Developing remote technologies to understand changes in seabird behaviour and ecology

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University of Oxford

A thesis submitted for the degree of

Doctor of Philosophy

Michaelmas 2024

This thesis is dedicated to my Dad, who supported all of my adventures growing up.
I wish you could have been here to see me complete this one.

Black-legged Kittiwake (*Rissa tridactyla*) in flight, Hvítabjarnarey, Iceland. Photo from time-lapse camera, provided by Róbert A. Stefánsson and Jón Einar Jónsson.

Abstract

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Seabirds are one of the most threatened groups of birds. Effective monitoring is therefore needed to understand population trends and the drivers of these trends, if we want to implement successful conservation action. Current monitoring methods are typically limited in their frequency and geographic reach, as many seabirds breed in remote and hard to access locations, which can make comprehensive fieldwork programs prohibitively expensive and time-consuming. Advances in remote technologies are providing opportunities to expand the scale of seabird monitoring at reduced cost and with less disturbance. In this thesis, I aim to develop methods to improve the scope of seabird monitoring and research, and apply these methods to improve our understanding of the impact of anthropogenic climate change on seabird phenology and breeding success. First, I consider the rapidly increasing application of drones in seabird research. I collate information from over 100 studies to develop an eight step framework for ensuring drone-seabird surveys are safe, effective, and within the law. Second, I use a time-lapse camera network, which has collected over 200 000 images between 2014 and 2023, to examine changes in Black-legged Kittiwake *Rissa tridactyla* phenology along a latitudinal gradient, as well as the impact of direct weather on kittiwake chick survival. Images were annotated by over 35 000 citizen scientists on the Seabird Watch citizen science project (hosted on the Zooniverse platform). I examine the cost-effectiveness of the citizen science camera network and look at patterns of volunteer engagement to understand the long-term success of the project. Having developed an algorithm to use the citizen science data, I find that while precipitation has a large and adverse effect on kittiwake chick survival (a 3.7-fold increase in daily chick failure rate per 1 mm increase in precipitation), other weather variables have no measurable impact. This suggests that the indirect effects of ocean warming may be having a greater impact on kittiwake breeding success than direct weather effects at present. Finally, I use a large geolocator tracking dataset, containing over 1400 individuals from 34 breeding colonies tracked between 2009 and 2022, to examine the mechanisms underpinning population level change in kittiwake phenology, in response to rising sea surface temperatures. I find that while some aspects of kittiwake migratory phenology are changing plastically, changes in breeding phenology were primarily due to turnover of individuals. I highlight that the direction, magnitude, and mechanism by which phenological change is mediated is context- and trait-dependent, and this has important implications for understanding and predicting how seabirds - and migratory animals more generally - can respond to ongoing climate change. Overall, I discuss the possibilities and challenges of incorporating remote technologies into seabird monitoring programs and their importance in the face of anthropogenic change.

Acknowledgements

This thesis was made possible by a graduate scholarship from the Natural Environment Research Council in conjunction with the Oxford DTP in Environmental Research. Further funding was provided by my college, St Edmund Hall, for additional fieldwork expenses and conference attendance.

Firstly, I would like to thank my supervisors, Tom Hart, Mark Jessopp, Ellie Owen, Matt Wood, and Katrina Davis for providing continued support and guidance throughout my PhD. I think it became apparent pretty quickly how much I love fieldwork, and I am grateful for all the amazing fieldwork opportunities that I had! From seeing polar bears in Svalbard, to driving a van full of paving slabs and scaffolding across Scotland, I loved every second. Visiting St Kilda was perhaps the highlight (sorry Tom, Svalbard was pretty epic too!) and I hope that one day I will have the opportunity to return there. To that end, thank you to the many, many people that made my fieldwork possible and helped me lug camera equipment across some pretty uneven terrain.

A special thank you also goes to Katrina, for providing pastoral support and adopting me into her research group in the final year of my PhD, after Tom moved to Oxford Brookes. Having a second research group was lovely, and reminded me that there is other interesting marine research outside of seabirds.

Thank you to everyone in Tom's research group for the beers and never-ending penguin talk over the past 4 years (Nacho, Chloe, Laure, and Jen). An extra thank you goes to Nacho, my PhD "big brother", who was always there to listen to my woes and rants, and provide pearls of wisdom (and chocolate). Likewise, Elliot and Lauren, thank you for providing much needed joy in the bleak ZRAB building. The Up in Arms trips and cycle path updates truly kept me going during the dark winters, and even after you moved to Australia Lauren, I loved sending long voicenotes (10 minutes at one point) about the flooding situation on the cycle path. I think that's when I realised I needed to get out more - but it was difficult when the fastest route into town was flooded.

I'd also like to thank my pals in OxNav (Lewis, Paddy, Morford, and Trina) for letting me become an honorary OxNav member. Thank you for all the pub trips and fun birdy times. The Oxford bird ringing scene might have been a real slog, but catching birds (or more often than not, just chatting sh*t in a field) was honestly so much fun. Therefore a special thanks to Thomas, Lewis, Joe Wynn, Paddy, and Alex for (almost) always being up for going ringing.

Thank you also to my climbing buddies for putting up with my shenanigans (Lewis, Harry, Ben, and Sam), and in Lewis' case, for teaching me to lead climb! One day I will learn to whinge less and just get on with it. I'm excited for our next adventure (provided Harry is there to help make Ben more tolerable).

Of course, I cannot get to the bottom of the Acknowledgments without giving a huge thanks to the Ferry Road gang (Fishy Joe, Anna, Sophie, and Luke). You were incredibly tolerant of my strange habits (e.g. the kayaks; waking up at 4 am to catch birds) and I couldn't have asked for better housemates. Coming home and watching trash TV just isn't the same without you guys.

Finally, I would like to thank my family for always believing in me and supporting me in my love of wildlife, and especially birds. Thank you Mum and Dad for letting my love of seabirds dominate our holidays around the UK as a teenager, and thank you Gig for being so tolerant of going on "yet another" seabird boat trip or island visit. I am very proud of your seabird identification skills (we will continue to work on other birds, don't worry). Thank you Dad for always being so excited about my next adventure; your enthusiasm was infectious and I only wish you were here to celebrate me finishing my PhD.

And last, but not least, thank you Joe. Thank you for always being there for me and for letting me be my weirdest self. Thank you for all the adventures, climbs, birds, and for working out that when I go quiet on a hike I just need food (Jelly bab babs all the way). There's no one I'd rather scramble around rocks with noosing seabirds.

∼ I am Walking on the Waves (Skippinish) ∼

Declaration and Author Contributions

The work presented in this thesis is primarily my own. Other authors contributed to the work in this thesis, and their contributions are acknowledged below.

Tom Hart contributed to the conception and manuscript preparation of Chapter 2, the conception, data collection, analysis, and manuscript preparation of Chapters 3 and 4, and the manuscript preparation of Chapter 5. Tom provided supervision for all chapters.

Mark Jessopp contributed to the conception and manuscript preparation of Chapter 2, the conception, data collection, analysis, and manuscript preparation of Chapters 3 and 4, and the manuscript preparation of Chapter 5. Mark provided supervision for all chapters.

Ellie Owen contributed to the data collection, analysis, and manuscript preparation of Chapters 3 and 4, and the manuscript preparation of Chapter 5. Ellie provided supervision for Chapters 3, 4, and 5.

Matt Wood contributed to the conception and manuscript preparation of Chapter 2, the data collection, analysis, and manuscript preparation of Chapters 3 and 4, and the manuscript preparation of Chapter 5. Matt provided supervision for all chapters.

Joe Wynn contributed to the analysis and manuscript preparation of Chapter 4, and the conception, analysis, and manuscript preparation of Chapter 5.

Maria Moiron contributed to the analysis and manuscript preparation of Chapter 5.

Carlos Arteta contributed to the analysis and manuscript preparation of Chapter 4.

Alex Banks contributed to the manuscript preparation of Chapter 2.

Rachel Bonnici contributed to the data validation and manuscript preparation of Chapter 4.

Lucy Clarke contributed to the manuscript preparation of Chapter 2.

Laure Cugnière contributed to the manuscript preparation of Chapter 2.

Jóhannis Danielsen contributed to the data collection and manuscript preparation of Chapters 3 and 4.

Sébastien Descamps contributed to the data collection and manuscript preparation of Chapters 3 and 4.

Jón Einar Jónsson contributed to the data collection and manuscript preparation of Chapters 3 and 4.

Kyle Elliot contributed to the manuscript preparation of Chapter 2.

Ignacio Juarez Martinez contributed to the manuscript preparation of Chapter 2, and the data validation and manuscript preparation of Chapter 4.

Alexandra Kilcoyne contributed to the manuscript preparation of Chapter 2.

Lewis Lancaster-Reeves contributed to the data validation and manuscript preparation of Chapter 4.

Flemming Merkel contributed to the data collection and manuscript preparation of Chapter 3 and the data collection, data validation, and manuscript preparation of Chapter 4.

Matthew Murphy contributed to the manuscript preparation of Chapter 2 and the data collection and manuscript preparation of Chapter 4.

Ruedi Nager contributed to the manuscript preparation of Chapter 2.

Norman Ratcliffe contributed to the manuscript preparation of Chapter 2.

Jonathan Rutter contributed to the data validation and manuscript preparation of Chapter 4.

Róbert Stefánsson contributed to the data collection and manuscript preparation of Chapters 3 and 4.

Claire Tanner contributed to the data validation and manuscript preparation of Chapter 4.

Danielle Thompson contributed to the manuscript preparation of Chapter 2.

Robin Ward contributed to the manuscript preparation of Chapter 2.

Tycho Anker-Nilssen contributed to the data collection of Chapter 5.

A variety of authors contributed to the data collection and manuscript preparation of Chapter 5 as part of the *SEATRACK* project. These include Tycho Anker-Nilssen, Maria

Bogdanova, Vegard Sandøy Bråthen, Jan Ove Bustnes, John Chardine, Olivier Chastel, Lorraine Chivers, Signe Christensen-Dalsgaard , Joshua Cunningham, Jóhannis Danielsen, Francis Daunt, Nina Dehnhard, Sébastien Descamps, Kjell Einar Erikstad, Alexey Ezhov, Annette Fayet, Morten Frederiksen, April Hedd, Maria Gavrilo, Yann Kolbeinsson, Aili Lage Labansen, Svein-Håkon Lorentsen, Mark Mallory, Flemming Merkel, Børge Moe, Anders Mosbech, Mark Newell, Stephen Newton, Bergur Olsen, Tone Reiertsen, Hallvard Strøm, Robert Swann, Geir Helge Rødli Systad, and Thorkell Lindberg Thórarinsson.

The intimate relationship of Britain and Ireland to their surrounding seas has meant that seabirds have long been a part of the culture of these islands. In historical times (and to a very limited extent in modern times) this relationship was one of exploitation by humans of seabirds as a source of food or feathers. As the necessity to use seabirds for these purposes declined in the 19th century, so the appreciation of their intrinsic value rose. Fears of over-exploitation, particularly as a source for feathers, coupled with evidence of decline at the massive colony of seabirds on Flamborough Head in north-east England, led both to the foundation of the organisation that is now the Royal Society for the Protection of Birds (RSPB) and to some of the first bird conservation legislation. The evidence of decline was based on diminishing harvest returns, and this might be argued as being the first evidence of seabird monitoring in the UK.

—M.L. Tasker, *The UK and Ireland seabird monitoring programme - a history and introduction (2000), JNCC*

Contents

1

Introduction

Contents

"When the sound of summer calls"

– Skippinish, *Summer Call*

1.1 Seabird monitoring and population change

Seabirds have long captivated the human imagination and formed the basis of many seafaring myths and legends. Returning to land only to breed, most seabirds spend the rest of the year at sea, and there is something quite fascinating about this connection between the land and the ocean. For island communities, seabirds form a deep-rooted part of their culture (Jenkins, 2005). In days gone by, many island communities hunted seabirds as a source of food and feathers and depended upon them to survive (Jenkins, 2005; Baldwin, 2013; Olsen et al., 2024). Such dependence would have led to an intricate understanding of these birds, with knowledge passed down from generation to generation. They knew the number of eggs in a clutch, whether a bird would re-lay, which ages of bird were best taken, and developed systems to limit the number of eggs and birds harvested to ensure the harvest would continue next year (Baldwin, 2012).

Today, our knowledge of seabirds and their populations is much more formalised, as they have been the subject of extensive scientific research over the past century. One of the earliest seabird censuses in the UK was a survey of breeding gannets, which estimated there were 75 000 gannets in Britain and Ireland across eight colonies in the early 20th century (Gurney, 1913; Lloyd et al., 2010). While gannets are currently showing an increasing population trend (BirdLife International, 2024b), continued monitoring has revealed that globally, seabirds are one of the most threatened groups of birds (Croxall et al., 2012). 31% of seabird species are globally threatened and almost half of seabird species are undergoing population decline (BirdLife International 2018).

The top three threats to seabirds in terms of number of species affected and average impact have been identified as invasive species, bycatch in fisheries, and climate change/severe weather (Fig. 1.1; Dias et al. 2019). However, seabirds are exposed to a multitude of other threats as well, including overfishing, light pollution, and disease, to name but a few. Most recently, outbreaks of Highly Pathogenic Avian Influenza (HPAI) have resulted in severe seabird mortality and breeding failure (Cunningham et al., 2022; Falchieri et al., 2022; Careen et al., 2024). While there is still limited understanding of the immunology

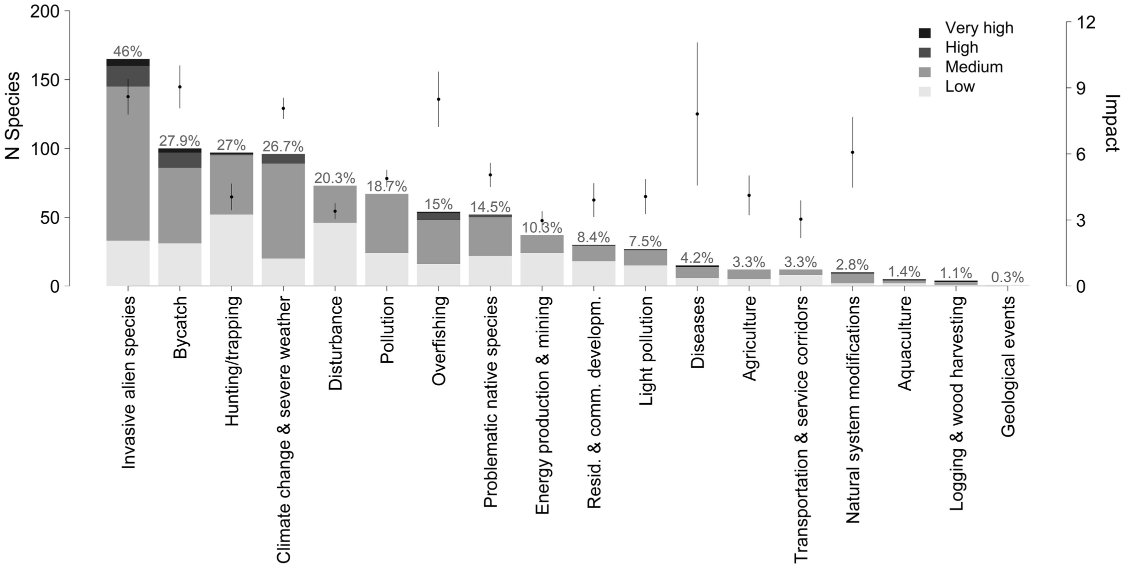

Figure 1.1: From Dias et al. 2019: Ongoing threats to all seabird species (ordered by the number of species affected). Left y axis: total number of species affected; Right y axis: average impact ± SE. Values atop bars indicate the percentage of species affected (n=359).

of HPAI and the extent to which individuals can develop immunity (Loeb, 2023; Lane et al., 2024), this disease has become one of the biggest immediate conservation threats to many seabird species (Tremlett et al., 2024).

In order for these threats to result in seabird population decline, they must act at one or more life stages, namely, they must reduce either adult survival, juvenile recruitment, or breeding success. Given that seabirds are long-lived and have low fecundity (Bennett et al., 2002), changes in seabird populations are often attributed to changes in post-fledging and adult survival, as short-term variation in breeding success may be buffered by a long life-span providing many opportunities to reproduce (Sæther & Bakke, 2000; Jenouvrier et al., 2005). Nevertheless, poor breeding success can also be an important driver of seabird population decline (Reiertsen, 2013), particularly when breeding success remains low in multiple consecutive years, or there is repeat breeding failure.

Identifying decreases in adult survival, juvenile recruitment, or breeding success could act as an early warning signal of future population decline, given that changes at the population level can take a long-time to become apparent. However, monitoring seabirds is not easy, not least because breeding individuals may spend up to half of the year at sea. Access to breeding colonies can be difficult and expensive (in terms of time and money) as seabirds often breed in remote locations, such as on islands or sea stacks (Mitchell & Parsons, 2007; Huffeldt & Merkel, 2013; Southwell & Emmerson, 2015; Edney & Wood, 2021). Nests can be equally hard to view even when at the colony, as many seabirds breed on exposed cliff faces that may not be visible from land, some species nest underground, and ground nesting birds may be concealed by vegetation or camouflage (Mitchell & Parsons, 2007; Robinson et al., 2010). There are also often concerns regarding disturbance to breeding seabirds during surveys (Walsh et al., 1995; Carney & Sydeman, 1999; Rush et al., 2018). As such, seabird monitoring programmes are often limited in their scope and data collected (Cook & Robinson, 2010; Paleczny et al., 2015).

For example, the UK Seabird Monitoring Programme consists of four key sites (Skomer Island in Wales, and Fair Isle, Canna, and the Isle of May in Scotland) where consistent long-term data is collected on abundance, breeding success, adult survival, phenology, and diet (British Trust for Ornithology, 2024). However, the UK has over 10 000 seabird colonies that are home to more than 8 million breeding seabirds (Mitchell et al., 2004; Burnell et al., 2023) where limited data collection occurs. Every year, the Seabird Monitoring Programme asks volunteers to measure the abundance and breeding success of local seabird colonies; yet, these surveys are by no means comprehensive, and rarely include additional measures of survival, phenology, or diet, unless being carried out as part of specific research projects. Every 10 to 15 years a census is conducted, with the most recent census, ‘Seabirds Count’, taking place from 2015 to 2021, following the three previous censuses, ‘Seabird 2000’ 1998-2002, ‘Seabird Colony Register’ 1985-88, and ‘Operation Seafarer’ 1969-70 (Burnell et al., 2023). While these censuses are crucial for understanding population trends, they do not provide information on what is driving these trends.

New technologies are increasingly helping to overcome some of the challenges posed by monitoring seabirds and can offer opportunities to expand the scale of monitoring. In this thesis, I focus on the use of drones, time-lapse cameras, and light level geolocators to monitor seabird abundance, phenology, breeding success, and chick survival.

1.2 General methods: remote technologies

1.2.1 Drones

In the past 10 years, the use of drones has seen enormous uptake in environmental biology, as platforms have become smaller, easier to fly, and more affordable (Nowak et al., 2018). Drones have been used for a wide range of ecological monitoring, including habitat classification and mapping (e.g. Ruwaimana et al., 2018), estimating species abundance (e.g. Lyons et al., 2019), and observing animal behaviour (e.g. Schad and Fischer, 2023). It is therefore unsurprising that drones have started to gain traction as a potential method for monitoring seabirds, particularly to measure abundance and distribution of species. There are many potential advantages of using drones for these purposes. For example, drones can access areas that are difficult, or even impossible, for fieldworkers to reach (e.g. sea stacks), and they can be angled to look into nests, the contents of which may otherwise be obscured from view. Drones can also survey areas faster in the field than direct field observations with binoculars which can allow entire breeding populations to be surveyed, rather than sub-plots due to access or time restrictions for fieldwork (McClelland et al., 2016; Rush et al., 2018). Additionally, drones can reduce disturbance relative to ground counts, as less time is spent in seabirds' breeding territory and observation is from the air rather than the ground (Sardà-Palomera et al., 2012). Manned aircraft have been used to count seabirds in remote locations; however, drones can offer a more affordable and less logistically difficult option for aerial surveys (Anderson & Gaston, 2013; Edney & Wood, 2021).

Nevertheless, with new technology come legitimate concerns regarding the safety and welfare of both birds and people during survey work (Borrelle & Fletcher, 2017). Reports of drones crashing into seabird colonies or flushing breeding birds from cliffs has led to concern among the seabird community about the potential for wildlife disturbance and putting wildlife and people in danger (Kobilinsky, 2021). Linked to this, there have been discussions about how to regulate flying drones around sensitive breeding sites, and make sure that tourists are discouraged from flying drones recreationally at nature reserves (Wallace et al., 2018; Jiménez López & Mulero-Pázmány, 2019; Rossi & Wiesmann, 2024). Furthermore, as with any new technology, understanding how to process the data output is paramount to its success.

Using drones to count seabird colonies has become relatively routine in my PhD research group, and so for the first chapter of my PhD, I wanted to produce best practice guidelines for using drones in seabird monitoring and research, by conducting a systematic review of the growing body of literature on this topic. Over the course of my PhD, there has been increasing use of drones in seabird monitoring, and so this review will hopefully serve as a useful document for practitioners and researchers alike to be confident that flights remain legal, safe, and obtain useful data that meets the survey objectives.

1.2.2 Time-lapse cameras

The second type of remote technology that I have utilised in my PhD are time-lapse cameras, which record images at set time intervals regardless of subject presence (Cutler & Swann, 1999). Advances in digital technology, such as increased affordability, reduced power consumption, and larger data storage capacity, has seen the field of time-lapse photography expand in recent years (Bolton et al., 2007). Time-lapse cameras are best used where a single vantage point gives a representative view of the study organisms, which should be frequently present at the location, but where the measurement of interest will not activate a motion-triggered camera (Cutler & Swann, 1999; Black et al., 2018). Breeding seabird colonies could therefore be monitored using this technology, allowing year-round observations and collection of data such as phenology and breeding success (Fig. 1.2 - 1.3).

Figure 1.2: Long-range time-lapse camera set-up at Fowlsheugh, Scotland. This system was developed by Time-lapse Systems (part of Hideaway Media Ltd). It used a Canon camera with a lens attached and was powered by a solar-panel. Photo by Alice Edney.

Figure 1.3: Short-range time-lapse camera set-up on St Margaret's Island, Wales. This set-up used a commercially available Reconyx camera which was attached to a metal tripod constructed from scaffolding poles. Photo by Steve Sutcliffe.

Time-lapse cameras have the main advantage that they can collect data year-round, at comparatively low cost, and thus allow monitoring at sites currently not visited by fieldworkers, either due to financial or logistical constraints. For example, cameras may only need to be serviced once every one to two years (e.g. to change batteries and SD cards), or potentially less if transmitting images via the mobile phone network, and can therefore be used to monitor remote colonies that are infrequently visited. Chapters 3 and 4 of my PhD used a network of time-lapse cameras to monitor the phenology (Chapter 3) and breeding success and chick survival (Chapter 4) of a cliff-nesting seabird, the Black-legged Kittiwake *Rissa tridactyla*.

Of course, with new technologies come additional challenges, such as how to store and process large amounts of data, as ecology increasingly becomes a big data field (Hampton et al., 2013; Farley et al., 2018). Machine learning and Artificial Intelligence (AI) are increasingly at the forefront of these discussions, but citizen science also provides important opportunities to engage members of the public in science and nature conservation (Dickinson et al., 2012; McClure et al., 2020; Pichler & Hartig, 2023). In Chapters 3 and 4, I utilised a large-scale citizen science project, Seabird Watch (www.seabirdwatch.org), to identify adult and chick kittiwakes in time-lapse images. I tested the validity of citizen science identification of birds and developed novel methodologies to extract accurate measurements of phenology and breeding success from this data. Chapter 3 specifically discusses the overall cost-effectiveness (both time and money) of the citizen science camera network and the importance of volunteer retention for maintaining citizen science projects long-term. The general discussion of this thesis (Chapter 6) goes on to look at the relative advantages and disadvantages of machine learning in comparison with citizen science, as rapid technological advances continue to change the future of image analysis.

1.2.3 Light level geolocators

The final type of remote monitoring technology that I have used in my thesis, are light level geolocators (or GLS), which are a type of biologging device used to track an animal's position. Geolocators work by recording ambient light levels, and these recordings can be used to determine the time of sunrise and sunset, and therefore calculate day length. Day length can then be used to derive latitude and solar noon can be used to derive longitude, with a spatial error of < 250 km (Lisovski et al., 2020). Although the spatial error is substantially more than other biologging devices, such as GPS, they have the advantage of being able to be record data year-round, as they are small enough to be attached onto a colour-ring or metal ring fitted around the bird's leg (Halpin et al.,

Figure 1.4: Black-legged kittiwake *Rissa tridactyla* with a light level geolocator attached to a colour-ring fitted around the bird's leg. Photo by Mark Jessopp.

2021, Fig. 1.4). In comparison, most GPS devices are attached onto feathers (often back or tail feathers) using tape and are therefore lost when the bird moults (Guilford et al., 2008). Geolocators have revolutionised our ability to understand the year-round movements and migration of seabirds.

Most geolocator devices also record salt-water immersion or conductivity, which, together with light data, can be used to infer bird behaviours, not just their position (Shoji et al., 2015; Wynn et al., 2022). This has been used to understand behaviours such as migratory timing, foraging patterns, and colony and nest attendance (Daunt et al., 2006; Grissot et al., 2023; van Bemmelen et al., 2024). However, many studies only focus on a single species and/or a single colony. In Chapter 5, I used an international geolocator dataset spanning 15 years, to investigate whether kittiwake phenology has changed over the past decade in response to sea surface temperature (SST). I further used repeat tracking of known individuals to determine if any such changes in migratory timing reflect within-individual plasticity or between-individual selection.

While a strong theme throughout this thesis is the development of novel methods for using remote technologies to monitor seabirds, the application of these technologies for advancing our understanding of seabird behaviour and ecology is of equal importance. Chapters 3 to 5 of this thesis focus specifically on monitoring the behaviour and ecology of the Black-legged Kittiwake *Rissa tridactyla*, and as such the following section introduces my main study species and provides background on why the behavioural and ecological questions answered in this thesis are of significance.

1.3 Study species: Black-legged Kittiwake

The Black-legged Kittiwake *Rissa tridactyla* (hereafter kittiwake) is a small, pelagic gull in the Laridae family, with a circumpolar breeding distribution in the northern hemisphere (BirdLife International, 2024a). Unlike other UK gull species, kittiwakes forage exclusively at sea and spend most of their lives here, only returning to land to breed (Coulson, 2011). Kittiwakes are a colonial breeding species, and breed on ledges on coastal cliffs, or increasingly, on manmade structures, such as buildings and oil rigs (Fig. 1.5, Christensen-Dalsgaard et al., 2020).

Despite a global population of 15 million and a widespread distribution, kittiwakes have experienced a 40% decline in only three generations, leading to their classification as Vulnerable on the IUCN Red List (BirdLife International, 2024a). This decline is thought to be primarily the result of climate change.

In the North Sea, increasing sea surface temperatures have been associated with declines in both adult survival and breeding success (Daunt & Mitchell, 2013). Specifically, kittiwakes breeding in eastern Scotland had lower over winter survival following winters with higher SST, and breeding success one year later was also reduced (Frederiksen et al., 2004b). However, this pattern has not been found across all of the UK, or even all

Figure 1.5: Black-legged Kittiwakes *Rissa tridactyla* breeding on the Mumbles Pier, Swansea, Wales. Photo by Alice Edney.

colonies in eastern Scotland. For example, winter SST was not a reliable indicator of kittiwake breeding success at Fowlsheugh on the east coast of Scotland (Eerkes-Medrano et al., 2017), and there was no relationship between SST in the Celtic Sea, and breeding success or population growth of kittiwakes breeding in Wales (Lauria et al., 2012; Lauria et al., 2013). This suggests potentially large regional variation in the impact of climate change on seabirds (Frederiksen et al., 2007; Carroll et al., 2015).

Kittiwakes have also been found to be affected by climate directly, albeit most of the research to date has focused on the indirect effects of warming. Severe winter storms have been associated with low survival, in some cases resulting in seabird wrecks (Morley et al., 2016; Clairbaux et al., 2021), and summer storms have reduced kittiwake breeding success by knocking or washing nests or their contents off cliffs (Newell et al., 2015). In other species of seabird, high temperatures have also been linked to breeding failure (Olin et al., 2023). Given that climate models have predicted an increase in climate variability and the frequency and severity of weather extremes (Rahmstorf & Coumou, 2011; Arias et al., 2021), there is an increasing need to research the direct effects of climate on seabirds.

The main mechanism by which increased temperature is thought to be affecting kittiwakes, and seabirds more generally, is via changes in prey availability, termed bottom-up effects (Rindorf et al., 2000; Oro & Furness, 2002; Frederiksen et al., 2006; Daunt et al., 2008; Parsons et al., 2008). Kittiwakes are surface-feeders and their primary prey are sandeels. Changes in prey availability are difficult to untangle but are in part due to changes in species abundance and distribution (for example, a northwards distributional shift in copepod *Calanus finmarchicus*; Frederiksen et al., 2012), but also due to changes in prey phenology (Burthe et al., 2012). In the North Sea, changes in the timing of sandeel life cycle events, have led to smaller sandeels of lower energy value being available during the chick rearing period, when seabird energy demands are highest (Wanless et al., 2004; Frederiksen et al., 2011; Burthe et al., 2012). This trophic mismatch between seabird energy demands and prey availability can lead to lowered reproductive success. This issue has been exacerbated in many areas by overfishing, such as the (now closed) sandeel fishery off south-each Scotland in the 1990s (Frederiksen et al., 2004b).

An individual seabird may maximise its fitness if it can adjust the timing of breeding to match the seasonal peak in food availability, by responding to environmental cues that predict this seasonal peak (Frederiksen et al., 2004a; Shultz et al., 2009). Individuals might respond to one or more environmental cues, such as photoperiod (e.g. Pinet et al., 2011), temperature (e.g. Moe et al., 2009), and wintering conditions (e.g. Dobson et al., 2017), at either the local level (e.g. local SST) or wider scale (e.g. North Atlantic Oscillation). In general, the timing of seasonal activities has been found to advance in both plants and animals over recent decades in response to climate change (Walther et al., 2002; Dunn, 2004; Visser & Both, 2005); however, a comprehensive meta-analysis of seabirds found that, on average, seabird populations worldwide have not advanced their breeding over time or in response to SST (Keogan et al., 2018). To date, research on kittiwake phenology has found variable results, with studies showing kittiwakes breeding earlier, (Coulson & Thomas, 1985), later (Frederiksen et al., 2004a; Moe et al., 2009; Wanless et al., 2009), or showing no detectable trend (Keogan et al., 2018; Gutowsky et al., 2022; Whelan et al., 2022). These divergent population-level responses might be better understood by examining the mechanisms that underpin them. Directional population change could result from individual plasticity, selective disappearance of individuals, or generational shifts caused by differential early life development (Piersma & Drent, 2003; Gill et al., 2019). However, very few studies have been able to examine this, due to the difficulty of collecting repeated individual data for wild seabirds (Moiron et al., 2022).

The international seabird tracking project, SEATRACK, has provided a unique opportunity to explore the processes generating changes in seabird phenology. The project has collected repeat tracks of over 1400 individual kittiwakes since 2007 across the species' range, allowing me to examine whether changes in kittiwake phenology in response to SST reflected within-individual plasticity or between-individual differences (Chapter 5). This will allow us to determine not only how animal behaviour is changing but also why; a key component in predicting responses to climate change going forward.

1.4 Thesis Outline

In this thesis, I aim to develop methods for utilising remote technologies to better understand changes in abundance, phenology, and breeding success of seabirds, in the face of environmental change. Chapter 2 is a systematic review, which synthesises a growing body of literature on the use of drones in seabird monitoring and research, to provide best practice guidelines given the increasing use of this comparatively new technology. Chapters 3 and 4 use time-lapse image data from the citizen science project, Seabird Watch, to investigate how kittiwake phenology and breeding success varies across the species' breeding range and in relation to direct weather effects. Chapter 3 further examines the utility of citizen science as ecology increasingly becomes a big data field, and its role with relation to machine learning and Artificial Intelligence. Chapter 5 goes on to investigate whether kittiwake phenology has changed over the past decade in response to SST, and whether any such changes reflect within-individual plasticity or between-individual differences, by using geolocator data from an international seabird tracking project, SEATRACK. Finally, Chapter 6 summarises the findings of this thesis and considers future directions of seabird monitoring and research with relation to continued development of remote technologies.

This research is of particular importance, given that seabirds are one of the most threatened groups of birds, and yet limited time and funding for conservation means that monitoring of basic demographic parameters is typically restricted to a small number of study sites and years. This research therefore aims to increase the geographical reach and international scope of seabird monitoring against a background of rapidly changing ecosystems and challenging funding landscapes.

Chapter 2: *Best practices for using drones in seabird monitoring and research*
Drones have become of global importance for surveying breeding seabirds, by providing opportunities to transform monitoring techniques and allow new research on some of the most threatened birds. However, such fast-changing and increasingly available technology presents challenges to regulators responding to requests to carry out surveys, and to researchers ensuring their work follows best practice and meets legal and ethical standards. This chapter collates information from over 100 studies and presents a framework comprising eight steps to ensure drone-seabird surveys are safe, effective, and within the law: 1) Objectives and Feasibility; 2) Technology and Training; 3) Site Assessment and Permission; 4) Disturbance Mitigation; 5) Pre-deployment Checks; 6) Flying; 7) Data Handling and Analysis; and 8) Reporting.

Chapter published: Edney, A.J., Hart, T., Jessopp, M.J., Banks, A., Clarke, L.E., Cugnière, L., Elliot, K.H., Juarez Martinez, I., Kilcoyne, A., Murphy, M., Nager, R.G., Ratcliffe, N., Thompson, D.L., Ward, R.M. & Wood, M.J. 2023. Best practices for using drones in seabird monitoring and research. *Marine Ornithology* **51**: 265 – 280.

Chapter 3: *Using citizen science image analysis to measure seabird phenology*
This study uses time-lapse camera data annotated by volunteers on the Zooniverse citizen science project, Seabird Watch, to measure kittiwake phenology. Time-lapse cameras collected > 200 000 images between 2014 and 2023 across 11 locations covering the species' breeding range (51.7°N – 78.9°N), with over 35 000 volunteers identifying adult and juvenile kittiwakes in images. This chapter aims to develop a standardised method to extract colony arrival and departure dates from citizen science annotations and to

use this data to investigate how phenology changes along a latitudinal gradient. This chapter further aims to understand the cost-effectiveness of the citizen science camera network and explores volunteer patterns of engagement.

Chapter published: Edney, A.J., Danielsen, J., Descamps, S., Jónsson, J.E., Owen, E., Merkel, F., Stefánsson, R.A., Wood, M.J., Jessopp, M.J. and Hart, T. (2025). Using citizen science image analysis to measure seabird phenology. *Ibis, 167(1),* 56-72. https://doi.org/10.1111/ibi.13317

Chapter 4: *Citizen science reveals precipitation – but not other weather variables – adversely affects chick survival in a threatened seabird*
This study uses the same citizen science dataset as Chapter 3, but aims to develop an algorithm to extract reliable chick count data from the citizen science classifications. It then aims to use this chick count data to test *a priori* hypotheses on the direct effects of local weather conditions on daily chick survival. Specifically, I test the predictions that increased precipitation, storminess, solar radiation, and colony direction measured as degrees from north (i.e. more southerly facing colonies) will increase daily chick failure rate.

Chapter in preparation for submission: Edney, A.J., Wynn, J., Arteta, C., Danielsen, J., Descamps, S., Einar Jónsson, J., Owen, E., Merkel, F., Murphy, M., Stefánsson, R.A., Bonnici, R., Juarez Martinez, I., Lancaster-Reeves, L., Rutter, J.D., Tanner, C.E., Wood, M.J., Jessopp, M.J.* & Hart, T.* Citizen science reveals precipitation – but not other weather variables – adversely affects chick survival in a threatened seabird.
*joint senior author

Chapter 5: *Individual-level plasticity only partially drives population-level phenological responses to climate change in a vulnerable seabird*
This study uses data from the international seabird tracking project, SEATRACK, to investigate whether population-level changes in kittiwake phenology in response to SST, can be explained by within-individual plasticity or between-individual differences. Where evidence of plasticity exists, it then aims to examine whether there is individual

variation in plasticity. The geolocator dataset used for this chapter contains repeat tracks of over 1400 individual kittiwakes since 2007, breeding at 34 colonies which span the species' breeding range.

Chapter in preparation for submission: Edney, A.J., Wynn, J., Moiron, M., Anker-Nilssen, T., Bogdanova, M., Bråthen, V.S., Chardine, J.W., Chastel, O., Chivers, L., Christensen-Dalsgaard, S., Cunningham, J.T., Danielsen, J., Daunt, F., Dehnhard, N., Descamps, S., Erikstad, K.E., Ezhov, A., Fayet, A., Frederiksen, M., Hedd, A., Gavrilo, M., Kolbeinsson, Y., Labansen, A.L., Lorentsen, S-H., Mallory, M.L., Merkel, F.R., Moe, B., Mosbech, A., Newell, M.A., Olsen, B., Owen, E., Reiertsen, T.K., Strøm, H., Systad, G.H.R., Thórarinsson, T.L, Wood, M.J., Jessopp, M.J., & Hart, T. Individual-level plasticity only partially drives population-level phenological responses to climate change in a vulnerable seabird.

Chapter 6: *Discussion*

This chapter aims to summarise and discuss the key findings of my thesis in the broader context of seabird monitoring and research. It also considers future directions and research based on my work.

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2

Best practices for using drones in seabird monitoring and research

Adapted from: Edney, A.J., Hart, T., Jessopp, M.J., Banks, A., Clarke, L.E., Cugnière, L., Elliot, K.H., Juarez martinez, I., Kilcoyne, A., Murphy, M., Nager, R.G., Ratcliffe, N., Thompson, D.L., Ward, R.M. & Wood, M.J. (2023). Best practices for using drones in seabird monitoring and research. *Marine Ornithology, 51,* 265 - 280.
http://doi.org/10.5038/2074-1235.51.2.1544

Contents

2.1 Abstract

Over the past decade, drones have become increasingly popular in environmental biology and have been used to study wildlife on all continents. Drones have become of global importance for surveying breeding seabirds by providing opportunities to transform monitoring techniques and allow new research on some of the most threatened birds. However, such fast-changing and increasingly available technology presents challenges to regulators responding to requests to carry out surveys and to researchers ensuring their work follows best practice and meets legal and ethical standards. Following a workshop convened at the 14th International Seabird Group Conference and a subsequent literature search, we collate information from over 100 studies and present a framework to ensure drone-seabird surveys are safe, effective, and within the law. The framework comprises eight steps: (1) Objectives and Feasibility; (2) Technology and Training; (3) Site Assessment and Permission; (4) Disturbance Mitigation; (5) Pre-deployment Checks; (6) Flying; (7) Data Handling and Analysis; and (8) Reporting. The audience is wide-ranging with sections having relevance for different users, including prospective and experienced drone-seabird pilots, landowners, and licensors. Regulations vary between countries and are frequently changing, but common principles exist. Taking-off, landing, and conducting in-flight changes in altitude and speed at $\geq$ 50 m from the study area, and flying at $\geq$ 50 m above ground-nesting seabirds/horizontal distance from vertical colonies, should have limited disturbance impact on many seabird species; however, surveys should stop if disturbance occurs. Compared to automated methods, manual or semi-automated image analyses are, at present, more suitable for infrequent drone surveys and surveys of relatively small colonies. When deciding if drone-seabird surveys are an appropriate monitoring method long-term, the cost, risks, and results obtained should be compared to traditional field monitoring where possible. Accurate and timely reporting of surveys is

essential to developing adaptive guidelines for this increasingly common technology.

“According to all known laws of aviation, there is no way a bee should be able to fly. Its wings are too small to get its fat little body off the ground.”

– Title Narrator, *The Bee Movie*

2.2 Introduction

In the past ten years, the use of aerial drones has seen enormous uptake in environmental biology (Nowak et al., 2018). As platforms have become easier to fly, smaller, and more affordable, drones have become an increasingly cost effective method of gathering finer spatial and temporal resolution data from the air. The number of publications on Web of Science referring to 'drone,' 'unmanned aerial,' 'unmanned aircraft,' 'remotely piloted aerial,' or 'remotely piloted aircraft' has increased by approximately 40% from 2015 to 2020 (Hyun et al., 2020). While drones are known under a variety of terms, including unoccupied aerial vehicles (UAVs), unoccupied aerial systems (UAS), and remotely piloted aircraft systems (RPAS), they are all characterised as small powered aerial vehicles that can be flown remotely or autonomously and carry a payload (Rush et al., 2018; Johnston, 2019; Edney & Wood, 2021). Here, we refer to all of the above as 'drones,' as the term is simple and in widespread use by non-specialists (Chapman, 2014).

Seabirds are one of the most threatened groups of birds, so effective monitoring is needed to understand reasons for decline (Croxall et al., 2012). While detailed protocols exist for manually surveying breeding seabirds (Walsh et al., 1995), challenges remain, such as access, viewing, disturbance, and cost (both time and money), which has often limited the scale of monitoring efforts (Carney & Sydeman, 1999; Mitchell & Parsons, 2007; Paleczny et al., 2015; Rush et al., 2018). Drones are providing opportunities to overcome some of these challenges and have been used for monitoring of a variety of seabird species and for a range of purposes, including measurement of abundance, distribution, and breeding success (Edney & Wood, 2021).

Drones can access areas that are difficult or dangerous for fieldworkers to reach, which means entire breeding populations may be surveyed, rather than sub-plots due to access or time restrictions for fieldwork (Rush et al., 2018). They are often able to survey areas faster than direct field observations with the naked eye or binoculars and are also capable of surveying larger areas than can be captured on-site with handheld cameras, although this depends on suitable weather for flying (McClelland et al., 2016). Furthermore, drones can be less disruptive than ground counts, as less time is spent in animals' territory and observation is from the air rather than the ground (Sardà-Palomera et al., 2012). These advantages are becoming particularly apparent in the face of disease outbreaks, such as highly pathogenic avian influenza (HPAI), where fast and non-invasive monitoring is needed to track rapidly changing populations (Cunningham et al., 2022; Gregor, 2022). Nonetheless, using drones for seabird monitoring is not without difficulties.

Public perception of drones can be an issue for survey work due to privacy concerns, an association with the military, the idea of drones ruining the natural landscape, encouraging tourists to fly drones in nature reserves, and potential disturbance to wildlife (Vacca & Onishi, 2017; Johnston, 2019; Duporge et al., 2021; Dukowitz, 2024). Novices attempting survey work without adequate knowledge of aviation regulations or animal behaviour are at risk of breaking the law and putting people and wildlife in danger (Krause et al., 2021). Yet, the steps to acquire this knowledge and the necessary qualifications can be unclear and time-consuming, and hence, there is a need to synthesise the current state of knowledge.

A workshop was convened at the 14th International Seabird Group Conference 2018 to discuss the use of drones in seabird monitoring and research and to develop guidance to ensure practitioners and researchers are confident that flights are legal, safe, and obtain the results required (Wood, 2022). This review focuses on eight key steps the workshop identified for this to happen: (1) Objectives and Feasibility; (2) Technology and Training; (3) Site Assessment and Permission; (4) Disturbance Mitigation; (5) Pre-deployment Checks; (6) Flying; (7) Data Handling and Analysis; and (8) Reporting. An advanced literature search collated information from over 100 studies that had not previously been brought together in one place. As a result, the overall audience is broad, with specific sections having more or less relevance for different users. The presentations from the workshop can be viewed online (Wood, 2022).

2.3 Literature Search

We performed an advanced search using scientific search engines Web of Science and Scopus on 13 February 2023, for published studies containing keywords: ‘seabird,’ ‘waterbird,’ or ‘penguin,’ and ‘UAV,’ ‘UAS,’ ‘RPAS,’ ‘Unmanned Aerial Vehicle,’ ‘Unmanned Aerial System,’ or ‘Remotely Piloted Aircraft System.’ We repeated this search using the Google Scholar search engine to identify grey literature, including conference papers and unpublished reports. Collated sources were screened and included in the final dataset if the study used drones to monitor/research seabirds, and personal communications were added. Scientific reviews summarising others’ research were excluded. The final dataset synthesised information on study aim; seabird species; life-history stage; assemblage; drone type; drone engine; image/video analysis method; disturbance information; and comparison with traditional monitoring techniques (Appendix 2.5, Table A1).

The literature search yielded 114 relevant studies, with the first study using drones to monitor abundance of a seabird colony being published in 2012 (Sardà-Palomera et al., 2012). Since then, the number of publications on this topic has steadily increased over time (Fig. 2.1). Most studies focused on breeding seabirds (84%) and measured their abundance (57%), although the diversity of study objectives has increased as the technology has developed (Fig. 2.1). Further results are discussed within the eight-step framework detailed below.

2.4 Framework

2.4.1 Objectives and Feasibility

Clear objectives are needed to determine whether drones are an appropriate monitoring method. While drones can offer a number of advantages compared to ground surveys and other aerial techniques, they may not be necessary, and the total time, cost, and

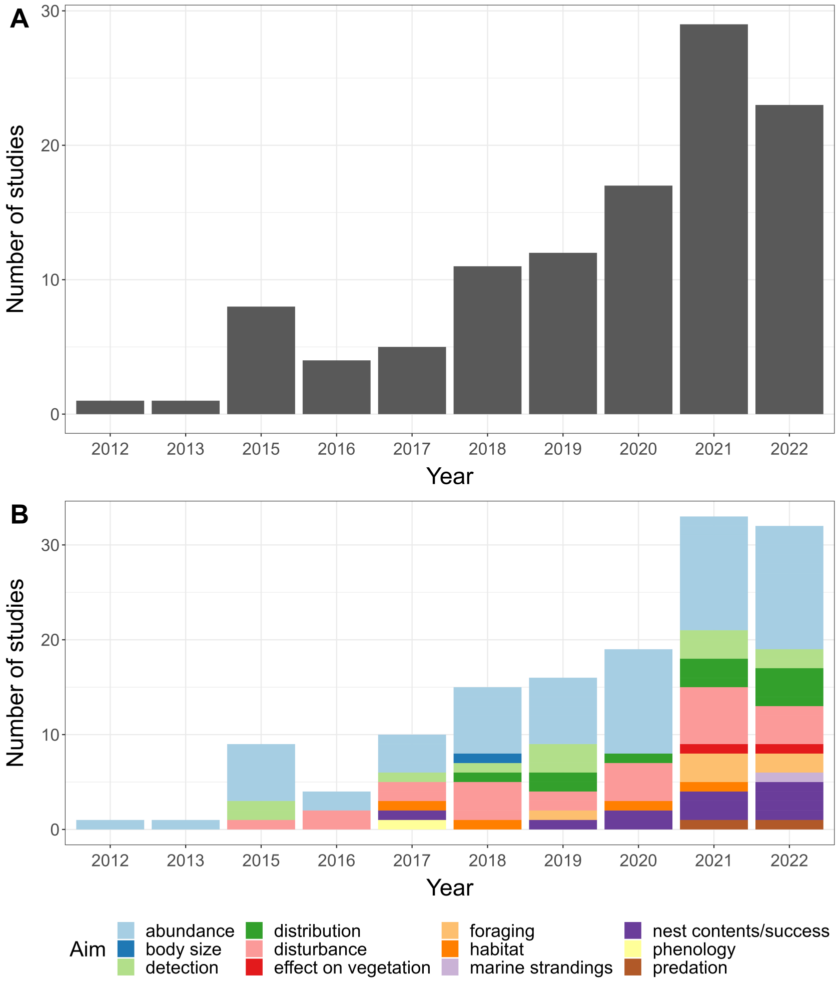

Figure 2.1: (A) Number of studies that have used drones to monitor/research seabirds each year from 2012–2022 (n = 114), as identified from our literature search. (B) Number of studies that used drones to monitor/research seabirds each year from 2012–2022, where the study aim has been categorised into one of twelve groups (n = 140, studies with multiple aims have been included more than once [i.e., once per aim]). Data from 2023 were excluded because the year was not yet complete at the time of publication.

disturbance incurred should be compared for each survey method (Tables 2.1, 2.2). The training and licensing procedure can take time and resources that may be better allocated elsewhere. Occasionally, cameras on long poles can achieve similar results (McDowall & Lynch, 2017), and for large species, satellite imagery may be available to count a population (Fretwell et al., 2017). The type of drone needed will also inform whether drones could be used, as they have a range of battery capacities, purposes, prices, and disturbance risks. This is an important first consideration when deciding whether drones are the most effective survey technique for a given task.

Table 2.1: Advantages and disadvantages of using drones to monitor seabirds compared with ground-based field observations; adapted from Edney and Wood, 2021

Advantages	Disadvantages
Operate at locations and times when field observations would be near-impossible. For example, remote locations (e.g. survey small islands from a boat), onshore and offshore, difficult terrain (Rush et al., 2018; Scarton & Valle, 2022). Surveying from a boat can avoid landing on remote islands, reducing risk posed to researchers from difficult boat landings in some cases, and minimising biosecurity risks and wildlife disturbance (Dickens et al., 2021). Reduced nest and site disturbance compared with walk-through surveys (Rush et al., 2018). Cover large areas in a short time (Valle & Scarton, 2021b; Corregidor-Castro et al., 2022). Combine habitat mapping and seabird occupancy from images, to investigate how habitat features affect populations (Oosthuizen et al., 2020). Georeferenced photographs allow for accurate geolocation of colonies and nests within and between seasons (Pfeifer et al., 2019). Permanent record viewable any number of times, available for independent verification, and re-analysis when new research questions and techniques become available (Thaxter and Burton, 2009; Buckland et al., 2012; Hodgson et al., 2018). Annotating images can improve accuracy of counts when presented with a large number of individuals, whereas field observers might find it hard to keep track of birds that have/have not been counted (Hurford, 2017; Hodgson et al., 2018).	Reduced use in areas with limited electricity and internet, which may be needed to charge batteries and update software. A fuel-powered generator may be required (Radjawali et al., 2017, Nowak et al., 2018). Vulnerable to damage or loss of control in adverse weather conditions, whereas field observations can often occur in more inclement weather. For example, small drones are unable to operate in windy conditions and low temperatures can reduce battery life or prevent take-off for some models (e.g. DJI). Waiting for the right conditions can make survey times longer than direct counts, and survey cancellations waste the opportunity costs of travelling to the site. (Chabot et al., 2015; McClelland et al., 2016). Large amount of data to handle and analyse, and processing and analysis requires specialised training and software (Rush et al., 2018). Data quality depends on operator skill, environment and meteorological conditions during flight. Birds flying over/in front of the colony could obscure the objects of interest behind them in images. (Nowak et al., 2018). Animals may modify their behaviour in response to a flying object, increasing intraspecific aggression, predation of eggs or chicks and nest abandonment. Some birds (e.g. raptors) may also attack the drone, and drone crashes in the colony could injure or kill birds. (Borrelle and Fletcher, 2017; Brisson-Curadeau et al., 2017; Rush et al., 2018). If an image is not clear, there is no opportunity to return/wait for a bird to move, unlike in the field. For example, field observers may wait for an adult to shift position to determine whether an egg/chick is present in the nest, but this is not possible when viewing an image afterwards (Walsh et al., 1995). Local, national and regional administrative regulations can affect possibility of data acquisition (Chabot et al., 2015; Nowak et al., 2018). Upfront cost of training and purchasing a drone makes surveys more expensive than field observations (e.g. using notebook, pencil and binoculars) for one-off or a small number of surveys; and multiple flights may be required to cover larger areas, increasing survey time (Albores-Barajas et al., 2018).

Table 2.2: Advantages and disadvantages of using drones to monitor seabirds compared with aerial surveys from occupied aircraft; adapted from Edney and Wood, 2021

Advantages	**Disadvantages**
Manoeuvrable, so can operate over small areas and monitor small objects (Nowak et al., 2018).	
Greater control over the scale, quality, and temporal and spatial resolution of images (Thaxter and Burton, 2009; Nowak et al., 2018; Korczak-Abshire et al., 2019)	Reduced use in areas with limited electricity and internet, which may be needed to charge batteries and update software. A fuel-powered generator may be required (Radjawali et al., 2017; Nowak et al., 2018).
Flexible angles of view can observe birds in a range of habitats and help reduce missed counts, especially when combined with thermal cameras to locate cryptic nests (Villegas et al., 2018; Shewring and Vafidis, 2021).	Operation generally limited to direct line of sight, which can prevent surveys of certain areas (e.g. headlands) from land. This requires the drone to be flown from a boat.
Portability and limited launch requirements allow operation in most locations and terrains, including from boats (Goebel et al., 2015).	More affordable (usually smaller) drones have sensors that take lower resolution images and often have lower battery life, increasing the number of flights needed to survey a given area, and thus survey time (Nowak et al., 2018).
Cost-effective (short survey time, low purchase, and operation costs) (Bibby, 2000; Buckland et al., 2012; Rush et al., 2018; Nowak et al., 2018; Villegas et al., 2018; Scarton and Valle, 2022).	

2.4.2 Technology and Training

Choice of Technology

There are many factors to consider when choosing a drone, including transportation, take-off and landing requirements, manoeuvrability, battery life, wind stability, temperature tolerance, water resistance, and sensor payload requirements. Drones commonly used for wildlife surveys can be classified into two main types: fixed-wing and multi-rotor (Table 2.3; Verfuss et al., 2019; Dunn et al., 2021). Out of 114 drone-seabird studies, 81% used multi-rotors. They are typically smaller, more manoeuvrable, and easier to fly, enabling easier transportation (e.g., in a rucksack), take-off from small spaces (e.g., boats), and reduced disturbance risk (see section '2.4.3 Disturbance Mitigation'). Fixed-wing drones may be more efficient for colonies containing many individuals (tens of thousands) and spread across large areas (km) because higher flight speed and longer flight duration means they can cover a larger area per survey, although such colonies can also be surveyed with multi-rotors given sufficient batteries and time (Lyons et al., 2019; Raoult et al., 2020). Improved battery endurance in recent years means survey coverage is more likely to be limited by regulations restricting flying Beyond Visual Line of Sight, rather than battery power.

Table 2.3: Comparison of multi-rotor and fixed-wing drones

Multi-rotor	**Fixed-wing**
Length usually from 35 to 150 cm and can normally be folded for transportation (e.g. can carry in a rucksack) (Johnston, 2019).	Wingspan usually from 90 to 350 cm, but can exceed 20 m (Johnston 2019).
Small multi-rotors (often <250 g) typically require less pilot training as they present a lower risk when flying.	Larger size means additional training and permits often needed.
Can take-off and land vertically in small areas (e.g. from the deck of a small boat) and from rugged terrain (Johnston, 2019; Raoult et al., 2020).	Often require launcher or runway for take-off, although some (expensive) models can take-off vertically (Chabot et al., 2015).
Agile manoeuvring and hovering and easier to fly. Allows image capture at appropriate angles for surveying cliff nesting seabirds, due to the aspect of the cliffs (Linchant et al., 2015).	Lower manoeuvrability, cannot remain stationary in flight. Harder to fly or require pre-programmed flight (e.g. SenseFly eBee X).
Safer, since they remain hovering when the control sticks are released. This means the pilot can let go in the event of an incident and allow the drone to hover while they regain composure and control.	Cannot hover, must be kept flying at all times, meaning problems can arise quickly.
Sound level is normally below the background noise from animals (e.g. seabird colony), ocean waves and wind (Goebel et al., 2015; Irigoin-Lovera et al., 2019).	Sound level of fixed-wing drones with petrol engines is greater than multi-rotors and can increase substantially with drone size (Christie et al., 2016). Electric fixed-wing drones have comparable sound levels to multi-rotors.
Lower speed and shorter flight duration ($\sim$20 min) so cover smaller area per survey (Rees et al., 2018; Colefax et al., 2019).	Higher speed and longer flight duration ($\geq$ 45 min), so cover larger area per survey (Rees et al. 2018).
Aerodynamically less stable, especially in windy conditions; although most reasonable sized multi-rotors perform well in moderate breeze (e.g. DJI Mavic 2 Enterprise Advanced is stable up to 29-38 km/h, Beaufort scale 4 to 5) (Goebel et al., 2015; Colefax et al., 2019; Corcoran et al., 2021; DJI, 2022).	Aerodynamically stable, less vulnerable to the effects of wind (Goebel et al., 2015; Corcoran et al., 2021).
Carry a limited range of sensors, often only one or two, so have to select the best sensor(s) to carry prior to take-off (e.g. DJI Mavic 2 Enterprise Advanced has RGB and thermal sensors; DJI, 2022).	Carry and capture from a greater range and number of sensors, due to their larger size. This includes carrying larger, heavier sensors which will reduce ground sample distance (GSD).

The type of payload will also affect drone choice. In the past, commercial multi-rotors have commonly used a digital camera that takes Red Green Blue (RGB) images and videos (Johnston, 2019; Raoult et al., 2020), but they are increasingly carrying additional sensors, such as active infrared (short wavelength infrared), thermal (mid-long wavelength infrared), and hyperspectral (wavelengths across the electromagnetic spectrum). Thermal sensors can be useful for detecting birds with cryptic colouration in environments where the animal's reflection in the visible wavelengths contrasts with the surrounding's reflection (Lee et al., 2019; Lethbridge et al., 2019; Corregidor-Castro et al., 2021). Most multi-rotors stabilise the payload with gimbals to improve image and video quality, especially when flying at higher speeds, while fixed-wings rarely use gimbals as their flight is more stable (Gašparović & Jurjević, 2017; Brinkman, 2020).

Camera specifications are important as well, as they will affect ground sample distance (GSD; the distance between two consecutive pixels in the image on the ground; small GSD means higher spatial resolution and more image detail) and risk of motion blur (O'Connor et al., 2017; Mustafa et al., 2019; Hayes et al., 2021). O'Connor et al., 2017 provide worked examples of how to achieve high-quality images by considering imaging configuration (pixel size, focal length, sensor size, and flight height) and exposure settings (ISO, aperture, shutter speed, focus and flight velocity). In summary, the GSD should be less than one-fifth of the size of the features of interest, and the flight height needed to obtain the required GSD can be calculated using:

$$GSD = \frac{(H * Sdet)}{f} \tag{2.1}$$

where H is flight height, f is focal length, and Sdet is width per pixel on the sensor (pixel pitch). If the required flight height is unsafe and may lead to disturbance (see '2.4.3 Disturbance Mitigation'), then lens focal length or sensor resolution could be increased to mitigate the challenge of maintaining GSD while operating at increased altitude. Motion blur should be kept < 1.5 times the GSD, and the required flight speed or shutter speed to achieve this can be calculated using:

$$b = \frac{(v * t)}{GSD} \tag{2.2}$$

where b is motion blur (in pixels), v is velocity, and t is shutter speed. In general, choosing cameras with larger sensors (to maximise sensitivity and reduce GSD) and minimum effective focal lengths of 24–35 mm (to minimise errors due to lens distortion), and optimising ISO (to ensure shutter speed is fast enough to minimise motion blur), will help provide suitable image quality at appropriate flight heights and speeds (O'Connor et al., 2017). Once the drone and payload have been chosen, it is important to consider how the specifications will affect flight training and permissions.

Flight regulations and training

Each operation should ideally have two people; a pilot and a visual observer, to aid with situational awareness given the pilot's attention is divided between aircraft and screen (Dickens et al., 2021). Flight regulations vary by country and the nature of flights (examples in Table A2 of 2.5 Appendix), but in general, drones > 250 g should be registered and have the registration number on the device, and pilots need certification to show they understand how to fly safely and legally (although in some regions, commercial work with < 250 g drones also requires relevant certification). This normally means taking a theoretical and sometimes practical flight assessment and flying $\leq$ 120 m high due to regulatory airspace restrictions and > 50 m from built-up areas and people (2.5 Appendix Table A2). This makes drone-seabird surveys in urban areas, like urban gull studies, challenging (Ross et al., 2016; Rush et al., 2018). Special permission and further qualifications are needed for these more complex operations that impinge general regulations, including flying Beyond Visual Line of Sight and flying with larger drones, typically > 25 kg (2.5 Appendix Table A2; Blight et al., 2019).

2.4.3 Site Assessment and Permission

Pre-site assessment

A pre-site assessment should be completed to assess whether the site is suitable for the designated work (2.5 Appendix Table A3). This should include details of the landscape to decide whether the objects of interest will be visible in drone images. Seabird nests may be camouflaged, hidden by vegetation and rocky outcrops, or be underground, with small entrance holes hard to see from the air (Albores-Barajas et al., 2018; Dickens et al., 2021). It should also document features that could affect site access (e.g., tidal forecasts for island surveys) or be a hazard to drone flight, namely physical obstructions (e.g., pylons, buildings), restricted areas in the vicinity (e.g., classified airspace and military operations), habitation and recreational activities, public access, and environmental regulations, as well as phone numbers to contact Air Traffic Control (ATC) at nearby aerodromes/airports if the pilot loses control of the drone.

Considering optimal survey date and time with relation to the study species and survey objectives is also important, as seabird breeding colony attendance varies on a daily and yearly cycle, and so restricted site access could bias data collected. For example, many species display diurnal variation in colony attendance; Brisson-Curadeau et al., 2017 found that the number of Thick-billed Murres *Uria lomvia* counted in drone images increased throughout the day, before peaking at 20h00. Because the number of birds present in the colony also changes through the breeding season and this differs among species, the optimal survey timing best reflecting, for instance, the breeding population size, needs careful consideration (Walsh et al., 1995).

Permissions

Provided the site is suitable for the planned survey, it is essential to get the necessary permissions to fly the drone at a specific site and time over the target species, beginning with permission from the landowner or local land manager. Several countries have banned drones in National Parks, including the United States, Canada (also banned in provincial parks in eight out of ten provinces), and South Africa due to disturbance concerns and potential use by poachers (2.5 Appendix Table A2; Dukowitz, 2024) although permission for research purposes may be granted by the countries' aviation authorities. Further consideration may be required for areas of any site that are sensitive to disturbance.

In the United Kingdom, most major seabird colonies are protected as Sites of Special Scientific Interest (SSSI), with many additionally protected as Special Protection Areas (SPAs). Every SSSI has a list of potentially damaging operations which can include the 'use of vehicles or craft likely to damage or disturb breeding seabirds' (Natural Resources Wales, 2021; Nature Scot, 2021); where such sites are also SPAs, conservation objectives (including those relating to minimising disturbance) must not be undermined by planned activity. It is also important to consider impacts on other features of these protected sites, like other bird species or particular habitats, that could result from seabird surveys.

Some seabird species are granted specific protection from disturbance when breeding, meaning it could be illegal to disturb them at certain times of year, although licenses can be applied for in some jurisdictions. For example, a license is required if you cannot avoid disturbing birds listed in Schedule 1 of the Wildlife and Countryside Act 1981 when they are nest building and rearing young in the UK (GOV.UK, 2015).

Even if additional licenses are not required, an ethics-related permit evaluating effects of potential disturbance by surveys on both target and non-target species' welfare may be requested by the research institution, funding body, or publisher if the study is later published. Whether animal welfare protocols are needed where drone work does not disturb wildlife is unclear, but possible direct and indirect environmental impacts must be considered during planning so the disturbance risks can be mitigated.

2.4.4 Disturbance Mitigation

Contamination and biosecurity

Contamination to the surrounding environment could occur from drone components shattering during collision and loss of drones in inaccessible locations where they cannot be retrieved, such as at sea. Anthropogenic debris can be physically hazardous to wildlife through entanglement, ingestion, alteration of habitats, or transport of non-native and pathogenic species (Engler, 2012; Rochman et al., 2016; Roman et al., 2020). It can also be chemically hazardous if chemical constituents adsorbed onto the debris are transferred to organisms by direct ingestion or via the food web (Engler, 2012; Rochman et al., 2016). Although the contribution of crashed drones to environmental pollution are minimal compared to that from other sources, these risks highlight the need for pilots to receive sufficient training to be competent, so the possibility of collision/loss is minimised.

Another concern when surveying seabirds is biosecurity, especially for birds breeding on remote islands. Introduction of invasive species and disease can have severe adverse consequences on seabird breeding success (Grimaldi et al., 2015; Caravaggi et al., 2019; Dias et al., 2019; Martin & Richardson, 2019), and so if drones can monitor populations without needing to go ashore, they can mitigate these risks (Dickens et al., 2021; Dewar et al., 2022). When drones do need to land, a landing pad should be used and the drone cleaned between sites to minimise spread of pathogens and non-native seeds and spores upon landing or in case of collision/loss (Council of Managers of National Antarctic Programs, 2021).

Wildlife disturbance

Another potential environmental impact is disturbance to breeding seabirds due to an unfamiliar aerial object in their territory, which may be perceived as an aerial predator (Mustafa et al., 2017; Mapes et al., 2020). This could disrupt behaviours like feeding, preening, and breeding, but it could also result in loss of nest contents. Adult seabirds displaced by a disturbance could knock eggs or chicks from nests, expose eggs or chicks to predation and the elements, or result in adults abandoning their breeding attempt (Borrelle & Fletcher, 2017; Brisson-Curadeau et al., 2017). Seabird colonies are often densely packed, with many birds occupying the surrounding airspace, and collision or crash landings could injure or kill individuals (Brisson-Curadeau et al., 2017; Ellett et al., 2021). Even if birds do not flush in response to the drone, they may still be stressed by its presence and experience other behavioural or physiological changes in response (Weimerskirch et al., 2018). This also applies for non-target species, such as marine mammals and raptors, which may be adversely affected by drone flight (Junda et al., 2015; Palomino-González et al., 2021). It is therefore essential that studies take appropriate measures to minimise disturbance to wildlife and monitor disturbance during surveys so that operations can cease if required (Hodgson & Koh, 2016).

Measuring and reporting disturbance

Existing studies vary in their measurement and reporting of disturbance, from research aimed at specifically testing and documenting drone-seabird responses (e.g., Rümmler et al., 2016; Brisson-Curadeau et al., 2017; Rümmler et al., 2018; Weimerskirch et al., 2018; Irigoin-Lovera et al., 2019; Krause et al., 2021; Rümmler et al., 2021) to ecologically focused studies that recorded responses as a by-product (e.g. Sardà-Palomera et al., 2012; Korczak-Abshire et al., 2016; Albores-Barajas et al., 2018; Mustafa et al., 2018; Rush et al., 2018; Blight et al., 2019; Rexer-Huber et al., 2020; Dunn et al., 2021; Mattern et al., 2021; Scarton and Valle, 2021). From our literature search, 72/114 studies (63%) provided some measure of disturbance and gave 132 'sub-studies,' for example, by measuring more than one species' and/or life-history stage responses, with different drone specifications and/or flight parameters. These are summarised in Table A4 (2.5 Appendix) with the aim of interpreting general guidance for best practice in measuring, reporting, and minimising disturbance. Out of 132 sub-studies, 50% reported a change in seabird behaviour in response to drone flight, although this should be interpreted with caution due to there being no standardised protocol for measuring and quantifying disturbance.

Several studies have compared the proportion of birds displaying specific behaviours before, during, and after a drone flight (2.5 Appendix Table A4). These behaviours are often associated with a disturbance score (typically, resting = 0, vigilance = 1, agonistic = 2, and escape = 3), which is used to determine whether drone flight causes adverse behavioural reactions (Korczak-Abshire et al., 2016; Rümmler et al., 2016; Mustafa et al., 2017; Rümmler et al., 2018; Weimerskirch et al., 2018; Barr et al., 2020; Krause et al., 2021). While this method is useful, studies often compare behaviour during drone flight to behaviour a short period (namely a few minutes) before and after drone flight, meaning the longer-term context of behavioural change is missing (Chabot et al., 2015; Barr et al., 2020). Seabirds show vigilance, agonistic, and escape behaviours across the breeding season in response to predators and competitors, and so the consequences of increased vigilance, agonistic, and escape behaviours due to drone flights might be minimal in comparison, but this is a topic that warrants future work.

Conversely, some studies recorded only the proportion of birds flushing in response to the drone (Sardà-Palomera et al., 2012; Reintsma et al., 2018), as escape behaviours may be more likely to have a significant fitness cost than vigilance, for example, due to energetically costly flight responses, loss of eggs or chicks by nest predation or exposure, and nest desertion (Brisson-Curadeau et al., 2017; Jarrett et al., 2020). Therefore, making comparisons between studies can be difficult due to different methods of categorising disturbance; for example, a study measuring changes in vigilance might report adverse behavioural reactions to drone flight, whereas a study only recording escape responses would not. It is also important to recognise that changes in behaviour do not necessarily have fitness consequences.

Even if a behavioural response is not observed, individuals might suffer physiological changes (e.g., heart and respiratory rates, hormonal stress response) due to drone flight (Weimerskirch et al., 2018), which studies rarely measure. To our knowledge, only two studies have investigated seabird physiological responses; one reported an increased heart rate in both parent and chick King Penguins *Aptenodytes patagonicu*s during drone flights (Weimerskirch et al., 2018), while the other found no change in Common Eider *Somateria mollissima* heart rate (Geldart et al., 2022; 2.5 Appendix Table A4). Quantifying these impacts may result in additional stress if birds need to be handled to attach loggers, such as heart rate monitors and respirometers. Studies should also consider drone-seabird responses relative to disturbance from traditional monitoring methods, such as ground counts (Mustafa et al., 2018). The pilot and visual observer do not need to be in close proximity to nesting seabirds during drone surveys, and so disturbance is likely to be reduced, especially compared with walk-through surveys (Chabot et al., 2015; Rush et al., 2018; Rümmler et al., 2021). It is therefore essential to consider the trade-off between the value of the data collected against potential disturbance from all methods of data collection.

Responses vary depending on a range of factors including drone features (e.g., size, shape, colour; Mulero-Pázmány et al., 2017), flight technique (including take-off/landing location, altitude, approach angle, flight pattern; Vas et al., 2015), target species (Borrelle & Fletcher, 2017; Barr et al., 2020), life-history stage (e.g., breeding vs. non-breeding; Brisson-Curadeau et al., 2017), age (e.g., adult vs. chick; Rümmler et al., 2021) and location (e.g., distance to an aerodrome affecting habituation to air traffic; Blight et al., 2019). Two studies investigated whether the sound of a multi-rotor drone was responsible for seabird behavioural changes, but both reported that the drone was no louder than ambient noise from the seabird colony (2.5 Appendix Table A4; Goebel et al., 2015; Irigoin-Lovera et al., 2019). We recommend detailed reporting of the equipment, flight methods used, and level of disturbance observed, as shown in Table A4, in all data published from drone surveys to help increase understanding of species' responses to different drone platforms in a range of environments and situations, leading to improved methods to minimise impacts (Hodgson & Koh, 2016; Barnas et al., 2020).

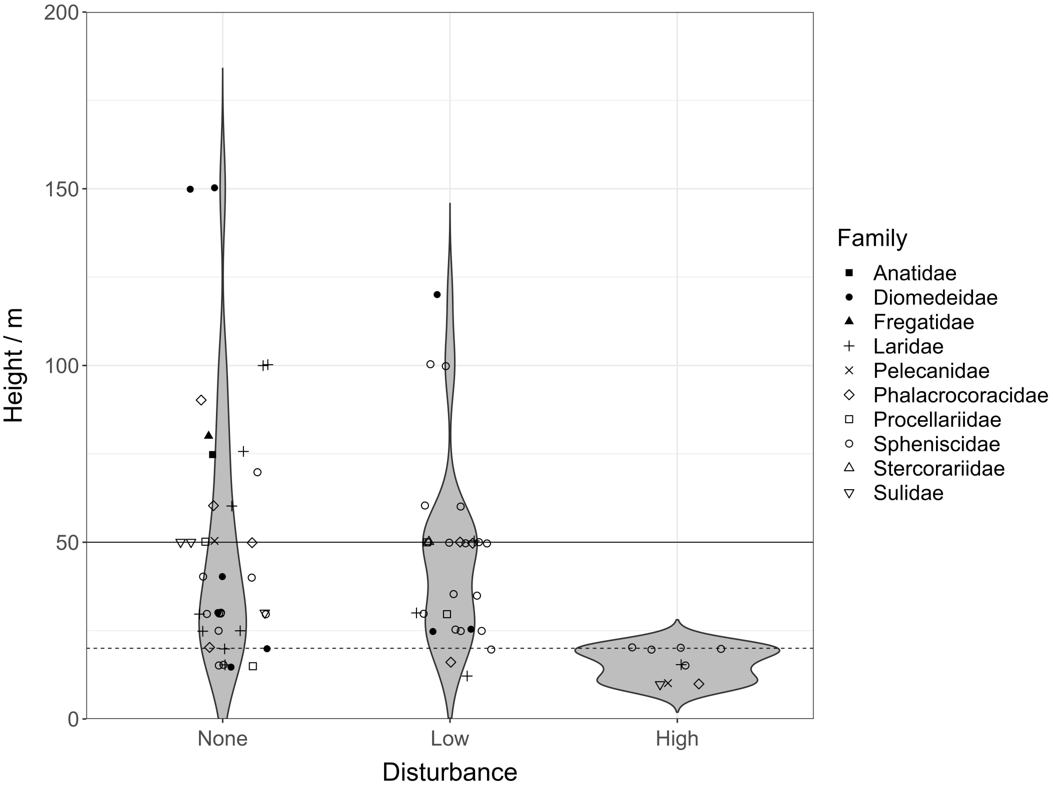

Figure 2.2: Violin plot of height above breeding ground-nesting seabirds at which a multi-rotor drone induced no (n = 38), low (n = 28), or high (n = 9) adverse behavioural responses for different seabird families (n: Anatidae = 1, Diomedeidae = 9, Fregatidae = 1, Laridae = 13, Pelecanidae = 2, Phalacrocoracidae = 8, Procellariidae = 4, Spheniscidae = 32, Stercorariidae = 1, Sulidae = 4). Flying at $\geq$ 50 m height (solid line) led to almost no disturbance. High disturbance only occurred when the drone flew $\leq$ 20 m height (dashed line). Data is available in Table A5, from studies summarised in Table A4 (see 2.5 Appendix). Disturbance categories were defined as: none = no behavioural response; low = a minor adverse behavioural response (e.g., vigilance); high = a marked increase in adverse behavioural response (e.g., escape).

Minimising disturbance

Summarising the disturbance data presented in Table A4, we find that for multi-rotor surveys of breeding ground-nesting seabirds, taking-off and landing 50 m from the study area (Brisson-Curadeau et al., 2017; Mustafa et al., 2017; Rümmler et al., 2018) and flying at greater than 50 m above the colony (n = 75, Fig. 2.2) is likely to have limited impact on many seabird species. If flight altitude or speed needs to be changed, the drone should be flown to the side of the colony and adjusted there, as vertical approach can cause more pronounced behavioural reactions than horizontal approach (Mustafa et al., 2017; Rümmler et al., 2018; Rush et al., 2018). For multi-rotor surveys of breeding cliff-nesting seabirds, the guidance is less clear due to few available studies (n = 9, Table A4), although flying at least 50 m horizontal distance from the cliff face is likely to prevent visible disturbance of species like guillemots and kittiwakes (Brisson-Curadeau et al., 2017; Park, 2020; Bishop et al., 2022, TH and AJE pers. comm, RMW pers. comm).

Nevertheless, when flying at a new site, a precautionary principle should always be adopted in the absence of evidence (Hodgson & Koh, 2016), and so we recommend that a trial is conducted to determine appropriate flight parameters (Mulero-Pázmány et al., 2017). Since there is a trade-off between image resolution and disturbance, we suggest starting at a height that is unlikely to cause disturbance and then working down to the maximum height (completing all changes in altitude away from the colony) at which the ground sampling distance is sufficient to accurately identify individuals without altering behaviour of both target and non-target species (Rush et al., 2018; Rexer-Huber et al., 2020; Dunn et al., 2021; Duporge et al., 2021). Flying higher will also give greater coverage in images and videos meaning fewer passes are needed over the colony, and extra altitude gives the pilot more time to move the drone away in the event of a problem.

Some researchers have suggested that post take-off, flying over the colony a few times can allow birds to habituate to the drone prior to the survey (Chabot et al., 2015; Reintsma et al., 2018; Rümmler et al., 2018). Equally, surveying sub-colonies that seem more sensitive to disturbance last, after they have seen calmer sub-colonies surveyed without incident, can reduce disturbance (e.g., Lesser Black-backed Gull *Larus fuscus*, MJW pers. comm). However, other studies have not observed short-term habituation, with seabird responses remaining the same after multiple flights during the same and consecutive days (Brisson-Curadeau et al., 2017; Mustafa et al., 2018; Rümmler et al., 2018). Habituation flights might therefore not reduce disturbance and only use up battery/opportunity time without justification of data collection. Instead, it is more important that an observer with seabird knowledge monitors the birds' behaviour and informs the pilot if flight needs to be adjusted or ceased due to disturbance (Junda et al., 2015; Hodgson & Koh, 2016; Mulero-Pázmány et al., 2017; Mustafa et al., 2018).

2.4.5 Pre-Deployment Checks

The pilot is responsible for having the necessary materials and supplies, and for ensuring both themselves and the drone are fit to fly in the local operating conditions on the day. Table A6 (see 2.5 Appendix) provides an example pre-deployment checklist to help achieve this, and extensive guidance can be found in operations manuals.

For seabird surveys, it is especially important to monitor local weather conditions leading up to the survey, as coastal sites are often windy and subject to sudden changes in weather (Bevan et al., 2015; Duffy et al., 2018; Raoult et al., 2020). Poor conditions (cold, precipitation, fog, glare, high wind speed) can decrease visibility, reduce the pilot's ability to control the drone, and distort or blur images (Raoult et al., 2020; Doukari et al., 2021). Maximum wind speed should be measured on-site using an anemometer, as winds > 20 km/h can reduce stability of multi-rotors (Bevan et al., 2015; Duffy et al., 2018; Raoult et al., 2020). A secondary landing site should be identified in case changing conditions prevent landing at the take-off location. For example, if worsening sea state prevents a boat landing, the drone should be landed remotely and recovered on land.

During set-up, the pilot must check that there is a global positioning system (GPS) signal, and that the compass and inertial measurement unit (IMU) are calibrated away from metal objects or other sources of interference. When operating from boats, it can be useful to ask the skipper to turn off radars during take-off and landing. The drone home point should also be set as the controller, not the take-off location, so if the batteries become low and the return to home failsafe is activated, the drone returns to the boat's current location and not over the ocean. For surveys of cliff-nesting seabirds, where take-off and landing are from the clifftop, the return to home failsafe must also be changed, so the drone flies vertically upwards above the clifftop, then horizontally to the landing point. Not all drones have object avoidance settings (Raoult et al., 2020), and so the standard return to home will return the drone to its take-off location via the shortest possible route: a diagonal upwards slope into the cliff.

2.4.6 Flying

Flying from a boat is sometimes recommended when surveying cliff-nesting seabirds (e.g., Bishop et al., 2022, T.H. & A.J.E. pers. comm., I.J.-M. pers. comm.) so direct visual contact can be maintained throughout flight, signal is maintained between the drone and controller, and the risk of pilot and observer standing too close to the cliff edge is removed. Furthermore, updrafts can be substantial at clifftops, making take-off and landing difficult (Duffy et al., 2018; Rexer-Huber et al., 2020). Surveying from a boat can also avoid landing on remote islands, minimising biosecurity risk and further wildlife disturbance (Dickens et al., 2021), as well as the risk posed to researchers by difficult boat landings. Taking off from a boat is best done from an observer's hand rather than the deck of the vessel (Johnston, 2019).

During take-off, the area downwind of the drone should be clear, as GPS compensation is only effective when it is a few feet above the ground, making the drone initially vulnerable to drift from wind gusts. Once airborne, a lawn-mower (grid) flight pattern is advised, with 70%–80% forward/backward overlap and 60% sideways overlap to prevent gaps in the stitched image (Parker & Rexer-Huber, 2020). The flight pattern can be pre-programmed with autonomous flight planning software (e.g., Map Pilot) and the same plan used over multiple years, making surveys repeatable, saving both preparation time for subsequent surveys and allowing assessment of temporal changes. However, this requires downloading the maps in advance for offline use when in the field (Dickens et al., 2021) and also relies on knowing the precise location of the target animals, which is not always possible if observing foraging behaviours, or if breeding colonies expand, contract, or shift location, as often occurs with penguins (Dickens et al., 2021). Manual flight is sometimes more appropriate, and the flight pattern chosen should be practiced in advance. If a bird starts interacting with the drone, the pilot should either continue slowly flying away from the area of disturbance until mobbing stops, or altitude should be immediately increased while remaining below any aviation flight height restrictions (often at $\leq$ 120 m high, but this varies by jurisdiction; 2.5 Appendix Table A2) to avoid further interactions. This contrasts with most non-bird emergency responses where altitude would be lowered, such as if a low-flying aircraft passed by.

Landing must occur away from the study area to minimise disturbance (Rush et al., 2018). If landing on a boat, multi-rotors are better hand-caught (protective gloves and eye protection are essential) due to movement of the vessel on the water increasing the risk of the drone landing overboard. Hand-catching is also preferred in windy conditions when the drone might otherwise fall over upon landing. Figure 2.3 provides a summary of the conditions that should normally be met when flying drones to survey breeding seabirds. More detailed information on steps to take when flying is given in 2.5 Appendix, Table A6.

2.4.7 Data Handling and Analysis

Image processing

Survey images can be examined individually or stitched together to form a composite image. An orthomosaic (where overlapping photos are joined together with distortions removed to create a positionally accurate representation of the surveyed area) can be produced using photogrammetry software such as Agisoft Metashape, previously called AgiSoft Photoscan (https://www.agisoft.com/), or ESRI Drone2Map (https://www.esri.com/en-us/arcgis/products/arcgis-drone2map/overview) (e.g., Albores-Barajas et al., 2018; Rush et al., 2018). This is difficult for surveys of vertical seabird colonies, as the software is designed to create a georeferenced image in the horizontal plane (i.e., a map), rather than the vertical plane. Instead, images can be stitched without embedded location data, using software like Hugin (http://hugin.sourceforge.net/) by finding fixed reference points in the images to create a panorama (Ratcliffe et al., 2015; Valle & Scarton, 2021a). Three-dimensional models of the surveyed area can be reconstructed from multiple overlapping drone images using

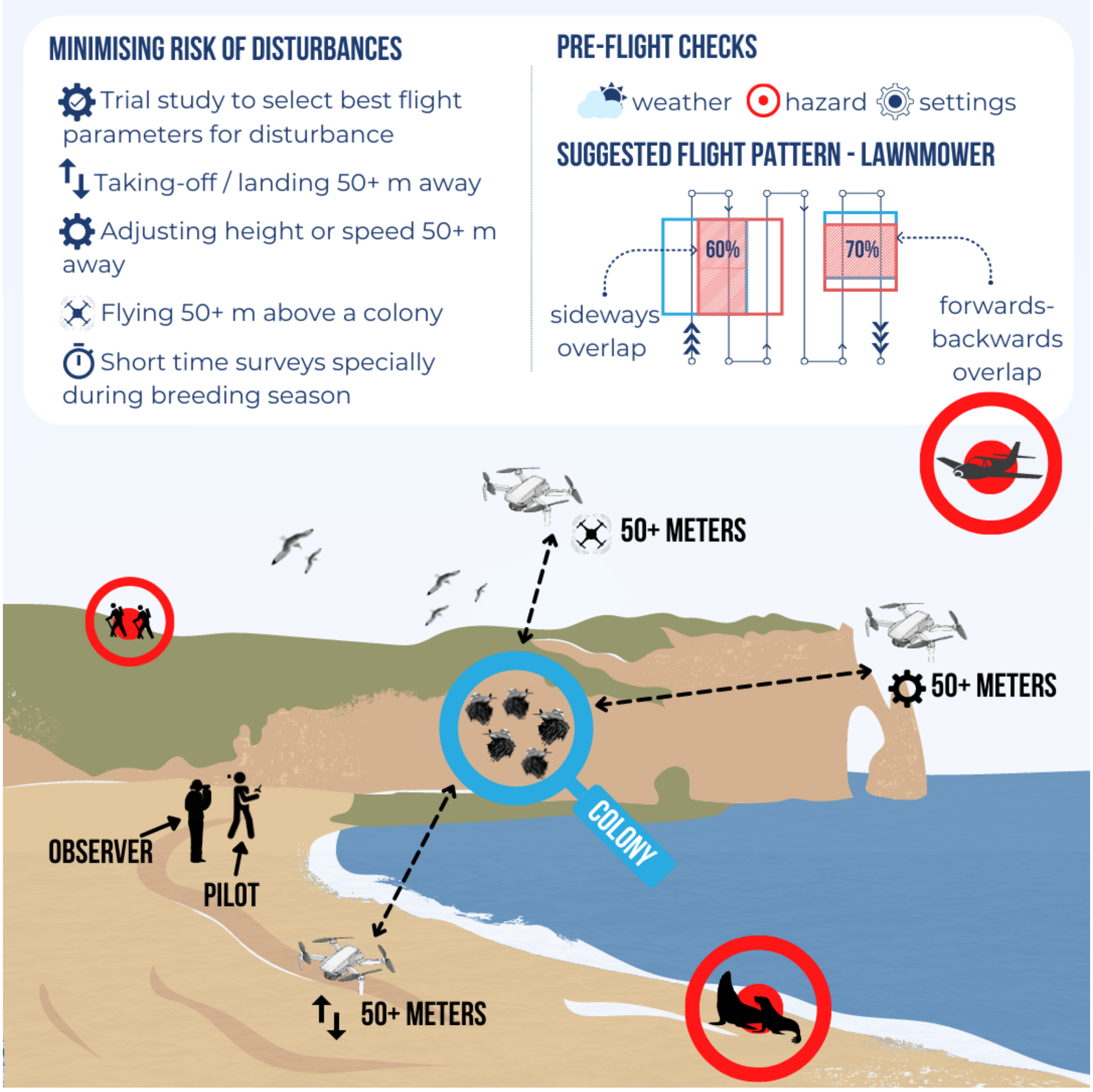

Figure 2.3: Summary of the conditions that should be met when flying drones to survey breeding seabirds, including pre-flight checks, methods to minimise wildlife disturbance, and possible flight pattern.

structure-from-motion processing (e.g., Oosthuizen et al., 2020) in software like Agisoft Metashape (https://www.agisoft.com/) or Pix4D (https://www.pix4d.com/). This has the advantage of capturing the 3D nature of cliff-based colonies.

Image analysis

After processing, images are analysed to obtain the measurements required. Thus far, manual image analysis has been most common (92 / 114 drone-seabird studies), where researchers examine the image and make the required measurement themselves (such as counting the number of nests, recording the stage of each nest, recording individual behaviours, etc.); however, because manual analysis is labour-intensive, semi-automated and automated methods are being increasingly applied (Shewring & Vafidis, 2021).

a) Manual image analysis

Many drone studies involve counting objects (e.g., birds, nests) (Nowak et al., 2018), with 80% of studies from our literature search (91 / 114) measuring seabird abundance. Tools which allow users to label objects in an image and then automatically sum the number of labels of each type can reduce counting errors (Ratcliffe et al., 2015; Hodgson et al., 2018). Suggestions for freely available software include ImageJ (e.g., Hodgson et al., 2018), DotDotGoose (e.g. Scarton and Valle, 2022), iTag (e.g. Ratcliffe et al., 2015), and QGIS (e.g. Espíndola et al., 2023), while Adobe Photoshop's count tool and ArcGIS (e.g. Bishop et al., 2022) must be purchased. To improve manual analysis, grid cells can be overlaid onto photographs to allow systematic counts grid-cell by grid-cell (Hodgson & Koh, 2016; Albores-Barajas et al., 2018; Korczak-Abshire et al., 2019; Valle & Scarton, 2021a), and images can be enhanced to improve clarity, such as by adjusting for shadows, highlights, and mid-tone contrast (Parker & Rexer-Huber, 2020). It is recommended that counts are repeated by both the same and different people, so that intra- and inter-observer error can be calculated and reported to assess confidence in results (Sutherland et al., 2004; Hodgson & Koh, 2016; Sinclair et al., 2017; Mallory et al., 2020).

The time required for manual identification and counting depends on the number of objects of interest in the image, image quality, and analyser experience, although it can be substantial. Analysing images of Gull-billed Tern *Gelochelidon nilotica* colonies took 176 minutes, which was 3.5 times longer than the drone inspection and surveys themselves (23 and 27 minutes, respectively; Scarton and Valle, 2021). Image processing time can be reduced by counting subsections of the image and scaling up to obtain a whole image estimate, provided counts from image sections are correlated (Sinclair et al., 2017).

For projects with large numbers of images to analyse, citizen scientists can represent a low-cost option to increase counting speed (Jones et al., 2018). The Zooniverse platform hosts over 50 active citizen science projects for free and has enabled annotations of over one million seabird images as part of the Penguin Watch and Seabird Watch projects (Zooniverse, 2021).

b) Semi-automated image analysis

Semi-automated classification is a type of supervised classification, meaning it is user-driven and cannot identify birds without human assistance, but is less time intensive than manual image analysis (Fretwell et al., 2012). Commercial ArcGIS software is commonly used and has given 98% and 96% mean agreement between semi-automated and manual counts of Lesser Black-backed Gulls (Rush et al., 2018) and Herring Gulls *Larus argentatus* (Corregidor-Castro et al., 2021), respectively. More recently, free ImageJ software has enabled 99.1% agreement for Mediterranean Gulls *Ichthyaetus melanocephalus*, providing a low-cost alternative (Corregidor-Castro & Valle, 2022).

Most semi-automated methods find a unique spectral signature for the target object (e.g., the head of a gull) that is used to identify all object occurrences in the image (Grenzdörffer, 2013; Waluda et al., 2014; Edney & Wood, 2021). This requires consistency in shape and colour of target objects and high contrast between objects and their background (Chabot & Francis, 2016; Andrew & Shephard, 2017; Hollings et al., 2018; Lyons et al., 2019). Animals with spectral properties similar to other species or the background—for instance, pale coloured gulls on guano-stained cliffs—will be harder to distinguish (Corregidor-Castro & Valle, 2022). Thermal imaging may help overcome this problem, as endotherms tend to be warmer than their surroundings and should therefore stand out (Lee et al., 2019). Nevertheless, in cold environments animals are often well insulated, leaving only a few small thermal hotspots that may be difficult to detect. In addition, differences in emissivity between animal tissue and substrate against which animals are viewed may mask the thermal difference between bird and background in thermal images (Witczuk et al., 2018).

c) Automated image analysis

Computer vision using deep neural networks (e.g., convolutional neural networks (CNNs)) is being increasingly used to automatically detect features in complex, ecological data (Christin et al., 2019; Jones et al., 2020; Hayes et al., 2021; Weinstein et al., 2022). However, accurate prediction of features, such as seabird location, abundance, and behaviour, will depend on technological constraints, environmental conditions, and ecological traits of target species (Corcoran et al., 2021). Detection is more accurate for images with uniform habitats, non-overlapping individuals of a single species, and individuals at rest rather than in flight (Dujon et al., 2021). Large training sets should improve detection and the network's ability to generalise to unseen imagery but are often unfeasible unless training annotations are outsourced to citizen scientists and/or micropayment sites (Arteta et al., 2016; Wang et al., 2019; Bowler et al., 2020). Lightweight CNN architecture and incorporating knowledge of bird spatial distribution within colonies can reduce the number of annotated images needed for training if species are abundant (e.g., Royal Terns *Thalasseus maximus*), but it is less accurate for species comprising < 10% of individuals (e.g., Caspian Terns *Hydroprogne caspia* and gulls; Kellenberger et al., 2021).

Automated image analysis can greatly increase efficiency compared to manual classification; Kellenberger et al., 2021 classified 21 000 seabirds in 4.5 hours, compared to three weeks of manual annotation. Nonetheless, building machine learning algorithms takes time, money, and experience. This might present a direct barrier to some users and make manual/semi-automated techniques more cost-effective if the drone survey is a one-off or infrequent occurrence.

Image analysis

The accuracy of results must be assessed to ensure data derived from drone images is suitable for use. Here, we can consider two types of accuracy: image-accuracy and observer-accuracy (Edney & Wood, 2021).

Image-accuracy is dependent on the image itself and whether it has captured all objects of interest, such as all active nests in the area being examined. It should predominantly be considered during the survey planning stage, as it will depend on image resolution (influenced by flight height and camera megapixels), weather conditions, and the landscape to be surveyed.

Observer-accuracy is the method's (e.g., manual observer's, computer's) intrinsic ability to correctly perform the required task (e.g., identify and count nests in the image) (Edney & Wood, 2021). For manual analysis, accuracy largely depends on user experience and the number of individuals in an image (Swanson et al., 2016; Jones et al., 2018). Large numbers of individuals increase the probability of some individuals being missed, although low numbers of individuals present fewer opportunities for the user to learn to recognise them (Swanson et al., 2016).

Ultimately, an accurate estimate is close to the true result (e.g., the true count in the wild), which is unknown. However, comparing results from drone imagery with traditional (often ground-based) monitoring methods can help decide if drone technology is an appropriate monitoring tool for the study objectives. If results from drone and traditional methods differ significantly, then the user needs to decide on the most accurate result. For example, drone imagery may achieve more accurate counts of breeding Thick-billed Murres than on-site ground counts, as the drone flushes non-breeding birds from the cliff (Brisson-Curadeau et al., 2017). Conversely, drones might give less accurate counts of species nesting in dense vegetation (e.g., gulls, terns, Macaroni Penguins *Eudyptes chrysolophus*) compared to traditional walk-through surveys, as nests will be hard to observe in photographs, but could be spotted on the ground (Dickens et al., 2021). As well, it may be difficult to discriminate between birds sitting on nests and nearby birds not on nests (especially for gulls) and impossible to distinguish between occupied and unoccupied burrows for burrow-nesting species. Where nests or burrows are difficult to spot from the air, sample areas should be counted in the field and on images to estimate counting error, so a correction factor can be used to estimate the true number of nests or burrows in images. Occupancy analysis, such as manual burrow inspection or playback of conspecific calls at burrow entrances in a sample area, can then estimate the proportion of burrows that are occupied (Walsh et al., 1995; Arneill et al., 2019).

Ideally, drone counts should give either the same or more accurate results than traditional methods before adopting them as common methodology; however, accuracy must also be balanced against variables such as time, money, and disturbance. Albores-Barajas et al., 2018 estimated that drone surveys of burrowing seabirds missed 5.6 burrows for every 100 compared to ground counts but saved 68% in person-hours, including additional image processing time. The monetary cost was higher due to the price of the drone, but this approach would become increasingly cost-effective per extra survey completed. Drone surveys might also be preferred at the expense of some accuracy if they significantly reduce disturbance to breeding seabirds, provided they do not limit the ability to detect, for example, population trends. In some cases, drones may even provide the only option for monitoring, for instance, if an island cannot be landed on or the terrain is impassable on foot (Benemann et al., 2022).

2.4.8 Reporting

A post-survey report is encouraged to allow continued guideline development and is typically required by regulators to determine how the survey went. This review offers practical guidance on how to survey seabirds with drones and obtain accurate data, and Barnas et al., 2020 complements it by providing a standardized protocol for reporting the methods in peer-reviewed articles, which we recommend. The protocol outlines information that should be included in each of six sections: Project Overview; Drone System and Operation Details; Payload, Sensor, and Data Collection; Field Operation Details; Data Post-Processing; and Permits, Regulations, Training, and Logistics. Table A4 in the Appendix (2.5) of this review further highlights key information that should be reported to help assess species' responses to drones and minimise disturbance.

2.5 Conclusions

In summary, drones offer many advantages for seabird monitoring and research. Time spent at a site is minimised if drones collect data faster than ground-based monitoring methods, and disturbance should be reduced as observers do not need to be in close proximity to seabirds. Furthermore, drones can minimise site travel and the potential to spread invasive species and damage vegetation. However, these benefits must be weighed against the costs, accuracy, operational utility, and potential impacts to seabird colonies and individuals. The recommendations outlined in this review are aimed at providing practitioners and researchers with a framework to ensure flights are effective, safe, and within the law. The need for accurate reporting and dissemination of operations is evident so we can continue to develop guidance for this comparatively new technology.

2.6 Appendix

The Appendix for this chapter is 77 pages long and is therefore not included in this thesis. Instead, it can be accessed online with the published article:

- http://www.marineornithology.org/article?rn=1544

Below is a summary of the tables contained in the Appendix:

Table A1. Final dataset generated from literature search for studies using drones to monitor/research seabirds. This yielded 114 relevant studies summarised below in chronological order.

Table A2. Regulations and permit requirements for flying drones in different countries in April 2022. At least one country is given for each continent. It is the responsibility of the pilot to ensure they are aware of the latest regulations in the country of operation at the time of flight, as requirements regularly change. In 2021, the European Union Aviation Safety Agency (EASA) divided drones into five classes from class C0 to class C4 based on different technical requirements, such as weight and noise level. The higher the number of the class, the greater the risk when flying. Since the classes have only recently been introduced drones without a class mark, including privately built aircraft, should be classed by their flying weight. VLOS = Visual Line of Sight, AGL = Above Ground Level.

Table A3. Example pre-site assessment form showing important information to record about the site. Useful sources of information include aeronautical chats, Google Earth, SkyVector, SkyDemon and NOTAMS.

Table A4. Summary of 72 studies, separated into 132 sub-studies, which measured seabird responses to drones. A single study (e.g., peer-reviewed journal article) can have contributed multiple table rows (termed a 'sub-study') for example, by measuring different species' and/or life-history stage responses, with different drone specifications and/or flight parameters. B = base, L = length, H = height, D = diagonally; TOLP = take-off and landing position; 'NA' if information not recorded in the study.

Table A5. Raw data for Figure 2.1, which is a violin plot of height above breeding ground-nesting seabirds at which a multi-rotor drone induced no (n=38), low (n=28) or high (n=9) adverse behavioural responses. These data are gathered from studies in Table A4 that used a multi-rotor drone to monitor breeding, ground-nesting seabirds and provided appropriate information on disturbance category and height (e.g. if disturbance could not be assigned to a single category the study could not be used). Disturbance categories are defined as: none = no behavioural response; low = a minor adverse behavioural response (e.g. vigilance); high = a marked increase in adverse behavioural response (e.g. escape). For studies where a range of heights were measured, height is the lower bound for disturbance category 'none' and the upper bound for disturbance categories 'low' and 'high'. For example, no disturbance (category 'none') at 20-30 m height in the original study, meant 20 m height used in Figure 2.1, because there was no disturbance as low as 20 m above breeding seabirds. Conversely, 'low' or 'high' disturbance at 20-30 m height in the original study, meant 30 m height used in Figure 2.1, because as high as 30 m there was still low- or high-level disturbance. Figure 2.1 therefore provides the minimum height at which no disturbance may be observed and the maximum height at which low and high disturbance may be observed, which are important parameters when trying to maximise image resolution but minimise disturbance.

Table A6. Example pre-deployment checklist for flying a multi-rotor drone, which should help ensure both drone and pilot are fit to fly in the local operating conditions on the day.

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3

Using citizen science image analysis to measure seabird phenology

Adapted from: Edney, A.J., Danielsen, J., Descamps, S., Jónsson, J.E., Owen, E., Merkel, F., Stefánsson, R.A., Wood, M.J., Jessopp, M.J. and Hart, T. (2025). Using citizen science image analysis to measure seabird phenology. *Ibis, 167(1),* 56-72. https://doi.org/10.1111/ibi.13317

Contents

3.1 Abstract

Developing standardized methodology to allow efficient and cost-effective ecological data collection, particularly at scale, is of critical importance for understanding species' declines. Remote camera networks can enable monitoring across large spatiotemporal scales and at relatively low researcher cost, but manually analysing images and extracting biologically meaningful data is time-consuming. Citizen science image analysis could reduce researcher workload and increase output from large datasets, while actively raising awareness of ecological and conservation issues. Nevertheless, testing the validity of citizen science data collection and the retention of volunteers is essential before integrating these approaches into long-term monitoring programmes. In this study, we used data from a Zooniverse citizen science project, Seabird Watch, to investigate changes in breeding timing of a globally declining seabird species, the Black-legged kittiwake *Rissa tridactyla*. Time-lapse cameras collected > 200 000 images between 2014 and 2023 across 11 locations covering the species' North Atlantic range (51.7°N – 78.9°N), with over 35 000 citizen science volunteers tagging adult and juvenile kittiwakes in images. Most volunteers (81%) classified images for only a single day, and each volunteer classified a median of five images, suggesting that high volunteer recruitment rates are important for the project's continued success. We developed a standardized method to extract colony arrival and departure dates from citizen science annotations, which did not significantly differ from manual analysis by a researcher. We found that kittiwake colony arrival was 2.6 days later and departure was 1.2 days later per 1° increase in latitude, which was consistent with expectations. Year-round monitoring also showed that kittiwakes visited one of the lowest latitude colonies, Skellig Michael (51.8°N), during winter, whereas birds from a colony at similar latitude, Skomer Island (51.7°N), did not. Our integrated time-lapse camera and citizen science system offers a cost-effective means of measuring changes in colony attendance and subsequent breeding timing in response to environmental change in cliff-nesting seabirds. This study is of wide relevance to a broad range of species that could be monitored using time-lapse photography, increasing the geographical reach and international scope of ecological monitoring against a background of rapidly changing ecosystems and challenging funding landscapes.

“~~Girls~~ Gulls on Film”

– Duran Duran, *Girls on Film*

3.2 Introduction

Biodiversity loss is threatening ecosystems, but there is increasingly limited time and funding for conservation (Waldron et al., 2013). Developing methods for cheaper, safer and more efficient ecological data collection is therefore of increasing importance to understand how and why species are declining, and to implement effective ecosystem management.

Seabirds are among the most threatened groups of vertebrates, with almost half of species globally threatened or near threatened with extinction (Croxall et al., 2012; Young & VanderWerf, 2022). Although seabirds are a well-studied faunal group (Richards et al., 2021), monitoring seabirds on land during the breeding season and at sea is often challenging (Edney & Wood, 2021). Difficulties accessing, viewing and disturbing breeding seabirds, as well as the time and money required to collect detailed life-history data (e.g. on phenology, breeding success, survival and diet) have often limited the scale of monitoring and precluded a globally standardized methodology (Mitchell & Parsons, 2007; Paleczny et al., 2015; Merkel et al., 2016; Edney et al., 2023).

Remote photography has a long history in seabird monitoring but has typically been limited to studies at a single site or conducted over a short time-period, often observing animals opportunistically, using handheld or animal-triggered cameras (Black et al., 2018b; Pascalis et al., 2018; Johnston et al., 2020). However, increased affordability, and continued improvements in power and data storage solutions, mean that large volumes of digital imagery can now be collected and stored with comparative ease (Bolton et al., 2007). This has seen the field of time-lapse photography (which records images at predetermined time intervals regardless of subject presence) rapidly expand in recent years (Edney & Wood, 2021). Remotely operated camera networks can enable monitoring across species' ranges, in remote locations and harsh conditions, at relatively low researcher cost and effort, as cameras need generally only be attended once per year (Southwell & Emmerson, 2015; Black, 2019; Edney & Wood, 2021). Collecting data year-round allows measurements of key breeding parameters, as well as additional variables such as colony arrival, colony departure and winter colony attendance, which are not captured by standard fieldwork, which typically focuses on determining breeding population counts and breeding success (Walsh et al., 1995; Black et al., 2017, 2018b). Higher frequency of observations than traditional fieldwork, which is often limited to a few repeat visits per season, can also provide finer temporal resolution data, potentially allowing dates of phenological events (e.g. chick hatch, fledge or failure) to be measured more precisely (Walsh et al., 1995; Black et al., 2018a). This can improve understanding of factors affecting chick survival or changes in fledging duration, for example (Knudson et al., 2020). Nonetheless, analysing images and extracting biologically meaningful data takes time, resulting in researcher workload being moved from the field to the desk (Merkel et al., 2016; Pascalis et al., 2018). One potential solution to prevent image collection exceeding researchers' processing capabilities is crowd-sourcing.

Citizen science engages non-professionals in scientific research (Dickinson et al., 2012) and has a long-standing history in ecology and conservation (Kobori et al., 2016; Swanson et al., 2016). Volunteers are primarily motivated to contribute to science, and citizen science projects can be effective in raising public awareness of ecological issues and increasing environmental stewardship (Raddick et al., 2010; Swanson et al., 2016; Viola et al., 2022). Despite this, citizen science projects often suffer criticism from professional researchers about the validity of data derived from non-experts, which can lower publication rates and grant funding (Foster-Smith & Evans, 2003; Dickinson et al., 2010; Bonter & Cooper, 2012; Swanson et al., 2016). It is therefore important that studies using citizen science data test that data's robustness before use (Hertzog et al., 2021; Gorleri et al., 2023; Jäckel et al., 2023). Citizen science projects have used a range of methods to improve the quality of volunteer data, including training volunteers before participation, requiring volunteers to pass a competency test, or aggregating the results of multiple users to form a consensus (Dickinson et al., 2010; Swanson et al., 2016). Recruiting enough volunteers to meet project workload is a further consideration for citizen science projects, and retaining volunteers can help to ensure project longevity, as well as minimizing the need for frequent training and/or testing of new participants.

When testing any new methodology, it is essential that it is ground-truthed against a well-understood phenomenon, but one which is of fundamental importance. Changes in the timing of key life cycle events (phenology) are one of the best-documented responses to rising global temperatures (Møller et al., 2008). Phenology of species occupying higher trophic levels, such as seabirds, may be less responsive to temperature-driven environmental change than those occupying lower trophic levels (Thackeray et al., 2010; Burthe et al., 2012; Thackeray et al., 2016; Keogan et al., 2018), making seabirds particularly sensitive to trophic mismatch (Hipfner, 2008; Shultz et al., 2009; Regular et al., 2014). This effect may be greater at higher latitudes, where Arctic amplification means Arctic ecosystems are being disproportionately affected by warming; yet, harsh abiotic conditions severely limit the time window that is favourable for seabird breeding and migration (Descamps et al., 2019; Sauve et al., 2019; Whelan et al., 2022). The timing of breeding is expected to be later at higher latitudes, driven by physical conditions (such as snow/ice cover on nest-sites) delaying the onset of breeding and/or by the timing of food availability near the colony (Moe et al., 2009; Burr et al., 2016). Investigating phenological changes across species' latitudinal breeding range is therefore important to assess which populations may be most at risk from trophic mismatch in a changing climate.

In this study, we investigated the potential for citizen science analysis of images collected from a time-lapse camera network, to measure breeding phenology of a globally declining seabird species, the Black-legged kittiwake *Rissa tridactyla* (hereafter kittiwake) (BirdLife International, 2024). Many bird phenology studies focus on a single species and site, while those spanning large spatial and temporal scales often rely on varying methods within the same study (Frederiksen et al., 2004; Moe et al., 2009; Wanless et al., 2009; Keogan et al., 2022) to obtain measures of breeding phenology across different sites and years (e.g. using both observed and estimated dates; using a combination of first, mean or median dates; changes in frequency and/or intensity of nest checks over time) meaning results are not always directly comparable and there is a clear need for standardization. We collected images at 11 colonies spanning an extensive latitudinal gradient (51.7°N – 78.9°N), providing a non-invasive, standardized technique for collecting data in remote locations that are visited infrequently by humans and often previously unmonitored (Edney & Wood, 2021). To process the large volume of imagery collected, we asked volunteers from the Zooniverse citizen science project, Seabird Watch, to classify adult and chick kittiwakes in these images. We tested the validity of citizen science data when images were classified by multiple volunteers and a consensus value was used, and predicted that such techniques would yield similar results to expert image annotation by a researcher. Using this standardized method would then enable assessment of spatiotemporal patterns of colony attendance, and we predicted that kittiwake arrival and departure would be delayed per degree increase in latitude, corresponding to the delayed egg-laying and hatching observed in previous studies (Burr et al., 2016; Keogan et al., 2022). We further considered the overall cost-effectiveness (both time and money) of the citizen science camera network. We predicted a monotonic relationship between the length of time volunteers participated in the project and the number of images they classified, in support of the idea that volunteer retainment is key to the system's long-term capacity to answer advanced ecological questions pertaining to seabird ecology and demography, in a standardized way.

3.3 Methods

3.3.1 Study sites and camera set-up

We used a network of 11 time-lapse cameras across eight countries that span the latitudinal breeding range of the Black-legged kittiwake (Fig. 3.1). The time-lapse cameras were most often commercially available Reconyx Hyperfire or Reconyx Ultrafire (Reconyx Inc., Holmen, WI, USA) mounted on either a pre-made camera tripod or a custom-built tripod (e.g. with scaffold poles), although some sites had specialist, custom-built cameras (Table 3.1, Fig. 3.2). Tripods were weighed down with ballast stones or attached to the ground/nearby rock to prevent movement. Each Reconyx camera contained a 16–64 GB SD card and 12 Ultimate Lithium batteries, or at UK sites, 12 rechargeable Eneloop batteries. Most cameras captured between 30 and 130 nests and were programmed to take

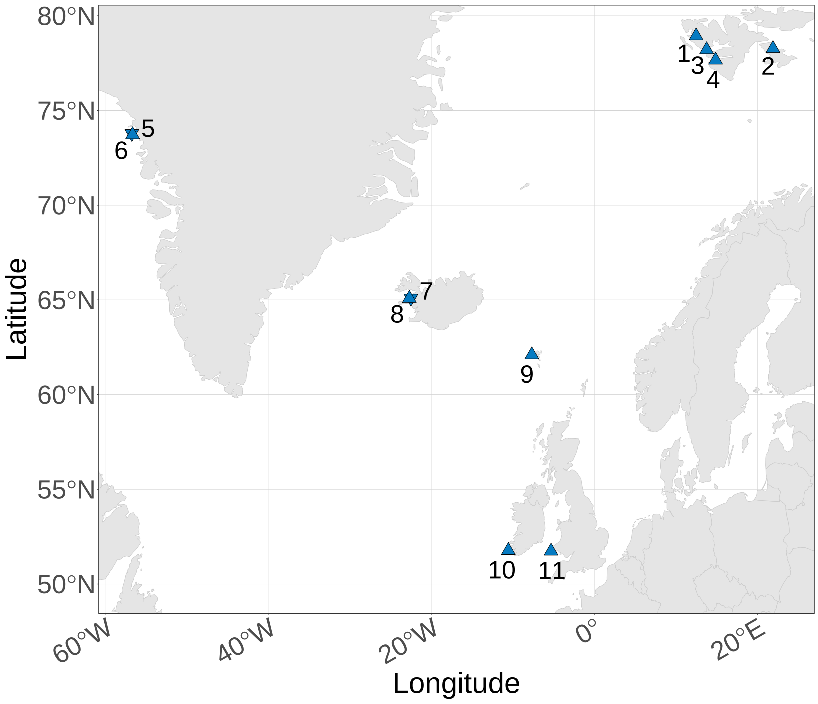

Figure 3.1: Locations of cameras included in this study. Key: 1 = Ossian Sarsfjellet, 2 = Kapp Waldberg, 3 = Alkhornet, 4 = Midterhukfjellet, 5 = Apparsuit, 6 = Kippaku, 7 = Elliðaey, 8 = Hvítabjarnarey, 9 = Mykines, 10 = Skellig Michael, 11 = Skomer. Closely spaced colonies are illustrated using upward and downward triangles to avoid complete overlap.

one image per hour year-round, although at high latitudes this was sometimes reduced to four photos per day to maximize battery lifespan at sites that were infrequently visited (e.g. in Alkefjellet, Svalbard, a Reconyx Ultrafire captured four images per day from 2018 to 2022, before its retrieval in 2022). Typically, batteries and SD cards only need to be changed once every 1–2 years for Reconyx cameras taking hourly images. The total cost of setting up one Reconyx camera is in the region of £800 (excluding travel expenses), depending on the camera model and mount used, and quantities ordered (e.g. c.£500–£600 per Reconyx camera; c.£200 per tripod; c.£20–£30 for batteries and SD cards). Cameras were visited once every 1–4 years depending on access and logistical constraints, to replace SD cards and batteries.

Table 3.1: Type of camera installed at each location used in this study.

Site (colony code)	Latitude, Longitude	Year	Camera type
Skomer Island, Wales (SKOM)	51.74, -5.30	2017	Reconyx UltraFire
		2018, 2019, 2020	Reconyx HC500 Hyperfire
Skellig Michael, Ireland (SKEL)	51.77, -10.54	2014, 2015, 2016	Reconyx HC500 Hyperfire
		2018, 2019, 2020, 2021	Reconyx Ultrafire
Mykines, Faroes (MYBR)	62.1, -7.66	2014, 2015	Reconyx HC500 Hyperfire
		2018	Reconyx Hyperfire 2 Covert
		2019, 2020	Reconyx HF2 Pro Convert
		2021	Reconyx Ultrafire
Elliðaey Island, Iceland (ELLI)	65.09, -22.49	2015, 2016, 2017	Reconyx HC500 Hyperfire
Hvítabjarnarey Island, Iceland (HVIT)	65.08, -22.68	2016, 2017	Reconyx HC500 Hyperfire
		2018, 2019, 2020, 2021	Bushnell
Kippaku Island, Greenland (KIPP)	73.72, -56.63	2016, 2017, 2018, 2019	Canon EOS 60D mounted in weatherproof box (see Merkel et al., 2016
Apparsuit Island, Greenland (APPA)	73.79, -56.72	2017, 2018, 2019	Canon EOS 70D mounted in weatherproof box (see Merkel et al., 2016)
		2020	Canon EOS 80D mounted in weatherproof box (see Merkel et al., 2016)
Midterhukfjellet, Svalbard (MITT)	77.66, 14.88	2014, 2015	Reconyx HC500 Hyperfire
		2016, 2017	Reconyx SC950 Security
		2019, 2020, 2021	Reconyx UltraFire
Alkhornet, Svalbard (ALKE)	78.21, 13.78	2015, 2016	Reconyx HC500 Hyperfire

Figure 3.2: (a) Example time-lapse camera set-up on Skomer Island, Wales. This camera is mounted on a pre-made tripod typically used for spotting scopes, whereas other cameras are mounted on custom-built tripods made from scaffolding poles. Tripods are attached to the ground/nearby rock or weighed down with ballast. (b) Image taken at Skellig Michael, Ireland, in winter (12 November 2016), with kittiwakes present on the cliffs.

3.4 Camera data extraction

3.4.1 Image annotation and processing

Images were annotated by volunteers on the Seabird Watch citizen science project, hosted on the Zooniverse platform. The Seabird Watch project contains multiple workflows (sequences of tasks, which volunteers are asked to complete) for analysing different image sets. Each workflow shows users a tutorial before being given their first image, which explains how to complete each task and provides examples of how birds appear in images. There is also a field guide of animals likely to be seen, a Frequently Asked Questions page and a discussion forum moderated by scientists, to answer volunteer questions and help ensure they understand the tasks to complete. For this analysis, the Timelapse workflow (launched on 19 October 2017) was used to click on birds and classify them as either adult or chick kittiwakes. Each image was viewed by multiple volunteers to increase data reliability. Specifically, four people were initially shown each image, and if any of them classified a bird, then the image was shown to 10 people in total. If the first four volunteers classified zero birds, the blank image was retired, meaning it was removed from the active dataset and not seen by further volunteers. As the presence of birds was easy to detect, recording four negatives was sufficient to be confident no birds were present and retire an image. Participants did not have to classify every bird in images, to help prevent loss of interest when photographs contained a large number of individuals, but at the end of each image, they were asked to select ‘Yes’ or ‘No’ for whether they had marked every bird (Jones et al., 2018). Previous research showed that for five colonies sampled, $> 99\%$ of images were classified by four or more volunteers who marked all birds, and $> 47\%$ were classified by seven or more volunteers who marked all birds (Edney, 2020). This suggests that across at least 10 independent viewers almost every bird should be classified.

As each image was classified by multiple volunteers, a clustering algorithm was used to aggregate raw classifications to generate one consensus classification for each object (i.e. bird) using Caesar software (Jones et al., 2018; Krawczyk et al., 2022). Classifications made by the same user in a single image (i.e. because they classified more than one bird) were placed in separate clusters, and consensus classifications had to be formed from at least three raw classifications to limit erroneous clicks (Jones et al., 2018; Krawczyk et al., 2022). The number of consensus classifications per image for each category (adult kittiwake, chick kittiwake) was summed to give an image count.

Images taken at night were removed from the dataset post-clustering, using the ‘suncalc’ package in R to either identify images taken after sunset but before sunrise, or at high latitude, to identify images without sunrise or sunset between October and February. This was important because the cameras do not have night vision, and so a count of zero birds in completely dark images is not necessarily a true zero (i.e. there might have been birds present, but they could not be observed); this is particularly relevant at high latitudes in winter when the sun does not rise. We chose to upload these images onto Seabird Watch and remove them post-clustering (rather than removing dark images prior to upload), because previous research found that blank images can increase citizen science participation (Bowyer et al., 2015).

For this analysis, we used counts from the 1:00 pm image, or the time closest to 1:00 pm, for each day. This was because different camera set-ups and image times processed in Seabird Watch across sites and years meant not all hours were available for every camera.

3.4.2 Changes in arrival and depature with latitude

Count data for adult kittiwakes were smoothed using a 3-, 5- and 7-day moving average to remove noise in the data. Smoothing was necessary because counts may be lower than expected (sometimes zero) as a result of the camera view being obscured, such as by snow, or a bird in the foreground partially obscuring the nests behind. The moving average chosen (i.e. 3, 5 or 7 days) was determined by comparison with researcher dates (see ‘3.4.2 Citizen science data validation’).

We defined an observation period as starting on 1 January and ending on 31 December with arrival occurring between January and May and departure between July and December.

Using these criteria, the available dataset for measuring colony arrival and departure was identified by removing years where the first image in the dataset was taken after May and where the last image in the dataset occurred before July (Table 3.2). Although we expected that kittiwakes would not depart until August, we included July in the departure dataset to potentially identify colonies where all breeding attempts failed and kittiwakes might leave early (Coulson, 2011). This could facilitate further investigation on the effect of extreme events (e.g. severe predation, food shortage, bad weather) on kittiwake breeding. Additional years were also removed where breaks in image capture (e.g. due to camera failure) meant arrival and/or departure were missed. Overall, 64% of possible arrival and departure dates were able to be used for analysis (Table 3.2).

Colony arrival was measured as the first day of X consecutive days of increase in the number of adult kittiwakes, and colony departure was measured as the last day of X consecutive days of decrease in the number of adult kittiwakes, where X took values from 2 to 7 days. The value of X used for analysis was chosen by comparison with researcher dates (see '3.4.2 Citizen science data validation') and thus provides a standardized method to measure arrival and departure, as the same value of X could be used if the method were applied again in other studies. We used a consecutive days approach, rather than the first and last day an adult kittiwake was recorded, to capture the gradual increase/decrease in colony abundance and reduce the likelihood of citizen science misclassifications recording too-early/too-late arrival/departure dates. For example, incorrectly classifying another bird species (such as a Herring Gull *Larus argentatus*, which may be present year-round in UK images) as a 'kittiwake' on 2 February, would give arrival as 2 February if this was the first day of the year a 'kittiwake' was seen. In comparison, the misclassified Herring Gull would be ignored using the consecutive days method, as it is unlikely that Herring Gull numbers would increase for multiple days in February.

We tested the relationship between latitude and arrival and departure dates using linear mixed-effects models, with either arrival or departure date as the response variable, latitude as a fixed effect and colony as a random effect, and computed P values using a Wald t-distribution approximation (Bates et al., 2015).

3.4.3 Citizen science validation

We compared arrival and departure dates calculated from 2 to 7 days of consecutive increase/decrease using 3-, 5- and 7-day moving averages of Seabird Watch consensus classifications, with arrival and departure dates from manual researcher analysis. The researcher (AJE) looked at the 1:00 pm images to identify the first time an adult kittiwake was seen in an image (arrival) and the last time an adult kittiwake was seen in an image (departure) for the season. Wilcoxon signed-rank tests tested for significant pairwise differences and Pearson product-moment correlations tested for pairwise correlations between Seabird Watch and researcher arrival and departure dates, for each combination of moving averages and consecutive days increase/decrease.

3.4.4 Citizen scientist participation and retention

To determine the long-term capacity of the camera–citizen science system to measure seabird demographic parameters, we extracted information on the number of images classified and volunteer contribution, for the Timelapse workflow, from 19 October 2017 to 19 October 2023 (excluding April to June 2023 when the workflow was inactive). Specifically, we measured the median number of images classified per month, the median number of volunteers who classified at least one image per month, the number of images each volunteer classified in total and the time period over which these images were classified. A Spearman's rank correlation test tested for a correlation between the number of images each volunteer classified and the time period over which they classified these images. All analyses were conducted in R, version 4.2.2 (R Core Team, 2022).

3.5 Results

3.5.1 Citizen scientist participation and retention

From 19 October 2017 to 19 October 2023, 799 917 images were classified using the Seabird Watch Timelapse workflow, which equates to 87 046 unique camera images (because each unique image was classified four to ten times by different volunteers). The median number of images classified per month was 3846 (interquartile range (IQR) 2003–9576) and the maximum number of images was 296 921, in October 2017 (Fig. 3.3). The total number of unique volunteers who classified an image was 36 889 (identified by their IP address or account login), of which 14 077 were logged into a registered account on the Zooniverse platform. The median number of unique volunteers participating per month was 193 (IQR 123–431), although the maximum was far higher (22 694 in October 2017). We found a positive correlation between the number of images classified by each volunteer and the length of time between the first and last image they classified ($r=0.26$, $P<0.001$; Fig. 3.3), despite 81% of volunteers classifying images for only a single day (Fig. 3.3). The median number of days between a volunteer's first and last classification was 0 (IQR 0–0) and the median number of images each volunteer classified during this time was 5 (IQR 2–12).

3.5.2 Citizen science data validation

Comparing arrival and departure dates derived from citizen science and researcher analysis using Wilcoxon signed-rank tests, we found that the 5-day moving average was the smallest moving average that gave similar estimates for both arrival and departure, for at least one value of consecutive days increase/decrease (Fig. 3.4; Table 3.3 and Fig. 3.8 in the Appendix). The 5-day moving average was chosen to smooth the citizen science data going forward, as stronger smoothing using larger moving averages (e.g. 7 days) might reduce the ability to detect the timing of key breeding season events more precisely (e.g. the kittiwake incubation period is typically 25–29 days; Coulson, 2011). Using this 5-day

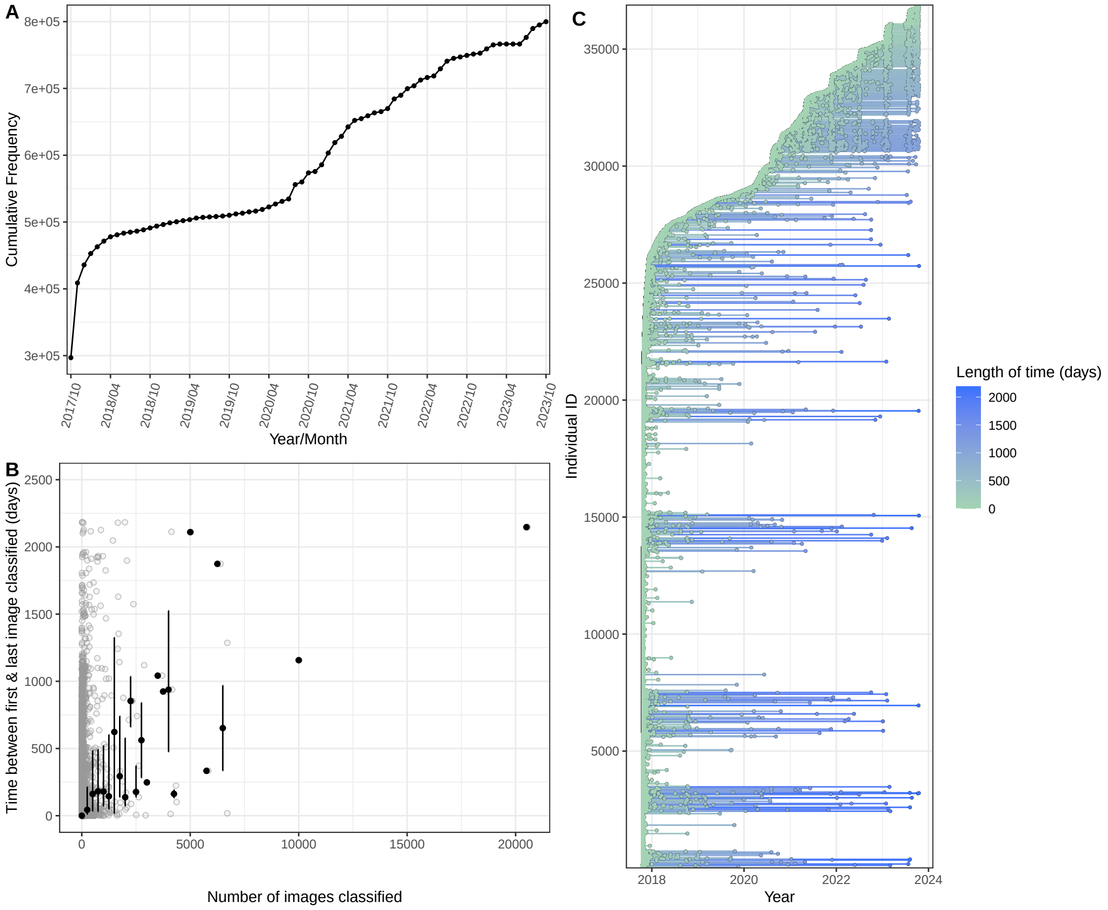

Figure 3.3: (a) The number of images classified using the Seabird Watch Timelapse workflow (19 October 2017 to 2023) has steadily accumulated across time, with high initial uptake when the project launched, and another notable increase during the COVID-19 pandemic in 2020. (b) There is a positive correlation (r=0.26, P<0.001) between the number of images classified by each volunteer and the length of time between the first and last image they classified (n=36 889). Points show raw data and transparency has been used to show density in areas of overlap. Black dots represent the median number of images classified, when binned into sets of 250, with whiskers showing the interquartile range. (c) Volunteer contribution pattern, showing the length of time (in days) between the first and last image each volunteer (individual ID) classified (n=36 889).

moving average, arrival and departure dates were both similar when 3 days of consecutive increase/decrease were used to identify arrival/departure respectively (Fig. 3.4; Table 3.3 and Fig. 3.8 in the Appendix). This was supported by the Pearson product-moment correlations, which found that the Pearson correlation coefficient was highest (R=0.9948) when the citizen science data was smoothed using a 5-day moving average and departure was measured as the last day of three consecutive days of decrease in the number of adult kittiwakes (Fig. 3.5; Table 3.4 in the Appendix). The Pearson correlation coefficient was similarly high (R=0.9937) when the citizen science data was smoothed using a 5-day moving average and arrival was measured as the first day of 3 consecutive days of increase (Fig. 3.5; Table 3.4 in the Appendix). As a result, we decided to smooth the citizen science data using a 5-day moving average and we measured arrival as the first day of three consecutive days of increase, and departure as the last day of three consecutive days of decrease, in the number of adult kittiwakes. For all combinations of moving averages and consecutive days, the departure dates for one colony, Skellig Michael, were outliers (departure date > q0.75+1.5*IQR; where q0.75 is the third quartile) (Fig. 3.4).

3.5.3 Changes in arrival and departure with latitude

Colony arrival and departure dates were determined by smoothing Seabird Watch consensus classification data using a 5-day moving average, and then determining the first day of 3 days of consecutive increase in number of adult kittiwakes (arrival) and the last day of 3 days of consecutive decrease in the number of adult kittiwakes (departure) (Fig. 3.6). Plotting the number of adult kittiwakes (smoothed using a 5-day moving average) counted from consensus classification data showed that birds visited the Skellig Michael colony during winter, resulting in skewed ‘departure’ dates in December that did not reflect colony departure post-breeding (Fig. 3.6). Most kittiwakes left the colony by mid-September and then returned in January before the start of the next breeding season, with small numbers of kittiwakes present in between. Consequently, we excluded winter attendance and re-defined departure as occurring from July to 15 September for Skellig Michael (compared with July to December for all other colonies), and measured

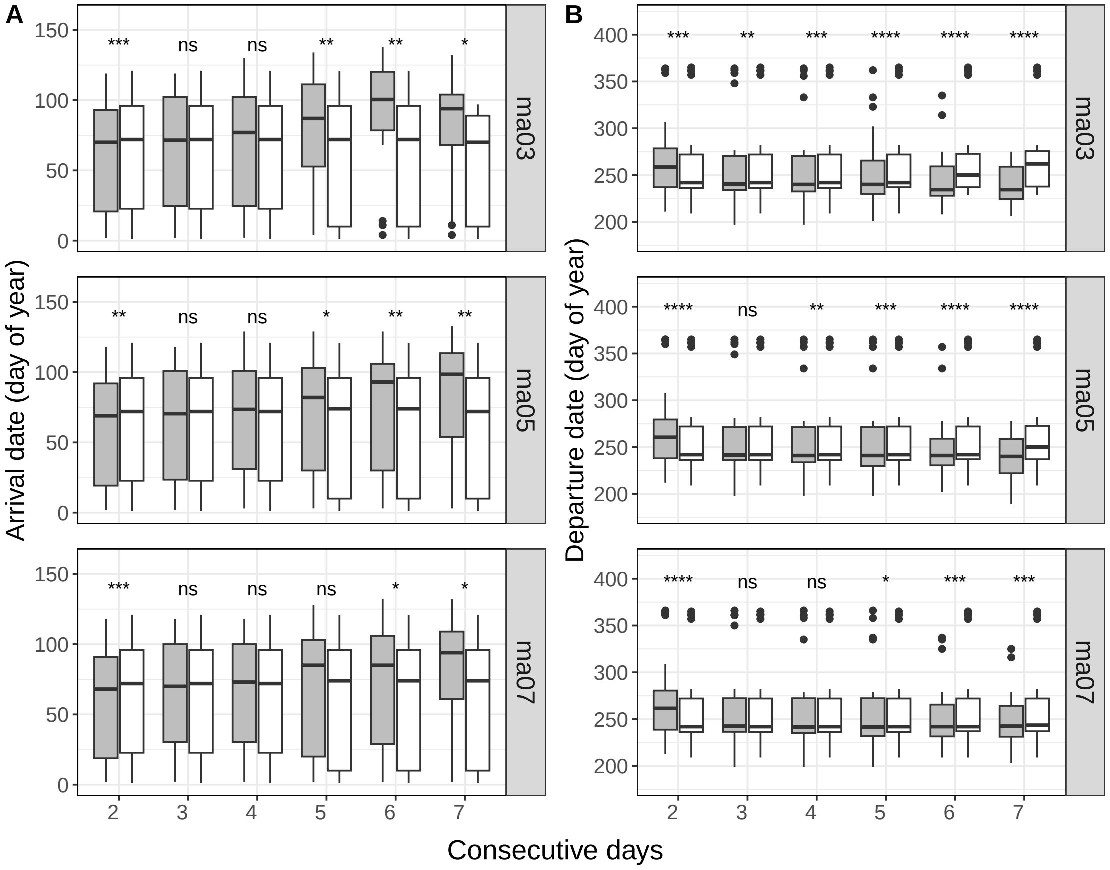

Figure 3.4: Boxplots comparing the median (a) arrival and (b) departure dates derived from citizen science consensus classifications (grey) and researcher analysis (white), when citizen science data were smoothed using 3-day (ma03), 5-day (ma05) and 7-day (ma07) moving averages, and arrival/departure was measured as the first/last 2, 3, 4, 5, 6 or 7 days of consecutive increase/decrease in the number of adult kittiwakes, respectively. Researcher dates were obtained by manually looking at the images and recording the first (arrival) and last (departure) date an adult kittiwake was seen at the colony each year. Outliers in (b) are departure dates from Skellig Michael, Ireland, where birds attended the colony over winter. Wilcoxon signed-rank tests tested for significant differences in citizen science and researcher arrival and departure dates, for each combination of moving averages and consecutive days increase/decrease.

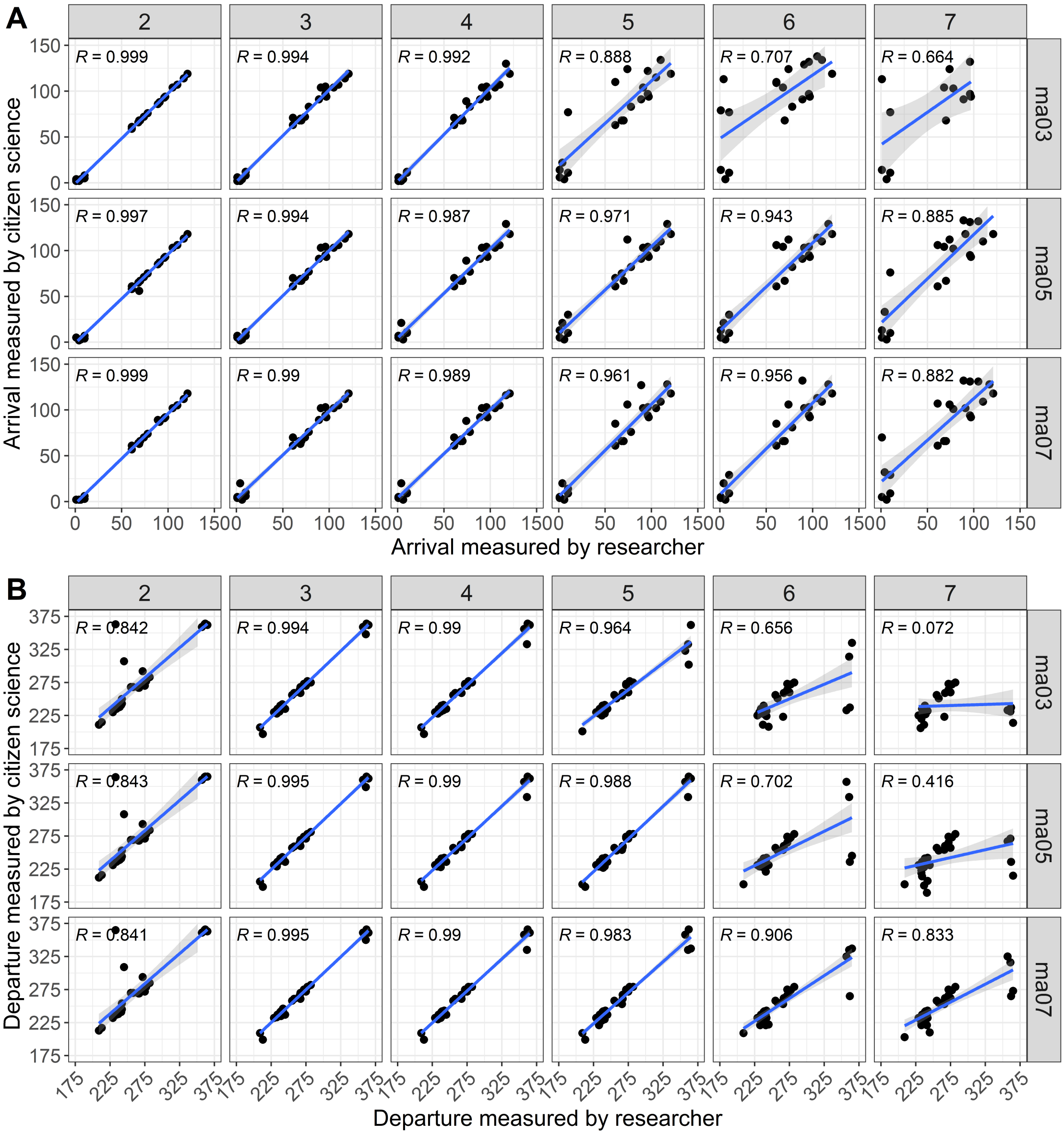

Figure 3.5: Relationship between the (a) arrival and (b) departure dates derived from citizen consensus classifications and researcher analysis, when citizen science data were smoothed using 3-day (ma03), 5-day (ma05) and 7-day (ma07) moving averages, and arrival/departure was measured as the first/last 2, 3, 4, 5, 6 or 7 days of consecutive increase/decrease in the number of adult kittiwakes, respectively. Researcher dates were obtained by manually looking at the images and recording the first (arrival) and last (departure) date an adult kittiwake was seen at the colony each year. Linear regressions between citizen science and researcher measured dates are shown in blue, with standard error as grey shading. Pearson product-moment correlations (R) tested for pairwise correlations between citizen science and researcher arrival and departure dates, for each combination of moving averages and consecutive days increase/decrease.

departure as the last day of three consecutive days of decrease within this time period. When all available Seabird Watch data were used, arrival was 2.6 (standard error (se) = ± 0.71) days later per 1° increase in latitude ($t(18) = 3.66$, $P < 0.01$), and departure was 1.2 (se = ± 0.49) days later per 1° increase in latitude ($t(36) = 2.42$, $P < 0.05$) (Fig. 3.7; arrival and departure data are provided in Tables 3.5 and 3.6 of the Appendix).

3.6 Discussion

Using images from the Seabird Watch time-lapse camera network, we demonstrate that citizen science can provide estimates of seabird colony arrival and departure that are comparable to expert data extraction. This method has several advantages over traditional field methods, including reduced cost, less disturbance, potential to cover a much larger geographical area, provision of standardized estimates across regions and increase in societal engagement in seabird monitoring. We found that at higher latitudes, adult kittiwakes return to the colony to breed later and depart later at the end of the breeding season, in line with previous studies. However, at one site, birds appeared to return to the colony during winter – an observation not previously detected there because of observer visits only occurring in the breeding season – suggesting regional differences in kittiwake over-winter behaviour.

3.6.1 Camera set-up

The kittiwake camera network has allowed the collection of an enormous quantity of data (> 200 000 images) from 2014 to the present. Time-lapse cameras have enabled monitoring at a large spatiotemporal scale, in infrequently monitored locations, and harsh environments, applying a standardized methodology to facilitate comparison across sites.

Maintaining such an extensive camera network is not without its challenges, especially in coastal environments in winter, where strong winds, waves and precipitation can knock cameras over, obscure camera lenses or cause camera failure (e.g. water ingress;

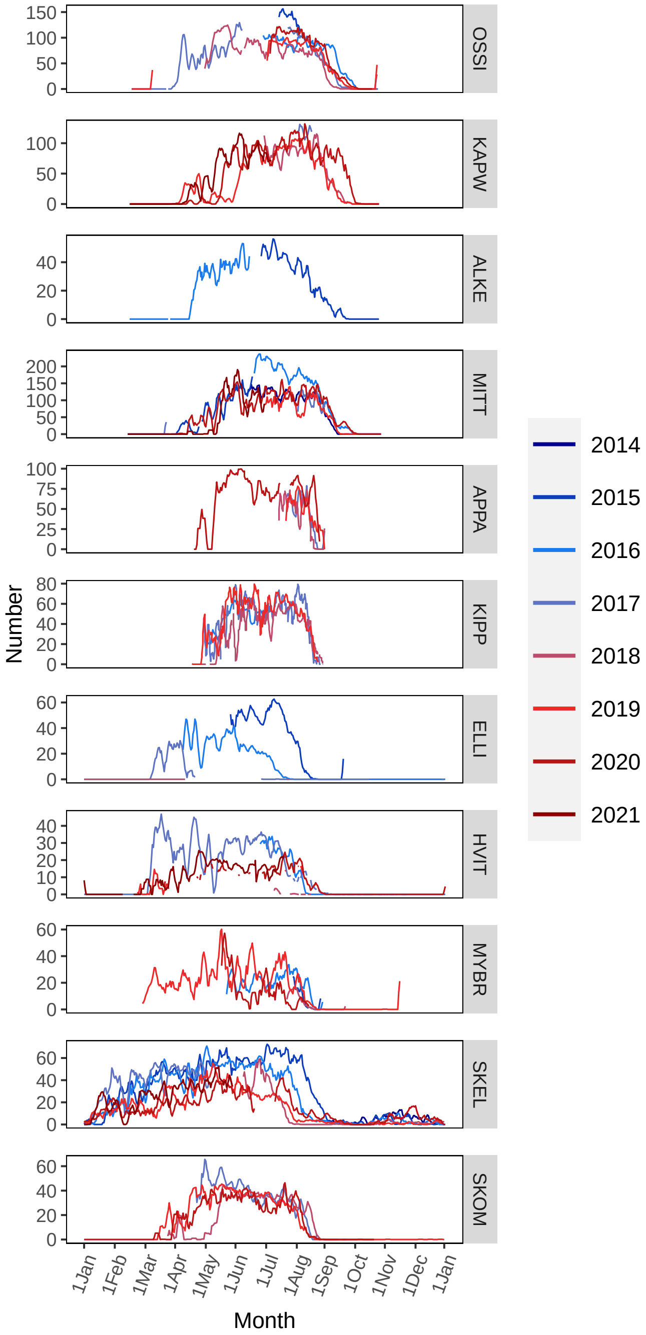

Figure 3.6: Number of adult kittiwakes (smoothed using a 5-day moving average) counted from citizen science consensus classifications for each day of the year, in different years. Colonies are arranged in latitudinal order: OSSI = Ossian Sarsfjellet, KAPW = Kapp Waldberg, ALKE = Alkhornet, MITT = Midterhukfjellet, APPA = Apparsuit, KIPP = Kippaku, ELLI = Elliðaey, HVIT = Hvítabjarnarey, MYBR = Mykines, SKEL = Skellig Michael, SKOM = Skomer.

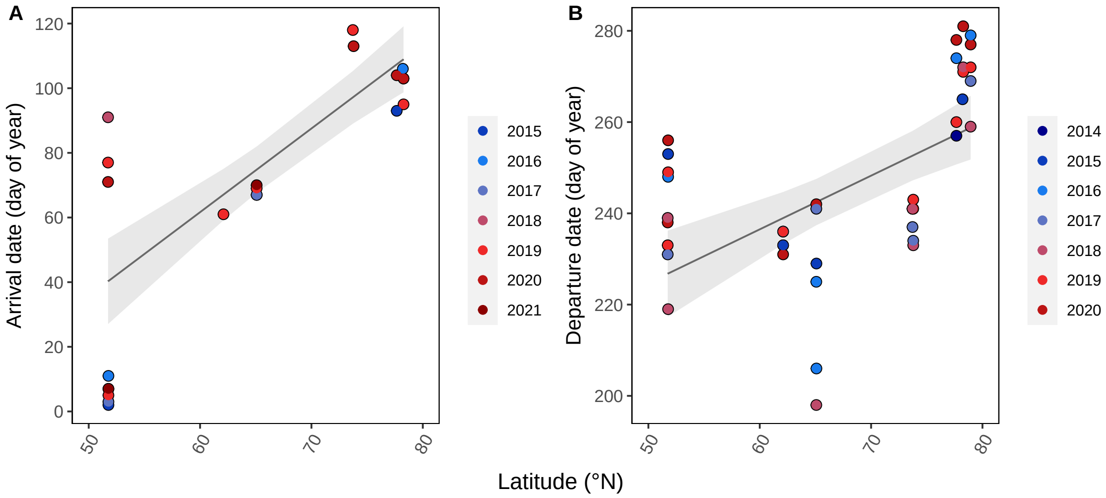

Figure 3.7: Relationship between latitude and kittiwake colony arrival date (n = 22) (a) and departure date (n = 40) (b), with standard error (grey shading). Arrival was 2.6 (se = ±0.71) days later per 1° increase in latitude ($t(18) = 3.66$, $P < 0.01$), and departure was 1.2 (se = ±0.49) days later per 1° increase in latitude ($t(36) = 2.42$, $P < 0.05$).

Merkel et al., 2016). As a result, the network contains gaps in data, where either cameras have failed or images are unusable, for example because they are blurred or the birds are obscured (e.g. condensation, precipitation on the lens). Furthermore, problems arising in winter are rarely identified until the following spring when fieldwork resumes. Remote image transmission could help overcome this problem, as images would be viewable online year-round, and issues with data capture could be identified and prioritized. Installing two cameras per colony could also increase the network's resilience, as if one camera fails, images would still be available from the other camera. Although this would increase cost in the short-term, cameras are comparatively cheap (c.£800 per camera and mount) compared with in-person field monitoring, especially when travel to remote islands is required and fieldworkers must be present regularly throughout the breeding season (Huffeldt & Merkel, 2013; Merkel et al., 2016). Although this study only tested the use of citizen science image analysis for measuring colony arrival and departure, the camera network also has the potential to answer questions about the possible drivers of change in seabird breeding phenology, success and chick survival, provided data can be efficiently analysed (Black et al., 2018a; Hinke et al., 2018; Youngflesh et al., 2021).

3.6.2 Citizen science data validation

The Zooniverse platform engages > 1.6 million registered users worldwide, who can participate in over 50 active projects that span a range of disciplines, from astronomy to ecology, to help analyse large datasets (Cox et al., 2015). Creating a Zooniverse project is free of cost, as development of the platform is funded by awards and grants (e.g. from the Alfred P. Sloan Foundation) (www.zooniverse.org). This makes the total monetary cost of the combined camera and citizen science system greatly reduced compared with other seabird monitoring techniques, such as traditional field observations and tagging, for the number of birds monitored.

When appropriate clustering and moving averages were applied, citizen science and expert data showed no significant differences in phenological parameters routinely used to determine responses to environmental change. This demonstrates how large citizen science datasets can answer important ecological questions with similar confidence to expert analysis, but at greater scales. Measuring colony-level arrival and departure with moving averages, rather than recording arrival and departure of birds at individual nests, removes the need for citizen science consensus classifications to accurately identify every bird in each image, provided the general trends of increase and decrease are present.

This study did not compare citizen science measures of phenology with those measured using traditional field methods. This is because fieldworkers are rarely present when adult kittiwakes first arrive at the colony (median arrival date 12 March) or when they leave (median departure date 29 August), as most fieldwork programmes are focused on the core breeding season, from egg-laying to chick fledging (Walsh et al., 1995). Future Seabird Watch studies aiming to measure additional breeding parameters, such as breeding success, will need to compare citizen science, expert image analysis and fieldworker identification of chicks and resultant metrics, where possible. Validation is crucial in the development of all novel and emerging technologies, to show that resultant data are equivalent to (or better than) the existing approach.

3.6.3 Citizen scientist participation and retention

For citizen science data to be integrated into monitoring programmes, it must reduce researcher workload and be capable of consistently collecting data in the long-term. The time required by volunteers to annotate images depends on the number of birds per image (affected by camera location/position, time of year, time of day), number of species present and the number of life-stages present (e.g. adults and/or chicks). Seabird Watch images are presented to users at random, meaning that these factors should vary across a series of images examined, which can help to retain volunteer interest. When two researchers annotated a random selection of images, they averaged 1.2 min per image (researcher 1 completed 42 images in 60 min; researcher 2 completed 60 images in 60 min). This means that volunteers have saved c.1740 h (over 10 months, if working a 40-h week) of researcher image processing time, for the c.87000 images classified using the Timelapse workflow to date.

However, to provide long-term monitoring solutions, citizen science projects also need to have enough volunteers in the long-term. Over the past 6 years, the Timelapse workflow has maintained sufficient volunteer effort (median number of images classified per month was 3700, IQR 2003–9576) to process the new images collected each year. Volunteer participation was highest during the first month of the project (Fig. 3.3), when it was featured on the UK TV programme Autumnwatch (https://www.bbc.co.uk/programmes/b0079t1) and peaked again during the COVID-19 pandemic, like many other Zooniverse projects (Ibrahim et al., 2021). Although participation has been sustained, the retention of individual volunteers was far less than expected. Most volunteers classified fewer than 10 images (median 5, IQR 2–12) in a single day (median number of days 0, IQR 0–0), and subsequently did not participate again. Similar volunteer patterns have been found for other Zooniverse projects, suggesting that it is much harder to maintain volunteer interest than it is to recruit new volunteers (Sauermann & Franzoni, 2015; Crall et al., 2017). In the long-term, this could affect the accuracy of data generated, as volunteers do not have time to learn and improve their classifications; although for this study, high turnover does not appear to have been an issue, as citizen science and expert phenology dates were comparable.

Hosting our project on a well-known and long-established citizen science platform has probably helped maintain a steady flow of new volunteers, particularly when Seabird Watch was featured on the Zooniverse homepage (different projects are chosen to be featured each week, by the Zooniverse team) (Crall et al., 2017). Equally, promoting the project on other platforms, such as SciStarter (https://scistarter.org/) and Twitter/X (https://twitter.com), has helped recruit people (Crall et al., 2017). Rewarding volunteers for their efforts might encourage long-term participation (West & Pateman, 2016), and Seabird Watch already provides volunteer certificates for a range of community engagement recognition programmes. Introducing competitive elements between volunteers, such as ranking and badging systems, can be rewarding (Robinson et al., 2021), as can receiving personal feedback from the project (e.g. via system-generated, but editable, emails) (Pecl et al., 2019). Regular project updates, and the opportunity to interact with the researchers, as well as other volunteers, can likewise ensure that volunteers know their contributions are valued and allow them to feel part of a wider community (West & Pateman, 2016; Robinson et al., 2021). Increased use of the Seabird Watch Talk function by both researchers and volunteers could promote this.

Increasingly, machine learning and artificial intelligence are being used for image object detection to reduce image processing time and provide long-term data processing solutions (Christin et al., 2019; Borowiec et al., 2022; Pichler & Hartig, 2023). Large training datasets are typically needed to train a model to recognize the objects of interest, and citizen science image annotations can provide such datasets, given that they are sufficiently accurate (Jones et al., 2020).

To date, artificial intelligence has predominantly been used to identify adult seabirds in drone and time-lapse images, but very few studies have attempted to identify seabird chicks (Jones et al., 2020; Hayes et al., 2021; Kellenberger et al., 2021; Weinstein et al., 2022). This might be because small chicks are difficult to detect when they first hatch, as they are often brooded by a parent (Coulson, 2011). Chick appearance then changes substantially as they grow-up, until they often look completely different just before fledging, which might make it hard to recognize the variable appearance of a (e.g. kittiwake) chick as the same object across time. Hentati-Sundberg et al., 2023 developed a video surveillance system combined with automated image processing to identify Common Guillemot *Uria aalge* adults, chicks and eggs and has been able to look at some aspects of nest attendance, breeding activity and phenology. The system was installed in a previously constructed artificial breeding cliff and uses five mains-powered cameras, mounted on five ledges to monitor c.23 pairs of Guillemots. As a result, the system is unlikely to be easily scalable, particularly in remote areas where reliable power is lacking. Specific camera set-ups can also impede the generalizability of neural networks, as models trained on a particular image set may not be able to make accurate predictions when faced with novel image sets (such as a different study site), even if they contain the same species. This means that models might have to be re-trained on new datasets, which increases computational time and costs, and requires further training data (Lamba et al., 2019). Citizen science annotations could provide such training data, which reiterates how citizen science and machine learning might complement each other to provide efficient and cost-effective image analysis techniques in the long-term.

3.6.4 Changes in arrival and departure with latitude

Using time-lapse cameras and citizen science annotations, we showed that kittiwake colony arrival was 2.6 days later per 1° increase in latitude from 51.7°N to 78.9°N. This is in line with previous research using traditional in-person monitoring showing that seabird breeding (namely average lay and/or hatching date) occurs later with increasing latitude at both the global (Keogan et al., 2018, 2022) and regional (Wanless et al., 2009; Burr et al., 2016) scale. Baker, 1939 predicted a 2- to 3-day delay in egg-laying for every 1° increase in latitude, and Burr et al., 2016 found kittiwake hatching was delayed by 2.3 days per latitudinal degree from 65°N to 79°N. Importantly, our result fits into this range of a 2- to 3-day delay per degree of latitude, showing that the novel methodology used here can detect known ecological patterns. The methodology can further be used to measure inter-annual variation in phenology, as cameras can provide long time-series of data. This is important for trying to understand the drivers of phenological change, and how environmental conditions can affect populations through breeding success and/or adult survival. The timing of arrival is of particular importance because it may affect the timing of breeding and subsequent reproductive success, and departure to the wintering grounds may consequently affect adult survival or cause potential carry-over effects the following breeding season.

In our study, we also expected departure to be delayed with latitude (because a later start should mean a later finish) and found this to be true, with a delay of 1.2 days per 1° latitudinal increase. The smaller magnitude delay in departure (1.2 days) relative to arrival (2.6 days) supports studies showing that breeding season length is shorter at latitudinal extremes, although we did not have sufficient data to test this directly (Hodum, 2002; Burr et al., 2016). At one of the lowest latitude sites, Skellig Michael, small numbers of kittiwakes were present between October and December, despite most of the colony leaving by mid-September, post-breeding. This supports previous studies showing that kittiwakes breeding around the Celtic–Biscay shelf (Rathlin, 55°N and Skomer 52°N; Frederiksen et al., 2012) (Rockabill 54°N; SEATRACK, 2024) tend to remain near the colony year-round, and do not necessarily migrate to the West Atlantic during winter like most other kittiwake populations (Frederiksen et al., 2012). Nevertheless, we did not observe kittiwakes in 1:00 pm images from Skomer between September 2019 and February 2020, suggesting that birds remaining near the colony do not always visit breeding sites during winter. Further research is needed on the occurrence and reasons for over-winter colony attendance in kittiwakes. Winter visitors might be young birds practising at establishing nests, adults maintaining a pair bond (Harris & Wanless, 1989) or adults competing for nests, with winter attendance being more likely at locations where competition for high-quality nest-sites is intense (Bennett et al., 2022). Our time-lapse camera and citizen science system represents a powerful tool to study such attendance patterns, given the lack of traditional field observations during winter.

3.7 Conclusions

In this study, we demonstrate how large-scale camera networks can measure phenological changes at remote colonies over a large geographical range, in a species of high conservation concern, and that this could be applied to cliff-nesting seabirds more widely. The potential to measure additional phenological parameters (such as chick hatch and chick fledge dates), nest survival and productivity, at comparatively low cost (Black, 2019) is high. Long-term maintenance of such camera networks and robust methods for analysing large quantities of images, such as citizen science, are essential if we hope to address temporal trends and explore how reproduction is affected by key drivers of environmental change.

3.8 Appendix

Table 3.2: Available Seabird Watch data that has been annotated on the Zooniverse platform, for sites used in this analysis. The first image must be taken January-May to capture kittiwake arrival, and the last image must be taken July-December to capture kittiwake departure; first image and last image cells shaded grey have been used in this analysis. Non-shaded cells indicate that data for this metric was not available for that colony/year and, where possible, the reason is provided. 'Camera not taking images' means arrival and/or departure dates were missed, because the first and/or last image in the dataset either already contained birds (arrival) or still contained birds (departure). The reason for this is unknown in most cases but could be for one of the following reasons: camera removed/disabled during winter, camera broke, batteries ran out, or the SD card reached maximum capacity.

Colony	**Season**	**First image**	**Last image**	**Reason why arrival/departure date is missing**	
				Arrival	**Departure**
ALKEa	s15-16	2015:06:23 16:00:00	2015:10:26 11:00:00	Camera not taking images	NA
	s16-17	2016:02:16 11:00:00	2016:06:22 07:00:00	NA	Camera not taking images
APPAa	s17-18	2017:07:17 22:59:59	2017:09:01 12:00:09	Camera not taking images	NA
	s18-19	2018:07:17 10:42:07	2018:09:01 12:01:14	Camera not taking images	NA
	s19-20	2019:07:08 16:37:07	2019:09:01 12:00:33	Camera not taking images	NA
	s20-21	2020:04:20 15:54:36	2020:09:01 12:01:09	NA	NA
ELLIa	s15-16	2015:05:23 12:00:00	2015:09:20 13:00:00	Camera not taking images	NA
	s16-17	2016:04:10 14:00:00	2016:12:31 15:00:00	Camera not taking images	NA
	s17-18	2017:01:01 12:00:00	2017:12:31 14:00:00	NA	Missing data between April and June (2017:04:23 to 2017:06:28). No birds seen in images after 2017:06:28, likely that colony failed.
	s18-19	2018:01:01 13:00:00	2018:08:02 14:00:00	One kittiwake returned on 2018-04-04 09:00:00. No other kittiwakes seen, colony did not return.	One kittiwake returned on 2018-04-04 09:00:00. No other kittiwakes seen, colony did not return.
	s16-17	2016:06:21 16:00:00	2016:12:31 15:00:00	Camera not taking images	NA

	s17-18	2017:01:01 13:00:00	2017:11:25 11:00:00	NA	NA
	s18-19	2018:07:12 16:29:35	2018:11:26 13:02:39	Camera not taking images	NA
	s19-20	2019:02:24 11:52:03	2019:09:01 12:30:39	NA	Missing data at end of August (2019:08:22 to 2019:09:01). Might have missed the first 13:00:00 image without adult kittiwakes.
HVITa	s20-21	2020:02:14 11:49:43	2020:12:31 13:58:51	Missing data in March and April(2020:02:29 to 2020:03:19 and 2020:03:30 to 2020:04:06)	NA
	s21-22	2021:01:01 11:58:50	2021:07:28 13:26:59	NA	Camera not taking images
KAPWa	s17-18	2017:07:29 14:00:00	2017:08:19 15:00:00	Camera not taking images	Camera not taking images
	s18-19	2018:07:02 11:00:00	2018:10:26 11:00:00	Camera not taking images	NA
	s19-20	2019:02:16 11:00:00	2019:10:26 12:00:00	NA	NA
	s20-21	2020:02:17 11:00:00	2020:10:25 11:00:00	NA	NA
	s21-22	2021:02:16 11:00:00	2021:07:15 13:00:00	NA	Camera not taking images
KIPPa	s16-17	2016:04:26 20:44:45	2016:06:30 23:41:24	Camera not taking images	Camera not taking images
	s17-18	2017:04:29 19:43:36	2017:08:31 05:57:19	Camera not taking images	NA
	s18-19	2018:04:28 15:44:20	2018:08:30 21:59:09	Snow covered camera early in season when kittiwakes arrived.	NA
	s19-20	2019:04:19 23:48:41	2019:09:01 12:00:38	NA	NA
	s14-15	2014:06:09 17:00:00	2014:10:28 11:00:00	Camera not taking images	NA
	s15-16	2015:02:14 11:00:00	2015:06:20 19:00:00	NA	Camera not taking images
	s16-17	2016:06:21 15:00:00	2016:10:27 12:00:00	Camera not taking images	NA
	s17-18	2017:02:14 11:00:00	2017:09:01 14:00:00	Missing data between March and August (2017:03:26 to 2017:08:04)	Camera not taking images

MITTa	s19-20	2019:07:03 11:00:00	2019:10:28 11:00:00	Camera not taking images	NA
	s20-21	2020:02:15 11:00:00	2020:10:27 11:00:00	NA	NA
	s21-22	2021:02:14 11:00:00	2021:07:09 13:00:00	Snow covered camera early in season when kittiwakes arrived.	Camera not taking images
MYBRa	s15-16	2015:07:28 11:00:00	2015:08:28 11:00:00	Camera not taking images	NA
	s16-17	2016:05:24 11:00:00	2016:08:29 12:00:00	Camera not taking images	NA
	s18-19	2018:07:25 11:00:00	2018:09:22 13:00:00	Camera not taking images	NA
	s19-20	2019:03:01 13:00:00	2019:11:16 13:00:00	NA	NA
	s20-21	2020:05:19 11:00:00	2020:08:21 12:00:00	Camera not taking images	NA
OSSIa	s15-16	2015:07:11 16:00:00	2015:08:07 15:00:00	Camera not taking images	Camera not taking images
	s16-17	2016:06:30 13:00:00	2016:10:24 12:00:00	Camera not taking images	NA
	s17-18	2017:02:18 12:00:00	2017:10:24 12:00:00	Snow covered camera early in season when kittiwakes arrived.	NA
	s18-19	2018:05:03 10:00:00	2018:10:24 12:00:00	Camera not taking images	NA
	s19-20	2019:02:18 12:00:00	2019:10:24 12:00:00	Missing data between March and July due to camera failure.	NA
	s20-21	2020:07:07 13:00:00	2020:10:24 12:00:00	Camera not taking images	NA
SKELa	s14-15	2014:09:03 15:00:00	2014:12:31 16:00:00	Camera not taking images	Camera not taking images, as departure might have occurred in August.
	s15-16	2015:01:01 09:00:00	2015:12:31 16:00:00	NA	NA
	s16-17	2016:01:01 09:00:00	2016:12:31 16:00:00	NA	NA
	s17-18	2017:01:01 09:00:00	2017:05:07 16:00:00	NA	Camera not taking images
	s18-19	2018:06:11 11:00:00	2018:12:31 13:00:00	Camera not taking images	NA
	s19-20	2019:01:01 11:00:00	2019:12:31 13:00:00	NA	NA
	s20-21	2020:01:01 11:00:00	2020:12:31 13:00:00	NA	NA
	s21-22	2021:01:01 11:00:00	2021:06:06 13:00:00	NA	Camera not taking images
	s17-18	2017:04:18 19:00:00	2017:08:25 13:00:00	Camera not taking images	NA

SKOMd	s18-19	2018:03:26 14:00:00	2018:09:23 13:00:00	NA	NA
	s19-20	2019:03:12 11:00:00	2019:12:31 13:00:00	NA	NA
	s20-21	2020:01:01 11:00:00	2020:10:26 13:00:00	NA	NA

Table 3.3: Results of paired samples Wilcoxon tests comparing the arrival and departure dates derived from citizen science consensus classifications and researcher analysis, when citizen science data was smoothed using 3- (ma30), 5- (ma05), and 7-day (ma07) moving averages, and arrival/departure was measured as the first two, three, four, five, six or seven days of consecutive increase/decrease in the number of adult kittiwakes, respectively. Researcher dates were obtained by manually looking at the images and recording the first (arrival) and last (departure) date an adult kittiwake was seen at the colony each year.

Stage	Moving average	Consecutive days	V	p-value	Significance
Arrival	3	2	212.5	0.000654	***
	3	3	101.5	0.635439	ns
	3	4	66	0.086643	ns
	3	5	23	0.003926	**
	3	6	20.5	0.001694	**
	3	7	14	0.029974	*
Arrival	5	2	201	0.002689	**
	5	3	113	0.778653	ns
	5	4	59	0.152287	ns
	5	5	26.5	0.010722	*
	5	6	20	0.004585	**
	5	7	15.5	0.004152	**
Arrival	7	2	207	0.000131	***
	7	3	106	0.671626	ns
	7	4	91	0.613556	ns
	7	5	63	0.120659	ns
	7	6	45	0.026187	*
	7	7	38	0.012987	*
Departure	3	2	44	0.00047	***
	3	3	323	0.006164	**
	3	4	412	0.000217	***
	3	5	416.5	1.73E-05	****
	3	6	395.5	1.21E-05	****
	3	7	290	6.66E-05	****
Departure	5	2	21.5	2.10E-05	****
	5	3	181	0.62607	ns
	5	4	278.5	0.001833	**
	5	5	341.5	0.000254	***
	5	6	385.5	3.30E-05	****
	5	7	336	4.77E-05	****
Departure	7	2	18	6.01E-06	****
	7	3	154.5	0.600005	ns
	7	4	265	0.304579	ns
	7	5	343	0.02292	*
	7	6	407	0.000317	***
	7	7	413	0.000203	***

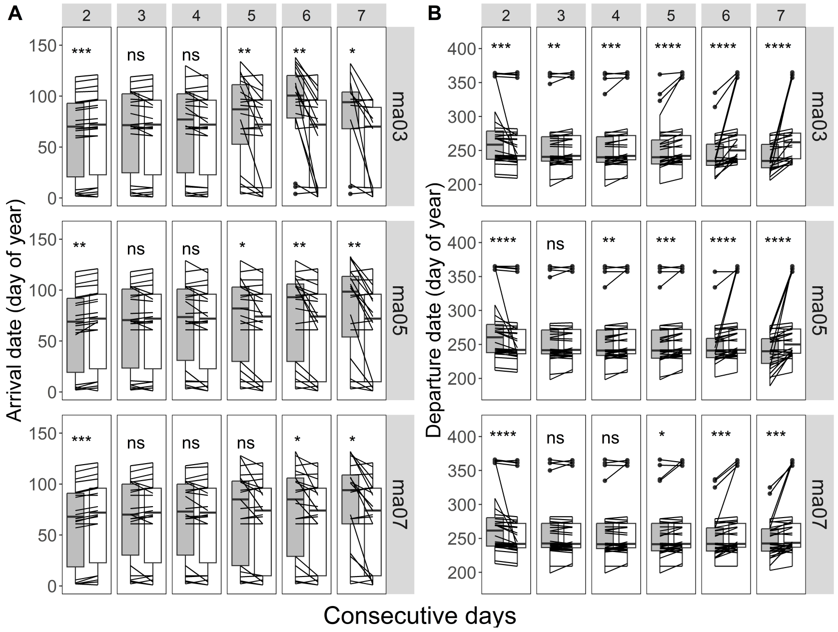

Figure 3.8: Boxplots and paired dot plots comparing the A) arrival and B) departure dates derived from citizen science consensus classifications (grey) and researcher analysis (white), when citizen science data was smoothed using 3- (ma030), 5- (ma05), and 7-day (ma07) moving averages, and arrival/departure was measured as the first/last two, three, four, five, six or seven days of consecutive increase/decrease in the number of adult kittiwakes, respectively. Researcher dates were obtained by manually looking at the images and recording the first (arrival) and last (departure) date an adult kittiwake was seen at the colony each year. Outliers in B) are departure dates from Skellig Michael, Ireland, where birds attended the colony over winter. Wilcoxon signed-rank tests tested for significant differences in citizen science and researcher arrival and departure dates, for each combination of moving averages and consecutive days increase/decrease.

Table 3.4: Results of Pearson product-moment correlations and linear regressions comparing the arrival and departure dates derived from citizen science consensus classifications and researcher analysis, when citizen science data was smoothed using 3-, 5-, and 7-day moving averages, and arrival/departure was measured as the first/last two, three, four, five, six or seven days of consecutive increase/decrease in the number of adult kittiwakes, respectively. Pearson correlation is the Pearson product-moment correlation coefficient. The F-statistic, R^2, p-value and significance are the linear regression results. The data is ordered from high to low Pearson correlations. Cells shaded grey are the moving average (5-day) and consecutive days (3) chosen for subsequent analysis, as they gave the highest Pearson correlation for departure and a similarly high value for arrival.

Stage	**Moving average**	**Consecutive days**	**Pearson correlation**	**F**	**R^2**	**p-value**	**Significance**
Arrival	3	2	0.9993	14549.74	0.999	4.19E-30	***
	7	2	0.9987	7728.54	0.997	2.32E-27	***
	5	2	0.9971	3438.44	0.994	7.39E-24	***
	3	3	0.9940	1652.94	0.988	1.06E-20	***
	5	3	0.9937	1565.72	0.987	1.81E-20	***
	3	4	0.9916	1168.97	0.983	3.22E-19	***
	7	3	0.9899	972.77	0.98	1.96E-18	***
	7	4	0.9888	875.54	0.978	5.49E-18	***
	5	4	0.9875	781.95	0.975	1.66E-17	***
	5	5	0.9707	309.51	0.942	3.23E-13	***
	7	5	0.9606	227.11	0.923	5.07E-12	***
	7	6	0.9561	202.42	0.914	1.39E-11	***
	5	6	0.9432	153.01	0.89	1.55E-10	***
	3	5	0.8885	67.47	0.789	1.68E-07	***
	5	7	0.8854	65.34	0.784	2.11E-07	***
	7	7	0.8824	66.8	0.779	1.22E-07	***
	3	6	0.7073	18.01	0.5	0.000488	***
	3	7	0.6643	8.69	0.441	0.013271	*
Departure	5	3	0.9948	2887.38	0.99	2.21E-31	***
	7	3	0.9947	2809.13	0.989	3.32E-31	***
	3	3	0.9945	2685.13	0.989	6.49E-31	***
	7	4	0.9904	1542.44	0.981	2.35E-27	***
	3	4	0.9900	1475.59	0.98	4.52E-27	***
	5	4	0.9898	1442.7	0.98	6.30E-27	***
	5	5	0.9885	1276.54	0.977	3.80E-26	***
	7	5	0.9828	848.79	0.966	1.46E-23	***
	3	5	0.9644	385.82	0.93	2.68E-18	***
	7	6	0.9057	132.45	0.82	2.48E-12	***
	5	2	0.8430	73.68	0.711	1.41E-09	***
	3	2	0.8422	73.18	0.709	1.52E-09	***
	7	2	0.8414	72.72	0.708	1.63E-09	***
	7	7	0.8333	63.6	0.694	1.10E-08	***
	5	6	0.7021	28.19	0.493	1.07E-05	***
	3	6	0.6558	19.62	0.43	0.000151	***
	5	7	0.4157	5.43	0.173	0.027784	*
	3	7	0.0722	0.12	0.005	0.737276	ns

Table 3.5: Kittiwake colony arrival dates measured for each colony using citizen science consensus classifications.

Colony	Year	Arrival date (day of year)
ALKE	2016	106
APPA	2020	113
ELLI	2017	67
HVIT	2017	67
	2019	69
	2021	70
KAPW	2021	103
	2020	103
	2019	95
KIPP	2019	118
MITT	2020	104
	2015	93
MYBR	2019	61
SKEL	2016	11
	2015	2
	2017	3
	2019	5
	2020	7
	2021	7
SKOM	2019	77
	2018	91
	2020	71

Table 3.6: Kittiwake colony departure dates measured for each colony using citizen science consensus classifications.

Colony	Year	Departure date (day of year)
ALKE	2015	265
APPA	2020	241
	2018	233
	2019	243
	2017	234
ELLI	2016	206
	2015	229
HVIT	2020	242
	2018	198
	2017	241
	2016	225
KAPW	2019	271
	2020	281
	2018	272
KIPP	2019	241
	2018	241
	2017	237
MITT	2020	278
	2019	260
	2016	274
	2014	257
MYBR	2020	231
	2018	233
	2016	236
	2019	236
	2015	233
OSSI	2020	277
	2017	269
	2018	259
	2019	272
	2016	279
SKEL	2015	253
	2016	248
	2018	219
	2019	249
	2020	256
SKOM	2019	233
	2020	238
	2018	239
	2017	231

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4

Citizen science reveals precipitation – but not other weather variables – adversely affects chick survival in a threatened seabird

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Contents

4.1 Abstract

Understanding how climate variability impacts species' demography and population dynamics is critical for protecting biodiversity. Seabirds are a prime example of a highly threatened taxa, with climate change being identified as one of the top three threats. However, most studies examine the indirect effects of sea surface temperatures (via the food web), rather than the direct effects of specific weather conditions, on breeding success and survival. Using remote cameras coupled to citizen science image analysis, we quantified the direct effects of local weather conditions on daily chick survival of a declining seabird, the Black-legged Kittiwake (*Rissa tridactyla*), at 13 colonies across the species breeding range (51.7°N – 78.9°N) from 2015 to 2022. We found that all chicks died when less than 15 days old and that daily chick failure rate increased by 3.7-fold per 1 mm increase in precipitation. We found no effect of storminess, temperature, or sun exposure. The lack of evidence for these other local weather effects might suggest the indirect effects of sea surface temperatures on food availability are indeed the more important drivers of decline. We highlight that using a large-scale citizen science camera system is a scalable, low-cost method for exploring landscape level patterns in breeding success, while also minimising disturbance to vulnerable breeding species.

> *"Humidity is rising, barometer's getting low*
> *According to all sources. The street's the place to go*
> *'Cause tonight for the first time. Just about half-past ten*
> *For the first time in history. It's gonna start raining men"*
>
> – The Weather Girls, *It's Raining Men*

4.2 Introduction

In the face of ongoing climate change, understanding the impact of climate and its variability on species' demography and population dynamics is of critical importance for protecting biodiversity (Sandvik et al., 2012). Seabirds are a prime example of a highly threatened taxa, with 31% of species globally threatened (Croxall et al., 2012). Although seabirds are affected by multiple stressors, climate change has been identified as one of the top three threats, alongside invasive species and bycatch (Dias et al., 2019). To date, many studies have focused on the indirect effects of warming sea surface temperatures on marine top predators, via bottom-up control of marine food webs (Frederiksen et al., 2004a, 2006; Moe et al., 2009; Lynam et al., 2017; Keogan et al., 2018), as well as the impact of changes in large scale oceanographic patterns such as the North Atlantic Oscillation and the El Niño–Southern Oscillation (Sandvik et al., 2008; Jenouvrier et al., 2009; Cubaynes et al., 2010; Siddiqi-Davies et al., 2024). Higher sea surface temperatures have been associated with lower breeding success (Frederiksen et al., 2004b; Carroll et al., 2015) and adult survival (Frederiksen et al., 2004b; Sandvik et al., 2005; Sandvik et al., 2012) in some species and regions, while in others these indirect effects are weak (Lauria et al., 2012; Lauria et al., 2013). There is an increasing understanding that the direct effects of climate change (i.e. the immediate effects of weather on, for example, breeding success and survival) are important too, despite this being largely understudied (Jenouvrier, 2013).

Many climate models have predicted increased weather variability and increased frequency and severity of weather extremes globally (Rahmstorf & Coumou, 2011; Arias et al., 2021). Among seabirds, severe winter storms have been associated with low survival, in some cases resulting in seabird wrecks (Frederiksen et al., 2008; Morley et al., 2016; Diamond et al., 2020; Acker et al., 2021; Clairbaux et al., 2021). For such long-lived species, even occasional large mortality events could contribute to population declines long-term. However, local weather conditions can also affect reproductive success. High winds, precipitations, temperatures, and sun exposure can all result in breeding failure, for example, due to nests being blown or washed off cliffs (Newell et al., 2015), death from cold or heat exposure (Yannic et al., 2014; Olin et al., 2023), or snow covering nest sites or blocking burrow/crevice entrances (Descamps et al., 2023). Breeding failure from local weather conditions could therefore be an important driver of population decline in some species (Sandvik et al., 2012; Reiertsen, 2013).

Nevertheless, the number of studies investigating these direct effects of local conditions on nest survival remains less than those investigating indirect effects of changing sea surface temperatures. Most previous studies have looked at only a single colony and/or in one year, where a noticeably extreme weather event was known to have occurred (Yannic et al., 2014; Newell et al., 2015), making research on this topic underpowered and potentially biased. This is because collecting data on breeding success is very time-consuming, given nests must be repeatedly visited throughout the breeding season (Walsh et al., 1995; Edney & Wood, 2021). For this reason, only a small proportion of seabird colonies have long-term breeding success data (Burnell et al., 2023). Where it does exist, the frequency of visitation is often too low to allow insight into daily survival rates, with most nests being visited a maximum of every few days and for only part of the breeding season (Walsh et al., 1995). With continued rapid developments in technology coupled with reduced cost, remote monitoring could offer a powerful tool to increase the temporal and spatial resolution of seabird breeding data collection and allow insight into the direct effects of climate.

In this study, we used data from a large citizen science project to examine the direct effects of local weather conditions on Black-legged Kittiwake (*Rissa tridactyla*) chick survival across the species' range (51.7°N–78.9°N). Despite a widespread distribution and a global population of 15 million individuals, the species has experienced a 40% decline in only three generations and is classed as Vulnerable on the IUCN Red List (BirdLife International, 2024). This decline has been associated with climate fluctuations indirectly (Descamps et al., 2017) affecting food availability via bottom-up effects, as well as overfishing (Frederiksen et al., 2004b, 2005). However, this may represent the tendency of studies to focus on the indirect effects of sea surface temperature and not specific local weather conditions, particularly in relation to breeding success (Descamps et al., 2015).

We collected time-lapse images between 2015 and 2022 at 13 colonies throughout the breeding season, and asked volunteers from the Zooniverse citizen science project, Seabird Watch, to to click on birds and classify them as either kittiwake adults or kittiwake chicks. We developed an algorithm to extract chick count data from the classifications to test *a priori* hypotheses on factors directly affecting daily chick survival. We predicted that increased precipitation, storminess, temperature, solar radiation, and colony direction measured as degrees from north (i.e. more southerly facing colonies) would increase the risk of chick failure. We hypothesised that increased solar radiation at more south facing colonies (i.e. increased sun exposure) would decrease chick survival, as sun exposure has been shown to have a large effect on heat gain in seabirds (Luskick et al., 1978; Olin et al., 2023).

4.3 Methods

4.3.1 Data collection

Study colonies and camera set-up

We used a network of 13 time-lapse cameras across eight countries that span the latitudinal breeding range of the Black-legged Kittiwake (hereafter kittiwake) (Fig. 4.1). The network comprised commercially available Reconyx Hyperfire or Reconyx Ultrafire cameras (see Edney et al., 2025 for details), although colonies in Greenland and Scotland had custom-built set-ups using Canon cameras developed by Time-lapse Systems (part of Hideaway Media Ltd) in Scotland, and by Merkel et al., 2016 in Greenland. Cameras were positioned opposite breeding kittiwakes and captured between 30 and 130 nests. They were typically programmed to take one image per hour year-round, although at high latitudes this was sometimes reduced to four photos per day to maximize battery lifespan at colonies that were infrequently visited.

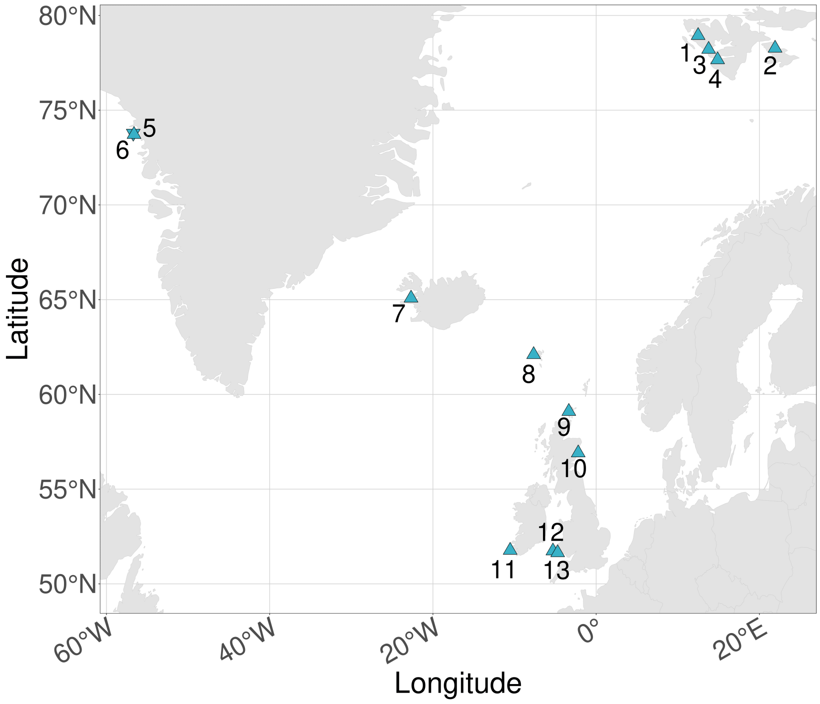

Figure 4.1: Locations of cameras included in this study. Key: 1 = Ossian Sarsfjellet, 2 = Kapp Waldberg, 3 = Alkhornet, 4 = Midterhukfjellet, 5 = Apparsuit, 6 = Kippaku, 7 = Hvítabjarnarey, 8 = Mykines, 9 = Marwick Head, 10 = Fowlsheugh, 11 = Skellig Michael, 12 = Skomer, 13 = St Margaret's Island. Closely spaced colonies are illustrated using upward and downward triangles to avoid complete overlap.

4.3.2 Image annotation and processing

Images were annotated by volunteers on the Seabird Watch (www.seabirdwatch.org) citizen science project, hosted on the Zooniverse platform (www.zooniverse.org). For this analysis, the 'Timelapse' and 'Kittiwake nests' workflows were used by volunteers to click on birds and classify them as either kittiwake adults or chicks. Volunteers were not asked to click on eggs or identify the start of incubation, due to eggs rarely being visible in images and uncertainty surrounding identification of behavioural states. Four people were initially shown each image, and if any of them classified a bird, then the image was shown to 10 people in total. If the first four people classified zero birds, the blank image was retired, meaning it was removed from the active dataset and not seen by further volunteers. Every animal marked in the image was stored as an x,y coordinate, termed a raw classification, and labelled as a chick or adult. Further information on camera set-up and the classification process is provided in Edney et al., 2025.

Images uploaded to Seabird Watch were aligned after classification was complete using the pengbot-aligner tool (https://github.com/CarlosArteta/pengbot-aligner). For each colony-year (i.e., one year of data at a specific colony), we selected a focal image, which all other images were aligned relative to, and created a nest diagram. This was a .png file that marked each Apparently Occupied Nest to be monitored. We selected three images per day for alignment (11:00 am, 12:00 pm, and 13:00 pm, or times closest to these) to prevent large differences in light levels (e.g. bright sun vs shade) between images reducing the effectiveness of the alignment. Image alignment removed movement between images created by camera shake, so that the x,y coordinates of nests were no longer shifted across a time-series. The output of the pengbot-aligner was a series of aligned nest diagrams (one nest diagram per image), rather than aligned images, because saving new time-lapse images was data heavy and would have increased algorithm processing time (see Appendix 4.6.1 for details on image alignment).

We converted raw classifications into the number of chicks per nest, per image. For every image, we first extracted the raw classifications from each nest in the nest diagram using the raster package in R (Hijmans et al., 2023). We counted the number of chicks that each volunteer clicked on per nest and converted this into a single chick count for different volunteer thresholds (Fig. 4.2). Kittiwake nests can have between zero and three chicks, and so to account for the possibility of multiple chicks, a threshold was set for each chick independently (Coulson & Porter, 1985). A worked example of this process is provided in Figure 4.2. To determine the most appropriate threshold value, we compared the sensitivity and precision of citizen science chick counts using different volunteer thresholds, with chick counts made by a researcher (see 'Citizen Science validation').

4.3.3 Citizen science validation

We selected one or two years of images from each colony for expert validation (Appendix 4.6.2). Two years were chosen if the size of the image uploaded to Seabird Watch changed

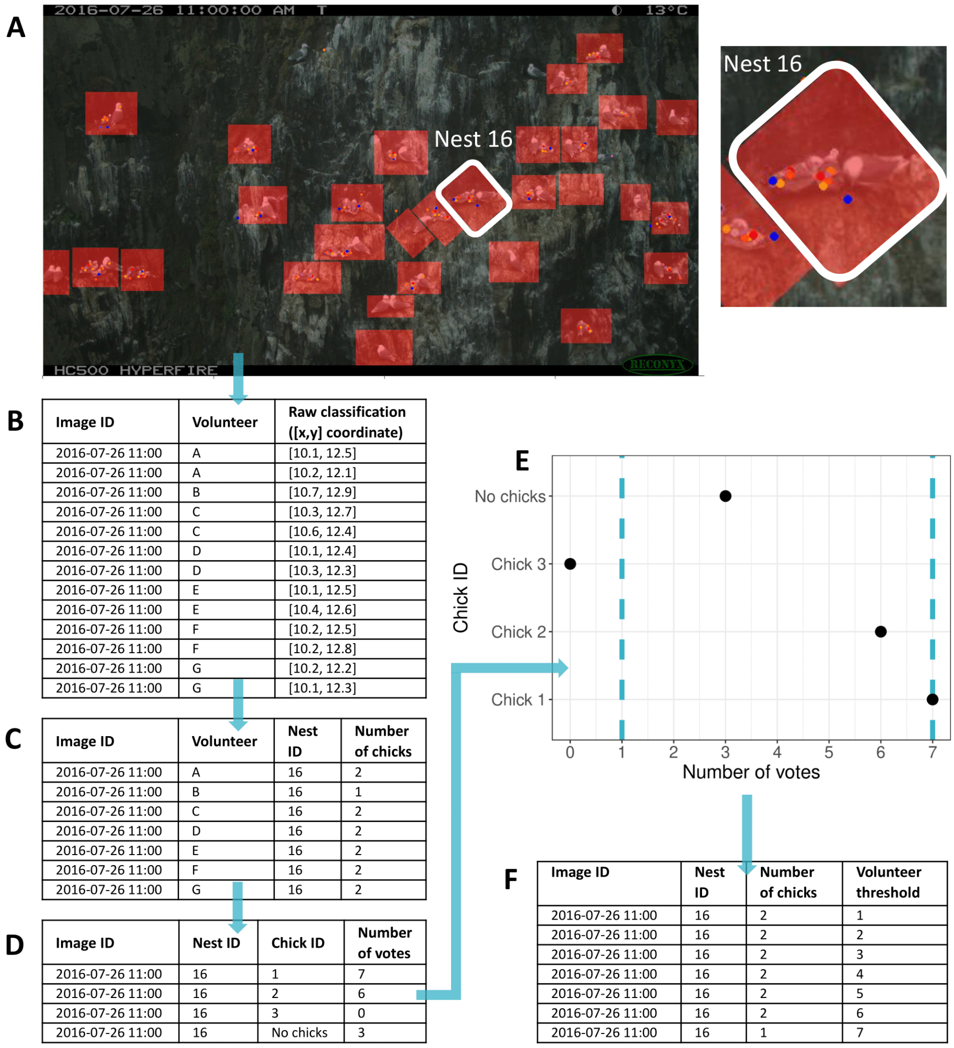

Image ID	Volunteer	Raw classification ([x,y] coordinate)
2016-07-26 11:00	A	[10.1, 12.5]
2016-07-26 11:00	A	[10.2, 12.1]
2016-07-26 11:00	B	[10.7, 12.9]
2016-07-26 11:00	C	[10.3, 12.7]
2016-07-26 11:00	C	[10.6, 12.4]
2016-07-26 11:00	D	[10.1, 12.4]
2016-07-26 11:00	D	[10.3, 12.3]
2016-07-26 11:00	E	[10.1, 12.5]
2016-07-26 11:00	E	[10.4, 12.6]
2016-07-26 11:00	F	[10.2, 12.5]
2016-07-26 11:00	F	[10.2, 12.8]
2016-07-26 11:00	G	[10.2, 12.2]
2016-07-26 11:00	G	[10.1, 12.3]

Image ID	Volunteer	Nest ID	Number of chicks
2016-07-26 11:00	A	16	2
2016-07-26 11:00	B	16	1
2016-07-26 11:00	C	16	2
2016-07-26 11:00	D	16	2
2016-07-26 11:00	E	16	2
2016-07-26 11:00	F	16	2
2016-07-26 11:00	G	16	2

Image ID	Nest ID	Chick ID	Number of votes
2016-07-26 11:00	16	1	7
2016-07-26 11:00	16	2	6
2016-07-26 11:00	16	3	0
2016-07-26 11:00	16	No chicks	3

Image ID	Nest ID	Number of chicks	Volunteer threshold
2016-07-26 11:00	16	2	1
2016-07-26 11:00	16	2	2
2016-07-26 11:00	16	2	3
2016-07-26 11:00	16	2	4
2016-07-26 11:00	16	2	5
2016-07-26 11:00	16	2	6
2016-07-26 11:00	16	1	7

Figure 4.2: Schematic showing how raw classifications of kittiwake chicks were converted into the number of chicks per nest. **2A)** Each volunteer (represented by a different coloured dot) marked kittiwake chicks in the image. The nest diagram was plotted on top of the image and marked out the Apparently Occupied Nests we wanted to monitor in different RGB shades of red. **2B-C)** Raw classifications were extracted from each nest, in this example from nest 16, to give the number of chicks that each volunteer identified per nest. **2D-F)** This was converted into a single chick count for different volunteer thresholds, where the threshold value was the number of votes a chick needed to be counted. Nests could have between one and three chicks. To account for the possibility of multiple chicks, a threshold was set for each chick (chick 1, chick 2, and chick 3) independently.

- In this example, six volunteers marked two chicks and one volunteer marked one chick, meaning chick 1 (the first chick) had seven votes (6+1), chick 2 (the second chick) had six votes, chick 3 (the third chick) had zero votes, and three people marked no chicks because ten people classified the image (10-7).
- If the threshold value was set to one, then a chick needed one or more votes to be counted, meaning both chick 1 and chick 2 were counted, and nest 16 had two chicks.
- Conversely, if the threshold value was set to seven, then a chick needed seven or more votes to be counted, meaning only chick 1 was counted, and nest 16 had one chick.
- Given the difficulty of spotting chicks, the nest was only determined to have zero chicks if the number of volunteers that did not see a chick exceeded the number of volunteers that marked a chick. For example, if two volunteers voted for chick 1, and eight volunteers marked no chicks, then at thresholds one and two we would count one chick, but at thresholds greater than two we would count zero chicks.

substantially between years. Most images were reduced in size prior to upload, as the Zooniverse platform has a maximum upload limit, but smaller images could be kept at their original size. Researchers with experience in seabird research and monitoring recorded the number of adults and number of chicks in ten nests, in three images per day (matching those from which citizen science classifications were extracted) from the 10th June to 31th August (or 30th September for colonies in Svalbard). Nests were selected by AJE to be representative of all possible nest positions in the image. This meant selecting nests in different positions relative to the centre of the image (e.g. to account for edge effects) and relative to one another (e.g. how isolated or crowded the nest was), so that comparison between researcher and citizen science data took into account a range of nest positions. Researchers viewed original sized images to maximise the probability of them accurately classifying chicks. It took on average 20 minutes to complete one nest, resulting in $\sim$66 hours of validation (22 colony-years, each taking 3 hours to validate 10 nests). In total, 55 808 images were validated.

We calculated the sensitivity (referred to in some studies as recall) and precision of citizen science chick identification, by comparing the number of chicks counted in each nest by citizen scientists with the number counted by researchers. Sensitivity measured the ability of the citizen science method to correctly identify kittiwake chicks and not let chicks go undetected, whereas precision measured the ability of the citizen science method to differentiate between kittiwake chicks and background noise or other objects (Kurnia et al., 2024). Sensitivity was therefore a measure of quantity and precision was a measure of quality. They were calculated as follows:

$$\text{Sensitivity} = \frac{\text{True Positives}}{\text{True Positives} + \textbf{False Negatives}}$$

$$\text{Precision} = \frac{\text{True Positives}}{\text{True Positives} + \textbf{False Positives}}$$

where a true positive was the number of objects correctly identified as a chick, a false positive was the number of objects/background noise incorrectly identified as a chick, and a false negative was the number of times citizen scientists failed to detect a present chick (Baratloo et al., 2015; Simons & Hinders, 2019).

We split the data into a training dataset (60%) and a test dataset (40%) (Appendix 4.6.2). For each colony-year in the training dataset, we calculated sensitivity and precision of chick 1, chick 2, and chick 3 separately for different threshold values. The threshold was the number of volunteers required to register a chick as present and count it (see Fig 4.2). We compared the sensitivity and precision at different threshold values to decide on the optimum threshold value for all colonies and years. Once this optimum threshold value was selected, we then calculated the mean sensitivity and precision for all colony-years in the test dataset and compared with the training dataset. We did this to ensure that the threshold selected was truly the optimum and was not overfitted to the training dataset.

4.3.4 Volunteer Threshold Algorithm to determine the number of chicks that failed and fledged

Once the threshold value for counting chicks was determined, we developed a Volunteer Threshold Algorithm to determine the number of chicks that failed and fledged per nest (see Appendix 4.6.3 for details). First, we counted the number of chicks per nest (see 'Image annotation and processing'), using the optimum threshold value. We then aggregated the data to daily resolution, to give the highest number of chicks seen in each nest over the course of the day.

Second, we calculated the dates that chicks were first and last seen. We used a consecutive days approach informed by the precision and sensitivity of each colony-year, rather than the exact first and last day a kittiwake chick was seen, to reduce the likelihood of citizen science misclassifications recording incorrect first and last seen dates. Specifically, we used the sensitivity and precision values calculated in the validation step (see above), to calculate tap-in and tap-out values for each colony-year. For colony-years that were not validated, we assigned them the same sensitivity and precision as images validated from the same colony and with the same image size.

The tap-in value was the number of consecutive days a chick had to be seen, to be 95% confident it was a chick and could therefore be recorded as first seen. The tap-out value was the number of consecutive days that a "known" chick must not be seen, to be 95% confident the chick was no longer present (i.e. it had fledged or died) and could therefore be recorded as last seen. Separate tap-in and tap-out values were calculated for chick 1, chick 2, and chick 3, as precision and sensitivity were calculated separately for chick 1, chick 2, and chick 3. The tap-in and tap-out values were calculated by solving the following equations:

$$(1 - precision)^{tapIN} = 1 - 0.95$$

$$(1 - sensitivity)^{tapOUT} = 1 - 0.95$$

To give:

$$tapIN = \frac{log(0.05)}{log(1 - precision)}$$

$$tapOUT = \frac{log(0.05)}{log(1 - sensitivity)}$$

The tap-in values were higher for colonies with low precision, as a chick needed to be present for a greater number of consecutive days to be 95% confident it was a chick and not a false positive. The tap-out values were higher for colonies with low sensitivity, as a chick had to be missing for a greater number of consecutive days to be 95% confident the chick had either fledged or died and was not a false negative.

Thirdly, we determined which chicks failed or fledged based on the number of days they were seen alive (i.e. the difference between the chick's last seen and first seen date). We grouped together colonies at similar latitude and for these groups, we used the normalmixEM function from the mixtools package (Benaglia et al., 2009) to fit two normal distributions to the number of days a chick was seen. We calculated the posterior probability of chicks falling into peak one (with a lower median number of days seen, indicating the chick had failed) and peak two (with a higher median number of days seen, indicating the chick had fledged) and assigned chicks the category (fail or fledge) for which they had a higher posterior probability. St Margaret's Island (MARG) and Alkhornet (ALKE) were not included here and were excluded from the subsequent survival analysis because no chicks were observed at these colonies in 2022 and 2015 respectively. Appendix 4.6.3 provides further details on the Volunteer Threshold Algorithm and how it was built to incorporate low sensitivity and precision estimates.

4.3.5 Validation of Volunteer Threshold Algorithm

We compared breeding success measured using the Volunteer Threshold Algorithm with already existing breeding success data measured by a researcher for colonies in Greenland, to determine the accuracy of our algorithm. Breeding success was calculated as the total number of chicks fledged divided by the total number of apparently occupied nests (AONs), as per standard seabird monitoring (Walsh et al., 1995). The researcher manually looked at the images and recorded the total number of AONs, incubation start and fledging dates, and estimated hatching dates as incubation start + 27 days, which allowed them to calculate breeding success (Coulson, 2011).

4.3.6 Environmental data

Weather data was obtained from the 'ERA5 hourly data on single levels from 1940 to present' dataset available through the Copernicus Climate Change Service (Hersbach et al., 2023). We calculated mean temperature (°C), mean surface solar radiation downwards (kWM^{-2}), mean daily total precipitation (mm), mean wind speed (ms^{-1}), mean significant height of total swell (i.e. wave height; m), and mean wave period (m) within a circle of 20 km radius from each colony, for each day. Studies have shown that seabird nests can be susceptible to gusting winds or high waves dislodging clutches or nests during storms, and so we conducted a Principal Component Analysis on wind speed, wave height, and wave period (Threlfall et al., 1974; Bonter et al., 2014; Newell et al., 2015; Christensen-Dalsgaard et al., 2018). We found that PC1 explained 68.9% of the variation, and therefore used PC1 as a storminess index (Appendix 4.6.4). We determined the direction each colony faced, as degrees from north (N facing = 0°, NW or NE = 45°, W or E = 90°, SW or SE = 135°, S = 180°).

4.3.7 Chick survival models

We tested whether local colony conditions predicted daily chick survival by fitting a Cox Proportional Hazards survival model with mixed effects using the coxme package in R (Therneau, 2024). We included fixed effects of precipitation, storminess, temperature, solar radiation, and colony direction measured as degrees from north, and an interaction term between solar radiation and colony direction. Colony direction measured the direction the colony faced, relative to due north. The interaction term provided a measure of sun exposure, as we predicted that increased solar radiation at more southerly facing colonies (i.e. increased sun exposure) would decrease chick survival. We included colony and nest ID as random effects to account for the lack of independence between chicks from the same nest and same colony.

We centred our chick dates within colony and year, such that day 0 was the first time a chick was seen at a specific colony and in a specific year. We left-censored chicks found after first hatching, by including them only from the day they were first seen. We right-censored chicks that fledged successfully by labelling them as still alive (event = 0) on the day of fledging. To incorporate time-varying covariates (i.e. daily values for precipitation, storminess, temperature, and solar radiation), encounter histories were coded separately for each day. For example, a chick that died at 10 days old, contributed nine encounters of event 0 (alive), and a tenth encounter of event 1 (dead).

We tested for collinearity between fixed effects by calculating Variance Inflation Factors (VIFs) for our model. All fixed effects had VIF < 2 except solar radiation and its interaction with colony direction which had VIF < 5; although, this was sufficiently small for an interaction term to assume collinearity was not an issue (James et al., 2013). We tested the proportional hazards assumption of the Cox regression model using the cox.zph function in the survival package in R (Therneau & Grambsch, 2000); p > 0.05 for the global model and all fixed effects.

When interpreting Cox Proportional Hazards models, the hazards ratio (i.e. exp(coef)) is the primary statistic of interest and can be interpreted as the instantaneous rate of occurrence of failure in chicks remaining at risk (Maag et al., 2022). Specifically, when exp(coef) < 1, the hazard decreases (and survival increases) per unit increase in a variable, and when exp(coef) > 1, the hazard increases (and survival decreases) per unit increase in a variable. The coefficients (coef) of the model can be interpreted as the multiplicative effect of each fixed effect on the hazard ratio (i.e. the relative influence of a variable on the daily failure rate; Maag et al., 2022).

4.4 Results

4.4.1 Validation

As the threshold number of volunteers required to mark a chick increased, sensitivity decreased, and precision increased (Fig 4.3; Appendix 4.6.5). We decided to use a threshold value of one to maximise chick sensitivity (Fig 4.3), and therefore the Volunteer Threshold Algorithm's ability to detect chicks, particularly second and third chicks. The mean sensitivity and precision for all colony-years was comparable between the test and training datasets, suggesting the algorithm was not overfitted to the training dataset (Table 4.1). Precision was zero when the chick was not observed for a given colony-year. This explained why precision was often low for chick 3, as very few colonies had nests containing a third chick.

Whilst the overall sensitivity and precision of citizen scientists appeared to be low, the Volunteer Threshold Algorithm was able to successfully use the sensitivity and precision of each colony-year to provide accurate measures of breeding success that were comparable to that measured by an experienced researcher. Breeding success calculated from the Volunteer Threshold Algorithm, using the chosen threshold value of one, significantly predicted breeding success measured by a researcher (slope = 1.21, SE = 0.18, $p < 0.01$; intercept = -0.16, SE = 0.11, p = 0.23) and the overall regression was statistically significant ($R^2 = 0.90$, $F_{1,5} = 45.5$, $p < 0.01$) (Fig 4.4). This enabled us to use the algorithm on the rest of the dataset to determine chick success and survival for each colony-year. More detailed results and justification for the optimum threshold selected are provided in Appendix 4.6.5.

Table 4.1: Sensitivity and precision (mean ± SD) of citizen science chick identification for the train and test datasets, when using a threshold value of one and two. Sensitivity and precision were calculated separately for chick 1, chick 2, and chick 3. *Precision was zero if the chick was not observed for a given colony-year. This explained why precision was so low for chick 3, as very few colonies had nests containing a third chick.

Threshold	Measurement	Chick	Train	Test
1	Sensitivity	1	0.71 ± 0.16	0.68 ± 0.20
		2	0.58 ±0.29	0.52 ± 0.25
		3	0.77 ± 0.32	0 ± 0 *
	Precision	1	0.60 (± 0.28 SD)	0.62 ± 0.30
		2	0.34 (± 0.31)	0.67 ± 0.28
		3	0.05 (± 0.12)	0 ± 0 *
2	Sensitivity	1	0.47 (± 0.22)	0.43 ± 0.25
		2	0.29 (± 0.21)	0.25 ±0.22
		3	0.18 ± 0.26	0 ± 0 *
	Precision	1	0.88 ± 0.13	0.82 ± 0.31
		2	0.60 ± 0.36	0.90 ± 0.10
		3	0.14 ± 0.29	0 ± 0 *

Figure 4.3: Sensitivity and precision of citizen science chick counts compared to researcher counts, when using a threshold of one, two, and three to determine the number of chicks in each nest. For all chicks, sensitivity was highest when using a threshold value of one, but precision was highest when using a threshold value of three. Both training and test datasets are presented here.

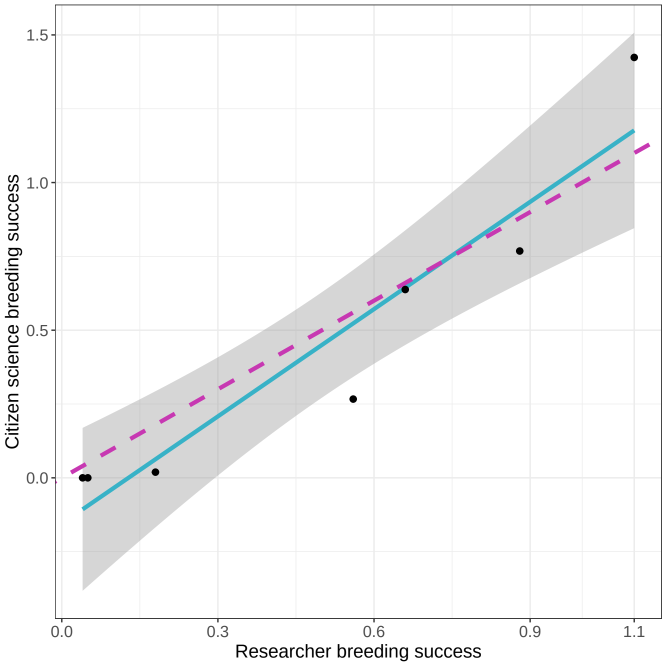

Figure 4.4: Breeding success measured using the Volunteer Threshold Algorithm (using threshold value one) plotted against breeding success measured by a researcher, for colonies in Greenland in different years. Breeding success measured using the algorithm significantly predicted breeding success measured by a researcher, shown by the solid blue line (slope = 1.21, SE = 0.18, $p < 0.01$; intercept = -0.16, SE = 0.11, p = 0.23). The pink dashed line shows a 1:1 line (slope = 1, intercept = 0.0). The overall regression was statistically significant ($R^2 = 0.90$, $F_{1,5} = 45.5$, $p < 0.01$).

4.4.2 Chick survival

We modelled the effect of local colony conditions on 1406 individual kittiwake chicks from 625 nests and 11 colonies over the period of 2015 to 2022 (Table 4.2). In total, 282 chicks died, all of which were less than 15 days old. Precipitation had a large negative effect on chick survival, with daily chick failure rate increasing by 3.7-fold per 1 mm increase in precipitation (hazard ratio = 3.68; Table 4.2, Fig 4.5). Storminess, temperature, solar radiation, colony direction, and the interaction between solar radiation and colony direction did not have a significant effect on daily chick survival (Table 4.2, Fig 4.5).

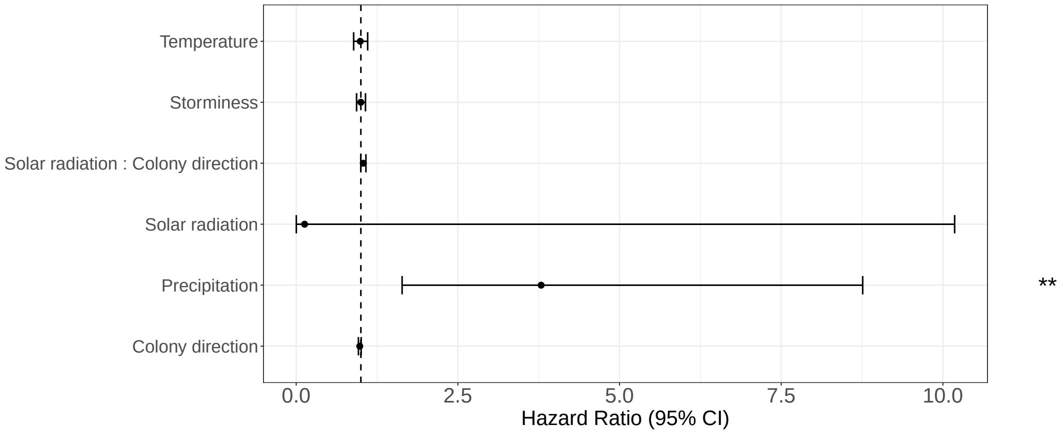

Figure 4.5: Hazard ratios estimated for each variable of a Cox mixed effects model. The dashed vertical line indicates hazard ratio = 1. When the hazard ratio is < 1 there is a reduced hazard of chick failure and so a positive effect on survival. When the hazard ratio is > 1 there is an increased hazard of chick failure and so a negative effect on survival. Precipitation was the only variable where the 95% CIs did not overlap 1, suggesting that daily chick failure rate significantly increased per 1 mm increase in precipitation.

Table 4.2: Model outputs of daily nest failure rate in relation to temperature, solar radiation, colony direction, storminess, precipitation, and the interaction of solar radiation and colony direction. The hazard ratio (exp(coef)), coefficient (coef), standard error (SE) and significance (p) are reported for each variable of a Cox mixed effects model. Significant p-values (p <0.05) are in bold. When exp(coef) <1 there is a reduced hazard of chick failure and when exp(coef) >1 there is an increased hazard of chick failure. A positive coef indicates a positive effect on chick failure rate, and therefore a negative effect on survival rate. Variance (Var) and standard deviation (SD) are reported for random effects.

Effect	**Variable**	**exp(coef)**	**Coef**	**SE**	**P**
Fixed	Solar radiation	0.13	-2.04	2.23	0.36
	Colony direction	0.98	-0.017	0.011	0.12
	Temperature	0.99	-0.0096	0.056	0.86
	Storminess	1.00	-0.000099	0.035	1.00
	Precipitation	3.79	1.33	0.43	**<0.01**
	Solar: colony direction	1.04	0.037	0.020	0.061
	Variable			**Variance**	**SD**
Random	colony	-	-	2.21	1.49
	nest ID	-	-	4.53	2.13

4.5 Discussion

Many studies have investigated the indirect effect of climate on seabird demography, but few have focused on the direct effects of weather on daily chick survival, and even fewer across multiple colonies and years (Mallory et al., 2009a). Understanding the impact of weather on seabird chick survival, and therefore breeding success, is of particular importance given predicted increases in climatic variability under future climate change scenarios (Rahmstorf & Coumou, 2011; Arias et al., 2021). Using images from the Seabird Watch time-lapse camera network, we developed an algorithm that used citizen science classifications to provide reliable breeding success data. This allowed us to quantify the direct effects of local weather conditions on kittiwake chick survival across large spatiotemporal scales with low cost and little disturbance (Edney et al., 2025). We found that precipitation had a large negative effect on chick survival, with daily chick failure rate increasing by 3.7-fold per 1 mm increase in precipitation. However, aside from the effect of precipitation, we found no evidence for the direct effect of other weather variables on chick survival, suggesting that these variables are at best of secondary importance.

4.5.1 Breeding success and chick survival

Our finding is supported by previous research, which reported a negative correlation between kittiwake breeding success and rainfall in Newcastle, England (Turner, 2010). This effect has also been found in seabirds breeding in Arctic Canada, where eggs and chicks were often lost during heavy snowstorms, rain or freezing-rain events accompanied by high winds (Mallory et al., 2009b). The mechanism via which rainfall modulates survival is not always clear, although in heavy rain adult seabirds will sometimes abandon their nests, leaving chicks exposed to the elements and in turn susceptible to chilling (Mallory et al., 2009b). Furthermore, it is possible that even brooding may be unable to protect chicks from high amounts of precipitation, particularly if water collects at the bottom of nests (Konarzewski & Taylor, 1989). There may also be interactive effects between precipitation and food availability which affect chick survival, for example if periods of high precipitation reduce adult foraging success (Baird, 1990; Finney et al., 1999; Clairbaux et al., 2021).

Precipitation is predicted to increase at high latitudes under climate change, meaning this threat may be heightened for northerly breeding seabirds, such as kittiwakes breeding in Svalbard (Intergovernmental panel on climate change, 2007). Modelling the effects of predicted future weather scenarios on chick survival at different colonies thus warrants future research. It is difficult to see how kittiwakes could respond to potentially unpredictable increases in precipitation, aside from adopting more sheltered breeding locations. Previously in Shetland, increased Great Skua (*Stercorarius skua*) predation was linked to increased numbers of kittiwakes breeding in sea caves, which afforded more protection (Heubeck & Mellor, 1994; Mousley & Kershaw, 2023). This could suggest that kittiwakes may be able to plastically alter their nesting site to minimise mortality. However, it is unclear how such a strategy might mitigate against the effects of precipitation on a large scale, and it is unlikely that this will allow populations to respond to increased precipitation in a meaningful way.

Breeding in more sheltered locations might be beneficial for other reasons, such as reduced sun or storm exposure; yet, neither sun nor storm exposure affected kittiwake chick survival in our study. This was surprising given that solar radiation has been shown to have a large effect on heat gain in seabirds (e.g. Olin et al., 2023), and so we expected increased sun exposure and associated increased temperatures to negatively affect chick survival. While we might suggest that sun exposure and temperature may not be of primary importance, at present, when considering the direct causes of kittiwake chick mortality, we acknowledge that our study is limited by only examining these variables at the colony level. Future studies should consider quantifying sun exposure at each nest, to determine whether survival differs between nests at the same colony.

Storminess likewise had no effect on kittiwake chick survival, despite previous studies showing that seabird nests can be directly impacted by gusting winds or high waves dislodging clutches or nests, particularly for birds breeding on the lower parts of cliffs (Threlfall et al., 1974; Bonter et al., 2014; Newell et al., 2015; Christensen-Dalsgaard et al., 2018). We acknowledge that our study could have been biased towards more sheltered breeding locations, or that violent storms may not have hit the colonies during the study period. However, the mean daily wind speed ranged from 0.2 to 16.3 ms^{-1} (equivalent to 36.5 mph) and mean wave height ranged from 0.003 to 3.5 m during our study, suggesting considerable variation with which to observe differential survival. It is, of course, possible that the extreme conditions required to cause storm-based mortality were not observed during our study, leading to a false negative. Nevertheless, given that we have multiple years of data from sites spanning much of the kittiwake breeding range, we might conclude that such storms are sufficiently rare so as not to be a major driver of population decline via an effect on chick survival, at present.

Understanding the impact of climatic conditions on egg survival is equally important, which unfortunately our study was not able to quantify. For example, the section of kittiwake colony monitored by our camera at St Margaret's Island (Wales) produced no chicks in 2022, meaning there was complete failure during incubation or before. We therefore point to this as an essential avenue for future study. We further recommend that future analyses might consider extending this research to explore the precipitation effect found here in greater detail. This could include investigating how chick age might influence the affect of precipitation on survival, and testing the effects of cumulative or successive days of precipitation.

4.5.2 Remote monitoring and citizen science

Using our camera-citizen science system, we were able to answer questions pertaining to seabird chick survival across multiple colonies and years at comparatively low cost and low disturbance (Edney et al., 2025). By investigating the effects of weather within a regular monitoring set-up, we improved on studies which only analysed data in years where a noticeably extreme weather event occurred, which may have potentially biased some previous studies of rare weather events.

Continued technological advancement has made it cheaper and easier to remotely monitor wildlife, however with this comes challenges associated with analysing large amounts of data (Pascalis et al., 2018). We showed that citizen science represents one possible solution that also engages people in science and raises awareness of ecological issues (Dickinson et al., 2012; Kobori et al., 2016). Even when volunteers displayed < 50% sensitivity compared to researchers, our algorithm was able to convert chick observations into count data that could be used to accurately measure breeding success and chick survival. AI detection of adult birds is now relatively routine (Hayes et al., 2021; Weinstein et al., 2022), but using our citizen science dataset to train machine learning algorithms to automatically detect chicks might require higher sensitivity (Jones et al., 2020). Chicks are especially difficult to detect by non-experts, because of their changing appearance throughout their development, and because they can be hard to see behind or below adults. Sensitivity could be increased in future studies by providing volunteers with images where the objects of interest are much larger, for example by cropping images to show only a single nest at a time. This would allow volunteers to focus in on each nest and might increase the likelihood of spotting second and third chicks.

4.5.3 Conclusion

In this study, we found that precipitation was the only local weather variable that had a measurable effect on kittiwake chick survival. Whilst this direct effect is important to consider given predicted increases in climate variability and the frequency and severity of weather extremes, the lack of evidence for other local weather effects might confirm that the indirect effects of warming sea surface temperatures via the food web are the more important drivers of decline, at present. That said, it is possible that the remote-sensing approach taken here is insensitive to certain parameters, and hence it is essential that other studies with different technologies are used to confirm these trends. Nonetheless, we propose that the use of a large-scale citizen science camera system is a scalable, low-cost method that has allowed us to explore these patterns over a wide area, while also minimising disturbance to a vulnerable breeding species. Increasing uptake of remote monitoring techniques will, therefore, be important for continued and widespread ecological monitoring across a wide and variably accessible landscape.

4.6 Appendix

4.6.1 Appendix: Image alignment using the pengbot aligner

The pengbot aligner (https://github.com/CarlosArteta/pengbot-aligner) was run on each set of images, where a set was one year of data at a specific colony (termed a colony-year). The user selected a focal image, which all other images were aligned relative to, and created a nest diagram. This was a .png file that marked each Apparently Occupied Nest in the image that the user wanted to study (Fig. 4.2). The nest diagram was created in Paint.Net, with each nest being marked a different RGB shade of Red, to enable them to be distinguished as separate nests when extracting raw classifications to count individual birds.

The alignment algorithm also required consensus or raw classifications to identify where birds were in the image. The algorithm first took the consensus or raw classifications and drew a bounding box around each classification (i.e. possible bird) and removed these areas from the image. This meant that the algorithm only attempted to align parts of the image that did not contain birds (e.g. features of the cliff face). This step was important to prevent the algorithm attempting to align images using birds, which change position across images. Instead, the algorithm aimed to align images based on inanimate objects (e.g. rocks) which should remain in the same position between images, unless the camera had moved, thus meaning the image needed to be aligned.

Once this step was complete, the algorithm went through each image in turn, and attempted to align it to the focal image. If successful, a new nest diagram was saved, in which the position of the nests in the nest diagram should match the position of the nests in the image, even if the camera view had changed. If the alignment algorithm could not align an image, the user was presented with the current nest diagram overlaid on top of the image and asked to select one of the following options: Keep diagram (snow); Keep diagram (other); Ignore (blurry); Ignore (other); Redraw. The ‘Keep diagram’ options used the current nest diagram for the image, while the ‘Ignore’ options created an entirely black nest diagram for the image, meaning the algorithm should not attempt to align this image (e.g. because the image was blurred by rain). The ‘Redraw’ option was selected if the nests in the nest diagram no longer matched the position of the nests in the image sufficiently well. The user had to then draw a new nest diagram for the image the algorithm failed to align, and then re-run the algorithm from that point onwards. This had the advantage of being able to ensure the nest diagrams remained accurate, especially when aligning a large number of images at once. Some image sets required multiple (> 5) nest diagrams to be drawn throughout the alignment process, which could be time-consuming, particularly if the image contained a lot of nests. This sometimes occurred due to large differences in light levels between images (e.g. bright sun vs. shade). Consequently, we decided to only process three images per day using the alignment algorithm, to minimise large variation in light that might be experienced from images captured throughout the day.

The output of the alignment algorithm was a series of aligned nest diagrams (one per image) and a .csv file that provided the outcome of each image (i.e. Aligned, Keep diagram (snow), Keep diagram (other), Ignore (blurry), Ignore (other), Redraw). The output was aligned nest diagrams, rather than aligned images, because saving new time-lapse images was data heavy and would have substantially increased the algorithm processing time, whereas saving new nest diagrams was much faster.

4.6.2 Appendix: Summary of camera data used in this study

Table 4.3: Summary of the camera data that has been used in this study. Image size refers to whether images uploaded to Seabird Watch were their original resolution or reduced prior to upload. Images that were validated by a researcher have been categorised as ‘Test’ or ‘Train’ to indicate whether they were included in the test or train dataset, and unvalidated images are given a ‘-’. Fowlsheugh and Marwick Head were split into separate test and train datasets because each single colony image was cropped and uploaded as two separate images to Seabird Watch (crop1 and crop2, or crop2 and crop3). Nests from separate cropped images were, however, considered to be from the same colony (i.e. Fowlsheugh or Marwick Head) for the survival analysis. The number of nests used in the survival analysis is fewer than the number of nesting attempts (Apparently Occupied Nests) at each colony. This is because we were only able to model chick survival and so could not include nests that failed during incubation or before. *SKEL2019 did not have a complete breeding season of data, as images after June were not analysed. It was included in the validation process, but survival analysis could not be performed for this colony-year.

Colony (colony code)	Latitude, Longitude	Year	Image size	Validation dataset	Number of nests in survival analysis
Skomer Island, Wales (SKOM)	51.74, -5.30	2018	Reduced	Test	33
		2022	Original	Test	
Skellig Michael, Ireland (SKEL)	51.77, -10.54	2015	Original	-	32
		2016	Original	Train	
		2019*	Reduced	Train	
St Margaret’s Island, Wales (MARG)	51.64, -4.72	2022	Original	Test	0
Fowlsheugh, Scotland (FOWL-crop1)	56.91, -2.20	2022	Original	Train	19
Fowlsheugh, Scotland (FOWL-crop2)		2022	Original	Test	
Marwick Head, Scotland (MARW-crop2)	59.10, -3.35	2022	Original	Train	40
Marwick Head, Scotland (MARW-crop3)		2022	Original	Test	
Mykines, Faroes (MYBR)	62.1, -7.66	2016	Original	Train	23
		2019	Original	-	
Hvítabjarnarey Island, Iceland (HVIT)	65.08, -22.68	2016	Original	-	48
		2017	Original	Test	
		2021	Reduced	Test	
Kippaku Island, Greenland (KIPP)	73.72, -56.63	2017	Reduced	-	24
		2018	Reduced	Test	
		2019	Reduced	-	
		2021	Original	-	
		2022	Original	Test	
		2017	Reduced	-	

Table 4.3 continued from previous page

Apparsuit Island, Greenland (APPA)	73.79, -56.72	2018	Reduced	-	150
		2019	Reduced	-	
		2020	Reduced	Train	
		2021	Original	Train	
Midterhukfjellet, Svalbard (MITT)	77.66, 14.88	2014	Original	-	86
		2016	Original	Train	
		2020	Reduced	Train	
Alkhornet, Svalbard (ALKE)	78.21, 13.78	2015	Original	Train	0
Kapp Waldburg, Svalbard (KAPP)	78.27, 21.92	2019	Reduced	Train	13
Ossian Sarsfjellet, Svalbard (OSSI)	78.94, 12.49	2016	Original	Train	157
		2017	Reduced	-	
		2018	Reduced	Train	
		2019	Reduced	-	
		2020	Reduced	-	

4.6.3 Appendix: Volunteer Threshold Algorithm to determine the number of chicks that failed and fledged

We developed a Volunteer Threshold Algorithm to determine the number of chicks that failed and fledged per nest. First, we counted the number of chicks per nest, (see ‘Image annotation and processing’ in the main text), using the optimum threshold value. Second, we calculated the dates that chicks were first and last seen. Third, we determined which chicks failed or fledged based on the number of days they were seen alive.

In order to do this, we aggregated the data to daily resolution, to give the highest number of chicks seen in a given nest over the course of the day. We also assigned sensitivity and precision values to all colony-years, based on the test and train validation colony-years. For colony-years that were not validated, we assigned them the same sensitivity and precision as images validated from the same colony and with the same image size. We then proceeded to build the algorithm to solve key challenges in working with citizen science camera data.

A) First and last seen dates

The first challenge was that erroneous classifications could lead to chicks being recorded when they did not exist, leading to first seen dates before the true value. To solve this, we said that chicks were only first seen when they were recorded for the tap-in number of consecutive days. The tap-in value was obtained by solving the following equation for n: $(1 - \text{precision})^n = 1 - 0.95$, where n was the tap-in value, and precision was the precision for chick 1, 2, or 3 (depending on the chick being considered) for that colony-year. Given that precision was the probability that the citizen scientists could differentiate between kittiwake chicks and the surrounding image, the tap-in value was the number of consecutive days that a chick must be identified for us to be certain it was a chick. The tap-in values for chicks 1, 2, and 3 were higher for colonies with low precision, as a chick needed to be present for a greater number of consecutive days to be 95% confident it was a chick and not a false positive.

Based on this, the first seen date for chicks 1, 2, and 3, was the first time any number of chicks were seen for the tap-in number of consecutive days, meaning all chicks in a given nest had the same first seen date. This was because it was difficult to spot small newly hatched chicks being brooded. Given chicks in the same clutch typically hatch within two days of each other (Gill et al., 2002), we assumed all chicks must have hatched by the time any one of them was seen.

The second problem to resolve was that once chicks started to fledge, they might return to nests that were not their own. This could result in nests that failed early in the season having chicks present later in the season, or nests that never hatched a chick having chicks suddenly appear later in the season, leading to very late first seen dates for some nests. In the latter scenario, it was likely that chicks would only be seen for a short period of time in the wrong nest. To solve this, for all nests where a chick was seen for more than one day, we calculated the median first seen date for that colony-year. Then, the first seen date for all chicks had to fall within ± 8.8 days of this median first seen date. If the first seen date fell outside of this window, we assumed the chick was not a true datapoint (i.e. it was an erroneous click early in the season, or a chick from another nest late in the season), and it was removed from the dataset. We chose ± 8.8 days because Coulson and

White, 1958 report that the standard deviation of the average kittiwake fledging period (i.e. time between hatching and fledging) was ± 4.4 days. We multiplied this standard deviation by two, to account for the range of hatching dates being larger than the standard deviation, and therefore to ensure we picked up as many real chicks as possible. Given the minimum kittiwake fledging period is typically around 36 days Coulson and White, 1958, excluding chicks that were first seen on the median first seen date + 8.8 days, should comfortably exclude fledged chicks that visited the wrong nest.

Finally, the last problem to solve, was that consecutive zeros in the dataset could indicate that either a chick was not present (i.e. had died/fledged), or they could exist because chicks were present but not spotted and clicked on; however, it was not obvious how to distinguish between these two scenarios. To solve this, we said that chicks were not present, if they had not been seen for the tap-out number of consecutive days. The tap-out value was obtained by solving the following equation for n: $(1 - \text{sensitivity})^n = 1 - 0.95$, where n was the tap-out value and sensitivity was the sensitivity for chick 1, 2, or 3 (depending on the chick being considered) for that colony-year. Given that sensitivity was the probability that the citizen scientists correctly identified a chick, the tap-out value was the number of consecutive days that a chick must not be seen, before we were certain the chick was not present, and had therefore either fledged or died. The tap-out value for chicks 1, 2, and 3 was higher for colonies with low sensitivity, as a chick had to be missing for a greater number of consecutive days before we were 95% confident the chick had either fledged or died.

B) Failed and fledged

Once the first and last seen dates were obtained, we calculated the total number of days each chick was seen. We grouped together colonies at similar latitude (Wales = Skomer Island, Skellig Michael, St Margaret's Island; Scotland = Fowlsheugh, Marwick Head; Faroes and Iceland = Mykines, Hvítabjarnarey Island; Greenland = Kippaku, Apparsuit; Svalbard = Midterhukfjellet, Alkhornet, Kapp Waldburg, Ossian Sarsfjellet) and for these groups, we used the normalmixEM function from the mixtools package in R (Bengali et al. 2009) to fit two normal distributions to the number of days a chick was seen.

We calculated the posterior probability of chicks falling into peak one (with a lower median number of days seen, indicating the chick had failed) and peak two (with a higher median number of days seen, indicating the chick had fledged) and assigned chicks the category (fail or fledge) for which they had a higher posterior probability (Fig. 4.6). Colonies were grouped by latitude because this is known to affect phenology, and therefore fledging period (Burr et al., 2016; Edney, 2020). St Margaret's Island (MARG) and Alkhornet (ALKE) were not included here and were therefore excluded from the survival analysis because no chicks were observed, and so both colonies failed before or during the incubation stage in 2022 and 2015 respectively.

For both Greenland and Wales, the normalmixEM function did not converge on a single solution, but instead output one of two solutions on any given run. For the Greenland data, both solutions appeared with equal frequency when the model was repeatedly run, and so we selected the distribution that provided breeding success data most similar to breeding success measured by a researcher. For Wales, we selected the solution that appeared more frequently when the model was repeatedly run.

It is important to note that the number of days a chick was seen is a proxy for fledging period and first seen dates are a proxy for hatching dates. We acknowledge that the date a chick was first seen might not be the date it hatched, namely because chicks are almost continuously brooded for the first few days after hatching and are therefore very difficult to spot in time-lapse images. As a result, first seen dates are likely to be a few days later than hatching dates, and the number of days chicks were seen are likely to be shorter than fledging periods for chicks that fledge. Given that the methods used to extract this data are the same for all colonies, this should not introduce bias into our results.

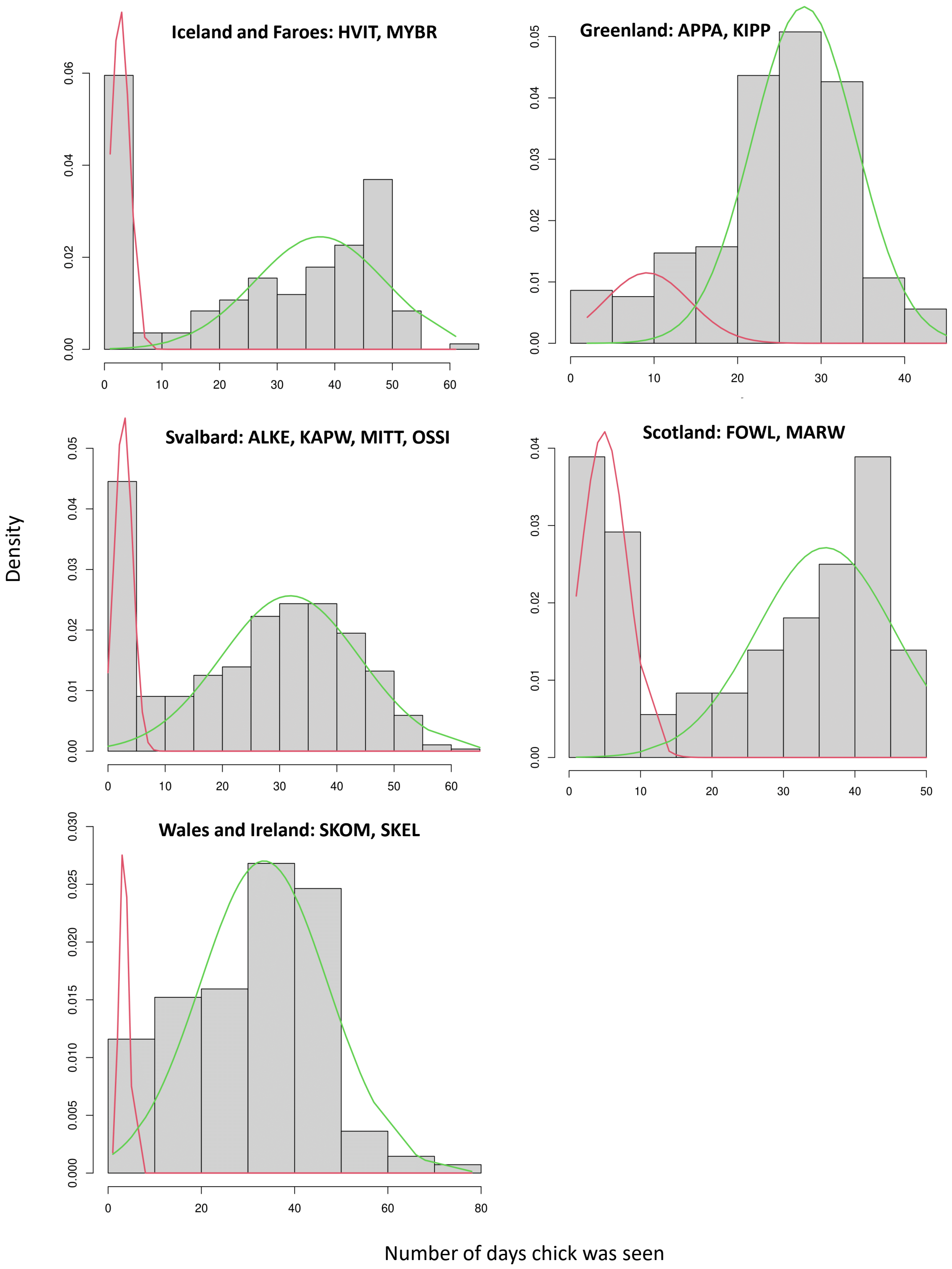

Figure 4.6: Two normal distributions fit to the number of days a chick was seen, for colonies grouped together at similar latitude. We calculated the posterior probability of chicks falling into the peak with a lower median number of days seen (fail; shown in red) and the peak with a higher median number of days seen (fledge; shown in green) and assigned chicks the category (fail or fledge) for which they had a higher posterior probability.

4.6.4 Appendix: Storminess index generated by Principle Component Analysis

We conducted a Principle Component Analysis on wind speed, wave height, and wave period, and found that PC1 explained 68.9% of the variation (Fig. 4.8, Fig. 4.7). We therefore used PC1 as a storminess index.

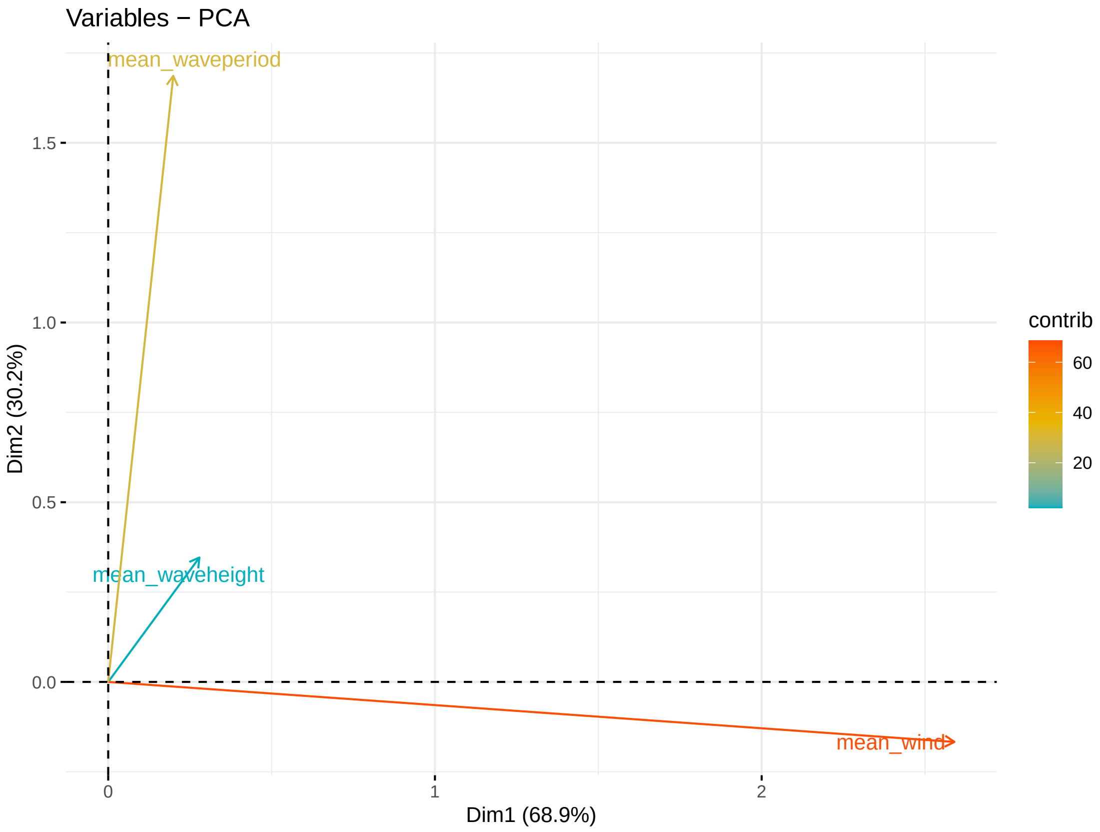

Figure 4.7: Principle Component 1 (x-axis) and Principle Component 2 (y-axis) for Principle Component Analysis on wind speed, wave height, and wave period.

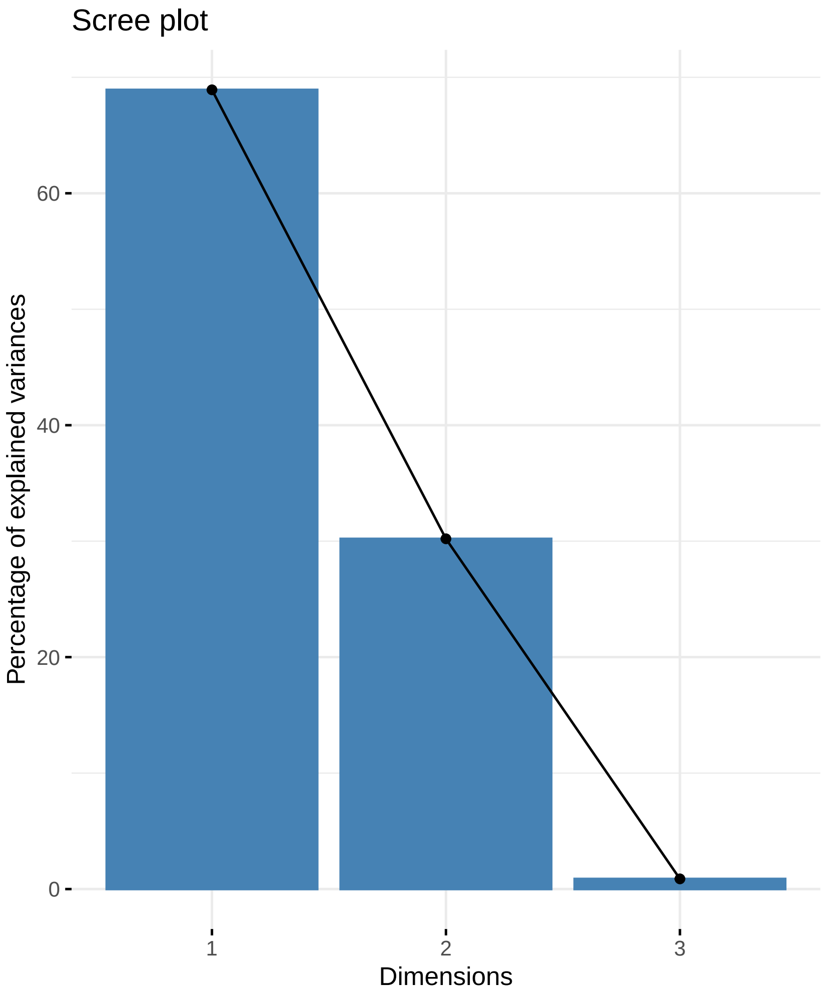

Figure 4.8: Scree plot for Principle Component Analysis on wind speed, wave height, and wave period.

4.6.5 Appendix: Results of citizen science validation

During the citizen science validation step, we measured the sensitivity and precision of each chick (chick 1, chick 2, and chick 3) when different threshold numbers of volunteers were required to have marked a chick for it to be counted. Sensitivity and precision were inversely proportional, such that as the threshold number of volunteers required to mark a chick increased, sensitivity decreased, and precision increased, as shown for all test and training datasets in Fig. 4.9, 4.10, and 4.11.

Precision was zero if the chick was not observed for a given colony-year. This was why precision was typically zero for chick 3, as very few colonies hatched a third chick in any of their nests. The sensitivity of chick 1 was generally higher than for chick 2, meaning in two chick nests, volunteers were more likely to spot one chick than both chicks. Overall, we decided to use a threshold value of one going forwards to maximise chick sensitivity, and therefore the algorithm's ability to detect chicks, particularly the second chick in two chick nests. The Volunteer Threshold Algorithm was built so that even colony-years with low sensitivity and/or precision could be used in the subsequent analysis, as explained in Appendix 4.6.3.

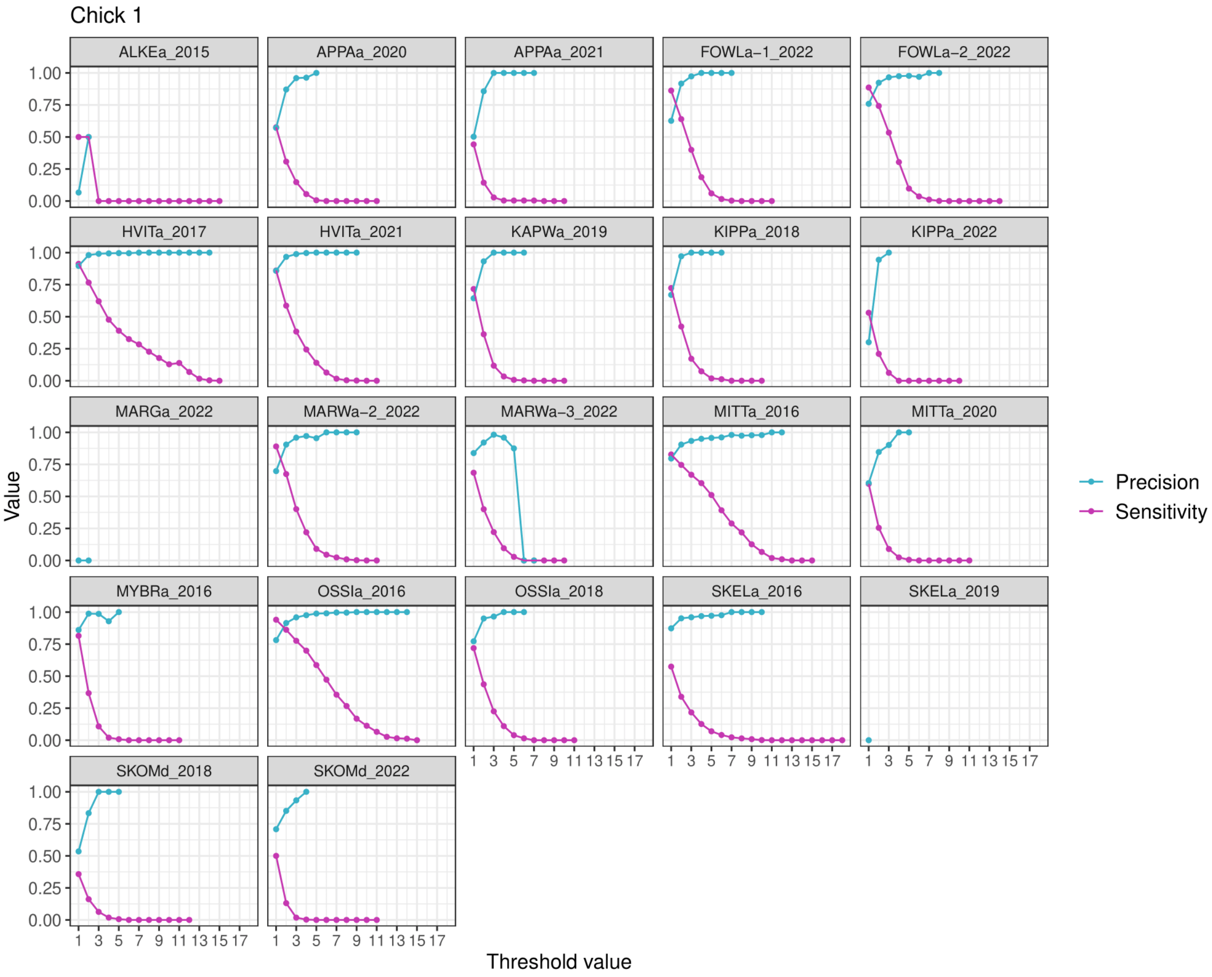

Figure 4.9: Relationship between the sensitivity and precision of citizen science compared to researcher counts of chick 1, as the threshold number of volunteers required to mark a chick increased. Each plot is for a separate colony year. Precision was zero if the chick was not observed for a given colony-year. The threshold value exceeds 10 for some colony-years, because a small proportion of images containing birds were seen by more than 10 volunteers.

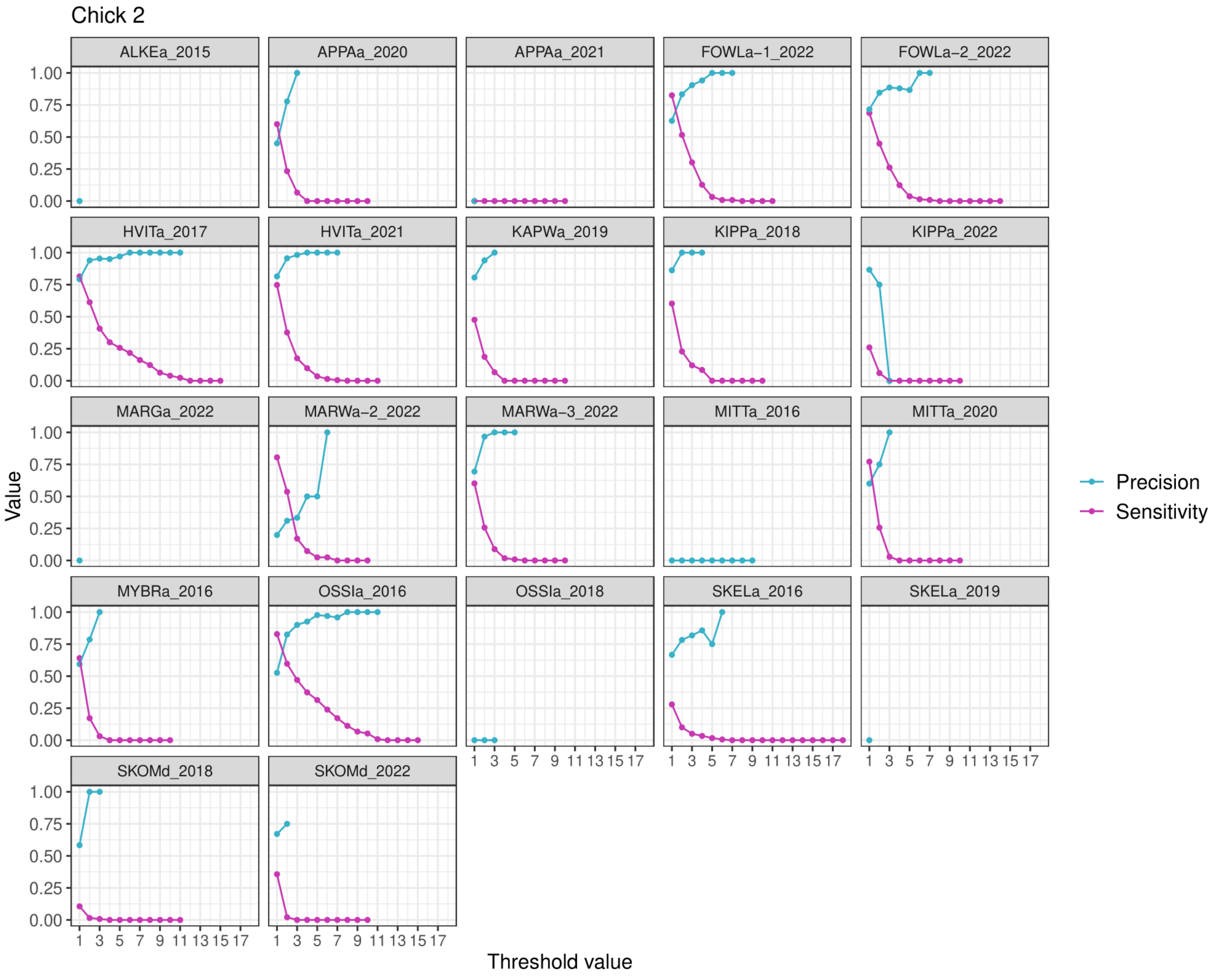

Figure 4.10: Relationship between the sensitivity and precision of citizen science compared to researcher counts of chick 2, as the threshold number of volunteers required to mark a chick increased. Each plot is for a separate colony year. Precision was zero if the chick was not observed for a given colony-year. The threshold value exceeds 10 for some colony-years, because a small proportion of images containing birds were seen by more than 10 volunteers.

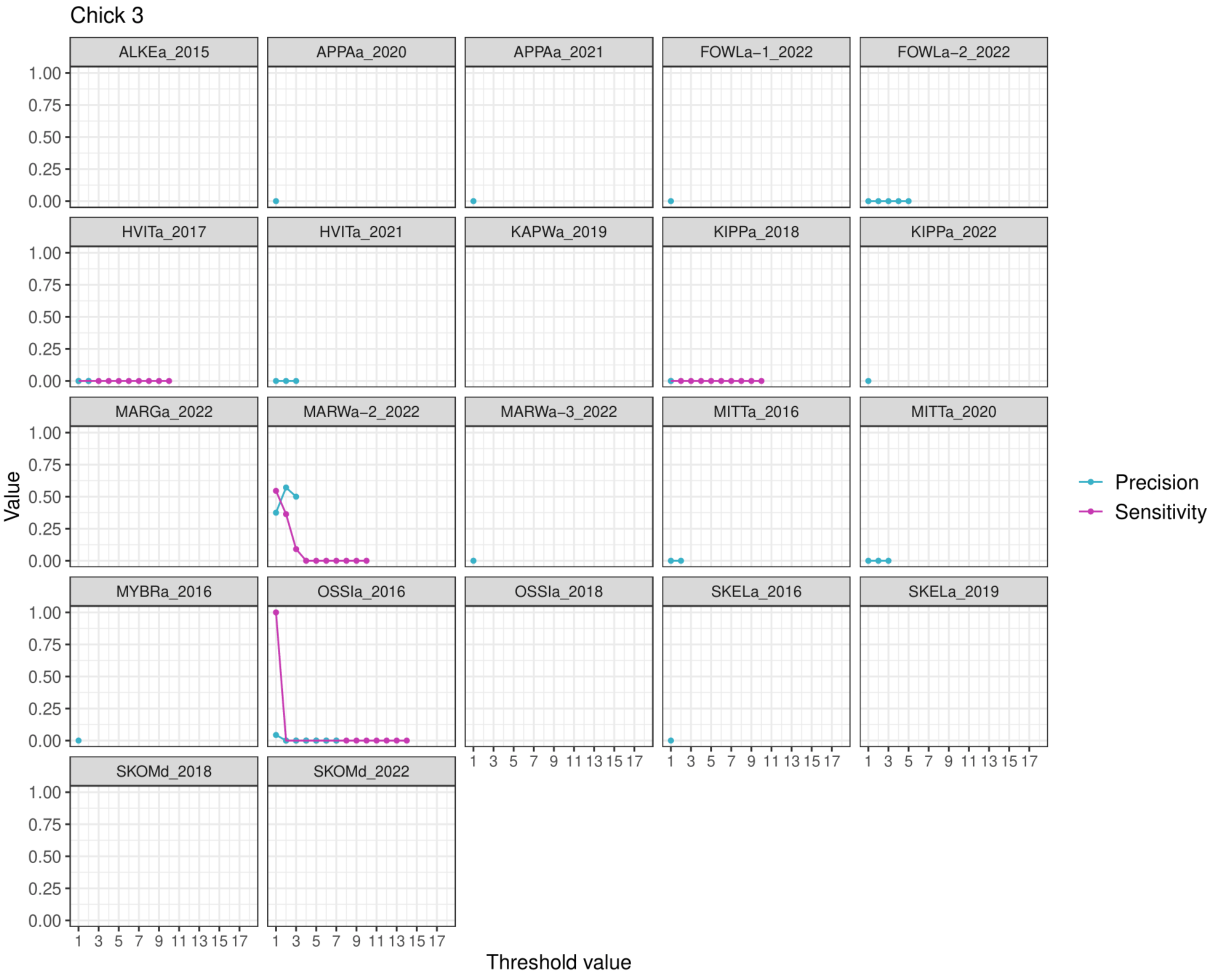

Figure 4.11: Relationship between the sensitivity and precision of citizen science compared to researcher counts of chick 3, as the threshold number of volunteers required to mark a chick increased. Each plot is for a separate colony year. Precision was zero if the chick was not observed for a given colony-year, and most plots here have no data as three chicks were recorded in very few nests. The threshold value exceeds 10 for some colony-years, because a small proportion of images containing birds were seen by more than 10 volunteers.

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5

Individual-level plasticity only partially drives population-level phenological responses to climate change in a vulnerable seabird

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Contents

5.1 Abstract

Given the distances they cover, migratory birds are uniquely vulnerable to anthropogenic change. One of the biggest threats facing migratory birds breeding in seasonal environments is trophic mismatch from global climate change decoupling climatic variables between geographically separate breeding and non-breeding areas. However, few studies examine how changes in individual behaviour underpin population-level changes in the timing of migration and breeding. Here, we use large-scale geolocator tracking of Black-legged Kittiwakes *Rissa tridactyla* between 2007 and 2023 (> 1400 individuals from 34 breeding colonies) to assess population-level changes in the timing of kittiwake migration and breeding in response to sea surface temperature, and investigate if these changes are due to within-individual plasticity and/or between-individual turnover. We found that, at the population level, kittiwakes arrived at the breeding grounds earlier and started incubating earlier as sea surface temperature increased. However, while changes in arrival were explained by within-individual plasticity, changes in incubation start were also explained by turnover of individuals (either via selective disappearance or generational shifts caused by differential early life development). Our study highlights that the direction, magnitude, and mechanism by which phenological change is mediated is thus context- and trait- dependent and has important implications for understanding and predicting how migratory animals can respond to ongoing climate change.

> *"~~Girl~~ Gull, it's so confusing sometimes to be a ~~girl~~ gull"*
>
> – Charli XCX, *Girl, so confusing*

5.2 Introduction

Climate change is predicted to have significant consequences for global ecosystems and biodiversity (Bellard et al., 2012). Migratory animals are uniquely vulnerable to such change, as they can be exposed to anthropogenic threats across large regions and different seasons, as they move between breeding, migration, and non-breeding areas (Wilcove & Wikelski, 2008; Robinson et al., 2009). Climate change acting at different parts of their annual cycle could thus adversely affect survival, reproduction, and cues used to optimise migration timing (Culp et al., 2017).

In seasonal environments, animals must time reproduction so that peak energy requirements, typically those required by rearing young, match seasonal peaks in food availability (Visser et al., 2012). In general, animals are advancing the timing of migration and breeding in response to earlier availability of seasonal resources, however, there are also examples of insufficient phenological responses leading to trophic mismatch and poor reproductive success (e.g. Thackeray et al., 2016; Keogan et al., 2018). The potential decoupling of climatic variables between geographically separate breeding and non-breeding areas, as well as other anthropogenic changes such as direct habitat alteration, pose significant threats to long-distance migrants being able to successfully optimise their arrival time at the breeding grounds (Møller et al., 2008; Culp et al., 2017). This vulnerability makes studying migratory timing of significant importance for understanding species' responses to climate change, which is necessary for developing effective conservation strategies.

Studying migratory birds is difficult given their wide-ranging movements, and it is only with recent advances in animal-borne tracking technologies that we have begun to reliably do so (Robinson et al., 2009; Bridge et al., 2011, 2013). Furthermore, while population-level phenological responses have been well-studied, the mechanisms driving population change in avian migratory timing are poorly understood. Directional population change in phenology could result from individual plasticity (e.g. Conklin et al., 2021; Linssen et al., 2023; Lewin et al., 2024), selective disappearance of individuals (e.g. Saraux and

Chiaradia, 2022; Wynn et al., 2025), or generational shifts caused by differential early life development (i.e. new recruits entering the population with a new phenotype based on early life learning, for example, recruitment of young individuals with increasingly early migration timing; Gill et al., 2019) (Piersma & Drent, 2003). However, the difficulty of collecting repeated individual data throughout the annual cycle means that the number of studies investigating these mechanisms in wild migratory birds is limited. Furthermore, studies tend to focus on either migratory or breeding timing, meaning it is not currently known how multiple phenological traits vary within a single migratory species.

Black-legged Kittiwake *Rissa tridactyla* is red-listed globally as a vulnerable seabird which breeds across the North Atlantic and North Pacific (Descamps et al., 2017; BirdLife International, 2024). Most individuals (∼80 %) migrate to winter in the West Atlantic, although some birds winter in the Barents Sea, some (mainly UK breeders) winter around the UK (including the North Sea, Celtic Sea, Irish Sea, and eastern Atlantic), and small numbers of individuals have been found to winter in the North Pacific (Bogdanova et al., 2011; Frederiksen et al., 2012; Ezhov et al., 2021). Several studies have investigated population-level changes in kittiwake phenology, most commonly egg laying and hatching dates, although they in several instances found weak or contrasting trends (Coulson & Thomas, 1985; Frederiksen et al., 2004; Moe et al., 2009; Wanless et al., 2009; Lauria et al., 2012; Keogan et al., 2018). While changes in phenology have typically been linked to changes in prey availability associated with rising sea surface temperatures (Burthe et al., 2012), it is unknown whether this is due to within-individual plasticity and/or between-individual turnover/selection, and thus whether individuals are flexible enough to cope with a changing climate (and avoid trophic mismatch), or whether change instead reflects micro-evolutionary responses to selection and early-life ontogeny (Piersma & Drent, 2003).

The international tracking project, SEATRACK, and preceding studies have collected tracks of over 1400 individual, with many repeat years of data, since 2007 across the species' Atlantic range (Frederiksen et al., 2012; Strøm et al., 2021). This has provided a unique opportunity to explore the processes generating changes in avian migratory and breeding timing at trans-oceanic spatial scales. Here, we used light-level geolocators to track kittiwakes breeding at 34 colonies between 2007 and 2023 to 1) determine whether population-level changes in the timing of arrival, incubation start, and departure from the breeding colony in response to Sea Surface Temperature (SST) were due to individual plasticity and/or between-individual differences, and 2) if there is evidence for plasticity, determine whether individuals showed variation in plasticity. This will allow us to determine not only how animal behaviour is changing but also why; a key component in predicting responses to climate change going forward.

5.3 Methods

5.3.1 Fieldwork and data collection

This study used data collected by the SEATRACK project, as well as earlier data processed using SEATRACK algorithms and stored in the SEATRACK database, between 2007 and 2023 (SEATRACK, 2024). In total, 1475 individual kittiwakes from 34 colonies were fitted with geolocator sensors attached onto a leg-ring and recaptured in following breeding seasons (Fig. 5.1). Geolocators were either from Migrate Technology (model c65 super), British Antarctic Survey (models mk13, mk14, mk18) or Lotek (Biotrack before 2020: models mk4083, mk4093), all of which recorded the maximum light and the total number of saltwater immersion events (where 0 = no contact with saltwater, and 1 = contact with saltwater) within each recording interval. As recording intervals differed among devices, data were interpolated to give such values for every 10 min period. These data were then standardised to values between 0 (completely dark; completely dry) and 1 (completely light; completely wet) to make outputs comparable among devices (e.g. because the value for maximum light differed among devices).

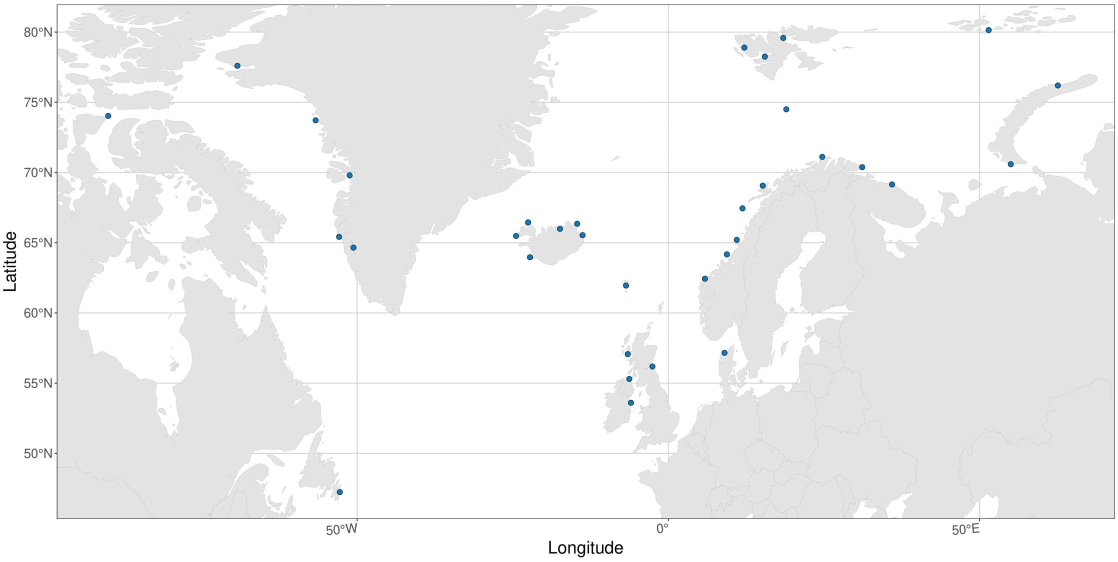

Figure 5.1: Locations of Black-legged Kittiwake colonies used in this study.

5.3.2 Geolocator processing and identification of phenological parameters

We used standardised light data, saltwater immersion data, and longitudinal position to identify when birds were present at the colony during daylight hours. Positions were estimated from raw light data using an automated process described in Bråthen et al., 2021. This method estimated positions with a threshold method using roof-top calibration and filtered inaccurate locations based on position, speed, and angle (Lisovski et al., 2020; Bråthen et al., 2021).

Tracked birds were determined to be present at the colony if the standardised light level was < 0.1 and standardised immersion was < 0.1 for each 10-minute interval, during daylight hours (i.e. between sunrise and sunset). This meant the device was dark when it should have otherwise been light (because the bird was sat on it, rather than because the sun had set), and dry (because the bird was not in the water). By choosing low cut-offs for light and immersion values, we aimed to remove birds in flight, either on migration or foraging trips, and select birds sitting at the colony.

Outside of the equinox, the sunrise and sunset were calculated using the suncalc package in R (Thieurmel & Elmarhraoui, 2022), based on the individual's mean estimated latitude and longitude position for each day. However, for a three-week period either side of the equinox (20th February to 3rd April and 8th September to 20th October) the latitude position could not be calculated (Bråthen et al., 2021). Given that some kittiwakes migrate during the equinox period, we risked missing the arrival and departure dates of many individuals in the study. To overcome this issue, we used the maximum and minimum latitude each individual reached outside of the equinox, and its mean longitude for each day during the equinox, to estimate the theoretical latest sunrise and earliest sunset it could have experienced for each day during the equinox. This allowed us to conservatively estimate if a bird was present at the colony for each 10-minute interval between sunrise and sunset (standardised light level was < 0.1 and standardised immersion was < 0.1). Whilst in principle, all latitudes have the same daylength at the equinox, in practice, the equinox period considered during geolocation was sufficiently large (three weeks) that we considered an estimated maximum and minimum latitude a more accurate and conservative approach.

For kittiwakes in the far north, position data was not available during the midnight sun (24-hours of daylight) and polar night (24-hours of darkness). However, for individuals experiencing typical day/night cycles and therefore with available position data, a second filtering step was included. For an individual to be present at the colony, the difference in longitude between the birds' current position and its colony position also had to be $< 2°$.

Overall, individuals were deemed to be at the colony if the device was dark and dry between sunrise and sunset and if the longitude was consistent with being at the colony (where longitude data was available). The number of 10-minute intervals where the bird was present at the colony was summed per day. We plotted the cumulative minutes spent at the colony per day, for each year an individual was tracked. Manual inspection of these graphs allowed us to extract three phenological parameters: arrival to the colony at the start of the breeding season, incubation start, and departure from the colony at the end of the breeding season. A worked example of how these were selected is provided in Appendix 5.7.1. The mean number of years of arrival, incubation start, and departure data provided by each individual was 1.99 (range 1-9), 1.60 (range 1-7), and 1.93 (range 1-9), respectively (Table 5.3. Fig. 5.4). To determine the accuracy of colony visits identified using light and immersion data, we compared our phenology estimates with dates provided in the literature. We used the “boot” package in R (Davison, A.C. & Hinkley, D. V., 1997) to perform bootstrapping (number of bootstrap replicates = 10 000) and calculated the 95% confidence intervals for the mean and/or median of our phenology estimates at different colonies, to see whether the corresponding mean and/or median estimate from the literature fell within these confidence intervals (Table 5.4). The average phenology calculated for each colony is provided in Table 5.5.

5.3.3 Environmental data

Sea Surface Temperature (SST) data was obtained from the ‘ERA5 monthly averaged data on single levels from 1940 to present’ dataset available through the Copernicus Climate Change Service (Hersbach et al., 2023). We calculated the mean SST within a circle of 37 km radius from each colony, for each month. The 37 km radius was the median of the maximum foraging range reported for kittiwakes in the literature (Table 5.6). For each colony, we calculated the median arrival, median incubation start, and median departure date across all years. We then calculated the mean SST for each colony and year one month prior to the colony’s median arrival, median incubation start, and median departure date, and also between the median arrival and median departure date (to give the mean SST during the breeding season). We calculated SST one month prior to arrival and incubation start, because many animals use environmental cues available before the breeding season to predict the seasonal peak in food availability and hence adjust their phenology accordingly (Frederiksen et al., 2004).

5.3.4 Statistical analyses

Statistical analyses and data processing were carried out in R version 4.2.2 (R Core Team, 2022). Models in section 1 (Sources of changes in phenology in response to

SST) were run using the “lme4” package (Bates et al., 2015). Models in section 2 (Variation in individual responses to SST) were run using “brms” (Bürkner, 2021) due to convergence issues in lme4.

1) Sources of changes in phenology in response to SST

We first fitted a linear-mixed effects model with SST during the breeding season as the response, year (continuous variable) as a fixed effect, and colony as a random effect to determine how SST changed during our study period. Next, we constructed linear-mixed effects models to test whether kittiwakes showed changes in phenology in response to SST at the population-level. SST was left-centred (minimum SST was subtracted from each SST value) to allow easier interpretation of the intercept. The models included the phenological parameter (either arrival, incubation start, or departure date) as the response variable and assumed they followed a Gaussian error distribution, in these models and hereafter. As fixed effects, we modelled the corresponding SST (SST one -month prior to arrival, one month prior to incubation start, or one month prior to departure) as a continuous, left-centered variable and year as a continuous, mean-centered and variance-standardised variable. As random effects, we fitted year , colony, and individual (all three modelled as factors) to control for the nonindependence of the observation at these different levels.

Second, we constructed linear mixed-effects models to test whether changes in phenology in response to SST represented within-individual (phenotypic plasticity) and/or between-individual (turnover) effects. Model construction followed the method of Van de Pol and Wright, 2009 to partition the population-level effect of SST into within-individual and between-individual effects, using within-subject centering (Conklin et al., 2021; Lewin et al., 2024). For each individual, we calculated its average SST as the mean SST for all the years when its phenology (either arrival, incubation start, or departure date) was measured. We calculated each individual’s delta SST as the difference between the SST when an individual’s phenology (either arrival, incubation start, or departure date) was measured and its average SST (i.e. delta SST = SST – average SST). Average

SST represented the between-individual SST effect and delta SST represented the within-individual SST effect on phenology (Van de Pol & Wright, 2009). A significant effect of the within-individual component (delta SST) suggested a plastic response. However, if the effect of the between-individual component (average SST) was significantly different from the within-individual variation (delta SST), this suggested that the population-level change was not fully explained by within-individual responses. This suggested turnover of individuals with different average behaviours, in addition to any plastic response.

The full model included the phenological parameter (either arrival, incubation start, or departure date) as the response variable, the corresponding average SST, delta SST, the interaction between average SST and delta SST, and mean centered and variance standardised year as fixed effects, and year, colony, and individual as random effects. The interaction term between average SST and delta SST allowed us to test for non-linear effects of SST (i.e. whether individuals varied their plasticity as SST changes). Null models included either average SST, delta SST, the interaction term, or year.

For all of the above models, likelihood ratio tests on nested full and null models were used to assess significance. Posterior distributions of fixed and random effects were estimated using simulations carried out in the “arm” package to get bootstrapped 95% Credible Intervals (CI) on model parameters (Gelman & Su, 2024).

2) Variation in individual responses to SST

We also constructed random regression models with the phenological parameter (either arrival or incubation start) as the response variable and included a random slope and intercept at the individual level to test whether individuals showed variation in their plastic responses of phenology along a SST gradient. Additionally, we also fitted the covariance between individuals’ intercepts and slopes to test whether individual variation in slopes and intercepts was (in)dependent from each other, for instance, whether individuals that had a higher average trait value (i.e., had the larger intercepts) also expressed a stronger plastic response to changes in SST (i.e., had the larger slopes). If there was a positive correlation between intercepts and slopes, we would expect to observe a pattern of fanning out, whereas a negative correlative would suggest a pattern of fanning in. Zero correlation would mean no pattern.

In this model, we fitted mean-centered and variance-standardized SST as the gradient for the slopes. By doing so, we ensured that the estimate of the intercepts' variance was calculated for the average SST value, and slopes were expressed as the effects of a change of two standard deviations in SST, facilitating cross-variable and cross-study comparisons. Ideally, in our study, one should model delta SST as the slope in the random regression model (because birds were measured in different years and years differed a lot), however, we did not do this because there was a significant interaction between delta SST and average SST (see Results). This meant there was non-linearity in the population slope, and by fitting delta SST as a random slope we could have generated spurious results.

As fixed effects, we fitted year and SST (both mean-centered and variance-standardized) instead of the partitioned components of SST (i.e. instead of the average and delta SST components). As random effects, besides the previously described random intercepts and slopes for individual identity, we also fitted colony and year as random intercepts. We compared this random regression model with random intercepts and random slopes, with a model that contained random intercepts only. All terms remained the same (mean centered and variance standardised SST and year as fixed effects, colony, year, and individual as random intercepts) but the random slope was removed. Comparison using "loo" (leave-one-out cross-validation) was used to test whether the model with random intercepts and slopes better fitted the data (indicated by a lower looic value) than the model with random intercepts only.

Simulations were carried out using the "arm" package to estimate bootstrapped 95% CI on effect size. For these models, we only included individuals where the phenological response had been measured for at least two years.

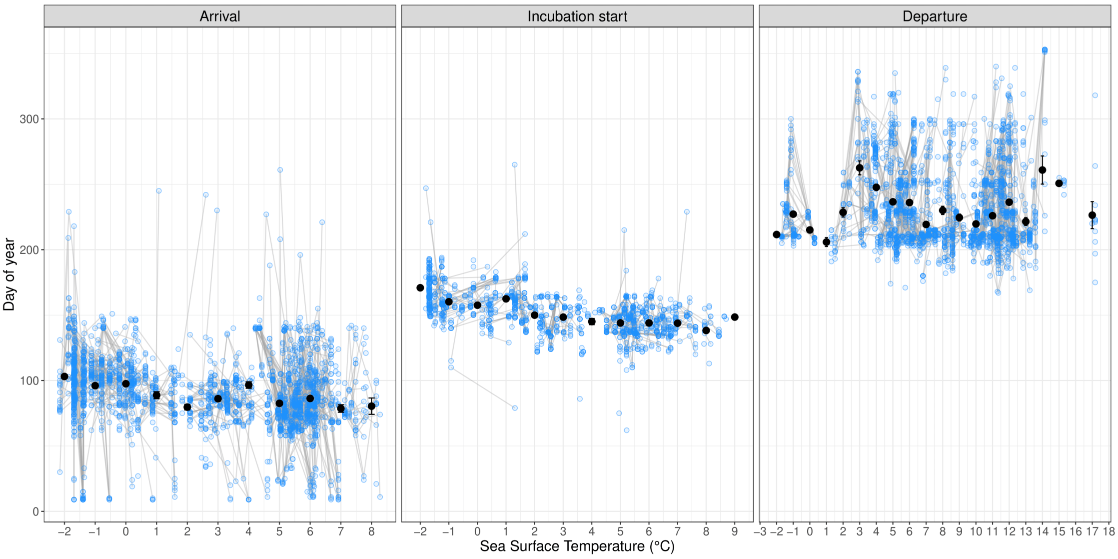

Figure 5.2: The relationship between arrival, incubation start and departure date and mean SST one month prior to arrival, departure, and incubation start respectively. All observations relating to a single individual are joined by grey lines. Black dots represent the median date when binned into sets of 1○C, with whiskers showing the interquartile range.

5.4 Results

5.4.1 1) Sources of changes in phenology in response to SST

SST during the breeding season significantly increased over the 17 year study period ($\chi^2_1 = 23.38$, $P < 0.0001$; Table 5.7). At the population-level, arrival became significantly earlier over the study period ($\chi^2_1 = 4.93$, $P < 0.05$) and as SST increased ($\chi^2_1 = 11.51$, $P < 0.001$; Table 5.7, Fig. 5.2). The timing of incubation start was not affected by year ($\chi^2_1 = 0.019$, $P = 0.89$), but became significantly earlier as SST increased ($\chi^2_1 = 21.05$, $P < 0.0001$; Table 5.7, Fig. 5.2). Conversely, departure date did not show significant changes across years ($\chi^2_1 = 2.09$, $P = 0.15$) or SST ($\chi^2_1 = 2.76$, $P = 0.10$; Table 5.7, Fig. 5.2).

We found that population-level changes in arrival were explained by within-individual plasticity in arrival date (delta SST: $\chi^2_1 = 7.01$, $P < 0.01$; average SST: $\chi^2_1 = 9.81$, $P < 0.01$). We also found a significant, positive effect of the interaction term between delta SST and average SST ($\chi^2_1 = 4.94$, $P < 0.05$), suggesting there was nonlinearity in the within-individual effect of SST (Table 5.1). Specifically, birds that, on average, experienced lower SST values had a greater plastic response than those birds that had, on average, experienced higher SST values (because the relationship between arrival date and SST was negative) and so were less flexible in their response. There was no within-individual effect of SST on incubation start date (delta SST: χ^2_1 = 1.69, P = 0.19) but there was a significant between-individual effect (average SST: χ^2_1 = 19.49, P < 0.0001). The difference between the average and delta SST was significant (95% CI of the difference did not overlap zero: 95% CI = -8.21, -1.52) indicating selective (dis)appearance of individuals with certain phenology, i.e., population-level changes in incubation start date were due to turnover of individuals (Table 5.1). There was also a significant, negative effect of the interaction term between delta SST and average SST on incubation start (χ^2_1 = 12.31, P < 0.001), suggesting evidence for plasticity as well. Birds that, on average, experienced higher SST values were more likely to be flexible in their response, but that at the intercept value there was no significant effect of the delta term (delta SST: χ^2_1 = 1.69, P = 0.19). There was no significant effect of the interaction term on departure date (χ^2_1 = 0.34, P = 0.56) and so this term was removed from the model and is reported as a rejected fixed effect in Table 5.1. Likewise, there was no within-individual or between-individual effect of SST on departure (delta SST: χ^2_1 = 0.34, P = 0.56; average SST: χ^2_1 = 2.09, P = 0.15).

Table 5.1: Results for linear mixed effects models investigating the sources of variation in phenology in response to SST (part 1). The fixed effect of year was mean centered and variance standardised. The 95% credible intervals were estimated using bootstrapping and the chi-squared and p-values were estimated from likelihood ratio tests on full and null models for each term. Significant predictors are highlighted in bold.

Response		Coefficient	Estimate	95% CI	Chi-squared	p-value
Arrival	Fixed effects	Intercept	10.4.05	88.56, 120.45	-	-
		Average SST (between-individual)	-1.48	-2.33, -0.63	9.81	**<0.01**
		Delta SST (within-individual)	-6.76	-11.5, -2.03	7.01	**<0.01**
		Average SST: Delta SST	1.08	0.13, 1.98	4.94	**<0.05**
		Year	-12.39	-23.45, -1.37	4.92	**<0.05**
	Random intercepts	Individual ID	29.88	27.28, 32.75	-	-
		Colony	55.48	33.06, 85.53	-	-
		Year	613.06	471.05, 860.71		
		Residual	497.51	470.69, 525.73	-	-
Incubation start	Fixed effects	Intercept	164.88	158.6, 171.33	-	-
		Average SST (between-individual)	-2.38	-3.1, -1.63	19.49	**<0.0001**
		Delta SST (within-individual)	2.31	-1.3, 6.27	1.69	0.19
		Average SST: Delta SST	-1.26	-2.00, -0.54	12.31	**<0.001**
		Year	0.3	-3.43, 3.81	0.023	0.88
	Random intercepts	Individual ID	2.87	2.55, 3.23	-	-
		Colony	55.38	31.76, 86.8	-	-
		Year	55.45	33.91, 89.86	-	-
		Residual	135.30	125.6, 145.74	-	-
Departure	Fixed effects	Intercept	242.87	225.31, 260.26	-	-
		Average SST (between-individual)	-0.87	-1.64, -0.08	2.09	0.15
		Delta SST (within-individual)	0.44	-1.09, 1.97	0.34	0.56
		Year	-8.19	-19.48, 3.01	0	0
	Rejected fixed effects	Average SST: Delta SST	0.12	-0.26, 0.54	0.34	0.56

Table 5.1 continued from previous page

Random intercepts	Individual ID	34.89	31.67, 38.3	-	-
	Colony	148.44	89.56, 220.26	-	-
	Year	655.67	567.6, 849.86	-	-
	Residual variance	275.94	260.48, 292.29	-	-

5.4.2 2) Variation in individual responses to SST

The model with random intercepts and slopes fit the data better for arrival date than the model with random intercepts only (looic of model with random intercepts and slopes: 16517.8; looic of model with random intercepts only: 16522.1). We found significant, among-individual variation in intercepts and slopes, explaining 6.1% and 8.5% of the variation respectively (Table 2). This means that individuals differed in their average arrival dates, and there was variation in their plastic responses of arrival date along a SST gradient. There was a significant positive correlation between intercepts and slopes (0.74; Table 5.2). This indicated a fanning-out pattern, meaning individual variation was larger at higher SST values and individuals with higher intercepts (later arrival) expressed a larger plastic response to SST. A large proportion of the variation in arrival date (41.7%) was explained by year and a smaller proportion was explained by colony (8.1%) (Table 5.2).

The model with random intercepts only fit the data better for incubation start than the model with random intercepts and random slopes (looic of model with random intercepts only: 6157.0; looic of model with random intercepts and random slopes: 6161.1), suggesting that individuals did not vary in their plastic responses of incubation start along a SST gradient. There was significant among-individual variance in intercepts. This means individuals differed in their average incubation start dates, with individual explaining 5.1% of the variation (Table 5.2). However, both year and colony explained a much larger proportion of the variation in incubation start (35.9% and 20.7% respectively; Table 5.2). Because we had previously found that there was no significant within-individual pattern for departure, we did not fit random regression models for this phenological variable.

Table 5.2: Results for random regression models investigating individual variation in arrival and incubation start in response to SST (part 2). All fixed effects were mean-centered and variance-standardized. Estimates shown are among-individual variance in intercepts (V_{IND} intercepts), among-individual variance in slopes (V_{IND} slopes), intercepts-slopes correlation (*r* intercepts-slopes), among-year variance (V_{YEAR}), among-colony variance (V_{COLONY}), and residual variance ($V_{RESIDUAL}$).

Response		**Coefficient**	**Estimate**	**95% CI**
Arrival	Fixed effects	Intercept	96.02	81.39, 110.75
		SST	-4.83	-7.39, -2.31
		Year	-13.11	-25.25, -0.86
	Random effects	V_{IND} intercepts	3.78	1.18, 6.48
		V_{IND} slopes	5.33	2.69, 7.48
		r intercepts-slopes	0.74	0.20, 0.99
		V_{YEAR}	26.01	17.05, 40.04
		V_{COLONY}	5.04	2.97, 7.99
		$V_{RESIDUAL}$	22.24	21.42, 23.10
Incubation start	Fixed effects	Intercept	152.87	145.08, 160.65
		SST	-7.37	-10.04, -4.29
		Year	0.39	-5.35, 6.12
	Random effects	V_{IND} intercepts	1.61	0.08, 3.71
		V_{YEAR}	11.22	6.73, 18.57
		V_{COLONY}	6.47	4.11, 9.99
		$V_{RESIDUAL}$	11.97	11.32, 12.62

5.5 Discussion

Understanding the mechanisms underpinning changes in migratory bird behaviour is essential for predicting responses to climate change. Here, we investigated how changes in SST – which are predicted to rapidly increase under climate change scenarios and increased over our study period (Intergovernmental Panel On Climate Change (Ipcc), 2023) – affect kittiwake phenology at both the population and individual level. Using data from 1475 individuals from 34 different colonies, we showed that at the population-level kittiwake arrival and onset of breeding (measured as incubation start) became earlier in response to increased SSTs. Changes in arrival date were explained by within-individual plasticity with individuals that, on average, experienced lower SSTs being more flexible in their response. However, changes in the start of incubation were due to turnover of individuals, with evidence for plasticity in individuals that experienced higher SSTs on average. Kittiwakes did not vary their departure date in response to SST. The direction, magnitude, and mechanism by which phenological change is mediated is thus context- and trait-dependent (Merkel et al., 2019) and might provide useful insight into why previous studies on seabird phenology have found diverse phenological trends. These include evidence for earlier (e.g. Gjerdrum et al., 2003; Gaston et al., 2005; Møller et al., 2006; Gaston et al., 2009; Moe et al., 2009; Wanless et al., 2009; Merkel et al., 2019) and later breeding (e.g. Frederiksen et al., 2004; Barbraud and Weimerskirch, 2006; Wanless et al., 2008; Moe et al., 2009; Wanless et al., 2009), as well as no detectable trend (e.g. Frederiksen et al., 2004; Gaston et al., 2005; Wanless et al., 2009; Keogan et al., 2018; Merkel et al., 2019).

5.5.1 Sources of changes in phenology in response to SST

Our results suggest that kittiwakes are not completely constrained in their phenology, as they exhibit plasticity in their timing of arrival at the breeding grounds and incubation start. As SST increases, kittiwakes may be able to flexibly alter their timing of breeding to match changes in prey phenology, such that peak chick energy demands match prey availability. Kittiwakes should therefore be able to compensate for anthropogenic climate change, at least partially.

However, this plasticity is context-dependent, as the interaction between average SST and delta SST goes in opposite directions for arrival and incubation start. Individuals that, on average, experienced lower SSTs were more flexible in their arrival date, whereas individuals that experienced, on average, higher SSTs were more flexible in the timing of incubation start. Higher SSTs will be generally experienced at lower latitudes, suggesting that kittiwakes breeding farther south might be better able to flexibly adjust the timing of incubation in response to SST, and therefore be better able to cope with a changing climate. It is unclear why the opposite trend would be true for arrival (with higher latitude birds potentially better able to flexibly adjust their arrival in response to SST). However, we recognise that this is correlative analysis, and so this trend could be explained by other and/or additional environmental variables.

Indeed, plasticity in arrival date may be less important than plasticity in incubation start. This is because the timing of egg laying and thus incubation start will directly affect whether peak chick energy demand matches lower trophic level resources, whereas the timing of arrival will affect these processes more diffusely. Between arrival and egg-laying, individuals establish and defend nest sites (Quillfeldt et al., 2014), build up body condition (in preparation for egg-laying and incubation demands; Mallory et al., 2008, and mate (Ismar-Rebitz et al., 2020). Some individuals might arrive very early (for example to defend the best nest sites; Bennett et al., 2022), but provided individuals arrive with enough time to complete the necessary tasks before egg laying, they should still be able to breed at the optimal time.

It is therefore particularly concerning that changes in incubation start date were explained by turnover of individuals, with evidence for plasticity only in individuals that, on average, experienced higher SSTs. Turnover will limit the rate at which individuals can respond to rising SSTs, and constraints on incubation start could make kittiwakes vulnerable to trophic mismatch with adverse consequences for breeding success (Keogan et al., 2018). Unfortunately, we cannot determine whether this turnover effect is due to selective disappearance based on phenotype, or generational shifts (i.e. new recruits entering the population with a new phenotype based on early life learning) because our dataset does not contain sufficient individuals of known age (Moiron & Bouwhuis, 2024; Wynn et al., 2025). Colony breeding birds often show high levels of synchronicity in breeding timing to reduce predation risk (predator swamping; Williams, 1975; Hatchwell, 1991), which might impose a constraint on the flexibility of incubation start.

5.5.2 Variation in individual responses to SST

We also found that individuals showed variation in their plastic responses of arrival date along a SST gradient, with individual random slope explaining 8.5% of this variation.

The positive correlation between individual intercepts and slopes suggested a fanning-out pattern, meaning that individual variation was larger at higher SST values and individuals with higher intercepts (later arrival) expressed a larger plastic response to SST. It is unclear what would give rise to this individual variation, for example genetics, early-life learning, or the individual's present situation (Piersma & Drent, 2003).

Previous studies have found that kittiwakes often demonstrate between individual differences in behaviour and behavioural flexibility (e.g. Collins et al., 2019; Harris et al., 2020a; O'Hanlon et al., 2024). It is possible, then, that the individual variation seen here could be part of some sort of behavioural syndrome (e.g. personality), with plastic responses correlated to other behavioural traits (Harris et al., 2020b), which may be of interest for future studies. More generally, it highlights the importance of considering individual variation when making conservation and policy decisions. For example, such variation can pose challenges when quantifying the impact of specific pressures, such as proposed offshore wind farms, on seabird populations (O'Hanlon et al., 2024). Focusing on population responses by averaging across individuals, may lead to studies under- or overestimating the impact of these threats on some individuals (O'Hanlon et al., 2024).

Nevertheless, a much larger proportion of the variation in arrival date was explained by year (41.7%). This could be because other factors that vary annually influence kittiwake arrival date which we were unable to model in this study. We speculate that carry-over effects linked to breeding success the previous year could be one possible explanation (Bogdanova et al., 2011; Fayet et al., 2016). Given that kittiwakes often show large variation in breeding success between years (Frederiksen et al., 2007), this could in turn lead to large inter-annual differences in arrival date.

5.6 Conclusion

Overall, study demonstrates the power of long-term tracking studies and the need for repeat information on known-individuals to be able to understand the mechanisms underpinning population-level change. We emphasise that the direction, magnitude, and mechanism by which phenological change is mediated is context- and trait- dependent and therefore has important implications for understanding and predicting how migratory animals can respond to ongoing climate change.

5.7 Appendix

5.7.1 Appendix: Identification of phenological parameters

We plotted the cumulative minutes spent at the colony per day for each year an individual was tracked. We used the locator function in R to manually identify and save instances of arrival, incubation start, incubation end, and departure from the colony. Arrival was identified as the first time a bird was present at the colony and had to occur before mid-June (day of year: 166). If the bird did not appear at the colony for more than 50 days after possible first arrival, then we assumed this was erroneous and the second time the bird was present at the colony was recorded as arrival. Incubation start was identified as the beginning of a sharp increase in gradient, such that the incubation period was represented by a consistent increase in the cumulative number of 10-minute intervals spent at the colony per day. Male and female kittiwakes tend to share the incubation period fairly evenly (46% by males, 54% by females; Coulson, 2011) and so we expected that the amount of time spent at the colony per day should stay the same during the incubation period for all birds. Incubation end was identified as the start of a gradual decrease in gradient, as birds would be no longer spending as much time at the colony per day (particularly as chicks developed and less time would be spent brooding, with an increasing amount of time spent foraging). To avoid including birds that failed at egg stage, incubation end had to be $\sim$25 days after incubation start, since the incubation period for kittiwakes is 27.3 ± 1.3 days (Coulson & Thomas, 1985). Departure was identified as the first time the line flattened, and stayed flat for at least 50 days, meaning the bird was no longer visiting the colony. Departure also had to occur after mid-June.

Below are two example graphs showing how these phenological parameters were identified (arrival = 1, incubation start = 2, incubation end = 3, departure = 4). Although geolocators were changed during the breeding season (e.g. in May/June) we plotted graphs to show a single calendar year. This meant that in years where the geolocator was changed, data from the first deployment is shown in red and data from the second deployment is shown in blue.

Incubation end was not included in the analysis in this chapter, as we were unable to extract enough incubation end dates for the models to be valid (see Table 5.7.2). This is because geolocators were often deployed/retrieved around the end of the incubation period/start of chick rearing, and so data was often missing for this period.

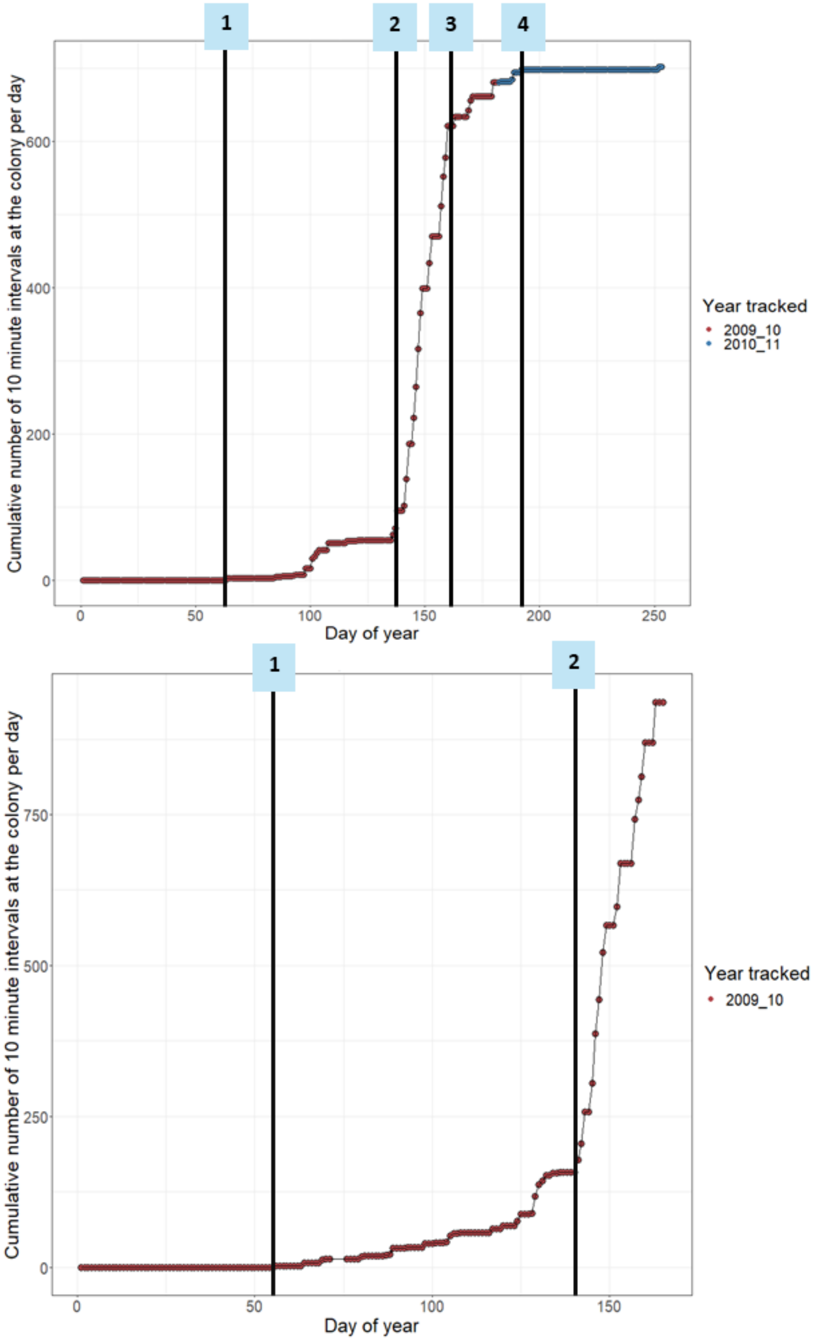

Figure 5.3: Identification of different phenological parameters from geolocator data. 1 = Arrival, 2 = Incubation start, 3 = Incubation end, 4 = Departure.

5.7.2 Appendix: Number of repeat years of data

Table 5.3: Number of individuals that contributed between one and nine years of data to the study. For example, 607 birds had arrival measured in one year, whereas three individuals had arrival measured for 9 years.

Number of years	**Number of individuals in each year of the study from which each phenological parameter was measured**			
	Arrival	**Incubation start**	**Incubation end**	**Departure**
1	607	503	240	592
2	299	182	40	304
3	155	74	11	143
4	70	30	2	68
5	43	11	1	29
6	20	1	NA	15
7	10	2	NA	8
8	4	NA	NA	2
9	3	NA	NA	4
Total	**1211**	**803**	**294**	**1165**

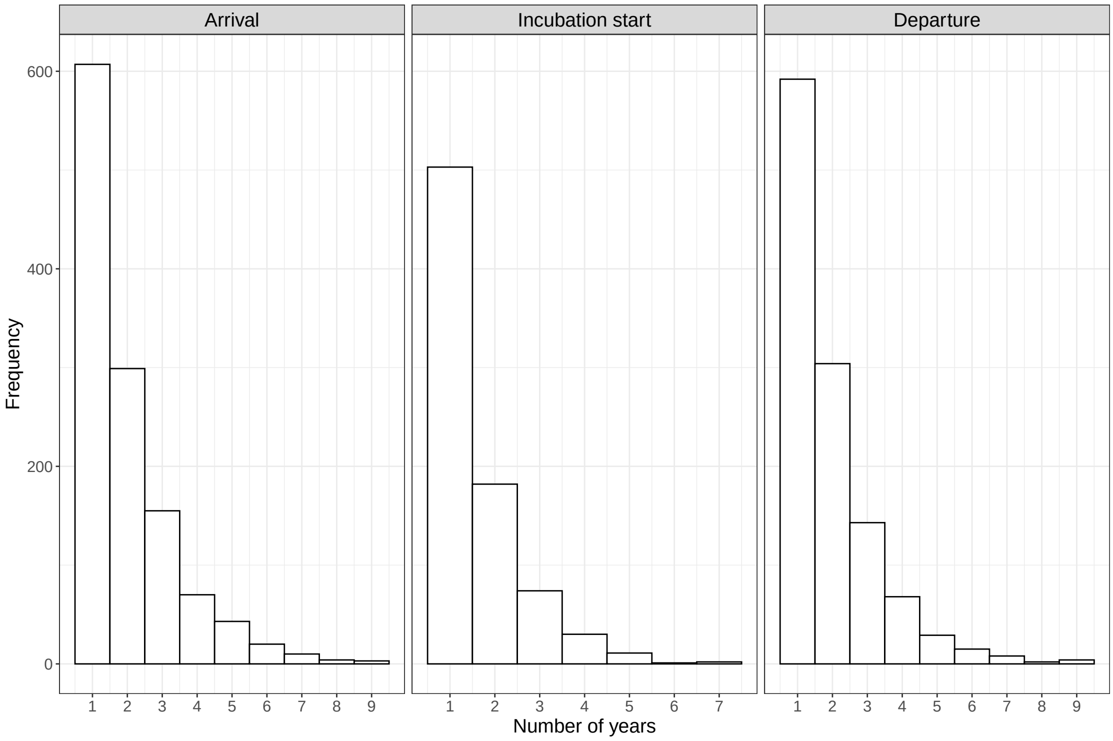

Figure 5.4: Number of individuals (frequency) that contributed between one and nine years of data to the study.

5.7.3 Appendix: Comparison of phenological parameters with cited literature

Table 5.4: Comparison of phenology measured in our study using geolocator data with observational data from previous studies. We obtained median and/or mean lay and/or hatch dates for five colonies (Anda, Hornøya, Isle of May, Kongsfjorden, and Røst) from Keogan et al., 2022. These averages were themselves calculated from observational data at each of the colonies. We used the groupwiseMedian and groupwiseMean functions in R to estimate the 95% confidence intervals of these median and mean lay and hatch dates and compared the results with bootstrapped median or mean estimates (Normal, R = 10 000) from our geolocator data processing. We also obtained estimates of mean arrival and departure dates (including the standard deviation) for Kongsfjorden from Léandri-Breton et al., 2021. These averages were based on geolocator processing and compared with bootstrapped mean estimates (Normal, R = 10 000) from our own geolocator data processing.

Colony	**Trait**	**Value & bootstrap 95% CI of GLS estimate**	**Sample size for GLS estimate**	**Value & bootstrap 95% CI or SD of literature estimate**	**Literature source**
Anda	Mean hatch date	174.5 (171.0, 177.8)	42	174.6 (171.5, 177.8)	Keogan et al. 2022
Hornøya	Mean hatch date	170.4 (163.5, 177.3)	8	170.7 (166.1, 175.3)	
Isle of May	Median lay date	145.1 (141.1, 149.2)	63	145.0 (141.2, 150.0)	
Kongsfjorden	Median hatch date	189.8 (182.8, 194.6)	45	190.0 (188.4, 190.7)	
Røst	Mean lay date	139.3 (137.0, 141.5)	109	133.7 (129.4, 138.0)	
Kongsfjorden	Mean arrival	101.1 (99.0, 103.2)	302	105 ± 5	Léandri-Breton et al. 2021
Kongsfjorden	Mean departure	245.8 (241.9, 249.8)	265	248 ± 9	

5.7.4 Appendix: Average phenology calculated for each colony

Table 5.5: Average arrival, incubation start, and departure date calculated for each colony in our study. SD = standard deviation and n = sample size.

Colony	Arrival			Incubation start			Departure		
	Mean	SD	n	Mean	SD	n	Mean	SD	n
Alkefjellet	89.9	39.2	109	171.9	13.6	56	231.0	24.5	86
Anda	84.9	30.9	186	148.2	15.3	133	227.7	23.2	177
Bjørnøya	83.7	24.5	120	156.7	17.6	75	230.0	32.1	95
Bulbjerg	96.4	24.2	14	128.6	10.5	4	226.4	35.8	12
Cape Krutik	86.4	11.4	131	144.9	14.3	91	224.0	25.7	138
Faroe Islands	81.0	25.6	157	143.8	6.8	70	221.1	26.0	157
Franz Josef Land	93.1	22.7	108	171.1	7.4	71	214.5	7.4	92
Hælavikurbjarg	135.2	60.6	5	NA	NA	NA	272.6	29.6	4
Hafnarholmi	64.0	26.4	14	141.7	3.4	11	254.8	37.1	18
Halten	71.4	35.2	8	136.7	8.8	4	284.3	18.3	10
Hjelmsøya	95.3	9.2	7	129.4	14.7	4	260.5	43.8	11
Hornøya	80.7	21.0	115	144.7	14.9	42	222.3	28.7	113
Isfjorden	103.4	29.0	183	161.9	14.6	97	241.3	35.7	129
Isle of Canna	81.7	25.9	70	141.7	10.6	29	218.6	24.0	53
Isle of May	95.5	30.6	147	145.4	14.4	63	221.9	29.6	134
Kara Gate	90.4	21.8	59	171.7	9.9	29	223.0	18.2	58
Kippaku	100.3	32.8	41	154.8	4.4	20	253.1	19.0	39
Kongsfjorden	101.1	18.8	302	158.2	14.6	151	245.8	33.2	265
Langanes	80.8	28.9	69	147.9	9.6	37	218.2	21.3	75
Latrabjarg	87.1	21.9	4	150.0	1.1	4	272.0	14.2	5
Nuuk	136.5	17.6	9	NA	NA	NA	252.8	10.5	14
Rathlin	96.9	14.1	4	NA	NA	NA	231.9	19.4	5
Reykjanes	NA	NA	NA	NA	NA	NA	240.9	NA	1
Ritenbenk	113.1	21.8	12	154.6	2.5	11	254.5	19.8	12
Rockabill	98.0	23.4	7	148.6	0.9	4	250.7	4.3	7
Røst	86.6	29.0	232	139.3	12.1	109	235.6	32.6	247
Runde and Ålesund	90.7	30.0	89	139.7	9.0	59	236.2	49.0	71
Russkaya Gavan	102.0	12.1	36	174.2	14.6	24	248.1	22.2	36
Sermilinnguaq	96.2	25.0	18	146.7	7.2	17	254.6	23.6	17
Skjalfandi	69.9	32.1	14	150.2	6.9	7	211.8	6.6	18
Sør-Gjæslingan	83.5	25.4	136	146.0	11.9	60	222.2	25.8	136
Witless Bay	103.8	31.4	8	157.1	4.2	2	242.3	10.8	9

5.7.5 Appendix: Kittiwake maximum foraging distance

Table 5.6: Maximum foraging distance reported for Black-legged Kittiwake in peer-reviewed studies. Foraging distance is either maximum foraging distance (maximum out of all individuals in the study) or average maximum foraging distance (average of the maximum foraging distance for each individual). Using these data, the median maximum foraging distance is 37 km. Thaxter et al. 2012 is a review paper and therefore was not conducted in a specific location or specific year(s).

Study	Tracking period	Foraging distance (km)	Location	Years
Thaxter et al. 2012	Incubation & chick rearing	120	NA	NA
Schlener et al. 2024	Incubation	59.5	Middleton Island, Alaska	2012-2020
	Chick rearing	50.6		2012-2020
Robertson et al. 2014	Incubation	50.95	Coquet Island, England	2012
	Chick rearing	9.03		2012
		28.02		2011
Redfern & Bevan 2014	Chick rearing	35.6	Brownsman, Farne Islands, England	2010-2012
	Chick rearing	56	Tyne Bridge, England	2010-2012
Ponchon et al. 2017	End of incubation to chick rearing	28.6	Boulogne-sur-Mer, France	2014
	End of incubation to chick rearing	36.7	Fécamp, France	2014
	End of incubation to chick rearing	31	Saint-Pierre-du-Mont, France	2014
Kotzerka et al. 2010	Incubation & chick rearing	59	Middleton Island, Alaska	2007
Irons 1998	Chick rearing	40	Shoup Bay, Prince William Sound, Alaska	1989
Daunt et al. 2002	Chick rearing	73	Isle of May, Scotland	1999
Cleasby et al. 2024	Incubation & chick-rearing	67	United Kingdom	2010-2015
		303.7	Sør-Gjæslingan, Norway (foraging in oceanic waters)	2011-2014

Table 5.6 continued from previous page

Study	Tracking period	Foraging distance (km)	Location	Years
Christensen-Dalsgaard et al. 2017	Chick rearing	27.66	Sør-Gjæslingan, Norway (foraging in coastal waters)	2011-2014
		63.5	Anda, Norway	2011-2014
		36.7	Anda, Norway	2011-2014
Chivers et al. 2012	Chick rearing	22.9	Rathlin Island, Northern Ireland	2009
		42.4		2010
		17.3	Lambay Island, Republic of Ireland	2009
		20.3		2010
Ainley et al. 2003	Chick rearing	41.7	Shoup Bay, Alaska	1995
		44.4		1997
		43.9		1998
		31.5		1999
		5.5	Eleanor Bay, Alaska	1995
		19.8		1996
		35.4		1997
		15.7		1998
		29.3		1999
		33.3	N. Icy Bay, Alaska	1996
		24.1		1997

5.7.6 Appendix: Linear-mixed effects models investigating changes in SST across the study period, and population-level changes in phenology in response to SST

Table 5.7: Results for linear mixed effects models investigating changes in SST during the breeding season (between arrival and departure) across the study period, and population-level changes in phenology in response to SST. The fixed effect of SST was left-centered and the fixed effect of year was mean centred and variance standardised. The 95% credible intervals were estimated using bootstrapping and the chi-squared and p-values were estimated from likelihood ratio tests on full and null models for each term. Significant predictors are highlighted in bold.

Response		Coefficient	Estimate	95% CI	Chi-squared	p-value
Breeding season SST	Fixed effects	Intercept	-5.25	-10.09, -0.1	-	-
		Year	0.0059	0.0034, 0.0082	23.38	**<0.0001**
	Random effects	Colony	15.22	15.11, 15.33	-	-
		Residual	0.24	0.23, 0.24	-	-
Arrival	Fixed effects	Intercept	104.10	88.11, 119.86	-	-
		SST	-1.54	-2.41, -0.72	11.51	**<0.001**
		Year	-12.5	-22.73, -2.53	4.93	**<0.05**
	Random intercepts	Individual ID	29.51	26.70, 32.30	-	-
		Colony	54.95	30.82, 84.64	-	-
		Year	605.06	468.04, 825.5	-	-
		Residual	498.87	471.21, 527.99	-	-
Incubation start	Fixed effects	Intercept	164.89	158.8, 170.7	-	-
		SST	-2.36	-3.01, -1.71	21.05	**<0.0001**
		Year	0.2	-3.45, 3.86	0.019	0.89
	Random intercepts	Individual ID	1.87	1.65, 2.12	-	-
		Colony	57.44	33.85, 87.73	-	-
		Year	54.98	33.22, 89.42	-	-
		Residual	138.24	127.17, 149.78	-	-
	Fixed effects	Intercept	239.16	222.66, 256.85	-	-
		SST	-0.59	-1.3, 0.11	2.76	0.096
		Year	-8.48	-20.33, 3.49	2.089	0.15
		Individual ID	35.08	31.93, 38.39	-	-

Table 5.7 continued from previous page

Departure	Random intercepts	Colony	145.07	85.3, 216.84	-	-
		Year	661.36	566.89, 895.93	-	-
		Residual	276.00	259.84, 292.61	-	-

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6
Discussion

Contents

"This ain't a love song, this is goodbye"

– Scouting for Girls, *This Ain't a Love Song*

The aim of this thesis was to develop the use of remote technologies to increase the scope of seabird monitoring and research and demonstrate their utility by investigating how anthropogenic climate change is affecting kittiwake phenology and breeding success. Thus, the findings of this thesis are really a story of two parts:

i) Development of large-scale remote technologies for seabird monitoring and research

Throughout this thesis, I explored how drones, time-lapse cameras, and light level geolocators could be used to collect data on seabird abundance (Chapter 2), phenology (Chapters 3 and 5), and breeding success (Chapter 4) at large geographic scales. A common theme of these technologies was the ability to collect data comparatively cheaply and easily at sites that were previously difficult, or even impossible, to regularly monitor. Nevertheless, the propensity to collect increasing amounts of data can present additional challenges associated with storing and processing such data. This could provide a notable barrier to progress for small research teams. This led to discussions in Chapters 2, 3, and 4, about possible solutions, and the relative advantages and disadvantages of citizen science compared with machine learning. As ecology increasingly becomes a big data field, it is of paramount importance that we develop appropriate techniques to deal with the ever-increasing volume of data.

ii) Application of remote technologies for investigating changes in kittiwake phenology and breeding success in response to anthropogenic climate change

The second aim of this thesis was to apply the remote technologies and methods developed to answer ecological questions, primarily investigating the impact of anthropogenic climate change on seabird phenology and breeding success. In Chapter 2, I discussed how drone technology could be used to monitor seabirds, with a focus on counting colony-nesting seabirds due to the lack of published studies on cliff-nesting species. This contrasted with the remaining chapters, which focused on a well-studied cliff-nesting seabird, the Black-legged Kittiwake. Previous research has examined changes in kittiwake laying and hatching dates at the population level, however I utilised time-lapse cameras and light level geolocators to examine arrival and departure dates (Chapters 3 and 5), which fieldworkers are not normally present to observe. I further explored how individuals are adjusting their phenology in response to climate change to provide insight into the mechanisms underpinning population change (Chapter 5). Both Chapters 4 and 5 have implications for kittiwake breeding success, with Chapter 4 focusing on the direct effects of weather – a topic notably understudied - and Chapter 5 looking at the indirect effects of SST on breeding timing. This could potentially lead to trophic mismatch which might have adverse effects on chick growth and survival. Overall, the results of this thesis highlight the ability of new and remote technologies to allow us to look at seabird ecology and behaviour across large geographic scales, and to answer questions at the level of the individual as well as the population. Below, I synthesise the key findings and implications of the research presented in this thesis and suggest future directions for research.

6.1 Key findings and future directions

6.1.1 1) Large-scale remote technologies for seabird monitoring and research

In the face of a biodiversity crisis, effective monitoring is essential if we are to understand population trends and their drivers, and to recommend appropriate conservation action. Identifying changes in demographics (such as decreases in adult survival, juvenile recruitment, or breeding success) could act as early warning signals of future population decline, given that changes at the population level can take a long-time to become apparent. Localised seabird monitoring programmes have achieved this at regional scales, allowing assessment of changing population abundance (e.g. Kissling et al., 2007), phenology (e.g. Frederiksen et al., 2004a; Moe et al., 2009), and demographics (e.g. Emmerson and Southwell, 2022), which has in turn lead to conservation policy and action. For example, a sandeel fishery off SE Scotland was closed in 2000 in response to research showing the fishery was having deleterious effects on seabird breeding performance at nearby colonies, such as the Isle of May (Frederiksen et al., 2004b; Daunt et al., 2008).

However, extrapolation of small-scale studies to wider regions, or even to species-level, may lead to incorrect assumptions and skewed perspectives, as population trends can vary markedly across a species' range. For example, within the UK there is substantial regional variation in kittiwake breeding success (Harris & Wanless, 1990; Frederiksen et al., 2005). Furthermore, variation can exist within even smaller geographic areas, for instance due to edge effects. Neighbouring areas of a seabird colony can have variable nest predation rates and thus breeding success (Tenaza, 1971; Jackson et al., 2005). Likewise, behaviour can vary across a species' range, but stand-alone studies on a small number of individuals could misinterpret a localised behaviour as a species-wide trait. Failure to understand such variation could lead to erroneous conclusions and skewed interpretations of population metrics and behaviours – with potential conservation implications - highlighting the importance of studies of greater geographic breadth.

The use of remote technologies has the potential to expand the scale of seabird monitoring, and this thesis has highlighted how drones, time-lapse cameras, and light level geolocators can do so, by examining trends in kittiwake breeding success and phenology across large parts of the species' breeding range. The UK has often been viewed as a shining example of seabird monitoring, having one of the oldest formalised seabird monitoring programmes (Tasker, 2000), yet it is really quite data poor. Yearly and standardised data collection on species' abundance, breeding success, phenology, adult survival, and diet are only collected at four key sites, despite the UK being home to over 10 000 seabird colonies (Burnell et al., 2023). Incorporating new and developing technologies into seabird monitoring could help expand the number of colonies monitored, by reducing the cost (both time and money) required per colony. However, for these technologies to be formally incorporated into seabird monitoring programmes such that their use becomes standard practice, will require us to think carefully about a) data collection, b) data storage and sharing, and c) data processing. Below, I discuss these key considerations and provide recommendations to facilitate the incorporation of remote technologies into seabird monitoring and research.

a) Data collection

Fieldworker involvement

To begin, new technologies require that people know how to use them. Many seabird monitoring programmes rely on trained volunteers to collect data alongside a small number of professional fieldworkers and researchers (Burnell et al., 2023). A sudden push for the use of new technologies could have the unintended consequence of making fieldworkers feel like their skills are no longer needed and that they are being replaced by technology. It is therefore important that we take time and care to ensure fieldworkers do not feel disenfranchised. There is still an important place for traditional field methods amidst the technological revolution (Strouk, 2023), and indeed new technology will in many cases depend on fieldworkers being trained to use it.

It is essential that current methodologies are not replaced in haste, as this could introduce unknown biases into long-term studies (Edney & Wood, 2021). For example, if more birds were identified from drone-derived imagery than during traditional field counts at a colony, then switching to the use of drones only could lead to an erroneous increase in estimated population size due to a change in technology rather than a true population increase (Hodgson et al., 2018; Rodway et al., 2024). It is therefore important that at locations considering replacing traditional methods with new technologies (for example, due to funding reasons), that traditional and new methods are run in parallel to understand potential biases in both. This could allow conversion factors to be generated so that estimates from traditional methods can be compared with estimates from new technologies, and vice versa (Rodway et al., 2024). The time period for which studies should run concurrently before traditional methods are phased out is, however, unclear and at a minimum should occur for several years so they capture sufficient variation in the system (Edney & Wood, 2021). Importantly, deciding to replace traditional methods is something that must not be rushed. In most cases, new technologies would be better used to expand existing monitoring and target knowledge gaps, rather than replacing pre-existing monitoring that is working well.

Of course, if we are to expand the geographic scale of monitoring, then fieldworkers will remain essential to this task. Providing opportunities for volunteers and professionals alike to learn how to use and facilitate the use of new technologies for seabird monitoring will ensure their experience is not lost. Below, I discuss some specific insights on doing so with regards to drones and time-lapse cameras.

Case study: drones

The best practice guidelines developed in Chapter 2 will hopefully be a useful starting point for those planning to use drones for seabird monitoring and research, and more documents like this will likely be needed for other forms of technology as it develops.

Nevertheless, using drones as a case study demonstrates the possible challenges and ethical considerations of attempting to roll out new technologies and make them widely available for use in seabird monitoring and research. This is because new technologies are often poorly regulated such that those with limited practical experience or knowledge of the study species could legally use the technology (Weston et al., 2020). Currently in the UK, pilots must obtain their A2 Certificate of Competency (A2 CofC) to be able to fly drones < 2 km in open areas (> 50 m from people), which would be sufficient for flying at remote seabird colonies (provided they had landowner permission to conduct the flights). However, the A2 CofC exam is a multiple-choice test that focuses on regulations to ensure safety to people and other aircraft, not wildlife, and does not involve any form of practical flight assessment. It is therefore unsurprising that many regulators and reserve managers are worried about the use of drones for surveying seabirds at their reserves, given there is no current system for ensuring that pilots know how to safely fly around seabird colonies, where a crowded airspace, difficult topography, and risk of disturbing sensitive breeding species makes this task especially difficult (Shamoun-Baranes et al., 2017; Dias et al., 2019; Sorrell et al., 2023).

Recently, several organisations in the UK (led by Oxford Brookes University and Natural England, and including Nature Scot, Natural Resources Wales, and the British Trust for Ornithology) have formed a 'Drones and Wildlife Group'. The aim of this group is to try and develop a suitable seabird-drone training course that could become socially recognised in the UK seabird community as a must have before pilots are allowed to survey seabirds with drones. Although this might be perceived as creating an additional barrier for fieldworkers learning new technologies, it would help ensure all pilots meet a minimum standard, reduce the risk of undue disturbance to wildlife, and help pilots feel more confident in their job.

Case study: time-lapse cameras

Compared to drone technology, data collection using time-lapse cameras is less likely to cause disturbance or pose a risk to wildlife. The time-lapse camera network used in Chapters 3 and 4 rely on researchers and volunteers to help maintain them, again highlighting the importance of training fieldworkers in the use of new data collection techniques. However, it is important not to underestimate the time and effort required to maintain remote technologies, especially if they are still in the development phase and may require iterative rounds of testing and updating.

As part of my fieldwork, I had access to 11 camera systems developed by the company Time-lapse Systems (part of Hideaway Media Ltd) for deployment in Scotland (Fig. 1.2). For four of these cameras a data package was purchased (renewal due annually) which allowed them to connect to the 4G network and upload images to an online platform, such that new data was available daily. The remaining seven cameras were non-networked and required the images to be downloaded from a USB stick when visiting the camera. Although we successfully deployed five cameras in total, several technological and logistical issues prevented the remaining cameras from being installed. Notably, software issues during the 2023 field season led to all cameras being returned to the company for trouble shooting and updates, thus preventing additional cameras being deployed.

Furthermore, installing the camera systems was quite complicated, including both the assembly of the scaffolding structure that the cameras were attached to, and setting the cameras up to take in-focus images at the correct time intervals. This made it difficult to train local people, such as reserve wardens, how to install and maintain the camera systems. It also raised questions about whether it was even fair to ask reserve wardens to maintain the cameras, given they already have full-time jobs. Of course, training local people would have made it easier to install more cameras and address technical faults, as regularly travelling from Oxford to Scotland was not practical. Based on these experiences, it seems clear that the following two points must be considered when developing new monitoring systems:

1) Has the equipment been properly tested?

Thoroughly testing each piece of equipment before taking it into the field can easily be overlooked, especially when companies have previously demonstrated that the technology works. Setting the equipment running in a back garden or office for several weeks, or indeed months, ahead of deployment can allow any issues to be identified and fixed before fieldwork commences.

2) Are there suitable trained (and ideally local) personnel, who are responsible for maintaining the technology, and have the time and money to do so?

Local reserve wardens should be invited to help with set-up and maintenance, as their investment in the research will help ensure the project runs smoothy, and long-term will hopefully assist with their monitoring work. However, we should not rely on local reserve wardens for assistance, given they often already have busy work schedules. Employing a dedicated field technician responsible for maintaining the camera network would ensure its continued success and should be seriously considered before embarking on future ambitious monitoring projects. However, employing a full-time technician requires sufficient funding; an issue that is often challenging to overcome when developing new technologies for wildlife conservation.

Time and money

New technologies may reduce survey time and cost long-term, but often require a large upfront cost to purchase or develop the equipment, making them initially more expensive than traditional methods (Albores-Barajas et al., 2018). This might be prohibitively expensive for small research programmes or in developing countries. Given the limited funding available for conservation, the introduction of new technologies in seabird monitoring programmes will likely need to be carefully planned and budgeted (Martin et al. 2018). Power analyses could be used to identify monitoring gaps, so that resources can be allocated to these priority areas and species (Anker-Nilssen et al., 1996; Hatch, 2003).

b) Data storage and sharing

The large-scale deployment of remote technologies also requires that there are appropriate data storage and processing pipelines in place to deal with the large volumes of data being collected. Big science fields, such as physics, astronomy, and genomics, already have standard data practices, as researchers collaborate extensively to use expensive instruments (Borgman et al., 2007; Cragin et al., 2010; McCray, 2014). For example, the Copernicus data platform provides free and open access Earth observation data from satellites, which I was able to use in Chapters 4 and 5 (https://dataspace.copernicus.eu/). However, data sharing in small science fields that often collect data through fieldwork is not common, and indeed these fields typically lack the tools and infrastructure to manage the growing deluge of data generated by new forms of instrumentation (Cragin et al., 2010; Hampton et al., 2013). While there is increasing encouragement within the scientific community for open-access publications, datasets, and code (and increasing numbers of publishers now require that data and code are made available alongside articles; Whitlock, 2011), there is still some reluctance from ecologists in general (Borgman et al., 2007; Hampton et al., 2013). This is perhaps due to concerns of data ownership, ethics, and accountability, and on the whole, researchers are less likely to share their data the more handcrafted the data collection and the more laborious the post-processing for interpretation (Borgman et al., 2007; Borgman, 2012).

Gray, 2007 described the data iceberg, which is the idea that most data remains out of view (unpublished or unarchived) with only the tip of the iceberg represented as a formal publication. This vast pool of inaccessible data has also been referred to as dark data (Hampton et al., 2013). Given that data collection is often expensive and time-consuming, particularly for ecologists working in remote locations or where specialist field equipment is needed, we should be encouraging data sharing. This will allow limited resources to be directed to research priorities and not spent gathering data that has already been collected by someone else. There is therefore a pressing need for the development and expansion of data-sharing platforms and a culture shift towards data sharing becoming the norm (Faniel & Zimmerman, 2011; Farley et al., 2018). This would facilitate accelerated rates of scientific discovery, and in the context of conservation, perhaps accelerated policy-implementation and conservation action (Jones, 2019).

c) Data processing

Alongside increased data sharing is the need for increased sharing of data processing techniques. As ecology becomes a big data field, we need reproducible data pipelines, and ideally integrated data storage and processing frameworks that researchers can use to analyse this data. Increased collaboration with big science fields, such as physics and computer science that have long used big data approaches like machine learning, will be essential.

For many tasks, researchers are increasingly looking to automated machine learning methods to drastically reduce data processing times. Relying on manual processing puts many remote technologies at risk of moving work from the field to the desk and increasing processing times compared to traditional methods. For example, manual image analysis is time-consuming, and can lead to substantial delays between data collection and results (e.g. abundance estimates) compared to field observations (e.g. where birds are counted in real time).

To date, machine learning has commonly been used in seabird research to identify and count seabirds in images and sometimes videos (e.g. Hayes et al., 2021; Kellenberger et al., 2021; Le et al., 2022; Cusick et al., 2024). Previously, large volumes of annotated images were required to train Convolutional Neural Networks (CNN) to identify the object(s) of interest (e.g. Jones et al., 2020), however this number is reducing and increasingly general bird detectors are being developed (Montserrat et al., 2017; Kellenberger et al., 2021). Many of these tools are becoming more off the shelf, with code and tutorials made publicly available to help those without extensive machine learning experience use them (Weinstein et al., 2022). Nevertheless, understanding how these algorithms work and being able to edit the code (for example to re-train an algorithm on additional data) is rarely easy, making many of these tools somewhat of a black-box to the average ecologist (Lucas, 2020; Borowiec et al., 2022; Pichler & Hartig, 2023).

Furthermore, some of these algorithms only identify ‘bird’ and do not differentiate between species or age classes of bird (Weinstein et al., 2022). Evidently, this can severely limit the utilisation of such algorithms for seabird monitoring, especially cliff-nesting seabirds where many species nest in close-proximity and so images are unlikely to contain a single species of seabird. Additionally, very few studies have attempted to identify seabird chicks, which limits their use for measuring breeding success. This could be because most seabird chicks are brooded by a parent when they first hatch, and so are difficult to spot. As well, chick appearance can change substantially as the bird develops, which might make it hard to recognise chicks at different stages of development as being from the same species (Edney et al., 2025).

The YOLOv5 deep learning algorithm is a notable exception, and has been used to identify Common Guillemot *Uria algae* adults, chicks, and eggs (Hentati-Sundberg et al., 2023). The recall (also termed sensitivity) for eggs was deemed too low ($R < 0.7$) to analyse the egg data further, due to too many eggs being missed as they were hidden under incubating parents. Nonetheless, the adult and chick data had precision and recall > 0.7 and could therefore be analysed. This led to a particularly novel approach, where the size of the bounding box that identified each bird could be used to monitor chick growth, as the bounding box should increase in size as the chick grows.

Crowd-sourcing presents an alternative solution to machine learning for reducing data processing time and might be more cost-effective for small scale studies that are not collecting new data every year. Platforms such as Amazon Mechanical Turk pay users to complete tasks (Mason & Suri, 2012), or citizen science platforms, like the Zooniverse, engage volunteers for free (Simpson et al., 2014).

Seabird Watch

The Seabird Watch citizen science project enabled 799 917 images to be processed from 19th October 2017 to 19th October 2023 (Chapter 3) and allowed investigation into the timing of seabird breeding and chick survival (Chapters 3 and 4). However, the time and effort required to maintain an active citizen science project should not be underestimated. In Chapter 3, I reported that the median number of images classified by each volunteer was 5 (IQR 2-12), with 81% of volunteers only participating in the project for a single day. This showed that the project predominantly relies on continued volunteer recruitment rather than retention to classify new images, as very few volunteers classify more than one image. This makes it difficult to improve the sensitivity and precision of chick identification, which I found to be lower than expected (< 80% sensitivity and < 70% precision) in Chapter 4, as volunteers do not have the opportunity to learn how to spot chicks and therefore get better at accurately identifying them. Although the Volunteer Threshold Algorithm was able to accurately measure breeding success despite low sensitivity and precision values (Chapter 4), these low values would make it difficult to use the raw data to train machine learning algorithms to accurately identify chicks. It is therefore evident that the Seabird Watch project needs to focus on developing ways to improve both volunteer accuracy and volunteer retention, as the two are likely closely linked.

1) Crop images so that volunteers are shown a single nest at a time

Cropping images could be particularly important for images containing a large number of nests (> 30), where volunteers might be liable to lose interest part way through, and therefore spend less time carefully examining nest contents. Showing volunteers a single nest at a time would hopefully encourage thorough inspection of each nest and lead to more chicks being spotted.

2) Provide more training material which specifically focuses on chick identification

Like all Zooniverse projects, Seabird Watch has a tutorial that new users must view to show them how to complete the required task. It also has a field guide which provides further information on species identification and distinguishing between adults and chicks. More detailed information on how to identify chicks could be included in the tutorial, however this must be balanced against making the tutorial so long that new users become bored and decide not to participate in the project. The optimal solution might therefore be to increase the training in the field guide, and state in the tutorial that it is highly recommended for new users to read this information before starting the task.

3) Include a volunteer testing phase - only allow volunteers that correctly classify a certain percentage (e.g. 90%) of images to proceed with classifying images from rest of the dataset

Incorporating a testing phase into the workflow would arguably be the most effective method for filtering out inaccurate volunteers and retaining those who are good at classifying kittiwake chicks. However, the current architecture of the Zooniverse makes it difficult to see how a testing phase could be easily incorporated into the project, without researchers needing to manually validate every single volunteer classification made in the testing phase. Furthermore, a testing phase might reduce the likelihood of some volunteers continuing with the project, although with improved outreach and public engagement this could hopefully be mitigated.

4) Increase communication with volunteers so they remain excited about the project and continue to feel that they are valued members of the project

At present, project updates are posted on the ‘Results’ and ‘Talk’ pages on the Seabird Watch project, but it is unclear how many volunteers regularly look at these pages. Sending regular email updates to volunteers might be a more effective method of communication, and including personal feedback (e.g. the number of images they classified that month, certificates for reaching certain milestones) via system-generated but editable emails might help keep volunteers onboard (Pecl et al., 2019; Spiers et al., 2019).

Overall, as technology continues to advance and ecologists become increasingly computer literate, it seems evident that machine learning will become the primary method of image processing. However, certain images might remain more suitable for analysis by citizen scientists, such as those partially obscured (e.g. by snow; Jones et al., 2020). Furthermore, there are many ways in which citizen science and machine learning can complement each other. For example, citizen science datasets can be used to train machine learning algorithms (Jones et al., 2020). Table 6.1 provides a comparison of citizen science and machine learning image analysis at present, highlighting the advantages and disadvantages of each method.

Table 6.1: Comparison between citizen science and machine learning image analysis

Citizen science	Machine learning
Engages members of the public in science and can help raise awareness of conservation issues.	Minimal public engagement opportunities.
Can be used as training data for machine learning.	May require a large amount of manually annotated data to train the algorithm.
Developing pipelines to process citizen science data should be less timing consuming than developing machine learning algorithms. However, understanding the error structure of citizen science datasets can take time and building algorithms that account for these inaccuracies can be difficult.	Can be time-consuming to develop machine learning algorithms that work well and provide sufficient accuracy, even for experienced programmers.
It can take a long time for citizen scientists to complete tasks, and this can be unpredictable as it depends on the number of active volunteers participating in the project. Consequently, there can often be large lags between data collection and results (e.g. upwards of one year).	Once the algorithm has been developed, data can be run through it at regular intervals. This means there can be a short time between data collection and results (e.g. weeks).
Less computing power required to process citizen science data. Can typically be processed on a normal laptop.	Large amount of computing power required to train and run machine learning algorithms. Typically requires access to a high-performance computing (e.g. supercomputers or clusters).
Volunteers might get bored if the task takes too long and stop participating in the project altogether. Citizen science therefore requires continued engagement and discussion with volunteers to maintain their interest and to recruit new volunteers where needed.	Once the algorithm is built it should run with minimal input or updates. Additional training may be required on new datasets if they significantly differ from the original training dataset.

Table 6.1 continued from previous page

Volunteers are likely to be less accurate at the task compared to researchers (i.e. produce less accurate results).	Machine learning algorithms may also be less accurate at the task compared to researchers. However, the error structure of machine learning outputs is likely to be more predictable than that produced by citizen scientists, who can sometimes differ in their answers in unpredictable ways.

6.1.2 2) Application of remote technologies for investigating changes in kittiwake phenology and breeding success in response to anthropogenic climate change

Direct weather effects

To date, most studies have focused on the indirect effects of rising SST on seabird phenology and breeding success, however, future climate scenarios also predict increased weather variability and increased frequency and severity of weather extremes (Rahmstorf & Coumou, 2011; Arias et al., 2021). Understanding the impact of direct weather effects on seabirds is therefore important too, to properly understand how anthropogenic climate change is affecting seabird population dynamics.

In Chapter 4, I found that only precipitation negatively affected kittiwake chick survival, with sun exposure and storminess having no measurable effect. This was surprising, because anecdotally researchers often point to heat waves and stormy weather as having severe adverse consequences on seabird breeding success, due to chicks overheating or nests/nest contents being dislodged by high winds or waves (e.g. Newman et al., 2021; Brown and Eagle, 2022). While these events do happen and might be important at single colonies (Newell et al., 2015; Olin et al., 2023) they are perhaps sufficiently rare or only result in the loss of a small numbers of chicks, to not have a measurable impact on kittiwake chick survival across multiple colonies and years.

The lack of evidence for local weather effects (aside from precipitation) might therefore suggest that the indirect effects of warming are perhaps more important drivers of kittiwake decline than direct weather effects at present. That being said, our study did not look at the interactions of direct weather with other variables, such as foraging success, which could be a more important mechanism by which weather is impacting kittiwake chick survival.

Storms can indirectly increase chick mortality by reducing adult foraging success (Christensen-Dalsgaard et al., 2018). This may be particularly challenging for surface feeders, like kittiwakes, where increased water turbidity and disruption to water stratification and prey aggregations (a washing-machine effect), could negatively affect foraging efficiency (Clairbaux et al., 2021). These interactive effects between weather conditions and food availability are, however, harder to study. For example, poorly fed chicks may be more susceptible to periods of high precipitation, which would increase energy expenditure needed to maintain their body temperature (Chapman et al., 2011).

However, determining chick diet and its energy content is often invasive and time-consuming (Gaglio et al., 2017). Species that hold prey in their bills can be easier to study through photography (Owen et al., 2024), and DNA metabarcoding of faeces can also provide insight into diet composition with minimal disturbance (de Leeuw et al., 2024). For future studies, quantifying food availability combined with local weather conditions could improve our understanding of how a changing climate might impact seabird chick survival and population dynamics long-term.

Indirect effects of SST

The indirect effects of increased SST on kittiwake phenology and breeding success are much better understood at the population level, with there being a general consensus that changes in prey availability linked to ocean warming are negatively affecting reproductive success (Lewis et al., 2001; Frederiksen et al., 2005; Shultz et al., 2009). Nevertheless, very few studies have been able to examine changes in seabird behaviour at the level of the individual, and thus understand the mechanisms underpinning population change (i.e. within-individual plasticity or between-individual differences). This is because of difficulties associated with collecting repeat individual data on wild seabirds.

The Common Tern *Sterna Hirundo* colony on the Banter See is a notable exception, where pedigrees of more than 1000 individuals have been collected over the past 30 years (Moiron et al., 2022, 2024). This study system provided inspiration for Chapter 5. Using a large geolocator dataset, I was able to show that while kittiwakes can vary some aspects of their migratory phenology plastically, they are less capable of varying their breeding phenology. I recommend that other long-term seabird studies with repeat data on known individuals likewise look at life-history studies for inspiration and consider whether they too can explore the mechanisms underpinning population change. This will allow us to determine not only how animal behaviour is changing, but also why; a key component in predicting responses to climate change going forward.

I further recommend that longitudinal seabird studies measure and record the age of individual birds, as known age birds are required to determine whether a turnover effect is due to selective (dis)appearance based on phenotype or generational shifts (i.e. new recruits entering the population with a new phenotype based on early life learning) (Moiron & Bouwhuis, 2024; Wynn et al., 2025). In Chapter 5, I found evidence for between-individual differences in incubation start date, but I was unable to conclude whether this was due to selective disappearance or early life learning, as most of the birds in the study were of unknown age. Advancements in molecular methods will make it increasingly easier to determine individual age, and I therefore encourage longitudinal studies to take blood samples (with appropriate permission and licenses) so individuals can be aged for future research (Roman et al., 2024).

6.2 Conclusion

In conclusion, the research presented in this thesis offers new insights into the use of remote technologies for expanding the geographic scope of seabird monitoring and research. Given that seabirds are one of the most threatened groups of birds, the application of these technologies will be important for improving our understanding of seabird population trends, as well as the drivers of such trends; both of which are necessary if we want to implement effective conservation action. While this thesis has focused on drones, time-lapse cameras, and geolocators, alongside the use of citizen science for image analysis, continued advancements in technology will present exciting possibilities for seabird research going forwards. I hope that the work presented here will spark continued interest in innovative seabird monitoring techniques and show how remote technologies can benefit wildlife monitoring more generally.

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