ENVIRONMENTAL CONSTRAINTS ON THE BREEDING PHENOLOGY OF GIANT PETRELS *MACRONECTES* SPP., WITH EMPHASIS ON SOUTHERN GIANT PETRELS *M. GIGANTEUS*

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ABSTRACT

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An organism's reproductive phenology is closely connected with environmental variables and resource availability, and an earlier reproduction is generally predicted as temperatures warm. Sibling giant petrels *Macronectes* spp. have a circumpolar Southern Hemisphere breeding distribution, which provides an opportunity to test predictions of phenological change in breeding stages over large environmental gradients. Mean comparisons confirmed a ~50 day separation in egg-laying phenologies for the two species, and linear regression showed that variation in phenology was not linked to latitude when the data were separated by species. There was a significant predictive interaction model for temperature and day length at onset of copulation in Southern Giant Petrels *M. giganteus*, but plots of the raw data suggested that temperature has little, if any, effect on gonad maturation. While day length was the most important factor related to onset of copulation, temperatures at hatching likely constrained the overall phenology of breeding, especially for populations reproducing at extreme high latitudes.

INTRODUCTION

Phenology—the timing of temporally distinct and seasonally recurring life-history events—has evolved through natural selection to occur when conditions are most favourable for species to maximise fitness (Lack 1950, Stenseth & Mysterud 2002). In birds, especially mid- to high-latitude species, the predictable, recurrent annual cycle of photoperiod (day length) is the predominant factor stimulating gonad development to a "pre-breeding" status, with immediate cues (e.g., temperature, precipitation) regulating the rates of development (Wingfield *et al.* 1997). Following photo-stimulation of gonad development, the deposition of yolk, laying of eggs, and hatching of chicks are timed to coincide more so, but not exclusively, with favourable air temperatures and resource availability (Raveling 1978, Gwinner 1996, Dawson *et al.* 2001, Dunn 2004, Visser *et al.* 2009).

Day length, immediate environmental conditions, and resources vary for geographically widespread species, and we therefore predict mean differences in breeding phenology among populations that are dependent on breeding locality. Generally, a later timing is observed for populations that breed poleward of the tropics and/or with increasing altitude (Baker 1939, Dunn & Winkler 1999, Morrison & Hero 2003, Hipfner *et al.* 2005, Rubolini *et al.* 2007, Wanless *et al.* 2008, Bears *et al.* 2009, Forrest & Miller-Rushing 2010, Burr *et al.* 2016, Keogan *et al.* 2018). However, there were inconsistencies in the direction and amplitude of those responses: some taxa showed no response to temperature change, some delayed their phenologies, while others advanced theirs (Dunn & Winkler 1999, Hindell *et al.* 2012, Keogan *et al.* 2018). The relative importance of key regulatory factors in determining the phenologies of free-ranging species is clearly inconsistent, but it is also complicated by a lack of studies both in the field and under controlled laboratory conditions (Lambrechts *et al.* 1996).

The Procellariidae (petrels, prions, and shearwaters) is a family of well-studied, long-lived seabirds with broad geographic distributions. The largest of the petrels, the aptly named Giant Petrels *Macronectes* spp. (GPs), have a circumpolar Southern Hemisphere (SH) distribution extending from mid-latitudes to the Antarctic coast, making them an excellent test case for investigating the effects of geography on reproductive phenology. Based on differences in morphology, genetics, and breeding phenology, the Northern Giant Petrel *M. halli* (NGP), which lays eggs earliest, has been separated from the Southern Giant Petrel *M. giganteus* (SGP) (Bourne & Warham 1966, Techow *et al.* 2010). Bourne & Warham (1966) also noted that egg-laying dates were later in colonies that were further south, suggesting that geography affects GP phenology. However, subsequent studies reported SGP chicks hatched later in East Antarctica compared with subantarctic Macquarie Island, but not later than at some intermediate latitudes (Johnstone 1972, Otovic *et al.* 2018). On the other hand, NGPs showed little variation in egg-laying phenology over their relatively narrow breeding range (Conroy 1972). Such results suggest that the phenologies of the GP species are not solely dependent on colony latitude, but fostered, perhaps, by an interplay between proximate environmental factors.

For this study, published data regarding aspects of the breeding phenology for the two GP species were collated from across their breeding ranges. The aim was to determine the relative importance of latitude, air temperature, and day length in shaping the phenologies of the two species.

METHODS

Response variables

Observational data concerning the breeding phenology for GPs at 17 separate locations were drawn from the published literature (1936–2018). Five studies (four SGP and one NGP) provided observations of first copulation date. The single NGP study reported that the time between copulation and first egg laying (hereafter "onset of incubation") was 12 d, and for SGPs it was a mean of 23.5 d. Therefore, to provide a proxy estimate of breeding readiness in male SGPs, 23.5 d were subtracted from all first incubation dates. A correction of 23.5 d seems reasonable because large-bodied Procellariiformes are known to undertake a three- to four-week pre-laying exodus from breeding colonies, during which time yolk deposition and egg formation occurs (Astheimer & Grau 1990, Whittow 2001).

Dates regarding the onset of incubation were collated from 16 studies encompassing 14 SGP and 7 NGP breeding locations, five of which have sympatric populations (Appendix 1); no data were available for the sympatric SGP population at Isles Kerguelen. Data quality fell into three categories. Category 1 entailed multi-year studies reporting direct observations of onset of egg laying. Category 2 studies reported a single onset date or a range of laying dates. Category 3 studies reported only general information (e.g., "last week of October"). For category 2 studies, the first date of a reported range was taken as the commencement of incubation. For category 3 studies, the date corresponding to the middle of the week reported was nominated (e.g., "the last week of October" was assigned 27 October).

Standard deviations of mean first incubation date were calculated for two of the seven NGP study locations and 11 of the 14 SGP sites. To account for differences in sample sizes across studies, standard deviations were converted to an inverse-variance weighting variable (i-vw). A conservative i-vw equivalent to the greatest variance was attributed to studies where $n = 1$.

Sixteen studies (12 SGP and 4 NGP) observed that incubation of the single egg took about 60 days, regardless of breeding location or species. Therefore, onset of hatching was projected 60 days forward of onset of incubation for both species across all breeding locations. Calendar dates were converted to equivalent Julian day, the exception being when onset of hatching occurred beyond 31 December; in those cases, day-number continued arithmetically.

Explanatory variables

Three possible explanatory variables—latitude, day length, and air temperature—were considered. Breeding latitude was taken directly from the source literature, and mean monthly air temperatures and total day length (hours:minutes) at the onset of each breeding stage were obtained from https://www.timeanddate.com (accessed 09 July 2018). Day lengths were converted to decimal hours. Sourced air temperatures were for the year 2018, and because there have been long-term regional temperature trends, those temperatures were corrected to the time of data collection using the mean monthly rates of decadal change in Richard *et al.* (2013). Where correction factors were not available for a specific breeding location, data for the next nearest location were used (e.g., Chatham Island and Antipodes Island); the exceptions were the Falkland Islands, South Georgia, and northern Patagonia, which were outside the scope of the Richard *et al.* study (2013). Temperatures for South Georgia were corrected using seasonal values from Thomas *et al.* (2018). No seasonal or monthly temperature correction factors were found for the Falkland Islands and northern Patagonia. However, the phenology data for those locations were collected within the past decade and the effect of correction factors would have been negligible.

Mean differences

Model diagnostics showed that the assumption of a near-normal (Gaussian) distribution was violated for some variables on some occasions, but the chances the samples were not normally distributed were modest (all Shapiro-Wilks tests produced P values > 0.02). Although ANOVA is considered robust to violations of the normality assumption, the significance of mean differences was analysed by non-parametric methods (Kruskal-Wallace H tests). To reduce the chances of Type I false positive outcomes, the P value to reject the
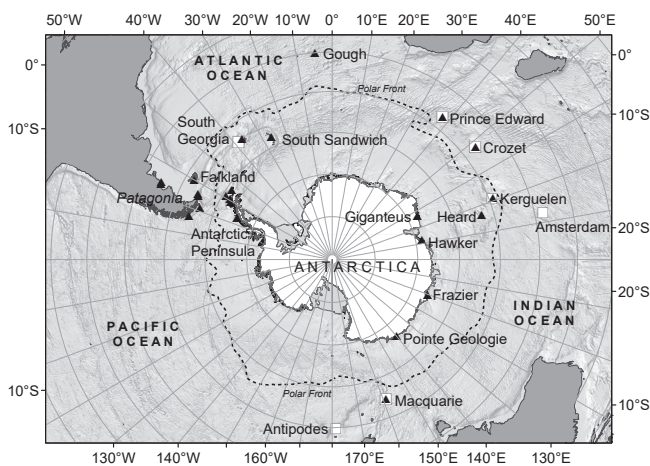

Fig. 1. Breeding locations for Southern Giant Petrels (solid triangles) and Northern Giant Petrels (open squares). Dotted line = average position of the Polar Front.
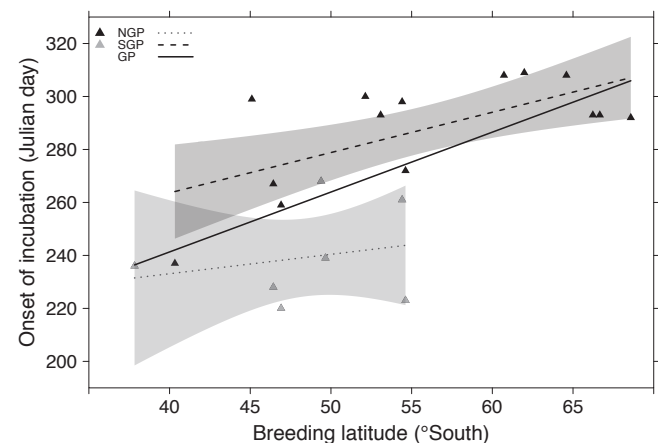

Fig. 2. Regression relationships between for the onset of incubation (Julian day) and breeding latitudes of Giant Petrel (GP) populations. Lines refer to the means and the shaded regions are the 95% confidence limits. SGP = Southern Giant Petrels; NGP = Northern Giant Petrels

null hypothesis that the means are the same was elevated from < 0.05 to < 0.001. Means are accompanied by standard error values.

Exploratory data analysis

The effects of day length and temperature on breeding phenology were assessed by linear regression (*lm*) of i-vw explanatory variables. Samples were sufficiently large to allow only first-order interactions to be considered. Since latitude has been considered a proxy for environmental gradients, it was omitted from models in favour of the direct environmental measures: day length and air temperature. Latitude was considered in a separate main-effects model to re-test findings by Bourne & Warham (1966), Conroy (1972), and Johnstone (1972).

Insufficient phenology data were available to test for the effects of day length and temperature on first copulation dates for the NGP (*n* = 1), and responses were therefore explored for male SGPs only. All analyses and plot graphics were achieved in the R environment (R Core Team 2018).

RESULTS

The seven NGP breeding populations were located between 37.8°S (Ile Amsterdam) and 54.6°S (Macquarie Island:

mean = 48.5°S ± 5.7°) with all but one, Ile Amsterdam, being fully encapsulated by the distributional range of the SGP (Gough Island at 40.3°S and Hawker Island at 68.6°S; mean = 55.8°S ± 9.1°, Fig. 1). Mean first copulation date for SGPs was 24 September (± 21 d) and occurred over a wide temperature range (−24 to 13 °C) at day lengths ranging from 9.6 to 14.3 h (Table 1). Compared with an average date of 15 October for SGPs, NGPs commenced incubation of the single egg approximately 50 days earlier, when mean temperatures were about 4 °C warmer than those experienced at SGP colonies. No NGPs incubated eggs at temperatures below 0 °C, yet SGPs incubated at −14 °C in East Antarctica (Table 1). Mean differences between the species continued to hatch date, but over the ~60-day incubation period, those differences converged from 4.2 °C at incubation to 1.7 °C at hatching (Table 1).

Colony latitude

Latitude had a positive (delaying) effect on the onset of incubation (first egg laid) in GPs at a mean rate of 1.67 d/°S (R^2_{adj} = 0.30, $F_{(1,19)}$ = 9.82, *P* = 0.005, Fig. 2). However, when the data were split by species, the relationship was only weakly positive and not significantly different from zero; change in onset of incubation with latitude for the SGP data was 0.92 d/°S (R^2_{adj} = 0.18, $F_{(1,12)}$ = 3.85, *P* = 0.07) and 0.86 d/°S for the NGP data (R^2_{adj} = −0.12, $F_{(1,5)}$ = 0.35, *P* = 0.58).

TABLE 1
Summary statistics for the mean (± standard deviation and range) first dates for breeding stages
in the phenology of northern (NGP, *n* = 7) and southern Giant Petrels (SGP, *n* = 14)

	Date (day/month ± days)		Air temperature (°C)		Day length (h)	
	NGP	**SGP**	**NGP**	**SGP**	**NGP**	**SGP**
Copulation	ID	24 Sept ± 21 (02 July–12 Oct)	ID	−1.7 ± 10.0 (−23.9–13.5)	ID	12.3 ± 1.4 (9.6–14.3)
Incubation	**27 Aug ± 18 (08 Aug–25 Sept)**	**15 Oct ± 21 (25 Aug–05 Nov)**	4.1 ± 3.9 (0–11)	−0.1 ± 7.8 (−13.9–13.0)	NR	NR
Hatching	**26 Oct ± 18 (07 Oct–24 Nov)**	**14 Dec ± 21 (24 Oct–04 Jan)**	5.6 ± 3.9 (1.5–12)	3.9 ± 5.9 (−2.6–18.0)	NR	NR

Bold values = Kruskal-Wallace H-test for mean differences, *P* values < 0.001. ID = Insufficient data. NR = Not required for analyses.

TABLE 2
Slope estimates (± standard error (SE)) and coefficients of determination (adjusted R^2)
for the interaction model and lines of best fit shown in Figs. 3A, B, C

Species	Response variable (onset date for)	Classification variables	Slope	SE	R^2 (adjusted)	*P*
NGP[a]	Copulation	ND	-	-	-	-
	Incubation	Air temperature	−1.15	2.24	−0.14	0.63
	Hatching	Air temperature	−0.35	2.33	−0.19	0.88
SGP	Copulation	Day length	13.51	0.63	0.96	< 0.001
		Air temperature	−9.57	2.30	−0.04	0.002
		Day length*Air temperature	0.77	0.18	0.98	0.002[b]
	Incubation	Air temperature	−0.39	0.57	−0.04	0.50
	Hatching	Air temperature	−0.63	0.82	−0.03	0.46

[a] NGP = Northern Giant Petrel (*n* = 7), SGP = Southern Giant Petrels (*n* = 14). Residuals were normally distributed (Shapiro-Wilks tests *P* > 0.05). ND = no data. * = interaction term.
[b] $F_{(3,10)}$ = 237.7.

Day length and air temperature

A plot of the significant interaction term (Table 2) predicted that onset of copulation would be little affected by day length at cold temperatures (−20 °C), although at warmer temperatures, it would be earlier at correspondingly shorter day lengths (10 °C, Fig. 3A). Onset of incubation and hatching tended to be earlier as temperature increased (Figs. 3B, C), but the effect was weak and non-significant for both species (Table 2).

Plots of change in air temperature over three successive breeding stages were split by species (Fig. 4, lower panels) and showed similarities and differences between and within the species. Temperatures at which NGPs began incubation and hatching fell within the range experienced by SGPs. At East Antarctic sites, Dumont d'Urville, Nelly Island, and Hawker Island, SGPs copulated and incubated at the lowest temperatures experienced for all GP populations. The difference, however, was not as marked at hatching as it was at copulation and incubation (Table 1, Fig. 4 lower panel, Fig. 5).

SGP populations clustered according to day length at copulation (Fig. 4, upper right panel), with three groups discerned. The first group was a putative short-day phenotype, which copulated at day lengths of ~10–11 h when temperatures were > 1.5 °C (mean = 4.03 ± 3.17 °C, Fig. 5) at their four oceanic breeding islands (situated north of the average position of the Antarctic Polar Front (Fig. 1)). With the extreme northern population at Gough Island included, onset of copulation was within a range of 34 days across populations (Fig. 4, lower right panel), but when Gough Island was excluded, onset was within 13 d across the remaining three populations.
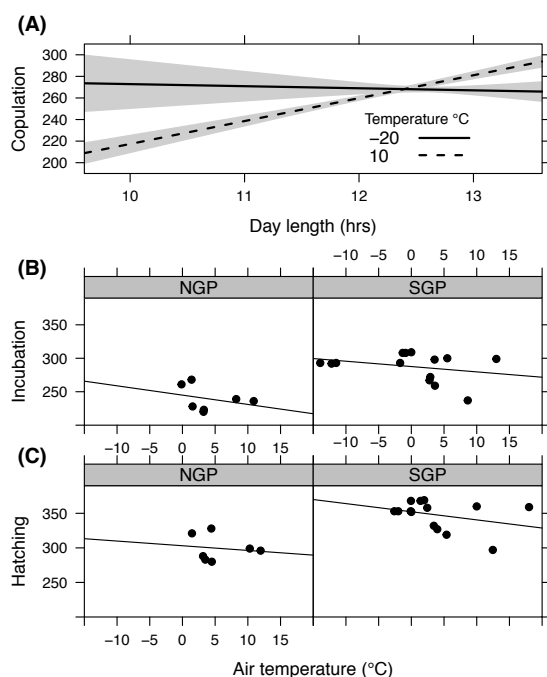
The second group was termed the intermediate phenotype, which commenced copulation at day lengths of 12.2–12.8 h when temperatures were −24 to 13 °C (mean = −4.71 ± 13.3 °C, Fig. 5). Onset of copulation for this intermediate phenotype varied by eight days across populations breeding at latitudes 45°–68.5°S, some of which were further south than the long-day group (Fig. 4, lower right panel).

The third group was designated the long-day SGP phenotype, which copulated at day lengths over 13.5 h when temperatures were < 0 °C (mean = −2.34 ± 1.33 °C, Fig. 5) at their near–Antarctic Peninsula (61°–65°S) breeding locations. In this group, the most time-constrained one, onset of copulation was within a day of one another (Fig. 4, lower right panel). Unfortunately, a lack of data concerning the onset of copulation for NGPs precluded similar comparisons as for the other two groups, but there was a suggestion of two possible phenotypes in the temperature plots (Fig. 4, lower left panel).

Mean temperatures within each day length phenotype changed little over the course of the three breeding stages (Fig. 5). Of interest were the marked seasonal warmings at the three East Antarctic SGP populations. At those locations, temperatures increased from lows of less than −14 °C at copulation to about −2 °C some 90 days later at hatching; the greatest change was approximately 21 °C at Dumont d'Urville (Figs. 4, 5).

DISCUSSION

There is little doubt that the small sample sizes available for this study restricted some statistical analyses, but the data collated represented all six NGP and 12 of the 14 SGP regions recognised in Patterson *et al.* (2008). Omitted were Isles Kerguelen, where only four SGP pairs have been recorded breeding, and the isolated South Sandwich Islands, where data collection is a challenge. Not all reproductive events identified by Otovic *et al.* (2018) were equally well represented across studies. More readily observable activities such as egg laying and hatching provided the most data, whereas less is known about the timing of copulation in either species. Perhaps future studies of GP phenology, especially for NGPs and at isolated locations (e.g., Gough Island), could incorporate the use of an automated camera array like that described by Otovic *et al.* (2018). In that way, data suited to phenology analyses might be standardised and maximised across populations.

Results confirmed earlier observations of a mean difference of ~50 days in egg laying phenology for the two species (Warham 1962, Bourne & Warham 1966, Hunter 1984, Cooper *et al.* 2001). The data collated also showed that NGPs at Iles Kerguelen laid later than SGPs at Gough Island, Marion Island (Prince Edward Islands), and Ile Possession (Iles Crozet, Fig. 4, Supplementary Table 1). Such clear differences in sibling-species' phenologies are thought to result from selective pressures to minimise competition and achieve a match between breeding and resource (food, nest sites) requirements (e.g., Visser *et al.* 1998, Stenseth & Mysterud 2002, Pfennig & Pfennig 2010). Studies of GP diets suggested that species preferences (e.g., NGP chicks were fed more pinniped carrion than SGPs chicks) could explain mean differences in breeding phenology at Bird Island (South Georgia, Hunter 1987) and Marion Island (Cooper *et al.* 2001). However, the substantial similarities in species' feeding ecologies at Macquarie Island provided no evidence of dietary specialisation resulting from competition, nor did it provide

Fig. 3. (A) Temperature × day length interaction for onset of copulation in Southern Giant Petrels. (B) and (C) Linear regression of onset of incubation and hatching, respectively, as a function of mean monthly air temperature. SGP = Southern Giant Petrels; NGP = Northern Giant Petrels

evidence that differences in phenology were the consequence of preferred diet, since chicks were fed similar diets (Johnstone 1977). Further studies have shown overlaps and differences in the suite of items fed to chicks, with the differences being more pronounced between the sexes than between the species (Hunter 1983; Hunter & Brooke 1992; Ridoux 1994; Cooper *et al.* 2001; de Bruyn *et al.* 2007; González-Solís *et al.* 2000, 2007). Moreover, naive fledglings dispersed thousands of kilometres from their natal islands to forage at spatially patchy mosaics of seasonally or continuously (aseasonal) available food resources within biologically productive eastern boundary currents (EBCs; Shaughnessy & Voisin 1981, Thiel *et al.* 2007, Trebilco *et al.* 2008, Montecino & Lange 2009, van den Hoff 2011, Thiers *et al.* 2014). Those similarities in diet and foraging behaviours suggest that one strategy is not favoured over the other, for if it were, one might expect to observe a shift in foraging ecology in the absence of competition (e.g., in allopatry) to match breeding with the most favourable environmental conditions and resource availability. No appreciable differences in contemporary diets of SGPs have been reported (Johnstone 1977, Rey *et al.* 2012), though nothing is known of historical differences during the some 700 000 years that have passed since the species were first separated (Techow *et al.* 2010).

A trend in reproductive phenology is predicted—and observed—for species breeding across broad latitudinal and altitudinal gradients (e.g., Morrison & Hero 2003, Wanless *et al.* 2008, Burr *et al.* 2016). Such a trend was exactly what Bourne & Warham (1966) reported when they stated "further [sic] south late laying is the rule" for Giant Petrels. The results of this study supported that finding, but only when the data were combined for both species (Fig. 2). When the data were split by species, the results supported Conroy
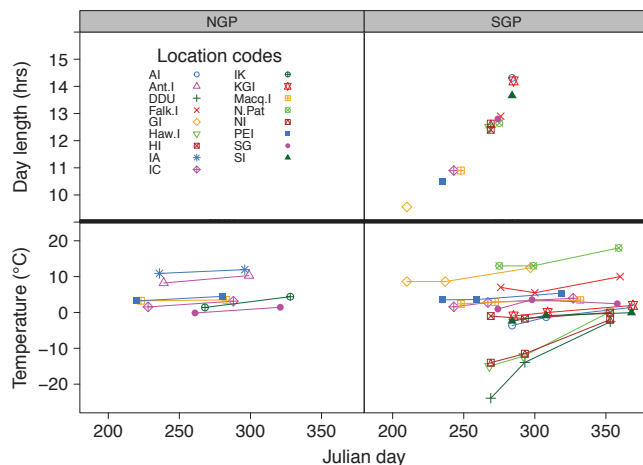
(1972) and Johnstone (1972), who commented that the relationship between latitude and phenology was less clear for the separated species. It seems likely the initial relationship Bourne & Warham reported owed its strength to the combined species data.

Like other Procellariiformes, the duration of chick development in GPs appears fixed, incubation is continuous, and breeding is highly predictable with little inter-annual variation (e.g., Williams & Ricklefs 1984, Astheimer & Grau 1990, Otovic *et al.* 2018). Such a constrained reproductive cycle suggests that GP phenology has a genetic basis, and in such circumstances, whether the stimulus is direct or indirect, changes in the physiology of reproduction (e.g., gonad maturation) occur principally in response to rate changes in or total lengths of photoperiod (Wingfield *et al.* 1997, Dawson 2007). Temperature is also recognised for its ability to directly affect and/or modulate avian phenology around photoperiod responses (Dawson 2007, Visser *et al.* 2009). SGPs are distributed across ~30° of SH latitude where temperatures at copulation range from −24 °C in high-latitude East Antarctica to 13 °C in mid-latitude Northern Patagonia. Therefore, one might expect GP breeding phenology to respond in some way to temperature gradients, as was observed for Great Tits *Parus major* (under both captive experimental and natural conditions; Sanz 1998, Visser *et al.* 2009) and for three of four wild populations of Northern Hemisphere seabird species (Burr *et al.* 2016). However, a variety of positive, negative, and nil effects of temperature on gonadotropin secretion and gonad development have been reported across a range of study species (Dawson 2007). Onset of copulation in SGPs could therefore respond in one of two opposing ways, or not at all.

Endocrine indicators of gonad maturation were not directly measured for this study. However, measures of environmental variables, such as day length and temperature, at pre-defined reproductive stages may be useful indicators of internal processes, such as changes in gonadotropin levels. If this is true, analysing the effects of temperature and day length on gonad maturation (onset of copulation)
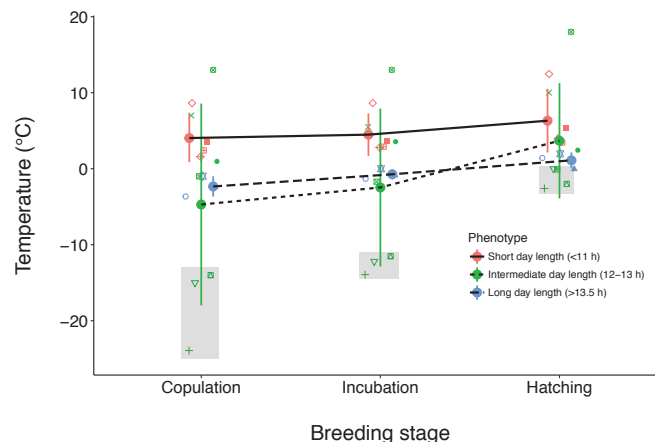

Fig. 4. Seasonal changes in mean monthly air temperature and day length at individual Northern Giant Petrel (NGP) and Southern Giant Petrel (SGP) breeding locations. First points in the SGP time series = onset of copulation dates, second points = onset of incubation dates, and third points = onset of hatching dates. No onset of copulation dates were determined for NGPs, and therefore their time series begins at incubation. Location abbreviations (also used in Fig. 5): AI = Anvers Island, Ant.I = Antipodes Island, DDU = Dumont d'Urville, Falk.I = Falkland Islands, GI = Gough Island, Haw.I = Hawker Island, HI = Heard Island, IA = Isle Amsterdam, IC = Isles Crozet, IK = Isles Kerguelen, KGI = King George Island, Macq.I = Macquarie Island, N.Pat = Northern Patagonia, NI = Nelly Island, PEI = Prince Edward Islands, SG = South Georgia, SI = Signy Island.

Fig. 5. Range of temperatures experienced at progressive stages in the breeding cycle of Southern Giant Petrels. Location symbols are the same as for Fig. 4 except they are now coloured according to three day-length phenotypes. Superimposed are the temperature means (dots ± 1 SD, bars). The grey shaded areas highlight the data for populations breeding at the extreme cold locations of Hawker Island, Nelly Island, and Dumont d'Urville along the East Antarctic coastline (Fig. 1).

in male SGPs produced some interesting outcomes. There was evidence for an interaction between day length and temperature at or before the onset of copulation that weakened as temperatures decreased from 10 to −20 °C (Fig. 3). Although the interaction model predicted that temperature would have a delaying effect on the onset of copulation, the overall range of temperatures at that time suggested otherwise. Summary statistics showed that copulation was uninhibited at temperatures from −24° to 13 °C (Table 1) and that the onset of copulation for the intermediate day length group was at lower temperatures on average than those experienced for both the shorter and the longer day length phenotypes (Figs. 4, 5). The results of this study suggest that day length (photo-stimulation) was of primary importance and that temperature had only a very weak secondary effect, if any, at copulation, as was proposed for species with predictable breeding seasons (Dawson *et al.* 2001). It is possible that the role of temperature at copulation was over-emphasised at the cold end of the temperature spectrum in the interaction model, where samples were smallest ($n = 3$ for temperatures below −5 °C).

The findings described above prompted the following question: if day length was the primary driver of copulation in SGPs (and probably NGPs, too), why were there such marked differences in day length (~10–14.3 h) at that time? It would seem reasonable, in the absence of a temperature effect, to expect males could be copulation-ready at day lengths of ~10 h. If so, delays in the date of onset of copulation might be the consequence of latitudinal (not longitudinal) differences in the day of the year when day length reaches 10 h. The situation does not appear to be so simple. The two SGP breeding locations at South Georgia and Macquarie Island share near-identical latitudes (54.4°S vs 54.6°S, respectively) and temperatures at onset of copulation (0.96 °C and 2.40 °C, respectively). If males at those two sites were copulation-ready at 10-h days, onset of copulation would be on day 235 (23 August), yet their actual onset dates differ by 26 d and the day lengths differ by 1.9 h. One possible explanation for the observed difference between those two populations is that secondary environmental factors, such as temperature, have acted upon their phenology at later breeding stages.

There was evidence to suggest that temperature influences SGP breeding phenologies, at least at severely cold East Antarctic breeding locations (Figs. 4, 5). Mean temperature differences between those sites and sub-Antarctic sites were most marked at onset of copulation, but due to the very different seasonal gradients of change in temperature that were due to extended sunshine hours and decreasing angles of incidence at higher latitudes, temperatures at hatching in East Antarctica were not so different from temperatures in the sub-Antarctic (Figs. 4, 5). Ultimately, no GP chicks hatched at temperatures below −2.6 °C. One conclusion that can be drawn is that very cold temperatures (−15 to −20 °C) do not deter gonad development and copulatory activities, but they have a selective effect at later stages of incubation and/or hatching. Take, for example, the phenology of a well-studied SGP breeding population at Hawker Island, East Antarctica. Imagine if copulation at Hawker Island had commenced at day lengths of ~10 h rather than 12.5 h; this would advance their breeding phenology by about 20 days. Such a change would result in a reduction in temperature of 2 °C and 6 °C at incubation and hatching, respectively. At such low air temperatures, it is possible that internal egg temperatures of 31–37 °C (Williams & Ricklefs 1984, Brown & Adams 1988) would be difficult to maintain and embryonic development would be compromised, as it was for experimentally chilled SGP eggs (Williams & Ricklefs

1984). Alternatively, if adults managed to incubate the single egg, the energetic demands of the newly hatched chick might exceed adult capabilities, with obvious ramifications on chick survival. Over generational time-spans, selection would thus favour later breeding at high latitudes, such that chicks would be incubated or hatched when temperatures are warm enough to tolerate. Ultimately, a stabilised change in phenology would ensure temperatures at hatching were above a critical minimum value of about −3 °C.

Over 40 years ago, Johnstone (1977) used diet analyses and breeding distribution observations to suggest that NGPs were adapted to a subantarctic existence and SGPs could be considered the more cold-adapted of the two species. The temperatures at which SGPs were able to copulate and incubate validate those remarks.

ACKNOWLEDGEMENTS

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