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TIMING OF CLUTCH INITIATION IN *PYGOSCELIS* PENGUINS ON THE ANTARCTIC PENINSULA: TOWARDS AN IMPROVED UNDERSTANDING OF OFF-PEAK CENSUS CORRECTION FACTORS

H.J. Lynch[1,2]✉, W.F. Fagan[1], R. Naveen[2],
S.G. Trivelpiece[3] and W.Z. Trivelpiece[3]

[1] Department of Biology, University of Maryland
College Park, MD 20742, USA
Email – hlynch@umd.edu

[2] Oceanites, Inc., PO Box 15259
Chevy Chase, MD 20825, USA

[3] Antarctic Ecosystem Research Division,
NOAA/SWFSC, La Jolla, CA 92038, USA

Abstract

Penguin censuses on the Antarctic Peninsula are often subject to logistical challenges that preclude nest counts being conducted at the peak of egg laying. Additionally, the historical literature includes many census counts with non-standard timing. The challenge is, therefore, to correct 'off-peak' census counts to make them comparable with current standard methods. Census correction involves knowing (i) how the census is timed relative to the peak of egg laying, and (ii) how nest numbers change through the breeding cycle. In this paper the authors present an analysis relating to both these challenges. Clutch initiation dates for four penguin breeding sites are examined (Cape Shirreff, Admiralty Bay, Humble Island and Petermann Island) in relation to potential drivers of clutch initiation (e.g. temperature, precipitation, sea-ice etc.). It is found that mean October temperatures constitute the most consistent significant factor related to the timing of clutch initiation in all three of the penguin species examined (Adélie (*Pygoscelis adeliae*), gentoo (*P. papua*) and chinstrap (*P. antarctica*)). A statistical model for determining the peak of clutch initiation is presented and, along with a simple estimation of species-specific nest attrition rates, is used to illustrate the procedure for correcting off-peak census counts.

Résumé

Les recensements des manchots sur la péninsule antarctique font souvent l'objet de défis logistiques qui empêchent le décompte des nids au pic de la période de ponte. De plus, les nombreux recensements publiés par le passé dans la littérature n'ont pas été réalisés à une époque standard. Le défi est donc de corriger les dénombrements « hors période de pointe » pour qu'ils puissent être comparés aux méthodes actuelles standard. Ces corrections nécessitent de savoir : i) situer les recensements dans le temps par rapport au pic de la période de ponte, et ii) de combien le nombre de nids change-t-il au cours du cycle de reproduction. Dans cet article, les auteurs présentent une analyse qui relève ces deux défis. Ils examinent les dates du début des couvées en quatre sites de reproduction de manchots (cap Shirreff, baie de l'Amirauté, îles Humble et île Petermann) par rapport à des facteurs déterminants susceptibles de lancer la couvaison (comme la température, les précipitations, les glaces de mer, etc.). Il est découvert que le facteur le plus significatif par rapport à la date du début de la couvaison est systématiquement constitué par les températures moyennes d'octobre chez les trois espèces de manchots examinées (Adélie (*Pygoscelis adeliae*), papou (*P. papua*) et à jugulaire (*P. antarctica*)). Accompagné d'une simple estimation du taux de perte de nids selon l'espèce, le modèle statistique présenté, visant à déterminer le pic du début de la couvaison, est utilisé pour illustrer la procédure de correction des décomptes réalisés en dehors de la période de pointe.

Резюме

Учет численности пингвинов на Антарктическом п-ове зачастую зависит от логистических проблем, не позволяющих проводить подсчет гнезд в пик периода кладки яиц. Кроме того, ранее опубликованные литературные источники включают много подсчетов численности с нестандартными сроками проведения. Следовательно, проблема заключается в том, чтобы откорректировать «внепиковые» подсчеты численности и сделать их сопоставимыми с существующими стандартными методами. Корректировка учета численности подразумевает знание того, (i) как выбрано время учета относительно пика периода кладки яиц, и (ii) как меняется число гнезд в течение цикла размножения. В настоящей статье авторы представляют анализ, касающийся обоих этих вопросов. Рассматриваются даты начала кладки для четырех участков размножения пингвинов (мыс Ширрефф, залив Адмиралтейства, о-в Хамбл и о-в Петерманн) по отношению к возможным определяющим факторам времени начала кладки (напр., температура, выпадение осадков, морской лед и т. д.). Показано, что средние температуры в октябре являются наиболее устойчивым существенным фактором, связанным со сроками начала кладки во всех трех рассматриваемых видах пингвинов (Адели (*Pygoscelis adeliae*), папуасские (*P. papua*) и антарктические (*P. antarctica*)). Представлена статистическая модель для определения пика начала кладки, которая используется наряду с простой оценкой темпов убыли гнезд по видам для того, чтобы проиллюстрировать процедуру корректировки внепиковых подсчетов численности.

Resumen

Los censos de pingüinos en la Península Antártica a menudo están sujetos a problemas logísticos que impiden el conteo de nidos durante el período de máxima puesta de huevos. Además, la información bibliográfica disponible incluye muchos recuentos de censos efectuados en distintas épocas. Por lo tanto, el desafío está en corregir los recuentos realizados durante los períodos de menos actividad para compararlos con los métodos estándar vigentes. Para poder efectuar la corrección de los censos, se debe saber (i) la fecha del censo en relación con el período de máxima puesta, y (ii) la variación en el número de nidos durante el ciclo de reproducción. En este trabajo los autores analizan el reto planteado por estas dos interrogantes. Se examinan las fechas de inicio de la puesta de huevos en cuatro sitios de reproducción de pingüinos (Cabo Shirreff, Bahía Almirantazgo, Isla Humble e Isla Petermann) en relación con los posibles factores determinantes del inicio de la puesta de huevos (vg. temperatura, precipitación, hielo marino etc.). Se encontró que las temperaturas promedio del mes de octubre son el factor significativo más constante relacionado con la fecha de inicio de la puesta de huevos en las tres especies de pingüinos examinadas (adelia (*Pygoscelis adeliae*), papúa (*P. papua*) y de barbijo (*P. antarctica*)). Se presenta un modelo estadístico para determinar la fecha punta de inicio de la puesta de huevos que, junto con una simple estimación de la tasa de pérdida de nidos por especie, se utiliza para ilustrar el método para corregir los recuentos realizados en épocas de menor actividad.

Keywords: breeding phenology, Antarctic Peninsula, clutch initiation, nest attrition, gentoo penguins, chinstrap penguins, Adélie penguins, census, CCAMLR

Introduction

Estimates of Peninsula-wide penguin populations require the use of all available information relevant to an estimation of the number of breeding pairs at a particular site, including the full integration of census estimates that may be historical (e.g. from the early Antarctic expeditions), opportunistic, or poorly timed relative to the current standard established by the CCAMLR Ecosystem Monitoring Program (CEMP) (CCAMLR, 2004). The logistical difficulties of Antarctic research mean that our understanding of penguin and seabird populations is necessarily piecemeal, and current data regarding penguin populations come from a mix of intensive long-term efforts carried out at a handful of sites (e.g. Admiralty Bay (King George Island), Palmer Station vicinity/Arthur Harbor (Anvers Island), Cape Shirreff (Livingston Island), Hope Bay, Goudier Island, Deception Island) and spatially extensive, but opportunistically timed, census work such as that carried out as part of the Antarctic Site Inventory (Naveen et al., 2000; Lynch et al., 2008). The Antarctic Site Inventory program, which has been censusing breeding bird populations on the Peninsula since 1994, is typical of many monitoring programs that cover a large area, in that the number of sites surveyed comes at the expense of the timing of surveys at any one location. In this sense, the techniques here developed are widely applicable to data that may have errors in the timing of censuses that must be accounted for along with other, more typical, sources of error.

One of the challenges associated with such an approach to penguin population research, one also shared with much of the historical data available, is the need to consider and account for the timing of the census relative to the breeding cycle, as the number of 'active' nests (the standard measure of the breeding population) at a site changes significantly over the course of the breeding season.

(Here and throughout, a count of nests or chicks is considered a special case of the broader concept of census, which can include additional population estimation procedures such as photodocumentation or sample plots.) At the beginning of the breeding season, penguins arrive, find mates and proceed to build nests. In an idealised situation, the distribution of clutch initiations (i.e. when the first egg is laid, and the point at which the nest is officially deemed 'active') follows a normal distribution, and the peak of egg laying is the mean (and in practice more usefully, the median) date of clutch initiation. CEMP Standard Methods require that the census count of the breeding population (i.e. the number of 'active' nests at the site) occurs one week after this peak. Note that the peak of egg laying and the maximum census count that could be obtained in any given year are not strictly coincident, and the maximum census count can occur either slightly before or slightly after the peak of egg laying. Although it is generally assumed that census counts after the peak of egg laying are biased downward from the standard count, this is not necessarily true over short time scales, because counts may actually increase for a short time if breeding birds continue to arrive at a rate faster than established nests fail (Lynch et al., unpublished data). Nevertheless, over longer time scales (weeks, months), the nest failure rate will overtake the rate of nest establishment, and 'off-peak' counts will be biased downward relative to the 'true' census count. So called 'off-peak' censuses are an empirical reality in the Antarctic, and despite the potential for errors in estimation, researchers routinely use off-peak data in their analyses (e.g. Trivelpiece et al., 1987; Sander et al., 2007; Lynch et al., 2008). In this paper, correction methods appropriate to off-peak penguin census counts are developed. These corrections involve two components. One is a model to estimate the date of peak egg laying for a given site in a given year, and the second is an estimate of the rate of nest attrition following the peak of egg laying. Using these two pieces of information, an opportunistically obtained count, along with its location and date, can be corrected to compensate for nest attrition to obtain an estimate of the breeding population compatible with the CEMP Standard Methods.

Data

Data for this analysis were taken from long-term studies of penguin colonies at four penguin breeding sites (Cape Shirreff, Livingston Island (62°28'S 60°46'W); Admiralty Bay, King George Island (62°10'S 58°30'W); Humble Island (64°46'S 64°06'W); and Petermann Island (65°10'S 64°10'W)) (Figure 1, Table 1). These sites included data on clutch initiation for three penguin species ((i) Adélie penguin (*Pygoscelis adeliae*), (ii) gentoo penguin (*P. papua*), (iii) chinstrap penguin (*P. antarctica*)). A total of 6 108 clutch initiation dates (CIDs) were recorded. Initially, it was not clear what potential environmental covariates might be related to the timing of clutch initiation, and an extensive set of potential covariates was investigated (see Methods: Exploratory data analysis). These covariates are listed in Table 2. Data on nest attrition rates were based on information available from the Antarctic Site Inventory. Some of these data come from opportunistic surveys based on commercial cruise ships, and nest attrition rates were estimated using sites for which multiple nest count surveys were completed within a single season. The rest of the data come from a field camp at Petermann Island, where the gentoo and Adélie penguin colonies on the island were surveyed multiple times throughout the breeding and incubation period. In total, there were eight sites and years for which multiple nest counts were available for each of the three penguin species studied (Adélie (*P. adeliae*), gentoo (*P. papua*) and chinstrap (*P. antarctica*)).

Methods

Exploratory data analysis

To determine which environmental covariates should be included in the final statistical model for the peak date of egg laying, a series of simple linear regressions were computed in which each potential covariate (Table 2) was regressed against mean CID for each site. Temperature, precipitation, Southern Oscillation Index (SOI), sea-ice and chlorophyll-*a* data were divided into monthly means so that each month was considered a separate potential covariate. Chlorophyll-*a* is widely used as a proxy for phytoplankton abundance (Bidigare et al., 1996; Smith et al., 2001; Murphy et al., 2007), and phytoplankton abundance has been linked to krill abundance (Weber and El-Sayed, 1985). For this reason, chlorophyll-*a* (specifically, monthly averages of chlorophyll-*a* within a 100 km radius of the sites considered) was included as a reasonable proxy for the amount of food available to breeding penguins in a given breeding season. Recent changes in sea-ice on the Western Antarctic Peninsula have come in the form of the timing of advance (shifting later) and retreat (shifting earlier) of the sea-ice, and not as a change in the maximum extent (Stammerjohn et al., 2008). For this reason, sea-ice data is considered at the monthly scale in order to investigate potential correlations between sea-ice phenology and breeding phenology. The Petermann Island data, which spanned only three years, were not used in the exploratory data analysis.

Table 1: Sources of clutch initiation data used in this analysis. ADPE – Adélie penguin, GEPE – gentoo penguin, CHPE – chinstrap penguin.

Site	Species	Years data available	Data source
Admiralty Bay, King George Island (62°10'S 58°30'W)	ADPE	1991–2006	W.Z. Trivelpiece and S.G. Trivelpiece, unpublished
Admiralty Bay, King George Island (62°10'S 58°30'W)	GEPE	1991–2006	W.Z. Trivelpiece and S.G. Trivelpiece, unpublished
Cape Shirreff, Livingston Island (62°28'S 60°46'W)	CHPE	1997–2006	W.Z. Trivelpiece and S.G. Trivelpiece, unpublished
Cape Shirreff, Livingston Island (62°28'S 60°46'W)	GEPE	1998–2006 (exc. 2005)	W.Z. Trivelpiece and S.G. Trivelpiece, unpublished
Humble Island (64°46'S 64°06'W)	ADPE	1991–1996[1] 1999–2000	LTER Palmer Station archive, online[2]; (Contributor: William Fraser) see Fraser (2004)
Petermann Island (65°10'S 64°10'W)	GEPE	2005–2007	H.J. Lynch, W.F. Fagan and R. Naveen (Antarctic Site Inventory), unpublished
Petermann Island (65°10'S 64°10')	ADPE	2005–2007	H.J. Lynch, W.F. Fagan and R. Naveen (Antarctic Site Inventory), unpublished

[1] Additional years of egg laying data were available but were not used because unusually clustered CIDs suggested that the data was not of sufficiently high temporal resolution to be used for this analysis.

[2] Data downloaded from: http://pal.lternet.edu/data/

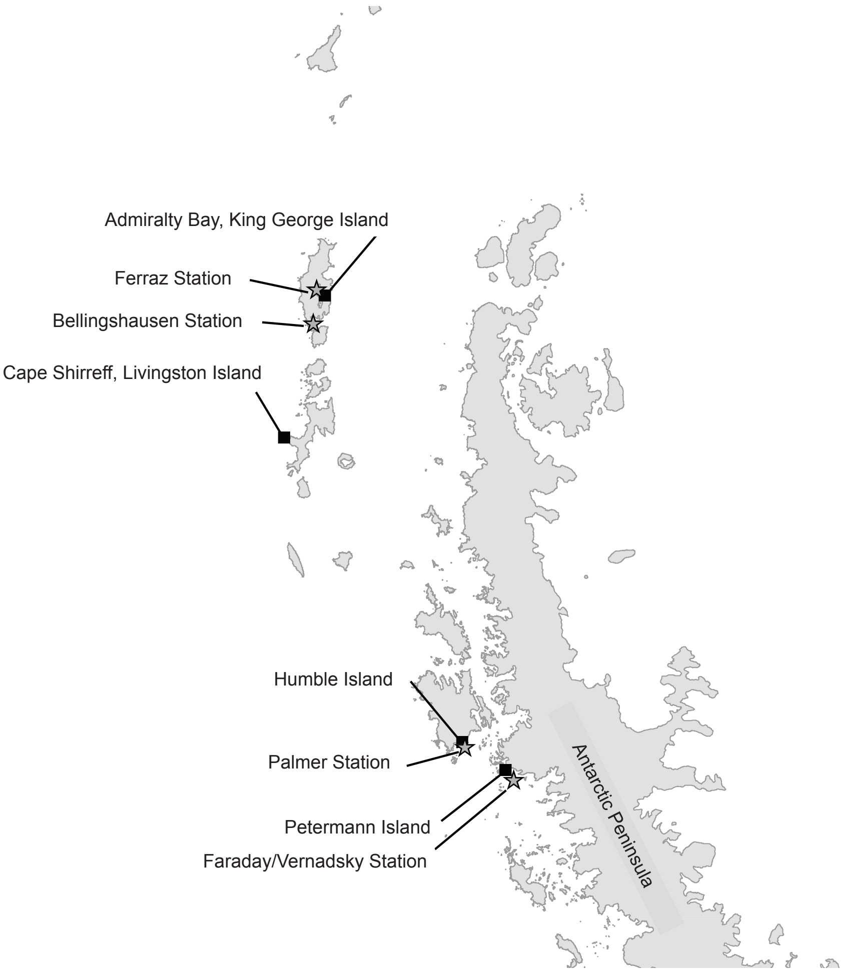

Figure 1: Map of the Antarctic Peninsula and the sites (black squares) and weather stations (grey stars) used in this analysis.

Table 2: Environmental covariates examined as potential drivers of the timing of clutch initiation.

Covariate	Source
Mean monthly temperature	For King George Island and Livingston Island, temperature data were obtained from Bellingshausen Station (data available from British Antarctic Survey, online[1]) . For Humble Island, temperature data used were from Palmer Station (data available from LTER Palmer Station archive, online[2] (Contributor: Karen S. Baker) see citation for Baker (2008). For Petermann Island, temperature data were obtained from Vernadsky Station (data available from British Antarctic Survey, online[3]).
Precipitation[4]	For King George Island and Livingston Island, precipitation data were obtained from Ferraz Base (data available from the Projeto de Meteorologia Antárctica[5]).
Sea-surface temperature anomalies	National Climatic Data Center Global Surface Temperature Anomalies Dataset[6].
Southern Oscillation Index (SOI)	University Center for Atmospheric Research Climate Analysis Section Data Catalogue[7].
Ice extent	Average monthly sea-ice coverage for all sites was taken as reported for the Palmer Station LTER region by the Monthly Averages Ice Coverage Dataset (Contributor: Sharon Stammerjohn)[8] see citation for Stammerjohn (2007).
Ice area	See above
Krill and salp abundance	Annual counts of krill and salp near Palmer Station, Antarctica, as reported for the Palmer Station LTER region (Contributors: Langdon Quetin, Robin Ross-Quetin)[9] see citation for Quetin and Ross-Quetin (2006).
Chlorophyll-*a*	GlobCOLOUR Project; monthly average level-3 CHL_1 0.25° resolution product.

[1] Data downloaded from www.antarctica.ac.uk/met/gjma/

[2] Data downloaded from http://pal.lternet.edu/data/data/weather/palmer/monthly7498temp and http://pal.lternet.edu/data/data/weather/palmer/daily8905 (Data from 2006–2008 obtained by personal communication with Palmer Station staff.)

[3] Data downloaded from www.antarctica.ac.uk/met/gjma/

[4] In order to avoid inaccuracies inherent in non-optical precipitation measurements, total precipitation was not used but was replaced by the total number of days in a month in which precipitation was recorded. Scheduled improvements in precipitation measuring in the Antarctic will allow consideration of the total amount of rain or snow (Alberto Setzer, pers. comm.), which is a better indicator of the amount of rain or snow experienced by breeding birds in a given season.

[5] Data downloaded from www.cptec.inpe.br/prod_antartica/weatherdata.shtml

[6] Data downloaded from www.ncdc.noaa.gov/oa/climate/research/anomalies/anomalies.html

[7] Data downloaded from www.cgd.ucar.edu/cas/catalog/climind/SOI.signal.ascii

[8] Data downloaded from http://oceaninformatics.ucsd.edu/datazoo/data/pallter/data/?action=list&ids[]=34

[9] Data downloaded from http://oceaninformatics.ucsd.edu/datazoo/data/pallter/datasets?action=summary&id=5

The results of this preliminary data analysis are reported in Appendix A. These results show that mean October temperature is the covariate most consistently correlated with mean CID, and is significantly ($p < 0.05$) correlated with four of the five datasets examined. In the four datasets for which mean October temperatures were significant, it explained between 51% and 78% of the variance in mean CID. The next most significant covariate ($p < 0.05$ for three of the five datasets) was September SOI, although a significant degree of co-linearity between the September SOI and mean October temperatures suggested that these two covariates did not represent independent factors in breeding phenology and should not be included in the model as such. Additionally, there are biological reasons why October temperatures might be expected to play a role in the timing of breeding in the three penguin species examined. At the sites considered in this analysis, all three species nest directly on rocks and breeding is conditional on the appearance of snow-free areas in October when penguins arrive at their breeding locations. The importance of snow-free areas to inter-season variability in the timing of gentoo penguin breeding has also been suggested by Gwynn (1953). Warm October temperatures hasten snow-melt in breeding areas and allow for earlier nest building and egg laying. Whereas other studies (Barbraud and Weimerskirch, 2006) in Eastern Antarctica have shown that the timing of penguin breeding is actually delayed by changes associated with climate change (specifically, reduced sea-ice extent), this analysis finds that warm temperatures in October are clearly associated with earlier clutch initiation. These differences imply different bottlenecks for populations breeding in different Antarctic regions, as discussed by Lynch et al. (in prep).

In addition to mean October temperatures, two additional variables were included in the final model. Due to the aforementioned requirements for snow-free breeding areas, there are compelling *a priori* reasons to suspect a strong latitudinal gradient in breeding chronology, with sites at higher latitude being delayed relative to sites at lower latitude (Croxall, 1984; Lishman, 1985). For this reason, latitude was included in the final statistical model. Finally, the model was used to investigate any temporal trend in CIDs separate from effects due to known environmental covariates such as temperature. For this reason, the year of measurement was included as a third covariate in the final model.

Final model for estimating the peak of egg laying

A three-stage hierarchical Bayesian model was used to understand breeding phenology. In the first stage, estimated clutch initiation dates (*CID.est*) for each nest (*i*) at each site (*j*) in each year (*t*) were modelled as being distributed around the actual clutch initiation dates (*CID.actual*) with an (asymmetric) error distribution which depends on the method used to estimate CID. Given the inescapably difficult nature of field work in the Antarctic and the multiple purposes for which data on penguin reproduction were originally collected, CID estimates were based on one of three methods: CID was recorded as the date at which the first egg (E1) was recorded (Method 1), CID was estimated based on the date that the second egg (E2) was recorded (Method 2), or CID was estimated based on the date on which the first egg hatched (Method 3). These three methods involve increasing amounts of uncertainty regarding the estimate of CID. For Method 1, there was an equal possibility of the CID being on the day it was recorded or on the day prior (after the visit of the previous day). For Methods 2 and 3, a multinomial error distribution was used representing the convolution of the type of error in Method 1 (i.e. that the second egg was laid (Method 2) or first chick hatched (Method 3) either on, or the day prior to, the recorded date) and an additional source of error. For Method 2, the additional error was due to the uncertainty of the time lag between E1 and E2 (taken as ±1 day), whereas for Method 3, the additional error arose from uncertainty associated with the literature-based estimates of the length of the incubation period. Because of the large number of nest records available and the relatively tiny fraction of records that used either Methods 2 or 3 (<3%), the results of the analysis are completely insensitive to the assumptions made regarding the error for Methods 2 or 3. Although these data points could have been excluded from the analysis, their inclusion highlights the flexibility inherent to the hierarchical Bayesian approach and illustrates how such heterogeneous data might be aggregated into a single analysis.

In the second stage of the hierarchical statistical model, the actual CID is modelled as being normally distributed with a mean equal to the mean CID for site (*j*) for year (*t*). Independent model fitting of gamma and normal distributions to the CID data showed that a gamma distribution provided a better fit slightly more than half the time (35 out of 64), but the interpretability of the normal distribution outweighed the slightly better fit of the gamma distribution, and a normal distribution was used instead. The variance of intra-site CIDs was modelled as species-specific, allowing us to simultaneously model inter-species differences in CID synchrony. Note that although the measurement error structure in the first stage of the model is pre-specified and fixed, the variance of actual CIDs around the year-, site- and species-specific mean is estimated by the model and contains biologically relevant information regarding breeding synchrony.

In the third and final stage of the model, the mean CID for a site (*j*) in year (*t*) was modelled as being a function of three covariates (in addition to a species-specific baseline): site latitude, mean October temperature for that site in that year, and a year effect used to capture overall trends in CID. Latitudinal and year effects were modelled as being shared across all three species, but the impact of temperature, which in a preliminary data analysis was shown to be highly species-specific, was modelled separately for each species. The implication of this species-specificity in temperature impacts will be discussed in more depth in the Results and Discussion.

The three-stage statistical model may be written as:

Stage 1:

$$CID.est_{i,j,t} \sim Multinomial \left(\begin{array}{l} \ldots, p_{CID.actual-1}, p_{CID.actual}, p_{CID.actual+1}, \ldots \\ \big| Method(i,j,t) \end{array} \right) \tag{1}$$

Stage 2:

$$CID.actual_{i,j,t} \sim N\left(CID.mean_{i,j,t}, \tau^2_{sp[i]}\right) \tag{2}$$

Stage 3:

$$\begin{aligned} CID.mean_{i,j,t} &= baseline_{sp[i]} + lat.eff * lat_j \\ &+ temp.eff_{sp[i]} * Oct.mean_{j,t} + year.eff * year_t \end{aligned} \tag{3}$$

where $baseline_{sp[i]}$ is the species-specific intercept for nest i, lat_j is the latitude of site j relative to the latitude of Admiralty Bay, King George Island (the most northerly of the study sites), $Oct.mean_{j,t}$ is the mean October temperature of site j in year t, and $year_t$ is measured relative to the year 2000. For convenience, all dates are measured relative to 1 October (e.g. $CID.mean_{i,j,t} = 15$ would imply a mean CID of 15 October). Note that due to the asymmetrical error structure, many of the multinomial probabilities in Stage 1 may be zero. The measurement error is fixed at its prescribed value (determined by the CID estimation method as described above), and the precision ($1/\tau^2$) of intra-season CIDs is given a vague gamma distribution. All of the covariate coefficients were given vague normal prior distributions. This model was fit to the data using the software package WinBUGS (Lunn et al., 2000). A burn-in period of 10 000 samples was used and the posterior distribution was constructed using every other sample from the following 20 000 samples in the Monte Carlo Markov Chain (MCMC) chain. In all cases, this was more than sufficient to achieve model convergence and adequate sampling of the posterior distribution.

Nest attrition

The second component necessary for correction of off-peak nest counts is the rate of nest attrition following the peak of egg laying. There is no reason to assume *a priori* that the rate of nest attrition is the same for each of the species studied, and the available data was insufficient to fit anything other than a linear function to the nest counts as a function of time. Note that this approach can be extended to correcting counts of chicks if there is a suitable function relating the number of chicks to the phase of the breeding cycle. Chick censuses are typically done at the peak of chick crèching, when most of the chicks in the colony are no longer being closely incubated but instead form large crèches with other chicks. Censuses done after this point may be negatively biased due to mortality and could be similarly corrected given an estimated rate of chick mortality after crèche. Census counts of adults are particularly difficult to interpret. Not only are breeding adults in constant flux into and out of the colony, but significant numbers of non-breeders, pre-breeders and failed breeders make it difficult to relate the number of adults present to the size of the breeding population. Census counts of adults can be used only as a rough measure of the breeding population, and correction techniques for adult counts are currently being developed.

Results

The results of this analysis are presented in Table 3. Each of the components of the model (the baseline date of breeding, latitudinal gradients in CID, the impact of mean October temperatures, the overall trend in breeding phenology and species-specific breeding asynchrony) have important biological and ecological interpretations. The species-specific baseline CID may be interpreted as the overall static shift in breeding phenology among the three penguin species. As noted by other authors (Trivelpiece et al., 1987), the three penguin species breed in a predictable sequence, with Adélie being the first to arrive and lay eggs (baseline CID = 26.2 (±0.2) days), followed by gentoo (baseline CID = 28.0 (±0.3) days) and then chinstrap (baseline CID = 46.9 (±0.2) days). (Results represent the mean of the posterior distribution followed by one standard deviation in parenthesis.) The results also indicate a strong latitudinal gradient in breeding phenology (–4.77 (±0.05) days/°C), with sites further south being delayed relative to more northerly sites. Consistent with the exploratory data analysis on environmental covariates to breeding phenology, it is found that mean October temperatures are significantly correlated with breeding phenology, and all three species show an advanced schedule of breeding in response to warmer October temperatures (–1.40 (±0.05) days/°C for Adélie, –3.4 (±0.1) days/°C for gentoo and –1.57 (±0.08) days/°C for chinstrap). Although all three species show some degree of 'elasticity' in breeding phenology, gentoo penguins are able to advance breeding more than twice as much as either Adélie or chinstrap penguins in response to warmer temperatures. In addition to the impact of warmer temperatures on CIDs, there is also an overall, and unexplained, trend towards

Table 3: Summary metrics of the model covariate posterior distributions. ADPE – Adélie penguin, GEPE – gentoo penguin, CHPE – chinstrap penguin.

Parameter	Interpretation	Mean (± s.e.)	(2.50%, median, 97.5%)
baseline[ADPE]	Baseline CID for Adélie penguin	26.2 days (± 0.2)	(25.8, 26.2, 26.5)
baseline[GEPE]	Baseline CID for gentoo penguin	28.0 days (± 0.3)	(27.4, 28.0, 28.7)
baseline[CHPE]	Baseline CID for chinstrap penguin	46.9 days (± 0.2)	(46.4, 46.9, 47.3)
lat.eff	Effect of latitude (latitude measured relative to Admiralty Bay, King George Island)	–4.77 days/° latitude (±0.05)	(–4.88, –4.77, –4.66)
temp.eff[ADPE]	Effect of mean October temperature on CID for Adélie penguin	–1.40 days/° C (±0.05)	(–1.51, –1.40, –1.29)
temp.eff[GEPE]	Effect of mean October temperature on CID for gentoo penguin	–3.4 days/° C (±0.1)	(–3.6, –3.4, –3.2)
temp.eff[CHPE]	Effect of mean October temperature on CID for chinstrap penguin	–1.57 days/° C (±0.08)	(–1.73, –1.57, –1.41)
year.eff	Overall trend in CID shared by all three species	–0.21 days/year (±0.01)	(–0.23, –0.21, –0.18)
τ[ADPE]	Intra-season breeding asynchrony for Adélie penguin	3.96 days (±0.06)	(3.85, 3.95, 4.07)
τ[GEPE]	Intra-season breeding asynchrony for gentoo penguin	7.0 days (±0.1)	(6.8, 7.0, 7.2)
τ[CHPE]	Intra-season breeding asynchrony for chinstrap penguin	3.06 days (±0.07)	(2.92, 3.06, 3.21)

earlier reproduction of 0.21 (±0.01) days/year. Finally, the model results show varying levels of intra-season breeding synchrony among the three penguin species, with chinstrap penguins showing the most synchronous breeding (intra-season standard deviation = 3.06 (±0.07) days), closely followed by Adélie penguins (intra-season standard deviation = 3.96 (±0.06) days). The gentoo penguin was significantly less synchronous than either the chinstrap or Adélie (intra-season standard deviation = 7.0 (±0.1) days).

Figure 2 illustrates the fit of the model in predicting mean CID at each of the sites and years for which data were available. On the x-axis is the mean day on which CIDs were recorded for each of the species at each site in each year. The y-axis represents the corresponding mean of $CID.actual_{i,j,t}$ as estimated by the model. It is expected that the actual recorded CIDs will lag the predicted CIDs by up to a day due to the asymmetric measurement error distribution previously discussed, and therefore the 1:1 line serves only as a visual guide and not as a metric of model fit. There are five points (circled in Figure 2) for which the model significantly underpredicts the mean CID. All of these points come from gentoo penguins at Cape Shirreff. It is hypothesised that gentoo penguins at Cape Shirreff have shifted their breeding phenology in response to their sympatric association with chinstrap penguins at that site. It is not fully understood what role sympatric associations play in driving breeding phenology and consequently the effects of such associations have not been included in the present model.

Rates of nest attrition were 0.9 ± 0.2 (p = 3.7 × 10^{-4}), 0.6 ± 0.3 (p = 0.06) and 1.0 ± 0.3 (p = 0.01) %/day for Adélie, gentoo and chinstrap penguins respectively (Figure 3). Note that while the rates of nest attrition for Adélie and chinstrap penguins are not significantly different from each other (the rate of nest attrition in the grouped dataset is 1.0 ± 0.2 (p = 1.1 × 10^{-5}), the rate of nest attrition for gentoo penguins is not significantly different from zero. This is consistent with the relatively asynchronous breeding reported for the gentoo penguins, as the continual arrival of gentoo penguins at the nest site roughly balances nest losses over a broad period of time around the peak of egg laying. The asynchrony of gentoo penguins makes it difficult to define the size of the breeding population or how it should be measured in the field. For practical purposes, however, it means that gentoo penguin census counts will remain flat over a wider time interval and, therefore, the timing of such censuses may be less critical.

Discussion

Season-to-season variability in the timing of pygoscelid egg laying has been explained as being a function of sea-ice and/or terrestrial snow and ice conditions at the nesting locations (Croxall, 1984). Alternatively, food availability has been suggested as explaining the large season-to-season changes in the timing of gentoo egg laying (Croxall and Prince, 1979; Croxall, 1984). These results strongly suggest that terrestrial snow and ice conditions play the predominant role in season-to-season variability in clutch initiation, and support neither the ideas that sea-ice or food availability are the principal driver of breeding phenology. The long lag between krill reproduction and availability as prey preclude any connection between mean October temperatures and prey availability in any given season, although it cannot be ruled out that long-term changes in sea-ice conditions and prey availability may play a role in the unexplained trend towards earlier clutch initiation (0.21 [0.18,0.23] days/year [square brackets represent the 95% confidence interval]) in all three species studied.

The model reproduces several features that would be predicted based on our biological understanding of these species. For example, the model shows that the spread of CIDs (τ) is significantly larger in gentoo penguins than either Adélie or chinstrap penguins, reflecting the relatively asynchronous breeding pattern seen in gentoo penguins relative to the other two species (Croxall, 1984; Bost and Jouventin, 1990a, 1990b). It has been hypothesised that this breeding asynchrony is a strategy to avoid intraspecific competition among gentoos which forage over a relatively small inshore feeding area (Croxall, 1984; Croxall and Prince, 1980). In addition, the model shows a strong and significant latitudinal gradient in breeding chronology, and the results show that mean CIDs are retarded 4.8 days [4.7,4.9] for every degree in latitude south of Admiralty Bay. This is consistent with the idea that the timing of breeding is limited by the availability of snow-free breeding areas, which will take longer to become available at higher latitudes.

It has been noted that season-to-season variability in the timing of gentoo penguin breeding is higher at more northerly sites (Bost and Jouventin, 1990a) with year-to-year variability reaching 4–5 weeks (Croxall and Prince, 1980). Over the relatively small latitudinal range examined here (relative to the overall gentoo penguin breeding range) it was not possible to verify a latitudinal gradient in inter-season variability, although the largest difference between consecutive seasons

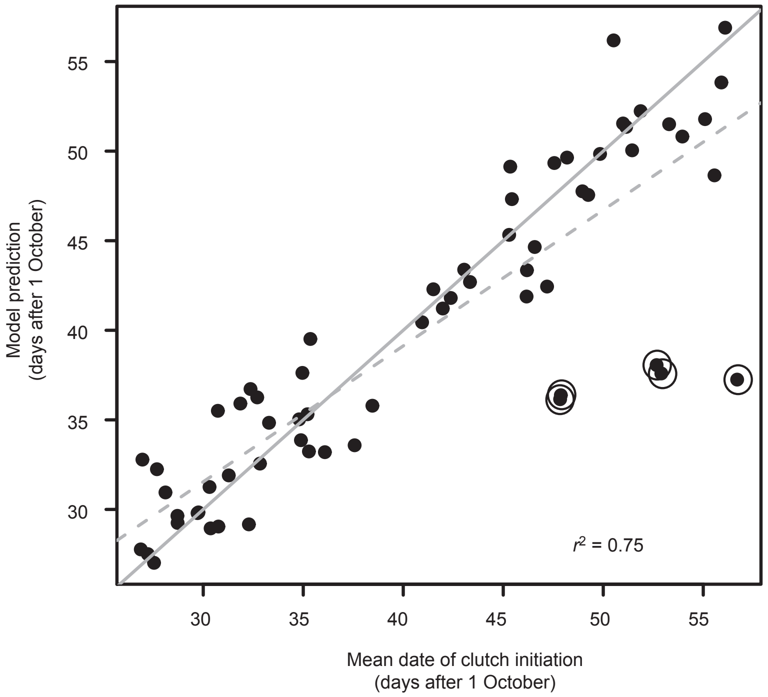

Figure 2: Scatterplot of model predictions for mean CID versus observed mean CID. Black circles indicate outliers (all from gentoo penguins at Cape Shirreff as noted in text). The 1:1 (solid) and best-fit (dashed) lines are shown for reference.

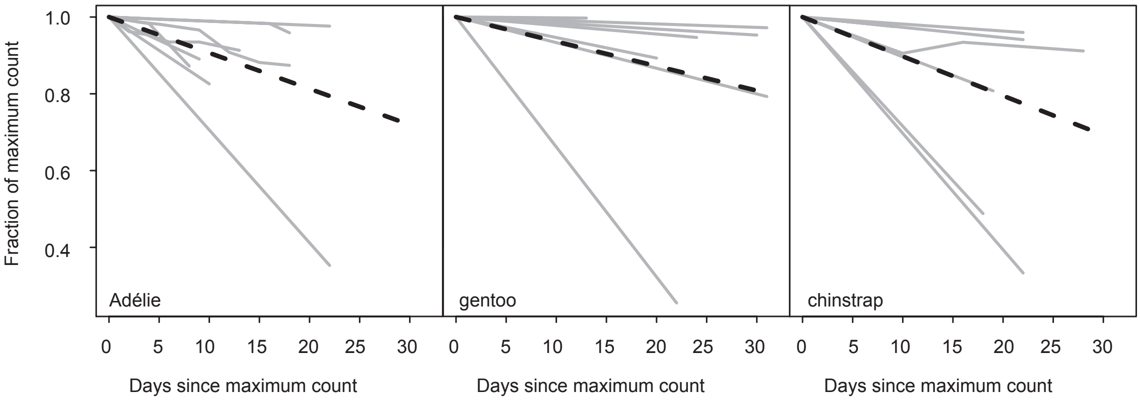

Figure 3: Nest attenuation following maximum census count for Adélie (left panel), gentoo (centre panel) and chinstrap (right panel) penguins. Individual year trends (gray solid lines) are included along with the species-aggregated best-fit regression lines (black dashed lines). The species-specific attenuation rates are 0.9% per day (σ = 0.2% per day) for Adélie, 0.6% per day (σ = 0.3% per day) for gentoo and 1.0% per day (σ = 0.3% per day) for chinstrap penguins.

in mean clutch initiation date was only ~15 days (between 2001 and 2002 at both Cape Shirreff and Admiralty Bay).

It has been assumed throughout that it is possible to closely estimate mean October temperature at a given site from the closest weather station. However, the combination of a strong latitudinal temperature gradient and a scarcity of weather stations on the Peninsula means that this may not always be possible. For example, the average October temperature difference between Faraday/Vernadsky Station and Palmer Station during 1974–1998 was 1.8°C. Using the Faraday/Vernadsky temperature record instead of the Palmer Station record for sites located between the two stations could lead to a difference in estimated CIDs as high as six days for gentoo penguins. The most accurate estimates of CIDs could be obtained by interpolating climatological data from all available weather stations on the Peninsula, a procedure which would introduce an additional source of error that would need to be considered.

The available data on rates of nest attrition (Figure 3) show a high amount of variability, with four trendlines showing much higher rates of nest attrition than the majority. Among these four are the only three sites with fewer than 100 nests of that species. This implies that smaller colonies (which may or may not be imbedded within larger colonies of other species) may have higher rates of nest attrition relative to larger colonies. Environmental factors are also likely to play a role in nest attrition rates, although the available data did not permit further investigation of this issue. Future advancements in the modelling of nest attrition rates will improve this component of the model. One of the advantages of this approach is the natural decomposition of the different model components, and improvements in any of the model components are easily incorporated into future versions.

Both models examined (breeding phenology and nest attrition rates) have important implications biologically, some of which have been discussed here. The motivation, however, was to use this model as a tool to predict mean CID for other sites and other years in which census data, but not data on CIDs, are available. To illustrate the utility of this model for correcting off-peak censuses, this model is applied to two census counts for which exact data on CID is unavailable.

Case 1:

Original data:

Site: Jougla Point
Count: 1 473 nests
Species: gentoos
Date of count: 2 January 2003

Additional information required (but available *post facto*):

Site latitude: –64.83°
Mean October (2002) temperature (from Palmer Station): –4.5°C

Model estimated mean CID
= 28.0 days +
–4.77 days/°latitude × (–64.83 – (–62.17)) °latitude +
–3.4 days/°C × (–4.5°C) +
–0.21 days/year × (2002 – 2000)
= 55.6 days (day 1 = 1 October)
= 25 November 2002

The nest count of 1 473 on 2 January 2003 is estimated to be 38 days after the peak of egg laying and, drawing on the estimate of nest attrition rates, the count is expected to be 22.8% less (38 days × 0.6%/day) than the true peak count. For this case, the true nest census count is estimated to be 1 908 ± 284. There are several things to note about this calculation. First, the error in this case comes only from propagating the uncertainty in the rate of nest attrition and the day of peak egg laying (Taylor, 1982). The intra-season variability in egg laying dates [i.e. Stage 2 of the model] is important for accurately predicting the spread in dates predicted for any given nest, but the population level mean is represented by *CID.mean* in Equations 2 and 3. Second, it has been assumed for purposes of demonstrating the technique that the original count had no error. Assuming 5% error in the original count increases the final uncertainty to ±299 (Appendix B). Finally, uncertainty in nest attrition rates, date of peak egg laying, and the original count (assumed 5%) represent 89.6%, 0.1% and 10.3% of the total uncertainty respectively. The uncertainty associated with the rate of nest attrition is by far the largest source of error in this census correction procedure, followed by the unavoidable error inherent in the original count, with the smallest contribution coming from the estimation of peak egg laying date. This emphasizes the need to understand better what processes drive nest attrition throughout a breeding season and the need for better data on this issue. Doing so would greatly improve the ability to correct off-peak nest census counts.

Case 2:

Original data:

Site: Berthelot Islands
Count: 402 nests
Species: Adélie
Date of count: 25 December 2006

Additional information required (but available *post facto*):

Site latitude: –65.33°
Mean October (2006) temperature (from Vernadsky Station): –1.9°C

Model estimated mean CID
= 26.2 days +
–4.77 days/°latitude × (–65.33 – (–62.17)) °latitude +
–1.40 days/°C × (–1.9°C) +
–0.21 days/year × (2006 – 2000)
= 42.7 days (day 1 = 1 October)
= 2 November 2006

The nest count of 402 on 25 December 2006 is estimated to be 43 days after the peak of egg laying, and this count is expected to be 43.0% less (43 days × 0.9%/day) than the true peak count (using the aggregated Adélie/chinstrap attrition rate). For this case, assuming the original count to be without error, the true nest census count is estimated to be 656 ± 95.

Conclusions

The model here developed is the first model the authors are aware of that takes into account year-, location- and site-specific information to correct 'off-peak' penguin nest census counts. Currently, the model accounting for nest attrition rates is limited by the available data, and additional data on this issue would help answer additional questions it was not possible to address here. One concern is that nest attrition may be non-linear through the breeding season. The available data were insufficient in temporal resolution (usually only encompassing two or three censuses a season) to consider non-linear models of nest attrition. Future field work specifically focused on obtaining multiple nest counts at a single location over the course of a season will help address this issue and will aid in the continued improvement in correction factors for off-peak census counts.

As previously noted and discussed in Lynch et al. (in prep.), there are reasons to believe that sympatric associations also play a role in the timing of clutch initiation. The role that sympatric associations may play in driving clutch initiation is currently being investigated, and future models would likely be improved by the inclusion of this information.

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APPENDIX A

Results of exploratory data analysis

Adélie penguin at Admiralty Bay:

Parameter	Estimate	Std. error	*t*-value	*p*-value (*Pr*(>|*t*|)
Mean October temperature	–2.18	0.38	–5.79	4.68e-05
September SOI	–1.41	0.51	–2.76	0.015
Mean May temperature	–0.90	0.34	–2.61	0.021
June ice area	5.58e-05	2.22e-05	2.52	0.025
June ice extent	4.59e-05	2.06e-05	2.23	0.043

Gentoo penguin at Admiralty Bay:

Parameter	Estimate	Std. error	*t*-value	*p*-value (*Pr*(>|*t*|)
Mean October temperature	–4.33	0.62	–7.03	5.97e-06
Mean May temperature	–2.11	0.56	–3.79	0.0020
June ice area	1.26e-04	3.77e-05	3.34	0.0048
September SOI	–2.95	0.91	–3.25	0.0059
June ice extent	1.03e-04	3.59e-05	2.87	0.012
October SOI	–1.97	0.85	–2.32	0.036
July ice extent	1.07e-04	4.83e-05	2.22	0.043

Chinstrap penguin at Cape Shirreff:

Parameter	Estimate	Std. error	*t*-value	*p*-value (*Pr*(>|*t*|)
Mean October temperature	–1.64	0.50	–3.28	0.011
November ice extent	4.88e-05	1.64e-05	2.97	0.018
November ice area	6.18e-05	2.39e-05	2.58	0.033
October SST	23.77	9.38	2.53	0.035

Gentoo penguin at Cape Shirreff:

Parameter	Estimate	Std. error	*t*-value	*p*-value (*Pr*(>|*t*|)
Krill abundance[1]	0.21	0.09	2.28	0.07

Adélie penguin at Humble Island:

Parameter	Estimate	Std. error	*t*-value	*p*-value (*Pr*(>|*t*|))
Mean February temperature	5.03	1.53	3.28	0.017
May SOI	–2.22	0.70	–3.16	0.020
November ice area	1.05e-04	3.39e-05	3.10	0.021
September SOI	–1.29	0.43	–3.03	0.023
Mean October temperature	–1.10	0.44	–2.49	0.047

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[1] No covariate examined was significantly ($p < 0.05$) correlated to mean CID for gentoo penguin at Cape Shirreff. Krill abundance was included because it was the most significant covariate for gentoo penguin at Cape Shirreff.

APPENDIX B

Error propagation

The relationship between the corrected count (q) and the original count (n) is given simply by

$$q(r,d,n)=\frac{n}{1-rd} \tag{A1}$$

where r is the rate of nest attrition and d is the number of days since the peak of egg laying. The error in q is the sum of squared errors from all the components with error which, assuming error in r, d and n (i.e. error in the original census count) is given by

$$\delta q=\sqrt{\left(\frac{\partial q}{\partial r}\delta r\right)^2+\left(\frac{\partial q}{\partial d}\delta d\right)^2+\left(\frac{\partial q}{\partial n}\delta n\right)^2} \tag{A2}$$

or, in this case,

$$\delta q=\frac{n}{(1-rd)^2}\sqrt{(d\delta r)^2+(r\delta d)^2+\left(\frac{\delta n}{n}(1-rd)\right)^2}\;. \tag{A3}$$

The relative importance of each source of error can be judged by the proportion each term contributes to the total sum under the square root.