

1 **King penguin populations increase on South Georgia but explanations remain elusive**

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13 **Abstract**

14 While dramatic increases in populations of King Penguins (*Aptenodytes patagonicus*) have been
15 documented throughout their range, population changes on the island of South Georgia have not
16 been assessed. We reconstructed time series of population size for six major colonies across
17 South Georgia using historical data stretching back to 1883 and new population estimates
18 derived from direct on-the ground censuses and oblique, high-resolution digital photographs. We
19 find evidence for a significant increase in the population of King Penguins at all colonies
20 examined over the 124 years of available survey data. We discuss our findings in the context of
21 four established hypotheses explaining King Penguin population growth: (1) favorable changes
22 in the pelagic food web; (2) climate forcing; (3) greater availability of breeding habitat; and (4)
23 the cessation of harvesting. While we do find evidence that glacial retreat may have increased
24 suitable breeding habitat at some colonies and facilitated population expansion, glacial retreat is
25 not associated with all of South Georgia's growing populations. Local anomalies in sea surface
26 temperature have increased in parallel with King Penguin population growth rate, suggesting that
27 climate forcing may contribute to colony growth, but a complete explanation for the island's
28 rapidly growing King Penguin population remains unclear.

29 **Keywords:**

30 Southern Ocean, high-resolution photography, population estimate, glacial retreat, climate
31 forcing

32

33 **Introduction**

34 Since the cessation of most whaling and sealing operations, the sub-Antarctic islands have seen
35 dramatic changes in ecosystem structure and composition. King Penguin (*Aptenodytes*
36 *patagonicus*) populations have received substantial attention because they were harvested in
37 great numbers for their oil (Bost et al. 2013) during the sealing epoch of the 19th and 20th
38 centuries. Populations on some islands, notably Heard and Macquarie Islands in the Indian and
39 Pacific Ocean sector of the Southern Ocean, respectively, suffered substantial declines and even
40 local extirpation (Budd 2000; van den Hoff et al. 2009; Bost et al. 2013), but relatively little is
41 known about the historic abundance, dynamics, or demographics of King Penguin colonies in the
42 Atlantic sector of the Southern Ocean. In this region, King Penguin abundance is concentrated on
43 South Georgia, a 170 km long crescent shaped island lying along the Scotia Arc. Upon its
44 discovery and exploration in the late 18th century, South Georgia became a hub for the
45 exploitation of seals, whales, and, to a lesser extent, penguins. In fact, throughout the 19th and
46 20th century, South Georgia was considered the primary location for all land-based whaling in
47 the Southern Ocean (Headland 1984) and hosted six permanent shore-based whaling stations
48 (Bannister 1964).

49 While island-wide King Penguin surveys are not regularly conducted at South Georgia,
50 the island is thought to possess the largest breeding colony of the *A. patagonicus patagonicus*
51 subspecies of King Penguin. Trathan et al. (1996) estimated there could be as many as 650,000
52 breeding pairs assuming a constant growth rate since 1976. In a more recent attempt, the IUCN
53 estimates the current breeding population consists of 450,000 pairs (BirdLife International 2017).
54 This, however, is only a rough estimate, as an island-wide survey of King Penguins has never
55 been conducted. Additionally, our understanding of their population dynamics are complicated

56 by the fact that recovery from historic exploitation is now occurring alongside environmental
57 fluctuations due to climate change (Jacka and Budd 1998; Gille 2002; Curran et al. 2003;
58 Trathan et al. 2007). Additionally, the breeding range of King Penguins appears to be extending
59 southward into the South Shetland Islands (Petry 2013; Juárez et al. 2014; Juárez et al. 2017),
60 and it has been suggested that these pioneer breeding pairs likely originated from South Georgia
61 (Juárez et al. 2014). Given the implications of range extension under climate change, it is
62 important to understand the population dynamics of potential source populations on South
63 Georgia.

64 While records clearly indicate the growth of King Penguin populations across their range
65 (Gales and Pemberton 1988; Budd 2000; Delord et al. 2004; van den Hoff et al. 2009), estimates
66 of abundance and hence analyses of trends are complicated by their unusual breeding phenology,
67 which takes more than a year to complete. Stonehouse (1956) observed a single colony of King
68 Penguins and suggested that their breeding cycle lasts approximately 14 months from egg laying
69 to chick fledging. He proposed that chick fledging success was highest when adults bred early,
70 with egg laying in December and hatching in late January, because first-year chicks are left at the
71 colony over the austral winter and receive only sporadic parental care and feeding during this
72 period. Consequently, chicks born to late-breeding adults enter the overwintering period with a
73 lower body mass than earlier hatched chicks and thus are prone to starvation and insufficient
74 thermoregulation (Stier et al. 2014). Due to this staggered breeding, individuals are present at the
75 colony throughout the year, with different ‘waves’ of chicks residing at the colony
76 contemporaneously. Since the number of chicks and attending adults varies over the course of
77 the year, it is difficult to directly compare population estimates. Moreover, count data derived
78 from infrequent logistical survey opportunities, as in the case of South Georgia, will often differ

79 with respect to their alignment with the colony's breeding phenology. While the challenge of
80 establishing a precise trend in King Penguin abundance at South Georgia remains an issue,
81 anecdotal evidence (Clark et al. 2012) suggests significant increases in abundance with potential
82 consequences for the health of terrestrial vegetation and interspecific competition for habitat and
83 resources (Ellis 2005; Bried and Jouventin 2002).

84 On other islands in the sub-Antarctic, four hypotheses have been proposed to explain
85 population increases of King Penguins (Conroy and White 1973). The first hypothesis suggests
86 that changes in the pelagic food web have led to favorable conditions for King Penguins (Sladen
87 1964; Laws 1973). Second, climate forcing has been suggested as a potential driver of population
88 increases. Third, it has been proposed that King Penguin colonies are limited by the availability
89 of breeding habitat, as discussed by Delord et al. (2004) based on observations at Crozet
90 archipelago. Lastly, the cessation of penguin harvesting has been proposed as an explanation for
91 population increases on other sub-Antarctic islands, though there is little evidence to suggest a
92 substantial industry in hunting King Penguins on South Georgia.

93 While some work has been conducted to understand how the population of King
94 Penguins has changed on South Georgia (Poncet and Crosbie 2005), there are no published
95 reports of population trend or abundance from within the last ten years. Additionally, because
96 many of the King Penguin colonies on South Georgia are so large, direct ground counting of
97 individuals, which had been the method used for previous surveys, is no longer feasible for much
98 of the population. In response to these issues, we sought to: (1) develop the appropriate methods
99 and best practices to census King Penguin populations; and (2) identify population trends of
100 King Penguin colonies on South Georgia and explore their potential drivers. Better identifying
101 the important drivers of change for King Penguins will facilitate our understanding of their

102 dynamics under climate change and their likely impact on the ecological community of South
103 Georgia.

104 **Materials & Methods**

105 *Estimation of Abundance*

106 King penguin breeding populations on South Georgia have been surveyed intermittently since
107 the late-1800s. However, due to their inaccessibility and the unusual breeding phenology of the
108 species, creating a coherent time series from these previous censuses is difficult. We used a two-
109 pronged approach to develop time series of abundance at six of South Georgia's King Penguin
110 colonies: (1) ground-based digital photographic counts were conducted for recently visited
111 colonies and (2) historical data were collected from available scientific reports and expedition
112 notes. Where known, the timing of each census was defined as either “optimal” or “suboptimal”.
113 Optimal nest and chick censuses were conducted January 15th - February 15th and October 1st -
114 November 15th, respectively. Photographs and ground counts were collected opportunistically at
115 these six colonies between October 2014 and February 2017. Direct *in situ* counts were
116 conducted and, where feasible, replicated three times by one or more trained observers. Larger
117 colonies (>5,000 pairs; see Online Resource) required counts to be made from photographs.
118 Digital photographs used for counting were taken from multiple viewpoints at higher elevation
119 locations surrounding the colony. For the largest colonies, a GigaPan EpicPro robotic camera
120 head was used to automate and assemble panoramas of the entire colony, which were then
121 stitched using Microsoft Research’s Image Composite Editor software.

122 Abundance was calculated by identifying nesting and loafing adults and chicks in each
123 panorama. Nesting penguins were defined as those actively incubating eggs or chicks. Loafing

124 penguins were defined as any penguin in adult plumage at the colony which was not actively
125 incubating eggs or chicks. Incubating penguins can be easily identified by their posture (Figure
126 2), as incubating penguins maintain a “c-shaped” body position, observable from any angle, and
127 a folded brood patch. At least one panorama from each site was counted independently by two or
128 more trained observers. Observers conducted all counts manually labelling each individual using
129 ArcMap software. Wherever possible, panoramas captured from different vantage points were
130 used to estimate the error associated with obstructed views of penguins within the colony. Taken
131 together, this information was used to estimate the overall precision of population estimates
132 derived using photographs.

133 Historic data were collected from scientific reports and expedition notes (Conroy and
134 White 1973; Lewis Smith and Tallowin 1979; Clark 1984; Clark 1985; Trathan, Daunt, and
135 Murphy 1996; Poncet and Crosbie 2005; Poncet Unpublished). Only data with estimates
136 associated with individual colonies were used in the present analysis. Count data were classified
137 according to the type of count (individual, adult, chick, pair, etc.) and, when known, the timing
138 of the count.

139 *Population Models*

140 Only historic counts that included breeding season, location, and information on count type
141 (individuals, adults, breeding adults, or chicks) were included in our time series. Given the
142 scarcity of existing data even for the six relatively well-surveyed colonies examined (Gold
143 Harbour, Right Whale Bay, Brisbane Point at Royal Bay, Salisbury Plain, St. Andrew’s Bay, and
144 Whistle Cove at Fortuna Bay; Figure 1), we fit simple log-linear models to the abundance data
145 available. This approach allowed us to estimate the average population growth rate for the site,

146 though it did not allow us to investigate non-linear or cyclic dynamics that may capture
147 fluctuations in abundance over shorter time scales (Woehler et al. 2001; Delord et al. 2004).

148 *Drivers of Population Change*

149 To determine whether glacial retreat might explain why King Penguin colonies on South Georgia
150 were growing, we used data on glacial front locations from Cook et al. (2010) to quantify the
151 change in glacial area between 1958 and 2003-2008 to determine if there was a correlation
152 between glacial retreat and colony growth. Colonies were identified as being in close proximity
153 to a glacier if they were within 1 km from a glacial front in 1958, and distant from a glacier if
154 they were more than 1 km from a glacial front in 1958. For this analysis we included three
155 colonies (Ample Bay, Cooper Bay, Elsehul) in addition to the six for which we were able to
156 construct reasonably complete time series, as they provide additional information on trends at
157 colonies proximal (Ample Bay) and distant (Cooper Bay, Elsehul) from glaciers.

158 **Results**

159 *Population Models*

160 The longest time series obtained was from St. Andrew's Bay, where the 19 available census
161 counts stretch back to 1883. The earliest records from Whistle Cove at Fortuna Bay were from
162 1905, creating a data set spanning 110 years. At three colonies, Right Whale Bay, Brisbane Point
163 at Royal Bay, and Salisbury Plain, the earliest observations were recorded from 1914, creating a
164 100 year data set ($n=4$, $n=9$, $n=14$, respectively). Lastly, the earliest reports from Gold Harbour
165 were from 1936, creating a 79 year data set ($n=22$).

166 Of the 33 duplicate colony counts (same panoramic, different observers), inter-observer
167 error rates ranged from 3-10%. Error associated with different vantage points ranged from 0-

168 47%. Larger errors associated with different vantage points were due to obstructed views in
169 some photographs. In these instances, the census derived from the larger estimate was used.
170 Across the six colonies evaluated, dramatic population increases were apparent, despite
171 considerable interannual variation (Figure 3). The rate of increase predicted by the log-linear
172 models varied across colonies (Table 1) with the fastest rate of increase observed at Whistle
173 Cove (4.3% per year) and the slowest rate of increase at Royal Bay (0.7% per year). Mean rate of
174 increase was 1.6% per year ($SD=1.4\%$).

175 *Glacial Retreat as a Driver of Population Change*

176 Six colonies in close proximity to glaciers were identified (Ample Bay, Whistle Cove, Gold
177 Harbour, Brisbane Point at Royal Bay, Salisbury Plain, and St. Andrew's Bay). Retreat of the
178 glacial front was prevalent across all of these sites, and in some cases, the present King Penguin
179 colony extent was completely within areas covered by the glacier for much of the time series
180 (Figure 4). While there is a weak, positive correlation between net annual glacial retreat and
181 King Penguin growth rate ($slope = 0.43$, $R^2=0.12$), this relationship is not statistically significant
182 ($p=0.28$) and the degree of causality is ambiguous (Figure 5a). Cooper Bay, Elsehul, and Right
183 Whale Bay are three colonies that are not within 1 km of a glacier but have grown in size
184 nonetheless over the available time series (Figure 5b).

185 **Discussion**

186 Despite limitations imposed by poor historical data and a complex breeding phenology, King
187 Penguin populations on South Georgia have unambiguously increased over the last century
188 (Figure 3). This is consistent with observations of King Penguin populations on other sub-
189 Antarctic islands, which have also increased in abundance over the last century (Gales and

190 Pemberton 1988; Budd 2000; Delord et al. 2004; van den Hoff et al. 2009). Conroy and White
191 (1973) proposed four primary hypotheses to explain the increases observed in King Penguin
192 populations. First, scientists have proposed that the removal of large whales and seals have
193 allowed for a surplus of food – namely Antarctic krill (*Euphausia superba*) – for marine
194 mesopredators (Sladen 1964; Laws 1973). This Krill Surplus Hypothesis is often cited as a
195 potential driver for rapid increases in seal and penguin populations throughout the Antarctic.
196 These effects become more complex in the case of King Penguins, whose diet consists primarily
197 of myctophid fish throughout much of their range (Olsson and North 1997; Raclot et al. 1998).
198 The degree to which these fish use krill resources is unclear (Williams 1985; Lancraft et al.
199 1989; Pakhomov et al. 1996; Pusch et al. 2004). Saunders et al. (2015) noted that the larger
200 myctophid species consistently consumed Antarctic krill and estimated that myctophid predation
201 could account for approximately 2% of the daily krill productivity in the Scotia Sea, amounting
202 to nearly 17 million tons per year. In fact, it has been proposed that large myctophids could be
203 the main consumer of krill in the Scotia Sea (Lancraft et al. 1989; Pusch et al. 2004; Hill et al.
204 2007), consistent with an apparent link between myctophid and krill abundance (Chamailé-
205 James et al. 2000). In contrast, Murphy et al. (2007) noted the importance of the mesopelagic
206 myctophid pathway in the Atlantic Sector of the Southern Ocean while omitting the krill-
207 myctophid link. Further complicating our understanding of the key trophic interactions,
208 commercial fishing operations harvest Southern Ocean myctophids. An estimated 200,000
209 tonnes of myctophid biomass were extracted from the South Georgia region of the Southern
210 Ocean between 1979 and 1992 (Collins 2008). The link between the Krill Surplus Hypothesis
211 and increasing King Penguin populations is thus indirect. While the causal pathways remain
212 unclear, several studies have implicated increased near-shore food availability with increases in

213 King Penguin populations (Crozet Islands: Weimerskirch et al. 1992, LeBohec et al. 2008;
214 Trucchi et al. 2014; Heard Island: Budd 2000; South Georgia: Woehler and Croxall 1997).

215 The second hypothesis for King Penguin population expansion focuses on the effect of
216 climate forcing. There are two primary mechanisms through which climate might affect King
217 Penguin populations. Studies have found correlations between breeding success and the Southern
218 Oscillation Index and associated changes in near-shore food availability (Delord et al. 2004;
219 LeBohec et al. 2008). Indeed, Trucchi et al. (2014) suggested that recolonization of King
220 Penguins on the sub-Antarctic islands following the Last Glacial Maxima was likely due to
221 climate forcing affecting food availability. Differences in the pelagic community between these
222 sites may have important consequences in foraging dynamics across summer and winter seasons.
223 Studies have demonstrated a link between King Penguin foraging habitat and oceanographic
224 conditions (Jouventin et al. 1994), however the relationship may be complicated by behavioral
225 differences across the breeding cycle. Jouventin et al. (1994) noted a preference for foraging near
226 the 5°C isotherm, which is associated with the Polar Front (Jouventin et al. 1994), but during
227 brooding, they preferentially forage at the Southern Antarctic Circumpolar Current, located
228 much closer to breeding colonies (Trathan et al. 2008). Additionally, recent studies have
229 suggested that a shift in the Polar Front's location, which is expected under most current climate
230 models (Turner et al. 2014; Gutt et al. 2015) and has already been observed (Sokolov and
231 Rintoul 2009), will likely have profound negative impacts on King Penguin populations
232 (LeBohec 2008).

233 Impacts of increasing sea surface (SST) and air temperature may have more direct
234 impacts on breeding colonies. Studies have demonstrated regional increases in mean SST across
235 the sub-Antarctic (Boyin et al. 2015), and more fine-scale analyses have demonstrated significant

236 warming of the waters around South Georgia over the 20th century (Figure 3; Whitehouse et al.
237 2008). Such changes in ocean conditions within the region have been linked to declining habitat
238 suitability for lower trophic level species in the sub-Antarctic (Whitehouse et al. 2008). Changes
239 in mean air temperature could also have important implications for King Penguin population
240 dynamics (Figure 3; Turner et al. 2004). Increases in winter air temperature have been linked to
241 wetter winter conditions in the region (Summerhayes et al. 2009; Constable et al. 2014; Gutt et
242 al. 2015). Because chicks overwinter at breeding colonies in their downy plumage, they are more
243 sensitive to changes in precipitation, particularly during colder weather (Boersma 2008;
244 Chapman et al. 2011; Ropert-Coudert et al. 2014).

245 The third hypothesis proposes that King Penguin populations are limited by the
246 availability of breeding habitat. Indeed, this was proposed as a possible mechanism regulating
247 the population size of King Penguins on the Crozet archipelago, where the rate of population
248 growth declined in association with a lack of suitable, flat, vegetation-free areas for nesting
249 (Delord et al. 2004). On South Georgia, 50% of the island is glaciated and a large proportion of
250 the remaining area is highly vegetated (Cook et al. 2010), which raises the possibility that habitat
251 for incubation and crèching may be a limiting factor. At the same time, however, there are many
252 coastal areas free of permanent snow and ice that might provide breeding habitat. At present it is
253 difficult to determine whether King Penguins are habitat limited because we lack a fine-grained
254 suitability model and suitable breeding habitat requirements are often difficult to determine in
255 seabirds because they frequently congregate in small areas, leaving apparently suitable habitat
256 space unoccupied (Bried and Jouventin 2002). Regardless of its potential role as a limiting factor
257 island-wide, recent analyses have indicated that 97% of the 103 coastal glaciers on the island

258 have retreated over the last 70 years (Cook et al. 2010) and, in doing so, may have exposed
259 additional suitable habitat for King Penguin breeding colonies near the glacier margins.

260 Our analysis suggests that glacial retreat may function as one mechanism for King
261 Penguin population regulation, however there are likely other mechanisms involved as well. The
262 Heaney and Cook Glaciers at St. Andrew's Bay have experienced a combined loss of nearly 6.5
263 km² since 1958, and the current extent of the penguin colony is contained entirely within this
264 recently exposed terrain (Figure 4). At other colonies, such as Cooper Bay, Elsehul, and Right
265 Whale Bay, no substantial glacial retreat has been observed near the penguin colonies and other
266 factors, separate from deglaciation, must be driving the increase in King Penguin populations
267 (Figures 3 & 5). It is worth noting in this context that some King Penguin colonies located in the
268 Falkland Islands, which are not glaciated, have also experienced substantial population growth
269 (Bingham 1998).

270 Lastly, and perhaps most obviously, the cessation of harvesting has been proposed as a
271 primary driver of King Penguin population increases. While this is certainly a plausible
272 explanation for much of their distribution (Budd 1970; Rounsvell and Copson 1982), it fails to
273 account for populations located on South Georgia, where it is unlikely a large-scale King
274 Penguin harvesting operation existed (Clarke 2012). There is evidence, however, to suggest that
275 small-scale harvesting almost certainly occurred and may have affected populations from small
276 breeding colonies. Upon returning from his 1912-13 trip to South Georgia, Robert Cushman
277 Murphy noted, "As an example of incidental vandalism, I saw many of the magnificent and
278 rapidly disappearing King Penguin (*Aptenodytes*) of the island destroyed in order that their gold-
279 collared skins might be used as *shoes* by New Bedford sealers." (Murphy 1915). Additionally,
280 the Russian explorer Bellingshausen reported observing the use of King Penguin skins to fuel

281 sealing tripot fires during his 1819 trip to South Georgia (Debenham 1945). Despite little
282 evidence supporting a large-scale King Penguin harvest, the historical record suggests that some
283 harvest did occur. If penguin populations during this time were already limited by other
284 ecological factors, even small-scale harvesting would have the potential to inhibit already-
285 depressed populations. Release from such harvest, especially if it co-occurred with release from
286 other inhibiting factors, may have allowed for rapid population expansion.

287 *Challenges of monitoring King Penguin populations*

288 Much interest has been focused on the issue of bias in wildlife survey methods (Pollock and
289 Kendall 1987; Bart et al. 2004), however most studies have focused only on the estimation of
290 error associated with the counting of individuals present at the study site rather than the
291 availability of individuals to be counted. In many populations, particularly asynchronous
292 breeders like the King Penguin, it cannot be assumed that all individuals are present at the time
293 of surveying (Fredrick et al. 2006). Indeed, studies have found substantial error associated with
294 estimating population sizes of phenologically asynchronous bird species (47% in wading birds
295 [Frederick et al. 2006] and 69-79% in shorebird populations [Farmer and Durbain 2006]),
296 because there is no single time when all breeding individuals will be present at the colony.
297 Future studies on king penguin populations should consider the impact of poorly timed surveys
298 and should seek to minimize biases associated with incomplete colony attendance at the time of
299 surveying. To best account for these biases, we propose a suite of best practices for the
300 estimation of King Penguin abundance on South Georgia that are easily tailored for populations
301 elsewhere in their range. (1) Chick counts should be completed in early spring, between October
302 1st and November 15th. This will allow for the quantification of chicks that have successfully
303 overwintered, but prior to fledging. (2) Nesting adult counts should be completed at peak

304 nesting, between January 15th and February 15th. This will allow for the survey of both early- and
305 late-breeding individuals at a single point in time, as this is when you would expect all breeding
306 adults to be present and nesting at the colony. Explicit mathematical models of colony
307 attendance and breeding phenology may be required to separate the underlying (but unknown)
308 abundance of breeding pairs and the flux of individuals into and out of the population available
309 for counting on any given day (e.g., Condit et al. 2007). In the meantime, only large changes
310 occurring over long time scales are probably interpretable from simple census counts.
311 Additionally, it is important to consider the impact of dispersal on the population dynamics
312 across their range. While it is possible that such metapopulation dynamics could play a role,
313 Clucas et al. (2016) noted that while most other King Penguin populations appear to be
314 genetically homogenous, the South Georgia population of King Penguins is significantly
315 differentiated from all other sub-Antarctic populations. Thus, it seems that metapopulation
316 dynamics could be important in other King Penguin populations, but are likely less substantial in
317 South Georgia.

318 *Looking ahead*

319 Surprisingly, the drivers allowing for dramatic growth in population remain elusive. Due to the
320 lack of evidence for consistent harvesting of King Penguins on South Georgia, release from
321 harvesting pressure is unlikely to explain these increases. Additionally, while there does appear
322 to be a relationship between glacial retreat and colony growth in some areas, glacial decline is
323 not a necessary condition for King Penguin population increases. Climate change may actually
324 play a more direct role in the complex life cycle of the King Penguin by controlling the extent to
325 which King Penguin chicks need to crèche. Studies have demonstrated that King Penguin
326 crèching behavior increases in colder and wetter weather (LeBohec 2005) presumably because

327 large breeding aggregations allow chicks to stay warm through the austral winter. Climate
328 change in this region is predicted to cause warmer (though wetter) winters (Summerhayes et al.
329 2009; Constable et al. 2014; Gutt et al. 2015), which may reduce the required crèche size and
330 facilitate more successful colonization of new colonies. By highlighting past trends, underlying
331 dynamics will help us understand their documented and likely continuing southward expansion
332 to the Antarctic Peninsula region (Petry et al. 2013; Juares et al. 2014; Juares et al. 2016).

333 Notwithstanding the inherent challenges of assessing King Penguin population
334 abundance, populations at South Georgia appear to have followed similar trajectories of other
335 sub-Antarctic island populations (Gales and Pemberton 1988; Budd 2000; Delord et al. 2004;
336 van den Hoff et al. 2009). Historical and current survey methodologies, however, have failed to
337 account for the demographic and population implications of the King Penguin breeding cycle,
338 leading to high errors associated with population estimates, and correction factors should be
339 developed to account for temporal differences in monitoring efforts across breeding seasons.
340 Moreover, while remote sensing methodologies may facilitate more regular monitoring of the
341 abundance of South Georgia’s King Penguin population, mark-recapture of individuals is likely
342 required if we are to understand the demographic drivers of these observed population increases.

343

344 **Compliance with Ethical Standards**

345 All research was conducted with under the approval of the Stony Brook University Institutional
346 Animal Care and Use Committee application 2011-1881- FAR- 6.19.20- BI and South Georgia
347 and South Sandwich Islands Permit #2015/018, and 2016/035.

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559 **Tables & Figures**

560

561 **Figure 1.** South Georgia is located in the Atlantic Sector of the Southern Ocean. Colony
562 locations described in this article are highlighted.

563

564 **Figure 2.** High-resolution digital photographs were used to create panoramas of breeding
565 colonies (a) which were used to quantify chicks and nesting adults. Nesting (b) and loafing (c)
566 King Penguins are distinguished by their posture. The brood patch of nesting penguins is folded
567 over the egg, resting on the feet (arrows), as penguins lean forward. Loafing penguins frequently
568 rest leaning back on the heels of the feet, with metatarsals exposed.

569

570 **Figure 3.** King penguin breeding colony population change at Gold Harbour, St. Andrew's Bay,
571 Royal Bay, Right Whale Bay, Whistle Cove, and Salisbury Plain (top) and regional air
572 temperature (blue; Turner et al. 2004) and ocean temperature anomalies (red; Boyin et al. 2015)
573 over the same period (bottom). Symbols denote count type: Adults (X); individuals (*); chicks
574 (○); and nests (□) or unknown (⊕). Filled symbols indicate optimal timing of the census. Open
575 symbols denote censuses with suboptimal or unknown timing.

576

577 **Figure 4.** Glacial retreat on South Georgia has been implicated as a potential driver for King
578 Penguin population growth. Sites such as St. Andrew's Bay have experienced substantial glacial
579 retreat exposing the (a) current extent of the expanded breeding colony. The glacial front (yellow
580 dashed line; background image: Landsat 2002/03 image mosaic [British Antarctic Survey 2018])
581 has consistently receded since observations in 1958 (b), 1977 (c) and 1993 (d). Red hatched area

582 indicates current colony extent. The last reported glacial front location was recorded in 2003 (e),
583 and leaves the entire current colony area exposed. Population data (f) collected during the
584 window of rapid glacial retreat which left the modern colony footprint exposed (blue shaded
585 region) indicates that this was likely a period of rapid population growth.

586

587 **Figure 5.** While there is a weak, positive relationship between annual population growth rate and
588 net glacial retreat (a), the causality is ambiguous. At other colonies (b), such as Cooper Bay and
589 Elsehul, there is no evidence of recent glacial retreat, however the populations have experienced
590 consistent growth. Symbols denote count type: Individuals (*); chicks (○); and nests (□) or
591 unknown (⊕). Filled symbols indicate optimal timing of the census (OC=Optimal Chick; ON =
592 Optimal Nest). Open symbols denote censuses with suboptimal or unknown timing
593 (SC=Suboptimal Chick; SN=Suboptimal Nest).

594

595 **Table 1.** Model description for the population growth at six colonies across South Georgia.

596

597

598 **Table 1.** Model description for the population growth at six colonies across South Georgia.
 599

| Colony | Latitude | Longitude | Model Slope | R² |
|------------------------------|-----------------|------------------|--------------------|----------------------|
| Gold Harbour | -54.6188 | -35.9457 | 0.007 | 0.508 |
| Royal Bay | -54.5764 | -36.0128 | 0.007 | 0.086 |
| St. Andrew's Bay | -54.4473 | -36.1810 | 0.026 | 0.792 |
| Whistle Cove, Fortuna Bay | -54.1402 | -36.8218 | 0.043 | 0.774 |
| Right Whale Bay | -54.0158 | -37.6814 | 0.022 | 0.651 |
| Salisbury Plain | -54.0544 | -37.3402 | 0.014 | 0.600 |

600
 601