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INTEGRATING COUNT EFFORT BY SEASONALLY CORRECTING ANIMAL POPULATION ESTIMATES (ICESCAPE): A METHOD FOR ESTIMATING ABUNDANCE AND ITS UNCERTAINTY FROM COUNT DATA USING ADÉLIE PENGUINS AS A CASE STUDY

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Abstract

This work describes a parametric bootstrap model for standardising animal count data to a common reference point of breeding chronology for species with a complex temporal function of sampling availability. ICESCAPE (Integrating Count Effort by Seasonally Correcting Animal Population Estimates) is a suite of routines that implements a general abundance estimator accounting for availability bias, detection bias and sampling fractions less than unity. Within this resampling framework, all reported measures of uncertainty associated with originally published counts are propagated through to the final adjusted estimates. Adjustment for availability bias is achieved by applying an adjustment factor based on independently measured time series of availability throughout a breeding season. Such time series are typically collected at only a limited number of sites, so surrogate availability information for a site is used when none exists. Importantly, a common standardisation procedure allows site-specific estimates to be aggregated to achieve region-scale population estimates. By way of illustration, the method is applied to several examples of published studies of Adélie penguin abundance at breeding sites in Antarctica. These examples focus on adjusting counts of adults to an effective number of breeding pairs, although the software has been developed to accommodate adjustment and aggregation of other count objects typical for penguin species, such as occupied nest or chick counts. While tailored for Adélie penguins, the method and implementation is sufficiently general to be easily adapted for other colonial land-breeding species showing seasonal variation in availability to sampling methodology.

Résumé

Ces travaux décrivent un modèle de bootstrap paramétrique pour uniformiser les données de dénombrement des animaux en fonction d'un point de référence commun dans la chronologie de la reproduction d'espèces dont la fonction temporelle de disponibilité pour échantillonnage est complexe. ICESCAPE (Intégration de l'effort de dénombrement par correction saisonnière des estimations de populations d'animaux) est une série de routines mettant en jeu un facteur d'estimation d'abondance générale qui tient compte des biais liés à la disponibilité et de détection et des fractions d'échantillonnage inférieures à l'unité. Dans le cadre de cette structure de ré-échantillonnage, toutes les mesures déclarées d'incertitude associée aux dénombrements qui ont été publiés par le passé sont utilisées jusqu'aux estimations finales ajustées. L'ajustement du biais lié à la disponibilité est effectué en appliquant un facteur d'ajustement fondé sur des séries chronologiques de la disponibilité mesurée indépendamment tout au long de la saison de reproduction. Normalement, ces séries chronologiques ne sont collectées qu'à un nombre limité de sites ; de ce fait, des données de substitution sur la disponibilité sont utilisées pour un site lorsqu'il n'en existe pas. Il est important de noter qu'une procédure de normalisation commune permet d'agréger les estimations par site pour obtenir des estimations de la population à l'échelle régionale. À titre d'illustration, la méthode est appliquée à plusieurs exemples d'études publiées sur l'abondance du manchot Adélie sur les sites de reproduction en Antarctique. Ces exemples se concentrent sur l'ajustement des dénombrements d'adultes pour atteindre un nombre efficace de couples reproducteurs bien que le logiciel ait été créé pour tenir compte de l'ajustement et de l'agrégation d'autres objets du dénombrement typiques des espèces de manchots, tels que le nombre de nids occupés ou de jeunes. Bien que conçue spécifiquement pour le manchot Adélie, la méthode est d'une application suffisamment générale pour pouvoir être facilement adaptée à d'autres espèces vivant en colonies et se reproduisant à terre, dont l'effectif disponible pour la méthode d'échantillonnage varie selon la saison.

Резюме

В данной работе описывается параметрическая модель бутстрап, использующаяся для стандартизации данных подсчета животных в соответствии с общей базисной точкой хронологии размножения видов со сложной временной функцией наличия для взятия проб. ICESCAPE (Интегрирование усилий по учету путем сезонной корректировки оценок популяций животных) представляет собой систему процедур, при помощи которой осуществляется общая оценка численности, учитывающая систематические ошибки наличия и обнаружения, а также доли выборки менее единицы. В рамках этой системы повторной выборки все приведенные показатели неопределенности, связанные с изначально опубликованными расчетами, распространяются на все вплоть до окончательных откорректированных оценок. Корректирование систематической ошибки для наличия происходит путем применения поправочного коэффициента на основе временных рядов независимо полученных данных по наличию в течение всего сезона размножения. Такие временные ряды обычно собираются только на ограниченном количестве участков, поэтому для участков, по которым не имеется информации, используется замещающая информация о наличии. Важно то, что общая процедура стандартизации позволяет агрегировать конкретные оценки по отдельным участкам с целью получения оценок популяции в региональном масштабе. В качестве иллюстрации данный метод применяется к нескольким примерам опубликованных работ о численности пингвинов Адели на участках размножения в Антарктике. Эти примеры концентрируются на корректировании подсчетов взрослых особей в соответствии с фактическим числом размножающихся пар, хотя программа была разработана для того, чтобы включать корректировку и агрегирование других объектов подсчета, типичных для различных видов пингвинов, например подсчет занятых гнезд или птенцов. Этот метод был специально разработан для пингвинов Адели, однако и сам метод, и его применение носят достаточно общий характер и могут без труда использоваться для других живущих колониями видов, которые размножаются на суше и доступность которых для проведения выборки подвержена сезонной изменчивости.

Resumen

Este trabajo describe un modelo paramétrico de bootstrap para normalizar los datos de recuentos de animales con respecto a un punto de referencia común de la cronología de reproducción para especies con una función temporal compleja de disponibilidad para el muestreo. ICESCAPE (integración del esfuerzo de conteo corrigiendo las estimaciones de las poblaciones de animales por temporada) es una serie de rutinas que aplica un estimador general de la abundancia para dar cuenta de sesgos debido a la disponibilidad, a la detección y a fracciones de muestreo menores que una unidad. Dentro de este marco para efectuar un nuevo muestreo, toda estimación de la incertidumbre notificada para los conteos publicados originalmente ha sido incorporada en las estimaciones ajustadas finales. El ajuste para el sesgo de la disponibilidad se consigue aplicando un factor basado en la serie cronológica de mediciones independientes de la disponibilidad durante una temporada de reproducción. En general las series cronológicas de este tipo sólo son recolectadas en un número limitado de sitios, de manera que cuando no se tiene información sobre la disponibilidad para un sitio, se utilizan datos sustitutivos. Lo que es más importante, un procedimiento de normalización común permite agregar las estimaciones para cada sitio a fin de obtener estimaciones de la población en escala regional. A modo de ilustración, se aplica el método a varios ejemplos de estudios publicados de la abundancia del pingüino adelia en colonias de reproducción en la Antártida. Estos ejemplos se concentran en el ajuste del conteo de adultos a un número efectivo de parejas reproductoras, si bien el software ha sido desarrollado para acomodar el ajuste y la agregación de otros sujetos de conteo característicos para las especies de pingüinos, como nidos con polluelos o conteo de polluelos. Si bien el método fue creado para el pingüino adelia, su implementación es lo suficientemente general como para ser fácilmente adaptado a otras especies que se reproducen en colonias terrestres y cuya disponibilidad para el muestreo varía con la temporada.

Keywords: abundance estimation, parametric bootstrap, availability bias, Adélie penguin, CCAMLR

Introduction

Counts of animal populations often need to be adjusted to provide unbiased estimates of abundance. Bias may result from a failure to count all animals present in searched areas (detection bias, often measured as a detection fraction; Thompson et al., 1998), or from the absence of some animals from search effort (availability bias; Williams et al., 2002; Pollock et al., 2004). A further adjustment issue, and one that interacts with the types of bias noted above, concerns sampling. Often, sample counts will be taken from some larger area of interest so that, in order to obtain estimates of total population size for the entire area, counts must be adjusted for the fraction of the total survey region that is searched (typically by up-scaling by a factor equivalent to the inverse of the sampling fraction). Adjustment to obtain unbiased estimates is imperative for monitoring temporal and spatial changes in populations, particularly for Antarctic vertebrate species where the difficulties in accessing a species' habitat can often result in detection, availability or sampling fractions being other than unity. However, despite the need for such adjustments, counts of Antarctic species such as penguins are often presented unadjusted, or adjustments are applied in an ad hoc manner. This is in part because one-off counts require relatively brief visits to sites, compared with collecting adjustment data that may require much longer sampling times and so are less often obtained. This difficulty is now being addressed through technical developments in sampling methodology, such as remotely operating cameras that allow automated collection of adjustment data (Newbery and Southwell, 2009; Southwell et al., 2010). Rigorous adjustment of census counts (including propagation of error) is also complicated by the difficulty of finding a closed-form solution when multiple sources of bias and uncertainty, each of which may have their own statistical distribution, need to be accommodated. The present study addresses these issues by developing a parametric bootstrap model (Davison and Hinkley, 1997) to correct counts for availability bias, detection bias and sampling fractions less than unity, while simultaneously combining all known variance information in these quantities.

Sources of bias such as those described above are evident in many studies estimating the abundance of colonial land-breeding vertebrate species in Antarctica and on sub-Antarctic islands, including penguins (e.g. Southwell, 2004a, 2004b) and flying seabirds (e.g. Creuwels et al., 2007). While the methods of this study are sufficiently general to be easily modified and applied to many land-breeding colonial species, Adélie penguins (*Pygoscelis adeliae*) have been chosen to demonstrate application of the technique. For penguins in general, and Adélie penguins in particular, most published count data are based on researchers attempting to undertake a census at one or more breeding sites; that is, a total count of all adult penguins (or nests or chicks) is taken over an entire site to estimate the breeding population. Consequently, the detection and sampling fractions are often either known or assumed to be unity, and no adjustment of counts to account for detection bias, or up-scaling to account for sampling, are required. However, because of logistic constraints, the timing of the counts within the breeding season is difficult for researchers to control and can be highly variable. The numbers of breeding Adélie penguins, nests and chicks present at a site are known to vary in association with breeding events such as initial arrival, egg-laying, incubation, provisioning of chicks and nest failure (Emmerson and Southwell, 2008). Patterns in availability will vary depending on the population unit being counted (adults, nests or chicks). A full description of the patterns in availability of adults, nests or chicks to sampling methodology is provided in a companion paper modelling availability curves (Southwell et al., 2010). Raw counts of adults, chicks or nests will therefore often be biased estimators of the breeding population unless adjusted for availability bias, with the magnitude of bias being dependent on the population object counted (adult, nest or chick) and the date of the count.

These issues are addressed by developing a parametric bootstrap model for adjusting counts to a common point of breeding chronology, optionally incorporating adjustments for detection fraction and sample fraction less than unity (if required), to derive estimates of the breeding population as the number of breeding pairs or nests present one week after the peak in egg laying (Southwell et al., 2010). Software to implement the method has been developed as a menu-driven suite of routines developed in the R language for statistical computing (R Development Core Team, 2009). Termed ICESCAPE (Integrating Count Effort by Seasonally Correcting Animal Population Estimates), the software takes as its input two types of data: (i) raw counts of adult penguins, occupied nests or chicks from breeding sites, along with auxiliary data including the object counted, date of the count, sampling fraction and detection fraction, and information on estimated precision of these elements; and (ii) time-series counts of adults, nests or chicks taken throughout a season, which provide an index of availability in relation to some optimal time point in the season. The former are typified by one-off counts collected from a relatively large number of sites at times during the breeding season when weather and other determinants of site access permit, while the latter comprise comparatively detailed longitudinal data throughout the breeding season derived from high-intensity sampling at a relatively small number of sites. Using these data, the bootstrap model adjusts counts to a common point of breeding chronology, if necessary adjusting counts for detection and sampling fractions less than unity. Importantly, the model attempts to preserve all aspects of uncertainty inherent in the count data, as well as uncertainty associated with adjusting for availability bias, detection bias and sampling fraction, and propagates these various sources of uncertainty through to adjusted breeding population estimates. Results arising from application of the procedure allow breeding population estimates to be reliably compared between sites and over time, and to be aggregated across sites to achieve regional estimates of total abundance.

Due to considerable variation in published counting methods and their reporting over time, ICESCAPE has been developed to be flexible in the way historical count data are interpreted. While most data appearing in the literature have a natural interpretation, ambiguities do exist and alternate interpretations have been accommodated as options to the estimation procedure. This flexibility is particularly useful for conducting sensitivity analyses to assess how certain decisions of interpretation affect adjusted estimates. While ICESCAPE has been developed in order to make full use of historical count data, it is just as useful for adjusting contemporary one-off counts to a common reference point of breeding chronology. At present, ICESCAPE has been tailored for the analysis of Adélie penguin data, and in particular for adjusting counts of adults, occupied nests and chicks for that species, but the procedure is sufficiently general to be relatively easily adapted for other species with similar biology.

In the remainder of this paper the bootstrap procedure, and methods associated with summarising the bootstrap object, are described. This is followed by three case studies utilising published counts of adult Adélie penguins to demonstrate the main features of the procedure. Finally, the Discussion focuses on known limitations of the work and plans for future improvements of the method. Models of time series of availability data, which provide a critical data input to the bootstrap model presented here, are described fully in a companion paper Southwell et al. (2010).

Methods

The general abundance estimator on which this bootstrap implementation is based is presented by Pollock et al. (2004), and is discussed in the context of Adélie penguins by Southwell (2004a). Here, a published estimate of a count $\hat{C}$ for a site is adjusted to provide an estimate of abundance at a fixed point of breeding chronology ($\hat{N}$) by:

$$\hat{N} = \frac{\hat{C}}{\hat{p}_{area} \cdot \hat{p}_a \cdot \hat{p}_{da}} \tag{1}$$

where $\hat{p}_{area}$ represents the estimator adjusting for the sample fraction, $\hat{p}_a$ is the estimator adjusting for availability bias, and $\hat{p}_{da}$ is the estimator for the conditional probability of detection given availability. The first and third denominator adjustment terms are bounded >0 and ≤1, while $\hat{p}_a$ is bounded >0 with an upper bound determined by the form of the species-specific availability function. For Adélie penguins, the upper bound for $\hat{p}_a$ is typically <2.5. Treatment of this model by some authors considers the count or the sample fraction to be known without error (e.g. the formulation of Pollock et al., 2004), however, many published studies of Adélie penguins provide estimates of uncertainty for one or both of these measures and this feature has been incorporated into the present model. For the purposes of this work on Adélie penguins, counts are adjusted for availability bias by standardising to a point seven days after the peak in egg laying (Southwell et al., 2010), consistent with the CCAMLR Ecosystem Monitoring Program (CEMP) Standard Method A3 (CCAMLR, 2004) for estimating breeding population size. This adjustment is intended to estimate the number of occupied nests, or equivalently breeding pairs, at their maximum value in a season (i.e. before any effect of nest attrition), and provides an alternative approach to that of Lynch et al. (2009) who simultaneously estimate clutch initiation and nest attrition using hierarchical Bayesian methods. To obtain a distribution of

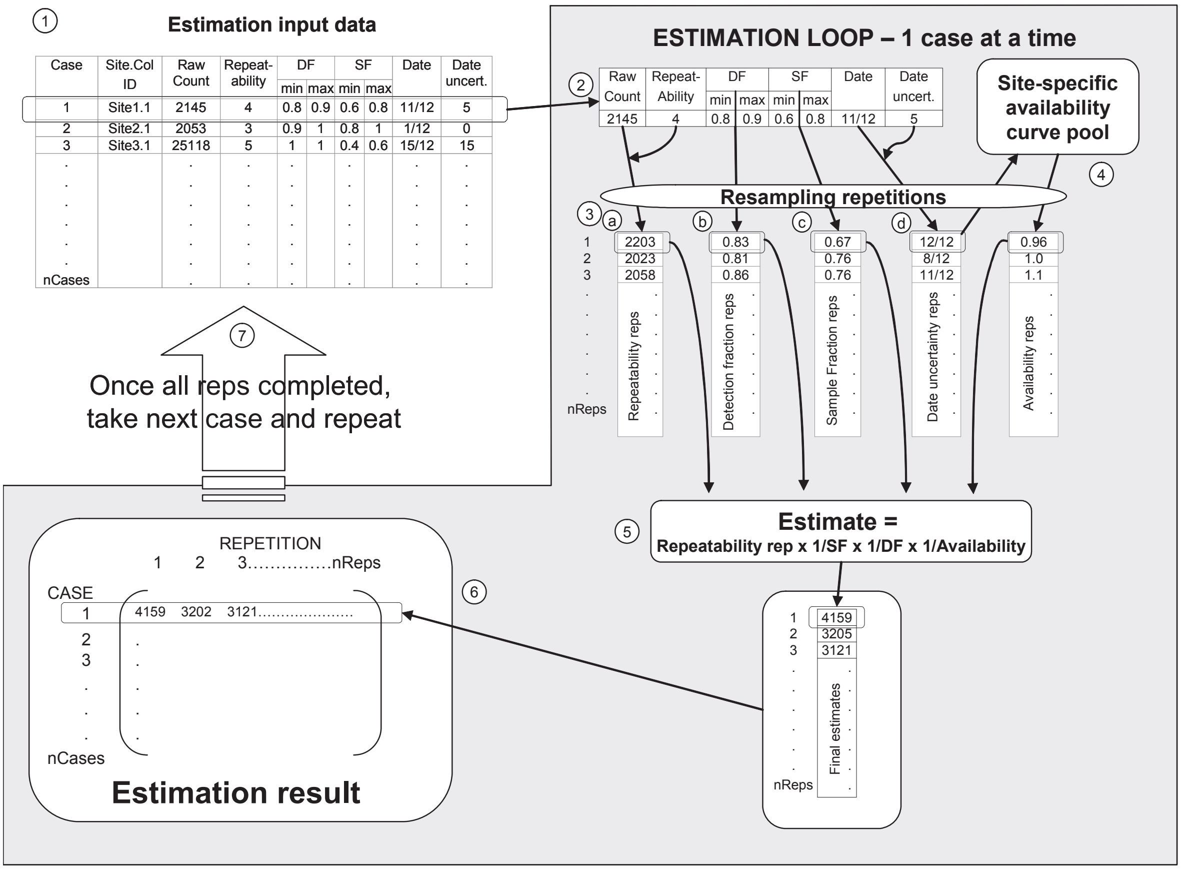

Figure 1: Representation of the ICESCAPE estimation procedure. The procedure is applied identically to raw, unadjusted counts of adults, nests or chicks, noting that object-specific availability curves are required for each type of count object.

adjusted counts ($\hat{N}$) for a given site in a season, bootstrap samples are generated for each of $\hat{C}$, $\hat{p}_{area}$, $\hat{p}_a$ and $\hat{p}_{da}$ taking into account known estimates of variance for each element. The distribution of adjusted estimates is then summarised for central tendency, and confidence bounds are obtained by considering appropriate percentile points.

The estimation procedure in ICESCAPE can be summarised as follows (Figure 1):

1. Data are presented to the routine in formats congruent with CCAMLR databases designed to store data of this kind; integrity checks take place, such as range checks and checks for the presence of essential fields; user-specified spatial and temporal subsetting occurs.

2. The procedure loops over the data one case at a time, taking all information relating to the raw count (information on precision, uncertainty in the count date, sample fraction, detection fraction).

3. Using known information about uncertainty in these quantities, bootstrap replicates are generated for the raw count, the date on which the count occurred, the sample fraction and detection fraction. Various options control how this uncertainty information should be treated (e.g. how Croxall and Kirkwood (1979) measures of repeatability should be interpreted, or the type of distribution to use when drawing replicates). Occasionally in the literature, counts are reported without any measure of uncertainty (e.g. Law, 1962; Ensor and Bassett, 1987). In the interests of promoting a precautionary approach to interpreting these counts, a minimum level of uncertainty in a reported count can be imposed by the user where none exists.

4. Availability fractions are generated by drawing samples from an availability curve for a site, or from a pool of surrogate availability curves if no availability information exists for a site. Surrogate curves, if necessary, are chosen from the total pool of such curves presented to the software. Curves are fitted to

availability time series using generalised additive models (GAMs) (Hastie and Tibshirani, 1990) using the methods of Wood (2006), and are described fully in Southwell et al. (2010). An adjustment factor for each replicated date is obtained by randomly selecting a curve from the pool available for a site and drawing from a Normal distribution with mean equal to the predicted value for that date and standard deviation equal to the standard error of the fitted function at that point. If multiple attendance curves are available in any one site-season combination within the surrogate pool (e.g. such as the replicate time series of attendance data arising from the remote camera sampling method detailed in Southwell et al. (2010)), then replicate curves are treated as subsamples and their probability of selection is appropriately down-weighted in the bootstrap model (i.e. weighted by the inverse of the number of subsamples, on a site by season basis).

5. The distribution of final adjusted estimates for a site-colony-season is calculated as the repeatability replicates (replicate counts resampled from a distribution based on the published repeatability information) multiplied by the inverse of the availability fraction replicates and, if necessary, detection fraction and sample fraction replicates.

6. Vectors of adjusted counts for a site are stored.

7. The procedure takes the next case (raw count) and repeats steps 3–7 until all cases are processed.

Once an estimation procedure has successfully completed, ICESCAPE saves an estimation object that must be summarised in order to obtain adjusted breeding population estimates for one or more sites. The summary routine performs several tasks:

1. Occasionally in the published literature, there may exist multiple count records for a single site in a season (e.g. counts taken on different days in a single season). Multiple count records are collapsed to just a single record by applying user-specified criteria specifying whether they should be averaged (point 3 below describes this process), or that the most or least precise estimate should be preferred.

2. Adélie penguin count data are published in a variety of forms. Some counts are published in their raw form with no attempt to adjust or interpret beyond this state (e.g. Ensor and Bassett, 1987). Sometimes counts are published in their raw form with no adjustment for availability bias, but are interpreted and presented as approximate estimates of the breeding population on the basis that the counts were undertaken around the time of the breeding season when availability adjustment factors are expected to be close to, or equal to, unity (e.g. Taylor et al., 1990). In other cases, only adjusted counts are presented and there is insufficient detail to infer the raw count data (e.g. Whitehead and Johnstone, 1990). Finally, in some cases both adjusted and unadjusted counts are presented (e.g. Barbraud et al., 1999). ICESCAPE has been designed to work with such variable count data in order that a consistent adjustment process can be applied across many sites, or through time for the same site. It is this common standardisation process that allows bias-corrected estimates to be plausibly aggregated. In cases where an author publishes an adjusted estimate and the unadjusted count on which it was based (or the unadjusted count can be inferred from the description of the adjustment process), then ICESCAPE will by default use the unadjusted count, ignoring the published adjusted estimate, so that a standardised adjustment is applied. However, if only an adjusted estimate is published and a raw count cannot be inferred, then 'pseudo-replicates' are generated from the adjusted estimate and associated measure of uncertainty in order to allow it to be combined during the aggregation process (Figure 2).

3. If specified by the user, records are aggregated to one of several spatial groupings by a summation of the bootstrap distributions of adjusted estimates for each site in the aggregation. This is accomplished by taking a random draw without replacement from the distribution of the adjusted population estimate for each site in the pool to be aggregated, summing the values to obtain a single aggregate estimate, and then repeating the process until all replicates making up the bootstrap distributions for each site have been processed. Bootstrap without replacement is appropriate here since each site distribution contributing to the aggregate distribution has already been formed using sampling with replacement. In the case of aggregating x distributions each with n elements, the resulting distribution by this method will comprise a random subsample (of size n) of all n^x permutations across members of the sets.

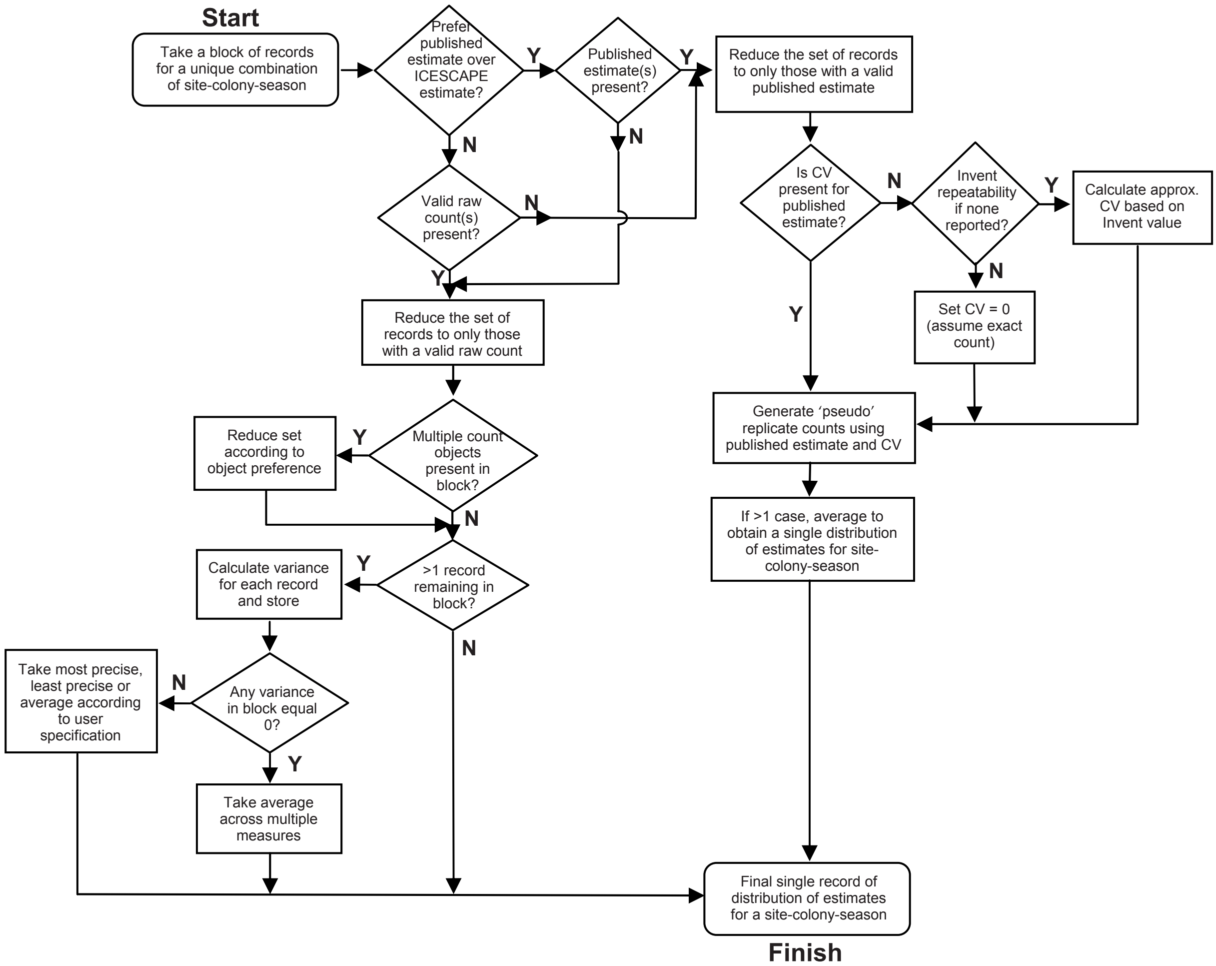

Figure 2: Representation of program flow associated with determining a single estimate for a site when multiple count records exist for a single site-colony-season combination. The term 'coefficient of variation' has been abbreviated to CV for reasons of brevity.

The aggregate distribution is then summarised to obtain regional estimates of abundance and associated uncertainty. A similar process is followed to obtain an average distribution of multiple counts taken at the same site in the same season, except that elements of each random draw are averaged instead of summed (see point 1 above).

4. The 100.(1 – alpha)% confidence interval is determined by examining the alpha/2 and 1 – alpha/2 percentile points of the (possibly aggregated or averaged) distribution of adjusted estimates.

In order to help understand how elements of the adjustment procedure contribute toward estimates of uncertainty, ICESCAPE has been developed to permit different interpretations of historically published data (where ambiguities exist), or to allow different components of the estimation process to be switched on or off. As an example, Croxall and Kirkwood (1979) measures of uncertainty, reported in the literature, present precision as a range of values (e.g. 0–5%, 5–10% etc.) around an estimated count. However, it is not clear what this range might represent in a statistical sense. Options are therefore provided to allow such ranges to be interpreted in different ways: either as representing 1, 2 or 3 standard errors around the estimate, with an additional option of allowing the lowest bound, midpoint or highest bound of the range to assume the point value for the interval estimate. Obtaining results under different interpretations of the data via settable options in ICESCAPE allows a user to easily assess relative contributions of different choices toward overall measures of uncertainty around an estimate, both at a site and an aggregated level. Such a feature is useful as a diagnostic tool at a site level, and may help to prioritise future survey work by identifying sites where existing data are inadequate.

It is intended that the ICESCAPE software be developed to a point where it can be released as an R package, however, at the present time it remains under active development and so is not yet available for general public release. A beta version for testing purposes can be made available on application to the authors.

Results

Results are presented by way of three case studies chosen to demonstrate the key features of ICESCAPE, namely: (i) adjustment of a single historical count taken at a site in a season; (ii) adjustment of several counts taken at a single site in a single season, with application of user-defined criteria for determining a preferred estimate; and (iii) adjustment of counts taken at several sites within a geographic area, which are then aggregated to achieve a regional estimate of abundance.

Adjusting raw counts for availability requires time-series counts of the relevant population object standardised to an appropriate reference point, with sufficient frequency in the time series to allow the functional form of the availability curve to be adequately modelled (Southwell et al., 2010). A search of the primary literature revealed a paucity of time-series data suitable for developing availability adjustment factors for adult Adélie penguins in East Antarctica, with only two suitable published series currently found. Watanuki and Naito (1992, Figure 1) provide time-series counts of adults at two breeding sites near Syowa station in the 1990/91 summer, and Southwell et al. (2010) provide standardised time-series counts of adults at Béchervaise Island in 2007/08. The Syowa data are somewhat limited in that time series do not extend beyond 24 December 1990. In demonstrating the utility of ICESCAPE here, the time-series data from these studies have been utilised, as well as previously unpublished data collected at Béchervaise Island in years other than 2007/08 and at sites in the Mawson region other than Béchervaise Island. In all, availability adjustment data from 14 site-seasons (two from the Syowa region, 12 from the Mawson region) were utilised.

Case Study 1 – Single estimate, single site

The first example demonstrates the estimation routine by applying it to a single historical count of adult Adélie penguins conducted during January 1979 at Haswell Island (66.52°S 92.99°E) in CCAMLR Statistical Division 58.4.1. The original description of the count information by Starck (1980) is '…the count performed on 24 January 1979 showed the presence of 36 000±500 individuals including 11 300 nestlings…', but the additional statement '…the observations were carried out… from 20 to 24 January 1979…' places some uncertainty on the exact date of the count. From this description it was interpreted that 24 700 adults and 11 300 chicks had been counted, that each of these counts had an associated repeatability of 1.4%, and, to be conservative, that the counts were made some time from 20 to 24 January 1979. This case was chosen because it represented four issues of the estimation process: adjustment of counts that are far from the optimum date in the breeding chronology for determining an effective number of breeding pairs attending a site; accounting for uncertainty in the count itself (repeatability); accounting for uncertainty in the date on which the count took place; and the use of surrogate availability data. As Starck (1980) made no mention of issues related to sample fraction or detectability, it was assumed that counting effort covered the entire island and all penguins were counted (i.e. sampling and detection fractions were assumed to be 1). The ICESCAPE estimation procedure was applied to the adult data, with distributions arising from 1 000 bootstrap replicates shown in Figure 3.

Resampling underestimated repeatability of the raw count produced a reasonably symmetric distribution of the (unstandardised) count ranging from around 24 200–25 200. Date uncertainty was interpreted as ±2 days, so resampling dates from a uniform distribution produced approximately 200 replicates from each of 5 days centred on 22 January 1979. Corrections for availability were obtained by resampling from 14 surrogate availability curves presented to the routine for the purpose of this example. However, only 12 of the 14 curves had data into late January when the Haswell Island count occurred, hence only these 12 curves were used to draw replicate availability fractions. The resulting distribution of availability ratios was centred around 0.5–0.6, but strongly positively skewed, resulting in a similarly skewed distribution of standardised estimates with mean 43 833, median 42 610, and 95% confidence interval by the percentile method of 19 220–86 358. This compares with an originally published unadjusted raw count value of 24 700.

Case Study 2 – Multiple estimates, single site

The second example demonstrates the ability of ICESCAPE to deal with multiple count records occurring in the same season for an individual site. Data comprise counts of adult Adélie penguins made three times during the 1990/91 season at Mame-zima Island (69.02°S 39.49°E), as reported

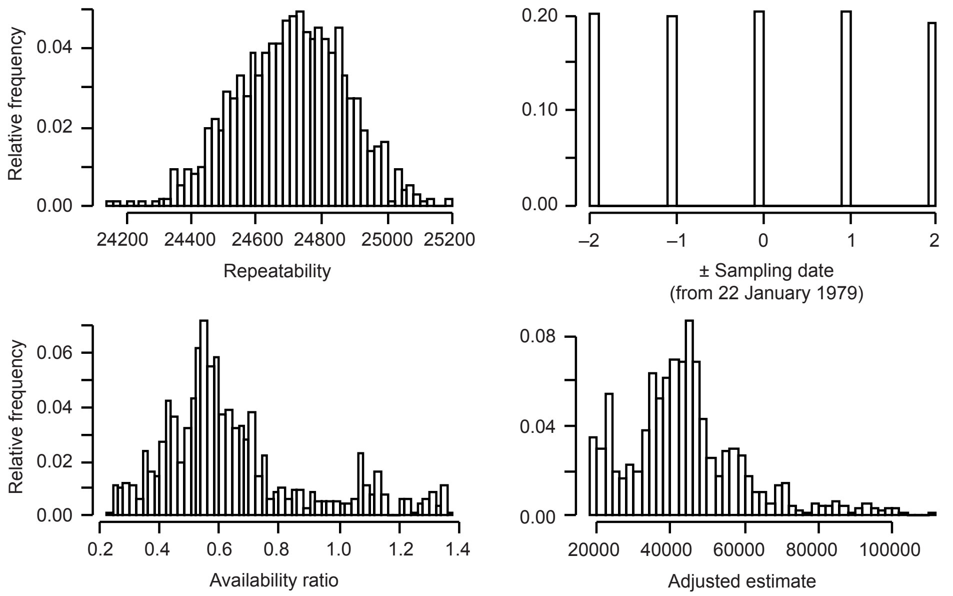

Figure 3: Distributions, based on 1 000 bootstrap replicates, arising from application of the ICESCAPE estimation routine to a count of adult Adélie penguins conducted in January 1979 on Haswell Island.

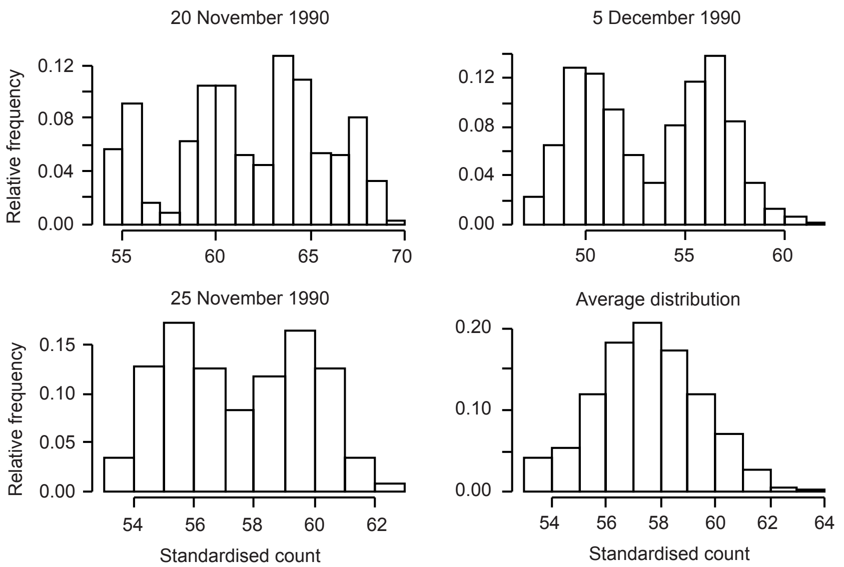

Figure 4: Distribution of standardised counts arising from application of ICESCAPE to each of three separate counts of Adélie penguins taken at Mame-zima Island in the 1990/91 breeding season, as well as the average distribution.

by Watanuki and Naito (1992): 115 adults on 18 or 21 November 1990, 75 adults on 25 November 1990, and 52 adults on 4 or 6 December 1990. Date uncertainty was taken to be ±1 day around 20 November and 5 December 1990. No repeatability information was reported for the counts, and since the counts are reasonably small it is assumed they were counted without error (i.e. an assumed level of repeatability was not introduced). Again, there was no reference to sample or detection fractions in the publication and these were assumed equal to unity. In this case, two of the 14 availability curves were derived from time-series data collected in the same season from islands adjacent to Mame-zima Island, so only these two availability curves were used as donor sites for the purpose of adjusting counts.

Results are presented as the distribution of final standardised estimates for each of the three sample dates, and the distribution of the average for the entire site (Figure 4). It should be noted that the spread of values in the distributions of standardised counts are wholly due to resampling from just two availability curves (incorporating date uncertainty of 1 for two of the sample dates), and resulting distributions of adjusted estimates show some evidence of bimodality as a result. Summarising the average distribution for location and spread gives a mean of 58 (median 58) and 95% confidence interval of 54–62, indicating the number of breeding pairs or, equivalently, the number of occupied nests at the standard time as defined by CEMP Standard Method A3 (CCAMLR, 2004). Watanuki and Naito (1992) also reported that 51 nests were counted on 4 or 6 December 1990 at this site, a number that is slightly lower than the lower bound of the 95% confidence interval calculated here. This discrepancy is possibly due to nest attrition occurring between the date of the reference count for adjustment and the date of their count.

Case Study 3 – Multiple sites

The final case study shows the estimation method applied to a number of sites within a specified spatial area to derive a regional estimate of abundance. On 17 November 1972, Jones (reported in Horne, 1983) counted Adélie penguins at several sites in the Rookery Island group in Division 58.4.2. For reasons of simplicity this study aggregates over only three of these sites, namely Rookery Islands 2 (67.60°S 62.53°E), 8 (67.61°S 62.52°E) and 11 (67.61°S 62.51°E), but note that the real advantage of this facility in ICESCAPE would be to aggregate data over multiple sites from much larger regions. The original published account of these data by Horne (1983) indicated that Jones made counts of adult penguins. However, Horne states that, in collating unpublished data, all unqualified counts of adults were divided by two to derive an estimate of the numbers of breeding pairs, and it is these estimates, rather than the original counts, that are reported. Therefore, it has been interpreted in this study that the estimates of 4 765, 698 and 326 breeding pairs for Rookery Islands 2, 8 and 11 represent raw counts of 9 530, 1 396 and 652 adults respectively, and applied the ICESCAPE estimation procedure to these raw counts. All counts were reported as having a repeatability score of 3 (10–25%) according to the Croxall and Kirkwood (1979) scheme. For the purposes of resampling during the estimation procedure, the mid-point of this range was assumed to represent an approximate 95% confidence interval (i.e. 17.5/100*count ≅ 2 standard errors). Estimates of sample fraction and detection fraction were not reported, and were assumed equal to one.

Results derived from 1 000 bootstrap replicates are presented as the distribution of final standardised estimates for each of the three islands, as well as the distribution of the total for all three sites determined by a summation of individual site distributions (i.e. by a summation of independent draws without replacement from each contributing distribution) (Figure 5). Measures of central tendency and dispersion are provided in Table 1.

The mean and median values for the three islands are remarkably similar to the original estimates provided by Horne (4 765, 698 and 326). However, this is a fortunate consequence of the counts being undertaken at a time of the breeding season when there are generally twice as many adults present as breeding pairs at the beginning of incubation; had adult counts been undertaken earlier or later, the differences between Horne's and this study's estimates would have been greater. Horne (1983) notes, as does Woehler (1993), that deriving estimates of the breeding population from adult counts by a simple division of two is likely to be 'less accurate' than deriving estimates from counts of nests. This sentiment is captured in the relatively large spread of the abundance distributions, which represents the uncertainty around the estimates.

Discussion

The bootstrap model described in this study provides an intuitive method of adjusting count data, often taken at sub-optimal times of a breeding season, to a common reference point of breeding chronology in order to assess spatial and temporal variability in population sizes. The model has several appealing features, including its relative ease of use, flexibility, extensibility and ability to perform sensitivity tests for different decisions made during application of the estimation procedure. Like all models of this kind, it is reliant on a correct specification of the underlying biological system. To help protect against model misspecification, care has been taken to provide methods that acknowledge and accommodate the CCAMLR precautionary paradigm. For example, a default level of count uncertainty can be introduced for originally published counts where none exists, flexibility is provided in deciding surrogate availability curves to be utilised for correcting a count at a site when no direct attendance information exists, and alternatives have been provided in how published repeatability information should be interpreted in a statistical sense. Choosing options conservatively will typically widen confidence intervals, which to some degree will protect against model misspecification. Nonetheless, users of ICESCAPE need to remain aware that the validity of estimates

Table 1: Mean, median and 95% confidence intervals (CIs) for individual and total distributions arising from application of the ICESCAPE estimation routine to surveys of three Adélie penguin colonies at three sites in the Rookery Islands group.

	Mean	Median	Lower 95% CI	Upper 95% CI
Rookery Islands 2	4783	4785	4097	5507
Rookery Islands 8	734	737	564	912
Rookery Islands 11	344	344	262	431
Total	5839	5824	5070	6551

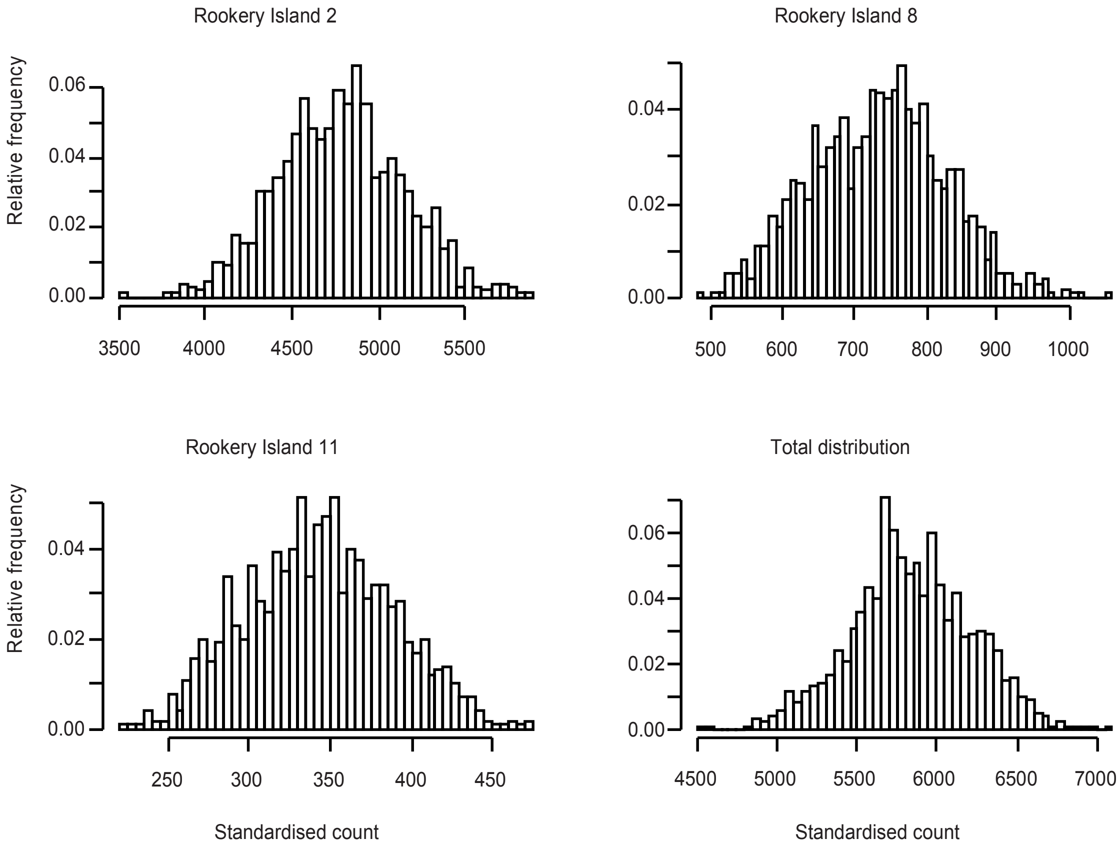

Figure 5: Distribution of standardised counts arising from application of ICESCAPE to counts of Adélie penguins taken on three separate islands in the Rookery Islands group (Division 58.4.2) on 17 November 1972, together with the aggregated distribution for all sites combined.

is predicated on the appropriateness of the underlying model linking attendance curve information to a raw count for a site.

Confidence bounds determined from considering percentiles of the bootstrap distribution of final estimates are not constrained to be symmetric about the mean, and results indicate they are sometimes not. This asymmetry is largely due to the relatively small pool of availability curves that currently exist. Included in this pool is one catastrophic breeding season that resulted in chick mortality and premature departure of adult birds. These events and their skewing effect on availability data are probably unusual and their impacts within the estimation procedure are likely to lessen as more availability data are collected.

One way to account for the extra variability introduced by inclusion of breeding failures in surrogate curve pools might be to use covariates in the process of determining which surrogate attendance curves should be used for correcting particular counts. At present, use of surrogate curves in lieu of an exact match for a site is implemented such that all possible curves presented to the estimation routines are used in the resampling procedure, irrespective of distance in time or space from the count being adjusted. An extension of this work might be to develop methods for utilising measures of spatial and temporal proximity between adjustment data and count data for selecting subsets of surrogate curves to use for purposes of adjustment. Initial investigations into such an approach indicates that, at the present time, the available pool of attendance curves is too limited in number for such subsetting to be of practicable benefit. This and other covariate-based approaches (e.g. using environmental covariates) to help allocate surrogate curves may help to improve the precision of estimates as more attendance data are collected and become available into the future.

Validation of model results is an important consideration, and two methods by which this might be accomplished are suggested here. The first approach takes advantage of the fact that many researchers do attempt to conduct counts at an optimal time for determining an effective number of breeding pairs at a colony. Using surrogate attendance curves to adjust counts that occur very near the optimal time should not appreciably alter their value, and the resulting confidence interval for the adjusted counts would be expected to include the raw count value since this was taken at a near-optimal time. Less frequently, a second count for a site may be undertaken in a season when a count at the optimal time has already occurred. In these circumstances, application of the routine for correction of the non-optimal count should also produce a distribution of adjusted counts with a median value close to that of the count taken at the optimal time. Divergence of these values may indicate bias introduced by the estimation routine, possibly due to the inclusion of atypical adjustment curves (e.g. breeding failures) in the pool of surrogate curves.

The second approach takes advantage of the fact that attendance curves themselves often comprise time series of closely spaced observations, including a count taken at the optimal time. A type of cross-validation can be performed by applying the estimation routine to all count values comprising a chosen attendance curve, using as the surrogate curve pool all available attendance curves *excluding* the time series containing the values being adjusted. Ideally, results should indicate that most precise estimates arise when adjusting count values close to the optimal time in the season. Bias should be low, providing attendance curves within the surrogate curve pool are similar in shape to the attendance curve containing the values being adjusted. This last point is critical: if the surrogate curve pool contains attendance functions appreciably different from the (usually unknown) attendance function applicable to the count being adjusted, then a distribution of adjusted counts for any given raw count value will be biased away from the true value. In practice, the nature of the true season-specific attendance function that should be used to correct a raw count for a site is never known. Instead, the distribution of attendance functions provided by the surrogate pool is relied on to be representative of the range of attendance behaviour that one might expect. The extent to which a surrogate pool of attendance curves can be contaminated by atypical curves, and the degree to which this affects adjusted estimates, is an area of continued investigation.

Estimation routines are currently structured to return estimates of adjusted population abundances from the most recent season within a specified time period for sites within the spatial subset presented to the software. This permits the possibility of developing time series of abundances by sequentially selecting and estimating for different time periods for the same spatial area. This is a perfectly legitimate use of the software, and is to be encouraged at the level of an individual site. However, care must be exercised should this approach be used for aggregations of sites, since not all sites will necessarily be surveyed in each time period. For this reason, it is unlikely that routines for automatically determining time series, except perhaps at the level of an individual site, will in future be implemented within the ICESCAPE framework.

While ICESCAPE was developed with the primary purpose of correcting and standardising count data, the facility in ICESCAPE to switch various components of the estimation process on or off and to select or invent different levels of uncertainty in the estimation components, in concert with the collection of adjustment data using the methods outlined in Southwell et al. (2010), could be used to simulate different survey design scenarios with the aim of developing optimal designs for future population surveys. For example, examination of the relative contributions of count and adjustment data to overall uncertainty in relation to different counting methods and timing of counts would help identify where improvements to future estimation could best be achieved.

Conclusions

Through use of a parametric bootstrap model, ICESCAPE provides an integrated way to standardise counts of Adélie penguins taken at any time in a breeding season to a point in the breeding chronology consistent with CEMP Standard Method A3 for estimating breeding population size. The model accommodates uncertainty in unadjusted raw counts, and sample fractions and detection fractions less than unity. Reported uncertainty associated with these quantities is preserved and propagated through to final estimates. Finally, results arising from sites where counts occurred at different points in a breeding season can be legitimately compared or aggregated to derive regional estimates of standardised abundance.

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