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Varying population size of the Cape Royds Adélie penguin colony, 1955–2020: a synthesis

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Abstract: Among the longest Antarctic biological time series is that of Adélie penguin *Pygoscelis adeliae* population size at Cape Royds, 1955 to the present. Demographic trends over the 66 years fall into five periods: 1) decrease then recovery due to control of tourism from McMurdo Station/Scott Base; 2) further increase responding to the removal of > 20 000 trophically competing Antarctic minke whales *Balaenoptera bonaerensis* from the colony's wintering area; 3) stabilization but not decrease upon the ban of whaling in 1982, and whale recovery, owing to increased winds facilitating McMurdo Sound Polynya presence (easier ocean access during nesting); 4) decrease in 2001–2005 when two mega-icebergs, B15A/C16, opposed the wind effect by increasing sea-ice cover, thus limiting ocean access; and 5) after iceberg departure, minimal recovery due to the increased velocity of the wind-generated Ross Gyre reducing penguin breeding probability. A multivariant model using 1998–2018 data confirmed the roles of gyre speed (negative) and open water (positive) in colony growth. Additional negative influence came from high nest predation by south polar skuas *Stercorarius maccormicki*, reducing chick production, as well as perhaps increased trophic competition from nearby Weddell seals *Leptonychotes weddellii*. Clearly, long time series increase our understanding of penguin population dynamics responding to a complexity of factors.

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Key words: Commercial fishing, McMurdo Sound Polynya, Ross Gyre, sealing, tourism, whaling

Dedication

We wish to dedicate this paper to two persons, one of whom initiated and then nurtured efforts to document the trends of the Cape Royds penguin colony, and the other who first collaborated on and then continued the effort, with both pondering the changes. For most of the time series upon which this paper is based they oversaw data acquisition, setting up so well an aerial census programme. Their successors in the endeavour were able to continue without interruption. We really owe so very much to the effort and foresight of these two ecologists and penguinologists!

Rowley H. Taylor, 18 October 1931–16 August 2021

Peter (Pete) R. Wilson, 6 February 1941–

Introduction

When populations change in size or distribution and we observe and conclude the reason and demographic mechanism involved, we have a better understanding of a species' ecology. This is a difficult task to accomplish for marine species that live in an environment to which humans make only brief visits (Ainley & Johns 2023). In modern times, as the human population increases beyond the oceans' capacity to sufficiently satisfy societal needs and the environment becomes more variable, it has become increasingly important to track marine biotic communities, particularly the portion that is exploited. That assessment is most fruitful when it is done within a historical context that can highlight the broader ecological significance of detected changes (Glantz & Thompson 1981, Pauly & Tsukayama 1987, Kittinger *et al.* 2015).

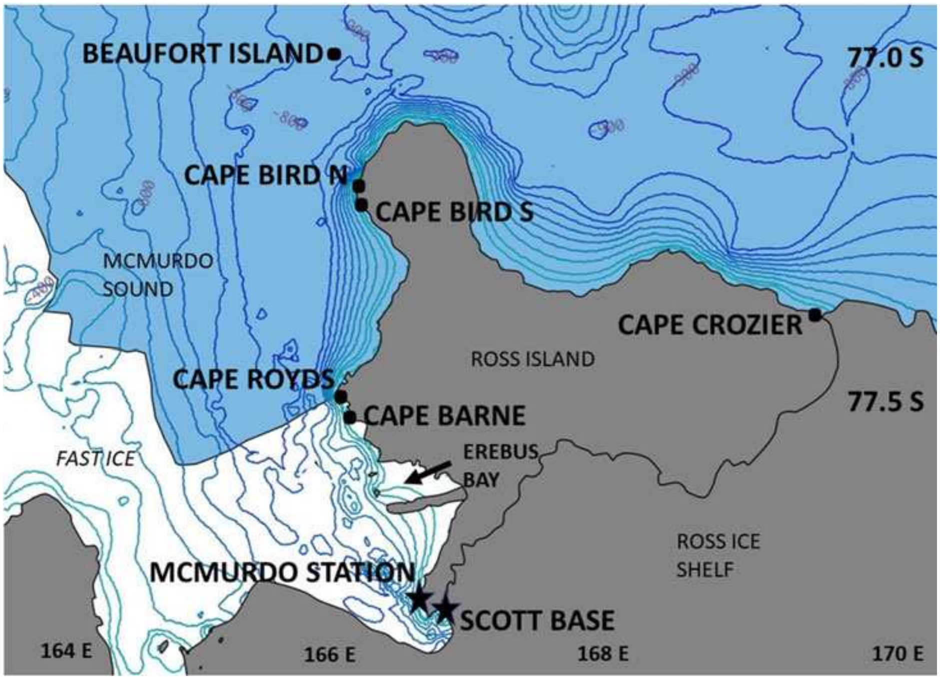

Figure 1. The Ross Island-McMurdo Sound portion of the southern Ross Sea, showing penguin colonies (dots) and modern station locations (stars), as well as other features mentioned in the text.

Due to the great expense involved in monitoring components of marine food webs, doing so for the economically valuable middle-trophic-level 'forage' species is generally quite problematic, as it rarely can be accomplished directly. Instead, monitoring is accomplished by using 'indicator species' that compete with humans for 'prey' (i.e. seabirds), such as in the Benguela (Crawford 2007, Crawford *et al.* 2015), Peru (Muck & Pauly 1987, Tovar *et al.* 1987) and California (Wells *et al.* 2017, Warzybok *et al.* 2018) currents. If the indicators are to be truly useful, significant correlations between prey and predator variability are not sufficient. Additional contextual information has to be obtained to distinguish between climate effects on the relevant ocean biophysics *vs* fishery effects (and other factors) that affect indicator species' population change (e.g. Velarde *et al.* 2004, 2019, Crawford *et al.* 2015, Wells *et al.* 2017, Ainley *et al.* 2018b). That is, we have to know specifically, and quantitatively, what processes were indicated by the changes in an 'indicator's' population or demography.

Amassing the fine-scale biological information necessary to understand the ecology of indicator species in the Southern Ocean has been an unsurpassed challenge, quite unlike the measurement of the physical environment, which has been made possible by advances in satellite imagery. Despite no specific, quantified link having been established between predator and prey resources, be they affected by climate or fisheries, the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) has designated a meso-predator, the Adélie penguin *Pygoscelis adeliae*, as one of several indicator species of the health of the Antarctic marine prey-scape (Agnew 1997, Constable *et al.* 2000, CCAMLR 2018a, 2018b). For sure, a long history of monitoring population change in this penguin species has been achieved in many locations around Antarctica (e.g. Taylor *et al.* 1990, Schofield *et al.* 2010, Lynch *et al.* 2012, Lyver *et al.* 2014, Southwell *et al.* 2015, Emmerson & Southwell 2022), most recently using satellite imagery (Lynch & LaRue 2014). However, determining any drivers of change in most cases remains related, with the least amount of speculation, to physical and specifically sea-ice change. Equivalent time series of the species' prey field for the most part have remained absent, thus lowering the explained variation. A recent analysis has found significant correlations between population change and climate/sea-ice factors, as well as a proxy for prey availability as affected by fishing at the capes Bird and Crozier, Ross Island colonies, 1997–2018 (D.G. Ainley *et al.* unpublished data). That is about as close as we have come to relating Adélie penguin population change to food web change, with other analyses being even more speculative (e.g. Trivelpiece *et al.* 2011, Lynch *et al.* 2012, Sailley *et al.* 2013, Gorman 2015).

The longest biological time series in the Antarctic, exceeded in years only slightly by counts of emperor penguins *Aptenodytes forsteri* at Pointe-Géologie, Adélie Land (Barbraud & Weimerskirch 2001), is that of Adélie penguin colony size at Cape Royds, Ross

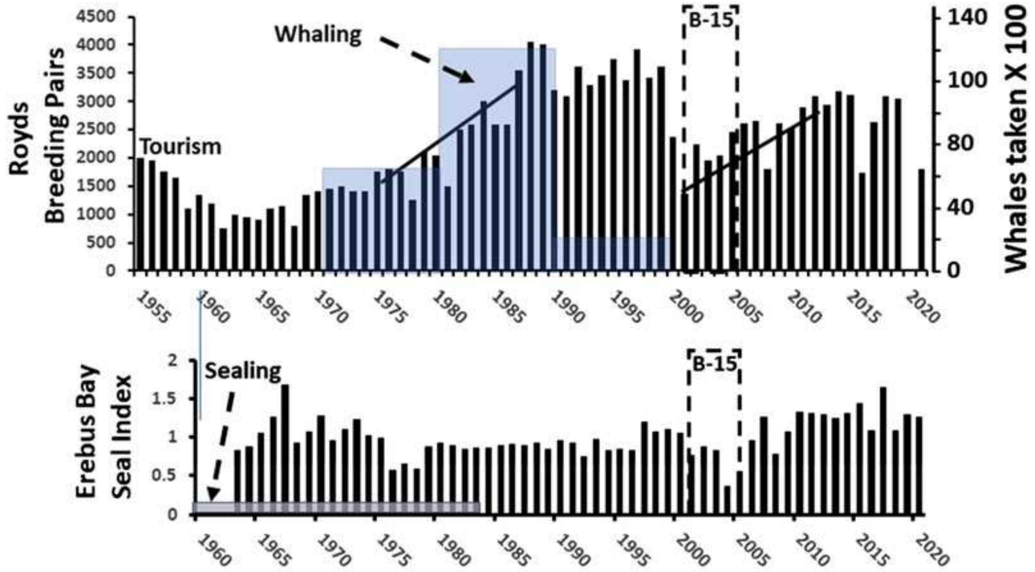

Figure 2. Variation in the size of the Cape Royds Adélie penguin colony (breeding pairs), 1955–2020, in the context of tourist visits to the colony, loss of whale competitors (histogram) and extensive sea-ice cover during 2002–2005 owing to B15A/C16 mega-iceberg presence. Also shown is variation in the size of the adjacent Erebus Bay Weddell seal population, including the effect of sealing. Penguin population increase during the whaling era is described by: $y = 137x + 1277$, $R^2 = 0.680$; and that of the B15A mega-iceberg recovery is described by: $y = 103x + 1681$, $R^2 = 0.582$.

Island, 1955 to the present. Details of its changing trajectories for early segments of its history have been discussed (e.g. Blackburn *et al.* 1990, Taylor & Wilson 1990, Taylor *et al.* 1990, Wilson *et al.* 2001, Ainley *et al.* 2005, 2007, Lyver *et al.* 2014), but not overall, nor recently. Tying together the various portions of the story is the goal of the present paper. Although measurement of physical aspects of this population's local and larger-scale environment have become more available, there is no accompanying time series of prey availability, other than perhaps by proxy (D.G. Ainley *et al.* unpublished data). Nevertheless, it would be instructive to consider the patterns of change during the several decades in which this colony has been monitored, with the identification of factors behind some of the earlier trends now being possible through retrospective application of current, better-quantified biophysical patterns through advanced satellite detection (e.g. Arrigo *et al.* 2015).

The importance of physical aspects, mainly open water and the extent of sea ice, is well known in general for Adélie penguins (summarized in Ainley 2002). For the southernmost of all penguin colonies this relationship to sea ice (or its lack) is evident from a well-documented geological timescale perspective (Stonehouse 1967, 1970, Spellerberg 1970, Emslie *et al.* 2003, 2007). In modern times, other factors also have come to bear, including tourism and the competitive release through exploitation of competing whales, seals and fish. The effect of some of these factors is described in greater detail as part of this review and synthesis. The ability to quantify the demographic response to a once-in-a-millennium 'natural experiment' brought about by the presence of mega-icebergs B15A and C16 (Arrigo *et al.* 2002) that hindered access to Ross Island breeding colonies for 5 years (2001–2005; Dugger *et al.* 2014) greatly enhanced our understanding of the effects of sea-ice cover on penguin productivity. On the other hand, although the Royds colony is now supposedly safe from fishery exploitation due to the waters surrounding Ross Island becoming part of a marine protected area as of 2017 (MPA; CCAMLR 2016), fishing still occurs nearby (for purposes of monitoring stocks; Ainley *et al.* 2016, Parker *et al.* 2016). Intensive fishing continues in the waters bordering the MPA, which include the region occupied by penguins from Ross Island colonies during the non-breeding season (Ballard *et al.* 2010, Jongsomjit *et al.* 2024). Before the late 1990s, fish extraction had been absent from the Ross Sea region (Ainley 2010).

Methods

Layout of the paper and hypotheses/variables considered

Necessarily, because multiple factors have affected Royds' penguin population trends over a 66 year period, this review will be covering multiple subjects, leading to a substantial list of references. Annual population size (breeding pairs) of Adélie penguins at Cape Royds

(Figs 1 & 2) is derived from counts made directly in early years and those from aerial photos in later years conducted and acquired by the New Zealand Adélie penguin programme (e.g. Lyver *et al.* 2014). Counts were made on 1 December or thereabouts, as by then all early failed and non-breeders have departed, with just one adult incubating eggs and the other being at sea (Ainley 2002).

The first portion of this paper contains a review of the literature, separating the Royds history into segments. Included later in the paper will be the use of publications/analyses to provide some ecological and statistical explanations of population change that apply to these earlier periods.

The second portion of the paper contains analyses of the trends during the most recent two decades, since 1998, as affected by a set of environmental variables that were not available for interpreting trends in earlier decades. Most of these variables have been derived from satellite imagery that was not available until the late 1990s. The result of these statistical analyses, using annual Royds population change as the dependent variable, help to confirm or inform interpretations of earlier trends. We looked at the following hypotheses and related variables for the period 1998–2018, sometimes with lags; some of the time series exceeded the length of that used in the modelling:

1) Ross Gyre speed (km/day) in July–October (data available 1992–2018) - stronger sea-ice movement (Kwok *et al.* 2017) probably impedes penguin arrival at Royds, thus precluding eventual nesting (Ainley 2002);
2) Wind (m/s) measured at McMurdo Station, October–February - affects ice formation and in turn the duration of open water adjacent to Royds (McMurdo Sound polynya), which affects penguin movement (see Ainley *et al.* 2005, Kim *et al.* 2018);
3) Open water area (km^2) in November - the area of open water in McMurdo Sound polynya at the time when penguins are arriving to nest (Arrigo *et al.* 2015); appreciable open water positively affects colony growth and productivity (Ainley 2002);
4) Open water date - day of year when the polynya reaches half its eventual size (see point 3); open water appearing early enough in November to affect penguin arrival (Ainley 2002, Dugger *et al.* 2010, 2014);
5) Mean air temperature (°C), November, measured at McMurdo Station - its relationship to penguins is not often obvious but the variable is used in many studies (e.g. Taylor & Wilson 1990);
6) Sea surface temperature (°C) is another variable often used, although it is a complex variable being affected by wind (mixing of surface with deep waters) and air temperature, as well as the amount and proximity of sea ice; its relationship to penguins or their prey is not obvious in this system;
7) Large-scale sea-ice extent (or area; SIE) in the Ross Sea sector of the Southern Ocean (km^2; Parkinson 2002, 2019) in the month it reaches its annual maximum, 1979–2019 - in the past, population change has exhibited a negative relationship with a 4–5 year lag and would have to do with recruitment and characteristics of the wintering area (Wilson *et al.* 2001);
8) Weddell seal *Leptonychotes weddellii* population size in adjacent Erebus Bay (Fig. 1) - count of pups born in October (Fig. 2); index of potential level of trophic competition for Antarctic silverfish *Pleuragramma antarcticum*, thus affecting intra- and interspecific competition (Ainley *et al.* 2015a, D.G. Ainley *et al.* unpublished data);
9) Catch in CCAMLR Area 88.1 of Antarctic toothfish *Dissostichus mawsoni* ≥ 134 cm total length (TL), totalled during the 3 years previous (tonnes) – owing to very conservative life history (e.g. maturity at 17 years and 134 cm TL), large fish taken in the commercial fishery are not readily replaced and thus the release of Antarctic silverfish, of about the size taken by penguins (Eastman 1985), to competing predators is cumulative (Ainley *et al.* 2017, D.G. Ainley *et al.* unpublished data). These large toothfish, having attained neutral buoyancy, occur high in the water column where penguins forage (D.G. Ainley *et al.* unpublished data). More silverfish would lead to growth in the penguin population.

Although we considered them, we did not include primary production or chlorophyll concentration because they were shown to be unimportant to Ross Sea Adélie penguins (Dugger *et al.* 2014, Morandini *et al.* 2022).

Source of environmental variables

Spring to summer averages of wind speed and air temperature were measured at McMurdo Station, which is at the southern edge of the study area (Fig. 1), and they are derived from daily data provided by the University of Wisconsin (http://amrc.ssec.wisc.edu/usap/mcmurdo/). Annual averages of the amount of open water in the McMurdo Sound polynya and sea-surface temperature (optimum interpolation SST) were derived from the Sea-viewing Wide-Field-of-View Sensor (SeaWiFS) and the Aqua satellite's Moderate Resolution Imaging Spectroradiometer (MODIS) using techniques described in Arrigo *et al.* (2015). The early part of that time series has been published (see also https://nsidc.org/data/g02202 and https://www.ncdc.noaa.gov/oisst; Reynolds *et al.* 2007, Meier *et al.* 2017). Annual average daily SIE in the Ross Sea sector of the Southern Ocean

Table I. Comparison using Akaike information criterion (AIC) between best models and models reduced one variable at the time for the Cape Royds Adélie penguin colony and first-order autocorrelation (null model).

	AIC	ΔAIC	K	Log-likelihood	Adjusted R^2
Best model					
Top model: Gyre SPD lag 5y, Open Water, Air Temp lag 5y, SIE lag 4y, CumFish_2y_1	-1.20	0	6	7.60	0.526
Without SIE lag 4y	1.17	2.37	5	5.42	0.247
Without CumFish_2y_1	2.02	3.22	5	4.99	0.387
First-order autocorrelation only	2.50	3.70	1	0.75	0
Without Air Temp lag 5y	4.15	5.35	5	3.92	0.485
Competitive model					
Top model: Gyre SPD lag 5y, Open Water	0.65	0	3	3.67	0.284
First-order autocorrelation only	2.50	1.85	1	0.75	0
Without Open Water	4.40	3.75	2	0.80	0.307
Without Gyre SPD lag 5y	5.05	4.40	2	0.48	-0.080

SIE = sea-ice extent; SPD = speed.

(130° W to 160° E) during the month of maximum were derived from passive microwave data from the Scanning Multichannel Microwave Radiometer (SMMR), Special Sensor Microwave Imager (SSMI) and SSMI Sounder (SSMIS) instruments on a series of NASA and Department of Defense satellites (described in Parkinson 2019).

Weddell seal pup counts are a ratio relative to the count in 1967 (Fig. 2; data from J. Rotella; see also Ainley *et al.* 2015a, D.G. Ainley *et al.* unpublished data). Toothfish catch data are from reconstructions of the length-frequency in the catch, using *Figi-analysis* software, published by CCAMLR (2008, 2019) for Food and Agriculture Organization (FAO)/CCAMLR Fishery Area 88.1 (summary of subareas S70, N70 and SRZ; D.G. Ainley *et al.* unpublished data).

Statistical methods

We used a Bayesian ensemble algorithm, the function *BEAST* from the package *Rbeast* (Li *et al.* 2023), to confirm the different periods of population change for change-point detection. For a given time series, *BEAST* outputs a model capturing the seasonality of the data, the long-term trend and the probability and location of break-points in the trend, combining several models into an average model (Bayesian model average).

The text provided in the Supplemental Materials describes the details of autoregressive integrated moving average (ARIMA) modelling (Box *et al.* 2015) and is adapted from D.G. Ainley *et al.* (unpublished data), in which an attempt was made to explain the recent increase in the populations of Adélie penguins at Cape Crozier and Cape Bird and that of Weddell Seals in Erebus Bay, McMurdo Sound (Fig. 1). Cape Royds was not included because it has been subjected to several factors, such as tourism and intensive predation by south polar skuas *Stercorarius maccormicki* that do not affect these other colonies. Moreover, of these Ross Island penguin colonies, only Royds is adjacent to a large breeding assemblage of Weddell seals that do affect the availability of silverfish to the penguins (Saenz *et al.* 2020). The present paper is complementary to D.G. Ainley *et al.* (unpublished data) and uses the same statistical procedure.

To establish the ARIMA modelling for the period 1998–2018, we calculated the year-to-year (annual) change for the Cape Royds Adélie penguin colony (breeding pairs, using the data shown in Fig. 2). We used the natural log of the ratio Nt/Nt - 1 as our growth metric (Nt = number at a given time). There are several advantages to using this metric. Lack of year-to-year growth (i.e. $Nt = Nt$ - 1) results in a 0 value (log(1) = 0). In addition, the log of the ratio of counts is relatively insensitive to substantial error in the estimation of the counts. The time series begins (1998) with the availability of data owing to new satellites (see above), and it ends (2018) when the person at the NASA Jet Propulsion Laboratory who had been calculating Ross Gyre speed, Ron Kwok, retired.

Model set construction and model selection. Models for the Royds colony size were fitted using the *ARIMA* function of the *forecast* package in *R* (http://www.r-project.org/); see Supplemental Materials for a full description. We built one model set relating change in population size (i.e. ln(Nt/Nt - 1)) to environmental (atmospheric and ocean) and fishing variables (Table I). Annual growth values for 1998/1999–2000/2001 were excluded from the analysed dataset in order to allow at least a 3 year lag for all the variables and 3 years of cumulative data for the total catch of toothfish ≥ 134 cm TL.

Per our hypotheses above, to consider age of recruitment of the penguins at Royds (1 year older than at the other Ross Island colonies; Kappes *et al.* 2021), temporal lags in effects were explored for toothfish removal, SIE, gyre

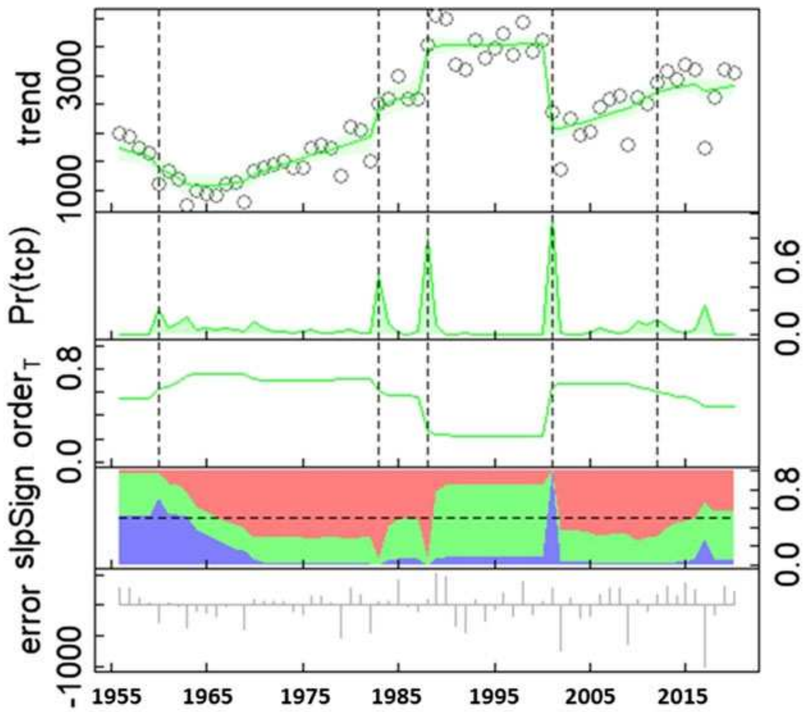

Figure 3. *Rbeast* mutation tests for Royds breeding pairs from 1955 to 2019. Top line = data points and trends; second line (Pr(tcp)) = point-wise probability of change-point occurrence over time; third line = order$_T$ curve, for which an average order towards 0 means that the trend is more likely to be flat and an average order close to 1 means that the trend is linear; lower lines = error; slpSign indicates a trend of change.

speed and open water area. A first model was built including all of the ocean and atmosphere variables (saturated model) for which we had previous consistent hypotheses. Because the geophysical variables are to varying degrees correlated with one another, we inspected and included only the set of variables whose degree of collinearity did not result in a variance inflation factor (VIF) > 10 (Kutner *et al.* 2004). Thus, all variables included had VIF < 10, with a maximum VIF of 4.43. We then used an information-theoretic approach (Burnham & Anderson 2002) with Akaike information criterion (AIC), inspection of effect sizes and likelihood ratio (LR) tests conducted by removing one variable at a time to determine the best model(s).

Fishing variables were selected from different combinations of the total tonnage of toothfish ≥ 134 cm TL caught (i.e. 3 years of cumulative data, 2 years of cumulative data, 1 year of data and including different percentage weights of the cumulative data per year; see Table I & Supplemental Table 1). The best combination was selected and included in the saturated model. We started from models including all main effects and proceeded iteratively backwards, deleting non-significant terms and checking for improvement in the AIC values. The non-significance of the removed terms was further confirmed by adding them back in one by one to the final model. During the selection process, when addressing our hypotheses (see above), 4 and 5 year lags and quadratic effects were included to check for significance and for improvement in the model score. Next, we compared results to a model with only the autocorrelation or intercept as a null model. We selected the model having the lowest AIC value to be our best model. Finally, the different combinations of fishing variables were tested by including them individually in our best model to check for any improvement to its AIC value. However, when evaluating competitive models, we examined the maximized log-likelihood by fitting the reduced (by one variable at a time) model to ensure that small ΔAIC values were not solely a result of adding an additional, uninformative covariate to a preferred, more parsimonious model (Arnold 2010). In our final selected models, all variables included, with one exception, were significant at or near $P = 0.05$, as determined by the LR test, a statistical test preferred to the Wald test, especially with small sample sizes (Hosmer *et al.* 2013).

All analysis code and data, including Jupyter Notebooks showing all the above work, are available at https://zenodo.org/doi/10.5281/zenodo.10602315.

Results and discussion

Results from the change-point analysis indicated a 31.7% probability that the trend component has five change-point (Pr(tcp = 5) = 0.32). Inflection points in trends occurred in (year (probability)): 1959 (0.51), 1982 (0.60), 1987 (0.92), 2000 (0.99) and 2011(0.38; Fig. 3). Thus, there is some element of approximation of the various dates. However, the 1959 point appears to have been thrown off by an usually low population that year, when it seems that *c.* 1965 is the actual overall low of the colony before it started to increase. The same is true for the 1982 point, which actually should be several years earlier (i.e. *c.* 1975).

Early years: International Geophysical Year to the mid-1970s

Following the heroic expeditions led by Robert Scott and Ernest Shackleton during the early twentieth century, the Cape Royds colony was free of human influence until preparations were initiated for participation in the International Geophysical Year (IGY; 1957–1958). In 1955, New Zealand began establishment of Scott Base and the USA began establishment of nearby McMurdo Station close to where the heroic expeditions based their operations (tip of Erebus Peninsula; Fig. 1). James Murray, a biologist of the first Shackleton expedition, resided at Cape Royds (with the entire crew) during 1907–1909 and made some of the first informed observations of nesting Adélie penguins (Murray 1909). The colony in those early years appears to have been ~60% of its size when next censused in 1956 (~2000 pairs). The early estimate was based on the number of eggs taken by the Shackleton over-wintering party, who apparently took them all (!) (Taylor 1962). What variation occurred during the intervening years, of course, is not known.

A few projects began the collection of data (e.g. Cape Royds penguin counts) prior to the IGY. The decrease in Royds colony size from 1955 to early 1960s (1965) was mainly the result of frequent, unchaperoned visitation by persons from Scott Base and McMurdo Station, arriving by over-ice vehicle or helicopter (Stonehouse 1967). The decrease was caused by disturbance that dissuaded pre-breeders from recruiting, although a decrease in chick production was also involved (Blackburn *et al.* 1991). As a result of the alarming decrease, tourist visitation became strictly controlled, beginning with designation in 1972 of the colony and surrounding area as Site of Special Scientific Interest (SSSI) No. 1, eventually becoming Antarctic Specially Protected Area No. 121. Once visitation was limited, the colony began to slowly increase, although the increase rate was not as fast as it could have been (as judged from modelling). However, the lack of fast recovery from tourism was in accord with an actual overall decrease in the Ross Island meta-population during the 1960s–1970s owing to severe sea-ice conditions in the Ross Sea (Ainley *et al.* 1983, Taylor *et al.* 1990).

Whaling era: mid-1970s to 1990

In *c.* 1975, the Royds colony began to exhibit a steep increase through the late 1980s (Fig. 2). Attempting to explain this trend, Blackburn *et al.* (1991) experimented with various demographic parameters, with results leading them to conclude that an increase in chick production (and, hence, post-fledging availability of juveniles) and a decrease in mortality of subadults and adults were required. Blackburn *et al.* (1991) grappled with deriving an explanation for the apparent improved conditions for Royds, as well as other Ross Sea Adélie penguin colonies (Taylor & Wilson 1990, Taylor *et al.* 1990). They thought it could be related to climate change (exemplified by increasing air temperatures measured at Scott Base) and discounted that it could be due to competitive release of forage by the demise of baleen whales in the Southern Ocean. They arrived at that conclusion because whaling had removed large baleen whales from the Ross Sea region before the 1940s, at least for the 'great whales' (see Ainley 2010).

Unknown to Blackburn *et al.* (1991) was that, once all of the large whales were gone, industry had turned to taking the smaller Antarctic minke whales *Balaenoptera bonaerensis* beginning *c.* 1970, with the take intensifying during the 1980s. More than 116 000 minke whales were taken, including an incredibly large number (> 20 000) just from International Whaling Commission (IWC) Areas V and VI during that time (Fig. 2; Brown & Brownell 2001). That area (i.e. the continental slope and adjacent waters of Victoria Land (western Ross Sea region) and eastern Adélie Land) subsequently was determined to be where Royds penguins spent their non-breeding period, or at least they did so into the early 2000s (Ballard *et al.* 2010). By the later 2000s, a portion of Royds penguins continued to do so (Jongsomjit *et al.* 2024). In further support of the connection, it has been shown that minke whales and Adélie penguins compete directly for food, with the whales' exploitation directly affecting the penguins' foraging behaviour and diet (Ainley *et al.* 2006, 2015b). Therefore, the close temporal overlap of the Royds population increase with the removal of large numbers of minke whales in an area important to the penguins raises the likelihood that the two factors were connected (Ballance *et al.* 2006, Ainley *et al.* 2007).

The commercial take of minke whales in the Ross Sea region, and elsewhere, ended with the whaling moratorium enacted by the IWC in 1982, except for a much smaller scientific take that occurred for a few additional seasons. The cessation of this whaling led to rapid recovery of the regional minke whale population by the early 2000s (Branch 2006). Hypothetically, this rapid recovery would explain why the penguin population ceased its increase when it did. However, why did the penguin population, if artificially raised by the loss of a competitor, not then decrease to its former level as the competitor returned, as surmised for the penguin population response to whaling in the Scotia Sea region (Ballance *et al.* 2006)?

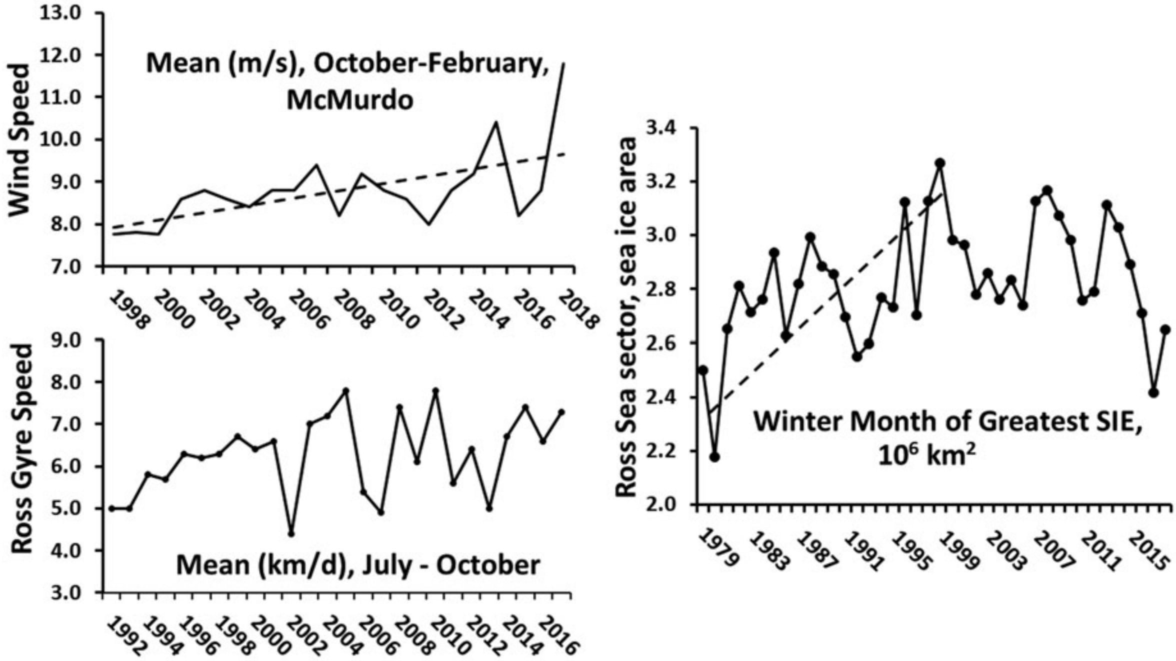

Figure 4. Selected environmental variables that have influenced Adélie penguin population change, or lack thereof, at Cape Royds. Lines serve to facilitate graphic presentation: for wind, adjusted $R^2 = 0.3023$, standard error (SE) = 0.028, $P = 0.006$; for gyre speed, adjusted $R^2 = 0.3630$, SE = 0.740, $P < 0.020$; for sea-ice extent (SIE), adjusted $R^2 = 0.2904$, SE = 0.200, $P = 0.007$.

Climate change becomes important: the 1990s

Essentially, the historical exploitation of the Ross Sea region biotic resources ended with the whaling moratorium enacted by the IWC in 1982, as well as with the Convention for the Conservation of Antarctic Seals enacted in 1978. The latter, in part, was instituted in response to the take of Weddell seals to feed sled dogs in the McMurdo Sound region beginning with the IGY (Ainley 2010, Ainley *et al.* 2015a). Although possibly just a coincidence, the rapid increase in the Royds penguin population described above occurred when the seal breeding and moulting populations of McMurdo Sound were at their lowest level (Fig. 2; Ainley *et al.* 2015a). It has been shown recently that within the Ross Sea region Adélie penguin colonies are smallest where Weddell seal numbers are highest (LaRue *et al.* 2019). However, remaining to be shown is why the seals would affect the penguins in this way given that the penguins forage for the more energetically valuable Antarctic silverfish mostly after the seals depart the Royds foraging area (chased away by seasonal arrival of killer whales *Orcinus orca*; Saenz *et al.* 2020). The departure of the seals is positive, as feeding fish to chicks is beneficial for their growth and subsequent survival (Ainley *et al.* 2018a, Jennings *et al.* 2021, 2023).

Nevertheless, by *c.* 1988 the Royds colony reached ~4200 pairs, nearly double the level from any earlier point in the historical record, at least considering the years when censuses were made beginning in 1909. In addition, the colony had expanded to include Cape Barne ~2.8 km away across Backdoor Bay (Taylor & Wilson 1990). That portion of the Royds-Barne colony attained a few dozen nests and continued into the early 2000s, although Adélie penguins had nested there as well during prehistoric times. Carbon dating of penguin parts and eggshells dug from the ornithogenic substrate indicated occupation 275–375 and 540–880 years earlier (Spellerberg 1970, Stonehouse 1970, Emslie *et al*. 2007), as well as 1170–790 years before present, when as many as 3000–4000 pairs nested at Cape Barne (Emslie *et al.* 2003). How many nested at Cape Royds then has not been estimated. At least by the mid-1990s small clusters of nests also occurred elsewhere on the Royds peninsula (D.G. Ainley, personal observation 1996–2000), a phenomenon also exhibited in prehistoric times (Spellerberg 1970, Emslie *et al*. 2007). Why the Royds colony (and other Ross Sea colonies) did not decrease with the recovery of the minke whale population is probably related to the significant change underway in the Ross Sea climate, especially related to wind and sea ice.

Climate change became a major player in the Ross Sea region, with the regime shift exhibited in the Southern Annular Mode (SAM), also known as the Antarctic Dipole (Yuan & Martinson 2001), turning positive in the late 1980s (Ainley *et al.* 2005). The SAM is measured by an index calculated as the difference in atmospheric pressure between Australia (40S) and the Amundsen Sea (65S), and until *c.* 1989 the shift had vacillated between negative and positive modes (relative to the long-term average) on a decadal scale. The more permanent shift to positive SAM (+SAM) in recent years was a result of atmospheric pressure effects brought about by the Antarctic ozone hole and mid-latitude warming (Thompson & Solomon 2002, Turner *et al.* 2009).

The significant feature of +SAM relevant to Royds penguins was the increase in winds (Ainley *et al.* 2005, a study that also considered air temperature change and other variables), which led to greater large-scale SIE (Fig. 4). More importantly for penguins, increased wind led to the greater size and persistence of coastal, latent-heat polynyas (Fig. 4; Parkinson 2002, Stammerjohn *et al.* 2008). Wind and temperature, both extending across the penguin count time series, best explained colony trends. More specifically, because of the changed wind regime, the McMurdo Sound polynya opened more often and earlier in the spring, corresponding to the timing when penguins are returning to the colony to nest (Arrigo *et al.* 2015, Kim *et al.* 2018). As confirmed by the B15A mega-iceberg 'natural experiment' in 2001–2005 (Dugger *et al.* 2010, 2014), open water near the colony leads to higher rates of recruitment and higher nesting success, hence increased colony productivity and population growth (akin to the variables that Blackburn *et al.* 1990 attributed to growth in earlier decades). These more frequent positive conditions seemingly allowed the Royds penguin population to overcome any negative effects brought about by the recovery of the regional whale population (as well as enhanced Ross Sea Gyre; see below). Thus, the colony size attained by the late 1980s continued through the 1990s rather than decreasing (Fig. 2). The retrospective analysis of ocean-ice variables below supports this supposition.

Mega-iceberg era: start of the twenty-first century

The arrival of the twenty-first century brought about a truly educational event, a 'natural experiment' - Royds colony penguin response to 4 years of extensive sea-ice cover brought about by two mega-icebergs, C16 and especially B15A (~175 km long), lodged against the north shore of Ross Island in 2001. During 3 of the 4 years, icebergs prevented the winds from clearing McMurdo Sound of sea ice (i.e. prevention of the McMurdo Sound polynya that otherwise would have formed each year). In one year (2003), exceedingly strong winds overcame the iceberg effect, and the polynya was present regardless of the icebergs. Breeding failure ensued in those years of total early breeding-season sea-ice cover, leading many penguins to move to Cape Bird or to recruit elsewhere that had open water (Dugger *et al.* 2010, 2014). The colony population dropped by more than half of what its level was in the year 2000, decreasing to just ~1500 pairs (Fig. 2). When the icebergs disappeared, the Royds colony began to recover at a rate similar to that shown in the 1980s when it became free from trophic competition with minke whales (Fig. 2).

The more complex environment of recent decades

The importance of ice cover and other bio-physical factors that could be affecting the Royds colony population trend is apparent in our multivariate analysis from 2006 (thus B15A years not included) to 2019. Two competitive models relating annual growth included gyre speed (speed of the Ross Gyre, July–October; Fig.4) with a 5 year lag and open water (i.e. size of McMurdo Sound polynya in November of the current year; Table I & Supplemental Table 1). The first competitive model included gyre speed with a 5 year lag, open water, air temperature with a 5 year lag, SIE with a 4 year lag and 2 years of cumulative fish (weights 20%, 100%; see Supplemental Table 1). Gyre speed with a 5 year lag was negative ($\hat{\beta}_{gyreSPD}$ = -0.1285, standard error (SE) = 0.0336). Conversely, air temperature with a 5 year lag, SIE with a 4 year lag and open water showed positive associations: when temperature or SIE decreased or open water was later in the season, the annual growth of the Cape Royds colony decreased ($\hat{\beta}_{airtemp}$ = 0.2148, SE = 0.0654; $\hat{\beta}_{OWdate}$ = 2.2077, SE = 0.4761; $\hat{\beta}_{SeaIceExt}$ = 0.2887, SE = 0.1222). When cumulative fish increased (more large, older fish removed from the food web), the Royds Adélie penguin colony size increased ($\hat{\beta}_{fish}$ = 0.0259, SE = 0.0099).

These results confirm an earlier analysis identifying wind speed as an important explanatory variable in population trends (Ainley *et al.* 2005). An adjusted R^2 of 0.526 of the model, although respectable, on the other hand indicates that other factors had to have been involved in driving the partial population recovery post-iceberg years. Skua predation and competition with seals for food do vary annually and so do not lend themselves as covariates on par with those of annual penguin population change nor the other climate variables used. However, they are ecological variables worth exploring further.

Lower chick production due to predation from skuas probably is involved only in the partial recovery (from B15A) of the Royds penguin colony, setting it apart from the other Ross Island colonies. During 2002–2017 (i.e. post-B15A), chicks per pair at Royds averaged just 0.83 ± 0.03 compared to 1.04 ± 0.02 at Crozier (Schmidt *et al.* 2021). This appears to be due to a greater level of predation of eggs and small chicks by south polar skuas, in accord with a ratio of skua pairs to breeding penguin pairs determined during 2011–2012 at Royds of 1:77 compared to 1:136 at Bird and 1:168 at Crozier (Wilson *et al.* 2016). That would be double the predation pressure at Royds compared to the other colonies. In 1985–1986, 15 years before the B15A iceberg, chick production was 1.1–1.2 chicks per breeding pair at Royds (Blackburn *et al.* 1990). The disproportionate relative representation of skuas at Royds, although increased post-B15A (owing to penguin population decrease), has been the case over the years due to proximity to McMurdo Station and its open dump just 20 km from Royds. The dump was regularly frequented by many skuas (Ainley *et al.* 1986). In 1981, 76 skua pairs were at Royds (Ainley *et al.* 1986), but with closing of the dump in the later 1980s, numbers fell to 29 pairs by 2002 (Wilson *et al.* 2016).

During the mega-iceberg experiment especially, the desertion of nests due to low penguin mate synchrony allowed skuas to intrude farther into sub-colonies than normal at Royds. As a result, more nests became located on sub-colony perimeters, in turn becoming 'easy pickings' for the skuas (Young 1994, Emslie *et al.* 1995). Several sub-colonies were reduced in size (five actually were completely obliterated (adult penguin desertion after nest contents stolen)). Owing to the high sub-colony perimeter-to-area ratio at Royds - relatively more edges for skuas to exploit (Schmidt *et al.* 2021) - skua predation has remained especially important, thus reducing total colony productivity. The resulting smaller Royds colony size does lead to less intraspecific trophic competition and larger chicks, hence greater post-fledging survival (Ainley *et al.* 2018a), but this is not enough to compensate for lower chick production.

Additional factors that could be involved in the Royds population trend are the recovery of the Erebus Bay Weddell seal population, matching levels in the 1960s, and a fishery for large Antarctic toothfish being inaugurated in the waters surrounding Ross Island and elsewhere in the Ross Sea in 1997 (Ainley *et al.* 2017). The seal recovery as well as growth of the adjacent Ross Island penguin colonies through to the present day appear to have been facilitated by the extraction of a competitor for silverfish (i.e. the toothfish), thus hypothetically leading to greater availability of energy-dense silverfish to penguins and seals. The seal colony adjacent to Royds and other Ross Island penguin colonies benefitted (Ainley *et al.* 2017, D.G. Ainley *et al.* unpublished data). All of these mesopredators - penguins, seals and toothfish - acquire forage fish (silverfish) high in the water column (Fuiman *et al.* 2002, Ballard *et al.* 2012, Ainley *et al.* 2021, Saenz *et al.* 2020). However, although the presence of fewer large toothfish may have increased the prevalence of silverfish in the upper water column, the growth of competing seal numbers and their foraging may have countered this factor.

Integration towards understanding Royds trends

More reliable presence of the polynyas (with stronger winds) typically corresponds to breeding productivity increases because penguins are more efficient at swimming in open water *vs* walking across sea ice. Easier access to the open water leads to a greater proportion of adults attempting to breed as well as higher pair nest-change synchrony and higher breeding success (Ainley 2002). During the period 1998–2018, when winds were 1 standard deviation (SD) above the mean (9.1 ± 0.9 m/s), McMurdo Sound polynya size averaged $5070 \pm 291\ \text{km}^2$ compared to $2930 \pm 885\ \text{km}^2$ when winds were < 1 SD below the mean - for the entire series, $r^2 = 0.6579$, not including the 2002–2005 iceberg years ($P < 0.05$). Another way to look at this is seen in the decrease in McMurdo Sound fast-ice extent (more open water) by 2 km/year during 2002–2014, a wind-driven phenomenon (Kim *et al.* 2018). The size and seasonal persistence of the polynya have been increasing or becoming of adequate size at a greater annual frequency with the greater winds brought by the SAM regime shift in the later 1980s (Arrigo *et al.* 2015). The seasonal timing of McMurdo Sound polynya formation has not changed to the degree that it affects population variation, unlike Ross Island colonies on the northern coast affected by the Ross Sea polynya (D.G. Ainley *et al.* unpublished data).

As noted above, this environmental change, which made it easier for Royds penguins to forage, overcame the increased trophic competition by minke whales as the whale population recovered. What this finding also accomplishes is that it makes more sense of covarying wind-driven variation in regional-scale SIE and its supposed effect on penguin colony size change (Wilson *et al.* 2001). It was found in that study that a greater SIE led to colony decrease 4–5 years later. Now that we have a more complete array of variables, it appears that it is the production (and subsequent recruitment 4–5 years later) of a larger number of young rather than some effect on juvenile survival due to greater SIE that brings about the lagged colony increase, as had been hypothesized by Wilson *et al.* (2001).

Simultaneously, and counter to the polynya facilitation, the increasing winds have led to a higher rate of ice movement in the Ross Gyre, where Royds birds spend the winter (Ballard *et al.* 2010, Jongsomjit *et al.* 2024). During years of greater gyre speed, SIE also is greater (Comiso *et al.* 2011, Holland & Kwok 2012). During 1992–2017 (gyre speed available), in years when gyre speed (mean 6.3 ± 0.9 km/day) is 1 SD above the mean, the Royds colony is smaller (mean size = 2326 ± 510 pairs) than the previous year; when gyre speed is 1 SD below the mean, colony size is greater (2742 ± 652 pairs). Thus, it appears that northward sea-ice movement, especially that along the Victoria Land coast in the spring, affects the opposite, southward movement of the penguins and thus the number able to show up in time to breed in a given year (and be included in the *c.* 1 December census). Ultimately, the overall production of chicks that year, and subsequently to recruit, is affected, consistent with the findings of the earlier Blackburn *et al.* (1991) demographic reconstruction (see also Dugger *et al.* 2014). Their movement along the Victoria Land coast from non-breeding/wintering areas to Royds (Ballard *et al.* 2010) against the direction of ice flow would slow the penguins' travel.

Younger birds make up the majority of new recruits and are later to arrive regardless (Ainley *et al.* 1983), and so further retardation results in them not showing up in time to breed. However, there is also a 5 year lag, which is consistent with the age of first breeding at Royds, which is 1 year older compared to in other Ross Island colonies (Kappes *et al.* 2021). It is the productivity 4–5 years earlier that is affected by number of recruits showing up (with large-scale SIE also correlating in a lagged fashion but being an artefact of gyre speed). Therefore, the increased gyre speed (and SIE) of recent decades (Kwok *et al.* 2017) appears to have been another of the factors that has had a negative influence on Royds colony recovery.

Conclusions

A number of factors have led to variation in the Cape Royds Adélie penguin colony size from 1955 to the present. Included are protection from unchaperoned tourism, decreasing and then recovering populations of cetacean trophic competitors, an inordinate level of south polar skua predation on penguin eggs and chicks thus decreasing production, more reliable presence of open water thus encouraging higher breeding propensity and success and increasing speed of ice movement in the Ross Sea region wintering habitat (lowering annual recruitment rate). The whale and climate factors have been important in affecting Adélie penguin population dynamics in other, larger Ross Sea colonies. What has proved not to be as important is competition for silverfish by an increasing (recovering) Weddell seal population, nor increasing silverfish availability due to reduced competition for silverfish from Antarctic toothfish. The latter two factors appear to cancel each other out, making the effect of silverfish availability much less important than for the two larger Adélie penguin colonies on Ross Island, which have few competing seals.

The most recent overall result has been a lack of population recovery from the extreme effects of too much local sea-ice cover brought about by the two mega-icebergs during 2001–2005, a pattern that is not consistent with the recovery (and further growth) of the other Ross Island colonies. Thus, the trends of the single Royds colony have been interesting and greatly instructive regarding Adélie penguin ecology, but for the purposes of monitoring larger-scale ecosystem/food web change a regional perspective clearly is required. The entire cluster of Ross Island colonies needs to be considered. The other lesson is that more than climate change (the subject of many recent Antarctic penguin analyses) can affect trends in Antarctic penguin colony growth.

Supplementary material

To view supplementary material for this article, please visit https://doi.org/10.1017/S0954102024000051.

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Author contributions

All authors conducted fieldwork, including some handling of the aerial photography and processing, that resulted in the penguin data analysed in the paper, and all contributed ideas to the paper's development as well as edits to the manuscript. Most of the writing was drafted by DGA and VM; data analysis was conducted by VM assisted by DGA.

Competing interests

The authors declare none.

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