

Spying on seabirds: a review of time-lapse photography capabilities and limitations

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Abstract

Remote monitoring of wildlife has a long history in ecological research but recent advances in technology have extended the possibilities of remote sensing methods, making camera systems more easily accessible, of higher resolution, and more relevant to a greater range of research interests. Time-lapse photography is most applicable to study animals frequently present at a photographed location or to study frequently repeated behaviours. Therefore, time-lapse photography methods are particularly relevant to study colonial animals at fixed locations. Here, I review literature using time-lapse photography methods in the context of their application to seabirds, focusing on distinct research aims. Cameras can be used to observe seabird behaviour in places or during times when human observation would be nearly impossible, including in remote locations, at night using infrared, and during harsh weather conditions. However, cameras are prone to mechanical failures and programming errors and need regular maintenance, depending on the frequency of photographs. Although many studies have used time-lapse photography techniques to understand seabird ecology, researchers can expand their study aims by examining how research on other taxa has used camera traps. In addition, as efficiency increases, demands for camera systems also increase; therefore, it is necessary to standardise data collection across sites and species to improve comparability across studies. Overall, for the study of colonial wildlife, time-lapse photography proves to be a cost-effective, relatively non-invasive method, which can help researchers save time during fieldwork when this is often limited.

Introduction

Recent technological advances in the remote monitoring of wildlife have extended the possibilities of remote sensing methods, making camera systems both easily accessible and relevant to a greater range of research interests (Swann *et al.* 2011). Traditionally, cameras have focused on photographing one individual, identified by distinct markings, by either taking motion-triggered photographs or using hand-held devices to study an animal opportunistically (Cutler & Swann 1999). However, in cases where wildlife can be photographed in groups, alternative methods may prove more effective in terms of data output, time in the field, and expense. In particular, time-lapse photography, defined here as a camera system installed at a field site and programmed to take an image at a set frequency, has

recently become more accessible to researchers and has great capabilities for the study of animals living in groups. To demonstrate these abilities and highlight possible limitations of time-lapse techniques, I review past uses of camera systems and how they may be applied, or have been applied, to the study of colonial wildlife with a focus on seabirds.

Camera use in ecology: a brief history

Cameras were first applied to the study of animal movement and the absence or presence of wildlife but, with technological advances, cameras have become capable of the remote monitoring popular today. Beginning in the nineteenth century, photography was initially used to examine patterns of horse running movements (Guggisberg 1977). Photography was only first applied to remotely observe wildlife ecology using stand-alone technology at the end of the 1950s in studies of rodent habitat use (Pearson 1959) and prey types in birds (Royama 1959). Beginning in the 1970s, nest box photography became popular to study breeding birds and today remains one of the most widespread uses of camera technology in ecological research (Cutler & Swann 1999). Technological advances led to trigger-sensor camera use, beginning in the 1980s, which, along with robust casings for use in harsh weather conditions, allows for autonomous remote monitoring of wildlife (Swann *et al.* 2011). Today, these systems often include a time and date stamp and air temperature record watermarked on each image, which provides accurate records of the sequence and timing of events. Improvements in camera systems eventually led to broader applications for time-lapse photography in the field of ecology, which are relevant for a range of species and locations and even allow for the tracking of animal movements and recording the absence or presence of wildlife.

Introduction to time-lapse photography

In contrast to motion-triggered cameras — which record individual, instantaneous events and are often deployed as transect networks — time-lapse photography is most applicable to study animals frequently present at a photographed location or to study frequently repeated behaviours, where regular sampling can be used to estimate the frequency or timing of activities and census a population (Swann *et al.* 2011). Therefore, time-lapse methods are particularly relevant to study colonial animals such as seabirds and seals, breeding in large groups. The range of camera equipment types has been reviewed elsewhere (Newbery & Southwell 2009; Swann *et al.* 2011), so will not be detailed in this review. It is important to note that not all camera types are capable of producing time-lapse images or are robust enough to withstand hazardous weather conditions.

Activity patterns

One of the most fundamental uses of time-lapse photography is to summarise activity patterns, which allows researchers to better understand time-budgets. In particular, postures (e.g. sleeping, sitting) have been characterised in several seabird species (Derksen 1977; Storch *et al.* 1999; Pacheco & Castilla 2001). However, the relevance of activity patterns to fitness and population dynamics is often difficult

to test, so the majority of studies have focused instead on nest activity patterns as they relate to chick survival. Only a few studies to date have examined feeding rates or prey types in seabirds using time-lapse photography. For example, one study used cameras to identify seabird species feeding in aggregations on scallops discarded from commercial fishing activity in the Irish Sea (Veale *et al.* 2000), while another observed feeding patterns on Grey Seal *Halichoerus grypus* carcasses by marine scavengers (Quaggiotto *et al.* 2016). However, all other foraging-related seabird studies have focused on the rates of provisioning of young by parents (Duffy 1996; Oswald *et al.* 2013; Sugishita *et al.* 2015; Sugishita *et al.* 2016). These feeding rates can have direct effects on the survival of chicks, which serves as another major focus of seabird studies using time-lapse photography techniques.

Breeding success and phenology

Time-lapse studies have proven to be particularly accurate in measuring breeding success when compared with direct observations (Southwell & Emmerson 2015a), providing researchers with an excellent alternative to measure fitness when time in the field is limited. Breeding success has been measured using time-lapse photography in several species with great accuracy (Lorentzen *et al.* 2010; Lorentzen *et al.* 2012; Wanless *et al.* 2012; Crofts and Robson 2015; Merkel *et al.* 2015, 2016). In addition, time-lapse photography, coupled with other survey techniques, was also used to understand adult and chick survival in guillemots following the Exxon Valdez oil spill (Boersma *et al.* 1995; Boersma & Clark 2001) and after a large population decline (Harris and Wanless 1984), demonstrating how this technique has potential to provide baseline information with which to measure change. Infrared time-lapse cameras have been used to measure breeding success in nocturnal and burrowing species, which are otherwise particularly difficult to measure and therefore often lack data on their basic biology (Wanless *et al.* 2007).

Time-lapse photography can provide information on phenology and nest attendance, replacing the need for direct observation. For example, a study on Adélie Penguins *Pygoscelis adeliae* found that phenological dates obtained from cameras were accurate but slightly more variable than direct observations; however, the study captured only one image daily and highlighted the strength of photographing seabirds at a higher frequency when measuring phenology (Southwell & Emmerson 2015a). The timing and duration of phenological periods, nest abandonment, and chick survival have also been studied in multiple penguin species using time-lapse photography (Black *et al.* 2018a). Nest attendance patterns during either incubation or the guard period prove to be one of the most common uses of time-lapse photography in seabird studies and have been utilised in the study of a variety of species (Hatch & Hatch 1989; Zador & Piatt 1999; Grémillet *et al.* 2000; Johnston *et al.* 2003; Harding *et al.* 2005; Harding *et al.* 2007a, 2007b; Hillman 2012; Arnold & Oswald 2013; Heggøy *et al.* 2015; Harris & Wanless 2016). In addition, nest occupation was recently observed in Shy Albatrosses *Thalassarche cauta* by using multiple cameras to take photographs simultaneously throughout the breeding season, which were then stitched together to create colony-wide panoramas (Lynch *et al.* 2015). Because nest

attendance is linked to egg temperature, chick growth, and the survival of fledglings (Deeming 2002), time-lapse photography can serve as a valuable method to better understand the health of a colony and individual fitness.

Population counts

Estimating population size is the primary method to understand how a colony or species is changing over both time and space. Counts should ideally take place at the peak of breeding to standardise data and remove bias across years and sites (Lynch *et al.* 2009). Time-lapse photography has been used to examine temporal and spatial variation in the attendance of Adélie Penguins at breeding sites to better understand the bias of direct counts (Southwell & Emmerson 2015a) and when future counts should take place (Southwell *et al.* 2014, 2015, 2017). Colony attendance has also been observed using time-lapse cameras installed next to colonies in a range of seabird species (Harris 1980; Piatt *et al.* 1990). More novel methods of counting populations include attaching time-lapse cameras to either 1) kites (Fraser *et al.* 1999) or 2) unmanned aerial vehicles (UAVs; Ratcliffe *et al.* 2015). Satellites take images over time in a similar fashion to time-lapse cameras and have also been used to count populations and identify locations of newly discovered colonies (Barber-Meyer *et al.* 2007; Fretwell *et al.* 2012; LaRue & Knight 2014; LaRue *et al.* 2014; Lynch & LaRue 2014).

Human-wildlife interactions

Time-lapse photography has been used as a tool to understand the effects of human disturbance and how scientists may be biasing their own datasets. The effects of both aircraft and recreational activity on several seabird species (Hillman 2012) and direct human disturbance on Adélie Penguins (Wilson *et al.* 1991) have been effectively studied using time-lapse cameras. In addition, to better understand whether scientific activities influence seabird behaviour, time-lapse photography was also used to examine the influence of human presence during direct observations on predation data (Parrish 1995) and the effects of stomach-retained temperature archival units (STAU), which are used to study feeding activity, on chick feeding rates (Wilson *et al.* 1998). However, more in-depth studies are needed to establish whether the presence of cameras themselves alter seabird behaviour and bias data before researchers can ultimately consider time-lapse photography methods as non-invasive.

Additional uses for time-lapse photography

Beyond the various outlined uses for time-lapse photography, researchers have also used this method to understand interspecific and intraspecific behaviour, habitat use and the geographic range of seabirds. Recent technological advances have decreased the size and weight of cameras, allowing for time-lapse cameras to be mounted directly on individuals (Sakamoto *et al.* 2009). Due to the vast number of recent studies using animal-borne cameras, including a published in-depth review paper (Moll *et al.* 2007), I will not discuss the applications of this method here. Time-lapse photography also serves as an excellent tool to better understand site fidelity, particularly during the rarely studied period of time outside of the breeding

season (Mudge *et al.* 1987; Black *et al.* 2017; Black *et al.* 2018b). Cameras with time-lapse functionality were also fixed on mussel farm buoys to understand how New Zealand King Shags *Phalacrocorax carunculatus* use these buoys (Fisher & Boren 2012), serving as a unique example of how time-lapse cameras can be applied to the study of habitat use. Time-lapse methods can help us to understand social behaviour, such as chick aggregations in Gentoo Penguins *Pygoscelis papua* (Black *et al.* 2016) and are relevant to the study of predator-prey interactions, identifying the causes of egg loss or chick fatality. Lastly, these camera methods have been used successfully to study chick predation, demonstrating how time-lapse photography can be customised, depending on the interests of the researcher and relevant questions being addressed (Powlesland *et al.* 2002; Sabine *et al.* 2005; Wanless *et al.* 2012; Collins *et al.* 2014; Merkel *et al.* 2015).

Capabilities

Time-lapse photography has been applied to the study of a range of interests in seabird research and has major advantages over alternative methods (Table 1). In particular, cameras may remove observer biases by allowing researchers to examine behaviours *ex situ*, therefore reducing the likelihood that they note behaviours they expect to see rather than what is actually occurring (Cowardin 1969). However, observer bias may still be present when observing behaviours in photographs, although this idea is yet to be tested in an animal behaviour and conservation context. Time-lapse photography can be used to observe seabird behaviour in places or during times when human observation would be nearly impossible, including in remote locations, at night using infrared, and during harsh weather conditions (e.g. Black *et al.* 2017). The collection of images also provides researchers with more accurate evidence for later identification of prey species, phenology events, and elusive behaviours, while also providing a time stamp for all events. Most notably, time-lapse cameras are cost effective and can provide researchers with large savings in time and money spent on fieldwork. Because cameras can provide more frequent observations, they are also able to observe more obscure behaviours or elusive species, depending on their set frequency. Time-lapse photography may also be preferred over videography, as it often provides researchers with the same high-resolution detail of the focal species' behaviour with less time needed to process the data.

Table 1. Capabilities and limitations of time-lapse cameras in seabird studies.

Capabilities	Limitations
Removes observer bias	Mechanical failures
Deployable in remote locations	Programming errors
Functions in harsh weather conditions	Regular maintenance
Records nocturnal behaviours	Affordable options produce lower resolution images
Records elusive behaviours	Potential nest disturbance and predator attraction
Saves time and money during fieldwork	Extensive networks expensive to maintain
	High volume of images to manage and note behaviours

Table 2. Overview of practicalities researchers must consider during the time-lapse camera preparation (batteries and storage capacity), set-up (settings and placement), data retrieval, and post-processing phases.

Phase	Specifics	Practicalities to consider
	Preparation	Batteries
	Storage capacity	Secure digital (SD) card size
Set-up	Settings	Resolution Frequency Time of day Start and end date
	Placement	Ecological questions to answer Distance to subject Angle
Data retrieval		<i>In situ</i> collection Satellite recovery
Post processing		Storage Organisation Metadata extraction Available software Citizen science Computer vision automation

Limitations

Naturally, there are disadvantages to time-lapse camera use, some of which may become irrelevant as technology progresses (Table 1). In a practical sense, cameras are prone to mechanical failures and programming errors and need regular maintenance, depending on the frequency of photographs (Table 2). In most cases, data cannot be obtained until a camera is visited for maintenance: a difficult task in remote regions (Table 2). Time-lapse cameras can produce image outputs in a range of qualities with some affordable options providing lower quality data (Table 2). Also, depending on the study species, it may be difficult to study multiple burrows at once in ground-nesting seabirds, making camera studies less affordable, and small seabirds may not be easily detected in the camera frame, leading to poor quality data. As mentioned, studies have not yet fully addressed how cameras influence seabird behaviour so there is a potential for nest disturbance, particularly abandonment (Cowie & Hinsley 1988), and either predator attraction or reduction to occur (Richardson *et al.* 2009) as a result of camera installation. However, cameras are typically fast to install and likely less invasive than direct observations. To date, there is little research on the potential effects of time-lapse or motion-trigger photography on animal behaviour and future

research should focus on the extent that these techniques may be altering behaviour to prove the non-invasiveness of camera use. In addition, if studying more elusive behaviours, such as predation events, or species across a large geographic range, camera purchases and maintenance can become expensive and logistically difficult, as both batteries and computer memory are generally limited.

Learning from other taxa

Although many studies have used time-lapse techniques to understand seabird ecology, seabird researchers can expand their study aims by examining how research on other taxa has used camera traps. For example, cameras methods can help us to understand environmental variables at study sites (e.g. sea ice, glaciers, volcanoes; Harrison *et al.* 1992; Smith *et al.* 2003; Orr & Hoblitt 2008; Ahn & Box 2010; Overeem *et al.* 2011, Figure 1). Aerial counts of birds have long served as a customary census technique and using time-lapse photography can increase the accuracy of seabird counts (Buckland *et al.* 2012). In cases where individuals can be identified either by natural markings or banding, as is the case in African

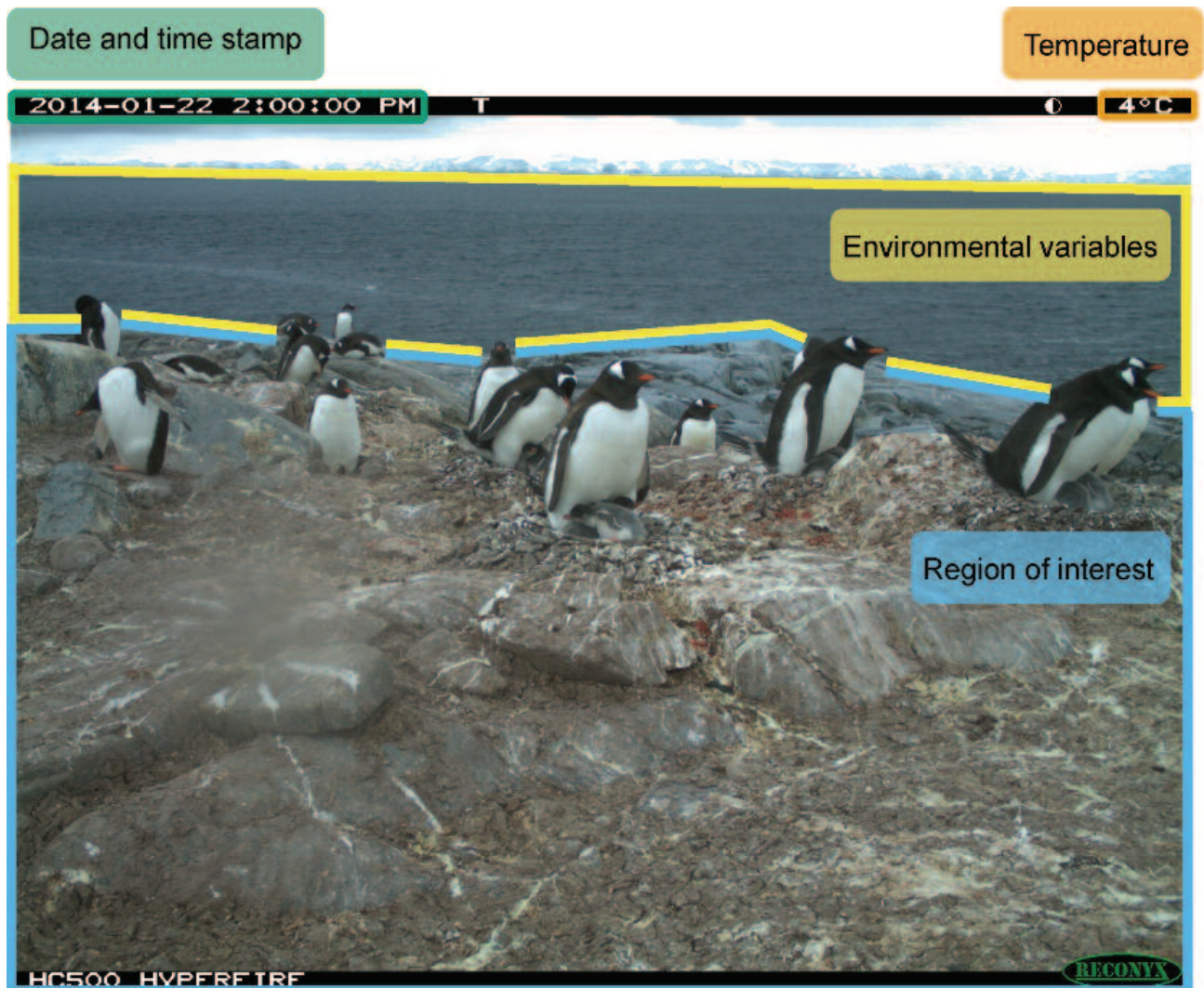


Figure 1. Example time-lapse camera trap image of Gentoo Penguin *Pygoscelis papua* colony, depicting the date and time stamp, temperature stamp, measurable environmental variables, and the region of interest.

Penguins *Spheniscus demersus* (Sherley *et al.* 2010), researchers can use time-lapse photography to study the physical condition of individuals (Kucera & Barrett 2011), a species range using time-lapse cameras along transects (Silveira *et al.* 2003), the parental investment of males compared to females, population structure (Ahumada *et al.* 2011; Hariyadi *et al.* 2011), and population estimates as an alternative to mark-recapture methods (Gardner *et al.* 2010). For an in-depth review of past studies using camera traps to study alternative taxa, including those using time-lapse photography, see Cutler & Swann (1999) and Swann *et al.* (2011).

Technological advances

As technology advances, camera systems are becoming more powerful, relevant, and efficient, particularly when studying seabirds inhabiting remote locations. Battery life and storage capacity have increased, allowing for greater time between servicing and lighter, smaller, more robust cameras (Table 2). Researchers can also take advantage of solar panels and rechargeable external batteries to reduce battery waste, and satellites can be used to obtain data more rapidly (Table 2). However, as efficiency increases and the usage of camera systems increases, it is necessary to standardize data collection across sites and species to improve comparability across studies (e.g. CCAMLR methods, CCAMLR 2004; Southwell & Emmerson 2015b; JNCC methods, Walsh *et al.* 1995). The research community would benefit from a data repository for camera data, such as those in place for tracking movements (Movebank, Kranstauber *et al.* 2011) and genetics (Genbank, Benson *et al.* 2008). Ultimately, the largest disadvantage of time-lapse photography is also its biggest advantage; enormous amounts of data are produced, which need to be processed. Cameras set to time-lapse mode typically take thousands of images, which, once retrieved, need to be noted for the focal behaviours to obtain usable data. This process can be laborious and time-consuming; however, solutions do exist to manage a high volume of images. A variety of software types are available to provide researchers with tools to manage databases and annotate images (Scotson *et al.* 2017); however, this step in the research process is often particularly labour intensive. To speed up post-processing, the use of both citizen science participation (e.g. Penguin Watch; Jones *et al.* 2018) and computer-vision and deep-learning automation (e.g. Dickinson *et al.* 2008; Dickinson *et al.* 2010; Gardner *et al.* 2010; Duyck *et al.* 2015) have been successfully explored; in the future these automation algorithms must be refined and made accessible to the research community at large.

Conclusion

Overall, for the study of colonial wildlife, time-lapse photography proves to be a cost-effective (Southwell & Emmerson 2015a) and relatively non-invasive method, which can help researchers save limited fieldwork time. Because of these advantages, and the method's relative ease of use, time-lapse photography can be — and has been — used to expand our knowledge of both interspecific and intraspecific behaviours and population dynamics over time and space, specifically in areas where studies were previously logistically impossible (Figure 2). Time-lapse photography can effectively replace other methods, including direct observation, tracking, surveys, and counts and are particularly efficient when studying elusive

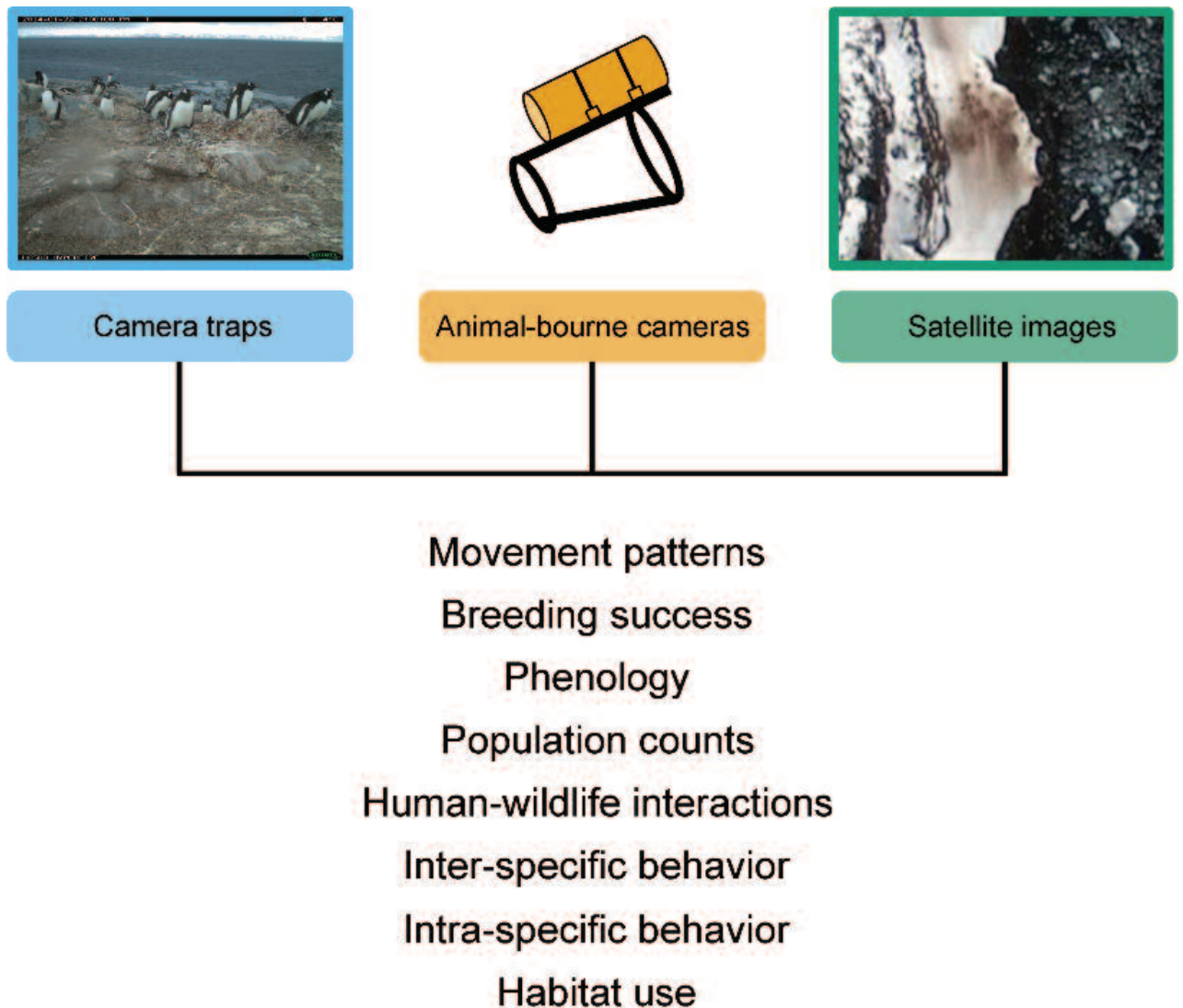


Figure 2. Camera traps, animal-borne cameras, and satellite images taken at set frequency time-lapse intervals can provide information on a variety of seabird behaviours.

and nocturnal species, as well as those sensitive to human presence. In addition, time-lapse methods can provide information on previously 'unseen behaviour' such as activity at night and during harsh weather conditions. However, researchers must budget time for troubleshooting, maintenance, and post-processing. To speed up the processing of image data, ecologists would benefit from greater collaboration with researchers from other disciplines, particularly computer scientists, to apply techniques that automate image notation and categorization, including those implementing computer-vision and deep-learning algorithms.

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References

- Ahn, Y. & Box, J. E. 2010. Glacier velocities from time-lapse photos: technique development and first results from the Extreme Ice Survey (EIS) in Greenland. *Journal of Glaciology* 56: 723–734.
- Ahumada, J. A., Silva, C. E., Gajapersad, K., Hallam, C., Hurtado, J., Martin, E., McWilliam, A., Mugerwa, B., O'Brien, T. & Rovero, F. 2011. Community structure and diversity of tropical forest mammals: data from a global camera trap network. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 366: 2703–2711.
- Arnold, J. M. & Oswald, S. A. 2013. First confirmed record of a Common Tern *Sterna hirundo* breeding at one year of age. *Bird Study* 60: 275–279.
- Barber-Meyer, S. M., Kooyman, G. L. & Ponganis, P. J. 2007. Estimating the relative abundance of emperor penguins at inaccessible colonies using satellite imagery. *Polar Biology* 30: 1565–1570.
- Benson, D. A., Karsch-Mizrachi, I., Lipman, D. J., Ostell, J. & Wheeler, D. L. 2008. GenBank. *Nucleic Acids Research* 36: D25–D30.
- Black, C., Collen, B., Johnston, D. & Hart, T. 2016. Why Huddle? Ecological Drivers of Chick Aggregations in Gentoo Penguins, *Pygoscelis papua*, across Latitudes. *PLoS ONE* 11: e0145676.
- Black, C., Rey, A. R. & Hart, T. 2017. Peeking into the bleak midwinter - investigating non-breeding strategies of penguins using a camera network. *Auk* 134: 520–529.
- Black, C., Collen, B., Lunn, D., Filby, D., Winnard, S. & Hart, T. 2018a. Time-lapse cameras reveal latitude and season influence breeding phenology durations in penguins. *Ecology and Evolution* 8: 8286–8296.
- Black, C., Southwell, C., Emmerson, L., Lunn, D. & Hart, T. 2018b. Time-lapse imagery of Adélie penguins reveals differential winter strategies and breeding site occupation. *PLoS ONE* 13: e0193532.
- Boersma, P., Parrish, J. K. & Kettle, A. B. 1995. Common murre abundance, phenology, and productivity on the Barren Islands, Alaska: The Exxon Valdez oil spill and long-term environmental change. Exxon Valdez oil spill: Fate and effects in Alaskan waters. *ASTM International*. DOI: 10.1520/STP19882S.
- Boersma, P. D. & Clark, J. A. 2001. Seabird recovery following the Exxon Valdez oil spill: why was murre recovery controversial? International Oil Spill Conference. *American Petroleum Institute* 2: 1521–1526
- Buckland, S. T., Burt, M. L., Rexstad, E. A., Mellor, M., Williams, A. E. & Woodward, R. 2012. Aerial surveys of seabirds: the advent of digital methods. *Journal of Applied Ecology* 49: 960–967.
- CCAMLR (2004) CCAMLR Ecosystem Monitoring Program: standard methods (<https://www.ccamlr.org/en/system/files/CEMP%20Standard%20Methods%20Jun%202014.pdf>). Accessed 22 November 2018.
- Collins, P. M., Green, J. A., Dodd, S., Shaw, P. J. & Halsey, L. G. 2014. Predation of Black-legged Kittiwake chicks *Rissa tridactyla* by a Peregrine Falcon *Falco peregrinus*: insights from time-lapse Cameras. *Wilson Journal of Ornithology* 126: 158–161.
- Cowardin, L. M. 1969. Use of flooded timber by waterfowl at the Montezuma National Wildlife Refuge. *Journal of Wildlife Management* 33: 829–842.
- Cowie, R. & Hinsley, S. 1988. Feeding ecology of great tits (*Parus major*) and blue tits (*Parus caeruleus*), breeding in suburban gardens. *Journal of Animal Ecology* 57: 611–626.
- Crofts, S. & Robson, B. 2015. First record of hybridisation between Northern *Eudyptes moseleyi* and Southern Rockhopper Penguins *E. c. chrysocome*. *Seabird* 28: 37–42.
- Cutler, T. L. & Swann, D. E. 1999. Using remote photography in wildlife ecology: a review. *Wildlife Society Bulletin* 27: 571–581.
- Deeming, C. 2002. *Avian Incubation: Behaviour, Environment and Evolution*. Oxford University Press, Oxford.
- Delord, K., Roudaut, G., Guinet, C., Barbraud, C., Bertrand, S. & Weimerskirch, H. 2015. Kite aerial photography: a low-cost method for monitoring seabird colonies. *Journal of Field Ornithology* 86:173–179.

- Derksen, D.V. 1977.** A quantitative analysis of the incubation behavior of the Adelie Penguin. *Auk* 94: 552–566.
- Dickinson, P., Freeman, R., Patrick, S. & Lawson, S. 2008.** Autonomous monitoring of cliff nesting seabirds using computer vision. In: *International Workshop on Distributed Sensing and Collective Intelligence in Biodiversity Monitoring, Amsterdam* (<http://eprints.lincoln.ac.uk/2207/1/biodivgrid08p1d.pdf>). Accessed 12 November 2018.
- Dickinson, P., Qing, C., Lawson, S. & Freeman, R. 2010.** Automated visual monitoring of nesting seabirds. In: *Workshop on Visual Observation and Analysis of Animal and Insect Behaviour, Istanbul* (http://homepages.inf.ed.ac.uk/rbf/VAIB10PAPERS/VAIB10p1dqc_final.pdf). Accessed 12 November 2018.
- Duyck, J., Finn, C., Hutcheon, A., Vera, P., Salas, J. & Ravela, S. 2015.** Sloop: A pattern retrieval engine for individual animal identification. *Pattern Recognition* 48: 1059–1073.
- Fisher, P. R. & Boren, L. J. 2012.** New Zealand king shag (*Leucocarbo carunculatus*) foraging distribution and use of mussel farms in Admiralty Bay, Marlborough Sounds. *Notornis* 59: 105–115.
- Fraser, W. R., Carlson, J. C., Duley, P. A., Holm, E. J. & Patterson, D. L. 1999.** Using kite-based aerial photography for conducting Adelie penguin censuses in Antarctica. *Waterbirds* 22: 435–440.
- Fretwell, P.T., LaRue, M.A., Morin, P., Kooyman, G.L., Wienecke, B., Ratcliffe, N., Fox, A.J., Fleming, A.H., Porter, C. & Trathan, P.N. 2012.** An emperor penguin population estimate: the first global, synoptic survey of a species from space. *PLoS ONE* 7: e33751.
- Gardner, B., Reppucci, J., Lucherini, M. & Royle, J. A. 2010.** Spatially explicit inference for open populations: estimating demographic parameters from camera-trap studies. *Ecology* 91: 3376–3383.
- Grémillet, D., Storch, S. & Peters, G. 2000.** Determining food requirements in marine top predators: a comparison of three independent techniques in Great Cormorants, *Phalacrocorax carbo carbo*. *Canadian Journal of Zoology* 78: 1567–1579.
- Guggisberg, C. A. W. 1977.** Early wildlife photographers. *Taplinger Publishing Company*.
- Harding, A. M. A., Piatt, J. F., Byrd, G. V., Hatch, S. A., Konyukhov, N. B., Golubova, E. U. & Williams, J. C. 2005.** Variability in colony attendance of crevice-nesting Horned Puffins: implications for population monitoring. *Journal of Wildlife Management* 69: 1279–1296.
- Harding, A. M., Piatt, J. F. & Schmutz, J. A. 2007.** Seabird behavior as an indicator of food supplies: sensitivity across the breeding season. *Marine Ecology Progress Series* 352: 269–274.
- Harding, A. M., Piatt, J. F., Schmutz, J. A., Shultz, M. T., Pelt, T. I. V., Kettle, A. B. & Speckman, S. G. 2007.** Prey density and the behavioral flexibility of a marine predator: the common murre (*Uria aalge*). *Ecology* 88: 2024–2033.
- Hariyadi, A. R. S., Priambudi, A., Setiawan, R., Daryan, D., Yayus, A. & Purnama, H. 2011.** Estimating the population structure of Javan rhinos (*Rhinoceros sondaicus*) in Ujung Kulon National Park using the mark-recapture method based on video and camera trap identification. *Pachyderm* 49: 90–99.
- Harris, M. 1980.** Breeding performance of puffins *Fratercula arctica* in relation to nest density, laying date and year. *Ibis* 122: 193–209.
- Harris, M. P. & Wanless, S. 1984.** The effect of the wreck of seabirds in February 1983 on auk populations on the Isle of May (Fife). *Bird Study* 31: 103–110.
- Harris, M. P. & Wanless, S. 2016.** The use of webcams to monitor the prolonged autumn attendance of Guillemots on the Isle of May in 2015. *Scottish Birds* 36: 3–9.
- Harrison, W. D., Echelmeyer, K. A., Cosgrove, D. M. & Raymond, C. F. 1992.** The determination of glacier speed by time-lapse photography under unfavorable conditions. *Journal of Glaciology* 38: 257–265.
- Hatch, S. A. 2002.** Activity Patterns and Monitoring Numbers of Horned Puffins and Parakeet Auklets. *Waterbirds* 25: 348–357.
- Hatch, S. A. & Hatch, M. A. 1989.** Attendance patterns of murrelets at breeding sites: implications for monitoring. *Journal of Wildlife Management* 53: 483–493.

- Heggøy, O., Christensen-Dalsgaard, S., Ranke, P. S., Chastel, O. & Bech, C. 2015.** GPS-loggers influence behaviour and physiology in the black-legged kittiwake *Rissa tridactyla*. *Marine Ecology Progress Series* 521: 237–248.
- Hillman, M.D. 2012.** *Evaluating the Responses of Least Terns, Common Terns, Black Skimmers, and Gull-billed Terns to Military and Civilian Aircraft and to Human Recreation at Cape Lookout National Seashore, North Carolina*. PhD thesis, Virginia Polytechnic Institute and State University.
- Huffeldt, N. P. & Merkel, F. R. 2013.** Remote time-lapse photography as a monitoring tool for colonial breeding seabirds: a case study using thick-billed murres (*Uria lomvia*). *Waterbirds* 36: 330–341.
- Johnston, R. B., Bettany, S. M., Ogle, R. M., Aikman, H. A., Taylor, G. & Imber, M. 2003.** Breeding and fledging behaviour of the Chatham Taiko (*Magenta petrel*) *Pterodroma magentae*, and predator activity at burrows. *Marine Ornithology* 31:193–197.
- Jones, F. M., Allen, C., Arteta, C., Arthur, J., Black, C., Emmerson, L. M., Freeman, R., Hines, G., Lintott, C.J., Macháčková, Z. & Miller, G. 2018.** Time-lapse imagery and volunteer classifications from the Zooniverse Penguin Watch project. *Scientific Data* 5: 180124.
- Kranstauber, B., Cameron, A., Weinzerl, R., Fountain, T., Tilak, S., Wikelski, M. & Kays, R. 2011.** The Movebank data model for animal tracking. *Environmental Modelling & Software* 26: 834–835.
- Kucera, T. & Barrett, R. H. 2011.** A history of camera trapping. In: O’Connell, A. F., Nichols, J. D. & Karanth, K. U. (eds.) *Camera Traps in Animal Ecology*: 9–26. Springer, New York.
- Larue, M. A. & Knight, J. 2014.** Applications of Very High-Resolution Imagery in the Study and Conservation of Large Predators in the Southern Ocean. *Conservation Biology* 28: 1731–1735.
- LaRue, M. A., Lynch, H. J., Lyver, P.O.B., Barton, K., Ainley, D. G., Pollard, A., Fraser, W. R. & Ballard, G. 2014.** A method for estimating colony sizes of Adélie penguins using remote sensing imagery. *Polar Biology* 37: 507–517.
- Lorentzen, E., Choquet, R. & Steen, H. 2012.** Modelling state uncertainty with photo series data for the estimation of breeding success in a cliff-nesting seabird. *Journal of Ornithology* 152: 477–483.
- Lorentzen, E., Steen, H. & Strøm, H. 2010.** Estimating chick survival in cliff-nesting seabirds - a hazard made easy with monitoring cameras. (<http://www.seapop.no/opencms/export/sites/SEAPOP/no/filer/short-reports/2010/SEAPOP-Short-Report-08-2010.pdf>) *SEAPOP Short Report*, 8-2010. Accessed 12 November 2018.
- Lynch, H. J., Fagan, W. F., Naveen, R., Trivelpiece, S. G. & Trivelpiece, W. Z. 2009.** Timing of clutch initiation in *Pygoscelis* penguins on the Antarctic Peninsula: towards an improved understanding of off-peak census correction factors. *CCAMLR Science* 16: 149–165.
- Lynch, H. J. & LaRue, M. A. 2014.** First global census of the Adélie Penguin. *Auk* 131: 457–466.
- Lynch, T. P., Alderman, R. & Hobday, A. J. 2015.** A high-resolution panorama camera system for monitoring colony-wide seabird nesting behaviour. *Methods in Ecology and Evolution* 6: 491–499.
- Merkel, F., Boertmann, D., Falk, K., Frederiksen, M., Johansen, K., Labansen, A. L., Linnebjerg, J. F., Mosbech, A. & Sonne, C. 2015.** Why is the last Thick-billed Murre *Uria lomvia* colony in central West Greenland heading for extinction? *Bird Conservation International* 26: 1–15.
- Merkel, F. R., Johansen, K. L. & Kristensen, A. J. 2016.** Use of time-lapse photography and digital image analysis to estimate breeding success of a cliff-nesting seabird. *Journal of Field Ornithology* 87: 84–95.
- Moll, R. J., Millspaugh, J. J., Beringer, J., Sartwell, J. & He, Z. 2007.** A new ‘view’ of ecology and conservation through animal-borne video systems. *Trends in Ecology & Evolution* 22: 660–668.
- Mosbech, A., Merkel, F. R., Boertmann, D., Falk, K., Frederiksen, M., Johansen, K. L. & Sonne, C. 2009.** *Thick-billed Murre studies in Disko Bay (Ritenbenk), West Greenland* (<https://www2.dmu.dk/pub/fr749.pdf>). National Environmental Research Institute, Technical Report 749, Aarhus University. Accessed 12 November 2018.

- Mudge, G. P., Aspinall, S. J. & Crooke, C. H. 1987.** A photographic study of seabird attendance at Moray Firth colonies outside the breeding season. *Bird Study* 34: 28–36.
- Murphy, E. C., Cooper, B. A., Martin, P. D., Johnson, C. B., Lawhead, B. E., Springer, A. M. & Thomas, D. L. 1987.** *The population status of seabirds on St. Matthew and Hall islands, 1985 and 1986.* Unpublished Minerals Management Service Report, Department of the Interior, USA.
- Newbery, K. B. & Southwell, C. 2009.** An automated camera system for remote monitoring in polar environments. *Cold Regions Science and Technology* 55: 47–51.
- Orr, T. R. & Hoblitt, R. P. 2008.** A Versatile Time-Lapse Camera System Developed by the Hawaiian Volcano Observatory for Use at Kilauea Volcano, Hawaii. *US Geological Survey* 4: 8.
- Oswald, S. A., Wails, C. N., Morey, B. E. & Arnold, J. M. 2013.** Caspian Terns (*Hydroprogne caspia*) Fledge a Ring-billed Gull (*Larus delawarensis*) Chick: Successful Waterbird Adoption Across Taxonomic Families. *Waterbirds* 36: 385–389.
- Overeem, I., Anderson, R. S., Wobus, C. W., Clow, G. D., Urban, F. E. & Matell, N. 2011.** Sea ice loss enhances wave action at the Arctic coast. *Geophysical Research Letters* 38: 1–6.
- Pacheco, C. J. & Castilla, J. C. 2001.** Foraging behavior of the American oystercatcher *Haematopus palliatus pitanay* (Murphy 1925) on the intertidal ascidian *Pyura praeputialis* (Heller 1878) in the Bay of Antofagasta, Chile. *Journal of Ethology* 19: 23–26.
- Parrish, J. K. 1995.** Influence of group size and habitat type on reproductive success in Common Murres (*Uria aalge*). *Auk* 112: 390–401.
- Pearson, O. P. (1959)** A traffic survey of *Microtus-Reithrodontomys* runways. *Journal of Mammalogy* 40: 169–180.
- Piatt, J. F., Roberts, B. D., & Hatch, S. A. 1990.** Colony attendance and population monitoring of least and crested auklets on St. Lawrence Island, Alaska. *Condor* 92: 97–106.
- Powlesland, R. G., Luke, I. J. & Jansen, P. 2002.** Predation by Australasian harrier (*Circus approximans*) of little shag (*Phalacrocorax melanoleucos*) clutches. *Notornis* 49: 266–268.
- Quaggiotto, M. M., Burke, L. R., McCafferty, D. J. & Bailey, D. M. 2016.** First investigation of the consumption of seal carcasses by terrestrial and marine scavengers. *Glasgow Naturalist* 26: 32–100.
- Ratcliffe, N., Guihen, D., Robst, J., Crofts, S., Stanworth, A. & Enderlein, P. 2015.** A protocol for the aerial survey of penguin colonies using UAVs. *Journal of Unmanned Vehicle Systems* 3: 95–101.
- Richardson, T. W., Gardali, T. & Jenkins, S. H. 2009.** Review and meta-analysis of camera effects on avian nest success. *Journal of Wildlife Management* 73: 287–293.
- Duffy, D. C. 1996.** APEX: Alaska predator ecosystem experiment. Exxon Valdez Oil Spill Restoration Project. Restoration Project 95163 (<http://www.evostc.state.ak.us/Store/AnnualReports/1995-95163-Annual.pdf>). *Alaska Natural Heritage Program*. Accessed 12 November 2018.
- Royama, T. 1959.** A device of an auto-cinematic food-recorder. *Japanese Journal of Ornithology* 15: 172–176.
- Sabine, J. B., Meyers, J. M. & Schweitzer, S. H. 2005.** A simple, inexpensive video camera setup for the study of avian nest activity. *Journal of Field Ornithology* 76: 293–297.
- Scotson, L., Johnston, L. R., Iannarilli, F., Wearn, O. R., Mohd-Azlan, J., Wong, W. M., Gray, T. N., Dinata, Y., Suzuki, A., Willard, C. E. & Frechette, J. 2017.** Best practices and software for the management and sharing of camera trap data for small and large scales studies. *Remote Sensing in Ecology and Conservation* 3: 158–172.
- Sherley, R. B., Burghardt, T., Barham, P. J., Campbell, N. & Cuthill, I. C. 2010.** Spotting the difference: towards fully-automated population monitoring of African penguins *Spheniscus demersus*. *Endangered Species Research* 11: 101–111.
- Silveira, L., Jacomo, A. T. & Diniz-Filho, J. A. F. 2003.** Camera trap, line transect census and track surveys: a comparative evaluation. *Biological Conservation* 114: 351–355.
- Smith Jr, K. L., Baldwin, R. J., Glatts, R. C., Chereskin, T. K., Ruhl, H., & Lagun, V. 2003.** Weather, ice, and snow conditions at Deception Island, Antarctica: long time-series photographic monitoring. *Deep Sea Research Part II: Topical Studies in Oceanography* 50: 1649–1664.

- Southwell, C., Low, M., Newbery, K. & Emmerson, L. 2014.** First comprehensive abundance survey of a newly discovered Adélie penguin breeding metapopulation in the Robinson Group of islands, Mac. Robertson Land, East Antarctica. *Antarctic Science* 26: 265–266.
- Southwell, C. & Emmerson, L. 2015a.** Remotely-operating camera network expands Antarctic seabird observations of key breeding parameters for ecosystem monitoring and management. *Journal for Nature Conservation* 23: 1–8.
- Southwell, C. & Emmerson, L. 2015b.** The importance of standardising and validating new methods for CEMP to maintain the robustness of long-term time series. *Commission for the Conservation of Antarctic Marine Living Resources: WG-EMM-15/44* (<https://www.camlr.org/en/wg-emm-15/44>). Accessed 22 November 2018.
- Southwell, C., Emmerson, L., Newbery, K., McKinlay, J., Kerry, K., Woehler, E. & Ensor, P. 2015.** Re-constructing historical Adélie penguin abundance estimates by retrospectively accounting for detection bias. *PLoS ONE*: e0123540.
- Southwell, C., Emmerson, L., Takahashi, A., Barbraud, C., Delord, K., & Weimerskirch, H. 2017.** Large-scale population assessment informs conservation management for seabirds in Antarctica and the Southern Ocean: A case study of Adélie penguins. *Global Ecology and Conservation* 9: 104–115.
- Storch, S., Grémillet, D. & Culik, B. M. 1999.** The telltale heart: a non-invasive method to determine the energy expenditure of incubating Great Cormorants *Phalacrocorax carbo carbo*. *Ardea* 87: 207–215.
- Sugishita, J., Torres, L. G. & Seddon, P. J. 2015.** A new approach to study of seabird-fishery overlap: Connecting chick feeding with parental foraging and overlap with fishing vessels. *Global Ecology and Conservation* 4: 632–644.
- Sugishita, J., McKenzie, M., Torres, L. G., & Seddon, P. J. 2017.** Automated techniques for measuring meal size in great albatrosses. *New Zealand Journal of Ecology* 41: 120–125.
- Swann, D. E., Kawanishi, K., & Palmer, J. 2011.** Evaluating types and features of camera traps in ecological studies: a guide for researchers. In: O’Connell, A. F., Nichols, J. D. & Karanth, K. U. (eds.) *Camera Traps in Animal Ecology*: 9–26. Springer, New York.
- Veale, L. O., Hill, A. S., Hawkins, S. J. & Brand, A. R. 2000.** Effects of long-term physical disturbance by commercial scallop fishing on subtidal epifaunal assemblages and habitats. *Marine Biology* 132: 325–337.
- Walsh, P. M., Halley, D. J., Harris, M. P., Del Nevo, A., Sim, I. M. W. & Tasker, M. L. 1995.** *Seabird monitoring handbook for Britain and Ireland: a compilation of methods for survey and monitoring of breeding seabirds*. Joint Nature Conservation Committee, Peterborough.
- Wanless, R. M., Ratcliffe, N., Angel, A., Bowie, B. C., Cita, K., Hilton, G. M., Kritzing, P., Ryan, P. G. & Slabber, M. 2012.** Predation of Atlantic Petrel chicks by house mice on Gough Island. *Animal Conservation* 15: 472–479.
- Wanless, R. M., Angel, A., Cuthbert, R. J., Hilton, G. M. & Ryan, P. G. 2007.** Can predation by invasive mice drive seabird extinctions? *Biology Letters* 3: 241–244.
- Wilson, R., Peters, G., Regel, J., Grémillet, D., Pütz, K., Kierspel, M., Weimerskirch, H. & Cooper, J. 1998.** Short retention times of stomach temperature loggers in free-living seabirds: is there hope in the spring? *Marine Biology* 130: 559–566.
- Zador, S. G. & Piatt, J. F. 1999.** Time-budgets of common murrelets at a declining and increasing colony in Alaska. *Condor* 101: 149–152.