Polar Biol
DOI 10.1007/s00300-014-1451-8

ORIGINAL PAPER

A method for estimating colony sizes of Adélie penguins using remote sensing imagery

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Received: 2 September 2013 / Revised: 29 December 2013 / Accepted: 4 January 2014

Abstract Adélie penguins (*Pygoscelis adeliae*) are important predators of krill (*Euphausia* spp.) and Antarctic silverfish (*Pleuragramma antarctica*) during summer, are a key indicator of the status of the Southern Ocean ecosystem, and are therefore a focal species for the Committee for the Conservation of Antarctic Marine Living Resources (CCAMLR) Ecosystem Monitoring Program. The ability to monitor the population size of species potentially affected by Southern Ocean fisheries, i.e., the Adélie penguin, is critical for effective management of those resources. However, for several reasons, direct estimates of population size are not possible in many locations around Antarctica. In this study, we combine high-resolution (0.6 m) satellite imagery with spectral analysis in a supervised classification to estimate the sizes of Adélie penguin breeding colonies along Victoria Land in the Ross Sea and on the Antarctic Peninsula. Using satellite images paired with concurrent ground counts, we fit a generalized linear mixed model with Poisson errors to predict the abundance of breeding pairs as a function of the area of current-year guano staining identified in the satellite imagery. Guano-covered area proved to be an effective proxy for the number of penguins residing within. Our model provides a robust, quantitative mechanism for estimating the breeding population size of colonies captured in imagery and identifies terrain slope as a significant component influencing apparent nesting density. While our high-resolution satellite imagery technique was developed for the Adélie penguin, these principles are directly transferrable to other colonially nesting seabirds and other species that aggregate in fixed localities.

Keywords Adélie penguin · Antarctica · Generalized linear mixed models · GIS · High-resolution imagery · Population estimation · Supervised classification

Introduction

Adélie penguins (*Pygoscelis adeliae*) are distributed around the Antarctic continent, with an estimated population of approximately 2.6 million breeding pairs (Woehler 1993). Considered an indicator of ecosystem change in the Southern Ocean (Ainley 2002a, b), Adélie penguins are heavily dependent on sea ice (Fraser et al. 1992; Wilson et al. 2001; Jenouvrier et al. 2006) and are sensitive to

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changes in the abundance and distribution of krill (e.g., *Euphausia superba, E. crystallorophias*) and fish (e.g., *Pleuragramma antarctica*; Schofield et al. 2010; Sailley et al. 2013), both of which comprise the majority of their diet (summarized in Ainley 2002a). In fact, the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), the agency responsible for managing fisheries in the Southern Ocean, considers Adélie penguins to be one of the core elements of their CCAMLR Ecosystem Monitoring Program (CEMP) with respect to the krill fishery. Concern over Southern Ocean resources has been fueled partly by evidence that Adélie penguin populations are declining rapidly on islands of the northern Antarctic Peninsula, but increasing in the southern Antarctic Peninsula region (Trivelpiece et al. 2011; Lynch et al. 2012a; Sailley et al. 2013) and the Ross Sea Region (Ainley et al. 2005, 2010; Lyver et al. 2011). The rapid and spatially varying changes in Adélie penguin populations and the implications of these changes to broader ecosystem integrity make it essential to understand the underlying environmental mechanisms, thus preserving this species' value to CEMP. However, the isolation and sporadic distribution of colonies (Woehler 1993; Ainley 2002a) and financial and logistical challenges associated with Antarctic field work challenge continental-scale, or even regional surveys of Adélie penguins. Only 10–15 % of known populations are monitored with any regularity, and it is likely that some Adélie populations remain undiscovered (Woehler and Croxall 1997; Ainley 2002a, Southwell and Emmerson 2013). The inaccessibility of portions of the breeding habitat for this important indicator species has driven a surge of interest in satellite imagery as a means for detecting and monitoring Adélie populations. Because of its life history (breeds in the open, in dense concentrations, with seasonal population dynamics well understood), the Adélie penguin is a model for assessing how remote sensing imagery can be used to track the distribution and abundance of seabirds with similar characteristics.

Remote sensing of penguin populations was first demonstrated with Landsat in the 1980s when it was discovered that guano at Adélie penguin colonies could be differentiated from the surrounding landscape (primarily in the visible range) and that there was a relationship between the number of pixels identified as guano and the number of breeding pairs of Adélie penguins on Ross Island, Antarctica (Schwaller et al. 1984, 1989). Since that time, many studies have used various remote sensing platforms (e.g., Landsat, SPOT, aerial photographs, QuickBird-2) to detect the distribution and change in penguin populations (Bhikharidas et al. 1992; Chamaillé-Jammes et al. 2000; Fretwell and Trathan 2009; Naveen et al. 2012; Fretwell et al. 2012; LaRue et al. 2013; Schwaller et al. 2013). For instance, Chamaillé-Jammes et al. (2000) used georeferenced aerial photography in a GIS to address population change in king penguins (*Aptenodytes patigonicus*) over several decades, and aerial photographs have been used to determine a strong relationship between subcolony area (m^2) and number of Adélie penguin pairs in east Antarctica (Woehler and Riddle 1998). Landsat was used to identify colonies of emperor penguins (*Aptenodytes forsteri*; Fretwell and Trathan 2009), a study that was followed by the first global census of a species from space using very high-resolution (VHR) images (Fretwell et al. 2012; 0.6-m resolution, e.g., QuickBird-2 from DigitalGlobe, Inc). Researchers documented a >50 % decline in chinstrap penguin (*Pygoscelis antarctica*) numbers during a 30-year period at Baily Head on Deception Island, Antarctic Peninsula, when ground counts were combined with VHR imagery (QuickBird-2 and WorldView-1; ~0.6-m resolution; Naveen et al. 2012). Finally, VHR images were recently combined with historic aerial photographs to quantify decadal population change of Adélie penguins on Beaufort Island, Ross Sea (LaRue et al. 2013). Clearly, remotely sensed data have the capacity to inform researchers, resource managers, and conservationists about distribution and population size of penguins, but the extent to which these can supplement or even replace field counts needs to be assessed.

Remotely sensed data of medium resolution (e.g., Landsat; 15-m resolution) provide distribution and presence/absence information (Schwaller et al. 2013), whereas higher-resolution images (up to 0.2-m resolution in the case of aerial photographs; 0.6 m in VHR satellite imagery) can be used to estimate population size of remote colonies of seabirds. Landsat images are likely too coarse to track Antarctica's smallest populations, and aerial surveys in remote areas can be prohibitively expensive. Further, overflights of some penguin colonies can be precluded by poor weather, remoteness, or prohibition related to conservation. Thus, VHR satellite images present a viable alternative for estimating Adélie penguin abundance and tracking changes in occupancy (e.g., colonizations and extinctions) at a regional or continental scale. However, to date no studies have identified specific methods for applying VHR imagery at such a range of scales. Thus, a model for predicting abundance from colony "footprint" is required before we can confidently estimate global abundance and trends of Adélie penguins. Herein, we describe the first comprehensive assessment of this technique using the guano footprint and the uncertainties associated with estimating abundances from high-resolution satellite imagery.

Based on the previous literature and our experiences in Antarctica, we hypothesized that the area of current-year guano, which is a different color, having a different spectral quality than older guano, would be correlated with the number of Adélie penguin breeding pairs and could therefore be used to estimate abundance (LaRue et al. 2013). We determined a relationship between the area of current-year guano and the number of breeding pairs counted during the same season by combining VHR satellite imagery (i.e., DigitalGlobe, Inc., GeoEye) with spectral analytic techniques adapted from Fretwell et al. (2012). Using colonies within the Ross Sea and near Palmer Station, Antarctic Peninsula, as test cases because ground-truthing was available, our goal was to develop a statistical model linking guano area to the number of breeding pairs that could be used for estimation in future population surveys of Adélie penguins.

Methods

Our study included 16 Adélie penguin colonies (as per Ainley 2002a; ten from the Ross Sea and six from the Antarctic Peninsula) that ranged in size from ~100 to >250,000 breeding pairs (Fig. 1) and were surveyed one or more times between 2004 and 2011. We calculated the area of current-year guano at each colony, first using a supervised classification and subsequently a maximum likelihood classification (MLC) of four bands of VHR imagery using ArcGIS 10.1 (Esri 2011). Briefly, a supervised classification allows the user to define pixels of known "class" identity (e.g., new guano, old guano, rock, snow) as a "training" dataset. A maximum likelihood classification identifies each pixel as belonging to one of the classes in a way that makes the training dataset classifications the most likely to occur; this model linking spectral signature and class is then applied to the rest of the image and the likely class of each pixel identified accordingly. The classification procedure allowed us to calculate the guano portion of each image. Our supervised classification approach is a hybrid between the fully manual delineation approach described in Lynch et al. (2012b) and the automated methods developed in Fretwell et al. (2012). This method benefits from on-the-ground experience of the classifier.

To model current-year guano area and population size, we first needed ground-truthed estimates overlapping with imagery (both temporally and spatially). To estimate the number of breeding pairs at Adélie penguin colonies along Victoria Land in the Ross Sea, we counted individual nesting territories from ground counts and aerial photographs taken approximately 800 m above ground level. We defined "nesting territories" as sites occupied and defended by adults during the egg-laying and early incubation periods (Taylor and Wilson 1990). We used photographs that were taken each year as close as possible to 1 December, a date on which colonies are represented almost entirely by one member of each penguin pair, incubating its eggs, with few nonbreeders present (Ainley 2002a). On islets adjacent to Anvers Island, Antarctic Peninsula, data for number of breeding pairs were gathered by ground counts during the breeding season in accordance with internationally recognized census protocols (CCAMLR 2004). These data are a public resource provided by the Palmer Long-Term Ecological Research database (http://pal.lternet.edu/data/).

We orthorectified (i.e., correct imagery for terrain and internal satellite platform errors) VHR images for Adélie colonies with the RAMP DEM (Liu et al. 2001) during seasons where ground counts and images overlapped and further converted images into an equal-area projection to ensure accuracy of area calculations. We then calculated reflectance on each image and loaded images into ArcGIS 10.1 (Esri 2011). On each image, we identified a colony by visually searching for the guano stain, which typically appears as a bright pink or light gray stain on the rocky or sandy terrain (Fig. 2; see also Lynch et al. 2012b; LaRue et al. 2013). Using the Spatial Analyst toolbox, we then extracted the part of the image with only the guano stain and pansharpened (creating a higher-resolution multispectral image based on the resolution of the associated panchromatic image) that image subset. We then classified a set of pixels based on the presence of different items on the landscape (e.g., new guano, old guano, rock, snow) and calculated the MLC. We checked the classified raster for errors of misspecification, and, if necessary, a second training dataset was developed to correct for errors in the first round of classification. Because raster datasets inherently contained area information (each pixel was 0.36 m^2), we were able to translate the area classified as "current-year guano" into an area (m^2) used by penguins each year.

Nesting densities of Adélie penguins within subcolonies do not vary substantially (Penney 1968; Volkman and Trivelpiece 1981; Woehler and Riddle 1998), at least in part because close nesting is a defense against skua (*Stercorarius* spp.) predation (Young 1994). Nests are little more than pecking distance apart, but internest distances can be greater where there are large rocks or terrain is steep, which also limit skua access. Because of this, we considered models including slope (which ranged from 0° to 14.65°) and aspect, which are both micro-topographic factors that may influence colony density. We used a 30-m digital elevation model (DEM) of Ross and Beaufort islands (Csatho et al. 2008), Ross Sea, and the RAMP DEM (Liu et al. 2001; 200-m resolution) for Peninsula colonies, to calculate slope and aspect, which were reported in degrees and prominent direction, respectively.

We also assessed the accuracy of our supervised classification: both the relationship between new guano and

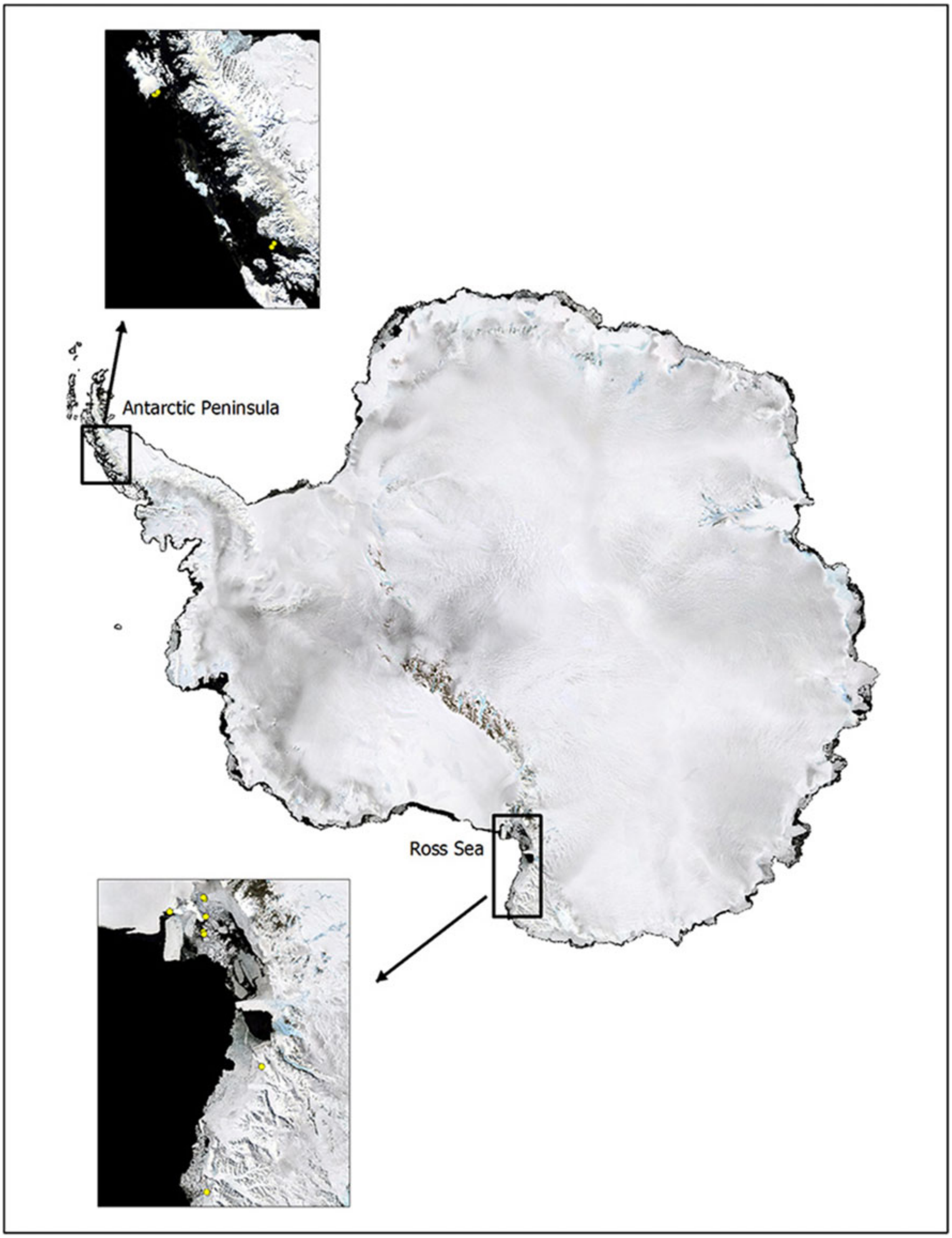

Fig. 1 Study areas and colony locations (dots on inset maps) in the Ross Sea and the Antarctic Peninsula for testing the relationship between guano area (m^2) and population size (number of breeding pairs) of Adélie penguins in Antarctica

population size, and also how our methods estimate area of new guano. Because true reference data (e.g., subcolony areas from GPS data or maps exactly coincident in time with satellite imagery) are almost nonexistent, we chose to assess accuracy by manually delineating areas at colonies where we had personal experience, ground photographs, and oblique air photographs to inform correct delineations on the satellite images. For our purposes, the manual

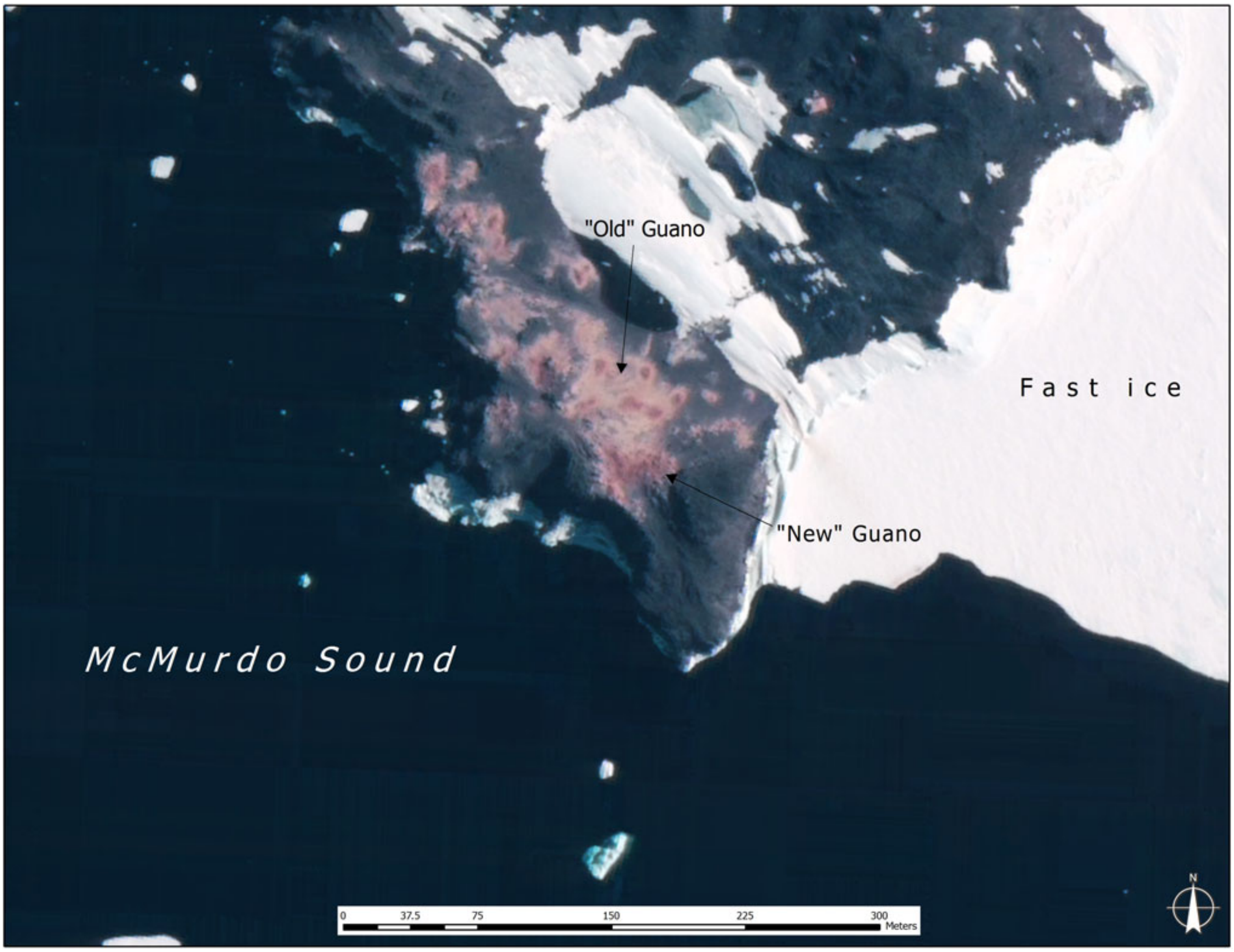

Fig. 2 VHR image, with color–infrared band combination, of Cape Royds colony on Ross Island, Antarctica. The "new" guano stain is *darker pink*, and its area is used in the supervised classification to estimate abundance, whereas the "residual" guano stain from previous years is located between the current-year guano and is *lighter in color.* Note Shackleton's historic hut, near the *top of the image*, just *right of center*. Image date is January 20, 2011; copyright DigitalGlobe, Inc. (Color figure online)

delineation at two colonies (Capes Crozier East, divided by a snow slope from West, treated separately, and Cape Royds) was therefore considered the "true" area used by penguins during that year. We then used these three areas as reference data to calculate accuracy for our supervised classification.

To determine accuracy of classification at the pixel scale, we randomly selected 800 points across images for these three colonies and extracted values from the classified rasters. Because in our classification system, we were only interested in accuracy of the current-year guano area, we further extracted points that represented pixels classified as such ($n = 330$). We then compared those points to the "true" delineations of current-year guano area and determined the percentage that fell within true boundaries.

We modeled colony abundance as a function of guano area and fit a generalized linear mixed model with Poisson errors to these data:

$$Y_i \sim \mathrm{Pois}(\lambda_i)$$

$$\log\left(\lambda_{i(j)}\right) = X\beta + \log\left(A_{i(j)}\right)$$

where X is the design matrix, β is the vector of model coefficients, and we indexed each data point by $i(j)$ to emphasize that each data point i is associated with a colony j (so multiple count/image pairs from the same colony share the same random effect for colony). We considered several fixed and random effects for $X\beta$ and used prediction bias and the width of the prediction intervals as metrics for the comparison of models with different sets of covariates.

We assessed the performance of our models by comparing the distribution of their predictions against the data. Model errors were significantly overdispersed. Therefore, to capture this overdispersion in our abundance predictions, we estimated the overdispersion factor for each model and drew predicted abundance from an overdispersed Poisson distribution (Gelman and Hill 2007). Following the procedure outlined in Gelman and Hill (2007), we assessed each model according to the precision and bias of its predictions for abundance under two scenarios. In the first, we dropped all the observations for a colony from the dataset, fit the model, and then predicted the abundance for the dropped observations. This represented the ability of our model to predict abundance for a new observation in a "new" colony, one for which a random effect had not previously been estimated. In the second approach, we used all the data in fitting the model and then predicted the abundance for an area that was represented in the dataset used for model estimation. This was analogous to using the model to predict abundance for a new observation for a "known" colony (for which the random colony effect had been estimated).

Results

The best model, scoring highest in three out of four categories (mean precision and bias assuming "known" and "new" colonies), included slope as a fixed effect and colony as a random effect. The random effect by colony permits narrower prediction intervals for "known" colonies (those with other counts, or with a priori information on apparent nesting density) since all counts from the same colony are used in the estimation of apparent nesting density. Modeled numbers of breeding pairs were highly correlated with current-year guano area (Fig. 3), and the resulting mean density of Adélie penguin nests was 0.67 [95th percentile CI (0.58, 0.77)] breeding pairs/m^2 (Table 1). Note that this represents an "apparent" density, because the area of current-year guano identified in the imagery may be slightly more or less than the actual area occupied by nests.

We found that 84 % ($n = 278$; range 81–89 %) of points classified as current-year guano fell within the true boundaries from manual delineations. The most common class for errors of commission, where points classified as current-year guano were actually a different class, was the "residual guano" class (remnant guano from previous years; Fig. 2). Despite strong correlations between guano area and Adélie penguin abundance, residual variability in nesting density produced relatively wide prediction intervals (Fig. 3).

Discussion

Adélie penguins are a critical indicator species for the Southern Ocean, and understanding status, distribution, and population trends is important to understand underlying factors affecting change given that direction of change varies by region (Ainley et al. 2005, 2010; Lynch et al. 2012a). With >200 colonies of varying sizes spread around the continent (Woehler 1993; Ainley 2002a), the promise of reliably tracking trends in abundance represents a significant advance toward understanding Southern Ocean ecosystems. Within the past decade, >25 new nesting locations have been discovered in east Antarctica and the Amundsen Sea, two little-visited regions (Low et al. 2007; Wilson et al. 2009; Southwell and Emmerson 2013; Schwaller et al. 2013). More broadly, our results offer the possibility of understanding metapopulation dynamics; Adélies are one of the few seabird species for which the interconnected demographics of clusters of one major cluster of breeding populations have been investigated (Ainley et al. 1995, 2002a; LaRue et al. 2013). Finally, understanding the drivers of the dramatic changes in colony size reported for the Ross Sea region (Lyver et al.

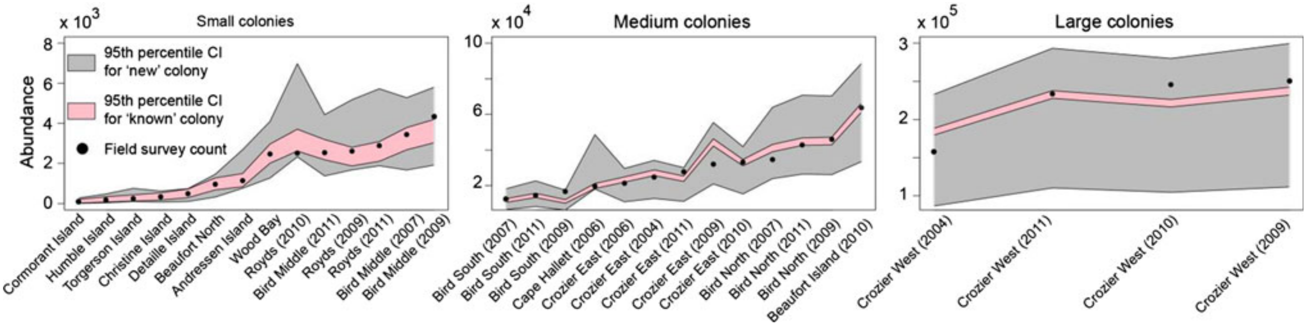

Fig. 3 Prediction intervals for estimates of abundance from guano area assuming each area is either from a "known" colony (using all data in model fit) or from a "new" colony (in which all counts for that location were removed prior to model fit). Colonies are arranged in increasing size based on field survey counts; note the different *y-axis scales* used for the *three panels* (*left* small colonies, *middle* medium colonies, *right* large colonies)

Table 1 Colony, date of image analyzed (date-month-year), calculated area of current-season guano stain, number of breeding pairs (BP) counted during aerial and ground surveys, and predicted abundance assuming a new observation at a known colony (see text) at Adélie penguin colonies in Antarctica

Colony	Image date	Area (m^2)	BP	Abundance estimated from imagery (95th percentile prediction interval)
Cormorant 2007	16-Jan-08	125.5	94	85 (22, 204)
Humble 2007	16-Jan-08	299.0	178	171 (71, 334)
Torgerson 2007	16-Jan-08	528.8	246	244 (121, 430)
Christine 2007	16-Jan-08	430.4	329	319 (172, 530)
Detaille 2009	16-Jan-08	278.0	486	474 (291, 721)
Beaufort North 2010	12-Dec-10	1,134.1	957	948 (676, 1,275)
Andressen 2009	16-Jan-08	1,366.0	1,139	1,133 (834, 1,496)
Wood Bay 2006	16-Dec-06	3,485.4	2,468	2,453 (2,006, 2,967)
Royds 2010	20-Jan-11	6,320.9	2,513	3,122 (2,615, 3,708)
Bird Middle 2011	8-Feb-12	3,716.4	2,534	2,655 (2,180, 3,191)
Royds 2009	13-Jan-10	4,662.6	2,609	2,302 (1,873, 2,806)
Royds 2011	30-Dec-11	5,200.1	2,887	2,567 (2,105, 3,090)
Bird Middle 2007	15-Dec-07	4,478.8	3,443	3,208 (2,679, 3,789)
Bird Middle 2009	16-Dec-09	5,008.6	4,333	3,581 (3,031, 4,195)
Bird South 2007	15-Dec-07	16,604.8	12,516	11,606 (10,598, 12,710)
Bird South 2011	8-Feb-12	20,687.8	14,481	14,494 (13,347, 15,717)
Bird South 2009	16-Dec-09	15,871.9	16,716	11,115 (10,125, 12,170)
Hallett 2006	23-Nov-06	45,938.8	19,744	19,736 (18,395, 21,204)
Crozier East 2006	11-Jan-07	27,260.9	21,374	23,406 (21,958, 24,913)
Crozier East 2004	4-Dec-04	31,680.9	24,775	27,224 (25,640, 28,839)
Crozier East 2011	12-Dec-11	27,786.0	27,786	23,852 (22,369, 25,400)
Crozier East 2009	7-Dec-09	51,551.7	32,062	44,275 (42,275, 46,318)
Crozier East 2010	18-Dec-10	38,293.9	33,220	32,896 (31,160, 34,696)
Bird North 2007	15-Dec-07	55,772.6	34,636	41,089 (39,059, 43,171)
Bird North 2011	8-Feb-12	60,744.3	42,860	44,728 (42,635, 46,821)
Bird North 2009	16-Dec-09	61,201.1	46,073	45,083 (42,935, 47,244)
Beaufort 2010	12-Dec-10	83,147.8	63,760	63,746 (61,292, 66,287)
Crozier West 2004	4-Dec-04	208,289.1	157,717	184,037 (179,606, 188,514)
Crozier West 2011	12-Dec-11	263,275.6	233,585	232,607 (227,696, 237,774)
Crozier West 2010	18-Dec-10	250,418.3	245,708	221,263 (216,418, 226,266)
Crozier West 2009	7-Dec-09	268,378.0	250,453	237,020 (231,958, 242,210)

2014) and Antarctic Peninsula (Lynch et al. 2012a; Sailley et al. 2013) requires broad perspective. Given the cost and logistical difficulties in surveying penguin colonies far from research stations, the method and model we provide here is a novel way forward in both colony identification and population estimation. We argue that a concurrent, continent-wide survey for Adélie penguin colonies cannot feasibly be done any other way.

Our model has limitations worth noting, particularly for future applications. First, the supervised classification portion of our methods cannot be used to automatically detect the presence of Adélie penguins on VHR imagery. Quite importantly, the areas we used for our analysis were known to us, and we had realistic expectations of relative size, area, and density. Had results been well outside our expectations, we would have been able to identify and search for mistakes, a luxury not afforded in areas where much less is known about Adélie presence. In areas where species overlap and guano stain may be indistinguishable, multiple images combined with knowledge of species phenology may be needed to assess sympatric pygoscelids (Lynch et al. 2012b). The most likely method for automatic detection of Adélie colonies would be identifying the spectral reflectance of guano (Schwaller et al. 2013). However, data indicate that reflectance is variable within and between seasons depending on diet (P.T. Fretwell unpublished data; M.A. LaRue unpublished data). A suite of spectral "endmembers" broad enough to include this variability may also lead to increased false positives, so even automated methods may require considerable validation by biologists experienced in the area of study and also further atmospheric and radiometric corrections. A study of spectral variability was outside the scope of our study but will be required to advance this technique into a fully automated process. The most robust approach for future monitoring would be a combination of multiple sensors merged with available field data, and the development of such an approach is already underway.

Our supervised classification calculated "current-year guano" pixels accurately [84 %, which is considered acceptable for the method (Foody 2002; Horning et al. 2010)]. The most common error was between the "current-year" guano and "residual" or old guano (Fig. 2). Currently, we have little capability to consistently eliminate these errors due to differences between colonies and between years, and so our methods had to rely on observer interpretation to amend results for errors of omission and commission. Observer interpretation is an important feature of land cover mapping (Horning et al. 2010) and was quite necessary in our study. It is important to understand that any future applications using this method alone will likely require observers experienced with Adélie penguins, and with interpretation of satellite images.

We did not address the bias inherent to a temporal mismatch between the image and the ground count, as most locations had limited amounts of useable images. Because images from too early or too late within a season could bias our abundance estimates, we specifically avoided images in November when the guano signature is more indicative of the previous breeding season's guano. Some of our images, however, were taken in January, when nonbreeders have returned to colonies. It is possible that the infiltration of young birds and their guano deposition could alter the area classified as current-year guano, although we suspect this discrepancy would be minimal. Young birds typically occupy areas recently abandoned by current-year breeders, then busily provisioning crèched chicks (Ainley and Ballard pers. obs). Our experience has been that December and January images are best for guano classification.

Our model is intended to provide information about apparent density and population size of breeding pairs of Adélie penguins for a given colony. Inference about population health, diet, or movement between colonies cannot be gained from our model alone. Wind, rain, snow, and snow/ice melt all have the capability of displacing substantial amounts of guano that we rely upon for our population estimate. Because environmental conditions are changing rapidly, particularly in the Antarctic Peninsula region (Ducklow et al. 2007; Cook et al. 2005; Montes-Hugo et al. 2009; Lynch et al. 2012a), ground-truthed data will remain critical for future model calibration.

High-resolution satellite imagery has been widely used for assessing potential habitat for several animal species (Gaston 2000; Nagendra 2001; Turner et al. 2003) and has thus played an indirect role in the assessment of population size and population viability since it first became available (Kerr and Ostrovsky 2003; Buchanan et al. 2008; Gillespie et al. 2008). However, there are extremely few cases in which satellite imagery has been used to directly estimate population abundance, and with a few notable exceptions (Abileah 2002; Thaxter and Burton 2009), the use of high-resolution imagery for direct census has been limited to polar ecosystems (Barber-Meyer et al. 2007; LaRue et al. 2011, 2013; Boltunov et al. 2012; Lynch et al. 2012b; Fretwell et al. 2012; Stapleton et al. unpublished data). These tools provide a complementary, cost-effective alternative to ground or aerial surveys, which as noted above in regard to "new" colonies discovered in little-visited regions, have proved impractical. Southwell et al. (2013) briefly synthesize caveats associated with the use of high-resolution imagery, which include the timing of satellite-derived estimates relative to the breeding phenology of the species (as we note above), and the prevalence of cloudy days. Despite the persistent cloudiness associated with much of coastal Antarctica, we were able to obtain a cloud-free image for each of the focal colonies in this study. Many of our guano area–ground count comparisons were quite close temporally, and given that the amount of guano seen on images likely does not change in size through the season, we are confident that our area estimations and subsequent comparisons are biologically reasonable. However, future work to confirm this would be beneficial.

Density estimates

To accurately assess the number of birds in a given area, it is crucial to understand nesting density of the species in

Table 2 Mean densities reported for Adélie penguins

Location	Mean density	Units	Reference
Peninsula	2.13	Nests	Stonehouse (1975)
Cape Crozier	1.46	Nests	Stonehouse (1975)
Cape Royds	0.82	Breeding pairs	Taylor (1961)
Wilkes Station	0.75	Nests	Penney (1968)
Ross Sea and Peninsula	0.67	Breeding pairs	This study
Mawson Region	0.63	Breeding pairs	Woehler and Riddle (1998)
Beaufort Island	0.49	Breeding pairs	LaRue et al. (2013)

question. Average apparent nesting density was 0.67 breeding pairs/m^2, which was a number consistent with the literature on nesting densities of Adélie penguins (Table 2; Taylor 1961; Penney 1968; Trivelpiece and Volkman 1979; Woehler and Riddle 1998). A factor that may influence density, or changes in density, at Adélie penguin colonies is competition for well-draining nesting areas. Throughout most of their range, Adélie penguins compete among themselves for habitat; only on the northern Antarctic Peninsula do they interact with the other two pygoscelid species: the gentoo penguin (*Pygoscelis papua*) and the chinstrap penguin. The model we created considers only physical factors that may affect density and does not take into account species interactions in predicting population estimates. However, we recognize that competition for resources (particularly, nesting habitat), and continuous changes in abundance of these resources due to changes in precipitation patterns, wind patterns, and glacial retreat (particularly on the Antarctic Peninsula; Fraser and Patterson 1997; Bricher et al. 2008) may impact numbers and density of Adélie penguins (see also LaRue et al. 2013).

Applications

The most direct use of this model would be its application to satellite images of all colonies of Adélie penguins and other Antarctic seabirds. By assessing the VHR imagery for the entire coastline, which is available patchily from 2004 to 2013, researchers can identify every extant colony and assess its population, thus providing key information necessary for resource extraction management. Indeed, a global census of Adélie penguins using VHR satellite imagery has recently been completed (Lynch and LaRue unpublished data), and future global analyses of this type will allow us to assess population change over spatial scales much larger than has been traditionally possible. Also, a combination of our approach with phenological information could easily be applied to the other Antarctic and sub-Antarctic penguin species [e.g., chinstrap, gentoo, macaroni (*Eudyptes chrysolophus*)], as species identification is possible via satellite imagery (Lynch et al. 2012b).

Our methods can be extended to other polar systems, where remote locations of animals preclude accurate estimates of populations. Combining spectral analysis with biological or environmental information could easily be implemented, for example, on walrus (*Odobenus* spp.). In Arctic Russia, USA, and Canada, walrus haul out at predictable rookeries every summer to raise offspring and are easily identifiable from satellite images (Boltunov et al. 2012), as they congregate in large groups with measurable densities. Given their site fidelity, gathering and analyzing images of walrus haulouts over several years is feasible. Another application of our method would be Crozet shags (*Phalacrocorax melanogenis*) on Marion Island, a sub-Antarctic island off the coast of Africa. That population has decreased by >70 % over a 10-year period, a trend that was similar in the sympatric gentoo penguin population (Crawford et al. 2003), both of which are identifiable on VHR imagery (Lynch and LaRue unpublished data).

Because satellite technology is likely to continue to improve, the methods we propose here are an important step in the process of advancing remote sensing, and data fusion in general, for use in estimation of animal populations. Climate and other environmental changes are advancing across the globe, so rapid, repeatable monitoring of species abundance and distribution using remote sensing is quickly becoming an urgent need (Horning et al. 2010). Additionally, ecologists and conservation biologists should be aware that VHR images can be used for finer-scale research purposes across broad geographic distributions. Adapting or combining our methods here with statistical models, other remote sensing platforms, or ground/reference data could easily advance our knowledge of ecosystem and species dynamics in similarly remote areas.

Acknowledgments This research was funded by National Science Foundation (OPP-0217282, OPP-0823101, ANT-0739515, ANT-0944411, OPP-1109962, PLR-1255058) and New Zealand's Ministry for Business, Innovation and Employment (C09X0510, C01X0505, C01X1001, CONT-21216-BKBN). Field logistics were provided by the US Antarctic Program and Antarctica New Zealand, and helicopter support was provided by PHI, Inc., and Helicopters NZ. We thank the team of counters over the years, but in particular Peter Wilson, Bruce Thomas, Brian Karl, Keven Drew, Caroline Thomson, Morgan Coleman, Quoyah Barr-Glintborg, and Mario Fichtner. The Polar Geospatial Center facilitated use of imagery for analysis, and we thank Claire Porter for assistance with image processing. We would like to thank the editor and 3 anonymous reviewers for their feedback and insight in previous drafts of this manuscript. Point Blue Conservation Science contribution #1945.

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