The Auk
Ornithological Advances
AmericanOrnithology.org

Volume 134, 2017, pp. 39–50
DOI: 10.1642/AUK-16-125.1

COMMENTARY

Recent studies overestimate colonization and extinction events for Adelie Penguin breeding colonies

Colin Southwell,[1]* Louise Emmerson,[1] Akinori Takahashi,[2] Akiko Kato,[2a] Christophe Barbraud,[3] Karine Delord,[3] and Henri Weimerskirch[3]

[1] Australian Antarctic Division, Department of the Environment, Kingston, Tasmania, Australia
[2] National Institute of Polar Research, Tachikawa-shi, Tokyo, Japan
[3] Centre d'Etudes Biologiques de Chizé, Station d'Écologie de Chizé-La Rochelle, Villiers en Bois, France
[a] Current address: Centre d'Etudes Biologiques de Chizé, Station d'Écologie de Chizé-La Rochelle, Villiers en Bois, France
* Corresponding author: colin.southwell@aad.gov.au

Submitted June 19, 2016; Accepted July 30, 2016; Published October 26, 2016

ABSTRACT

Modeling metapopulation dynamics is potentially a useful and powerful tool for ecologists and conservation biologists. However, the key processes driving metapopulation dynamics are colonization and extinction events, which are notoriously difficult to study. A recent global assessment of Adelie Penguin (*Pygoscelis adeliae*) breeding populations reported multiple potential colonization and extinction events from occupancy observations using recent high-resolution satellite imagery and examination of historical occupancy literature, but emphasized that the events should be confirmed with direct observations. We evaluated these conclusions by developing a comprehensive database of direct observations of Adelie Penguin breeding site occupancy across East Antarctica. The database allowed 16 of 19 proposed colonization and extinction events in this region to be evaluated using direct observations that were concurrent in space and time (same breeding season) with observations from satellite imagery. We concluded that none of the 16 proposed colonization and extinction events had occurred. One true extinction event may have been correctly identified from satellite imagery, but a conclusive evaluation was not possible because the direct and satellite observations were not concurrent in time. The evaluation identified several sources of error in observations from satellite imagery, including errors of omission through failure to detect small colonies and errors of commission through misidentification of other biological and physical features as Adelie Penguin guano. The occupancy database corrected issues of poor precision and accuracy in locations of historical occupancy data. Our results improve understanding of key parameters for Adelie Penguin metapopulation dynamics and facilitate improved interpretation of satellite imagery in the future.

Keywords: Antarctica, high-resolution satellite imagery, historical data, metapopulation dynamics, occupancy

Estudios recientes sobreestiman los eventos de colonización y extinción de *Pygoscelis adeliae* en reproducción

RESUMEN

El modelamiento de la dinámica metapoblacional es una herramienta potencialmente útil para ecólogos y biólogos de la conservación. Sin embargo, los procesos clave que influyen en la dinámica poblacional (colonización y extinción) son notablemente difíciles de estudiar. Un estudio global reciente sobre las poblaciones reproductivas de *Pygoscelis adeliae* reportó múltiples eventos potenciales de colonización y extinción a partir de observaciones satelitales recientes de ocupación de alta resolución y del estudio de la literatura sobre ocupación histórica, pero hizo énfasis en que dichos eventos debían ser confirmados con observaciones directas. Evaluamos esas conclusiones con el desarrollo de una base de datos exhaustiva de las observaciones directas de la ocupación de individuos anidantes de *P. adeliae* a través del oriente de Antártica. Esta base de datos permitió evaluar 16 de los 19 eventos de colonización y extinción propuestos en esta región usando observaciones directas que coincidían en tiempo y espacio (misma temporada reproductiva) con las observaciones satelitales. Concluimos que ninguno de los 16 eventos de colonización y extinción ocurrieron. Un evento verdadero de extinción podría haber sido correctamente identificado a partir de las imágenes satelitales, pero no fue posible una evaluación concluyente debido a que las observaciones directas no eran simultáneas con las observaciones satelitales. La evaluación identificó varias fuentes de error en las observaciones satelitales, incluyendo errores de omisión por la falla en detectar colonias pequeñas y errores de comisión por la identificación errónea de características físicas y biológicas como guano de *P. adeliae*. La base de datos de ocupación corrigió los problemas de poca precisión y exactitud en las localidades con datos históricos de ocupación. Nuestros resultados mejoran el entendimiento de los parámetros clave en la dinámica de la metapoblación de *P. adeliae* y facilitan la interpretación mejorada de las imágenes de satélite en el futuro.

Palabras clave: Antártica, datos históricos, dinámicas de metapoblaciones, imágenes satelitales de alta resolución, ocupación

INTRODUCTION

Metapopulation theory and models are powerful tools in ecology and conservation (Day and Possingham 1995, Oro 2003, Schippers et al. 2009). With appropriate model structure and accurate parameter estimates, these models can be used to predict the consequences of environmental change or management actions on animal populations over large spatial scales. Colonization and extinction events and rates are key processes driving metapopulation dynamics but are extremely difficult to observe and estimate, especially for species distributed over large spatial scales or with low colonization and extinction rates (Hanski and Gilpin 1991, Harrison 1991). For such species, there is a tradeoff between making frequent observations of site occupancy over sufficiently large spatial scales and detecting changes in occupancy accurately, because colonizations and extinctions are by their nature often at the edge of the detection range.

As a colonially breeding Antarctic species with breeding habitat restricted to ice-free areas close to the ocean, Adelie Penguins (*Pygoscelis adeliae*) form a series of discrete occupied breeding patches along the Antarctic coastline. Estimates of colonization and extinction rates at these breeding sites are extremely difficult to obtain because a large proportion of potential breeding sites is difficult to access along the remote Antarctic coastline. In a recent global assessment of Adelie Penguin breeding populations, Lynch and LaRue (2014) approached this problem by using satellite imagery to make contemporary occupancy observations at potential breeding sites, and examined the literature for historical occupancy observations to infer possible colonization and extinction events in recent decades. They reported 11 Adelie Penguin colonizations and up to 13 colony extinctions around Antarctica in recent decades. In further satellite developmental work, Lynch and Schwaller (2014) noted that another 5 unreported colonies were possible recent colonizations. These results suggest that Adelie Penguins may have a greater capacity to colonize unoccupied sites over ecological time scales, and hence may be less philopatric, than previously thought. Lynch and LaRue (2014) acknowledged, however, that their conclusions on colonization and extinction events required confirmation from field surveys. This is important because biased estimates of key parameters such as colonization and extinction rates can reduce the accuracy of metapopulation model predictions (Hanski and Gilpin 1991), particularly for species such as seabirds in which colonization and extinction events occur infrequently.

In this commentary, we provide a field evaluation of 16 of 19 potential Adelie Penguin colonization and extinction events in East Antarctica reported by Lynch and LaRue (2014) and Lynch and Schwaller (2014) by comparing their results with direct occupancy observations from field studies in East Antarctica, and discuss potential implications from this evaluation. We also develop and make publicly available a breeding site, occupancy, and bibliographic database based on direct observations to provide a foundation for eliminating uncertainty over site locations and historical occupancy. We recommend that these databases form the basis of future assessments of Adelie Penguin colonization and extinction events in East Antarctica, and note that similar efforts for other regions and species would be valuable.

METHODS

In the classic metapopulation paradigm, a metapopulation comprises spatially discrete subpopulations separated by a continuum of unsuitable habitat and connected by interpatch dispersal (Hanski and Gilpin 1991). For colonial breeders, habitat patches or colonies exist only during the breeding season and habitat unsuitable for breeding, such as the ocean in this case, may be used for nonbreeding activities such as foraging (Matthiopoulos et al. 2005). In the context of our evaluation, potential breeding habitat was considered occupied if breeders were present during the breeding season, colonization refers to a potential breeding site that was unoccupied in a previous breeding season but that became occupied by breeders in a subsequent season, and an extinction occurred if a breeding site that was occupied in a previous season was not occupied by breeders in a subsequent season (Taylor and Hall 2012).

To undertake the evaluation, we compiled contemporary and historical direct field observations of Adelie Penguin breeding site occupancy across East Antarctica into a comprehensive database, and compared these field observations with the most recent compilation of occupancy observations and conclusions by Lynch and LaRue (2014) and Lynch and Schwaller (2014). The field observations presented here were obtained from published and unpublished data collected by the Australian, Japanese, and French Antarctic research programs and during private expeditions.

The occupancy database contains linked tables of (1) all geographic sites in the region defined as potential Adelie Penguin breeding habitat, (2) observations of occupancy (presence or absence) by breeding Adelie Penguins at

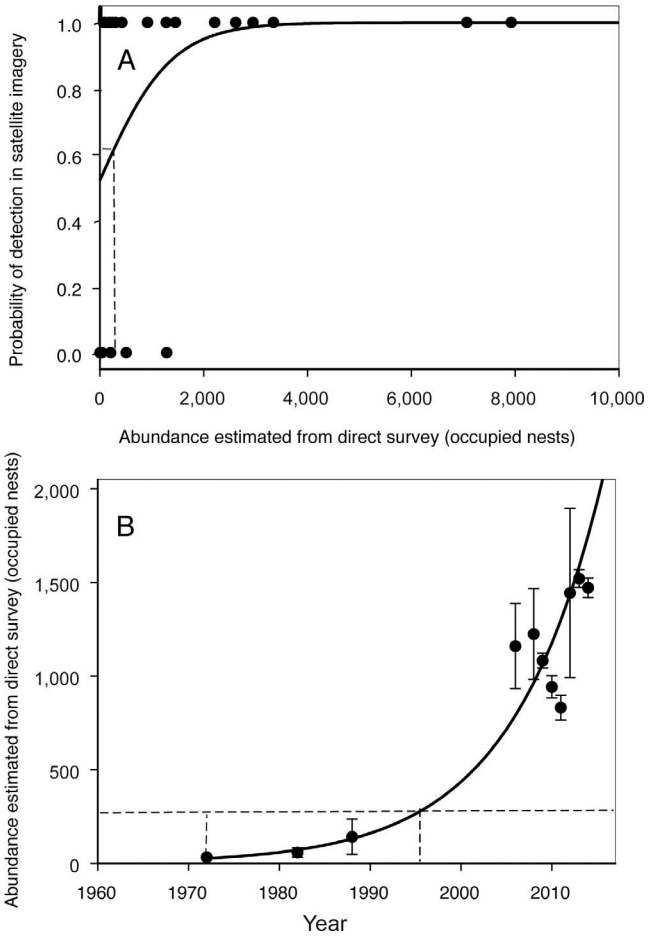

FIGURE 1. Detectability and false negative conclusions of breeding Adelie Penguin occupancy from high-resolution satellite imagery. (**A**) Logistic regression of occupancy estimated from observations from satellite imagery against breeding abundance estimated from direct surveys. The dashed lines indicate that a colony needs to be ≥250 occupied nests in size to be detected from high-resolution satellite imagery with >60% probability. (**B**) Growth in a small Adelie Penguin colony on the Mac. Robertson Land Coast, East Antarctica. The dashed lines indicate that this initially small colony, undergoing a long-term population increase, could take >20 yr to reach a size of 250 occupied nests, when the probability of being detected from high-resolution satellite imagery will be >60%.

those sites, and (3) additional information on the sites where breeding has been observed. The table of potential breeding sites was based on the sites identified by Southwell et al. (2009) between longitudes 45°E and 136°E and 142°E and 160°E (the Australian Antarctic Territory), with the coverage extended to 37°E–160°E for this work (Southwell et al. 2016a). This table has an accompanying set of maps. Each geographic site in the table and on a map has a unique identifying label for accurate and consistent identification and location of occupancy observations. The table also includes the names of sites in the SCAR Composite Gazetteer (Scientific Committee on Antarctic Research; https://data.aad.gov.au/aadc/gaz/scar/). The occupancy table includes known observations of presence and absence by geographic site and split-year breeding season (Southwell et al. 2016b). The table of actual breeding sites includes all names used for those sites in the literature, the exact location of colonies at the site, and comments to aid correct interpretation or identification of the breeding site. We considered a breeding site to be a geographic feature (island or outcrop of continental rock) that has been observed to be occupied by live breeding Adelie Penguins. Multiple breeding sites can occur in the same geographic site if separated by a distance of >1 km. Long-extinct breeding sites (old guano only, no signs of recent occupation) are not included in the breeding site table.

RESULTS

The database provided evidence to evaluate 6 of the 8 extinction events reported from observations made from satellite imagery by Lynch and LaRue (2014) in East Antarctica. We conclude from the field evidence that none of these 6 extinction events occurred (see details in Appendix Table 1). In all 6 cases, field and satellite observations were made in the same breeding season, but colonies observed on the ground were not detected in satellite imagery. We could not conclusively assess a proposed extinction at the Kuzira Point breeding site because there was no concurrent direct observation, but the most recent direct observation in 1994 (16 years previous to satellite imagery) found no breeding penguins, so this was a true past extinction event for this population. This would constitute a correctly detected extinction event if the breeding site had not been recolonized by the time that the satellite images were taken.

Most of the colonies that were not detected in satellite imagery were relatively small. The largest undetected colony (Rumpa; ~2,000 occupied nests) may have been obscured from satellite detection by heavy snowfall shortly before the satellite image was obtained. Figure 1A shows the fit of a logistic regression of occupancy observations from satellite imagery against breeding abundance estimated from direct surveys in the same breeding season. The regression predicts a decreasing chance of colonies being detected via satellite as colony size decreases below 2,000 occupied nests, with colonies of <250 occupied nests having <60% chance of being detected. One consequence of size-related detection bias is that there may be a substantial delay between the time when a new colony is established and when it is large enough to detect. Figure 1B shows the growth of an initially small Adelie Penguin colony in Mac. Robertson Land, East Antarctica, across 4 decades. Given the detection probabilities predicted by the logistic regression in Figure 1A, the

colony could have taken >20 yr to reach a size where the probability of being detected with high-resolution satellite imagery was >60%.

We were able to evaluate 10 of the 11 potential colonization events and similarly concluded that none of these 10 events had occurred (Appendix Table 1). The supporting evidence for our conclusions includes (a) satellite detection of guano associated with other seabird species (3 cases), (b) satellite detection of a physical feature mistaken for guano (1 case), (c) incomplete searching of the historical literature (5 cases), and (d) mistaken or erroneous location of occupied sites (1 case). These cases involved both false positive and false negative occupancy observations.

DISCUSSION

Our evaluation highlights a number of difficulties and challenges for correctly identifying colonization and extinction events. One of the main difficulties in accurately documenting extinction events is that the populations which are most prone to extinction (small populations which are disproportionately affected by genetic and demographic stochasticity; Caughley 1994) are the same populations that have the least certainty of being detected because of their small size. For similar reasons, it can be difficult to accurately document seabird colonization events and their timing (but see Oro and Ruxton (2001) and Kildaw et al. (2005) for circumstances where this was possible) because colonization events typically involve just a few individuals initially, and there may be a delay in detecting new colonies until they have grown to a critical size. Size bias, or incomplete detection of small objects, is one aspect of detectability that has long been recognized in wildlife abundance estimation theory (Drummer and McDonald 1987) and is most pertinent to the detection of colonization and extinction events, which by their nature occur at the edge of the size and hence detection range.

A recent renaissance in using satellite imagery as an observation tool for estimating penguin populations has focused attention on incomplete detection (or errors of omission) of penguin colonies in Landsat imagery in relation to colony size (Schwaller et al. 2013, Lynch and Schwaller 2014). Our evaluation extends this focus to errors of omission in high-resolution imagery and finds that extinction events were overestimated. In addition to colony size, other possible explanations for incomplete detection in satellite imagery include fragmentation of colonies into small, scattered subcolonies or individuals, the timing of image acquisition within the breeding season, presence of snow or shadow, and image quality. Further comparison of observations from satellite imagery and direct observations will help to elucidate these issues. If detection bias cannot be eliminated through improved resolution and interpretation of satellite imagery, it may be possible to employ methods that use repeated observations to account for detection bias when estimating colonization and extinction rates (Barbraud et al. 2003, MacKenzie et al. 2003) from occupancy observations from satellite imagery.

In addition to the false negative observations discussed above, our evaluation also shows some circumstances in which false positive observations (or errors of commission) can confound occupancy observations from satellite images. As penguins are too small to see and count individually in currently available satellite imagery, they are currently detected indirectly from guano stains on the ground or ice (Fretwell and Trathan 2009, LaRue et al. 2014), leading to the chance of erroneously detecting guano from other species as shown here. Although Emperor Penguins (*Aptenodytes forsteri*) breed on ice almost exclusively, they are known to breed on land at 2 locations around Antarctica, and direct observations of ice-breeding populations at Amanda Bay and Dumont d'Urville show that they also spend time on nearby land during the breeding season, and that this guano can be detected in satellite imagery (Figure 2A). Guano from land-breeding flying seabirds also can be mistaken for Adelie Penguin guano (Figure 2B, Appendix Table 1), and guano deposited by molting penguins (Figure 2C) could confound identification of breeding sites in satellite images. Lynch and Schwaller (2014) have also found abiotically driven false positive errors from geological features such as wet alluvial fans, sediment runoff, and iron-tinting in rock (Figure 4D). False positive occupancy observations can lead to an overestimation of colonization rates, which can in turn lead to overinflation of metapopulation persistence, which can be particularly serious for isolated patches (Moilanen 2002). New methods and strategies for distinguishing between species, and between breeding and molting sites, will be important if guano-based satellite methods are to be used to accurately identify colonization events in the future.

Correctly identifying colonization and extinction events requires accurate recording and interpretation of historical as well as contemporary occupancy data. Lynch and LaRue (2014) noted that discrepancies in names and locations in the historical record made the identification of true colonization and extinction events challenging. Their nondetection of some important references in the dispersed historical literature also emphasizes the difficulty of correctly finding and interpreting historical occupancy data. We have tried to address these issues, as well as capturing the collective direct and long-term experience of researchers from multiple national Antarctic research programs operating in the East Antarctic region, when collating and clarifying the Adelie Penguin occupancy data used in this evaluation.

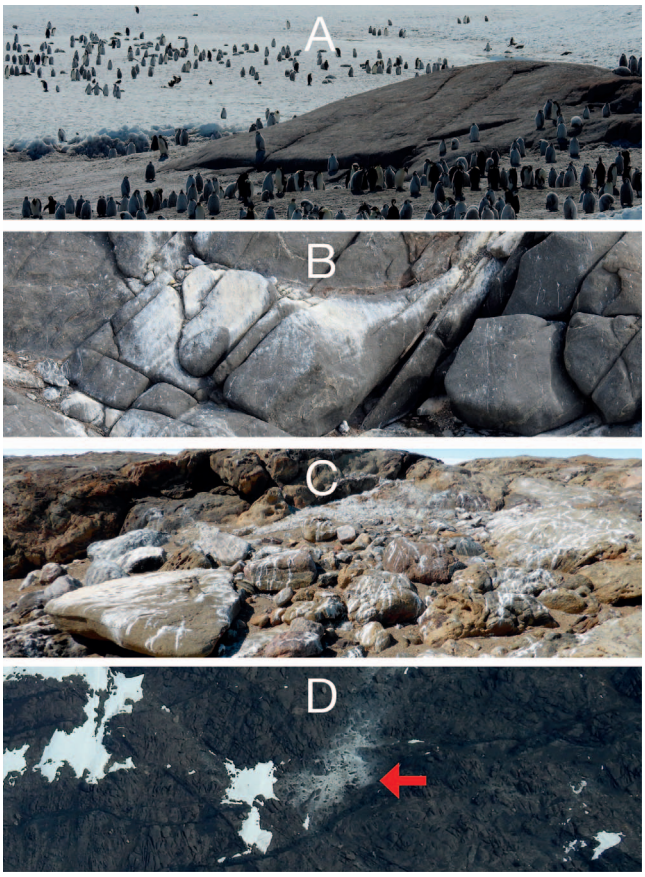

FIGURE 2. Some features that could lead to false positive observations of breeding Adelie Penguin occupancy from satellite imagery: (**A**) ice-breeding Emperor Penguins (background) occupying land (foreground) at Amanda Bay, East Antarctica; (**B**) flying seabird guano at Ardery Island, East Antarctica; (**C**) an Adelie Penguin molting site; and (**D**) a physical feature (shown by arrow) on Barrier Island, East Antarctica.

Modeling studies have shown that site fidelity has important consequences for the metapopulation dynamics of colonially breeding species (Matthiopoulus et al. 2005). Although genetic and ecological studies indicate that Adelie Penguins can disperse over large spatial scales within geological timeframes (Millar et al. 2012) and that environmental perturbations can induce local movement among colonies in the short term (Dugger et al. 2010, LaRue et al. 2013), most studies show that Adelie Penguins have strong natal site return, and the species is generally considered to be highly philopatric. The conclusion of multiple colonizations and extinctions by Lynch and LaRue (2014) could suggest that the Adelie Penguin has a greater capacity to colonize unoccupied sites over ecological timescales and hence is less philopatric than previously thought, but in this case these colonization and extinction events were unsubstantiated by direct evaluation. Nevertheless, the frequency and circumstances of colonization and extinction events are important phenomena for metapopulation studies. Although direct observations also can be subject to incomplete detection, they are currently the most reliable source of occupancy information. The direct observations of Adelie Penguin colonizations and absence of extinctions in East Antarctica in the context of increasing populations (Southwell and Emmerson 2013, Southwell et al. 2015) has provided insight into the processes driving these events. However, it will be challenging to continue the broadscale direct observations on which this work was based into the future with regular or high frequency. Here we concur with Lynch and LaRue (2014) on the potential offered by high-resolution satellite imagery for efficient occupancy observation in the future if the technology is able to address the issues raised in this commentary. By highlighting some of these issues here, our intention is to provide the most accurate record of colonization and extinction events to this time, and to direct further evaluation of satellite technology into areas that will maximize the accuracy of satellite occupancy observations in the future. Given that perfect knowledge of colonization and extinction events is unlikely from either direct or indirect methods, it could also be instructive to examine the sensitivity of metapopulation model predictions to errors of varying magnitude in estimates of colonization and extinction rates.

ACKNOWLEDGMENTS

We thank Heather Lynch, Michelle LaRue, and Matt Schwaller for welcoming our direct observations and enthusiastically discussing their satellite observations with us for the long-term goal of improved satellite imagery interpretation.
Funding statement: This work was supported by the Australian Antarctic Program (recently under AAS projects 2722, 4087, and 4088), the Japanese Antarctic Research Expeditions (recently under programs AMB1 and AP12), and the Institut Paul Emile Victor (IPEV program 109), Zone Atelier Antarctique (CNRS-INEE), and Terres Australes et Antarctiques Françaises. None of the supporters had any influence on the content of the submitted or published manuscript nor required approval of the final manuscript to be published.
Ethics statement: All work was conducted in accordance with permits issued by the Australian Antarctic Ethics Committee, the Committee on Bioscience Program at the National Institute of Polar Research for Japanese Antarctic Research Expeditions, and Terres Australes et Antarctiques Françaises authorities under the Institut Paul Emile Victor, Zone Atelier de Recherches sur l'Environnement Antarctique et Subantarctique (CNRS-INEE), and Terres Australes et Antarctiques Françaises.
Author contributions: C.S. and L.E. conceived the idea; C.S., L.E., A.T., A.K., C.B., K.D., and H.W. performed experiments; C.S., L.E., A.T., A.K., C.B., K.D., and H.W. wrote the paper;

C.S., L.E., A.T., A.K., C.B., K.D., and H.W. designed methods; and C.S. analyzed the data.

LITERATURE CITED

Barbraud, C., and S. C. Baker (1998). Fulmarine petrels and South Polar Skua *Catharacta maccormicki* populations on Ardery Island, Windmill Islands, Antarctica. Emu 98:234–236.

Barbraud, C., K. C. Delord, T. Micol, and P. Jouventin (1999). First census of breeding seabirds between Cap Bienvenue (Terre Adelie) and Moyes Islands (King George V Land), Antarctica: New records for Antarctic seabird populations. Polar Biology 21:146–150.

Barbraud, C., J. D. Nichols, J. E. Hines, and H. Hafner (2003). Estimating rates of local extinction and colonization in colonial species and an extension to the metapopulation and community levels. Oikos 101:113–126.

Caughley, G. (1994). Directions in conservation biology. Journal of Animal Ecology 63:215–244.

Day, J. R., and H. P. Possingham (1995). A stochastic metapopulation model with variability in patch size and position. Theoretical Population Biology 48:333–360.

Drummer, T. D., and L. L. McDonald (1987). Size bias in line transect sampling. Biometrics 43:13–21.

Dugger, K. M., D. G. Ainley, P. O'B. Lyver, K. Barton, and G. Ballard (2010). Survival differences and the effect of environmental instability on breeding dispersal in an Adélie Penguin metapopulation. Proceedings of the National Academy of Sciences USA 107:12375–12380.

Fretwell, P. T., and P. N. Trathan (2009). Penguins from space: Faecal stains reveal the location of Emperor Penguin colonies. Global Ecology and Biogeography 18:543–552.

Hanski, I., and M. Gilpin (1991). Metapopulation dynamics: Brief history and conceptual domain. Biological Journal of the Linnean Society 42:3–16.

Harrison, S. (1991). Local extinction in a metapopulation context: An empirical evaluation. Biological Journal of the Linnean Society 42:73–88.

Hoshiai, T., T. Sweda, and A. Tanimura (1984). Adélie Penguin census in the 1981–82 and 1982–83 breeding seasons near Syowa station, Antarctica. Memoirs of the National Institute of Polar Research 32:117–121.

Kato, A., K. Watanabe, and Y. Naito (2004). Population changes of Adélie and Emperor penguins along the Prince Olav coast and on the Riiser-Larsen Peninsula. Polar Bioscience 17:117–122.

Kildaw, S. D., D. B. Irons, D. R. Nysewander, and C. L. Buck (2005). Formation and growth of new seabird colonies: The significance of habitat quality. Marine Ornithology 33:49–58.

LaRue, M. A., D. G. Ainley, M. Swanson, K. M. Dugger, P. O'B. Lyver, K. Barton, and G. Ballard (2013). Climate change winners: Receding ice fields facilitate colony expansion and altered dynamics in an Adélie Penguin metapopulation. PLOS One 8:e60568. doi:10.1371/journal.pone.0060568

LaRue, M. A., H. J. Lynch, P. O. B. Lyver, K. Barton, D. G. Ainley, A. Pollard, W. R. Fraser, and G. Ballard (2014). A method for estimating colony sizes of Adélie Penguins using remote sensing imagery. Polar Biology 37:507–517.

Lewis, D., and M. George (Editors) (1984). The initial scientific reports of the Mawson Anniversary and Frozen Sea expeditions. Oceanic Research Foundation, Windsor, NSW, Australia.

Lynch, H. J., and M. A. LaRue (2014). First global census of the Adélie Penguin. The Auk: Ornithological Advances 131:457–466.

Lynch, H. J., and M. R. Schwaller (2014). Mapping the abundance and distribution of Adélie Penguins using Landsat-7: First steps towards an integrated multi-sensor pipeline for tracking populations at the continental scale. PLOS One 9: e113301. doi:10.1371/journal.pone.0113301

MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin (2003). Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology 84:2200–2207.

Matthiopoulos, J., J. Harwood, and L. Thomas (2005). Metapopulation consequences of site fidelity for colonially breeding mammals and birds. Journal of Animal Ecology 74:716–727.

Millar, C. D., S. Subramanian, T. H. Heupink, S. Swaminathan, C. Baroni, and D. M. Lambert (2012). Adélie Penguins and temperature changes in Antarctica: A long-term view. Integrative Zoology 7:113–120.

Moilanen, A. (2002). Implications of empirical data quality to metapopulation model parameter estimation and application. Oikos 96:516–530.

Oro, D. (2003). Managing seabird metapopulations in the Mediterranean: Constraints and challenges. Scientia Marina 67 (Suppl. 2):13–22.

Oro, D., and G. D. Ruxton (2001). The formation and growth of seabird colonies: Audouin's Gull as a case study. Journal of Animal Ecology 70:527–535.

Orton, M. N. (1963). A brief survey of the fauna of the Windmill Islands, Wilkes Land, Antarctica. Emu 63:15–22.

Robertson, G., B. Wienecke, L. Emmerson, and A. D. Fraser (2014). Long-term trends in the population size and breeding success of Emperor Penguins at the Taylor Glacier colony, Antarctica. Polar Biology 37:251–259.

Schippers, P., R. P. H. Snep, A. G. M. Schotman, R. Jochem, E. W. M. Stienen, and P. A. Slim (2009). Seabird metapopulations: Searching for alternative breeding habitats. Population Ecology 51:459–470.

Schwaller, M. R., C. J. Southwell, and L. M. Emmerson (2013). Continental-scale mapping of Adélie Penguin colonies from Landsat imagery. Remote Sensing of Environment 139:353–364.

Secretariat of the Antarctic Treaty (2014). Management Plan for Antarctic Specially Protected Area No. 169 (Amanda Bay, Ingrid Christensen Coast, Princess Elizabeth Land, East Antarctica). In Final Report of the Thirty-seventh Antarctic Treaty Consultative Meeting and Seventeenth Committee on Environmental Protection Meeting, Brasilia, Brazil, 28 April 2014–7 May 2014. http://www.ats.aq/documents/recatt/Att550_e.pdf

Secretariat of the Antarctic Treaty (2015). Management Plan for Antarctic Specially Protected Area No 101 (Taylor Rookery, Mac.Robertson Land). In Final Report of the Thirty-eighth Antarctic Treaty Consultative Meeting and Eighteenth Committee on Environmental Protection Meeting, Sofia, Bulgaria, 1 June 2015–10 June 2015. www.ats.aq/documents/recatt/att439_e.pdf

Southwell, C., and L. Emmerson (2013). Large-scale occupancy surveys in East Antarctica discover new Adélie Penguin

breeding sites and reveal an expanding breeding distribution. Antarctic Science 25:531–535.

Southwell, C., L. Emmerson, J. McKinlay, K. Newbery, A. Takahashi, A. Kato, C. Barbraud, K. DeLord, and H. Weimerskirch (2015). Spatially extensive standardized surveys reveal widespread, multi-decadal increase in East Antarctic Adélie Penguin populations. PLOS One 10:e0139877. doi:10.1371/journal.pone.0139877

Southwell, C., L. Emmerson, D. T. Smith, and A. Bender (2016a). Sites of potential habitat for breeding Adelie Penguins in East Antarctica. Australian Antarctic Data Centre. doi:10.4225/15/5758F4EC91665

Southwell, C., L. Emmerson, A. Takahashi, A. Kato, C. Barbraud, K. Delord, and H. Weimerskirch (2016b). Site occupancy by breeding Adelie Penguins in East Antarctica. Australian Antarctic Data Centre. doi:10.4225/15/57590498D301C

Southwell, C., J. McKinlay, M. Low, D. Wilson, K. Newbery, J. L. Lieser, and L. Emmerson (2013). New methods and technologies for regional-scale abundance estimation of land-breeding marine animals: Application to Adélie Penguin populations in East Antarctica. Polar Biology 36:843–856.

Southwell, C., D. Smith, and A. Bender (2009). Incomplete search effort: A potential source of bias in estimates of Adélie Penguin breeding populations in the Australian Antarctic Territory. Polar Record 45:375–380.

Takahashi, A., K. Sato, J. Nishikawa, M. Kouno, and Y. Naito (2000). Distribution and size of Adelie Penguin colonies in Amundsen Bay, Enderby Land, Antarctica. Antarctic Record 44:38–41.

Taylor, C. M., and R. J. Hall (2012). Metapopulation models for seasonally migratory animals. Biology Letters 8:477–480.

Van Franeker, J. A., P. J. Bell, and T. L. Montague (1990). Birds of Ardery and Odbert Islands, Windmill Islands, Antarctica. Emu 90:74–80.

Whitehead, M. D., and G. W. Johnstone (1990). The distribution and estimated abundance of Adelie Penguins breeding in Prydz Bay, Antarctica. Polar Biology 3:91–98.

Wienecke, B., and P. Pedersen (2009). Population estimates of Emperor Penguins at Amanda Bay, Ingrid Christensen Coast, Antarctica. Polar Record 45:207–214.

APPENDIX TABLE 1. Comparisons of observations from satellite imagery and direct observations of Adelie Penguin breeding colonization and extinction events in East Antarctica.

Name and location of site given in [a, e]	Satellite observations		Direct observations	
	Conclusion	Commentary	Conclusion	Commentary
Kuzira Point (69.6000°S, 38.2667°E)	Extinct [a]	Cannot find colony in DigitalGlobe (Westminster, Colorado, USA) satellite imagery obtained on February 11, 2010 [a]	Unable to assess, but may have been unoccupied at the time of satellite observation	The Kuzira Point breeding population is located at 69.6110°S, 39.6000°E in site IS_251 [b,c]. No direct observations are available after the 1994–1995 breeding season. No breeding birds were present during the last direct observation on November 12, 1994.
Benten (69.0417°S, 39.2500°E)	Extinct [a]	No sign of Adelie Penguin colony in DigitalGlobe satellite imagery obtained on December 22, 2008 [a]	Occupied [c]	The Benten breeding population is located at 69.0398°S, 39.2451°E in site IS_105 [b,c]. Breeding Adelie Penguins were observed by an observer on the ground on December 3, 2008 [c]. This small colony was not detected by satellite.
Rumpa (69.1441°S, 39.3905°E)	Not found, extinct [a]	Colony not found at location given in [d] in DigitalGlobe satellite imagery obtained on February 21, 2011 [a]	Occupied [c]	The Rumpa breeding population is located at 69.1452°S, 39.3948°E in site IS_120 [b,c]. Breeding Adelie Penguins were observed by an observer on the ground on December 1, 2010, and from a helicopter on January 25, 2011 [c]. Heavy snow falls shortly before the satellite image was obtained may have obscured guano from detection by satellite.
Ytrehovdeholmen (69.2167°S, 39.4333°E)	Extinct [a]	No sign of Adelie Penguin colony in DigitalGlobe satellite imagery obtained on February 10, 2011 [a]	Occupied [c]	The Ytrehovdeholmen breeding population is located at 69.2100°S, 39.4400°E and 69.2226°S, 39.4132°E in sites IS_128 and IS_136 [b,c]. Breeding Adelie Penguins were observed by an observer on the ground on November 16, 2010, and from a helicopter on January 25, 2011 [c]. This small colony was not detected by satellite.
Mame-zima (69.0167°S, 39.4833°E)	Extinct or merged with Meholmen [a]	No sign of Adelie Penguin colony in DigitalGlobe satellite imagery obtained on February 10, 2011 [a]	Occupied [c]	The Mame-zima breeding population is located at 69.0251°S, 39.4782°E in site IS_101 [b,c]. The location for Mame-zima in [a] is incorrect. The true location of Mame-zima was mistakenly assigned to Meholmen Island in [a]. Breeding Adelie Penguins were observed at Mame-zima by an observer on the ground on December 1, 2010 [c].
Torinosu Cove (69.4833°S, 39.5667°E)	Extinct [a]	Unable to locate colony in DigitalGlobe satellite imagery obtained on February 11, 2010 [a]	Occupied [c]	The Torinosu Cove breeding population is located at 69.4940°S, 39.5611°E in site R_1171 [b,c]. Breeding Adelie Penguins were observed by an observer on the ground on November 17, 2009 [c].

APPENDIX TABLE 1. Continued.

Name and location of site given in [a, e]	Satellite observations		Direct observations	
	Conclusion	Commentary	Conclusion	Commentary
Mizukuguri Cove (69.1917°S, 39.6333°E)	Extinct [a]	No sign of Adelie Penguin colony in DigitalGlobe satellite imagery obtained on February 10, 2011 [a]	Occupied [c]	The Mizukuguri Cove breeding population is located at 69.1972°S, 39.6146°E in site R_1090 [b,c]. The location for Mizukuguri Cove in [a] is incorrect. Breeding Adelie Penguins were observed at Mizukuguri Cove by an observer on the ground on December 1, 2010 [c].
Unnamed location (69.187°S, 39.714°E)	Occupied, previously unreported [e]	Unreported penguin colony in Landsat (U.S. Geological Survey, Reston, Virginia, USA) satellite imagery [e]	Unoccupied	The unnamed location given in [a] is in site R_1090 [b]. No penguins were observed in photos taken during ground surveys in the area on February 6, 2011, and January 27, 2013. We suggest that the satellite observation is a detection of a dried lake (Ichijiku Lake).
Cape Omega (68.5667°S, 40.9833°E)	Not found [e]	Colony not found at location given in [d] in DigitalGlobe satellite imagery obtained on November 15, 2009, or December 12, 2010 [a]	Unable to assess	The Cape Omega breeding population is located at 68.5820°S, 41.0230°E in site R_1018 [b,c]. The longitude given in [f] is incorrect (42°1.4′E, should have been 41°1.4′E). No direct observations are available after the 2000–2001 breeding season.
Kirby Head (67.2726°S, 46.5372°E)	Occupied, new colony [a]		Unable to assess	Kirby Head is located at site R_517 [b]. No direct observations have been made at this site.
Sheelagh Islands (66.5464°S, 50.1804°E)	Occupied, new colony [a]	New Adelie Penguin colony in DigitalGlobe satellite imagery obtained on January 26, 2010 [a]	Occupied, previously reported colony [c]	The Sheelagh Islands are located at sites IS_70652 and IS_70654 [b,c]. Adelie Penguin breeding populations were first reported on the Sheelagh Islands from an aerial survey in 1998–1999 [c,g].
Mount Gleadell (66.9410°S, 50.4400°E)	Occupied, new colony [a]	New Adelie Penguin colony, or breeding location not previously seen and reported, in DigitalGlobe satellite imagery obtained on January 26, 2010 [a]	Occupied, previously reported colony [c]	Mount Gleadell is located at site R_395 [b,c]. An Adelie Penguin breeding population was first reported at Mt. Gleadall from an aerial survey in 1998–1999 [c,g].
Unnamed location (67.455°S, 60.882°E)	Occupied, previously unreported [e]	Unreported penguin colony in Landsat satellite imagery [e]	Unoccupied [c]	The unnamed location given in [e] is at site R_626 [b]. We conclude that the satellite observation is a detection of Emperor Penguin guano. The location given in [e] matches the location of an Emperor Penguin colony at the Taylor Glacier Antarctic Specially Protected Area [h]. The Emperor Penguin colony at Taylor Glacier was first reported in 1954 [i]. Numerous visits and direct observations of the Emperor Penguin colony have been reported since then [i]. No breeding Adelie Penguins have been observed in >60 yr of ground-based observation at this location. However, Emperor Penguins breed on land at this location [i].

APPENDIX TABLE 1. Continued.

Name and location of site given in [a, e]	Satellite observations		Direct observations	
	Conclusion	Commentary	Conclusion	Commentary
South Svenner (69.1341°S, 76.7442°E)	Occupied, new colony [a]	New colony, not previously reported, in DigitalGlobe satellite imagery obtained on December 29, 2008 [a]	Occupied, previously reported colony [c]	The location given in [a] is at site IS_72982 [b,c]. We conclude that the satellite observation is very likely the same Adelie Penguin colony reported in [j,k]. This site is previously reported to have had breeding Adelie Penguins [k], is likely to be the breeding site named Svenner 3 in [j] (see [c]), and was observed to have breeding Adelie Penguins in a regional aerial survey of the Svenner Islands in November 2009 [l].
Unnamed location (69.273°S, 76.833°E)	Occupied, previously unreported [e]	Unreported penguin colony in Landsat satellite imagery [e]	Unoccupied [c]	The unnamed location given in [e] is at site IS_73016 [b]. We conclude that the satellite observation is a detection of Emperor Penguin guano. The location given in [e] matches the location of an Emperor Penguin colony at the Amanda Bay Antarctic Specially Protected Area [m]. The Emperor Penguin colony at Amanda Bay was first reported in 1956 [n]. No breeding Adelie Penguins have been observed in >60 yr of intermittent ground observations of Emperor Penguins at Amanda Bay. Emperor Penguins breeding on ice at Amanda Bay can venture onto nearby land (C. Southwell personal observation; Figure 1A) where guano may be detected.
Unnamed location (69.148°S, 77.269°E)	Occupied, previously unreported [e]	Unreported penguin colony in Landsat satellite imagery [e]	Occupied, previously reported colony [c]	The unnamed location given in [e] is at sites IS_72984, IS_72986, and IS_72987 [b,c]. We conclude that the satellite observation is very likely the same colony or colonies reported in [j,k,l]. These sites were previously reported to have had breeding Adelie Penguins in October 1983 [k], are very likely to be the breeding sites observed in December 1981 and named 'Islands NE of Brattstrand Bluffs' in [j], and were observed to have breeding Adelie Penguins in a regional aerial survey of the Svenner Islands in November 2009 [l].

APPENDIX TABLE 1. Continued.

Name and location of site given in [a, e]	Satellite observations		Direct observations	
	Conclusion	Commentary	Conclusion	Commentary
Barrier Island (68.4163°S, 78.3240°E)	Occupied, new colony [a]	New colony, not previously reported, in DigitalGlobe satellite imagery obtained on December 14, 2011 [a]	Unoccupied [c]	The location given in [a] is at site IS_73413 [b]. We conclude that the satellite observation is most likely an Adelie Penguin colony previously reported for this site that has been incorrectly attributed to Barrier Island (IS_73442), or possibly detection of a physical feature mistaken for penguin guano. The entry for Barrier Island in the supplementary table of [a] refers to Landsat observations in [°]. The supplementary KML file in [°] shows a location matching colony site 6 in figure 3 of [j], which we interpret is IS_73413. Direct aerial observation at IS_73413 in 2008–2009 found breeding Adelie Penguins [c]. The location of Barrier Island (68°28′S, 78°23′E) given by the National Geospatial-Intelligence Agency (Springfield, Virginia, USA) is ~3 km east of IS_73413. Direct ground and aerial observations at IS_73442 in November 2014 and November 2015 found no evidence of occupation by any penguin or seabird species, but the aerial observation found a physical feature that was easily distinguished from surrounding rock and could have been mistaken for penguin guano (Figure 1A).
Unnamed location (66.368°S, 110.453°E)	Occupied, previously unreported [e]	Unreported penguin colony in Landsat satellite imagery [e]	Unoccupied [c]	The unnamed location given in [e] is at site IS_73838 [b]. We conclude that the satellite observation is a detection of flying seabird guano. The location given in [e] matches Ardery Island. Flying seabird colonies at Ardery Island were first reported in 1960 [p]. Numerous visits and direct observations of flying seabirds have been reported since then [q,r]. No breeding penguins have been observed in >50 yr of ground-based observations at Ardery Island.

APPENDIX TABLE 1. Continued.

Name and location of site given in [a, e]	Satellite observations		Direct observations	
	Conclusion	Commentary	Conclusion	Commentary
Retour Island (66.7670°S, 141.5669°E)	Occupied, new colony [a]	New colony in DigitalGlobe satellite imagery obtained on February 5, 2011 [a]	Occupied, previously reported colony [c]	The location given in [a] is at site IS_73901 [b]. An Adelie Penguin colony was first reported at this location from an aerial survey in 1997–1998 [c,s], when it was reported as the Curzon Islands, with location coordinates of 66°46′S, 141°34′E.

[a] Lynch and LaRue (2014).
[b] Southwell et al. (2016a).
[c] Southwell et al. (2016b).
[d] Hoshiai et al. (1984).
[e] Lynch and Schwaller (2014).
[f] Kato et al. (2004).
[g] Takahashi et al. (2000).
[h] Secretariat of the Antarctic Treaty (2015).
[i] Robertson et al. (2014).
[j] Whitehead and Johnstone (1990).
[k] Lewis and George (1984).
[l] Southwell et al. (2013).
[m] Secretariat of the Antarctic Treaty (2014).
[n] Wienecke and Pedersen (2009).
[o] Schwaller et al. (2013).
[p] Orton (1963).
[q] Barbraud and Baker (1998).
[r] Van Franeker et al. (1990).
[s] Barbraud et al. (1999).