

1 *REVIEW ARTICLE*

2
3 **Update on the global abundance and distribution of breeding Gentoo Penguins (*Pygoscelis***
4 ***papua*)**

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ABSTRACT

Though climate change is widely known to negatively affect the distribution and abundance of many species, few studies have focused on species that may benefit. Gentoo Penguins (*Pygoscelis papua*) have undergone population growth along the Western Antarctic Peninsula (WAP), a region accounting for ~30% of their global population. These trends are in stark contrast to the Adélie Penguin (*P. adeliae*) and the Chinstrap Penguin (*P. antarcticus*), which have experienced considerable population declines on the WAP attributed to environmental changes. The recent discovery of previously unknown Gentoo Penguin colonies on the WAP and evidence for southern range expansion since the last global assessment in 2013 motivates this review of the abundance and distribution of this species. We compiled and collated all available recent data for every known Gentoo Penguin colony in the world and report on previously unknown Gentoo Penguin colonies along the Northwestern section of the WAP. We estimate the global population of Gentoo Penguins to be 432,144 (338,059 – 534,114) breeding pairs, with approximately 364,359 (95th CI: 324,052 – 405,132) breeding pairs (85% of the population) living in the Atlantic sector. We estimate that the global population has increased by approximately 11% since 2013, with even greater increases (23%) along the WAP. The Falkland Islands population, which comprises 30% of the global population, has remained stable, though only a subset of colonies have been surveyed since the last comprehensive survey in 2010. Our assessment identifies South Georgia and sub-Antarctic islands in the Indian Ocean as being the most critical data gaps for this species.

Keyword: Gentoo Penguins, range expansion, global census, Antarctic Peninsula, glacial retreat, sea ice

INTRODUCTION

Climate change is widely known to affect the distribution and abundance of species, with some taxa experiencing range retractions and extinctions and others experiencing latitudinal shifts in response to warming conditions (Thomas et al. 2006; Hickling et al. 2006; Chen et al. 2011; Pecl et al. 2017). While attention has focused largely on species at risk due to the impacts of climate change, less attention has focused on species that may benefit. One such species is the Gentoo Penguin (*Pygoscelis papua*), whose populations along the rapidly warming Antarctic Peninsula (Vaughan et al. 2003) have not only undergone population growth since the early 2000s, but have expanded their breeding range southwards with the establishment of many new breeding colonies (Lynch et al. 2013).

These trends stand in stark contrast to their sister species, the Adélie Penguin (*P. adeliae*) and the Chinstrap Penguin (*P. antarcticus*), which have experienced considerable population declines on the Western Antarctic Peninsula (WAP), the principle drivers of which are still being debated (Forcada and Trathan 2009; Trivelpiece et al. 2011; Lynch et al. 2012). Current hypotheses for population increases and range expansion of Gentoo Penguins in this region include: plasticity in their breeding phenology (Lynch et al. 2011), generalist foraging strategies and a flexible trophic niche (Polito et al. 2015; Herman et al. 2017; McMahon et al. 2019), and breeding habitat preferences (Cimino et al. 2013) vis a vis warming temperatures and declines of sea ice (Stammerjohn et al. 2008) throughout the waters around the WAP.

Gentoo Penguins are one of the most widespread of the penguin species, with a circumpolar breeding distribution and a wide latitudinal range stretching from 46°00' S in the Crozet Islands (2,350 km SSE of Madagascar) to 65°16' S on the Antarctic Peninsula (Lynch

2013). Current taxonomy of Gentoo Penguins identifies two subspecies, *P. papua papua* and *P. papua ellsworthi*, found north and south of 60°S, respectively (Dinechin 2012; Clements et al. 2017). However, recent genomic evidence suggests Gentoo Penguins found on South Georgia are more closely related to the southern subspecies and there is a deep divergence of Indian Ocean populations compared to other Gentoo Penguin colonies in the Atlantic sector, suggesting taxonomic revisions may be required at the subspecies level (Levy et al. 2016; Vianna et al. 2017; Clucas et al. 2018; Pertierra et al. 2020).

Since the last global assessment of approximately 387,000 breeding pairs (Lynch 2013), many new data have been collected across the Gentoo Penguin's distributional range. While the WAP population has been generally increasing, these trends are not homogenous, as some colonies have experienced recent declines (Petry et al. 2018; Dunn et al. 2019). In addition, the population in the Falkland Islands, where approximately one third of all Gentoo Penguins breed, increased overall by 105% between 2005 and 2010 (Baylis et al. 2013), though a subset of annually monitored colonies have since declined (Crofts and Stanworth 2019). In contrast, the majority of Indian Ocean colonies, approximately 16% of the global population, are rarely surveyed and represent areas of significant uncertainty for both abundance and trends.

To update our understanding of Gentoo Penguin abundance and distribution, we compiled all census data available to estimate the current global abundance and distribution of breeding Gentoo Penguins including new ground count survey data from previously unknown colonies along the northwestern section of the WAP and on the Danger Islands. This updated population assessment allows us to identify gaps and associated priorities for future research, and forms the basis for our forecasts of continued range expansion along the WAP.

METHODS

The majority of the Gentoo Penguin distribution falls within the area governed by the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR), which is divided into three statistical areas: Area 48 (Atlantic Ocean sector), Area 58 (Indian Ocean sector) and Area 88 (Pacific Ocean sector). Gentoo Penguins are found throughout Area 48 (including the Antarctic Peninsula, the South Shetland Islands, the Danger Islands, the South Sandwich Islands, the South Orkney Islands, and South Georgia) and Area 58 (including Marion and Prince Edward Islands, Crozet Island, Heard Island, and Kerguelen Islands (Figure 1). Outside the CCAMLR area, Gentoo Penguins have a large breeding population on the Falkland Islands, and smaller populations on Martillo Island in Tierra Del Fuego, Argentina, and Macquarie Island in the southwestern Pacific Ocean.

Much of the census data from the Antarctic Peninsula and South Shetland Islands are collected via opportunistic vessel-based field surveys (Lynch et al. 2013), though several additional surveys near permanent stations have been published (Pettry et al. 2018; Smagol et al. 2018; Dunn et al. 2019). Most surveys were conducted via manual ground counts of individual nests, counting individual nests in panoramic photos taken from the ground or from an offshore vessel, or counting individual penguins from photographs captured by drone imagery (Borowicz et al. 2018). The majority of surveys used in this assessment are precise to within 5% (i.e., they are Accuracy 1 counts, following Croxall and Kirkwood 1979).

The South Sandwich Island census data were collected via direct ground counts and using satellite imagery to estimate the aerial extent of the colony (as described in Lynch et al. 2016). The Falkland Island data are from the most recent island-wide census from Baylis et al. (2013) and from an annual census of a subset of colonies by the Falkland Islands Seabird Monitoring

Program (Crofts and Stanworth 2019). Although some sites on South Georgia have been recently surveyed during short landings at popular tourist landing spots, the majority of Gentoo Penguin colonies have not been surveyed recently. The last published comprehensive census data for many South Georgia colonies derives from Trathan et al. (1996), which were based on field data collected between 1985 and 1987 by P.A. Prince and S. Poncet (Unpublished). Many CCAMLR Area 58 populations (Indian Ocean) have not been surveyed comprehensively since the 1980s and 1990s (Weimerskirch et al. 1988; Woehler 1993; Jouventin 1994) with the exception of Marion Island and Prince Edward Island, which were last surveyed in 2008 (Crawford et al. 2009). We include a subset of site-specific census data from Lescroël and Bost (2006) and Weimerskirch (*pers. comm.*) in Online Resource 1, but chose to use the most recent comprehensive survey data for the Kerguelen and Crozet Island Archipelagos for our global population estimates (Weimerskirch et al. 1988; Jouventin 1994). We also collated the most recent count data for Heard Island (Woehler 1993), Marion Island and Prince Edward Island (Crawford et al. 2009), Macquarie Island (Parks and Wildlife Service 2006), and Martillo Island (Ray et al. 2014).

We used a method for denoting census accuracy used in many other penguin assessments, denoting five levels of accuracy: 1) accurate to better than $\pm 5\%$; 2) accurate to 5-10%; 3) accurate to 10-15%; 4) accurate up to 25-50%; 5) accurate to the nearest order of magnitude (Croxall and Kirkwood 1979; Naveen et al. 2012; Lynch et al. 2016; Borowicz et al. 2018). We assumed a truncated $[0, \infty)$ Normal distribution for census errors and propagated observation error to total and regional abundances by drawing from the corresponding Normal distribution ($n=1000$) centered on each individual count with a standard deviation appropriate for count accuracy (See Online Resource 1). Summing across draws for multiple sites allows us to extract

a population estimate (the mean of the distribution for the sum) and 95% confidence intervals for the total abundance within that region of interest. Recognizing that our uncertainty on current abundance reflects both the uncertainty of the original survey and the time elapsed since the most recent survey of a colony, we have downgraded (for the purposes of summing up abundances at the regional scale and propagating our uncertainty in those regional abundances) the precision of counts older than 2015 by either one step (e.g., from accuracy=2 to accuracy=3) for counts 2005-2014, by two steps for counts (1995-2004) by three steps for counts from 1985-1994, and by four steps for counts prior to 1985, noting that the accuracy code saturates at 5. All analyses were performed in the R computing environment (R Development Core Team 2017).

To explore deglaciation as a possible mechanism for range expansion and colonization in Gentoo Penguins (Cole et al. 2019), we analyzed high-resolution satellite imagery provided through Google Earth for eight of 14 recently-colonized areas and compared it with digitized aerial photography taken in December, 1956 by the Falkland Islands and Dependencies Aerial Survey (FIDASE 1956).

RESULTS

We estimate the global population of Gentoo Penguins to be 432,144 (338,059 – 534,114) (Table 1). Colony specific census data, where available, are detailed in Online Resource 1. Approximately 364,359 (95th CI: 324,052 – 405,132) breeding pairs (85% of the population) live in the Atlantic Sector. We report on 14 colonies in the Danger Islands and along the northern coast of Joinville Island unknown at the time of the last global review of Gentoo Penguin abundance and distribution (Lynch 2013; see Online Resource 1 for full details). Including these new populations, the total abundance of Gentoo Penguin breeding pairs on the Antarctic

Peninsula is 127,320 (95th CI: 118,199 -137,208). In addition to population growth on the WAP, Gentoo Penguins have colonized at least eight new islands since 1994, with six of those islands contributing to a recent southward expansion of this species' range by approximately 60 km (Figure 2). One of these newly established colonies is on Green Island, part of the Berthelot Islands, as predicted by Lynch et al. (2012). There has been rapid population growth at these sites (Figure 3), and there are currently 1,789 breeding pairs in this expansion zone as of 2018. These colonization events have occurred in a cascading latitudinal pattern such that the most recent colonies are at the southernmost end of the species current range.

Comparing our assessment of the global Gentoo Penguin breeding population with Lynch (2013), we estimate that the global Gentoo Penguin breeding population has increased by 11% since 2013. The Western Antarctic Peninsula population (excluding the Joinville and Danger Island colonies) estimated to be 116,521 (95th CI: 107,692 – 126,331) has increased by approximately 23% since 2013. The Falkland Islands current breeding pair population estimate is 131,059 (95th CI: 129,036 – 133,123). This estimate combines a new subset of colony census data and the most recent comprehensive survey in 2010.

Of the eight newly established colonies in the Danger Islands and Joinville Island region for which historic aerial imagery were available, two sites appear to have recently experienced glacial retreat, exposing land that is now occupied by breeding penguins (Figure 4).

DISCUSSION

Population growth and range expansion on the Antarctic Peninsula

The estimated 11% increase in the total global Gentoo Penguin population to 432,144 breeding pairs since the last global estimate published in 2013 can be attributed largely to increases on the

Antarctic Peninsula, which has experienced warming air temperatures, increasing precipitation, and declines in the extent, seasonal duration, and thickness of sea ice (Trivelpiece et al. 2011; Turner et al. 2017; Shepherd et al. 2018). One of the more interesting aspects of Gentoo Penguin population growth and range expansion on the Antarctic Peninsula is that these trends are in direct contrast to population trends of Adélie and Chinstrap Penguins in the same region. Since the 1980's, both Adélie and Chinstrap Penguin populations have been declining throughout the peninsula, even as Gentoo Penguin populations have grown steadily. While the drivers of decline for Adélie and Chinstrap Penguins are hotly debated (Forcada and Trathan 2009; Trivelpiece et al. 2011; Lynch et al. 2012) there is considerable evidence that Gento Penguin life history provides some relative advantages. In particular, Gentoo Penguins have more flexibility in diet, foraging behavior, and breeding phenology, which suggests they may be more resilient to environmental change and better able to colonize newly exposed territory (Lynch et al. 2011; Masello et al. 2017; McMahon 2019),

In some colonial nesting bird species, the major contribution to rapid population growth at newly established breeding colonies has been large-scale immigration of individuals (Oro and Ruxton 2001; Dunlop 2009; Santoro et al. 2016). Given their fast growth rates, it is unlikely that growth of newly-established Gentoo Penguin colonies can be explained by reproductive success and subsequent offspring recruitment alone; continued immigration from other locations over a period of several years would also be required.

Intraspecific competition could be one possible explanation for the range expansion exhibited by Gentoo Penguins. Density-dependent decline in habitat quality of current breeding locations could result in individuals relocating to new, unused habitat and establishing new colonies. Another driver of immigration to new colonies may be newly-available habitat

resulting from increased snow melt or glacial retreat. It is possible that sites beyond the former southern range margin were previously inaccessible due to heavy winter sea ice conditions that would preclude foraging in the overwinter period; declines in the extent or concentration of overwinter sea ice might make these sites available for breeding and overwinter residency and explain the Gentoo's southern range expansion. Historically, deglaciation and terrestrial ice sheet retreat has led to the expansion and proliferation of Antarctic and sub-Antarctic penguin populations since the last glacial maximum (LaRue et al. 2013; Clucas et al. 2014; Younger et al. 2015; Cole et al. 2019). The Western Antarctic Peninsula has continued to experience rapid thinning of the ice shelves and their tributaries since the 1990s, which is attributed to increases in upper ocean heat content (Pritchard et al. 2012; Paulo et al. 2015). While Gentoo Penguins are expanding their range further south, they have also colonized two areas that appear to have become available due to very recent deglaciation. Aerial photographs of Noble Rocks in the Neumayer Channel and Moot Point in the Penola Strait, both taken in 1956, show these regions as previously covered by terrestrial ice sheets (Figure 4). For Noble Rocks, the advent of Landsat satellite imagery corresponds to the period in time in which the ice covering this small island began disintegrating, resulting in its full exposure, probably early in the 1990s. These sites now have exposed bare rock and are physically separated from the glaciers by ocean and both have been colonized by Gentoo Penguins.

While we do not have data to determine the pace of colonization at these sites, the imagery for Noble Rocks indicates that a colony of 40 nests can establish in as little as 25 years post-exposure. Moreover, this colony, situated on a space-limited small rock, seems likely to be at carrying capacity and may be serving as a source population for other bare rock patches in the vicinity. As glacial retreat continues to occur on the Antarctic Peninsula, and perhaps especially

on its ice sheet-covered islands whose ice masses are no longer connected to the continental ice sheets, it is likely that expanding Gentoo Penguins may continue to seek out newly-exposed areas of the rocky coastline as potential breeding habitat.

Population changes in Indian Ocean Sector

Though the last comprehensive survey of the breeding Gentoo Penguins on the Kerguelen Archipelago was conducted in 1985, the colonies on Courbet Peninsula, Penn Island, and Longue Island, have been regularly monitored since the 1980's. Lescroél and Bost (2006) reported an approximately 30% drop in breeding numbers from the mid 1980's to the mid-2000s on the Courbet Peninsula, which they suggested was the result of inshore food shortages where Gentoo Penguins typically forage (Lescroél and Bost 2005). However, a 2018 survey found that the colony had recovered, surpassing its 1985 breeding population size by 9% (Weimerskirch pers. comm.). In contrast, Possession Island, part of the Crozet Archipelago, was also surveyed in 2018 and found to have declined in breeding population size by 32% (Weimerskirch pers. comm). Similarly, the breeding population at Marion Island has declined by 52% since 1994 (Crawford et al. 2014). With the exception of Courbet Peninsula, these population trends suggest an overall decline among colonies found in the Indian Ocean sector, likely related to declines in food availability due to environmental changes.

Notable data gaps and future work

South Georgia's last population estimate was in the mid-1980s (P.A. Prince and S. Poncet Unpublished) and estimated at 98,867 breeding pairs (Trathan et al. 1996), which constitutes over 25% of the last global Gentoo Penguin census. As this population sits between the Antarctic

Peninsula, where populations have increased, and the Falkland Islands, where they appear in decline, it is essential that future efforts be made to fully survey this region. Similarly, the Indian Ocean Gentoo Penguin breeding colonies found on Kerguelen and Crozet Island Archipelagos and those on Heard Island, approximately 14% of the global population, have not been comprehensively surveyed since the early 1970's to late 1980's (citation). Given recent genetic evidence for at least one distinct subspecies in the Indian Ocean (Levy et al. 2016; Vianna et al. 2017; Clucas et al. 2018), updated census data for these regions is particularly urgent.

Monitoring of changes in marine predators is critical to our understanding of marine ecosystem responses to climate change and other environmental perturbations. Predators are sensitive to shifts in prey resources and foraging habitat and can therefore act as proxies for identifying environmental perturbations (Weimerskirch et al. 2003; Sandvick et al. 2005; Cherel et al. 2007; Baylis et al. 2015). While much research is focused on species undergoing declines, few studies focus on species that are robust to – or even benefit from – environmental change (Somero et al. 2010; Fulton et al. 2011; Clucas et al. 2014). Gentoo Penguins are one of the few examples of a marine predator that appears to be adaptive and resilient to environmental change, resulting in continued population growth and range expansion. Future work should focus on the mechanisms of population growth and range expansion in Gentoo Penguins, as well as the creation of habitat suitability models to identify future potential habitat. Updated census data for large populations on South Georgia and the colonies of the sub-Antarctic islands in the Indian Ocean should be considered of high priority.

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COMPLIANCE WITH ETHICAL STANDARDS

The authors declare no conflicts of interest.

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456 **Table 1:** Estimated abundance (in breeding pairs) of Gentoo Penguins (*Pygoscelis papua*) for
 457 each major region and sub-regions. *Note that we did not include the 2018 Possession Island and
 458 Courbet Peninsula counts in the global estimate because we cannot directly differentiate them
 459 from the historical overall population counts of the Crozet and Kerguelen island groups.

CCAMLR Sector	Region/Island Group	Abundance (95 th Percentile CI)	Average Year of Survey
- -	Falkland Islands	131,059 (129,036 – 133,123)	2010
48.1	Antarctic Peninsula	127,320 (118,199 – 137,208)	2007
	WAP	116,521 (107,692 – 126,331)	2007
	Danger Islands	4,523 (4,398 – 4,655)	2015
	Joinville Island	6,022 (5,857 – 6,189)	2015
48.2	South Orkney Islands	5,364 (3,081 – 7,810)	1990
48.3	South Georgia	98,867	1985-1987
48.4	South Sandwich Islands	1,902 (1,790 – 2,022)	2010
- -	Martillo Island, Tierra del Fuego	31	2013
58.7	Marion Island	550	2012
58.7	Prince Edward Island	40	2008
58.6	Crozet Islands	9,000	1970-1982
	Possession Island	577	2018*
58.5	Kerguelen Islands	35,000	1985
	Courbet Peninsula	8392	2018*
58.4	Heard Island	16,574	1987
- -	Macquarie Island	3,800	2006
Total Estimate		432,144 (338,059 – 534,114)	

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Figure 1: Global Gentoo Penguin (*Pygoscelis papua*) breeding distribution (triangles) and CCAMLR statistical sections (bold numbers).

Figure 2: Locations of all Gentoo Penguin (*Pygoscelis papua*) breeding colonies on the Antarctic Peninsula (purple circles). Newest colonies formed after 1994 are in orange triangles.

Figure 3: Population trends for six new Gentoo Penguin (*Pygoscelis papua*) breeding colonies of interest (data from MAPPPD; Humphries et al. 2017; see Online Resource 1).

Figure 4: Glacial retreat at newly colonized Gentoo Penguin (*Pygoscelis papua*) breeding sites: A – Historic aerial imagery of Moot Point (1956; FIDASE); B - Recent high-resolution satellite imagery taken of Moot Point (2016; Google, CNES/Airbus); C – Historic aerial imagery (FIDASE) taken December 1956 of Noble Rocks; D - Recent satellite imagery taken of Noble Rocks (2012; Google, Maxar Technologies).

APPENDIX

Online Resource 1 (see attachment ESM_1.xlsx)