due to the island's topography. We also monitored only clearly visible nests occupied by *bona fide* breeders (i.e., nests that contained a chick in February). In total, we monitored 24 nests at Hawker Island and 20 nests at Nelly Island.

Image analysis

We adapted an open source image analysis program, *Penguin Nest Picture Analyser* Version 4 (Newbery 2016), for this study. All images were imported into the software and visually assessed for quality. Images that were significantly out of focus or underexposed were discarded from analyses, as were images taken when the lens cover failed or when considerable lens-flare obscured the image content.

The dates for various breeding activities/events were recorded for each nest throughout the breeding season to determine the timing of key events (e.g., onset of laying), and to estimate the duration of certain periods (e.g., incubation). Descriptions of activities were adapted from Conroy (1972) and Hunter (1984) (Table 1). The guard period includes two phases: 1) the brooding guard, when chicks are still thermally dependent on their parents; and 2) the non-brooding guard, when chicks reach homeothermy and are only covered in inclement weather (Rice & Kenyon 1962, Cooper *et al.* 2001). We refer to the former as “brood stage” and the latter as “guard stage.”

A nest-specific template of active nests was created for each camera. Nests containing chicks in mid-February were circled in the software for each year and pooled across years to obtain the number and location of all potentially active nests. Only nests that were clearly visible in the images were considered; some active nests were partially obscured by rocks, which made the determination of the timing of certain events impossible. Nests were individually numbered; the numbers remained constant throughout the study period regardless of the level of activity in a given season. A

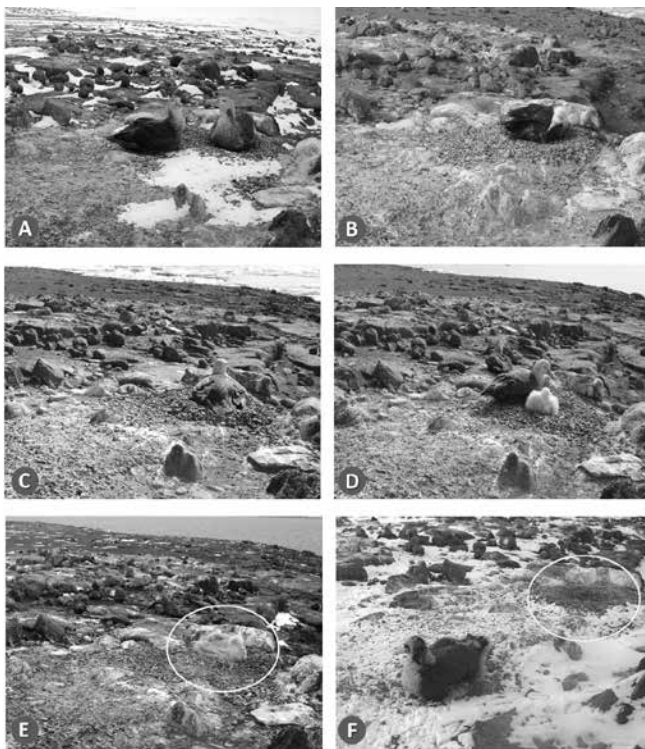


Fig. 2. Example images taken during the various stages of the breeding period of Southern Giant Petrel *M. giganteus* at the same nest. (A) Pair formation: both parents occupy the nest; (B) Hatching: the chick's beak is just visible next to the tip of the parent's beak; (C) Brooding: the chick is entirely covered by the parent; (D) Start of guard: the chick now regulates its own body temperature and is left for increasingly longer periods by itself on the nest; (E) Chick by itself on nest while both parents are foraging; (F) Near fledging: the chick has started to moult into its flight feathers and has moved off the nest. The circle in (E) and (F) indicates nest position.

template identifying all observed nests was laid over each image to ascertain the activities for individual nests. This approach allowed a quick narrowing down of key periods and enabled rapid scanning of a large number of images. Activities and contents of marked nests were recorded for later statistical analyses (Table 1, Fig. 2).

Exploratory statistics

For statistical purposes, we needed “date” to be a continuous variable. Since the breeding season of SGPs spans two calendar years, observation dates were converted to days since 31 May, i.e., June 1 became day 1 in the annual cycle, and 31 May of the following year was day 365. The last day of May was chosen after scans of multiple images revealed a period in early winter when SGP attendance at colonies was minimal (see Results).

The observations arising from this study provide some challenges for statistical analysis. A key feature of the data is that the phenological events of interest are clearly related, since the samples at any point of the breeding cycle are dependent on those sampled at previous times. This suggests that a MANOVA-type approach would be appropriate to account for this dependence among response variables. However, this would have been problematic for several reasons, including: i) our sample sizes were too small to accommodate all dependent responses simultaneously; ii) only some stages of the annual cycle are wholly dependent on those that come before; iii) it was difficult to identify and track individuals, and a repeated measures MANOVA relies on individuals being measured at each stage of the annual cycle; and, iv) each stage usually involves some natural attrition (e.g., death of a chick), so observations become “censored.”

Due to these difficulties, our preferred approach was to treat each stage as independent, and to use two-way ANOVAs to assess

temporal (*year*) and geographic (*island*) differences—and the possibility of an interaction between these terms—for a range of response variables corresponding to key events. Model diagnostics revealed that the usual assumptions of ANOVA were met. Therefore, more flexible and generalised linear model approaches proved unnecessary. Model assumptions were checked by developing standard residual diagnostics (plots of residuals against predictors and fitted values, and Normal quantile plots), all of which proved satisfactory (Appendix 1).

Assuming independence between response variables, we acknowledge that conducting several separate analyses will increase Type I error rates when the suite of models we fit are considered as a whole (Armstrong 2014). One of the objectives of the present study was to use the automated camera as a proof of concept for obtaining suitable observations for long-term monitoring, and consequently we place less importance on formal treatments of significance. Nonetheless, in the spirit of Bonferroni, we restrict our interpretation to only those ANOVA effects considered strongly significant ($P < 0.001$), whilst understanding that doing so may increase the chance of committing Type II error (Gelman *et al.* 2012). Rather than present individual ANOVA tables for each variable considered, many of which were non-significant even at conventional levels, we instead present a summary table of P -values from all models (Appendix 1), and the full ANOVA tables for the two analyses where one or more effects were highly significant ($P < 0.001$) (Appendix 2). Means \pm SD are given unless stated otherwise.

Geographic comparisons

Dates for egg-laying and incubation at other colonies were taken from published studies. Where a range in egg-laying was reported, the first date within the range was considered representative of

TABLE 2
Mean dates (\pm SD), durations, and inter-island differences for key activities and periods in the annual cycle of Southern Giant Petrels *M. giganteus* at their East Antarctic breeding colonies at Hawker and Nelly islands

Event/Activity	Hawker Island		Nelly Island		Inter-Island
	Mean Date	Mean Duration (d)	Mean Date	Mean Duration (d)	Difference Hawker Island:Nelly Island (d)
First Adult on Nest	17 Jul \pm 28		8 Jul \pm 25		– 9
Pair Formation	20 Aug \pm 26		10 Aug \pm 27		– 10
Pre-Laying Period		102 \pm 30		83 \pm 28	
Egg Laying	27 Oct \pm 3		27 Oct \pm 4		+/-0
Incubation Period		57 \pm 2		59 \pm 5	
Hatching	22 Dec \pm 4		24 Dec \pm 5		+ 2
Brooding Period		18 \pm 3		16 \pm 4	
Guard	26 Jan \pm 6	17 \pm 6	18 Jan \pm 8	8 \pm 6	– 8
Guard Period ^a		35 \pm 6		24 \pm 7	– 11
Last Adult on Nest	20 Feb \pm 10		28 Feb \pm 39		+ 8
Last Chick in Colony	18 Apr \pm 6		6 Apr \pm 12		– 12
Chick Rearing Period ^b		116 \pm 6		107 \pm 12	

^a Number of days from onset of brooding to end of guard

^b Number of days between hatching and fledging

first egg observed. Where multiple studies contributed data over multiple years at one location, the mean onset date and variance were calculated. Some colonies were regarded as representative of a broader breeding location. For example, data gathered at Arce Island (45°00'S, 65°30'W) and Gran Robredo (45°08'S, 66°03'W), Argentina, were deemed to be representative of the colonies in northern Patagonia, and Bird Island (54° 00'S, 38°03'W) was considered to be representative of nearby South Georgia.

RESULTS

Camera efficacy

Over 17000 digital images were compiled over three years (2012–2015) at Hawker Island and Nelly Island. Only a few images were unusable due to the factors mentioned above. For example, at Hawker Island one camera took 2123 images in 2013. Of those, three images had been affected by lens flare, eight were black because the shutter had frozen shut, and 33 had been taken when it was too dark. Thus, 44 images (<0.5%) in this round had to be discarded. However, on all days, except those when the shutter had frozen ($n = 3$), the loss of one image was not an issue because several other images taken on the same days were of excellent quality.

Colony activities

Figure 2 provides representative images for the key breeding activities described in Table 1, such as pair formation (Fig. 2A)

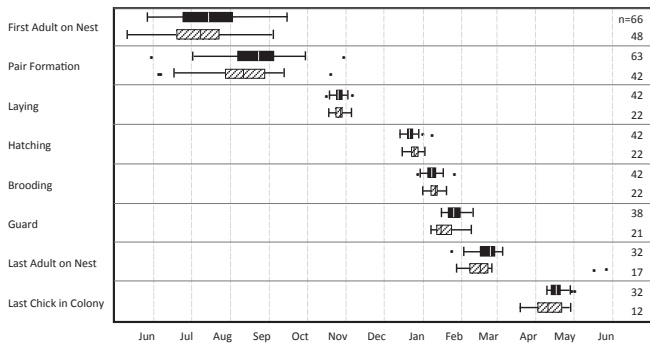


Fig. 3. A comparison box plot of the three years of data for each variable in the annual cycle of Southern Giant Petrels *M. giganteus* in at Hawker Island (grey) and Nelly Island (hatched).

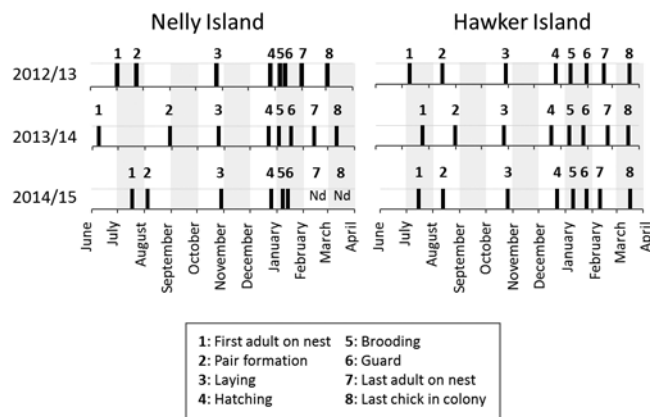


Fig. 4. Comparison of breeding phenology of Southern Giant Petrel *M. giganteus* at Nelly and Hawker islands over three seasons (2012–2015).

and chick fledging (last chick seen) (Fig. 2F). Based on the commencement and cessation dates for the activities described, six event periods were also identified and their durations estimated (Tables 1 and 2).

Annual cycle in colonies

Adult SGPs visited nests as early as the first week of July, but usually only for one or two days (Fig. 3). Pair formation (two birds on the same nest) typically occurred in mid-August, but was highly variable (Table 2, Appendix 1). Pairs often remained on or near the nest for several days engaging in courtship behaviours and nest repair. Both birds then disappeared and re-appeared several times—together or individually—from the cameras’ field of view until the egg was laid in the last week of October (Table 2, Fig. 3).

Mean incubation of the single egg took 57 ± 2 d at Hawker Island and 59 ± 5 days at Nelly Island. The first eggs hatched in the final week of December (Table 2). Newly hatched chicks were closely brooded for 18 ± 3 d at Hawker Island and 16 ± 4 d at Nelly Island before the guard phase commenced; thermally independent nestlings sat next to the guarding parent, usually without direct contact with the adult. The mean start date of the guard phase was the only variable with a statistically strong island effect ($F_{1,53} = 972.2$, $P < 0.001$; Appendix 2); at Nelly Island, chicks were consistently left unattended 9–14 d earlier than those at Hawker Island (Fig. 4 and 5B, Table 2), where the guard phase lasted 17 ± 6 d compared to 8 ± 6 d at Nelly Island. Thus, the overall guard period was shorter at Nelly Island than at Hawker Island.

Generally, adults were last recorded on or near nests in late February; many left several weeks before their chicks. Fledglings were last seen in mid-to-late April. At Nelly Island, fledglings left about two weeks before those at Hawker Island. The chick rearing period from hatching to fledging lasted, on average, 107 ± 12 d at Nelly Island and 116 ± 6 d at Hawker Island (Table 2).

Annual variability in events and activities

Temporal variability between the study islands was greatest in the timing of the return of the first adult and the duration of the pre-laying period (Fig. 4). In 2013/14, SGPs were first seen at Nelly Island on 8 June, but not until on 24 July at Hawker Island. Early arrival did not necessarily result in early pair formation. In 2013/14, SGPs started to frequent Nelly Island earlier than in the other two

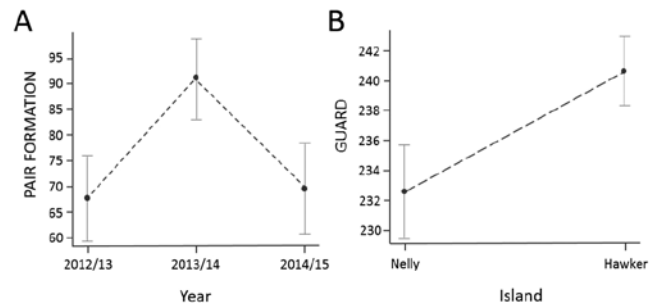


Fig. 5. Effect plots for (A) year (PAIR FORMATION), and (B) island (GUARD), showing the differences in mean dates in the annual cycle of Southern Giant Petrels *M. giganteus* in East Antarctica, 2012–2015. Days on y-axis are days since 31 March \pm 95% CI.

years, but pairs formed 88 d later; for the 2012/13 and 2014/15 seasons, this period was 38 d and 18 d, respectively. At Nelly, the period between first arrival and pair formation ranged from 28 to 61 d (Fig. 4).

Mean commencement dates for nest-based activities were near-synchronous at both islands; inter-island differences were all <10 d, except for pair formation (Table 2). Only the date of pair formation had a significant *year* effect (Fig. 5A; $F_{2,99} = 10.6$, $P < 0.001$; Appendix 2). At both islands in 2013/14, pairs formed later than in the other two years, especially at Nelly Island where adults were first seen earlier than in the other years. Since in 2013/14 laying still occurred around 27 October, the timing of events in the remainder of the breeding season was similar to the other two seasons. There were no statistically significant *year:island* interactions for any of the response variables considered.

Geographic comparisons

Various researchers have described and reported breeding events differently. Most provided only a range for lay dates and estimates of incubation length; year-round observations are rare as researchers are often limited by logistic and other constraints. Some studies only reported a general time (month) for laying. The earliest onset of laying was reported for Gough Island (mid-August; Cooper *et al.* 2001), and the latest for Signy Island (4–26 November; Conroy 1972), a difference of ~68 d. At both of our study colonies, the onset of egg laying fitted nearest in timing with the dates at breeding locations south of 50°S (Table 3). Mean incubation lasted 59 ± 5 d (range 57–67) at Nelly Island and 57 ± 2 d (range 51–63) at Hawker Island, similar to the incubation times reported elsewhere (Table 3).

DISCUSSION

Evaluation of automated camera system

The automated cameras performed exceptionally well at both sites, but they had some minor limitations. First, the field of view was restricted to a fixed focal area and direction, possibly leading to missed observations, especially during times when birds were not confined to the nest. Missed colony observations may have influenced the temporal range estimated for activities, such as the date of first arrival and chick fledgling. Second, despite the protective housing, cameras were occasionally affected by inclement weather. During blizzards, the external shutter of the camera case sometimes froze shut, preventing the servo motor from opening the shutter. At Nelly Island, data were lost after one solar panel failed after 449 d. At Hawker Island, another issue was sun lens flare, which occurred when a camera pointed directly into the rising sun, rendering some images unusable. However, acute flare (most of the image over-exposed) affected this camera for only a few days per year at low angles of incidence. When this issue occurred, several images were taken per day and the loss of information was minimal. Some images were taken at light levels too low to provide detailed information. This can be avoided by improving the schedule of image capture.

Overall, the number of poor images was small, and the advantages of an automated camera system far outweighed these challenges. The systems allowed for year-round, simultaneous observations at numerous colonies or sub-colonies, and provided, in a cost-effective manner, meaningful data for comparisons between distinctly separated geographic areas. Human disturbance, considered globally a major contributing factor in the decline of seabird

TABLE 3
Dates for egg laying, duration of laying, and incubation period for eggs of Southern Giant Petrels *M. giganteus* throughout their breeding range

Breeding location	Latitude (south)	Egg laying		Incubation (days)	Source
		Mean onset (\pm SD)	Range		
Gough Island	40.32	Nd ^a	2nd week Aug–end Sep	~60	Voisin and Bester (1981)
Northern Patagonia	45.13	Nd ^a	4th week Oct	60	Quintana <i>et al.</i> (2005)
Possession Island	46.40	Nd ^a	26 Sep–17 Oct	63 (\pm 4)	Voisin (1968)
Marion Island	46.75	27 Sep (\pm 1.9 d)	12 Sept–25 Oct	60	Cooper <i>et al.</i> (2001)
Falkland Islands	51.70	Nd ^a	late Oct	58–60	Falklands Conservation ^b
Heard Island	53.10	3 Oct	17 Oct–?	~70	Downes <i>et al.</i> 1959
Bird Island	54.00	10 Nov (\pm 1.7 d)	30 Oct–24 Nov	~60	Hunter (1984)
Macquarie Island	54.58	Nd ^a	27 Sep–19 Oct	~60	Johnstone (1978)
Signy Island	60.72	13 Nov (\pm 4.0 d)	4 Nov–26 Nov	~60	Conroy (1972)
King George Island	62.01	Nd ^a	31 Oct–?	~60	Sierakowski <i>et al.</i> (2017)
Dumont d'Urville	66.66	Nd ^a	20 Oct–15 Nov	59	Mougin (1968)
Nelly Island	66.23	28 Oct (\pm 5.0 d)	19 Oct–6 Nov	60 (\pm 3)	This study
Hawker Island	68.61	27 Oct (\pm 4.0 d)	20 Oct–7 Nov	57 (\pm 2)	This study

^a No published data

^b www.falklandsconservation.com/wildlife/albatross-and-petrels/105-southern-giant-petrelmacronectesgiganteus (accessed 17/8/2017)

populations (Croxall *et al.* 2012), was limited to the setup of the camera systems, data retrieval, and general maintenance, all of which (logistics and weather permitting) can occur outside sensitive periods in the breeding cycle.

For long-term observational work, the frequency of image capture is important. We wanted to determine the activities of SGPs throughout their annual cycle. Due to limited daylight during the austral winter, our cameras took only one image at local noon from 1 June to 31 October. From September onwards, the number of images increased at two hourly intervals as more daylight became available. This schedule kept the number of images at manageable levels, and avoided overburdening the storage capacity of the memory cards. If more detailed observations were needed, more images could be taken at shorter intervals during key periods. Furthermore, images provide archival records that can be stored, re-analysed and used to answer a variety of different questions. The cameras have the added benefit of capturing environmental information, such as storm events, coincident with behavioural observations. Although outside the scope of this study, the relationship between weather, changes in environmental variables, and life history parameters—such as breeding success and foraging trip duration—can also be investigated. In the absence of local weather information, data from the nearest research station could be used. However, while these data may be useful for the determination of large scale events such as snow storms, they may not be representative of events at a study site (e.g., wind run, which is the “quantity” of wind that passed a meteorological station (km of wind/d), or wind strength). In long term studies aiming to relate observations of changes in local conditions to the population dynamics of SGPs, the installation of automated weather stations for recording even basic meteorological data would provide valuable local information and improve the quality of the analysis.

The breeding cycle: annual variability in study colonies

This multi-year study allowed some preliminary comparisons between two sites over three years. Overall, the seasonal activities at the study colonies were similar in terms of their timing and duration, with some unexpected differences.

Non-breeding SGPs of undetermined age or sex visited the colonies at both study sites in all months, but were rarest during the coldest, darkest period; birds were observed only occasionally from mid-May until mid-June. We set the start of the annual cycle to 1 June and declared the date of first arrival to be any date after that. Only two adult SGPs (one at each island) were seen 3 and 4 d, respectively, before this date. At both colonies, the date of first adult arrival varied up to 31 d among individuals at both colonies. This variability probably arose because, in winter, the SGPs had not yet committed to breed in the coming season (Hunter 1984, Voisin 1988). However, maintaining a bond with a nest site may be important for established breeders. Not every nest visited during winter became an active nest in the subsequent breeding season. Regardless, adults returned to known nest sites with varying regularity, at times engaging in nest maintenance, and probably generally laying claim to the site. At Possession Island, site fidelity was high. SGPs appeared to breed roughly every other year, with some pairs breeding in five consecutive years (Voisin 1988).

Because the identity of individual birds was unknown, some birds attending a colony in winter may have originated from other colonies. Yearlings, recognisable by their evenly dark plumage,

were noticed at both study sites throughout the year. They disperse widely before they settle into a breeding population (Trivelpiece & Trivelpiece 1998, van den Hoff 2011). Also, some SGPs that had fledged at Hawker or Nelly islands emigrated in both directions (van den Hoff 2017). However, many SGPs roosted at known nest locations in winter, even when the ground was covered by snow obscuring the nests. On sub-Antarctic islands such as Îles Crozet, SGPs use vegetation to build their nests, and may move a few metres from the previous nest location to acquire a fresh reserve of nest-building materials (Voisin 1988). In Antarctica, SGP nest locations are more permanent. The small pebbles gathered into shallow mounds get scattered through the activity of the birds during the breeding season but remain largely in the vicinity of the nest. When SGPs roost in known nests, the occupants are most likely familiar with the area. Established breeders are highly philopatric and return to their breeding colonies and nest sites year after year (Conroy 1972, Mougouin 1975, Hunter 1984, Voisin 1988). Even juveniles—although they disperse widely post-fledging (e.g., Trebilco *et al.* 2008, van den Hoff 2011)—appear to prefer to return to their natal colonies rather than settle elsewhere (Techow *et al.* 2010, van den Hoff 2017).

As yet, nothing is known about the at-sea distribution of post-breeding SGPs in East Antarctica. However, birds intending to breed may not travel significant distances from their colonies, even in winter, if sufficient food supplies can be located. In the sub-Antarctic (southern Indian Ocean), adult SGPs satellite-tracked during winter remained relatively close to their breeding colonies (Thiers *et al.* 2014). Gathering tracking data from SGPs at our study sites would provide valuable information about their wintering areas, and potentially survivorship and links with other colonies.

Similar to the date of first arrival, the duration of the pre-laying period fluctuated between islands, albeit inconsistently. In 2012/13, SGPs paired 38 d and 61 d after adults first returned to Nelly Island and Hawker Island, respectively. In the following season, pairs formed at Nelly Island 88 d after the first adults had returned, compared to only 39 d at Hawker Island. Our study sites lie about 1500 km apart, yet the ANOVA results were not significant for the interaction term *year:island* effect. This indicates that the drivers associated with pair formation during the annual cycle of SGPs in East Antarctica were experienced across the broader geographical region. Which drivers were involved remains elusive.

SGPs started to populate the islands in increasing numbers from early September onwards. The cameras occasionally captured birds copulating during this period. Snow usually still covered the ground and nest occupancy was initially intermittent but became ongoing from the time the hens laid their eggs and incubation commenced. Laying was the most synchronous event in our study. The mean lay date was 27 October on both islands across three years (Table 2). At more northerly breeding locations, a high degree of synchronicity in lay dates has also been observed, although the timing is different (see Table 3). At high latitudes, synchrony may be expected because the most favourable time to reproduce is limited to the relatively short austral summer when food is abundant. Furthermore, among Procellariids, incubation periods tend to be longer than estimated based on the weight of their eggs (see Rahn & Ar 1974). Delays in lay dates may lead to unsuccessful breeding attempts when the window of opportunity is limited. This raises the question of the ability of SGPs to adapt to marked changes in their environment.

On average, the mean incubation periods were two days shorter at Hawker (57 d) than at Nelly Island (59 d), but the difference was not significant and may have been related to the detectability of a change in body posture of brooding adults (Fig. 2). When viewed from the front or from behind the change is obvious, but is less so when the bird appears side-on in an image.

Given the synchrony in laying dates, the mean hatching dates were equally contemporaneous at the study sites and ranged from 16 to 21 December at Hawker Island, and from 18 to 21 December at Nelly Island. SGP hatchlings are semi-precocious, and although covered in down they are unable to thermoregulate at an early age. The duration of the brood phase varied by 2–4 d within islands and 1–3 d between islands. Also, the brood stage was slightly shorter at Nelly than at Hawker each year. Homeothermy is achieved gradually as the chicks grow; increases in muscle mass lead to increases in the production of metabolic heat per unit muscle mass, and this increases thermogenic heat production (Ricklefs 1979). Parental brooding offers energy savings as the chick develops (i.e., energy not expended on thermoregulation can be used for growth) (Visser 2002). For example, chicks of Antarctic terns *Sterna vittata* saved up 46%–81% of energy when brooded (Visser 2002). SGP chicks gain weight rapidly from the day they hatch (Voisin 1976, Hunter 1984). Since very young chicks are limited in the amount of food they can receive, it must be advantageous to invest energy into growth rather than thermoregulation.

In contrast to the synchronicity of the lay and hatching dates, guard phase ended significantly earlier (13–14 d) at Nelly Island compared to Hawker Island (Table 2). Since Hawker Island is about 255 km farther south than Nelly Island, the situation could have been expected to be reversed if a latitudinal gradient was the main determinant. It appears that other, perhaps local, factors are more important to lay and hatching dates than latitude. Hence, we examined whether differences in mean temperatures could be a contributing factor. In the absence of site-specific measurements of ambient temperatures, we compared mean maximum and minimum air temperatures recorded at the meteorology stations, Casey (66°16'S, 110°31'E) and Davis (68°34'S, 77°58'E), respectively. Hawker Island lies 2.0° (~215 km) south of the Antarctic Circle, and Nelly Island just 0.4° (~40 km) north of it; however, there were no significant differences in ambient summer temperatures. During December–January, the mean maximal and minimal ambient temperatures were similar and were on average 1–1.5 °C colder at Nelly Island than at Hawker Island (www.bom.gov.au/climate/data/stations). The open topography of Hawker Island compared to the craggy topography of Nelly Island may induce localised differences in microclimate that we have not measured (e.g., wind chill). Furthermore, Nelly Island lies about 13 km offshore, while Hawker Island is located at the seaward side of the Vestfold Hills. Other differences in the large-scale features in the islands' surroundings, such as the proximity of the ice-free Vestfold Hills near Hawker Island, are likely to influence local weather conditions. The installation of automated weather stations would enable access to more detailed and precise information—about temperature, wind strength and direction, and other variables, for example—that could be used to further examine the influence of microclimate on the breeding phenology and success.

In the absence of predators of SGPs on the islands, protection from predators also does not explain the difference in the length of the guard stage. Whether or not differences in foraging strategies

may contribute to the variability in the guard duration is currently unknown; tracking data and diet analysis would help elucidate possible links. As the guard periods were consistently longer at Hawker Island than at Nelly Island, it is also possible that the birds in these locations traditionally behave somewhat differently.

Comparison with other sites

The dates when the first adults attended the colony (but not necessarily a nest site) were 9 ± 15 d and 16 ± 11 d June for Nelly Island and Hawker Island, respectively. In comparison, at Pointe Géologie, SGPs were first sighted at the colony from 31 June to 12 July. Conroy (1972) did not report precise dates but noted that only a few SGPs were seen in June and that their numbers increased throughout July. Previously, the date of first adult arrival in the colony was used as a possible indicator to examine whether the breeding phenology of SGPs and other Antarctic flying birds was influenced by climate shifts (Barbraud & Weimerskirch 2006). Among SGPs, the date of first arrival was highly variable and no significant change was detected in over a 55-yr period. One potential issue with this variable is that this datum is strongly related to observation effort (Møller *et al.* 2008). Given the great variability in this parameter (Sparks & Mason 2004), perhaps a more sensitive measure, such as date of first laying, would provide a better alternative for these kind of analyses (see below). Our study shows that a conservative variable, such as onset of laying, can be monitored more precisely even at small colonies in the absence of human disturbances.

The information gathered to date on the onset of laying points to a relationship between SGP breeding phenology and latitude (see Table 3). Although the biology of SGPs at their northernmost breeding location, Gough Island (40°S), is poorly documented and data on actual laying dates are not available, there are indications that laying commenced in mid-to-late August (Shaughnessy 1976, Voisin & Bester 1981). This is about one month earlier than Marion Island (46°S), where SGPs laid from 12 September to 17 October, varying about 7 d within a year (Cooper *et al.* 2001). In comparison, at Pointe Géologie (66°S), first eggs were laid 100–106 d after adults returned, and laying lasted from 20 October to 15 November (Mougin 1968). SGPs at Signy Island (61°S) laid from 4 to 26 November, somewhat later than anywhere else, with the onset of laying varying by <2 d over a 13-year study period (Conroy 1972). At Hawker and Nelly islands, the dates for egg-laying (19 October–2 November at Nelly, 24 October–1 November at Hawker) were similar to those recorded for other colonies in Antarctica and for some sub-Antarctic locations (Table 3). At both islands, the inter-annual variation was 4 d on average. The laying period at northern locations was six to seven weeks, compared to three to four weeks in the southern colonies, including Bird Island, Pointe Géologie, and our study sites. This may be related to a potentially longer breeding season at lower latitudes (e.g., Burr *et al.* 2016 and references therein).

Latitudinal differences in breeding phenology are often driven by gradients in environmental variables (Wanless *et al.* 2008, Carey 2009, Ockendon *et al.* 2013). However, despite the differences in the timing of other activities, the mean incubation length appeared unaffected; SGP incubated their eggs for ~60 d (Table 3). One exception was Hawker Island, the southernmost colony, where incubation (57 ± 2 d) was 2–3 d shorter than elsewhere. It is unlikely that this small difference is biologically significant.

The estimated length of the entire chick rearing (hatching to fledging) period at our study sites was about 120 d and fell well within the range reported elsewhere (e.g., Warham 1962, Hunter 1984, Quintana *et al.* 2005, Copello & Quintana 2009).

CONCLUSION

The automated camera system designed by Newbery & Southwell (2009), and used during this study, proved successful in delivering useful data throughout the annual cycle of SGPs; the system maximised data collection while simultaneously ensuring that human disturbance was minimal. We are confident that the activities recorded for SGPs in this study were natural and representative of the species at the study sites. These results improve our understanding of the site-specific nature of SGP phenology, and they allow comparisons with other colonies. The results also provide data to examine the inter-annual variation of many parameters—including many not explored in this study—in detail. Many published studies suffer from a lack of detail and continuity; on the ground, observations are usually made by researchers only a few times, and for short periods, throughout the breeding season. This study has demonstrated the usefulness and effectiveness of an automated camera system to provide continuous data over long time periods. Such automated systems could be deployed at difficult-to-access locations for many species for which data are currently sparse (e.g., giant petrels at Heard and Gough islands). Automated camera systems will not enable us to answer all questions about the dynamics and drivers of populations, but they do enable the collection of data year-round. They may also provide information about the best time to conduct a census. Finally, when several cameras are deployed, they not only provide contingency in case of failure, but they also allow comparisons of a number of subpopulations. The system has also proven far more cost effective than the manual methods often used to gather similar data.

Because variation of biological processes occurs at different spatial and temporal scales (e.g., Wiens & Rotenberry 1981), ongoing observations of events throughout the annual cycle of SGPs are necessary to monitor the health of their populations. The SGP population at Hawker Island has remained at roughly 30 occupied nests since it was discovered in 1963 (Wienecke *et al.* 2009), despite the fact that it does not appear to be limited by habitat or food resources during the breeding season, and that far more birds are frequently seen in the vicinity of the islands. Some adults that received leg bands in the 1990s still breed here, but there are no data on breeding success and recruitment. The former can be examined based on the data of automated cameras; the latter will require more effort, including the tracking of juveniles. Imagery provided by automated cameras will also assist in determining how habitat may change. To improve our understanding of the drivers of population dynamics and change, including breeding success and habitat occupancy, future analyses should include comprehensive meteorological data, such as the number and duration of storm events, local temperatures, and wind run. Establishing automated weather stations at study sites would greatly improve the relevance of meteorological data. Where predator and prey populations live in proximity of each other, monitoring more than one species would provide deeper insights into habitat changes than single species studies.

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