



UNIVERSITY OF
GLOUCESTERSHIRE

This is a peer-reviewed, post-print (final draft post-refereeing) version of the following published document, This is the peer reviewed version of the following article: Edney, A.J. and Wood, M.J. (2020), Applications of digital imaging and analysis in seabird monitoring and research. *Ibis*. doi:10.1111/ibi.12871, which has been published in final form at <https://onlinelibrary.wiley.com/doi/full/10.1111/ibi.12871>. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Self-Archiving. and is licensed under All Rights Reserved license:

Edney, Alice J. and Wood, Matthew J ORCID: 0000-0003-0920-8396 (2021) Applications of digital imaging and analysis in seabird monitoring and research. *Ibis: International Journal of Avian Science*, 163 (2). pp. 317-337. doi:10.1111/ibi.12871

Official URL: <http://dx.doi.org/10.1111/ibi.12871>

DOI: <http://dx.doi.org/10.1111/ibi.12871>

EPrint URI: <https://eprints.glos.ac.uk/id/eprint/8812>

Disclaimer

The University of Gloucestershire has obtained warranties from all depositors as to their title in the material deposited and as to their right to deposit such material.

The University of Gloucestershire makes no representation or warranties of commercial utility, title, or fitness for a particular purpose or any other warranty, express or implied in respect of any material deposited.

The University of Gloucestershire makes no representation that the use of the materials will not infringe any patent, copyright, trademark or other property or proprietary rights.

The University of Gloucestershire accepts no liability for any infringement of intellectual property rights in any material deposited but will remove such material from public view pending investigation in the event of an allegation of any such infringement.

PLEASE SCROLL DOWN FOR TEXT.

Applications of digital imaging and analysis in seabird monitoring and research

ALICE J. EDNEY* & MATT J. WOOD

School of Natural & Social Sciences, University of Gloucestershire, Francis Close Hall, Cheltenham, GL50 4AZ, UK

*Corresponding author.

Email: aliceedney4@gmail.com

Twitter: [@animal__alice](https://twitter.com/animal__alice)

Rapid advances in digital imaging technology offer efficient and cost-effective methods for measuring seabird abundance, breeding success, phenology, survival and diet. These methods can facilitate understanding of long-term population trends, and the design and implementation of successful conservation strategies. This paper reviews the suitability of satellites, manned aircraft, unmanned aerial vehicles (UAVs), and fixed-position, handheld and animal-borne cameras for recording digital photographs and videos used to measure seabird demographic and behavioural parameters. It considers the disturbance impacts, accuracy of results obtained, cost-effectiveness and scale of monitoring possible compared with 'traditional' fieldworker methods. Given the ease of collecting large amounts of imagery, image processing is an important step in realizing the potential of this technology. The effectiveness of manual, semi-automated and automated image processing is also reviewed. Satellites, manned aircraft and UAVs have most commonly been used for population counts. Spatial resolution is lowest in satellites, limiting monitoring to large species and those with obvious signs of presence, such as penguins. Conversely, UAVs have the highest spatial resolution, which has allowed fine-scale measurements of foraging behaviour. Time-lapse cameras are more cost-effective for collecting time-series data such as breeding success and phenology, as human visits are only required infrequently for maintenance. However, the colony of interest must be observable from a single vantage point. Handheld, animal-borne and motion-triggered cameras have fewer cost-effective uses but have provided information on seabird diet, foraging behaviour and nest predation. The last of these has been important for understanding the impact of invasive mammals on seabird breeding success. Advances in automated image analysis are increasing the suitability of digital photography and videography to facilitate and/or replace traditional seabird monitoring methods. Machine-learning algorithms, such as Pengbot, have allowed rapid identification of birds, although training requires thousands of pre-annotated photographs. Digital imaging has considerable potential in seabird monitoring, provided that appropriate choices are available for both image capture technology and image processing. These technologies offer opportunities to collect data in remote locations and increase the number of sites monitored. The potential to include such solutions in seabird monitoring and research will develop as the technology evolves, which will be of benefit given funding challenges in monitoring and conservation.

Keywords: conservation photography, population ecology, remote sensing, seabird, videography.

Seabirds are one of the most threatened groups of birds, with almost half of seabird species experiencing population declines (Croxall et al. 2012). Effective monitoring is essential to understand long-term population trends, so that conservation action can be implemented (Walsh et al. 1995, Anker-Nilssen et al. 1996, Petersen et al., 2008). However, monitoring seabird populations can be challenging. Pelagic species spend most of the year at sea, only returning to land to breed. Many nest on exposed cliffs with difficult access, especially during periods of inclement weather, ground-nesting birds may be concealed by camouflage or vegetation, and some species nest underground (Mitchell & Parsons 2007, Robinson & Ratcliffe 2010). Furthermore, visiting breeding colonies regularly is logistically difficult in remote locations, can cause disturbance, and is often expensive in terms of time and money (Anker-Nilssen et al. 1996, Field et al. 2005, Huffeldt & Merkel 2013, Southwell & Emmerson 2015). As a result, monitoring efforts are often restricted to small temporal and spatial scales (Evans 1986, Lynch et al. 2012a, Paleczny et al. 2015).

Recent advances in digital imaging technology offer considerable potential for overcoming some of the challenges associated with monitoring seabird populations. Digital photography has a long history in wildlife monitoring but has previously been limited to small studies that observe animals opportunistically, using handheld or animal-triggered cameras (Black 2018). Now, increased battery life, increased data storage and better optics have transformed the potential of remote photography and videography and made it possible to monitor populations that are hard to access (Bolton et al. 2007, Kucera & Barrett 2011, Anderson & Gaston 2013, Black 2018). Nevertheless, the wide range of technology available can make it challenging to decide which type of equipment is most suitable for a specific monitoring purpose, and how to handle and analyse large amounts of digital data.

Here we summarize the main technologies available for collecting digital data on seabird populations and offer a critical assessment of each data collection method. The suitability of each technology for measuring demographic and behavioural parameters is assessed in relation to the disturbance caused, accuracy of results obtained, cost-effectiveness and scale of monitoring possible, compared with non-digital (termed 'traditional') methods. In particular, we focus on the ability of satellites, manned aircraft, unmanned aerial vehicles (UAVs) and handheld, animal-borne and fixed-position (including time-lapse, video and motion-triggered) cameras to monitor the abundance, breeding success, phenology, survival and diet of seabird populations at sea and on land. This includes surface-nesting and cliff-nesting seabirds, sea-ducks on inland bodies of water, and seabirds at sea. We assess the accuracy and cost of manual, semi-automated and automated image analysis methods, as well as considering future developments needed in the field. Our hope is that by drawing information together from many individual studies, this review can help researchers decide where digital photography and videography could facilitate seabird monitoring, in a world that can be short of time and money for conservation endeavours (Waldron et al. 2013).

COLLECTION OF DIGITAL IMAGERY

Satellites

One of the first developments in remote sensing technology was the use of satellites for aerial surveys. Although more commonly used to survey vegetation, satellite imagery was used for seabird monitoring as early as the 1980s (Schwaller et al. 1989, Nowak et al. 2019). Images have been used to locate and count seabird populations, including penguins, Masked Booby *Sula dactylatra* and Wandering Albatross *Diomedea exulans* (Fig. 1) (Schwaller et al. 1989, Guinet et al. 1995, Fretwell & Trathan 2009, Hughes et al. 2011, Fretwell et al. 2012, 2014, 2017, Lynch et al. 2012b, Waluda et al. 2014, Borowicz et al. 2018, Dolliver, 2019). The downward-facing perspective of satellites means images are unlikely to provide a representative view of cliff-nesting species but they are suitable for observing surface-nesting seabirds, seabirds at sea and sea-ducks inland.

The primary advantage of satellite imagery is its global coverage. This has allowed the discovery of previously unknown populations, often in remote, inaccessible areas (Fretwell & Trathan 2009, Fretwell et al. 2012, 2014, Ancel et al. 2017, Borowicz et al. 2018). Moreover, satellite data collection occurs at such a high altitude that it does not disturb birds or habitats, unlike ground, boat or other aerial surveys, making satellites ideal for monitoring sensitive species and locations.

This high-altitude view and the lack of control over the spectral, spatial and temporal resolution of images means that many populations are not visible in enough detail to be counted accurately from satellites (Rush et al. 2018, Nowak et al. 2019). The trade-off between spatial and temporal resolution also limits their ability to collect the frequent, high-resolution images needed to measure breeding success. Terra and Aqua satellites with MODIS sensors have high temporal resolution (four images every 24 h) but very low spatial resolution, whereas Landsat or Sentinel-2 satellites have high spatial resolution (10–30 m) but low temporal resolution (one image every 16 days) (Nowak et al. 2019). A fixed re-visit time means image frequency may be further reduced if poor weather conditions such as low cloud obscure the area of interest when in the satellite's view (Müllerova et al. 2017, Nowak et al. 2019). Ground cover will also affect bird visibility, making satellite imagery unsuitable for monitoring burrow-nesting species and those nesting in dense habitat such as long grass. Furthermore, none of the freely available satellite images has < 1 m spatial resolution and acquiring images from commercial suppliers is expensive (Nowak et al. 2019). Consequently, satellites can offer a cost-effective method of counting some seabird populations, but only if they can be viewed at the necessary spatial and temporal resolution from freely available images. This means satellites are most likely to be cost-effective in remote locations that are not readily accessible, and are more suitable for monitoring bigger species, such as penguins, and those that leave obvious signs of presence, such as substantial areas of faecal staining (Fretwell & Trathan 2009). Satellites are unlikely to facilitate monitoring of large numbers of small breeding seabird colonies.

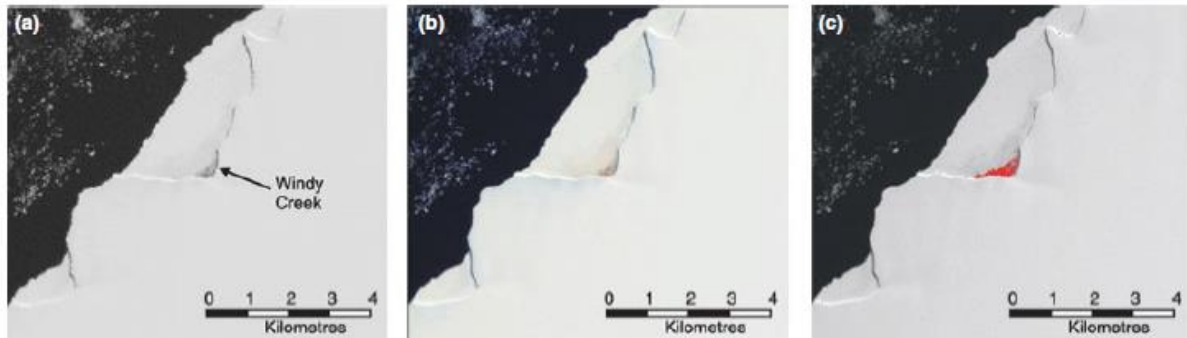


Figure 1. Landsat ETM imagery used to identify the Windy Creek Emperor Penguin *Aptenodytes forsteri* colony from faecal stains. (a) Data viewed online from the Landsat Image Mosaic of Antarctica (LIMA) website showed a potential penguin colony. (b) Data downloaded from the LIMA website and viewed in GIS clearly showed the brown faecal staining of the colony. (c) Spectral analysis identified areas where the red band had a higher value than the blue band. The resulting positive area, shown in red, located the exact area of the colony (Fretwell & Trathan, 2009). Images: MAXAR.

Manned aircraft

Aerial seabird surveys are more commonly conducted with manned aircraft (Fig. 2) or UAVs, rather than satellites (Loarie et al. 2007, Rush et al. 2018). Compared with boats, manned aircraft afford a more cost-effective technique for surveying large areas of sea and inland bodies of water (Camphuysen et al., 2004). The shorter survey time of manned flights at high speed reduces the risk of double-counting, which increases count accuracy. However, this benefit may be negated by reduced time to detect and identify smaller or less abundant species, meaning that surveys of inshore seabirds rarely detect grebes, Common Goldeneye *Bucephala clangula* or Black-throated Diver *Gavia arctica* (Joint Nature Conservation Committee 2010). As a result, land- and boatbased counts are often used alongside aerial surveys to ensure that birds are not missed (Joint Nature Conservation Committee 2010). This increases survey effort and thus the time and money required for effective monitoring using manned aircraft.

Installing manned aircraft with cameras might reduce the need for accompanying land- and boat-based surveys. Photographs and videos provide a permanent record that can be used to identify additional individuals that surveyors might have missed (Hutchinson 1980). This is supported by a study in Carmarthen Bay (Wales, UK), which found that visual aerial surveys gave lower estimates of Common Scoter *Melanitta nigra* abundance compared with digital images and videos taken from an aeroplane (Buckland et al. 2012). Digital aerial surveys could also be used to count surface-nesting seabirds, including Arctic Skua *Stercorarius parasiticus*, terns, and Lesser Black-backed *Larus fuscus* and Great Black-backed Gull *Larus marinus*. Aerial surveys reduce habitat disturbance compared with traditional colony walkthrough methods and reduce disruption to nesting birds (Brisson-Curadeau et al. 2017, Rush et al. 2018). Taking digital photographs and videos from manned aircraft can further lower behavioural stress responses, as this allows the vehicle to be flown at higher altitude. This is because aerial surveyors must be close enough to the birds to allow accurate identification and counts, whereas images can be magnified during analysis (Thaxter & Burton 2009, Kemper et al. 2016).



Figure 2. Aerial photograph of the gannetry on Grassholm Island, UK, 2015. Image: Sarah Money.

The benefits of reduced disturbance and increased accuracy must be balanced against the high purchase and operational costs of manned aircraft (Hutchinson 1980). This includes the price of fuel, hiring a pilot with a professional aviation licence and, if photographs or videos are desired, camera installation and hiring a camera operator (Wilhelm et al. 2015, Nowak et al. 2019). In the past, photographs were taken through windows using handheld cameras, whereas most studies today install fixed cameras to improve image quality and consistency (Hutchinson 1980, Wilhelm et al. 2015). Additionally, manned aircraft are restricted in where they can operate, as they require a nearby airport, fulfilment of aviation procedures and are not manoeuvrable over small areas (Nowak et al. 2019). Moreover, at-sea aerial surveys are not advised in winds greater than Beaufort 4 to reduce the likelihood of inaccurate counts, as can happen, for example, if white wave caps are confused with gulls (Thaxter & Burton 2009).

Monitoring seabirds using imagery from manned aircraft has some disadvantages. The high cost means that temporal resolution is typically low, so manned flight surveys are best deployed to obtain infrequent population counts, rather than time-series data such as breeding success (Anderson & Gaston 2013, Lyons et al. 2019). Manned aircraft are unlikely to reduce disturbance to surface-nesting seabirds that can be monitored from a single vantage point, although they could be a useful alternative to walk-through surveys. The benefits of using manned aircraft are therefore context- and species-dependent but could appreciably benefit sensitive species and sites. Increasingly, many studies are now turning to UAVs for aerial monitoring to overcome some of the challenges faced by manned aircraft (Anderson & Gaston 2013).

Unmanned aerial vehicles (UAVs)

The number of environmental biology studies using UAVs has increased markedly in the past 20 years, particularly since 2011 (Nowak et al. 2019). UAVs are known under a variety of terms, including: unmanned aerial systems, remotely piloted aircraft and, colloquially, 'drones'. They are small, powered aerial vehicles that can be flown remotely or autonomously and can carry a payload, such as a camera (Fig. 3).

To date, UAV imagery has mainly been used for counting nests or individuals and has even identified 'new' populations (Nowak et al. 2019, Pfeifer et al. 2019). A wide range of seabirds have been monitored using UAVs, including penguins (Spheniscidae) (Hodgson et al. 2016, Borowicz et al. 2018, Korczak-Abshire et al. 2019, Pfeifer et al. 2019), albatrosses (Diomedidae) (McClelland et al. 2016), terns and gulls (Laridae) (Sardà-Palomera et al. 2012, Grenzdörffer 2013, Chabot et al. 2015, Hodgson et al. 2016, Brisson-Curadeau et al. 2017, Rush et al. 2018), shags and cormorants (Phalacrocoracidae) (Irigoin-Lovera et al. 2019, Korczak-Abshire et al. 2019, Oosthuizen et al. 2020), auks (Alcidae) (Brisson-Curadeau et al. 2017), frigatebirds (Fregatidae) (Hodgson et al. 2016, Villegas et al. 2018), boobies (Sulidae) (Irigoin-Lovera et al. 2019), pelicans (Pelecanidae) (Irigoin-Lovera et al. 2019) and giant petrel species (*Macronectes* spp.) (Korczak-Abshire et al. 2019). As most UAVs allow camera rotation, cliff-nesting seabirds can be readily surveyed – a feat more difficult to achieve with satellites (Brisson-Curadeau et al. 2017). However, unlike satellites and manned aircraft, distant sea surveys are limited, as UAVs must typically remain in the line of sight of the controller to satisfy flight regulations (Nowak et al. 2019).

Increasingly, UAVs are being used for monitoring purposes other than population or nest counts. For example, UAV surveys have recorded fine-scale foraging behaviour of terns in relation to wakes created by strong currents interacting with man-made structures (Lieber et al. 2019). In addition, UAVs might also collect time-series data, for example to measure nesting success. They create less disturbance than manned aircraft due to being smaller and less noisy and are cheaper to purchase and operate (Goebel et al. 2015). This means multiple flights throughout the breeding season are more feasible in terms of animal welfare and cost, and flight height can be lower, which increases spatial resolution and accuracy. For example, minimum flight height for at-sea surveys using manned aircraft is 450 m, whereas UAVs are regularly flown at < 100 m (Thaxter & Burton 2009). Nonetheless, UAVs can still disturb breeding seabirds. The behavioural response to UAV flight should be measured before studies to ensure that it does not exceed that of traditional field monitoring methods such as walk-through surveys.



Figure 3. DJI Inspire 1 quadcopter unmanned aerial vehicle (UAV) fitted with a DJI FC350 camera being used to survey Lesser Black-backed Gull nests on Skokholm Island, UK, 2016 (Rush et al. 2018). Image: Matt Wood.

The magnitude of behavioural response depends on the type of UAV; flight parameters, including altitude and speed; take-off location relative to the colony; and the species being monitored (Rümmler et al. 2016, Brisson-Curadeau et al. 2017, Mulero-Pázmány et al. 2017, Rush et al. 2018, Weimerskirch et al. 2018, Irigoien-Lovera et al. 2019). Rümmler et al. (2018) found that Adélie Penguins *Pygoscelis adeliae* reacted to a small octocopter UAV at the highest test altitude of 50 m, whereas Gentoo Penguins *Pygoscelis papua* only reacted below 30 m. In another study, Adélie Penguins did not respond to fixed-wing electric UAVs at 350 m altitude but did show vigilance and increased activity levels in response to UAVs flown at the same height but powered by a piston engine (Korczak-Abshire et al. 2016). Deciding on a suitable flight protocol to minimize disturbance is therefore difficult, as it will vary between and within species depending on a variety of factors. For example, there may be intra-species variation in response at different locations due to variable aerial predation levels or variation in response by the same colony at different times of the year. Consequently, it seems wise that test flights should always be conducted before using UAVs for seabird monitoring.

National flight regulations mean that both a pilot and ground-level observer are often required for UAV flights (Nowak et al. 2019). Although this increases the cost of UAV studies, especially as pilots require training, it allows a dedicated ground-level observer to focus on monitoring disturbance levels to ensure that flights are conducted safely. Legal restrictions also limit UAV flight parameters, including maximum altitude, speed and use over reserves, which can affect the possibility of data acquisition (Nowak et al. 2019). This may be further limited by adverse weather conditions, as UAVs are more vulnerable to damage during aerial surveys than are manned aircraft and satellites. For example, many small, lightweight UAVs, such as the AI-Multi (by Aerial Insight, Brandon, MB, Canada), cannot operate during precipitation, and wind often reduces image quality due to camera movements during flight (Chabot et al. 2015, Goebel et al. 2015).

Overall, UAV-based monitoring is likely to be effective for measuring breeding success or counting nesting seabirds, provided disturbance is not greater than traditional monitoring methods. UAVs are particularly cost-effective if the window for fieldwork is short, and they can survey areas inaccessible by foot or vehicle, such as sea-stacks (Lyons et al. 2019, Oosthuizen et al. 2020). On the other hand, aerial surveys are not necessary for seabirds that can be viewed from a single vantage point (Table 1). In that case, time-lapse photography may be a better alternative to traditional point surveys than UAVs.

Table 1. Advantages and disadvantages of using unmanned aerial vehicles (UAVs) to monitor seabirds.

Advantages	Disadvantages
Cost-effective: short survey time, low purchase and operation costs (Bibby et al. 2000, Buckland et al. 2012, Rush et al. 2018, Villegas et al. 2018, Nowak et al. 2019)	More affordable UAVs take lower resolution images (Nowak et al. 2019)
Portability and limited launch requirements allow operation in most locations and terrains (Goebel et al. 2015)	National and regional administrative regulations can affect possibility of data acquisition (Nowak et al. 2019)
Manoeuvrable, so can operate over small areas and monitor small objects (Nowak et al. 2019)	Reduced use in areas with limited electricity (Radjawali et al. 2017, Nowak et al. 2019)
Operate at locations and times when ground-based field observations would be near-impossible. For example, remote locations, onshore and offshore, difficult terrain, at night (Rush et al. 2018)	Vulnerable to damage in adverse weather conditions (McClelland et al. 2016)
Greater control over the scale, quality, and temporal and spatial resolution of images (Thaxter & Burton 2009, Rush et al. 2018, Korczak-Abshire et al. 2019, Nowak et al. 2019)	Large amount of data to handle and analyse (Rush et al. 2018)
Downward-facing view can observe birds in a range of habitats and help reduce missed counts (Rush et al. 2018, Villegas et al. 2018)	Data quality depends on operator skill, environment and meteorological conditions during flight (Nowak et al. 2019)
Combine habitat mapping and seabird occupancy from images, to investigate how habitat features affect populations (Oosthuizen et al. 2020)	Animals may modify their behaviour in response to a flying object, increasing intraspecific aggression, predation of eggs/chicks and nest abandonment (Rush et al. 2018, Nowak et al. 2019)
Permanent record viewable any number of times and available for independent verification (Thaxter & Burton 2009, Buckland et al. 2012, Rush et al. 2018)	
Reduced nest and site disturbance compared with walk-through surveys (Rush et al. 2018)	
Reduced disturbance when flown at the same height as manned aircraft (Goebel et al. 2015, Korczak-Abshire et al. 2019)	
Removes observer bias from variation in surveyor experience and alertness over a long period. This is useful when observers are swamped with a large number of birds to count (Bibby et al. 2000, Thaxter & Burton 2009, Rush et al. 2018)	

Fixed position cameras

Time-lapse cameras

Time-lapse photography records images at predetermined time intervals regardless of subject presence (Cutler & Swann 1999). It has been used for avian studies since the technology first became commercially available, although its potential uses in ornithology are quickly increasing with advances in digital technology (Dodge & Snyder 1960, Green & Anderson 1961, Cowardin & Ashe 1965, Temple 1972, Weller & Derksen 1972, Harris 1982, Huffeldt & Merkel 2013). The increased availability of affordable cameras, requiring less frequent maintenance, with reduced power consumption and larger data storage capacity, has seen the field of time-lapse photography expand rapidly in recent years (Bolton et al. 2007).

Time-lapse cameras are most appropriate for studying animals frequently present at a location, where a single vantage point gives a representative view of individuals and where the measurement of interest will not activate a motion-triggered camera (Cutler & Swann 1999, Black 2018). Species that aggregate at high densities at some point in their life-history, such as breeding seabirds, therefore represent ideal candidates for use (Fig. 4) (Black 2018). Time-lapse cameras are suited for collecting data as part of long-term studies, principally time-series data such as annual breeding success and phenology, and have a number of advantages over traditional field observations (Southwell & Emmerson 2015, Merkel et al. 2016, Hinke et al. 2018, Black et al. 2018a). First, time-constraints placed on fieldworkers and external conditions such as weather mean that direct observations of nesting success are typically recorded less frequently than time-lapse photographs (Walsh et al. 1995). Most studies set cameras to record one image per hour and are only returned to once per year to change SD cards and batteries (Southwell & Emmerson 2015, Black et al. 2018a). This means that time-lapse photography can improve temporal resolution and data accuracy with reduced time investment.

High temporal resolution also makes time-lapse photography suitable for measuring numerous other parameters. This includes nest activity (such as nest attendance and division of labour between parents), re-sighting marked birds to determine adult survival and foraging behaviour, and population counts of breeding birds year-round, allowing insights into over-winter site attendance (Weller & Derksen 1972, Mudge et al. 1987, Black et al. 2017, 2018b, Pascalis et al. 2018). Additionally, time-lapse cameras can provide evidence of infrequent events not purposefully monitored (Harris 1982, Black et al. 2017, 2018b). For example, time-lapse photographs have recorded Black-legged Kittiwake *Rissa tridactyla* chick predation by a Peregrine Falcon *Falco peregrinus* (Collins et al. 2014). Predation may be under-recorded by fieldworkers and aerial surveys, as both human and aircraft presence could deter predatory activity. Similarly, cameras might capture adult seabirds carrying prey, which could give information on chick diet.



Figure 4. Time-lapse photograph of nesting Black-legged Kittiwakes at Protheroes Dock, Skomer Island, UK, 2018. Image: Seabird Watch.

As well as their diverse range of uses, time-lapse cameras are unlikely to have an adverse effect on the wildlife they monitor, provided they are installed and maintained outside the breeding season and are located at a safe distance from breeding birds (Merkel et al. 2016). Determining a 'safe' distance is difficult, but the distance kept by fieldworkers could be a provisional minimum (Joint Nature Conservation Committee 2016). Limited disturbance also means cameras can collect data regardless of abiotic conditions. For example, the UK 'Seabird Count' instructs surveyors to avoid visiting colonies in winds stronger than Beaufort 4 or during heavy and continuous rain, as disturbance during wet weather can leave eggs and chicks vulnerable to chilling and weather conditions can affect colony attendance, so that this strict protocol helps to ensure count comparability across years and colonies (Joint Nature Conservation Committee 2016).

The infrequency of human visits (i.e. yearly maintenance) allows time-lapse cameras to capture images in locations and at scales otherwise unfeasible in terms of time, money and human capabilities, such as in harsh conditions and remote places (Weller & Derksen 1972, Black et al. 2017, 2018a, 2018b, Black 2018, Pascalis et al. 2018). Already, extensive camera networks in the Antarctic have provided data on previously unmonitored penguin colonies (Southwell & Emmerson 2015). Nonetheless, maintaining camera networks is expensive and, if only visited once annually, a large amount of data could be lost from mechanical failure between visits. Camera set-up is also a crucial consideration to ensure useful and reliable data are obtained (Lorentzen et al. 2010). Increasing the distance between camera and colony will increase the number of birds viewed per frame but will lower image resolution. A study on pygoscelid penguins suggested approximately 20 nests could be reliably monitored for the duration of the breeding season, but this depended on nest density and topography (Hinke et al. 2018). The optimal camera angle and horizontal and vertical distance from the colony will therefore be specific to location, study species and study purpose

(Lorentzen et al. 2010). A summary of the advantages and disadvantages of time-lapse photography as a tool for monitoring seabirds is given in Table 2.

Table 2. Advantages and disadvantages of using time-lapse photography to monitor seabirds.

Advantages	Disadvantages
Cost-effective: saves time and money during fieldwork. For example, difficult for a single researcher to record detailed nest activity across multiple nests at a colony (Weller & Derksen 1972, Black 2018, Pascalis et al. 2018)	Mechanical failures (Cutler & Swann 1999, Merkel et al. 2016, Black 2018)
Increased spatial and temporal scale of monitoring (Southwell & Emmerson 2015, Merkel et al. 2016)	Programming errors (Cutler & Swann 1999, Black 2018)
Operates at locations and times when field observation would be near-impossible. For example, remote locations, harsh weather conditions, at night (Cutler & Swann 1999, Southwell & Emmerson 2015, Black et al. 2017, Sinclair et al. 2017, Black 2018, Black et al. 2018a, 2018b)	Maintenance required. For example, images are vulnerable to camera movements caused by harsh weather conditions (Merkel et al. 2016, Black 2018)
Removes observer bias from variation in surveyor experience and alertness over a long period (Cowardin & Ashe 1965, Weller & Derksen 1972, Cutler & Swann 1999, Black 2018)	More affordable cameras take lower resolution images (Black 2018)
More frequent observations than fieldworkers allows observation of elusive species, obscure behaviours and phenology (Cutler & Swann 1999, Black 2018)	Large camera networks needed to monitor an entire colony, which are expensive to install and maintain (Black 2018)
Permanent record viewable any number of times and available for independent verification (Cutler & Swann 1999, Merkel et al. 2016, Sinclair et al. 2017, Black, 2018)	Large amount of data to handle and analyse (Merkel et al. 2016, Black 2018)
Easier to maintain comparable study effort between years (Merkel et al. 2016)	Cameras rarely possess thermal imaging or infra-red sensors, making night monitoring difficult (Black et al. 2018a, 2018b)
Infrequent visitation lowers nest and site disturbance (Cutler & Swann 1999)	

Video cameras

Videography is similar to time-lapse photography, except that observations are recorded continuously. It may be preferable when constant field measurements are required, as time-lapse cameras might miss an event that occurred between photographs and results would not be comparable with field observations, introducing bias into long-term studies. Examples include recording incubation behaviour, thermoregulatory responses and rate of adult provisioning (Frederiksen et al. 2019, Cook et al. 2020, Williams & DeLeon 2020).

Frederiksen et al. (2019) used video surveillance to measure chick feeding rates of Little Auk *Alle alle* in northeast Greenland. Traditional methods required 12- or 24-h surveillance in the field,

which is time-consuming, physically demanding and renders results liable to error from observer fatigue, even when monitoring is conducted in shifts (Harding et al. 2007, Mosbech et al. 2017). Although videos take a long time to analyse manually, the ability to increase playback speed means that periods of inactivity can be watched quickly and important events can be slowed down, re-wound and re-watched innumerable times to ensure that accurate records are made. Moreover, processing can take place independently of external abiotic conditions that inhibit direct observations in the field. Having said this, poor weather can reduce image quality, meaning that neither video nor time-lapse cameras deliver useable data in all conditions.

Unfortunately, the large amount of data recorded by video cameras per unit time means that SD cards and batteries must be replaced regularly, often daily (Mosbech et al. 2017, Frederiksen et al. 2019). This makes continuous videography only suitable in locations readily accessible by humans. For most studies requiring data with high temporal resolution, time-lapse cameras are a more cost-effective option.

Motion-triggered cameras

For studies where measurements do not need to be made at regular intervals or continuously, motion-triggered cameras are an alternative to static time-lapse or video cameras. Movement in front of the sensor triggers photographs or a short video sequence to be recorded, allowing capture of individual, instantaneous events (Black 2018). So far, motion-triggered cameras have been most frequently deployed in seabird research to examine the impact of nest predation on breeding success (Hervías et al. 2013, Thiebot et al. 2014, Davies et al. 2015, Ekanayake et al. 2015, Luna et al. 2018, Whelan et al. 2018, Stolpmann et al. 2019). In some cases, this has provided support for removal of introduced predators at seabird colonies (Davies et al. 2015). Motion-triggered cameras are likely to be more effective at monitoring predation than time-lapse cameras, as the camera should be triggered whenever a predator enters the field of view, rather than at specific time points. Another use of motion-triggered cameras has been to understand nesting seabird behaviours, such as incubation and foraging patterns. They can record the time at which parents exchange incubation duty or when one parent returns from a foraging trip to feed the young (Hart et al. 2016, Mendez et al. 2017). This could allow assessment of seabird diet for species that load prey in their bills.

One of the difficulties of deploying motion-triggered cameras is to prevent irrelevant motion in the surrounding environment causing false triggers. This is often due to vegetation moving in the wind, and although some vegetation could be removed from the camera's zone of detection, the environment should ideally be altered as little as possible (Van Berkel 2014). Alternatively, positioning cameras closer to the object of interest, such as a seabird nest, can reduce false triggers but severely limits spatial coverage (Van Berkel 2014). Each camera might therefore only view one or two nests. This greatly increases the number of cameras required, and thus cost, if many nests need to be monitored.

Handheld cameras

Another form of digital photography that has been used to investigate seabird diet is the handheld camera (Table 3). Although time-lapse and motion-triggered cameras may capture seabirds with prey, purposefully taken photographs of prey-carrying seabirds can record the diet of a greater number of individuals, given that handheld cameras do not have a fixed field of view. Traditional techniques to investigate seabird diet predominantly focus on morphological analysis and include visual identification of prey species and size in the field, as well as mist-netting adults to obtain whole prey or regurgitates or collecting regurgitates from chicks, either from the ground or using ligatures (Votier et al. 2003, Barrett et al. 2007, Forsys & Hevesh 2017, Gaglio et al. 2017). More recently, the use of molecular and biochemical techniques in diet studies has dramatically increased, particularly DNA and stable isotope analysis of blood and faecal samples (Horswill et al. 2018). Each method of diet analysis has its own advantages and limitations. In general, sample collection has the obvious disadvantage of disturbing birds, while direct observation is more likely to result in incorrect identification, especially when trying to estimate prey size in the field. Conversely, taking photographs of adult seabirds carrying prey is non-invasive provided that a safe distance is kept between bird and photographer. It also produces a permanent record for checking identification of species and size and is more likely to capture the entire prey item. For example, terns often only regurgitate the posterior body and caudal fin, making identification of similar species challenging (McLeay et al. 2009).

Gaglio et al. (2017) showed that photo-sampling produced similar estimates of Greater Crested Tern *Thalasseus bergii* prey composition and size compared with regurgitations, and at a faster species accumulation rate. Over three breeding seasons they were able to double the known diversity of prey taken by two Great Crested Tern colonies. Likewise, photo-sampling increased the known number of fish species fed to Black Skimmer *Rynchops niger* chicks by 29% (Forsys & Hevesh 2017).

Handheld cameras could allow seabird diet to be monitored at greater scales than before, as photographs can be accumulated faster than prey samples. There is already a large wildlife photography community capturing seabirds with prey, offering a rich source of diet data. This use of citizen science was recognized by Forsys and Hevesh (2017), who used Facebook and Flickr to ask for photographs of Black Skimmer adults carrying prey. From 211 photographs, they conducted a small study of chick diet during the 2015–2016 breeding season. At a much larger scale, the RSPB Project Puffin UK is currently requesting photographs of Atlantic Puffins *Fratercula arctica* carrying prey from any year, to better understand spatial and temporal variation in diet (Fig. 5; RSPB 2020).

Table 3. Advantages and disadvantages of photo-sampling for obtaining information on seabird chick diet.

Advantages	Disadvantages
Non-invasive, assuming photographers remain a safe distance from birds (Gaglio et al. 2017)	Only suitable for species that carry prey in their bills (Gaglio et al. 2017)
Possible in a range of locations, including from land and boat (Gaglio et al. 2017)	Large amount of data to handle and process (Gaglio et al. 2017)
Large amounts of data can be collected in a short time-period	Repeated photography of individuals carrying the same prey load (Gaglio et al. 2017)
Minimal training to use cameras (Gaglio et al. 2017)	Observer bias (Gaglio et al. 2017)
Equipment relatively affordable and durable (Gaglio et al. 2017)	Chick diet is not always representative of adult diet, or diet outside the breeding season (McLeay et al. 2009, Gaglio et al. 2017)
Permanent record of observations available for independent verification and re-analysis without loss of quality. For example, prey samples degrade over time (Gaglio et al. 2017)	Challenging in poor weather conditions (Gaglio et al. 2017)
Only requires one individual to collect photographs (Gaglio et al. 2017)	Large-scale studies across multiple locations/species are time-consuming, unless multiple people are deployed
More likely to record the entire prey item than regurgitations, aiding accurate identification (McLeay et al. 2009, Gaglio et al. 2017)	



Figure 5. Photograph of an Atlantic Puffin carrying prey, submitted to RSPB Project Puffin UK. Image: Alice Edney.

Of course, using photography to investigate diet is only feasible for seabirds that carry prey in their bills. Moreover, photographs take time to process and strict protocols are required to minimize bias. For example, birds should be photographed at random, rather than focusing on individuals carrying large, interesting or multiple prey items. For studies using citizen science, it can be hard to ensure that protocols have been followed, especially when mining existing databases, and so quantification of suspected biases in method is essential. Project Puffin UK suspected that Puffins carrying large prey were more likely to be spotted and photographed than those carrying small prey. To quantify this potential size-bias, a researcher took photographs of any Puffin approaching a colony on the Farne Islands (England, UK) regardless of whether it appeared to have prey. Photographs containing prey will be compared with images taken by members of the public at the same location and in the same year to quantify any size-bias (E. Owen pers. comm.).

Animal-borne cameras

The final type of digital imaging device to consider is an animal-borne camera. Originally, the large size of these devices limited their deployment to mammals and captive and/or flightless birds (Watanuki et al. 2008). However, gradual miniaturization of the technology has since allowed use on unhabituated, free-ranging seabirds (Moll et al. 2007, Watanuki et al. 2008). Bird-borne cameras can record still images or videos and are unique in that they provide observations from the perspective of the animal (Moll et al. 2007, Tremblay et al. 2014). This makes them particularly well suited for understanding fine-scale interactions between seabirds and their environment (Moll et al. 2007). Cameras on seabirds have been particularly useful for providing insight into foraging behaviours. This includes foraging habitat selection (Watanuki et al. 2008), movement patterns (Ponganis et al. 2000, Tremblay et al. 2014), and interactions with prey (Grémillet et al. 2006, Handley & Pistorius, 2016, Handley et al. 2018), fisheries (Votier et al. 2013), conspecifics (Takahashi et al. 2004, Yoda et al. 2011) and other predator species during foraging (Sakamoto et al. 2009, Yoda et al. 2011, Thiebault et al. 2014).

One of the main limitations of animal-borne cameras is system lifespan (Moll et al. 2007). The ethical requirement for minimized camera size limits battery capacity and means that recording duration is often under 2 h, especially for continuous video recordings (Grémillet et al. 2006, Moll et al. 2007, Hooker et al. 2008, Yoda et al. 2011, Thiebault et al. 2014, Tremblay et al. 2014, Handley et al. 2018). Battery power is a greater limitation than data storage capacity for cameras connected to a transmitter because the data can be relayed to a remote downloading station (Moll et al. 2007, Hays 2015). Downloading data remotely is advantageous because it means data are not lost if the device cannot be retrieved. However, constraints on bandwidth available through data relay platforms, such as the Argos service, can again limit the duration of camera deployment (Hays 2015).

Recapturing birds to recover cameras can be challenging and frequently restricts studies to breeding adults that can be re-caught on the nest (Watanuki et al. 2008, Sakamoto et al. 2009, Votier et al. 2013, Tremblay et al. 2014). Equally, the difficulty of recapture, ethical implications of handling

and attaching devices to birds, and high cost of each device, means most studies only deploy cameras on a small number of individuals, commonly < 10 (Ponganis et al. 2000, Takahashi et al. 2004, Grémillet et al. 2006, Moll et al. 2007, Bluff & Rutz 2008, Watanuki et al. 2008, Sakamoto et al. 2009, Yoda et al. 2011, Bicknell et al. 2016). Small sample size can sacrifice robust population-level inferences, although the ability to collect novel data from the field of view of the seabird should not be overlooked (Hebblewhite & Haydon 2010).

Night-vision

One advantage of using any form of digital imaging technology for seabird monitoring is the improved ability to make observations at night using infra-red illumination and/or thermography. Infra-red illumination allows cameras to take photographs and videos in the dark by shining infrared light on the area of interest. This reduces disturbance to burrow-nesting seabirds and seabirds being monitored at night compared with visible light flash photography, as infra-red wavelengths are invisible to birds and mammals (Perkins et al. 2018). Collins et al. (2014) were able to observe night-time predation of Black-legged Kittiwake nests on Puffin Island (Wales, UK) from infra-red images captured by an Lti-Acorn 5210MC time-lapse camera. Conversely, infra-red thermography (thermal imaging) does not itself emit light, but instead detects infra-red radiation (heat) emitted by animals (McCafferty 2013). It is often used to detect and count nesting sites, with Israel and Reinhard (2017) using a UAV-borne thermal camera to detect camouflaged Northern Lapwing *Vanellus vanellus* nests. This has potential for locating inconspicuous nests of surface-nesting seabirds, such as gulls and terns.

Limitations of digital image collection

In summary, digital imaging technology has the potential to increase accuracy, cost-effectiveness and scale of seabird data collection, while reducing disturbance to breeding birds. Nevertheless, it is not a 'silver bullet' solution. Different technologies have different uses and some species cannot easily be monitored using digital imagery, such as burrow-nesting seabirds. Perkins et al. (2018) concluded that infra-red filming was a costly and inefficient method for counting European Storm Petrels *Hydrobates pelagicus* relative to tape playback, due to the large amount of expensive equipment and reviewing time needed. It would only be beneficial at sites that cannot otherwise be surveyed safely or where disturbance is a concern.

One of the main trade-offs for most digital imaging technologies is between cost and image resolution, which affects how well the object(s) of interest can be identified in photographs and videos. Image resolution is clearly affected by the choice of camera, including the number of pixels and optical quality of the lens. However, it is also influenced by factors specific to the image capture method. For example, reducing the flight speed of manned aircraft will improve video quality but increase flight time, and the latter increases costs of fuel and pilot hire (Mellor et al. 2007). Conversely, higher speeds can be achieved with less reduction in quality if higher frame rates are

used or the number of pixels is increased, both of which increase camera cost (Mellor et al. 2007). Increasing the depth of frame from 1000 pixels to 2500 pixels means a bird would stay in frame for the same amount of time at double the flight speed, or alternatively stay in frame for over twice as long at a given speed (Mellor et al. 2007). Dealing with this trade-off between cost and image resolution is difficult when funding is limited for wildlife monitoring (Waldron et al. 2013). Users must remember that image quality should be 'good enough' to provide data of equal or better accuracy than traditional non-digital methods, but it does not need to be 'exceptional'. Selecting an affordable method that will provide imagery of sufficient quality for the monitoring purpose is therefore all that can be recommended.

DATA PROCESSING AND ANALYSIS

For seabird species where digital photography and videography could aid data collection, it is important to consider current data processing and analysis methods. These must be feasible, in terms of time and money, and provide accurate data for the technology to be of value to seabird monitoring. So far, manual methods have been deployed most often, although rapid advances in semi-automated and automated information extraction are revealing that digital imagery can be a powerful and cost-effective monitoring technique.

Manual image analysis

Manual image analysis requires researchers to examine photographs individually and make the appropriate measurement, such as count the number of each species present or record re-sighted birds. If multiple images have been collected over time, then parameters such as breeding success and phenology can be calculated. For photographs taken by UAVs and manned aircraft, the images must be orthorectified prior to analysis to produce an orthomosaic (mosaic image with positional accuracy) using software such as AGISOFT PHOTOSCAN (Rush et al. 2018).

Accuracy

One of the most important considerations when deciding whether to analyse images manually is accuracy. An 'accurate' estimate can be defined as one that is close to the true value, for example the true population count (Gregory et al. 2004, Hodgson et al. 2016). The accuracy of manual counts firstly depends on the researchers' intrinsic ability to correctly identify and count individuals in an image. This can be termed 'count-accuracy'. Secondly, it depends on the image itself and whether it has captured all the individuals of interest, for example all active nests on the section of cliff being examined. This is 'image-accuracy'.

To increase count-accuracy by reducing misidentification of birds and counting errors, most studies have used counting tools. Users click on a bird to mark it, and the computer program automatically sums the number of marks to give a total count per image. Software commonly used

includes ImageJ (Merkel et al. 2016, Hurford 2017, Hodgson et al. 2018), Adobe Photoshop's count tool (Chabot et al. 2015, Goebel et al. 2015, Hodgson et al. 2016, Sinclair et al. 2017) and GIS environments (Sardà-Palomera et al. 2012, Lyons et al. 2019). ImageJ and QGIS are free, whereas users must pay for ARCGIS and Adobe Photoshop. Some researchers have built their own purpose-designed annotation software, such as 'Penguin Nest Picture Analyser' in JAVA (Southwell & Emmerson 2015) and the *Penguin Watch* interface on ZOOIVERSE (Black et al. 2017, Jones et al. 2018, 2020). Overall, the availability of free, easy-to-use counting tools means that researchers should not be limited by software in their ability to analyse digital images. To assist further with manual counting, several studies have overlaid grid cells on photographs and then made systematic, cell-specific counts (Hodgson et al. 2016, Korczak-Abshire et al. 2019). Count-accuracy can also be increased by brightening dull photographs (Sinclair et al. 2017).

It is not possible to assess count-accuracy directly unless the true image count is known. Instead, precision within counts of the same and different observers should be calculated (Sinclair et al. 2017). This means calculating the variance and/or standard deviation between replicated counts by the same and different counters attempting to count the same sample (Gregory et al. 2004, Hodgson et al. 2016, Sinclair et al. 2017, Korczak-Abshire et al. 2019). Unfortunately, this increases the time required for an already laborious task, so it has not become common practice.

As with count-accuracy, it is not possible to assess image-accuracy unless the true count in the wild is known. Nevertheless, comparison between traditional and digital photography methods can be informative. If results from traditional monitoring and digital image analysis do not differ significantly, then digital photography is at least 'as accurate as' traditional techniques. For example, no significant difference was found between ground and UAV-derived counts of penguins in Antarctica and terns in Australia, suggesting UAVs were suitable for these population counts (Goebel et al. 2015, Hodgson et al. 2016). Equally, a significant correlation between direct and time-lapse photography measurements of penguin breeding success in Antarctica supports the use of time-lapse cameras for measuring nesting success (Southwell & Emmerson 2015, Hinke et al. 2018). It is important that different researchers conduct ground surveys and image analysis to allow valid comparison of methods (Goebel et al. 2015).

Alternatively, if there is a statistically significant difference between traditional and digital image-derived results, then interpreting the accuracy of digital photography is more complicated. Further analysis of the data is required to assess whether traditional or digital methods are more accurate. For example, counts of Common Tern *Sterna hirundo* from UAV-derived images were 93–94% of traditional ground counts in North America (Chabot et al. 2015). UAV-derived counts were presumed to be less accurate, due to variable visibility of birds with ground cover, weather conditions and image quality. Conversely, UAV-derived counts of penguins and frigatebirds in Australia were significantly larger than ground counts. The authors suggested the downward-facing perspective of UAV images reduced the number of birds missed by topography and other birds obscuring the counters' line of sight in ground surveys (Hodgson et al. 2016). Such problems are likely to be species- and habitat-specific, thus reinforcing the notion that assessment of accuracy should be made on a case-by-case basis.

Depending on the parameters being measured, it may not be possible to perform statistical analyses with small sample sizes. Southwell and Emmerson (2015) found that the first date of Adélie Penguin arrival was 0–2 days later in time-lapse images than with direct observation, over 8 years, and the first egg was seen 2–6 days later in camera images, over 2 years. Later detection of first arrival was expected given the restricted spatial coverage of cameras compared with direct observers, and first egg detection was limited by temporal resolution. Incubating parents huddle tightly on the egg and reliable detection requires near-continuous observation (Southwell & Emmerson 2015). But should these small differences in dates prevent time-lapse cameras being used to measure penguin phenology? The answer will depend largely on the individual situation. Do the other advantages of time-lapse cameras compared with direct observation outweigh the costs of marginally different phenology measurements?

Moreover, in some locations, monitoring has only occurred with digital photography, making comparison with traditional methods impossible. This is typical of remote locations at high latitude with harsh environmental conditions and highlights how digital imaging technology can greatly increase the scale of monitoring (Black et al. 2017, 2018a, 2018b, Korczak-Abshire et al. 2019). For these studies, it is particularly important to calculate the variance of intra- and interobserver counts of the same image to ensure high count-accuracy.

Cost

One of the main disadvantages of manual image analysis is the time required. This has probably prevented the wide-scale use of digital imaging methods such as time-lapse photography to date, as the volume of raw imagery collected can quickly exceed researchers' processing capabilities (Pascalis et al. 2018). To date, most studies have monitored only a single colony of interest (Southwell & Emmerson 2015, Black et al. 2017). The time required per image depends on the number of birds per photograph, image quality and the experience of the analyser, although this can be decreased using a variety of methods. Sinclair et al. (2017) assessed how manual counts of Common Guillemot *Uria aalge* were affected if only one-quarter of the original image was counted. They found that counts from all quarters of an image were significantly correlated, meaning only the top right-hand corner needed to be sampled. This reduced post-processing from 7 to 3 min per photo. However, this method is only possible when seabirds are evenly distributed across the image.

Another and increasingly common method to reduce the time researchers spend processing images, at little extra cost, is to engage volunteer citizen scientists. Two projects currently advocating citizen science for seabird monitoring are *Penguin Watch* and *Seabird Watch* on the ZOOVERSE platform (<https://www.zooniverse.org>). Time-lapse photographs are uploaded onto the platform and volunteers click on birds to classify them as either adult or juvenile penguins (*Penguin Watch*), Black-legged Kittiwakes or guillemots (*Seabird Watch*) (Fig. 6). Each image is shown to four participants and if no animals are identified or the image is too dark/blurry to classify, the image is retired from the active dataset and not viewed by further volunteers. If any of the four participants identifies an animal, then the image is shown to an additional six people before being retired (Jones et al. 2018). Having

multiple people view each image increases data reliability and a field guide is available to aid bird identification and increase accuracy. For *Penguin Watch*, comparison between annotations made by citizen scientists and 'gold standard' researchers has validated the use of citizen science for identifying penguins in time-lapse photographs (Jones et al. 2018). This process is currently being followed for Seabird Watch, as well as a comparison between results from field observations and 'gold standard' researcher-analysed images (A. Edney unpubl. data).

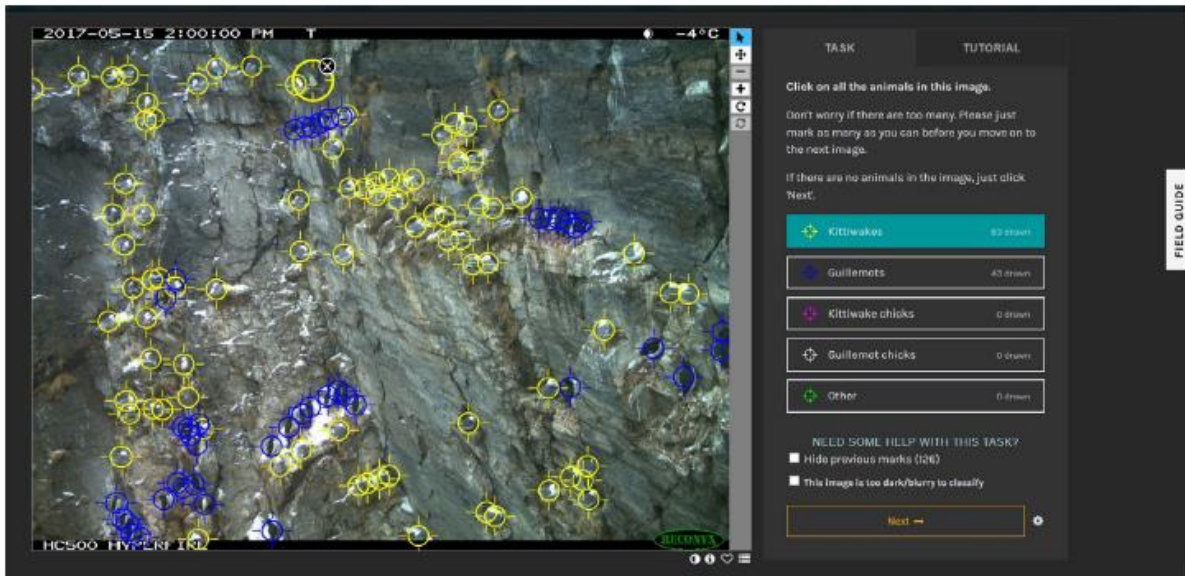


Figure 6. Annotated Seabird Watch image on the ZONIVERSE platform. Yellow circles mark adult Black-legged Kittiwakes and blue circles mark adult guillemots. Image annotated by Alice Edney.

Although citizen scientists reduce researcher post-processing time, the total amount of time for images to be analysed is often much longer. Volunteers cannot be given strict deadlines like paid researchers, meaning a large number of volunteers are needed for images to be analysed quickly. There are also concerns that an increasing number of citizen science projects will effectively 'flood the market', resulting in fewer participants per project. The most effective way to increase cost-efficiency of digital image analysis is to develop semi-automated and automated techniques.

Semi-automated image analysis

Semi-automated classification is a form of supervised classification. It is user-driven and cannot identify and count birds without human guidance (Fretwell et al. 2012, Rush et al. 2018). Most semi-automated classification involves finding a unique spectral signature for the object in question (e.g. the head of a gull) that can be used to identify all occurrences of this object in the image (Schwaller et al. 1989, Fretwell et al. 2012, Grenzdörffer 2013, Waluda et al. 2014, Hodgson et al. 2018).

Rush et al. (2018) offer a comprehensive description of one approach to semi-automated classification of nesting Lesser Black-backed Gulls counts from UAV images. In brief, the training sample manager tool in ARCGIS identified different spectral signatures of three species of gull and surrounding habitat features. The maximum likelihood tool performed supervised classification and identified the gull species in each image. A shapefile, with the outlines of objects identified as birds, was overlaid on every original image for manual editing. This process was quick to complete and involved systematically scanning the image and confirming whether objects in the shapefile were indeed birds. Non-bird objects were deleted. The number of Lesser Black-backed Gulls from semi-automated classification had a mean agreement of 104% with manual counts, due to some non-bird objects being incorrectly identified as gulls. Agreement was reduced to 98% via manual editing. This demonstrates that semi-automated classification of UAV images can provide accurate counts of a surface-nesting seabird with minimal disturbance.

Semi-automated classification would be especially useful for classifying birds in time-lapse photographs, as the sheer number of raw images collected can make manual classification unfeasible. Although it may be difficult to use for species that do not have good contrast with their surroundings, such as shags and cormorants on dark rocks, initial spectral analysis can quickly determine this (Grenzdörffer 2013, Lyons et al. 2019). It is also important to remember that human vision is limited to visible light, so different objects that appear the same colour to the human eye might still have a unique spectral signature that allows them to be separated.

Automated image analysis

Automated image analysis is a rapidly developing field that has the potential to vastly increase the scale of seabird monitoring. Automatic cell counting is frequently performed by cell biologists in ImageJ, using the 'Automatic cell counter' tool, but its transferability to seabird monitoring is limited due to the complexity of seabird colonies (Grishagin 2015).

The automated counter of ImageJ cannot differentiate between species and is most accurate when birds occur against a plain background (Hurford 2017). It is liable to underestimate the true count, due to overlapping birds being counted as one object, whereas birds with strongly contrasting plumage patterns may be overestimated (Hurford 2017). The high nest density of cliff-breeding species and the complex background created by the natural environment mean that automated counts in ImageJ are unlikely to be accurate for most seabird colonies. Nest density, terrain and vegetation should be carefully considered when choosing seabird colonies suitable for automated image analysis (Hinke et al. 2018).

Recently, more studies are developing machine-learning algorithms to identify birds in images, including those obtained from videos (Williams & DeLeon 2020). One example is the *Pengbot* algorithm, developed by the *Penguin Watch* team, to automatically identify and count penguins in time-lapse photographs (Jones et al. 2020). A similar tool is in the process of being developed for *Seabird Watch* (T. Hart pers. comm.). *Pengbot* uses a Convolutional Neural Network (CNN) to estimate an object (penguin) density map from which the number of objects (penguins) can be

obtained. Training the algorithm to recognize penguins and then testing it required in the order of 82 000 pre-annotated images provided by citizen scientists via *Penguin Watch* (Arteta et al. 2016). Without citizen science, labelling photographs is expensive in terms of time and money, especially if professionals are paid to do so via micropayment sites such as Amazon Mechanical Turk (Arteta et al. 2016, Wang et al. 2019).

Consequently, although automated image analysis can be cost-effective once machine-learning algorithms are up and running, it is important to remember the effort that goes into their development. For small-scale studies on a single species, manual or semi-automated analysis may be more achievable. Nevertheless, automated analysis of time-lapse photographs could monitor species at very large scales, by installing time-lapse cameras across their range.

CONCLUSIONS

We have critically assessed the use of a wide range of digital imaging methods for seabird monitoring, both from a data collection and from a data analysis perspective. All types of digital photography and videography create a permanent record of observations that can be validated and re-analysed. Many offer a cost-effective means of overcoming the challenges associated with 'traditional' methods for measuring specific demographic and behavioural parameters. The extent to which digital imaging methods are incorporated into seabird monitoring over the coming years will depend largely on advances in automated image analysis.

This leaves researchers to consider whether digital imaging technology could facilitate and/or replace their traditional monitoring techniques. There is a trade-off between potentially increased accuracy, cost-effectiveness and reduced disturbance, with reduced consistency in long-term studies. Long-term research conducted in the same way for many years needs to consider the risk of new methods biasing results. Where digital imaging could replace traditional methods, researchers must also consider the transition time required: how long should traditional and new methods be run in parallel before traditional methods are phased out? Decisions like this must be made on a case-by-case basis. Despite these unanswered questions, digital imaging technology has the potential to greatly assist seabird monitoring in a research environment with increasingly limited time and funding for conservation (Waldron et al. 2013).

We would like to thank Sarah Money and Peter Fretwell for providing photographs to include in the paper. We would also like to thank the University of Gloucestershire's Environmental Dynamics and Governance RPA for awarding A.J.E. a bursary to undertake an MSc by Research. Two anonymous reviewers provided helpful feedback on the manuscript.

AUTHOR CONTRIBUTIONS

Alice Jane Edney: Writing-original draft (lead); Writing-review & editing (lead). Matt Wood: Supervision (lead); Writing-original draft (supporting).

Data Availability Statement

This work has no associated data.

REFERENCES

- Ancel, A., Cristofari, R., Trathan, P.N., Gilbert, C., Fretwell, P.T. & Beaulieu, M. 2017. Looking for new Emperor Penguin colonies? Filling the gaps. *Global Ecol. Conserv.* 9: 171–179.
- Anderson, K. & Gaston, K.J. 2013. Lightweight unmanned aerial vehicles will revolutionize spatial ecology. *Front. Ecol. Environ.* 11: 138–146.
- Anker-Nilssen, T., Erikstad, K.E. & Lorentsen, S.-H. 1996. Aims and effort in seabird monitoring: an assessment based on Norwegian data. *Wildlife Biol.* 2: 17–26.
- Arteta, C., Lempitsky, V. & Zisserman, A. 2016. Counting in the wild. *Eur. Conf. Comput. Vis. LNCS*, 9911: 483–498. https://doi.org/10.1007/978-3-319-46478-7_30
- Barrett, R.T., Camphuysen, K. (.C.J.), Anker-Nilssen, T., Chardine, J. W., Furness, R. W., Garthe, S., Hüppop, O., Leopold, M. F., Montevecchi, W. A. & Veit, R. R. 2007. Diet studies of seabirds: a review and recommendations. *ICES J. Mar. Sci.* 64: 1675–1691.
- Bibby, C.J., Burgess, N.D., Hill, D.A. & Mustoe, S. 2000. *Bird Census Techniques*. London: Elsevier.
- Bicknell, A.W., Godley, B.J., Sheehan, E.V., Votier, S.C. & Witt, M.J. 2016. Camera technology for monitoring marine biodiversity and human impact. *Front. Ecol. Environ.* 14: 424–432.
- Black, C. 2018. Spying on seabirds: a review of time-lapse photography capabilities and limitations. *Seabird* 31: 1–14.
- Black, C., Rey, A.R. & Hart, T. 2017. Peeking into the bleak midwinter: investigating nonbreeding strategies of Gentoo 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. *Ecol. Evol.* 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.
- Bluff, L.A. & Rutz, C. 2008. A quick guide to video-tracking birds. *Biol. Lett.* 4: 319–322.
- Bolton, M., Butcher, N., Sharpe, F., Stevens, D. & Fisher, G. 2007. Remote monitoring of nests using digital camera technology. *J. Field Ornithol.* 78: 213–220.
- Borowicz, A., McDowall, P., Youngflesh, C., Sayre-McCord, T., Clucas, G., Herman, R., Forrest, S., Rider, M., Schwaller, M., Hart, T., Jenouvrier, S., Polito, M.J., Singh, H. & Lynch, H.J. 2018. Multi-modal survey of Adélie Penguin mega-colonies reveals the Danger Islands as a seabird hotspot. *Sci. Rep.* 8: 1–9.
- Brisson-Curadeau, E., Bird, D., Burke, C., Fifield, D.A., Pace, P., Sherley, R.B. & Elliott, K.H. 2017. Seabird species vary in behavioural response to drone census. *Sci. Rep.* 7: 1–9.
- 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. *J. Appl. Ecol.* 49: 960–967.
- Camphuysen, K.J., Fox, A.D., Leopold, M.F. & Petersen, I.K. 2004. *Towards standardised seabirds at sea census techniques in connection with environmental impact assessments for offshore wind farms in the UK: a comparison of ship and aerial sampling methods for marine birds, and their applicability to offshore wind farm assessments*. NIOZ Report Commissioned by COWRIE Ltd., Texel: NIOZ.
- Chabot, D., Craik, S.R. & Bird, D.M. 2015. Population census of a large Common Tern Colony with a small unmanned aircraft. *PLoS One* 10: e0122588.
- Collins, P.M., Green, J.A., Dodd, S., Shaw, P.J.A. & Halsey, L.G. 2014. Predation of Black-legged Kittiwake Chicks *Rissa tridactyla* by a Peregrine Falcon *Falco peregrinus*: insights from time-lapse cameras. *Wilson J. Ornithol.* 126: 158–161.
- Cook, T.R., Martin, R., Roberts, J., Häkkinen, H., Botha, P., Meyer, C., Sparks, E., Underhill, L.G., Ryan, P.G. & Sherley, R.B. 2020. Parenting in a warming world: thermoregulatory responses to heat stress in an endangered seabird. *Conserv. Physiol.* 8: coz109.

- Cowardin, L.M. & Ashe, J.E. 1965. An automatic camera device for measuring waterfowl use. *J. Wildl. Manage.* 29: 636–640.
- Croxall, J.P., Butchart, S.H.M., Lascelles, B., Stattersfield, A.J., Sullivan, B., Symes, A. & Taylor, P. 2012. Seabird conservation status, threats and priority actions: a global assessment. *Bird Conserv. Int.* 22: 1–34.
- Cutler, T.L. & Swann, D.E. 1999. Using remote photography in wildlife ecology: a review. *Wildl. Soc. Bull.* 27: 571–581.
- Davies, D., Dilley, B., Bond, A., Cuthbert, R. & Ryan, P. 2015. Trends and tactics of mouse predation on Tristan Albatross *Diomedea dabbenena* chicks at Gough Island, South Atlantic Ocean. *Avian Conserv. Ecol.* 10.
- Dodge, W.E. & Snyder, D.P. 1960. An automatic camera device for recording wildlife activity. *J. Wildl. Manage.* 24: 340–342.
- Dolliver, J.E. 2019. *Using Satellite Imagery to Count Nesting Albatross from Space*. Master's thesis. Corvallis, OR: Oregon State University.
- Ekanayake, K.B., Sutherland, D.R., Dann, P. & Weston, M.A. 2015. Out of sight but not out of mind: corvids prey extensively on eggs of burrow-nesting penguins. *Wildl. Res.* 42: 509–517.
- Evans, P.G.H. 1986. Monitoring seabirds in the North Atlantic. In Monbailliu, X. (ed) *Mediterranean Marine Avifauna*: 179–206. Berlin: Springer.
- Field, S.A., Tyre, A.J. & Possingham, H.P. 2005. Optimizing allocation of monitoring effort under economic and observational constraints. *J. Wildl. Manage.* 69: 473–482.
- Forys, E.A. & Hevesh, A.R. 2017. Investigating Black Skimmer chick diets using citizen science and digital photography. *Southeast. Nat.* 16: 317–325.
- Frederiksen, M., Mosbech, A., Andersson, A.W., Castro, A.C., Egevang, C., Fort, J., Grémillet, D., Linnebjerg, J., Lyngs, P., Haaning Nielsen, H. & Rømer, J.K. 2019. *Population size and habitat use of breeding seabirds in northeast Greenland. Field studies 2017–2018*. Danish Centre for Environment and Energy Scientific Report 337. Roskilde: Aarhus University.
- Fretwell, P.T. & Trathan, P.N. 2009. Penguins from space: faecal stains reveal the location of Emperor Penguin colonies. *Glob. Ecol. Biogeogr.* 18: 543–552.
- 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.
- Fretwell, P.T., Trathan, P.N., Wienecke, B. & Kooyman, G.L. 2014. Emperor Penguins breeding on iceshelves. *PLoS One* 9: e85285.
- Fretwell, P.T., Scofield, P. & Phillips, R.A. 2017. Using super-high resolution satellite imagery to census threatened albatrosses. *Ibis* 159: 481–490.
- Gaglio, D., Cook, T.R., Connan, M., Ryan, P.G. & Sherley, R.B. 2017. Dietary studies in birds: testing a non-invasive method using digital photography in seabirds. *Methods Ecol. Evol.* 8: 214–222.
- Goebel, M.E., Perryman, W.L., Hinke, J.T., Krause, D.J., Hann, N.A., Gardner, S. & LeRoi, D.J. 2015. A small unmanned aerial system for estimating abundance and size of Antarctic predators. *Polar Biol* 38: 619–630.
- Green, G.W. & Anderson, D.C. 1961. A simple and inexpensive apparatus for photographing events at pre-set intervals. *Can. Entomol.* 93: 741–745.
- Gregory, R.D., Gibbons, D.W. & Donald, P.F. 2004. Bird census and survey techniques. In Sutherland, W.J., Newton, I. & Rhys, G. (eds) *Bird Ecology and Conservation: A Handbook of Techniques*. 17–52. New York, NY: Oxford University Press.
- Grémillet, D., Enstipp, M.R., Boudiffa, M. & Liu, H. 2006. Do cormorants injure fish without eating them? An underwater video study. *Mar. Biol.* 148: 1081–1087.
- Grenzdörffer, G.J. 2013. UAS-based automatic bird count of a common gull colony. *Int. Arch. Photogramm. Remote Sens. Spatial Inf. Sci.* 2: 169–174.
- Grishagin, I.V. 2015. Automatic cell counting with ImageJ. *Anal. Biochem.* 473: 63–65.

- Guinet, C., Jouventin, P. & Malacamp, J. 1995. Satellite remote sensing in monitoring change of seabirds: use of SPOT IMAGE in King Penguin population increase at Ile aux Cochons, Crozet Archipelago. *Polar Biol* 15: 511–515.
- Handley, J.M. & Pistorius, P. 2016. Kleptoparasitism in foraging Gentoo Penguins *Pygoscelis papua*. *Polar Biol* 39: 391–395.
- Handley, J.M., Thiebault, A., Stanworth, A., Schutt, D. & Pistorius, P. 2018. Behaviourally mediated predation avoidance in penguin prey: in situ evidence from animal-borne camera loggers. *Royal Soc. Open Sci.* 5: 171449.
- Harding, A.M.A., 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.
- Harris, M.P. 1982. Promiscuity in the Shag as shown by time-lapse photography. *Bird Study* 29: 149–154.
- Hart, L.A., Downs, C.T. & Brown, M. 2016. Sitting in the sun: nest microhabitat affects incubation temperatures in seabirds. *J. Therm. Biol.* 60: 149–154.
- Hays, G.C. 2015. New insights: animal-borne cameras and accelerometers reveal the secret lives of cryptic species. *J. Anim. Ecol.* 84: 587–589.
- Hebblewhite, M. & Haydon, D.T. 2010. Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. *Philos. Trans. R Soc. Lond. B Biol. Sci.* 365: 2303–2312.
- Hervías, S., Henriques, A., Oliveira, N., Pipa, T., Cowen, H., Ramos, J.A., Nogales, M., Gerales, P., Silva, C., de Ybáñez, R.R. & Opper, S. 2013. Studying the effects of multiple invasive mammals on Cory's Shearwater nest survival. *Biol. Invasions* 15: 143–155.
- Hinke, J.T., Barbosa, A., Emmerson, L.M., Hart, T., Juárez, M.A., Korczak-Abshire, M., Milinevsky, G., Santos, M., Trathan, P.N., Watters, G.M. & Southwell, C. 2018. Estimating nest-level phenology and reproductive success of colonial seabirds using time-lapse cameras. *Methods Ecol. Evol.* 9: 1853–1863.
- Hodgson, J.C., Baylis, S.M., Mott, R., Herrod, A. & Clarke, R.H. 2016. Precision wildlife monitoring using unmanned aerial vehicles. *Sci. Rep.* 6: 1–7.
- Hodgson, J.C., Mott, R., Baylis, S.M., Pham, T.T., Wotherspoon, S., Kilpatrick, A.D., Segaran, R.R., Reid, I., Terauds, A. & Koh, L.P. 2018. Drones count wildlife more accurately and precisely than humans. *Methods Ecol. Evol.* 9: 1160–1167.
- Hooker, S.K., Heaslip, S.G., Matthiopoulos, J., Cox, O. & Boyd, I.L. 2008. Data Sampling Options for Animal-Borne VideoCameras: Considerations Based on Deployments with Antarctic Fur Seals. *Mar. Technol. Soc. J.* 42: 65–75. <https://doi.org/10.4031/002533208786829179>
- HorswAncelill, C., Jackson, J.A., Medeiros, R., Nowell, R.W., Trathan, P.N. & O'Connell, T.C. 2018. Minimising the limitations of using dietary analysis to assess foodweb changes by combining multiple techniques. *Ecol. Ind.* 94: 218–225.
- 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.
- Hughes, B.J., Martin, G.R. & Reynolds, S.J. 2011. The use of Google Earth™ satellite imagery to detect the nests of Masked Boobies *Sula dactylatra*. *Wildlife Biol.* 17: 210–216.
- Hurford, C. 2017. Improving the accuracy of bird counts using manual and automated counts in ImageJ: an open-source image processing program. In Díaz-Delgado, R., Lucas, R. & Hurford, C. (eds) *The Roles of Remote Sensing in Nature Conservation: A Practical Guide and Case Studies*: 249–276. Cham: Springer International Publishing.
- Hutchinson, A.E. 1980. Estimating numbers of colonial nesting seabirds: a comparison of techniques. *Proc. Colonial Waterbird Group* 3: 235–244.
- Irigoin-Lovera, C., Luna, D.M., Acosta, D.A. & Zavalaga, C.B. 2019. Response of colonial Peruvian guano birds to flying UAVs: effects and feasibility for implementing new population monitoring methods. *PeerJ* 7: e8129.

- Israel, M. & Reinhard, A. 2017. Detecting nests of lapwing birds with the aid of a small unmanned aerial vehicle with thermal camera. In: *2017 International Conference on Unmanned Aircraft Systems (ICUAS)*, pp. 1199–1207. Miami: IEEE.
- Joint Nature Conservation Committee 2010. *Seaduck survey data*. Available at: <http://archive.jncc.gov.uk/page-4570> (accessed 21 January 2020).
- Joint Nature Conservation Committee 2016. *Seabirds count: A census of breeding seabirds of Britain and Ireland. Census Instructions and Recording Form*. Available at: <http://archive.jncc.gov.uk/page-7485> (accessed 21 January 2020).
- 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., Simpson, R., Southwell, C., Torsey, H.R., Zisserman, A. & Hart, T. 2018. Time-lapse imagery and volunteer classifications from the Zooniverse Penguin Watch project. *Sci. Data* 5: 180124.
- Jones, F.M., Arteta, C., Zisserman, A., Lempitsky, V., Lintott, C.J. & Hart, T. 2020. Processing citizen science and machine-annotated time-lapse imagery for biologically meaningful metrics. *Sci. Data* 7: 1–15.
- Kemper, G., Weidauer, A. & Coppack, T. 2016. Monitoring seabirds and marine mammals by georeferenced aerial photography. *Int. Arch. Photogramm. Remote Sens. Spatial Inf. Sci.* 8: 689–694.
- Korczak-Abshire, M., Kidawa, A. & Zmarz, A. 2016. Preliminary study on nesting Adélie Penguins disturbance by unmanned aerial vehicles. *CCAMLR Sci.* 23: 1–16.
- Korczak-Abshire, M., Zmarz, A., Rodzewicz, M., Kycko, M., Karsznia, I. & Chwedorzewska, K.J. 2019. Study of fauna population changes on Penguin Island and Turret Point Oasis (King George Island, Antarctica) using an unmanned aerial vehicle. *Polar Biol.* 42: 217–224.
- Kucera, T.E. & 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: Methods and Analyses*: 9–26. Tokyo: Springer Japan.
- Lieber, L., Nimmo-Smith, W.A.M., Waggitt, J.J. & Kregting, L. 2019. Localised anthropogenic wake generates a predictable foraging hotspot for top predators. *Commun. Biol.* 2: 123.
- Loarie, S.R., Joppa, L.N. & Pimm, S.L. 2007. Satellites miss environmental priorities. *Trends Ecol. Evol.* 22: 630–632.
- Lorentzen, E., Steen, H. & Strøm, H. 2010. Estimating chick survival in cliff-nesting seabirds – a hazard made easy with monitoring cameras. *SEAPO Short Rep.* 8: 1–10.
- Luna, N., Varela, A.I., Brokordt, K. & Luna-Jorquera, G. 2018. Assessing potential predation risk by introduced predators on unattended eggs in the Red-Tailed Tropicbird, *Phaethon rubricauda*, on Rapa Nui (Easter Island). *Tropic. Conserv. Sci.* 11 <https://doi.org/10.1177/1940082918785079>
- Lynch, H.J., Naveen, R., Trathan, P.N. & Fagan, W.F. 2012a. Spatially integrated assessment reveals widespread changes in penguin populations on the Antarctic Peninsula. *Ecology* 93: 1367–1377.
- Lynch, H.J., White, R., Black, A.D. & Naveen, R. 2012b. Detection, differentiation, and abundance estimation of penguin species by high-resolution satellite imagery. *Polar Biol.* 35: 963–968.
- Lyons, M., Brandis, K., Wilshire, J., Murray, N., McCann, J., Kingsford, R. & Callaghan, C. 2019. A protocol for using drones to assist monitoring of large breeding bird colonies. *EcolEvolRxiv*. <https://doi.org/10.32942/osf.io/p9j3f>
- McCafferty, D.J. 2013. Applications of thermal imaging in avian science. *Ibis* 155: 4–15.
- McClelland, G.T., Bond, A.L., Sardana, A. & Glass, T. 2016. Rapid population estimate of a surface-nesting seabird on a remote island using a low-cost unmanned aerial vehicle. *Mar. Ornithol.* 44: 215–220.
- McLeay, L.J., Page, B., Goldsworthy, S.D., Ward, T.M. & Paton, D.C. 2009. Size matters: variation in the diet of chick and adult Crested Terns. *Mar. Biol.* 156: 1765–1780.

- Mellor, M., Craig, T., Baillie, D. & Woolaghan, P. 2007. Trial High Definition Video Survey of Seabirds. Cowrie Ltd. Mendez, L., Prudor, A. & Weimerskirch, H. 2017. Ontogeny of foraging behaviour in juvenile Red-footed Boobies (*Sula sula*). *Sci. Rep.* 7: 13886.
- 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. *J. Field Ornithol.* 87: 84–95.
- Mitchell, P.I. & Parsons, M. 2007. Strategic Review of the UK Seabird Monitoring Programme. *JNCC Unpubl. Rep.*
- Moll, R.J., Millsbaugh, J.J., Beringer, J., Sartwell, J. & He, Z. 2007. A new 'view' of ecology and conservation through animal-borne video systems. *Trends Ecol. Evol.* 22: 660–668.
- Mosbech, A., Lyngs, P. & Johansen, K.L. 2017. Estimating Little Auk (*Alle alle*) breeding density and chick-feeding rate using video surveillance. *Polar Res.* 36: 1374122.
- 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.
- Mulero-Pázmány, M., Jenni-Eiermann, S., Strebler, N., Sattler, T., Negro, J.J. & Tablado, Z. 2017. Unmanned aircraft systems as a new source of disturbance for wildlife: a systematic review. *PLoS One* 12: e0178448.
- Müllerová, J., Brůna, J., Bartaloš, T., Dvořák, P., Vítková, M. & Pyšek, P. 2017. Timing is important: unmanned aircraft vs. satellite imagery in plant invasion monitoring. *Front. Plant Sci.* 8: 887.
- Nowak, M.M., Dziób, K. & Bogawski, P. 2019. Unmanned aerial vehicles (UAVs) in environmental biology: a review. *Eur. J. Ecol.* 4: 56–74.
- Oosthuizen, W.C., Krüger, L., Jouanneau, W. & Lowther, A.D. 2020. Unmanned aerial vehicle (UAV) survey of the Antarctic shag (*Leucocarbo bransfieldensis*) breeding colony at Harmony Point, Nelson Island, South Shetland Islands. *Polar Biol.* 43: 187–191.
- Paleczny, M., Hammill, E., Karpouzi, V. & Pauly, D. 2015. Population trend of the world's monitored seabirds, 1950–2010. *PLoS One* 10: e0129342.
- Pascalis, F., Collins, P. & Green, J. 2018. Utility of time-lapse photography in studies of seabird ecology. *PLoS One* 13: e0208995.
- Perkins, A.J., Bingham, C.J. & Bolton, M. 2018. Testing the use of infra-red video cameras to census a nocturnal burrow-nesting seabird, the European Storm Petrel *Hydrobates pelagicus*. *Ibis* 160: 365–378.
- Petersen, A., Irons, D., Anker-Nilssen, T., Artukhin, Y., Barrett, R., Boertmann, D., Egevang, C., Gavrilov, M.V., Gilchrist, G., Hario, M., Mallory, M., Mosbech, A., Olsen, B., Osterblom, H., Robertson, G. & Strøm, H. 2008. *Framework for a Circumpolar Arctic Seabird Monitoring Network. CAFF CBMP Report No. 15.* Akureyri: CAFF International Secretariat.
- Pfeifer, C., Barbosa, A., Mustafa, O., Peter, H.-U., Rümmler, M.-C. & Brenning, A. 2019. Using fixed-wing UAV for detecting and mapping the distribution and abundance of penguins on the South Shetlands Islands, Antarctica. *Drones* 3: 39.
- Ponganis, P.J., Dam, R.P.V., Marshall, G., Knower, T. & Levenson, D.H. 2000. Sub-ice foraging behavior of Emperor Penguins. *J. Exp. Biol.* 203: 3275–3278.
- Radjawali, I., Pye, O. & Flitner, M. 2017. Recognition through reconnaissance? Using drones for counter-mapping in Indonesia. *J. Peasant Stud.* 44: 817–833.
- Robinson, R.A. & Ratcliffe, N. 2010. *The Feasibility of Integrated Population Monitoring of Britain's Seabirds. BTO Research Report No. 526.* Thetford: British Trust for Ornithology.
- RSPB 2020. *Puffarazzi*. Available at: <https://www.rspb.org.uk/reserves-and-events/events-dates-and-inspiration/puffarazzi/> (accessed 27 January 2020).
- Rümmler, M.-C., Mustafa, O., Maercker, J., Peter, H.-U. & Esefeld, J. 2016. Measuring the influence of unmanned aerial vehicles on Adélie Penguins. *Polar Biol.* 39: 1329–1334.
- Rümmler, M.-C., Mustafa, O., Maercker, J., Peter, H.-U. & Esefeld, J. 2018. Sensitivity of Adélie and Gentoo Penguins to various flight activities of a micro UAV. *Polar Biol.* 41: 2481–2493.

- Rush, G.P., Clarke, L.E., Stone, M. & Wood, M.J. 2018. Can drones count gulls? Minimal disturbance and semiautomated image processing with an unmanned aerial vehicle for colony-nesting seabirds. *Ecol. Evol.* 8: 12322–12334.
- Sakamoto, K.Q., Takahashi, A., Iwata, T. & Trathan, P.N. 2009. From the eye of the Albatrosses: a bird-borne camera shows an association between albatrosses and a killer whale in the Southern Ocean. *PLoS One* 4: e7322.
- Sardà-Palomera, F., Bota, G., Viñolo, C., Pallarés, O., Sazatornil, V., Brotons, L., Gomáriz, S. & Sardà, F. 2012. Fine-scale bird monitoring from light unmanned aircraft systems. *Ibis* 154: 177–183.
- Schwaller, M.R., Olson, C.E., Ma, Z., Zhu, Z. & Dahmer, P. 1989. A remote sensing analysis of Adélie Penguin rookeries. *Remote Sens. Environ.* 28: 199–206.
- Sinclair, N.C., Harris, M.P., Nager, R.G., Leakey, C.D.B. & Robbins, A.M. 2017. Nocturnal colony attendance by Common Guillemots *Uria aalge* at colony in Shetland during the pre-breeding season. *Seabird* 30: 51–62.
- Southwell, C. & Emmerson, L. 2015. Remotely-operating camera network expands Antarctic seabird observations of key breeding parameters for ecosystem monitoring and management. *J. Nat. Conserv.* 23: 1–8.
- Stolpmann, L.M., Landers, T.J. & Russell, J.C. 2019. Camera trapping of Grey-faced Petrel (*Pterodroma gouldi*) breeding burrows reveals interactions with introduced mammals throughout the breeding season. *Emu* 119: 391–396.
- Takahashi, A., Sato, K., Naito, Y., Dunn, M.J., Trathan, P.N. & Croxall, J.P. 2004. Penguin-mounted cameras glimpse underwater group behaviour. *Proc. R. Soc. Lond. B* 271 (Suppl 5): S281–S282.
- Temple, S.A. 1972. A portable time-lapse camera for recording wildlife activity. *J. Wildl. Manage.* 36: 944–947.
- Thaxter, C.B. & Burton, N.H.K. 2009. *High Definition Imagery for Surveying Seabirds and Marine Mammals: A Review of Recent Trials and Development of Protocols*. British Trust for Ornithology Report Commissioned by Cowrie Ltd. Thetford: British Trust for Ornithology.
- Thiebault, A., Mullers, R.H.E., Pistorius, P.A. & Tremblay, Y. 2014. Local enhancement in a seabird: reaction distances and foraging consequence of predator aggregations. *Behav. Ecol.* 25: 1302–1310.
- Thiebot, J.-B., Barbraud, C., Delord, K., Marteau, C. & Weimerskirch, H. 2014. Do introduced mammals chronically impact the breeding success of the world's rarest albatross? *Ornithol. Sci.* 13: 41–46.
- Tremblay, Y., Thiebault, A., Mullers, R. & Pistorius, P. 2014. Bird-borne video-cameras show that seabird movement patterns relate to previously unrevealed proximate environment, not prey. *PLoS One* 9: e88424.
- Van Berkel, T. 2014. *Camera Trapping for Wildlife Conservation: Expedition Field Techniques*. London: Geography Outdoors.
- Villegas, P., Mena, L., Constantine, A., Villalba, R. & Ochoa, D. 2018. Data imaging acquisition and processing as a methodology for estimating the population of frigates using UAVs. In: 2018 *IEEE ANDESCON*, pp. 1–4.
- Votier, S.C., Bearhop, S., MacCormick, A., Ratcliffe, N. & Furness, R.W. 2003. Assessing the diet of Great Skuas, *Catharacta skua*, using five different techniques. *Polar Biol.* 26: 20–26.
- Votier, S.C., Bicknell, A., Cox, S.L., Scales, K.L. & Patrick, S.C. 2013. A bird's eye view of discard reforms: bird-borne cameras reveal seabird/fishery interactions. *PLoS One* 8: e57376.
- Waldron, A., Mooers, A.O., Miller, D.C., Nibbelink, N., Redding, D., Kuhn, T.S., Roberts, J.T. & Gittleman, J.L. 2013. Targeting global conservation funding to limit immediate biodiversity declines. *Proc. Natl. Acad. Sci. USA* 110: 12144–12148.
- 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*. Peterborough: JNCC/RSPB/ITE/ Seabird Group.

- Waluda, C.M., Dunn, M.J., Curtis, M.L. & Fretwell, P.T. 2014. Assessing penguin colony size and distribution using digital mapping and satellite remote sensing. *Polar Biol.* 37: 1849–1855.
- Wang, D., Shao, Q. & Yue, H. 2019. Surveying wild animals from satellites, manned aircraft and unmanned aerial systems (UASs): a review. *Remote Sens.* 11: 1308.
- Watanuki, Y., Daunt, F., Takahashi, A., Newell, M., Wanless, S., Sato, K. & Miyazaki, N. 2008. Microhabitat use and prey capture of a bottom-feeding top predator, the European Shag, shown by camera loggers. *Mar. Ecol. Prog. Ser.* 356: 283–293.
- Weimerskirch, H., Prudor, A. & Schull, Q. 2018. Flights of drones over sub-Antarctic seabirds show species- and status-specific behavioural and physiological responses. *Polar Biol.* 41: 259–266.
- Weller, M.W. & Derksen, D.V. 1972. Use of time-lapse photography to study nesting activities of birds. *Auk* 89: 196–200.
- Whelan, R., Clarke, C., Almansoori, N., Jaradat, A., Qadi, N.S.A. & Muzaffar, S.B. 2018. Demographic consequences of native fox predation on Socotra cormorants on Siniya Island, United Arab Emirates. *Wildlife Biol.* 2018: 1–13.
- Wilhelm, S.I., Mailhiot, J., Arany, J., Chardine, J.W., Robertson, G.J. & Ryan, P.C. 2015. Update and trends of three important seabird populations in the western North Atlantic using a geographic information system approach. *Mar. Ornithol.* 43: 211–222.
- Williams, H.M. & DeLeon, R.L. 2020. Deep learning analysis of nest camera video recordings reveals temperature-sensitive incubation behavior in the Purple Martin (*Progne subis*). *Behav. Ecol. Sociobiol.* 74: 7.
- Yoda, K., Murakoshi, M., Tsutsui, K. & Kohno, H. 2011. Social interactions of juvenile Brown Boobies at sea as observed with animal-borne video cameras. *PLoS One* 6: e19602.