Antarctic penguins and Climate Change: Long-term behavioural monitoring and Conservation.

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Thesis abstract

The Antarctic Peninsula is the second fastest warming region on Earth. In this thesis, I intend to understand the impacts of environmental change on the three *Pygoscelid* penguin species: the Adélie, Chinstrap and Gentoo penguins (*Pygoscelis adeliae*, *P. antarctica* and *P. papua* respectively). Population changes and shifts in the area of distribution are already late indicators in the timeline of population collapse, so in this thesis I developed ways to access early impact indicators like changes in behaviour (e.g. phenology) and demographic metrics (e.g. breeding success). To do this I used the Penguin Watch camera network, consisting of 87 cameras taking hourly time-lapse imagery in 37 colonies across the Antarctic Peninsula and the Sub-Antarctic Islands between 2012 and 2023. An introduction to the ecosystem and the study system can be found in Chapter 1.

In this thesis, I found all three penguin species have advanced their phenology at record levels in relation to rapid warming (0.3ºC/year) at their colonies (Chapter 2). In order to find out whether this is an adaptation mechanism to environmental change or, conversely, this is impacting their survival I decided to study their breeding success. In order to do this, I needed to build a tool to estimate this metric from volunteer annotations of selected time-lapse images in the citizen science platform Zooniverse.org (Chapter 3). I found breeding success has remained high overall but there are ever-more-frequent catastrophic breeding failures due to an increasing amount of snowfall. Breeding success was also influenced by breeding synchronicity, carry-over effects, in-season effects and human visitation (Chapter 4). Finally, I successfully tested a new type of camera, the Event Camera, in order to detect and extract a specific type of at-nest penguin behaviour (the Ecstatic Display) in an automated and non-invasive way (Chapter 5).

I expect these results can be of use for penguin conservation and I hope the tools developed here can be used to monitor potential impacts in these and other species' populations.

Author Contributions

The work in this thesis is primarily my own. I devised most of the research questions in this thesis, prepared and conducted fieldwork (five seasons), collected much of the data in Antarctica, run all the analyses, produced all the plots and wrote the text in its entirety.

All of this I have done with and thanks to the counsel and guidance of Tom Hart and Alex Kacelnik. I have benefitted greatly from many conversations and debates with both of them during all the steps that led to the completion of this thesis. They have also generously contributed with ideas and feedback for all chapters and all parts of this thesis. My gratitude to them must exceed the acknowledgements section.

Apart from my supervisors, many people contributed to the completion of this thesis in one or more ways:

In Chapter 2: This chapter benefits from the time-lapse imagery gathered by Jefferson Hinke (Copacabana cameras, King George Island), Mike Dunn (Signy Island) and Andrea Raya Rey (Isla Martillo, Argentina). Gathering the PenguinWatch time-lapse dataset has required the collaboration of a number of researchers in the field apart from those mentioned above and myself. To name a few: Fiona Jones, Gemma Clucas, Catie Foley, Mike Polito, Zofia Burr, Caitlin Black, Jen Mannas, Heather Lynch, Alex Kacelnik, Carlos Arteta, Samanta Dodino, Casey Youngflesh, Rachael Hermann, Michael Schrimpf, Chloe Kaczvinsky, Chris Lintott, Ted Cheeseman, Meagan Dewar, Louise Emmerson, Grant Miller, Craig Nisbet, Carole Hall, Kelton McMahon, Kate Blackwell among others. The idea for this project stems partially from conversations with Heather Lynch, who also helped with comments.

In Chapter 3: Carlos Arteta built the alignment tool and wrote part of appendix 3.2, regarding such tool.

In Chapter 4: Clare Flynn extracted breeding success estimates for colonies BROW, LOCK and SPIG.

Chapter 5 stems from a greater collaboration between the University of Oxford and the Technical University of Berlin. The Robotic Interactive Perception (RIP) lab, led by Guillermo Gallego provided the event cameras, CPU and SSDs necessary to obtain the data. Friedhelm Hamann and Suman Gosh, two of the PhD students in the lab, were responsible for building the AI tool capable of detecting Ecstatic Display that resulted in a sister publication at the prestigious CVPR conference. All three contributed decisively with their ideas to the inception of this piece of research as well as providing analysis tools and valuable feedback.

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Chapter 1

General Introduction

The Southern Ocean ecosystem.

Penguins are truly marine creatures, spending the vast majority of their life at sea and adapted to a fully pelagic lifestyle (Ainley, 1980). They come in land to breed and take care of their offspring but when free of that burden will spend their life at sea making thousands of kilometres across the icy waters (Hinke et al., 2015) and diving deeper than any other bird (Kooyman & Kooyman, 1995). Penguins are true sea-birds and it is worth having a look at the particularities of the Southern Ocean ecosystem where the species of study in this thesis live.

Abiotic elements of the Southern Ocean

The main features of the Southern Ocean come from its unique geographical position surrounding a continent, Antarctica, which (also uniquely) roughly extends over most of the South polar area (i.e. south of the Antarctic Circle). This particular location gives the Southern Ocean its main characteristics:

1. Low temperatures: The Polar Regions are cold because their position on the globe means solar irradiation is necessarily oblique and light scatters over a greater surface compared to lower latitudes. Over the continent, this causes a very strong and persistent high-pressure system over the South Pole. The icy continent cools the air above it, making it denser and causing it to come down all throughout its extension. The only way out for all that air is to flow close to the continent's surface and on towards the sea. These are the katabatic winds that can reach hundreds of kilometres per hour and cools down Antarctic waters. A cold Southern Ocean allows for better solubility of dissolved gases (mainly O_2 and CO_2), which facilitates algal photosynthesis as well as respiration and, in turn, ocean productivity. Katabatic winds are also responsible for the formation of polynyas (ice-free areas

of great productivity) as well as for creating Ekman spiral currents that facilitate layer-mixing in the water column (Lenn & Chereskin, 2009).

2. The Southern Ocean's biggest feature is the Antarctic Circumpolar Current (ACC), a strong continuous easterly current that encircles the Antarctic Continent. The ACC is the strongest ocean current in the world due to the concurrence of the Coriolis effect on wind and water, the current's uninterrupted path around the Antarctic continent and the Ekman effect of katabatic winds. This is the only current linking all three major oceans (Atlantic, Indian and Pacific) meaning it has a key role in global ocean circulation. The ACC also creates the Ross and Weddell Sea Gyres of importance in regional Ocean Circulation.

3. High seasonality: Due to the Earth's axis being tilted 23.5 degrees, the poles of the globe experience great seasonality. Beyond the polar circles (66.5 degrees) there is close to 6 months of light and 6 months of night; the situation is similar but less extreme for lower (i.e. more northern) latitudes of the Southern Ocean. This creates various limits to life in the Antarctic, from photosynthesis to the presence of sea-ice and the opening and closing of breeding grounds.

The combination of a closed-circuit circumpolar current (1) together with cold temperatures (2) make an oceanographic barrier called the Polar Front or Antarctic Convergence between the Southern Ocean and adjacent sub-Antarctic oceans. The Polar Front is one of the most marked oceanographic barriers in the world, with changes in water temperature of around 2.8ºC within 10-30 km. Usually, colder Antarctic waters sink next to warmer waters, mixing the water column and resulting in a high productivity area all around the continent. Despite its richness, the Polar front is also a strong ecological barrier with only a handful of species spanning both sides of its border.

Strong seasonality (3) drives the ACC (1) and the Polar Front northwards and southwards at different times of the year. This creates further opportunities for upwelling at different latitudes. Strong seasonality (3) in a context of near-zero temperatures (2) create the conditions for the dynamic appearance and disappearance of the last of its main features: Ice.

During the winter months the Southern Ocean undergoes a radical transformation, as temperatures fall below the sea-water freezing point (approximately -1.8° C) and sea-ice forms in the surface of the Ocean. Sea-ice is only a few meters thick (it appears in winter and mostly melts in summer) but it will expand hundreds of miles north around the whole continent. Sea-ice is very dynamic depending on wind, currents and local topography, receiving different names and creating different physical ecosystem constraints and opportunities for the species living at sea. A small glossary of ice-related terms that I am going to refer to throughout the thesis would be:

- *Fast ice*: 'Fast' as in 'secured' or 'land-fastened'. This is sea-ice attached to land or to an ice shelf. It forms continuous sheets of ice that may crack with the tides but do not move with the currents or wind.
- *Drift-ice*: As opposed to fast ice, drift ice is free-floating sea-ice. Its pieces are generally flat and somewhat rounded.
    - Its biggest pieces are called *ice-floes* if >20m across although they can reach dozens of kilometres.
    - *Pack-ice*: Sea-ice is considered pack-ice whenever drift-ice is pushed together by winds or currents and sea-ice reaches >70% surface coverage.
- *Ice-shelves*: None of the above types of sea-ice should be mistaken for Ice-shelves. These are old expansions of ice that form when glaciers pour into the ocean. They are permanent, fresh-water, mostly year-round and kilometres-thick, so they generally rest on the sea floor.
    - When pieces of the ice-shelves or glaciers calve (i.e. break off) they receive various names depending on their size: Icebergs (>15m across), bergy bits (<15m across) and growlers (<2m across and less than 1m above the water).

Sea-ice creates its own dynamics that interact with all the other abiotic features of the Southern Ocean. For example, upon freezing, seawater releases its salt, creating a layer of saline and cold water (very dense) just under the sea-ice. This water sinks, and it becomes a component of the thermohaline circulation. In addition, sea-ice delays warming up of the region after winter by reflecting sunlight back to space.

Biotic elements of the Southern Ocean

Sea-ice (and its corresponding lack of open water) represents a completely different marine habitat for species living in the Southern Ocean, both enabling and limiting their opportunities. For example, sea-ice decreases light availability for phytoplankton by up to 99%, especially if it gets snowed over (Arrigo, 2014). At the same time, sea-ice is key for the survival of plankton overwinter. It serves as insulation against the frigid air temperatures and keeps cells and spores at the top of the water column, safe from currents and predation, either frozen within or at its rugged bottom surface (Lizotte, 2001).

In areas of complete darkness algae survive inside the ice for up to ten months living off their nutrient reserves, at a minimal metabolic rate (Palmisano & Sullivan, 1982) and sometimes even resorting to heterotrophy (Bunt & Lee, 1972). Further north, algae can keep a basal metabolism even with minimal amounts of light, usually surviving within brine channels formed as the water solidifies and expels salts out.

Algae surviving overwinter in sea-ice serve a crucial function on the following spring as it keeps. Sea-ice keeps algae and various plankton spores at the top of the water column. Despite only a fraction of the algae surviving overwinter (McMinn et al., 2010), this is enough to trigger a spring algal bloom driven by low grazing pressure, an increase in light availability and a temporary increase in micronutrients from those deposited on top of the ice shelf overwinter.

The main consumer of phytoplankton is Antarctic krill (*Euphausia superba*). They do this either filtering open water using six pairs of modified front legs covered in fine bristles (thoracopods) or by raking ice-algae growing underneath the sea-ice (Hamner, 1988). In either way, adult krill (4-6cm) is able to prey directly on phytoplankton down to 1-5µm, rather than through microzooplankton (usually copepods; Constable et al., 2014). This makes energy transfer between trophic levels very efficient and is one of the reasons allowing for krill to be so abundant in the Southern Ocean. Krill swarms can span kilometres and contain billions of individuals (Nicol, 2006) with densities of up to 30.000 individuals per cubic meter (Tarling & Fielding, 2016).

Krill has a complex life cycle, with nine life stages, and individuals live up to six years, although they only become breeding adults after their second season (Nicol, 2006). Each of their life-stages occur at a certain depth, level of ice-cover, geographical region and time of the year; for a detailed review see Nicol (2006). The relationship with sea-ice is especially complex (Nicol, 2006; Saba et al., 2014; Walsh et al., 2020), with krill relying heavily on it for the first stages of development (Veytia et al., 2021) as well as for the shelter and feeding of adults overwinter (Brierley et al., 2002). In general, greater extensions of sea-ice favour krill recruitment in the following season (Veytia et al., 2021), but even changes in timing (Moline et al., 2008) or the speed at which ice melts in spring can have very different effects on krill availability and quality on a given season (Beaulieu et al., 2010). The high abundance and distribution throughout Antarctic waters make krill preferred food for most mesopredators in the area, including fish, squid, baleen whales, seals and, of course, penguins.

On land

The Antarctic continent is a huge landmass (twice the size of Australia) covered by ice in 99% of its extension. Most of its surface is a central high plateau that lies on average at 2500 meters above sea level, partly due to the accumulation of kilometres of ice in the continent's valleys. Despite this abundance of fresh water over the continent, Antarctica is technically a desert as average precipitation is consistently under 50mm. This is mostly because the strong katabatic winds keep weather systems away from it.

All the animals that need to breed on land (all birds and some seals) do it on the 1% of the territory that is not covered by ice, usually in northern and maritime areas. Their breeding grounds and colonies are located normally on the continent's coast close to the ocean, since they all forage in the ocean or prey or scavenge on birds that do. Exceptionally, Antarctic petrels (*Thalassoica antarctica*) breed hundreds of kilometres inland making use of ice-free surfaces in nunataks and north-facing crags. Despite the lack of ice, these areas are still subject to heavy snows throughout the winter, affecting the timing and the space availability for breeding.

In the sub-Antarctic Islands north of the continent the temperatures are warmer, precipitation is more frequent and ice cover is restricted mostly to glaciers. These gentler conditions allow low vegetation to grow in low altitudes. These areas are still subject to heavy snows that limit breeding but these are much more infrequent and usually happen much earlier in the season.

Climate change in the Antarctic Ecosystem.

The Antarctic ecosystem described above has changed in many ways over the last decades due to climate change (Meredith et al., 2019). Particularly our area of study, the Antarctic Peninsula, is experiencing the second fastest warming in the planet after the north east Atlantic (Clem et al., 2020; Vaughan et al., 2003). This warming has happened especially in the last decades of the 20th century and again since 2015 (Carrasco et al., 2021). This warming is driven mostly by the rise in winter temperatures with increases of over 6 degrees in 50 years (Vaughan et al., 2003). The current overall trend for the Western Antarctic Peninsula is one of heating, having increased +0.36°C between 2015 and 2020 (Carrasco et al., 2021).

Warming directly affects the survivability of Antarctic specialist species with narrow temperature tolerances (Morley et al., 2012). This is especially relevant for fish, whose many physiological adaptations to cold but stable temperatures leave them with a temperature tolerance of only a few degrees (Mintenbeck et al., 2012). Currently their recruitment has already been impacted as a result of rising sea surface temperatures (Belchier & Collins, 2008) and their populations are expected to move south (Morley et al., 2019; Navarro et al., 2019).

Temperature increases affect the pattern, type and amount of precipitation occurring in the southern Ocean (Vignon et al., 2021). This is important as the presence of snow is a limiting factor for nesting, both delaying the start of the season (Boersma, 2008) and affecting breeding success (Patterson, 2001). Throughout the season precipitation also affects chick survival, especially because rain can saturate chicks' down and cause hypothermia (Boersma & Rebstock, 2014; Demongin et al., 2010). In the future precipitation is expected to increase, especially in the Antarctic Peninsula (Tewari et al., 2022) and especially in the form of rain (Vignon et al., 2021).

The effects of warming on the Antarctic ecosystem that are of greatest significance for the studies in this thesis are mostly mediated through sea-ice loss (Meredith et al., 2019). The sea-ice season has shortened by three months since 1980 in the Antarctic Peninsula and the Bellingshausen Sea (Stammerjohn et al., 2012). This is really important for marine primary production (Schofield et al., 2010) but also on krill abundance and distribution food distribution (Loeb et al., 1997; Wiedenmann et al., 2009). In our area of study, both phytoplankton blooms and krill abundance are projected to decrease and to move southwards as a result of Sea-ice retreat and ocean acidification(Meredith et al., 2019).

For now, changes in sea-ice extent and food availability are already the two main drivers of population change in the Southern Ocean (Meredith et al., 2019; Schofield et al., 2010). This has been found to shift the foraging distribution and behaviour of Antarctic seabirds and mammals (Bost et al., 2015; Carpenter-Kling et al., 2019; Hindell et al., 2016), affecting their phenology (Barbraud & Weimerskirch, 2006; Sauser et al., 2021) and modifying demographic parameters like breeding success (Rombolá et al., 2010), mortality (Chen et al., 2020) and body condition (Dugger et al., 2014). In the future, these effects are projected to severely impact penguin and other krill predator populations both in the Antarctic Peninsula and the Scotia Sea under every warming scenario (Klein et al., 2018).

Pygoscelids: The three penguin species of study.

This thesis focuses on three related species of penguins that inhabit Antarctica and the sub Antarctic islands: the Adélie penguin (*Pygoscelis adeliae*), the Chinstrap penguin (*P. antarcticus*) and the Gentoo penguin (*P. papua*).



Figure 1: Photographs of the three species of study: Adélie penguin (*Pygoscelis adeliae*; left), Chinstrap penguin (*P. antarcticus*; centre) and Gentoo penguin (*P. papua*; right). Photo credit: Ignacio Juarez.

The three species of the *Pygoscelis* genus are known as the brush-tailed penguins because of their characteristically long tail feathers. These species of penguins are mostly monogamous with long lasting pair bonds and high pair and nest-site fidelity. All three species build substantial nests (10 to 20cm in height and 45cm in diameter), typically using pebbles or gravel to form an elevated platform within which they lay the eggs. They normally lay two eggs of which both can be raised successfully in good conditions despite the first one being generally bigger (Williams, 1995). Replacement clutches are infrequent and have only been observed at northern (Sub Antarctic) colonies. Chicks are semi-altricial and leave the nest within about five weeks forming loose huddles called crèches. Their crèche period coincides with the chicks' fastest growing rate, allowing for both parents to bring food until they finish moult. After chicks fledge, adults spend a special foraging period before undergoing their own moult before winter.

All three species primarily consume krill in the AP region (Trivelpiece et al., 1987), fish can be of occasional relevance and they will sometimes consume squid and salps (Williams, 1995). All of them hunt their prey by pursuit diving and hence most of their foraging happens diurnally (Williams, 1995).

Adélie penguins

The Adélie penguins can be easily identified by their completely black head and the white ring of feathers around their eyes. They show a slight sexual dimorphism; males are bigger and heavier than females and have a significantly greater bill size (Williams, 1995). Adélies breed mostly in Antarctica, the South Shetland Islands and the South Orkney Islands (but with some smaller colonies in the South Sandwich and Bouvet Island), making them the only species considered truly Antarctic together with the Emperor penguins (*Aptenodytes forsteri;* Williams, 1995). Their colonies are located in all sort of rocky areas, as long as they are ice-free from exposure to either the sun or the wind. Their breeding range seems to be limited by the presence of heavy sea-ice cover (70-100% ice cover; Ainley et al., 1998). This limits their colonies to the range between the ice shelf to the south and the disappearance of pack-ice to the north (Emmerson & Southwell, 2008). They also display high breeding synchronicity within colonies (Williams, 1995).

Adélie Penguins in the Antarctic Peninsula primarily consume krill, frequently reaching over 90% of stomach content mass. Fish are also frequently present although they seldom make more than 10% of the mass. Krill dominating the Adélies diet has been observed throughout the AP during the guard and crèche periods: in King George Island (Juáres et al., 2018; Volkman et al., 1980), Antarctic Sound (N. R. Coria et al., 1995) as well as in South Orkney (Lishman, 1985; Lynnes et al., 2004). In other parts of the continent, Adélies are known to show greater flexibility in their diet and although krill is still the main food source both in Adélie Land (Ridoux & Offredo, 1989; Wienecke et al., 2000) and the Ross Sea (Watanuki et al., 1994). Fish can become a substantial part of the diet depending on environmental conditions (D. G. Ainley et al., 1998; Jarman et al., 2013).

Krill abundance has been linked to breeding success in the AP region (Lynnes et al., 2004) and elsewhere (Tierney et al., 2009) although this might be a function of meal mass (Tierney et al., 2009) as other studies show fish-fed chicks fledge well at the Ross Sea too (Ainley et al., 2018).

At the end of summer, Adélies vacate the colonies completely as sea-ice starts to close in around their colonies and they do not normally return until the start of the following season. During winter, their distributions seem to be determined by the species' ecological preference for a heavy pack-ice cover (D. G. Ainley et al., 1993) with no evidence of colony-specific segregation (Hinke et al., 2015).

Adélie penguins in winter exploit an area of dense pack-ice (>80% cover) near the ice-shelf (100 to 200km away from shore) moving relatively little (100km/week) other than to follow their preferred sea-ice conditions (Dunn et al., 2011). Adélies spend most of their winter days out of the water resting on ice floes off which they forage during daylight (Takahashi et al., 2018). There is some niche flexibility however: in East Antarctica sea ice can go down to 20% at Adélie wintering locations without much change to their daily habits (Takahashi et al., 2018). Adélies have only been seen on land over winter in the WAP, where favourable pack-ice conditions do occur close to the coast (Black et al., 2018). In the peninsula GPS tracking revealed the Weddell sea as the preferred area for peninsular Adélies' in the South Shetlands and South Orkney (Dunn et al., 2011; Hinke et al., 2015). Tagged Adélies from the West Antarctic Peninsula concentrated around Marguerite bay, although they use a variety of locations provided there is dense sea-ice and shallow waters (Erdmann et al., 2011). Tagged penguins in East Antarctica moved with the ice to the suitable areas close to the colony (Takahashi et al., 2018). Their diet changed somewhat to that of the summer months, with squid as the main component by mass followed by krill (*E. superba*) and Myctophids (deep ocean lanternfish) (D. Ainley et al., 1992). Also stomach content was much smaller in winter than in the breeding period (D. Ainley et al., 1992). Simultaneous initiation of the return migration around the equinox suggests photoperiod as a cue to trigger homing behaviour (Dunn et al., 2011) and maybe as an initiator of hormonal changes in preparation for the breeding season.

Their global conservation status is "Least Concern" due to their relatively stable populations and the regional population increase in East Antarctica (BirdLife International, 2020a). However, in the colonies studied in this thesis numbers are in decline (Humphries et al., 2017) except for those in the Weddell Sea, which are stable or growing (Wethington et al., 2023).

CHINSTRAP PENGUINS

Chinstrap penguins are easily recognisable by a thin strip of black feathers running from ear to ear under their chin. This species is slightly taller than Adélies, but it is the lightest of the three Pygoscelids. They only breed in the maritime Western Antarctic Peninsula and in the subantarctic islands of the Scotia Sea south of the Polar Front. On land, they establish their colonies at ice-free areas, normally at steeper slopes than its congeners, often at cliff ledges and headlands. At sea they prefer open maritime areas of light ice-cover (10-30%; Williams, 1995). In winter (May-Sept) they migrate away from the colonies north of the ice-pack (Ainley et al., 1994).

Chinstraps feed almost exclusively on Euphausiids (several types of krill) throughout their range, both for themselves and to feed their offspring. Diet analysis show krill selection for decades across their range: from the South Shetland (Miller et al., 2010; Rombolá et al., 2010; Volkman et al., 1980) and South Orkney Islands

(Lishman, 1985; Lynnes et al., 2004; Rombolá et al., 2010) and Bouvet Island (Niemandt et al., 2016). They are strict krill specialists with fish or amphipods being only of occasional importance in their diet (Williams, 1995). Krill availability has been linked to their breeding success (Lynnes et al., 2004).

At the end of summer, Chinstraps also vacate the colonies completely after the breeding season for the whole winter. Chinstraps winter much further north than Adélies, at the open waters on the edge of the pack-ice (Hinke et al., 2019), not seen to venture more than a dozen kilometres into it and mostly in areas of big, scattered floes (Ainley et al., 1993, 1994). This takes them to cold (<2ºC), deep (up to 2500m) waters between the ice edge and the Polar Front (Hinke et al., 2015, 2019). Tracked adults and juveniles do not concentrate on particular locations or aggregate in any way overwinter, but seem to loosely distribute themselves over areas of favourable conditions regardless of their colony of origin (Hinke et al., 2015, 2019). Tagged Chinstraps in the WAP mostly migrated west into the Pacific Sector of the Southern Ocean (up to 2700km away from their colony). Some stayed directly north of the peninsula and some migrated East, North of the Wedell Sea, where there was some degree of overlap with Adélies throughout winter (Hinke et al., 2015). Normally Chinstraps and Adélies do not overlap, their wintering areas being separated by a wide "dynamic" area of too fast-changing ice cover changes for penguins to adapt (Ainley et al., 1993). Regarding their diet not much has been done in winter other than assessing the differences with Adélies in Stable Isotope analyses (Hinke et al., 2015).

Chinstrap penguins fall into "Least Concern" (BirdLife International, 2020b) although their numbers are decreasing throughout our colonies of study in the AP (Humphries et al., 2017). Reasons behind their decline seem to be related to declining krill abundance in the Southern Ocean, probably through fishing (Strycker et al., 2020).

GENTOO PENGUINS

Gentoo penguins have characteristic white patches above their eyes, and a bright orange bill. Their distribution is circumpolar across most sub-Antarctic Islands and the north of the Antarctic Peninsula. There is great variation in breeding and migratory behaviour between the populations North and South of the polar front. There is little to no evidence of mixing between those regions and there is an ongoing discussion about whether these populations consist of different species and if so, how many (Pertierra et al., 2020; Tyler et al., 2020; Vianna et al., 2017).

Gentoos establish smaller colonies than the other two species, normally in snow-free low flat areas, although sometimes they claim some elevated headlands if clear of snow. Often they participate in mixed colonies, adding dozens of nests to existing Adélie and Chinstrap colonies. In the subantarctic islands they breed on vegetated areas (Tussock grass, *Poa flabellata*) and often change their colony location year to year after trampling the vegetation. In their feeding habits Gentoos are foraging generalists, foraging in ice-free inshore waters close to the colonies (Wilson et al., 1998). They exhibit remarkable foraging variability depending on the state of the sea and the time of year (Lescroël et al., 2004).

In the sub-antarctic, fish is often the main prey, followed by crustaceans and occasionally cephalopods. However, there is great variability between seasons and colonies and even inter-individual variability seems to be quite high (Camprasse et al., 2017). The preference for fish over crustaceans and Cephalopods holds true for most of their subantarctic range including: the Falklands/Malvinas (Clausen & Pütz, 2002; Pütz et al., 2001), South Georgia (Croxall et al., 1988), Marion Island (Adams & Klages, 1989; Carpenter-Kling et al., 2019), Kerguelen (Lescroël et al., 2004) and Heard Island (Klages et al., 1990). Only in one study in Macquarie Island were crustaceans negligible and cephalopods took a modest second place in the diet (Hindell, 1989; Robinson & Hindell, 1996). In the subantarctic islands the percentage of fish frequently oscillates between 30-90% and the percentage of crustaceans between 0-60%. The presence of cephalopods in the diet is frequent, but only rarely making up more than 15% of the stomach content (Borboroglu & Boersma, 2015). This variability has been suggested to arise from great foraging versatility, as they have been seen to eat food items depending on the local availability (Clausen et al., 2005; Lescroël et al., 2004)

In the Antarctic, krill is the main prey item, by far making a greater proportion of prey by mass than any other group. In the South Shetlands, krill is the main prey always at >60% by weight and usually at >90% (Juáres et al., 2016; Miller et al., 2010; Volkman et al., 1980). This is maintained throughout the breeding season and both on King George (Juáres et al., 2016; Volkman et al., 1980) and in Livingston Islands (Miller et al., 2010). However, the proportion of prey was observed to change throughout the year with fish peaking before and after the breeding season and krill making up most of their diet during the breeding season (Juáres et al., 2016). Cephalopods were not found in any of the samples taken in the Antarctic (Borboroglu & Boersma, 2015). The only study in South Orkney found both krill and fish can be the main item although none ever falling below 30% by mass (Coria et al., 2000); an intermediate situation for this intermediate location.

Gentoos are non-migratory and they will stay overwinter in areas where there are inshore open waters throughout the winter. This happens almost exclusively in the Western Antarctic Peninsula. In fact, our camera network often records them at the breeding colonies throughout the winter. These near-shore foragers stay on land, often at their breeding colony, close to ice-free coastal locations in order to maximise foraging time during the scarce daylight hours (Hinke & Trivelpiece, 2011; Wilson et al., 1998). This is possibly more energetically efficient than staying in the water or on ice and can help exchange information or avoid predation. In fact, Gentoos return to land most nights after foraging (Hinke & Trivelpiece, 2011; Tanton et al., 2004). These penguins will vacate the colony for periods of up to six weeks if environmental conditions deteriorate and fast-ice forms in the waters around the colony closing their access to food (Black et al., 2017). This is possibly why they spend more time at the colony in temperate locations (i.e. in the subantarctic), although they show up at least every month even at their southernmost colonies (Black et al., 2017). Gentoos winter diet is similar compared to their summer diet. This was mostly fish in Marion island, Macquarie, Kerguelen and South Orkney (N. Coria et al., 2000; Hindell, 1989; LaCock et al., 2010; Lescroël et al., 2004), squid and fish at the Falklands (A. Clausen & Pütz, 2003) with no specific winter diet studies found at the Antarctic Peninsula or Patagonia. The closest to a study on winter diet are the isotope analysis studies performed on pre and post breeding specimens (egg membranes and feathers) from Gentoos on King George Island. These show a krill dominated diet (60-80%) with an increase in fish consumption (up to 30%) over in the pre and post breeding periods (Juáres et al., 2016). The weight of the stomach contents is generally smaller than that of the summer throughout studies (N. Coria et al., 2000; Hindell, 1989; LaCock et al., 2010; Lescroël et al., 2004).

Currently their conservation status is “Near Threatened” although in the Antarctic Peninsula their populations are increasing, and their range is expanding (Wethington et al., 2023). Their conservation status may change for some populations once the taxonomy is clarified (BirdLife International, 2020c).

Penguins, Sentinels of the Southern Ocean.

Seabirds, including penguins, are considered *marine sentinels* since they are easy to monitor at their colonies (i.e. on land), but are vulnerable to a number of threats at sea (Dias et al., 2019) and are thus able to 'report' on possible alterations of their environment.

Seabirds can be exposed to these threats anytime over their long lifespans and long breeding cycles (Davis & Darby, 2012), at any point across their broad geographical ranges (while foraging or during migration; Ropert-Coudert et al., 2019) and through the various trophic levels they feed upon. Apart from these seabird-wide reasons, penguins are uniquely placed to monitor the health of the Southern Ocean. Penguins are distributed all along the coast of Antarctica (Santora et al., 2020) and are among the top consumers of marine productivity alongside seals and whales (McCormack et al., 2021). Finally, high colony fidelity allows for the building of long time-series that can allow us to witness system change through time (Barbraud & Weimerskirch, 2006; Burr et al., 2016; Hinke et al., 2007).

Penguins therefore 'report' on critical threats that may exist anywhere in their lifecycles by way of changes in their breeding patterns (Trivelpiece et al., 1990). For this reason, penguins (as seabirds) are considered "ocean sentinels" (Boersma, 2008; Croxall et al., 2012), a sort of canary in the cold mine that can quickly signal disruptions in the marine ecosystem through the disruption of their own life cycles (Furness, 1997; Paleczny et al., 2015; Pichegru et al., 2010). In the longer term this alters their breeding success (Boersma, 2008), decreasing (Trathan et al., 2015) or increasing (LaRue et al., 2013; Pichegru et al., 2010); their productivity depending on the trajectory of changing environmental conditions.

This is unfortunately what makes penguins the most endangered group within seabirds, together with albatrosses, (Dias et al., 2019) and one of the most endangered bird groups worldwide (McClure & Rolek, 2020). Currently half of the penguin species are threatened to some degree (BirdLife International, 2020d). At sea, the main threats to penguins are fishing (mostly through competition but also bycatch), and changes in oceanographic conditions induced by climate change and pollution (Dias et al., 2019). At the colony, penguins are mainly affected by severe weather events and invasive species (mostly in temperate areas; Croxall et al., 2012).

Current environmental changes are seeing Gentoos expanding their numbers and range southward throughout the Antarctic Peninsula (Herman et al., 2020) while Adélie (Wethington et al., 2023) and Chinstraps (Strycker et al., 2020) are receding. As these species are closely related and greatly sympatric it is likely that these different responses are related to the distinct specialisations of each congener. Understanding the impacts of climate change on each species can therefore be a key to understanding how the Southern Ocean and its food web are changing without studying them directly. I will explore these possibilities by studying penguin phenology and breeding success in chapters 2 and 4; please refer to them for a discussion on what these findings mean for the broader Antarctic environment.

Aims of this thesis.

Population changes and range shifts are already late indicators in the timeline of population collapse. Earlier indicators like changes in behaviour (including phenology), morphological features or demographic metrics (e.g. breeding success) are much better suited to assess disturbance scenarios before populations start declining and, once they are, assess the path to extinction (Cerini et al., 2023).

In this thesis, I aim to understand several aspects of the breeding biology and behaviour of the three pygoscelid species that are important to their conservation:

Chapter 2. To understand how climate change is affecting breeding phenology in Pygoscelids, I study the initiation of the breeding season over a decade of monitoring and across 87 locations in 37 colonies in the Antarctic Peninsula and the Sub-Antarctic Islands. In this chapter, I relate the phenological changes to local environmental variables in order to understand the proximate environmental causes behind the observed phenological shifts. The differences serve as a hint on the reasons behind the observed divergence between Adélie and Chinstrap penguins from Gentoo penguins despite being largely sympatric in the Antarctic Peninsula.

Chapter 3. I need to build a tool capable of extracting biologically meaningful metrics from time-lapse images in order to delve deeper into the effects of climate change on the breeding ecology of the three Pygoscelid species. I will use volunteer annotations (obtained from Zooniverse, a Citizen Science platform) in order to track the presence of chicks in each nest throughout the season. With this data I intend to estimate hatching and crèching dates, chick mortality dates and breeding success.

Chapter 4. Phenological shifts such as those reported in Chapter 2 could be due to penguins adapting to new environmental conditions or whether they are being pushed to breed at suboptimal timing. In order to do this, I in this chapter I study how Pygoscelid breeding success has changed at a selection of colonies over the last ten years in the Antarctic Peninsula. I also test some of the known environmental and non-environmental factors known to affect breeding success.

Chapter 5. In this final chapter, I study the occurrence of Ecstatic Display (ED) in a colony of Chinstrap penguins. Ecstatic display has never been studied in Chinstrap Penguins other than a few references in general books and on papers studying the vocalizations they emit while displaying. In this chapter, I characterise the behaviour and compare its occurrence to ED in other species as a way to hypothesise about its function. To do this I pilot the use of a new type of camera (called event or neuromorphic cameras) as a way to test its possibilities to automate behaviour data acquisition.

Methods Overview.

In order to conduct this research I use image data captured thanks to the Penguin Watch camera network (Figure 2a). This camera network currently consists of 87 cameras deployed over throughout the Antarctic Peninsula and the Atlantic Sub-Antarctic Islands (See Appendix S2.1 for information on camera codes, location and amount of data available). These cameras are commercially available camera-traps (or trail cameras) set in timelapse mode so they can take one picture per hour of at least ten nests during the whole year. The cameras we use are Reconyx Ultrafire, Reconyx Hyperfire 1 and Hyperfire 2.

a)



b)



Figure 2: Fieldwork context. a) Example of an experimental setup. The camera trap is attached to the top of a weigthed metal tripod and set to time-lapse mode so it can take 1 picture per hour of a subset of a penguin colony. Here we can see camera BOOTb, which monitors a series of Gentoo Penguin nests on Booth Island with Port Charcot in the background. b) An example of the expedition cruise ships that we use as logistic platforms in order to access remote penguin colonies. In the image it is possible to see the Gentoo colony at Neko Harbour on Andvord Bay with the Ocean Endeavour in the background. I conducted my two first field seasons on board that ship. Photos: IJM.

This network was originally deployed by my supervisor Tom Hart with the first time-lapse camera deployments happening in the 2011-2012 season. Since then many PhD students and collaborators have helped maintain and enlarge this network with approximately 2-5 teams for two members taking aprt in every season (Except 2020-2021 when only Tom reached Antarctica). Among the students we can mention Fiona Jones, Gemma Clucas, Caitlin Black, Chloe Kaczvinsky and Hila Levy. Regarding collaborators: Andrea Raya Rey from CADIC-CONICET (Argentina) has contributed data from Martillo and Estados Islands in Patagonia, Jefferson Hinke (NOAA, USA) has contributed data from Copacabana Beach (King George Island, Antarctica) and Mike Dunn (BAS, UK) has contributed data from Signy Island (South Orkney, Antarctica). Other collaborators that have helped us collect data in the field are: Heather Lynch, Catie Foley, Mike Polito, Zofia Burr, Caitlin Black, Jen Mannas, Alex Kacelnik, Carlos Arteta, Casey Youngflesh, Rachael Hermann, Michael Schrimpf, Samanta Dodino, Chris Lintott, Ted Cheeseman, Meagan Dewar, Louise Emmerson, Grant Miller, Craig Nisbet, Carole Hall, Kelton McMahon Kate Blackwell among others.

I personally started collaborating with the acquisition of data for Penguin Watch in my first season in 2018-2019. I have participated in every season since until the present 2023-2024 except for the first covid season (2020-2021), where only my supervisor Tom Hart was able to go south. During the season 2021-2022 I was deployed for two months at the Gabriel de Castilla research station (Deception Island, South Shetland,

Antarctica) as part of a collaboration with Andrés Barbosa from the Spanish Antarctic Mission in order to conduct the Event Camera study in Chapter 5.

Our research is reverse-engineered in order to be able to be conducted in a span of 2-3 hours per colony as our group usually conducts research aboard tour vessels (Quark, National Geographic, Hurtigruten, Cheeseman, among others; Figure 2b). Antarctic tourism is based on selling access to a continent marketed as pristine, unsoiled continent so they often land in penguin colonies far away from research stations. This makes tour ships great logistic platforms from which to study those colonies far from bases and thus fill a knowledge gap left by the national programmes. Usually we are deployed in two colonies per day and in that deployment time we are usually able to service 1-4 timelapse cameras, take 30 (non-invasive) guano samples per species present, 30 feathers (non-invasively as well), perform a drone survey of the colony and change a glycerol pollen trap, if present.

This is a landscape-level study that covers a great -if not most- part of these species' distributions. This spread is useful to capture a range of responses to environmental factors but also it is key to observe broader geographical patterns like edge-of-range effects. This is especially interesting for Gentoo penguins, who are currently expanding their range along the Antarctic Peninsula.

The nature of the data in this thesis means these chapters have a strong technical development aspect in order to extract biologically-meaningful metrics out of imagery. I intend to publish these findings and developments separately in technical journals and here these are kept mostly in the appendices in order to focus on the biological questions in the main body of the chapters.

Time-lapse cameras make data acquisition relatively easy in a harsh environment, in a way that is also relatively cheap and non-invasive. However, extracting biologically-meaningful metrics from them requires a great deal of technical development work. To start, the metrics themselves need to either be adapted to a fixed camera view setup (e.g. 'Breeding success' in Chapter 3) or to develop new metrics altogether (e.g. 'colony settlement' in Chapter 2). Both require a trial-and-error process where each of those tries requires the coding of new ground-truthing tools as well as the coding of the final implementation tools. In chapter 4, I even pilot the use of an altogether new type of camera, the event camera. This required major machine learning development through a collaboration with the Technical University of Berlin. Most of this technical development has been reported in the appendices, in order to focus on the biological questions in the main body of the chapters.

I hope both the behavioural and ecological results in this thesis are useful contributions to the understanding of the current situation of Pygoscelids. I equally hope the tools and metrics developed here will help the study and conservation of these and other species in the future.

References.

Adams, N. J., & Klages, N. T. (1989). Temporal Variation in the Diet of the Gentoo Penguin Pygoscelis papua at Sub-Antarctic Marion Island. *Colonial Waterbirds*, *12*(1), 30. https://doi.org/10.2307/1521309

Ainley, D., Dugger, K., La Mesa, M., Ballard, G., Barton, K., Jennings, S., Karl, B., Lescroël, A., Lyver, P., Schmidt, A., & Wilson, P. (2018). Post-fledging survival of Adélie penguins at multiple colonies: Chicks raised on fish do well. *Marine Ecology Progress Series*, *601*, 239–251. https://doi.org/10.3354/meps12687

Ainley, D. G. (1980). Birds as marine organisms: A review. *CalCOFI Rep*, *21*, 48–53.

Ainley, D. G., Ribic, C. A., & Fraser, W. R. (1994). Ecological Structure among Migrant and Resident Seabirds of the Scotia—Weddell Confluence Region. *The Journal of Animal Ecology*, *63*(2), 347. https://doi.org/10.2307/5553

Ainley, D. G., Ribic, C. A., & Spear, L. B. (1993). Species-Habitat Relationships among Antarctic Seabirds: A Function of Physical or Biological Factors? *The Condor*, *95*(4), 806–816. https://doi.org/10.2307/1369419

Ainley, D. G., Wilson, P. R., Barton, K. J., Ballard, G., Nur, N., & Karl, B. (1998). Diet and foraging effort of Adélie penguins in relation to pack-ice conditions in the southern Ross Sea. *Polar Biology*, *20*, 311–319.

Ainley, D., Ribic, C., & Fraser, W. (1992). Does prey preference affect habitat choice in Antarctic seabirds? *Marine Ecology Progress Series*, *90*, 207–221. https://doi.org/10.3354/meps090207

Arrigo, K. R. (2014). Sea Ice Ecosystems. *Annual Review of Marine Science*, *6*(1), 439–467. https://doi.org/10.1146/annurev-marine-010213-135103

Barbraud, C., & Weimerskirch, H. (2006). Antarctic birds breed later in response to climate change. *Proceedings of the National Academy of Sciences*, *103*(16), 6248–6251. https://doi.org/10.1073/pnas.0510397103

Beaulieu, M., Dervaux, A., Thierry, A.-M., Lazin, D., Le Maho, Y., Ropert-Coudert, Y., SpÃ©e, M., Raclot, T., & Ancel, A. (2010). When sea-ice clock is ahead of Adélie penguins' clock. *Functional Ecology*, *24*(1), 93–102. https://doi.org/10.1111/j.1365-2435.2009.01638.x

Belchier, M., & Collins, M. A. (2008). Recruitment and body size in relation to temperature in juvenile Patagonian toothfish (Dissostichus eleginoides) at South Georgia. *Marine Biology*, *155*(5), 493–503. https://doi.org/10.1007/s00227-008-1047-3

BirdLife International. (2020a). *Pygoscelis adeliae. The IUCN Red List of Threatened Species 2020*. https://dx.doi.org/10.2305/IUCN.UK.2020-3.RLTS.T22697758A157660553.en

BirdLife International. (2020b). *Pygoscelis antarcticus. The IUCN Red List of Threatened Species 2020*. https://www.iucnredlist.org/species/22697761/184807209

BirdLife International. (2020c). *Pygoscelis papua. The IUCN Red List of Threatened Species 2020*. https://dx.doi.org/10.2305/IUCN.UK.2020-3.RLTS.T22697755A157664581.en

BirdLife International. (2020d). *The IUCN Red List of Threatened Species 2020*. https://www.iucnredlist.org/search?query=penguins&searchType=species

Black, C., Rey, A. R., & Hart, T. (2017). Peeking into the bleak midwinter: Investigating nonbreeding strategies of Gentoo Penguins using a camera network. *The Auk*, *134*(3), 520–529. https://doi.org/10.1642/AUK-16-69.1

Black, C., Southwell, C., Emmerson, L., Lunn, D., & Hart, T. (2018). Time-lapse imagery of Adélie penguins reveals differential winter strategies and breeding site occupation. *PLOS ONE*, *13*(3), e0193532. https://doi.org/10.1371/journal.pone.0193532

Boersma, P. D. (2008). Penguins as Marine Sentinels. *BioScience*, *58*(7), 597–607. https://doi.org/10.1641/B580707

Boersma, P. D., & Rebstock, G. A. (2014). Climate change increases reproductive failure in Magellanic penguins. *Plos One*, *9*(1), e85602.

Borboroglu, P. G., & Boersma, P. D. (2015). *Penguins: Natural History and Conservation*. University of Washington Press.

Bost, C. A., Cotté, C., Terray, P., Barbraud, C., Bon, C., Delord, K., Gimenez, O., Handrich, Y., Naito, Y., Guinet, C., & Weimerskirch, H. (2015). Large-scale climatic anomalies affect marine predator foraging behaviour and demography. *Nature Communications*, *6*(1), Article 1. https://doi.org/10.1038/ncomms9220

Brierley, A. S., Fernandes, P. G., Brandon, M. A., Armstrong, F., Millard, N. W., McPhail, S. D., Stevenson, P., Pebody, M., Perrett, J., Squires, M., Bone, D. G., & Griffiths, G. (2002). *Antarctic Krill Under Sea Ice: Elevated Abundance in a Narrow Band Just South of Ice Edge*. *295*, 4.

Bunt, J. S., & Lee, C. C. (1972). DATA ON THE COMPOSITION AN DARK SURVIVAL OF FOUR SEA-ICE MICROALGAE1. *Limnology and Oceanography*, *17*(3), 458–461. https://doi.org/10.4319/lo.1972.17.3.0458

Burr, Z. M., Varpe, Ø., Anker-Nilssen, T., Erikstad, K. E., Descamps, S., Barrett, R. T., Bech, C., Christensen-Dalsgaard, S., Lorentsen, S., Moe, B., Reiertsen, T. K., & Strøm, H. (2016). Later at higher latitudes: Large-scale variability in seabird breeding timing and synchronicity. *Ecosphere*, *7*(5). https://doi.org/10.1002/ecs2.1283

Camprasse, E., Cherel, Y., Bustamante, P., Arnould, J., & Bost, C. (2017). Intra- and inter-individual variation in the foraging ecology of a generalist subantarctic seabird, the Gentoo penguin. *Marine Ecology Progress Series*, *578*, 227–242. https://doi.org/10.3354/meps12151

Carpenter-Kling, T., Handley, J. M., Connan, M., Crawford, R. J. M., Makhado, A. B., Dyer, B. M., Froneman, W., Lamont, T., Wolfaardt, A. C., Landman, M., Sigqala, M., & Pistorius, P. A. (2019). Gentoo penguins as sentinels of climate change at the sub-Antarctic Prince Edward Archipelago, Southern Ocean. *Ecological Indicators*, *101*, 163–172. https://doi.org/10.1016/j.ecolind.2019.01.008

Carrasco, J. F., Bozkurt, D., & Cordero, R. R. (2021). A review of the observed air temperature in the Antarctic Peninsula. Did the warming trend come back after the early 21st hiatus? *Polar Science*, *28*, 100653. https://doi.org/10.1016/j.polar.2021.100653

Cerini, F., Childs, D. Z., & Clements, C. F. (2023). A predictive timeline of wildlife population collapse. *Nature Ecology & Evolution*, *7*(3), Article 3. https://doi.org/10.1038/s41559-023-01985-2

Chen, X., Cheng, X., Zhang, B., Meng, H., Wu, D., Zhang, M., Ji, M., & Li, X. (2020). Lagged response of Adélie penguin (Pygoscelis adeliae) abundance to environmental variability in the Ross Sea, Antarctica. *Polar Biology*, *43*(11), 1769–1781. https://doi.org/10.1007/s00300-020-02743-x

Clausen, A. P., Arkhipkin, A. I., Laptikhovsky, V. V., & Huin, N. (2005). What is out there: Diversity in feeding of Gentoo penguins (Pygoscelis papua) around the Falkland Islands (Southwest Atlantic). *Polar Biology*, *28*(9), 653–662. https://doi.org/10.1007/s00300-005-0738-1

Clausen, A. P., & Pütz, K. (2002). Recent trends in diet composition and productivity of Gentoo, magellanic and rockhopper penguins in the Falkland Islands. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *12*(1), 51–61. https://doi.org/10.1002/aqc.476

Clausen, A., & Pütz, K. (2003). Winter diet and foraging range of Gentoo penguins (Pygoscelis papua) from Kidney Cove, Falkland Islands. *Polar Biology*, *26*(1), 32–40. https://doi.org/10.1007/s00300-002-0443-2

Clem, K. R., Fogt, R. L., Turner, J., Lintner, B. R., Marshall, G. J., Miller, J. R., & Renwick, J. A. (2020). Record warming at the South Pole during the past three decades. *Nature Climate Change*, *10*(8), 762–770.

Constable, A. J., Melbourne-Thomas, J., Corney, S. P., Arrigo, K. R., Barbraud, C., Barnes, D. K. A., Bindoff, N. L., Boyd, P. W., Brandt, A., Costa, D. P., Davidson, A. T., Ducklow, H. W., Emmerson, L., Fukuchi, M., Gutt, J., Hindell, M. A., Hofmann, E. E., Hosie, G. W., Iida, T., … Ziegler, P. (2014). Climate change and Southern Ocean ecosystems I: How changes in physical habitats directly affect marine biota. *Global Change Biology*, *20*(10), 3004–3025. https://doi.org/10.1111/gcb.12623

Coria, N., Libertelli, M., Casaux, R., & Darrieu, C. (2000). Inter-Annual Variation in the Autumn Diet of the Gentoo Penguin at Laurie Island, Antarctica. *Waterbirds: The International Journal of Waterbird Biology*, *23*(3), 511. https://doi.org/10.2307/1522192

Coria, N. R., Spairani, H., Vivequin, S., & Fontana, R. (1995). Diet of Adélie penguins Pygoscelis adeliae during the post-hatching period at Esperanza Bay, Antarctica, 1987/88. *Polar Biology*, *15*(6), 415–418. https://doi.org/10.1007/BF00239717

Croxall, J. P., Butchart, S. H. M., Lascelles, B., Stattersfield, A. J., Sullivan, B., Symes, A., & Taylor, P. (2012). Seabird conservation status, threats and priority actions: A global assessment. *Bird Conservation International*, *22*(1), 1–34. https://doi.org/10.1017/S0959270912000020

Croxall, J. P., Davis, R. W., & O'Connell, M. J. (1988). Diving Patterns in Relation to Diet of Gentoo and Macaroni Penguins at South Georgia. *The Condor*, *90*(1), 157–167. https://doi.org/10.2307/1368444

Davis, L. S., & Darby, J. T. (2012). *Penguin Biology*. Elsevier.

Demongin, L., Poisbleau, M., Strange, I. J., & Quillfeldt, P. (2010). *Effects of severe rains on the mortality of southern rockhopper penguin (Eudyptes chrysocome) chicks and its impact on breeding success*. https://jlupub.ub.uni-giessen.de/bitstream/handle/jlupub/268/ON_21_(3)_439-443.pdf?sequence=1

Dias, M. P., Martin, R., Pearmain, E. J., Burfield, I. J., Small, C., Phillips, R. A., Yates, O., Lascelles, B., Borboroglu, P. G., & Croxall, J. P. (2019). Threats to seabirds: A global assessment. *Biological Conservation*, *237*, 525–537. https://doi.org/10.1016/j.biocon.2019.06.033

Dugger, K. M., Ballard, G., Ainley, D. G., Lyver, P. O., & Schine, C. (2014). Adélie penguins coping with environmental change: Results from a natural experiment at the edge of their breeding range. *Frontiers in Ecology and Evolution*, *2*. https://www.frontiersin.org/articles/10.3389/fevo.2014.00068

Dunn, M. J., Silk, J. R. D., & Trathan, P. N. (2011). Post-breeding dispersal of Adélie penguins (Pygoscelis adeliae) nesting at Signy Island, South Orkney Islands. *Polar Biology*, *34*(2), 205–214. https://doi.org/10.1007/s00300-010-0870-4

Emmerson, L., & Southwell, C. (2008). Sea ice cover and its influence on Adélie penguin reproductive performance. *Ecology*, *89*(8), 2096–2102.

Erdmann, E. S., Ribic, C. A., Patterson-Fraser, D. L., & Fraser, W. R. (2011). Characterization of winter foraging locations of Adélie penguins along the Western Antarctic Peninsula, 2001–2002. *Deep Sea Research Part II: Topical Studies in Oceanography*, *58*(13), 1710–1718. https://doi.org/10.1016/j.dsr2.2010.10.054

Furness, R. (1997). Seabirds as monitors of the marine environment. *ICES Journal of Marine Science*, *54*(4), 726–737. https://doi.org/10.1006/jmsc.1997.0243

Hamner, W. M. (1988). Biomechanics of filter feeding in the Antarctic krill Euphausia superba: Review of past work and new observations. *Journal of Crustacean Biology*, *8*(2), 149–163.

Herman, R., Borowicz, A., Lynch, M., Trathan, P., Hart, T., & Lynch, H. (2020). Update on the global abundance and distribution of breeding Gentoo Penguins (Pygoscelis papua). *Polar Biology*, *43*(12), 1947–1956. https://doi.org/10.1007/s00300-020-02759-3

Hindell, M. A. (1989). The Diet of Gentoo Penguins *Pygoscelis papua* at Macquarie Island: Winter and Early Breeding Season. *Emu - Austral Ornithology*, *89*(2), 71–78. https://doi.org/10.1071/MU9890071

Hindell, M. A., McMahon, C. R., Bester, M. N., Boehme, L., Costa, D., Fedak, M. A., Guinet, C., Herraiz-Borreguero, L., Harcourt, R. G., Huckstadt, L., Kovacs, K. M., Lydersen, C., McIntyre, T., Muelbert, M., Patterson, T., Roquet, F., Williams, G., & Charrassin, J. (2016). Circumpolar habitat use in the southern elephant seal: Implications for foraging success and population trajectories. *Ecosphere*, *7*(5), e01213. https://doi.org/10.1002/ecs2.1213

Hinke, J. T., Polito, M. J., Goebel, M. E., Jarvis, S., Reiss, C. S., Thorrold, S. R., Trivelpiece, W. Z., & Watters, G. M. (2015). Spatial and isotopic niche partitioning during winter in Chinstrap and Adélie penguins from the South Shetland Islands. *Ecosphere*, *6*(7), art125. https://doi.org/10.1890/ES14-00287.1

Hinke, J. T., Salwicka, K., Trivelpiece, S. G., Watters, G. M., & Trivelpiece, W. Z. (2007). Divergent responses of Pygoscelis penguins reveal a common environmental driver. *Oecologia*, *153*(4), 845–855. https://doi.org/10.1007/s00442-007-0781-4

Hinke, J. T., Santos, M. M., Korczak-Abshire, M., Milinevsky, G., & Watters, G. M. (2019). Individual variation in migratory movements of Chinstrap penguins leads to widespread occupancy of ice-free winter habitats over the continental shelf and deep ocean basins of the Southern Ocean. *PLOS ONE*, *14*(12), e0226207. https://doi.org/10.1371/journal.pone.0226207

Hinke, J. T., & Trivelpiece, W. Z. (2011). Daily activity and minimum food requirements during winter for Gentoo penguins (Pygoscelis papua) in the South Shetland Islands, Antarctica. *Polar Biology*, *34*(10), 1579–1590. https://doi.org/10.1007/s00300-011-1018-x

Humphries, G. R. W., Naveen, R., Schwaller, M., Che-Castaldo, C., McDowall, P., Schrimpf, M., & Lynch, H. J. (2017). Mapping Application for Penguin Populations and Projected Dynamics (MAPPPD): Data and tools for dynamic management and decision support. *Polar Record*, *53*(2), 160–166. https://doi.org/10.1017/S0032247417000055

Jarman, S. N., McInnes, J. C., Faux, C., Polanowski, A. M., Marthick, J., Deagle, B. E., Southwell, C., & Emmerson, L. (2013). Adélie Penguin Population Diet Monitoring by Analysis of Food DNA in Scats. *PLOS ONE*, *8*(12), e82227. https://doi.org/10.1371/journal.pone.0082227

Juáres, M. A., Casaux, R., Corbalán, A., Blanco, G., Pereira, G. A., Perchivale, P. J., Coria, N. R., & Santos, M. M. (2018). Diet of Adélie penguins (Pygoscelis adeliae) at Stranger Point (25 de Mayo/King George Island, Antarctica) over a 13-year period (2003–2015). *Polar Biology*, *41*(2), 303–311. https://doi.org/10.1007/s00300-017-2191-3

Juáres, M. A., Santos, M., Mennucci, J. A., Coria, N. R., & Mariano-Jelicich, R. (2016). Diet composition and foraging habitats of Adélie and Gentoo penguins in three different stages of their annual cycle. *Marine Biology*, *163*(5), 105. https://doi.org/10.1007/s00227-016-2886-y

Klages, N. T. W., Pemberton, D., & Gales, R. P. (1990). The Diets of King and Gentoo Penguins at Heard Island. *Wildlife Research*, *17*(1), Article 1. https://doi.org/10.1071/WR9900053

Klein, E. S., Hill, S. L., Hinke, J. T., Phillips, T., & Watters, G. M. (2018). Impacts of rising sea temperature on krill increase risks for predators in the Scotia Sea. *PloS One*, *13*(1), e0191011.

Kooyman, G. L., & Kooyman, T. G. (1995). Diving behavior of emperor penguins nurturing chicks at Coulman Island, Antarctica. *The Condor*, *97*(2), 536–549.

LaCock, G. D., Hecht, T., & Klages, N. (2010). THE WINTER DIET OF GENTOO PENGUINS AT MARION ISLAND. *OSTRICH*. https://www.tandfonline.com/doi/abs/10.1080/00306525.1984.9634486

LaRue, M. A., Ainley, D. G., Swanson, M., Dugger, K. M., Lyver, P. O. B., Barton, K., & Ballard, G. (2013). Climate change winners: Receding ice fields facilitate colony expansion and altered dynamics in an Adélie penguin metapopulation. *PLoS One*, *8*(4), e60568.

Lenn, Y.-D., & Chereskin, T. K. (2009). Observations of Ekman Currents in the Southern Ocean. *Journal of Physical Oceanography*, *39*(3), 768–779. https://doi.org/10.1175/2008JPO3943.1

Lescroël, A., Ridoux, V., & Bost, C. A. (2004). Spatial and temporal variation in the diet of the Gentoo penguin (Pygoscelis papua) at Kerguelen Islands. *Polar Biology*, *27*(4), 206–216. https://doi.org/10.1007/s00300-003-0571-3

Lishman, G. S. (1985). The food and feeding ecology of Adélie penguins (Pygoscelis adeliae) and Chinstrap penguins (P. antarctica) at Signy Island, South Orkney Islands. *Journal of Zoology*, *205*(2), 245–263. https://doi.org/10.1111/j.1469-7998.1985.tb03532.x

Lizotte, M. P. (2001). The Contributions of Sea Ice Algae to Antarctic Marine Primary Production1. *American Zoologist*, *41*(1), 57–73. https://doi.org/10.1093/icb/41.1.57

Loeb, V., Siegel, V., Holm-Hansen, O., Hewitt, R., Fraser, W., Trivelpiece, W., & Trivelpiece, S. (1997). Effects of sea-ice extent and krill or salp dominance on the Antarctic food web. *Nature*, *387*(6636), Article 6636. https://doi.org/10.1038/43174

Lynnes, A. S., Reid, K., & Croxall, J. P. (2004). Diet and reproductive success of Adélie and Chinstrap penguins: Linking response of predators to prey population dynamics. *Polar Biology*, *27*(9), 544–554. https://doi.org/10.1007/s00300-004-0617-1

McClure, C. J. W., & Rolek, B. W. (2020). Relative Conservation Status of Bird Orders With Special Attention to Raptors. *Frontiers in Ecology and Evolution*, *8*. https://www.frontiersin.org/articles/10.3389/fevo.2020.593941

McCormack, S. A., Melbourne-Thomas, J., Trebilco, R., Blanchard, J. L., Raymond, B., & Constable, A. (2021). Decades of dietary data demonstrate regional food web structures in the Southern Ocean. *Ecology and Evolution*, *11*(1), 227–241. https://doi.org/10.1002/ece3.7017

McMinn, A., Martin, A., & Ryan, K. (2010). Phytoplankton and sea ice algal biomass and physiology during the transition between winter and spring (McMurdo Sound, Antarctica). *Polar Biology*, *33*(11), 1547–1556. https://doi.org/10.1007/s00300-010-0844-6

Meredith, M., Sommerkorn, M., Cassotta, S., Derksen, C., Ekaykin, A., Hollowed, A., Kofinas, G., Mackintosh, A., Melbourne-Thomas, J., & Muelbert, M. M. C. (2019). *Polar Regions. Chapter 3, IPCC Special Report on the Ocean and Cryosphere in a Changing Climate*.

Miller, A. K., Kappes, M. A., Trivelpiece, S. G., & Trivelpiece, W. Z. (2010). Foraging-Niche Separation of Breeding Gentoo and Chinstrap Penguins, South Shetland Islands, Antarctica. *The Condor*, *112*(4), 683–695. https://doi.org/10.1525/cond.2010.090221

Mintenbeck, K., Barrera-Oro, E. R., Brey, T., Jacob, U., Knust, R., Mark, F. C., Moreira, E., Strobel, A., & Arntz, W. E. (2012). Impact of climate change on fishes in complex Antarctic ecosystems. In *Advances in*

ecological research (Vol. 46, pp. 351–426). Elsevier. https://www.sciencedirect.com/science/article/pii/B978012396992700006X

Moline, M. A., Karnovsky, N. J., Brown, Z., Divoky, G. J., Frazer, T. K., Jacoby, C. A., Torres, J. J., & Fraser, W. R. (2008). High Latitude Changes in Ice Dynamics and Their Impact on Polar Marine Ecosystems. *Annals of the New York Academy of Sciences*, *1134*(1), 267–319. https://doi.org/10.1196/annals.1439.010

Morley, S. A., Barnes, D. K. A., & Dunn, M. J. (2019). Predicting Which Species Succeed in Climate-Forced Polar Seas. *Frontiers in Marine Science*, *5*. https://www.frontiersin.org/articles/10.3389/fmars.2018.00507

Morley, S. A., Hirse, T., Thorne, M. A. S., Pörtner, H. O., & Peck, L. S. (2012). Physiological plasticity, long term resistance or acclimation to temperature, in the Antarctic bivalve, Laternula elliptica. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *162*(1), 16–21. https://doi.org/10.1016/j.cbpa.2012.01.009

Navarro, J. M., Paschke, K., Ortiz, A., Vargas-Chacoff, L., Pardo, L. M., & Valdivia, N. (2019). The Antarctic fish Harpagifer antarcticus under current temperatures and salinities and future scenarios of climate change. *Progress in Oceanography*, *174*, 37–43. https://doi.org/10.1016/j.pocean.2018.09.001

Nicol, S. (2006). Krill, Currents, and Sea Ice: Euphausia superba and Its Changing Environment. *BioScience*, *56*(2), 111–120. https://doi.org/10.1641/0006-3568(2006)056[0111:KCASIE]2.0.CO;2

Niemandt, C., Kovacs, K. M., Lydersen, C., Dyer, B. M., Isaksen, K., Hofmeyr, G. J. G., Mehlum, F., & Bruyn, P. J. N. de. (2016). Chinstrap and macaroni penguin diet and demography at Nyrøysa, Bouvetøya. *Antarctic Science*, *28*(2), 91–100. https://doi.org/10.1017/S0954102015000504

Paleczny, M., Hammill, E., Karpouzi, V., & Pauly, D. (2015). Population Trend of the World's Monitored Seabirds, 1950-2010. *PLOS ONE*, *10*(6), e0129342. https://doi.org/10.1371/journal.pone.0129342

Palmisano, A. C., & Sullivan, C. W. (1982). Physiology of Sea Ice Diatoms. I. Response of Three Polar Diatoms to a Simulated Summer-Winter Transition1. *Journal of Phycology*, *18*(4), 489–498. https://doi.org/10.1111/j.1529-8817.1982.tb03215.x

Patterson, D. L. (2001). *The effects of human activity and environmental variability on long-term changes in Adélie penguin populations at Palmer Station, Antarctica* [PhD Thesis, Montana State University-Bozeman, College of Letters & Science]. https://scholarworks.montana.edu/xmlui/bitstream/handle/1/8056/31762103446934.pdf?sequence=1

Pichegru, L., Grémillet, D., Crawford, R. J. M., & Ryan, P. G. (2010). Marine no-take zone rapidly benefits endangered penguin. *Biology Letters*, *6*(4), 498–501. https://doi.org/10.1098/rsbl.2009.0913

Pütz, K., Ingham, R., Smith, J., & Croxall, J. (2001). Population trends, breeding success and diet composition of Gentoo Pygoscelis papua , magellanic Spheniscus magellanicus and rockhopper Eudyptes chrysocome penguins in the Falkland Islands. A review. *Polar Biology*, *24*(11), 793–807. https://doi.org/10.1007/s003000100293

Ridoux, V., & Offredo, C. (1989). *The Diets of Five Summer Breeding Seabirds in Ad61ie Land, Antarctica*. *9*, 137–145.

Robinson, S. A., & Hindell, M. A. (1996). Foraging ecology of Gentoo Penguins Pygoscelis papua at Macquarie Island during the period of chick care. *Ibis*, *138*(4), 722–731. https://doi.org/10.1111/j.1474-919X.1996.tb08829.x

Rombolá, E. F., Marschoff, E., & Coria, N. (2010). Inter-annual variability in Chinstrap penguin diet at South Shetland and South Orkneys Islands. *Polar Biology*, *33*(6), 799–806. https://doi.org/10.1007/s00300-009-0757-4

Ropert-Coudert, Y., Chiaradia, A., Ainley, D., Barbosa, A., Boersma, P. D., Brasso, R., Dewar, M., Ellenberg, U., García-Borboroglu, P., Emmerson, L., Hickcox, R., Jenouvrier, S., Kato, A., McIntosh, R. R., Lewis, P., Ramírez, F., Ruoppolo, V., Ryan, P. G., Seddon, P. J., … Trathan, P. N. (2019). Happy Feet in a Hostile World? The Future of Penguins Depends on Proactive Management of Current and Expected Threats. *Frontiers in Marine Science*, *6*. https://www.frontiersin.org/articles/10.3389/fmars.2019.00248

Saba, G. K., Fraser, W. R., Saba, V. S., Iannuzzi, R. A., Coleman, K. E., Doney, S. C., Ducklow, H. W., Martinson, D. G., Miles, T. N., Patterson-Fraser, D. L., Stammerjohn, S. E., Steinberg, D. K., & Schofield, O. M. (2014). Winter and spring controls on the summer food web of the coastal West Antarctic Peninsula. *Nature Communications*, *5*(1), 4318. https://doi.org/10.1038/ncomms5318

Santora, J. A., LaRue, M. A., & Ainley, D. G. (2020). Geographic structuring of Antarctic penguin populations. *Global Ecology and Biogeography*, *29*(10), 1716–1728. https://doi.org/10.1111/geb.13144

Sauser, C., Delord, K., & Barbraud, C. (2021). Sea ice and local weather affect reproductive phenology of a polar seabird with breeding consequences. *Ornithological Applications*, *123*(4), duab032. https://doi.org/10.1093/ornithapp/duab032

Schofield, O., Ducklow, H. W., Martinson, D. G., Meredith, M. P., Moline, M. A., & Fraser, W. R. (2010). How Do Polar Marine Ecosystems Respond to Rapid Climate Change? *Science*, *328*(5985), 1520–1523. https://doi.org/10.1126/science.1185779

Stammerjohn, S., Massom, R., Rind, D., & Martinson, D. (2012). Regions of rapid sea ice change: An inter-hemispheric seasonal comparison: REGIONS OF RAPID SEA ICE CHANGE. *Geophysical Research Letters*, *39*(6), n/a-n/a. https://doi.org/10.1029/2012GL050874

Strycker, N., Wethington, M., Borowicz, A., Forrest, S., Witharana, C., Hart, T., & Lynch, H. J. (2020). A global population assessment of the Chinstrap penguin (Pygoscelis antarctica). *Scientific Reports*, *10*(1), Article 1. https://doi.org/10.1038/s41598-020-76479-3

Takahashi, A., Ito, M., Nagai, K., Thiebot, J., Mitamura, H., Noda, T., Trathan, P., Tamura, T., & Watanabe, Y. (2018). Migratory movements and winter diving activity of Adélie penguins in East Antarctica. *Marine Ecology Progress Series*, *589*, 227–239. https://doi.org/10.3354/meps12438

Tanton, J. L., Reid, K., Croxall, J. P., & Trathan, P. N. (2004). Winter distribution and behaviour of Gentoo penguins Pygoscelis papua at South Georgia. *Polar Biology*, *27*(5), 299–303. https://doi.org/10.1007/s00300-004-0592-6

Tarling, G. A., & Fielding, S. (2016). Swarming and Behaviour in Antarctic Krill. In V. Siegel (Ed.), *Biology and Ecology of Antarctic Krill* (pp. 279–319). Springer International Publishing. https://doi.org/10.1007/978-3-319-29279-3_8

Tewari, K., Mishra, S. K., Salunke, P., & Dewan, A. (2022). Future projections of temperature and precipitation for Antarctica. *Environmental Research Letters*, *17*(1), 014029. https://doi.org/10.1088/1748-9326/ac43e2

Tierney, M., Emmerson, L., & Hindell, M. (2009). Temporal variation in Adélie penguin diet at Béchervaise Island, east Antarctica and its relationship to reproductive performance. *Marine Biology*, *156*(8), 1633–1645. https://doi.org/10.1007/s00227-009-1199-9

Trathan, P. N., García-Borboroglu, P., Boersma, D., Bost, C.-A., Crawford, R. J. M., Crossin, G. T., Cuthbert, R. J., Dann, P., Davis, L. S., De La Puente, S., Ellenberg, U., Lynch, H. J., Mattern, T., Pütz, K., Seddon, P. J., Trivelpiece, W., & Wienecke, B. (2015). Pollution, habitat loss, fishing, and climate change as critical threats to penguins. *Conservation Biology*, *29*(1), 31–41. https://doi.org/10.1111/cobi.12349

Trivelpiece, W. Z., Trivelpiece, S. G., Geupel, G. R., Kjelmyr, J., & Volkman, N. J. (1990). Adélie and Chinstrap Penguins: Their Potential as Monitors of the Southern Ocean Marine Ecosystem. In K. R. Kerry & G.

Hempel (Eds.), *Antarctic Ecosystems* (pp. 191–202). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-84074-6_20

Trivelpiece, W. Z., Trivelpiece, S. G., & Volkman, N. J. (1987). Ecological Segregation of Adélie, Gentoo, and Chinstrap Penguins at King George Island, Antarctica. *Ecology*, *68*(2), 351–361. https://doi.org/10.2307/1939266

Vaughan, D. G., Marshall, G. J., Connolley, W. M., Parkinson, C., Mulvaney, R., Hodgson, D. A., King, J. C., Pudsey, C. J., & Turner, J. (2003). Recent Rapid Regional Climate Warming on the Antarctic Peninsula. *Climatic Change*, *60*(3), 243–274. https://doi.org/10.1023/A:1026021217991

Veytia, D., Bestley, S., Kawaguchi, S., Meiners, K. M., Murphy, E. J., Fraser, A. D., Kusahara, K., Kimura, N., & Corney, S. (2021). Overwinter sea-ice characteristics important for Antarctic krill recruitment in the southwest Atlantic. *Ecological Indicators*, *129*, 107934. https://doi.org/10.1016/j.ecolind.2021.107934

Vignon, É., Roussel, M.-L., Gorodetskaya, I. V., Genthon, C., & Berne, A. (2021). Present and Future of Rainfall in Antarctica. *Geophysical Research Letters*, *48*(8), e2020GL092281. https://doi.org/10.1029/2020GL092281

Volkman, N. J., Presler, P., & Trivelpiece, W. (1980). Diets of Pygoscelid Penguins at King George Island, Antarctica. *The Condor*, *82*(4), 373. https://doi.org/10.2307/1367558

Walsh, J., Reiss, C., & Watters, G. (2020). Flexibility in Antarctic krill Euphausia superba decouples diet and recruitment from overwinter sea-ice conditions in the northern Antarctic Peninsula. *Marine Ecology Progress Series*, *642*, 1–19. https://doi.org/10.3354/meps13325

Watanuki, Y., Mori, Y., & Naito, Y. (1994). Euphausia superba dominates in the diet of Adélie penguins feeding under fast sea-ice in the shelf areas of Enderby Land in summer. *Polar Biology*, *14*, 429–432.

Wethington, M., Flynn, C., Borowicz, A., & Lynch, H. J. (2023). Adélie penguins north and east of the 'Adélie gap' continue to thrive in the face of dramatic declines elsewhere in the Antarctic Peninsula region. *Scientific Reports*, *13*(1), Article 1. https://doi.org/10.1038/s41598-023-29465-4

Wiedenmann, J., Cresswell, K. A., & Mangel, M. (2009). Connecting recruitment of Antarctic krill and sea ice. *Limnology and Oceanography*, *54*(3), 799–811. https://doi.org/10.4319/lo.2009.54.3.0799

Wienecke, B. C., Lawless, R., Rodary, D., Bost, C.-A., Thomson, R., Pauly, T., Robertson, G., Kerry, K. R., & LeMaho, Y. (2000). Adélie penguin foraging behaviour and krill abundance along the Wilkes and Adélie land coasts, Antarctica. *Deep Sea Research Part II: Topical Studies in Oceanography*, *47*(12), 2573–2587. https://doi.org/10.1016/S0967-0645(00)00036-9

Williams, T. D. (1995). *The Penguins: Spheniscidae*. Oxford University Press.

Wilson, R. P., Alvarrez, B., Latorre, L., Adelung, D., Culik, B., & Bannasch, R. (1998). The movements of Gentoo penguins Pygoscelis papua from Ardley Island, Antarctica. *Polar Biology*, *19*(6), 407–413. https://doi.org/10.1007/s003000050266

2

Chapter 2

Record phenological responses to climate change in three sympatric penguin species

Abstract.

The timing of breeding and its flexibility are important aspects of many species' realised niche, reflecting adaptations to synchronise with food supplies, dilute predation, avoid competition, and exploit abiotic seasonal fluctuations. Breeding phenology is typically studied through long-term monitoring of focal populations, making it difficult to characterize species-wide traits and trends. Here I analyse the start of the breeding season of three sympatric Pygoscelid species of penguins (Adélie, Chinstrap and Gentoo) at a sub-continental scale for a decade (2011-2021). I use a network of 83 time-lapse cameras to monitor 37 colonies across the Antarctic Peninsula and sub-Antarctic islands. I find the breeding seasons for all three species advanced at record rates (10.2 ± 2, 10.4 ± 1.5, and 13 ± 4 days/decade, respectively) showing great adaptive capabilities. Phenological change shows great intra- and inter-species variability but, in all three species, advances are related to local environmental warming. The differences in response between the foraging generalist Gentoos (with local populations increasing) and the foraging specialists Adélies and Chinstraps (local populations decreasing) suggest recent changes selectively handicap Chinstraps and Adélies while Gentoo populations grow. If these trends continue, they could lead to increased competition between species, a risk of trophic mismatch, and a reshape of community assemblages in the near future.

Introduction.

In seasonally breeding organisms, the timing of breeding (phenology) is one of the most important aspects of a species' realised niche, reflecting adaptations to match the best possible conditions for reproduction (Perrins, 2008; Visser & Both, 2005). This often means synchronizing the maximal offspring growth period to the maximum (Perrins, 2008) or best quality (Rubenstein & Wikelski, 2003) of resources.

For birds, the start of the season constrains the timing of all subsequent life-history events (Ainley, 2002; Perrins, 2008). Early breeding is especially favoured by colonial breeders such as seabirds, since early arrivals occupy prime breeding areas (Bennett et al., 2022; Sergio et al., 2007) and enjoy increased reproductive success (Madsen et al., 2007; Verhulst & Nilsson, 2008), with more experienced birds being more successful (Bennett et al., 2022; Daunt et al., 1999). Early breeding is further favoured as early completion can be linked to increased breeding success in the following breeding season (Fayet et al., 2016).

Other factors constrain how early individuals can breed, such as food availability at the breeding (Regehr & Rodway, 1999; Whelan et al., 2022) or wintering areas (Dobson et al., 2017), since starting the breeding season in good body condition is key for reproductive success (Vleck & Vleck, 2002). In polar environments phenology is chiefly constrained by 'hard limits' to the season, most importantly the possibility to access nesting or foraging areas (Madsen et al., 2007; Stenson & Hammill, n.d.; Whelan et al., 2022). Finally, colonial birds need to ensure breeding occurs synchronously (Burr et al., 2016), since being an outlier results in agreater predation risk (Davis, 1982).

To respond to these needs (combining early onset of breeding with optimal conditions for reproductive success) many species have evolved sensitivity to a variety of external biotic and abiotic cues. One of the most common is temperature (Burnside et al., 2021; Samplonius et al., 2021) although rainfall (Cayuela et al., 2014), flowering (McGrath et al., 2022), photoperiod (Dawson et al., 2001) or changes in food quality (Rubenstein & Wikelski, 2003) have been described as proximate cues for different species. Cue determination is difficult since they are not exclusive, are often hierarchical (Chmura et al., 2020) and in migratory species they can be linked to remote over-wintering areas (Winkler et al., 2014).

Following these cues in a context of environmental change risks a phenological mismatch between predators and their prey (Parmesan, 2006; Samplonius et al., 2021; Thackeray et al., 2016; Visser et al., 2012) since different taxa tend to respond to different cues (or differently to the same cues) (Thackeray et al., 2010, 2016). This risk exists both for species that have changed their phenology (mostly advancing it (Cole et al., 2021; Parmesan, 2006; Visser et al., 2012) though with notable exceptions (Barbraud & Weimerskirch, 2006; Dobson et al., 2017; Whelan et al., 2022)) as well as for those that have not (most seabirds) (Keogan et al., 2018). Even if predators match their prey's shift (Matthysen et al., 2011; Parmesan, 2006; Visser et al., 2012) these changes might not be cost-free, as breeding outside the usual times have other costs like carry-over effects (Fayet et al., 2016; Parmesan, 2006; Regehr & Rodway, 1999; Shoji et al., 2015). Predator phenology monitoring is therefore an early indicator of disturbance to the individuals (Cerini et al., 2023) but also to their environment (Croxall et al., 2012).

In this study I monitor colonies of three sympatric Pygoscelid penguins that inhabit the Antarctic Peninsula (AP), the Adélie (*Pygoscelis adeliae*), Chinstrap (*P. antarcticus*) and Gentoo penguins (*P. papua*). These species are key sentinels of the Southern Ocean given their distribution throughout the Antarctic coast (Santora et al., 2020) and their role of top consumers of marine productivity alongside seals and whales (McCormack et al., 2021). High colony fidelity allows for the building of long time-series that allow us to witness system change through time (Barbraud & Weimerskirch, 2006; Burr et al., 2016; J. T. Hinke et al., 2007).

All three species nest on snow-free ground, forming colonies that range in size between the dozens and the tens of thousands of nests. Each pair lays on average two eggs per season and it takes approximately three months to fledge. While Adélies and Chinstraps are krill specialists, Gentoos are generalists and can switch to fish for large portions of their diet. In winter, Adélie and Chinstrap penguins migrate away from the colony, while Gentoo penguins tend to be more resident (Williams, 1995).

Despite their similarities and their sympatry, the three species are currently experiencing diverging population trends. Adélie penguin populations have been decreasing throughout the AP despite general increases in the cooler east Antarctica (Che-Castaldo et al., 2017). Chinstrap penguins are the most abundant of the genus, but are in general decline throughout their range (Strycker et al., 2020). Gentoos, a more-temperate species (or group of species), are increasing in number and establishing new colonies throughout the AP (Clucas et al., 2015; Herman et al., 2020).

Due to the challenging logistics of Antarctic work, most studies have been conducted at and around research stations. Recently, this has been partially overcome by using remote sensing techniques to track population changes either by conducting detailed drone surveys (Borowicz et al., 2018; Pfeifer et al., 2019) or using satellites to estimate population size (Fretwell et al., 2012; H. J. Lynch, White, et al., 2012). Still, population counts of such long-lived species can only warn us of disruptions once numbers have fallen and the breeding population decline is already underway. More nuanced behavioural or productivity studies that can warn of a disruption before populations collapse are still beyond those techniques (Cerini et al., 2023; McDowall & Lynch, 2019).

To overcome these difficulties I use an extensive remote network of time-lapse cameras to acquire high-resolution behavioural metrics at remote colonies unstrained by proximity to a research station. Here I focus on the phenology at the start of the breeding season and how recent changes in the environmental conditions along the AP have impacted breeding behaviour. I do this over a period of ten years and across most of the breeding range of each of these species in the AP as well as on a number of sub-Antarctic islands around the Scotia Sea. The AP has been one of the fastest warming areas in the world in the late 20th century (Vaughan et al., 2003) and again in the 2015-2020 period (Carrasco et al., 2021). Our aim is to quantify the magnitude of phenological shifts and to examine possible environmental drivers behind those shifts. Finally, I look at phenology data from the historical literature to understand how the current situation compares to those prior to marked warming.

Materials and Methods.

Remote time-lapse cameras (Reconyx HC500 Hyperfire and Reconyx Ultrafire Trail Cameras; commercially available from Reconyx Inc., Holmen, WI, USA) were used to monitor penguin colonies at 83 locations over various time periods between the 2010-2011 and 2020-2021 breeding seasons (Figure 1; See Appendix S2.1 for camera numbers, locations and abbreviations). I personally joined this effort in the 2018-2019 season and have participated in data collection since, however it is important to note the Penguin Watch Network forms part of a collective effort as 2 to 5 teams of two are deployed every year in the field to gather this data. Cameras were located overlooking nests (Southwell & Emmerson, 2015) with each camera fixed to an aluminium scaffold pole secured using a tripod or wire rock basket (Jones et al., 2018). Each unit was constructed during the austral summer (October to February), and serviced over subsequent summers when weather and ice conditions permitted. Cameras were programmed to capture images once per hour five to twenty-four times a day.

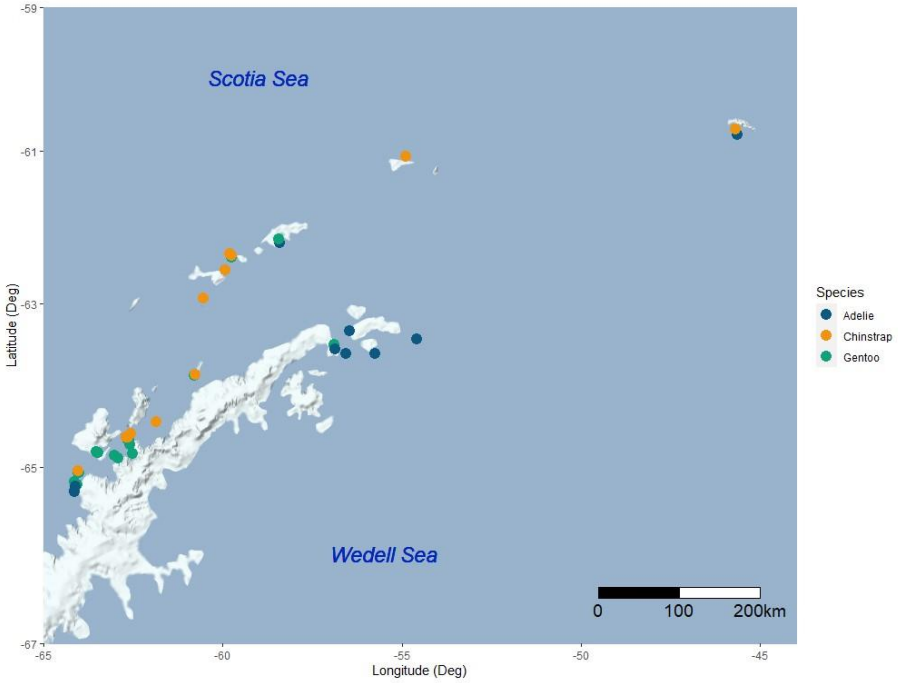
Upon recovery, time-lapse images were processed using custom R (version 4.0.5; R Core Team, 2020) scripts and Exiftool to extract date, time and temperature metadata. Images were referenced to a unique code including location, season and image number.

Settlement dates

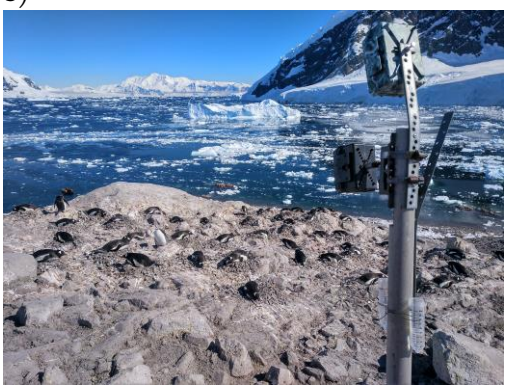
To study breeding phenology I have chosen “colony settlement” as a parameter to signal season start since it offers a more standardized metric to compare between years and colonies over “first arrival”. Individual first arrivals are by definition outliers and their use is discouraged as a phenological measure as not representative of their population (Inouye et al., 2019). Gentoos particularly have an intermittent presence throughout winter, rendering the traditional first arrival metric inadequate and it proved impossible to justify choosing any single arrival over any other. I defined colony settlement as the first date with no images of an empty field of view that stays as such for the rest of the season.

In order to estimate camera settlement dates, I manually examined 475 season starts in a randomized order to avoid anchoring bias within colonies (Appendix S2.1). Of those, 277 seasons had enough images (sometimes cameras run out of battery before I get to them) and enough visibility (often cameras get snowed over) to reliably determine a date.

a)



b)



c)



Figure 1: Study setup. a) Map of the study area, showing the geographic extent of the cameras across the Antarctic Peninsula, South Shetland Islands and the South Orkney Islands. b) Example of monitoring camera at Neko Harbour. c) An example of a single image from the camera deployed at Neko Harbour.

Temperature variables

These two variables related to warming were selected to test the effect of climate change on breeding behaviour. Both were constructed using the dataset including the 11am to 1pm in-built camera temperature log, since these are the hours common to all cameras. I ground-truthed camera-based temperature measurements against several years of measurements from the weather station at Jane Col, Signy Island (Polar Data Centre, U. K et al., 2021) to check for accuracy and bias (See Appendix S2.2). The result of that analysis shows there is a consistent bias throughout the temperature range of +2ºC that I corrected for in our analysis.

I derived median spring temperature (September to November) as a broad measure of season warmth at each colony. I also extracted the proportion of days with any temperature readings above zero degrees in October (the month in which all three species settle on average). This latter variable captures freezing temperatures and was chosen as a proxy for ice-allowing conditions at and around the colony.

Statistics

I modelled settlement using mixed models using latitude as well as all three combinations of the two environmental variables as fixed effects and colony as random effect to account for possible pseudoreplication (Appendix S2.3). These models were fitted with the *lmer* function (*lme4* package in R) and compared and tested for colinearity using the *performance* package. The final model was selected according to Akaike's Information Criterion (AIC); in case of a draw ($\Delta AIC < 2$) the simplest model was kept. The t-value is also presented for all fixed effects and marked red if |t-val|>2 (the equivalent of a significative result in usual linear models). All other models (latitude, temperature rise, etc) included a random effect for colony unless stated otherwise. Collinearity was low among all covariates in all models. Further details on model building and selection can be found in Appendix S2.3 (Tables 3, 4, and 5 respectively for Adelies, Chinstraps and Gentoos).

Results.

Decadal phenological shift

Over the ten year study period, all three species shifted towards earlier colony settlement across all latitudes (Figure 2). The rate and geographical pattern of this advance differs between species.

Adélie Penguins

Adélie Penguins on the AP started their breeding on average on the 15th of October ± 4.07 days, the earliest of the three species. During the study period settlement date has been moving forward at a rate of 1.02 ± 0.2 days per year (t-value = -4.9; model details in Appendix S2.3, Table S1). This phenological shift is not uniform among Adélies and differs according to geographic region (Figure 2). The southernmost PETE and YALO colonies both show a steady advance of the settlement date at a similar rate (purple; Figure 2). All three colonies in Signy Island show almost identical slopes despite their differences in settlement date (Yellow; Figure 2). Colonies in the Weddell Sea (BROW, HERO and PAUL in light blue) all show a stable trend (Figure 2). The exception are the colonies on King George Island (South Shetland), where LLAN colonies show some of the steepest advancements in phenology. The only Adélie colony in this study outside Antarctica is located on Saunders Island (South Sandwich Islands) and also seems to advance in its settlement dates (See Appendix S2.4 for sub-Antarctic Islands figures).

Chinstrap Penguins

Chinstrap Penguins settle in their colonies on average on the 29th of October ± 6.4 days; that date has been advancing almost year on year at a rate of 1.04 ± 0.15 days per year (t-value = -6.6; Appendix S2.3 Table S1). All the Chinstrap colonies in the AP display similar advances in their settlement date regardless of latitude (Figure 2). The only exception is their northernmost colonies: Signy Island, South Orkney (Figure 2) and Saunders Island, South Sandwich Islands (Appendix S2.4).

Gentoo Penguins

Gentoo Penguins on the AP are the last to settle (1st November ± 16.0 days). Their settlement dates span over a very wide "window" of almost six weeks inside which they display great variability both within and among colonies (Figure 2). Despite the greater variation in trends and rates, their phenology has overall been advancing at a greater rate than that of the other two species; this is true for the colonies on the AP (-1.3 ± 0.4 days/year. t-value = -2.7; Appendix S2.3 Table 1) as well as for their colonies around the Scotia Sea (-2.0 ± 1.2 days/year. t-value = -1.7; Appendix S2.3 Table 1). Gentoo penguins around the Scotia Sea displayed the earliest settlement dates, on average on the 4th of October ± 11.8 days.

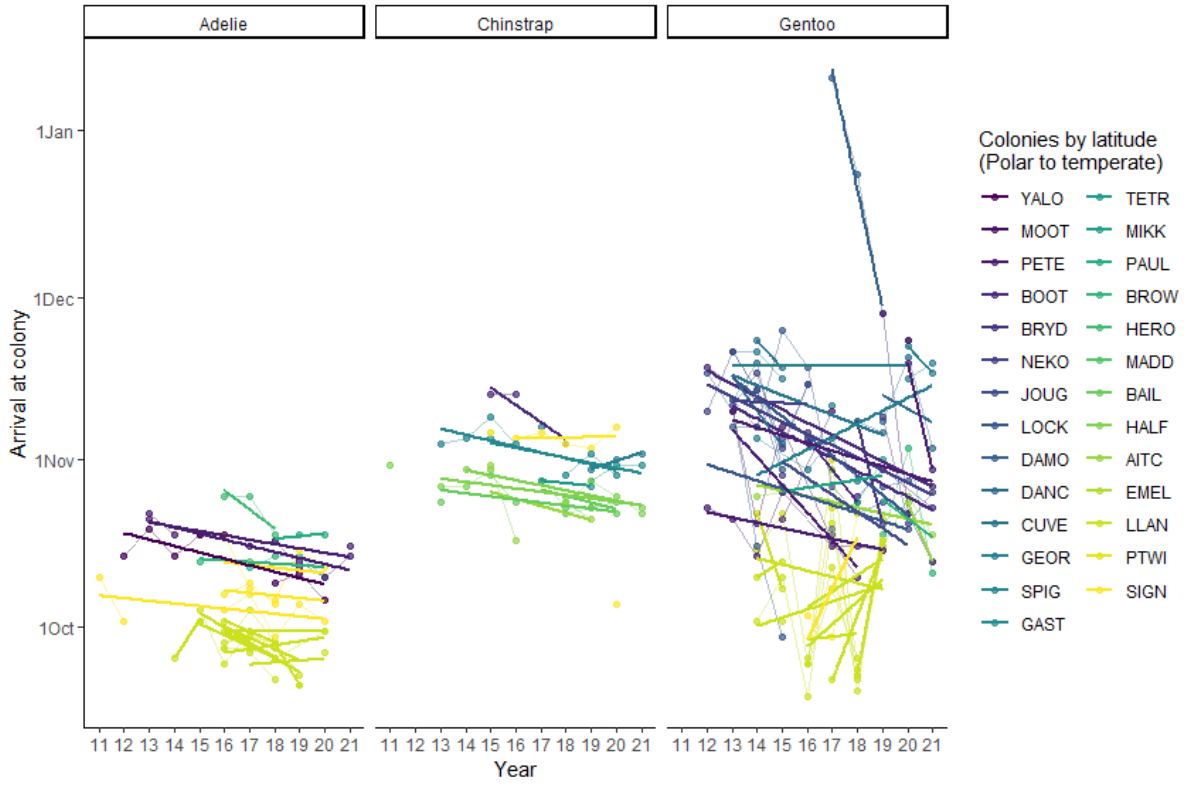


Figure 2: Colony settlement is occurring consistently earlier in Antarctic penguins. The main plots show the time series for the settlement date as estimated from each monitoring camera for each species through the period of study. Settlement data for each camera is overlaid with their respective regression lines to ease interpretation and coloured according to their latitude from higher -more polar- latitudes (darker) to lower -more temperate- latitudes (brighter). For the equivalent plot on colonies in the Scotia Sea see Appendix S2.4. Full details of all camera locations are provided in Appendix S2.1.

Latitudinal gradient

Spatially, the phenology of all three species on the AP depends heavily on the latitude of their colonies, with southern (more polar) colonies displaying later starts than northern (more temperate) ones (Figure 3, Table 1). The relationship established between latitude and colony settlement only applies to colonies in the AP. The trend does not hold for any sub-Antarctic colonies (they breed much earlier; Appendix S2.4) nor for colonies on the South Orkney Islands (SIGN) or even on Elephant Island (PTWI).

Environmental factors

During the study period I observe widespread rises in the average midday temperatures throughout the whole study area at almost all colonies for all species and at every latitude (Appendix S2.3 Figure S1). The average temperature change per year for the relevant months (once controlling for colony effect) are 0.37± 0.05ºC/year (August), 0.41 ± 0.08ºC/year (September), 0.2 ± 0.05ºC/year (October) and 0.44 ± 0.04ºC/year (November; Appendix S2.3 Table S2). In all three species phenological advance is related to at least one of the two warming-related variables in study (Figures 4 and 5, Table 1).

Adélie Penguin settlement date depends greatly on local conditions, since the variable 'colony' explains 64% of the variance as a random effect (Table 1). Latitude of the colony and both environmental variables are considered significant ($|$ t-val $|$ >2). It is worth noting that while settlement advance is related to an increase in spring air temperature, a greater proportion of days above zero in October actually delays settlement. Settlement of Chinstrap Penguins, contrary to Adélies, does not seem to be greatly influenced by colony as a random effect (22% of variance explained; Table 1). Regarding fixed effects, both environmental variables are retained in the model with similar estimates to those in the Adélie model. Gentoo Penguins were quite influenced by local conditions with colony accounting for almost 50% of the variance as a random effect. In this species, median spring air temperature was dropped from the model and only the proportion of October days above zero was retained (Table 1). Finally, I did not find the rate of phenological change to be related with latitude for any of the species.

Historical data

Comparing our settlement data with the historical records on "Return to colony" data available for our colonies (as gathered from Black (2016)) shows differences between regions of the area of study (See Appendix S2.6). In colonies at South Orkney and the Weddell Sea "return to colony" is recorded generally before or at the same time as our records for settlement. At the South Shetland Islands half of our data falls within intervals of dates seen in historical data. Finally, at colonies on the Western Antarctic Peninsula our "settlement" data happens clearly earlier than historical "return to colony data". Unfortunately, the amount of data per region is not enough to go beyond a qualitative description.

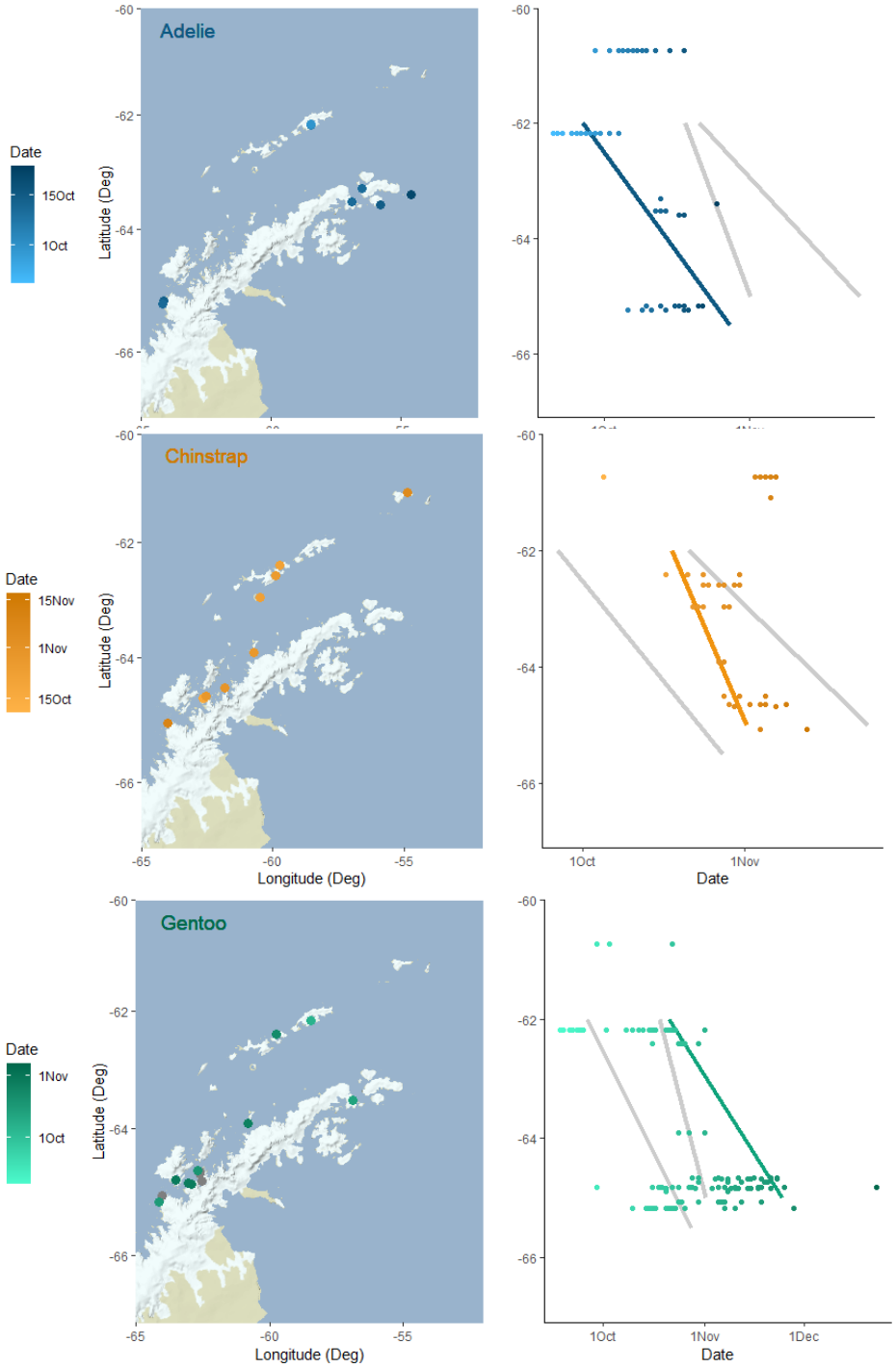


Figure 3: Arrival to and departure from the colony are influenced by latitude in the AP. The left hand map of each species shows the location of camera-monitored colonies. Colour indicates mean arrival date, as defined in the main text. Right: Scatterplot showing the relationship between arrival and departure dates and latitude. Datapoints are overlaid with a simple regression line to make the relationship more evident; regression lines from the other two species are shown in grey colour to ease comparison.

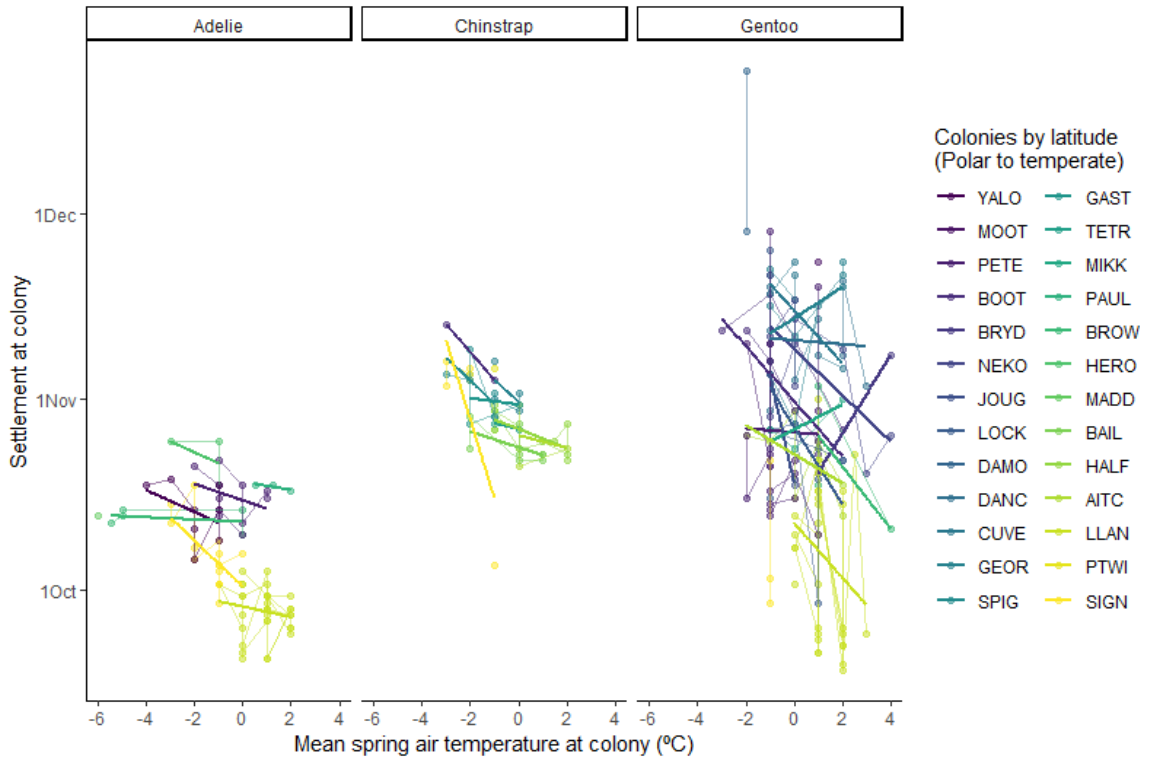


Figure 4: Arrival happens earlier in warmer years. Estimated settlement date by median spring air temperature for all cameras present at Antarctic Colonies. Points belonging to the same camera are linked together and a linear regression is shown for each colony to ease interpretation. Regressions as well as linked datapoints are coloured by colony according to their latitude from more polar (darker) to more temperate (brighter). For colonies around the Scotia Sea see Appendix S2.4.

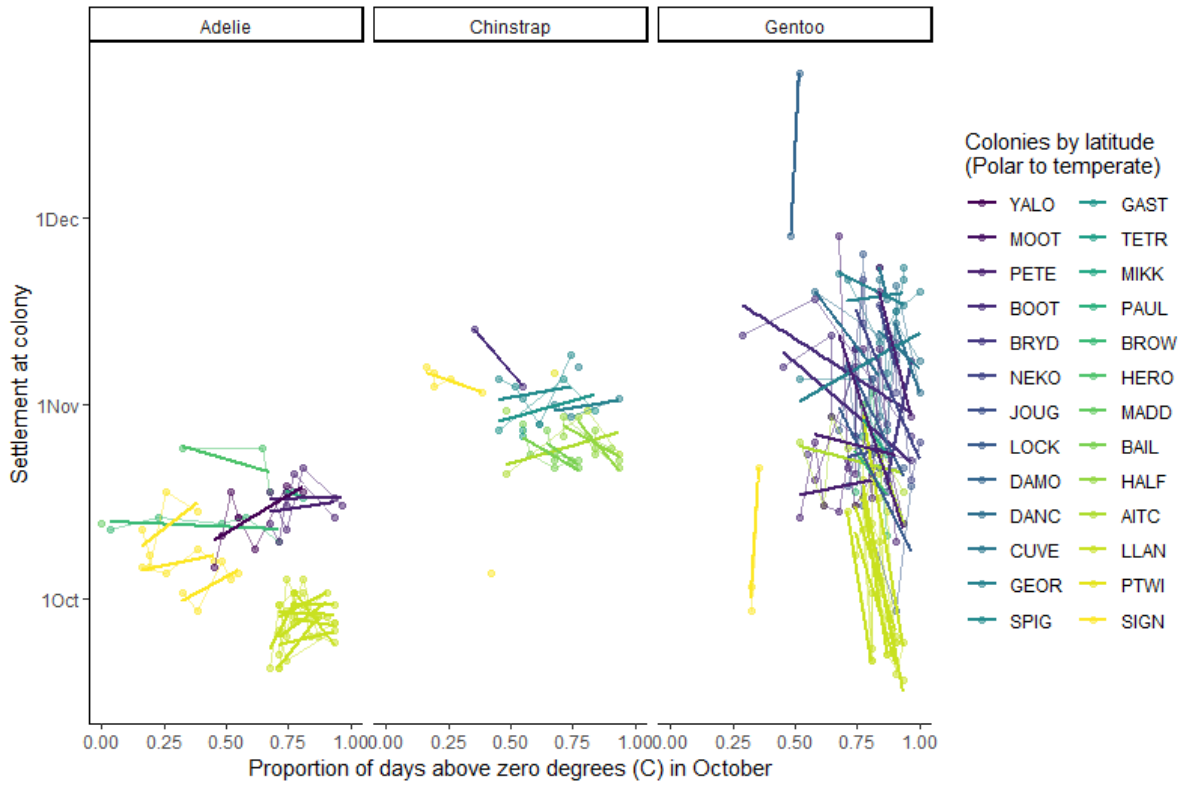


Figure 5: Settlement and proportion of days above freezing. Estimated settlement date by the proportion of days above zero in October for all cameras in Antarctica. Points belonging to the same camera are linked together and a linear regression is shown for each colony to ease interpretation. Regressions as well as linked datapoints are coloured by colony according to their latitude from polar (darker) to more temperate (brighter) locations. For colonies around the Scotia Sea see Appendix S2.4.

Table 1: Model summary. The three models that best explain the settlement of penguins at their respective colonies correspond to the following three models. These were models were selected using AIC from all combinations of models including: median spring air temperature, percentage of days above zero degrees in October and latitude as the fixed effects while controlling for colony as random effect. T-values are presented for all fixed effects and marked red if |t-val|>2 (the equivalent of a significant result in usual linear models). More on model selection in Appendix S2.3, Tables 3, 4 and 5 respectively for Adelie, Chinstrap and Gentoo penguins.

Adélie settlement date model Fixed Effects: Median spring air temperature + October days above zero + Latitude. Random Effects: Colony		Variable (Random)	Variance explained
		Colony	6.4 (64%)
		Residual	3.5 (35.4%)
Variable (Fixed)	Estimate	Std. Error	T-value
Intercept	-284.6	110.4	-2.56
Latitude	-5.927	1.6	-3.67
Median spring air temp.	-1.8	0.5	-3.3
October Days above 0ºC	13.2	4.9	2.6
Chinstrap settlement date model Fixed Effects: Median spring air temperature + October days above zero + Latitude. Random Effects: Colony		Variable (Random)	Variance explained
		Colony	2.9 (22.5%)
		Residual	7.9 (77.5%)
Variable (Fixed)	Estimate	Std. Error	T-value
Intercept	-75.3	55.6	-1.4
Latitude	-2.96	0.87	-3.4
Median spring air temp.	-2.47	0.57	-4.3
October Days above 0ºC	9.85	4.92	2.0
Gentoo settlement date model Fixed Effects: October days above zero + Latitude. Random Effects: Colony		Variable (Random)	Variance explained (and %)
		Colony	9.7 (48.5%)
		Residual	10.3 (51.5%)
Variable (Fixed)	Estimate	Std. Error	T-value
Intercept	-528.9	134.6	-3.93
October days above 0ºC	-29.3	8.8	-3.33
Latitude	-10.5	2.1	-5.01

Discussion.

Main findings

- Penguin colonies are warming at record speeds throughout the Antarctic Peninsula (Appendix S2.3 Table S2 and Figure S1).
- All three species of penguins are advancing their settlement phenology at record speeds regardless of the latitude of their colonies (Figure 2 and Table 1).
- Settlement phenology is also greatly influenced by the latitude of the colony with more northern colonies settling earlier (Figure 3 and Table 1).
  Their shift in phenology is related to warming, although this affects Gentoos differently to Adélies and Chinstraps (Figures 4 and 5 and Table 1).

Main discussion

I conducted this study during a period of rapid warming across the Western Antarctic Peninsula (Appendix S2.3 Figure S1). This is a well-established trend (Meredith et al., 2019) and concerns of ecosystem collapse pre-date this study (Kriegler et al., 2009). I note that the rates of change measured directly at our study colonies show an unprecedented temperature rise throughout the AP over the last decade (Appendix S2.3, Table S2). Our measurements (0.34 ± 0.07 °C/year; SM Table S2.3.2) show a rate of increase several times greater than the last estimates of warming for Antarctica (+0.061 ± 0.034 °C /year; (Clem et al., 2020)) or specifically the Western Antarctic Peninsula (+0.36°C between 2015 and 2020 (Carrasco et al., 2021)).

These results are not representative of the warming of the AP as a whole since these sampling locations are not random, but represent penguin choice based on favourable snow-free conditions (Williams, 1995). Despite these caveats, our data indicates that many penguin colony locations are warming much faster than any other region on Earth. Such temperature variation could significantly impact affected populations, particularly through changes in the seascape for sea-ice dependent penguins.

Record phenological advance

Over the ten-year study period all three species advanced their breeding season in relation to warming in the region (Figure 4; Table 1). Adélie and Chinstrap Penguins showed steady advances in their settlement date at their Antarctic colonies at a rate of just over 10 days over a decade (Table S3.1). Only colonies around the Weddell Sea show no phenological advance (SIGN for Chinstraps and HERO, MADD, PAUL for Adélies; Figure 2). Gentoo Penguins have advanced their breeding phenology at an overall rate of 13 days in a decade (Table 1). Variance in settlement data for Gentoos is much greater than in the other two species both between years and among colonies (Figure 2). Phenological advance happens in most individual colonies and also for the overall window in which colony establishment is observed to happen (Figure 2). This is consistent with previous studies on the phenology of incubation and hatching, that also agree on Gentoo's greater plasticity (J. Hinke et al., 2012; H. Lynch et al., 2012).

These shifts are among the fastest phenological changes observed in any animal (Romano et al., 2022). Relative to Cohen et al.'s (Cohen et al., 2018) global review of animal phenological responses to climate change, our data indicates Gentoos are undergoing the fastest phenological shift on record for *Aves* while Adélies and Chinstraps are respectively fourth and fifth. Relative to all vertebrates, these species would be first, fifth and sixth respectively (Cohen et al., 2018).

It is worth considering that the framing of each of the cameras sometimes changes year to years due to wind, ground shifting, mistakes made by the researchers upon servicing the cameras and snow. Despite these changes, each camera code is maintained for as long as the camera keeps looking at the same region of the colony so I do not expect these changes in framing to change the results of the settlement phenology greatly.

Environmental factors and species ecology

The phenological advance reported here is significantly related to a rapid increase in air temperatures for all three species (Figures 4 and 5; Table 1) despite differences in their ecology.

Adélie Penguins show a steady advance through the decade with colonies displaying similar shift rates in each region; colonies within either the Weddell Sea, South Shetland, South Orkney or Western Antarctic Peninsula all show similar rates of advance (Figure 2, Table 1). This is supported by the random factor location (colony) retaining most of the variance (64% of the model in Table 1). It is clear the advance is related to warming (Table 1, Figures 4 and 5), but how it translates into regionally-distinct phenological advance is a matter of speculation. In the past, sea ice extent has been known to impact breeding start date for Adélies (Arrigo et al., 2002; Kooyman et al., 2007) although snowfall or ocean productivity are also distinct regionally.

Chinstrap penguins show a similar rate of advance across their range (Figure 2) with little influence of local factors (only 22.5% of model variance; Table 1). Given their winter use of the Antarctic and sub-Antarctic maritime areas (Davis & Darby, 2012; J. T. Hinke et al., 2019), it is likely that the start of the breeding season is influenced by broad oceanic factors rather than local or regional events. Equivalent peninsula-wide similarities in Chinstrap behaviour across their range have also been found for incubation (J. T. Hinke et al., 2018).

Adélie and Chinstrap settlement dates are both influenced by the same two environmental variables (Table 1): spring air temperatures (Figure 4) and percentage of days below freezing in October (Figure 5). Both species are advancing their season in relation to an increase of the overall spring temperatures (Figure 4; Table 1), however the loss of days below freezing is concurrently delaying their phenology (Figure 5; Table 1). This is a complex scenario since they both mean warming, yet significantly relate to phenology change in opposite directions.

Temperature increases have previously been recorded to advance penguin phenology locally in response to warming (H. Lynch et al., 2012), and conversely, to delay breeding in cooling locations (Barbraud & Weimerskirch, 2006). The rate advance is also similar (Table 1) to those calculated previously for incubation in Adélies and Chinstraps (J. Hinke et al., 2012; H. Lynch et al., 2012). Rising temperatures might be allowing opportunities for earlier breeding; either through penguins using temperature as a proximate cue (Burnside et al., 2021; Winkler et al., 2014) or because of the melting of colony snow or sea-ice physically allowing the settlement (Madsen et al., 2007; Stenson & Hammill, n.d.). These observations are consistent with the lack of advance in colonies around the Weddell Sea (Figure 2) where I did not observe temperature change (Figure S3.1).

In opposition, the loss of freezing days is significantly pushing against the phenological advance in Adélies and Chinstraps (Figure 5, Table 1). I hypothesise this variable captures a known trend of sea-ice loss in the AP (Stammerjohn et al., 2008; Trivelpiece et al., 2011) or at least a loss of ice-forming conditions, since sea-ice is scarce north of Anvers Island even in winter (Stammerjohn et al., 2008).

This study also provides further evidence of a previously observed divergence between Adélies and Chinstraps in the AP, and Gentoos in the same region. The main divergence in our analysis between these species comes from the differing response to the loss of freezing conditions (Figure 2c, Table 1). Gentoos settled earlier in years with fewer freezing days (Figure 2c; Table 1), the factor that delayed its two congeners. I hypothesise this difference comes from Adélies and Chinstrap being differentially affected by sea-ice loss through their diet as Adélies in the AP and Chinstraps both overwhelmingly select for Antarctic krill (*Euphausia sp.*) [39,66,70–72] while Gentoos can frequently switch to fish [39,71,81,82].

The relationship between krill and sea-ice is complex and greatly depends on the life stage of krill and local conditions (Nicol, 2006; Walsh et al., 2020). Nonetheless, lack of ice hampers successful krill recruitment in the early season even in the relatively ice-free northern AP (Fraser & Hofmann, 2003; Saba et al., 2014; V & V, 1995). For Chinstraps and Adélies in the AP krill abundance is directly linked to reproductive success (Lynnes et al., 2004) and population declines (Trivelpiece et al., 2011). In fact early sea-ice retreat causes a diet shift towards fish consumption over krill in Adélies (Beaulieu et al., 2010) which increases foraging effort and

impacts juvenile recruitment (Fraser & Hofmann, 2003). Early sea-ice retreat has been seen to force Adélies to increase their fish consumption (Beaulieu et al., 2010).

I suggest these two species could be delaying their breeding season if they are taking longer to gain enough body condition to start the breeding process (Davis & Darby, 2012; Trivelpiece et al., 1990; Vleck & Vleck, 2002). Lack of krill would make it difficult for penguins to attain an adequate breeding weight, pushing against breeding advance. In general, food scarcity is the main and most common reason found to delay breeding in seabirds (Dobson et al., 2017; Regehr & Rodway, 1999; Whelan et al., 2022) and the need to gain weight prior to breeding is widely established as a factor of breeding success in penguins and other seabirds (Davis & Darby, 2012; Trivelpiece et al., 1990; Vleck & Vleck, 2002; Williams, 1995). In these two particular species krill loss has been linked to population declines in Adélies and Chinstraps, both krill specialists (Davis & Darby, 2012; Lynnes et al., 2004; McMahon et al., 2019; Williams, 1995).

The reduction of sea ice and the increase of ice-free days in the AP (Nicol, 2006; Walsh et al., 2020) likely makes this region more suitable for Gentoo penguins since they are non-migratory and need sea-ice-free winters (Korczak-Abshire et al., 2021). As Gentoos are generalists (McMahon et al., 2019; Miller et al., 2009, 2010; Williams, 1995), they would likely be less affected by a reduction in krill in the early season, other than through the effect on fish availability. Gentoos would not be as hampered by the effects ice-loss has on krill (Nicol, 2006), since Gentoos are foraging generalists that frequently switch between fish and krill. These concurrent factors possibly facilitate Gentoos' record phenological shift and their current expansion throughout the AP (Herman et al., 2020) or even the Weddell Sea (Wethington et al., 2023).

Adélie and Gentoos' phenological advance is more heavily influenced by local conditions (64% and 48% of variance respectively; Table 1) than Chinstraps' (22% of variance; Table 1). This influence of local conditions in Adélie and Gentoo's breeding phenology has been previously described (J. T. Hinke et al., 2007; H. Lynch et al., 2012) and has been attributed to snow accumulation at the colony location (Bricher et al., 2008; H. Lynch et al., 2012). There is a difference, however, since variance in Adélies is regional while Gentoos seem to vary colony to colony (Figure 2).

All three species show a similar and significant trend in relation to latitude (Figure 3). This differs from Black's (Black, 2016) analyses on historical data. This is possibly due to the use of Arrival as opposed to settlement as a metric and to the narrower latitudinal scope of this study. Here, the relationship of latitude and settlement date only holds for the AP with Scotia Sea colonies (and South Orkney colonies) falling out of the AP trend (Figure 3).

I have not identified the proximate signals that trigger the start of each species' breeding season. The strong dependence on temperature-related environmental variables suggest that fixed variables like daylight hours might not be the (only) environmental cues used to start the breeding season as suggested by Emmerson et al. (Emmerson et al., 2011). Photoperiod serves a role in marking the time to return from migration (Dunn et al., 2011) and in stimulating hormone production in preparation for the season (Ainley, 2002). Such a signal can be a pre-requisite of breeding initiation but could not explain the phenological advance seen here, since daylight hours are constant among years. Photoperiod-induced hormone control might still yet play a role in the future by serving as a hard limit on how early penguins can reproduce.

Increased competition

These three sympatric congeners have historically avoided competition through segregating their niches regarding breeding chronology, foraging behaviours, and life history traits (Trivelpiece et al., 1987). The increasingly less polar conditions of the AP will likely favour generalists (Gentoos) at the expense of polar specialists (Chinstraps and Adélies) (Clucas et al., 2015).

Foraging behaviour: Gentoos display a much more flexible diet than Adélies and Chinstraps (McMahon et al., 2019). Prey flexibility will be a great advantage to the Gentoos if sea-ice loss is affecting krill recruitment as discussed above. Gentoo colonies will be further favoured by sea-ice loss given their use of ice-free coastal waters both during summer and winter (Korczak-Abshire et al., 2021).

Life history: Gentoos stay at or close to their breeding colonies in winter while the other two Pygoscelids migrate. As Lynch et al. (H. J. Lynch, Naveen, et al., 2012) discuss, there are extra advantages to residents staying close to the colony over winter. They would benefit from access to local food resources in the early season and to immediate local knowledge (proximate breeding factors) over when to move on to land (H. J. Lynch, Naveen, et al., 2012) and give them a selective advantage over nesting space as seen in other bird species (Ahola et al., 2007).

Breeding chronology: In our cameras the average settlement order is Adélies-Chinstrap-Gentoos at every latitude of the AP studied (Figure 3) in contrast to many studies that report Gentoos as the first arrival (Black, 2016). Gentoo penguins' greater phenological advance weakens Pygoscelids' traditionally staggered breeding chronology understood to be a result of their respective sea-ice tolerances (Trivelpiece et al., 1987). This reduces their niche separation (J. Hinke et al., 2012; H. Lynch et al., 2012) and will likely mean increased inter-specific competition (Trivelpiece et al., 1987). It is very common to see intermittent Gentoo presence on nests in September or even throughout the winter. In mixed colonies, Gentoo's very early arrivals (weeks before any species settles) allow them to occupy Adélie and Chinstrap nests for days, although they are eventually displaced by the other two species upon arrival. The possibility of evicting Gentoos may become more difficult to displace if they have active nests when another species arrives.

In summary, Gentoos seem poised to win in a scenario of increased inter-specific competition given their greater flexibility in foraging behaviour, their year-round resident nature and the fact that Adélies and Chinstraps have a migration constraint.

Winners and losers of climate change

Worldwide, there is evidence that climate change allows generalist species to outcompete specialists as the latter lose their habitat while generalists' higher phenotypic plasticity allows them to cope better with high environmental variance (Davey et al., 2012; Morley et al., 2019). This contributes to a dynamic of "Winners and losers of climate change" among the three sympatric Pygoscelid species (Clucas et al., 2015) and is supported by the observed population trends recorded by MAPPPD at the study colonies ((Humphries et al., 2017); Appendix S2.5).

Over the last ten years, Gentoo penguin numbers have increased steadily (Appendix S2.5) and the species has established new colonies throughout the AP and into what was previously Adélie-only territory (Wethington et al., 2023). In contrast, most of the Adélie and Chinstrap colonies in our study have declined in recent years (Appendix S2.5). Some of the few colonies that have not experienced a decline are those that have remained phenologically stable (Figure 2), the Adélie colonies in the Weddell Sea, the same that have not seen warming (Appendix S2.3 Figure S1) or loss of sea ice (Kumar et al., 2021).

It has been difficult to establish population and phenology baselines before this study. The available 'Arrival' data generally lacks standardisation (records of different moments of the season and estimation methods) and is often an opportunistic occurrence in expeditions (resulting in a disparity of locations and sampling effort) (Black 2016; Humpfries et al., 2017). Comparing our settlement data to Black's (2016) review on historical phenology it is possible to see that our latest settlement data happens at the earliest recorded ranges of dates (Except for the Weddell Sea; Appendix S2.6). As "arrival" necessarily happens before "settlement", historical dates of settlement were likely much later than the arrival data reported. This means settlement phenology is advancing well beyond the oscillations in historical data. Although the ten year period of our study is relatively limited, the phenological advance identified is occurring at earlier dates than at any time in the 20th century.

Comments on the method

Camera traps have proven themselves as a cheap, autonomous, uninvasive and reliable way to acquire time-lapse imagery for wildlife monitoring in some of the harshest environments on Earth. It allows straightforward monitoring standardisation as well as reanalysis of the data should new methods or new research questions arise.

From marked penguin experiments I know Adélie and Gentoo adults often reoccupy nests in proximity to past nests (Spurr, 2008; Williams & Rodwell, 1992). It is impossible for us to know if this is our case but this would mean that samples from year to year would not be independent. However previous studies on phenology found the effect of ageing of a population in clutch initiation date was minimal (Youngflesh et al., 2018).

Next steps

This study has shown the three species are capable of a remarkable response to great environmental changes but it is unknown how much more elasticity will they be capable of displaying if temperatures keep rising at this rate. Previous studies have already shown evidence of phenological mismatch happening seasonally for Adélie Penguins (Youngflesh et al., 2017) as well as phenology changes affecting breeding output in the three species (J. Hinke et al., 2012). I am concerned either or both of these could be happening across the AP given the widespread phenological shifts shown in this paper. For this reason I encourage further studies on prey (krill and fish) availability and its phenology in coastal waters especially in the late winter and early breeding period.

References.

Ahola, M. P., Laaksonen, T., Eeva, T., & Lehikoinen, E. (2007). Climate change can alter competitive relationships between resident and migratory birds. *Journal of Animal Ecology*, *76*(6), 1045–1052. https://doi.org/10.1111/j.1365-2656.2007.01294.x

Ainley, D. G. (2002). *The Ad[]lie Penguin: Bellwether of Climate Change*. Columbia University Press.

Arrigo, K. R., van Dijken, G. L., Ainley, D. G., Fahnestock, M. A., & Markus, T. (2002). Ecological impact of a large Antarctic iceberg. *Geophysical Research Letters*, *29*(7), 8-1-8–4. https://doi.org/10.1029/2001GL014160

Barbraud, C., & Weimerskirch, H. (2006). Antarctic birds breed later in response to climate change. *Proceedings of the National Academy of Sciences*, *103*(16), 6248–6251. https://doi.org/10.1073/pnas.0510397103

Beaulieu, M., Dervaux, A., Thierry, A.-M., Lazin, D., Le Maho, Y., Ropert-Coudert, Y., SpÃ©e, M., Raclot, T., & Ancel, A. (2010). When sea-ice clock is ahead of Adélie penguins' clock. *Functional Ecology*, *24*(1), 93–102. https://doi.org/10.1111/j.1365-2435.2009.01638.x

Bennett, S., Harris, M. P., Wanless, S., Green, J. A., Newell, M. A., Searle, K. R., & Daunt, F. (2022). Earlier and more frequent occupation of breeding sites during the non-breeding season increases breeding success in a colonial seabird. *Ecology and Evolution*, *12*(9), e9213. https://doi.org/10.1002/ece3.9213

Black, C. E. (2016). A comprehensive review of the phenology of Pygoscelis penguins. *Polar Biol*, 29.

Borowicz, A., McDowall, P., Youngflesh, C., Sayre-McCord, T., Clucas, G., Herman, R., Forrest, S., Rider, M., Schwaller, M., Hart, T., Jenouvrier, S., Polito, M. J., Singh, H., & Lynch, H. J. (2018). Multi-modal survey of Adélie penguin mega-colonies reveals the Danger Islands as a seabird hotspot. *Scientific Reports*, *8*(1), 3926. https://doi.org/10.1038/s41598-018-22313-w

Bricher, P. K., Lucieer, A., & Woehler, E. J. (2008). Population trends of Adélie penguin (Pygoscelis adeliae) breeding colonies: A spatial analysis of the effects of snow accumulation and human activities. *Polar Biology*, *31*(11), 1397–1407. https://doi.org/10.1007/s00300-008-0479-z

Burnside, R. J., Salliss, D., Collar, N. J., & Dolman, P. M. (2021). Birds use individually consistent temperature cues to time their migration departure. *Proceedings of the National Academy of Sciences*, *118*(28), e2026378118. https://doi.org/10.1073/pnas.2026378118

Burr, Z. M., Varpe, Ø., Anker-Nilssen, T., Erikstad, K. E., Descamps, S., Barrett, R. T., Bech, C., Christensen-Dalsgaard, S., Lorentsen, S., Moe, B., Reiertsen, T. K., & Strøm, H. (2016). Later at higher latitudes: Large-scale variability in seabird breeding timing and synchronicity. *Ecosphere*, *7*(5). https://doi.org/10.1002/ecs2.1283

Carrasco, J. F., Bozkurt, D., & Cordero, R. R. (2021). A review of the observed air temperature in the Antarctic Peninsula. Did the warming trend come back after the early 21st hiatus? *Polar Science*, *28*, 100653. https://doi.org/10.1016/j.polar.2021.100653

Cayuela, H., Besnard, A., Bonnaire, E., Perret, H., Rivoalen, J., Miaud, C., & Joly, P. (2014). *To breed or not to breed: Past reproductive status and environmental cues drive current breeding decisions in a long-lived amphibian*. 10.

Cerini, F., Childs, D. Z., & Clements, C. F. (2023). A predictive timeline of wildlife population collapse. *Nature Ecology & Evolution*, *7*(3), Article 3. https://doi.org/10.1038/s41559-023-01985-2

Che-Castaldo, C., Jenouvrier, S., Youngflesh, C., Shoemaker, K. T., Humphries, G., McDowall, P., Landrum, L., Holland, M. M., Li, Y., Ji, R., & Lynch, H. J. (2017). Pan-Antarctic analysis aggregating spatial estimates of Adélie penguin abundance reveals robust dynamics despite stochastic noise. *Nature Communications*, *8*(1), 832. https://doi.org/10.1038/s41467-017-00890-0

Chmura, H. E., Wingfield, J. C., & Hahn, T. P. (2020). Non-photic environmental cues and avian reproduction in an era of global change. *Journal of Avian Biology*, *51*(3). https://doi.org/10.1111/jav.02243

Clem, K. R., Fogt, R. L., Turner, J., Lintner, B. R., Marshall, G. J., Miller, J. R., & Renwick, J. A. (2020). Record warming at the South Pole during the past three decades. *Nature Climate Change*, *10*(8), 762–770.

Clucas, G. V., Dunn, M. J., Dyke, G., Emslie, S. D., Levy, H., Naveen, R., Polito, M. J., Pybus, O. G., Rogers, A. D., & Hart, T. (2015). A reversal of fortunes: Climate change 'winners' and 'losers' in Antarctic Peninsula penguins. *Scientific Reports*, *4*(1), 5024. https://doi.org/10.1038/srep05024

Cohen, J. M., Lajeunesse, M. J., & Rohr, J. R. (2018). A global synthesis of animal phenological responses to climate change. *Nature Climate Change*, *8*(3), 224–228. https://doi.org/10.1038/s41558-018-0067-3

Cole, E. F., Regan, C. E., & Sheldon, B. C. (2021). Spatial variation in avian phenological response to climate change linked to tree health. *Nature Climate Change*, *11*(10), Article 10. https://doi.org/10.1038/s41558-021-01140-4

Croxall, J. P., Butchart, S. H. M., Lascelles, B., Stattersfield, A. J., Sullivan, B., Symes, A., & Taylor, P. (2012). Seabird conservation status, threats and priority actions: A global assessment. *Bird Conservation International*, *22*(1), 1–34. https://doi.org/10.1017/S0959270912000020

Daunt, F., Wanless, S., Harris, M. P., & Monaghan, P. (1999). Experimental evidence that age-specific reproductive success is independent of environmental effects. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *266*(1427), 1489–1493. https://doi.org/10.1098/rspb.1999.0805

Davey, C. M., Chamberlain, D. E., Newson, S. E., Noble, D. G., & Johnston, A. (2012). Rise of the generalists: Evidence for climate driven homogenization in avian communities. *Global Ecology and Biogeography*, *21*(5), 568–578. https://doi.org/10.1111/j.1466-8238.2011.00693.x

Davis, L. S. (1982). Timing of Nest Relief and Its Effect on Breeding Success in Adélie Penguins (Pygoscelis adeliae). *The Condor*, *84*(2), 178. https://doi.org/10.2307/1367665

Davis, L. S., & Darby, J. T. (2012). *Penguin Biology*. Elsevier.

Dawson, A., King, V. M., Bentley, G. E., & Ball, G. F. (2001). Photoperiodic Control of Seasonality in Birds. *Journal of Biological Rhythms*, *16*(4), 365–380. https://doi.org/10.1177/074873001129002079

Dobson, F. S., Becker, P. H., Arnaud, C. M., Bouwhuis, S., & Charmantier, A. (2017). Plasticity results in delayed breeding in a long-distant migrant seabird. *Ecology and Evolution*, *7*(9), 3100–3109. https://doi.org/10.1002/ece3.2777

Dunn, M. J., Silk, J. R. D., & Trathan, P. N. (2011). Post-breeding dispersal of Adélie penguins (Pygoscelis adeliae) nesting at Signy Island, South Orkney Islands. *Polar Biology*, *34*(2), 205–214. https://doi.org/10.1007/s00300-010-0870-4

Emmerson, L., Pike, R., & Southwell, C. (2011). Reproductive consequences of environment-driven variation in Adélie penguin breeding phenology. *Marine Ecology Progress Series*, *440*, 203–216. https://doi.org/10.3354/meps09265

Fayet, A. L., Freeman, R., Shoji, A., Kirk, H. L., Padget, O., Perrins, C. M., & Guilford, T. (2016). Carry-over effects on the annual cycle of a migratory seabird: An experimental study. *Journal of Animal Ecology*, *85*(6), 1516–1527. https://doi.org/10.1111/1365-2656.12580

Fraser, W. R., & Hofmann, E. E. (2003). A predator's perspective on causal links between climate change, physical forcing and ecosystem response. *Marine Ecology Progress Series*, *265*, 1–15. https://doi.org/10.3354/meps265001

Fretwell, P. T., LaRue, M. A., Morin, P., Kooyman, G. L., Wienecke, B., Ratcliffe, N., Fox, A. J., Fleming, A. H., Porter, C., & Trathan, P. N. (2012). An Emperor Penguin Population Estimate: The First Global, Synoptic Survey of a Species from Space. *PLoS ONE*, *7*(4), e33751. https://doi.org/10.1371/journal.pone.0033751

Herman, R., Borowicz, A., Lynch, M., Trathan, P., Hart, T., & Lynch, H. (2020). Update on the global abundance and distribution of breeding Gentoo Penguins (Pygoscelis papua). *Polar Biology*, *43*(12), 1947–1956. https://doi.org/10.1007/s00300-020-02759-3

Hinke, J., Polito, M., Reiss, C., Trivelpiece, S., & Trivelpiece, W. (2012). Flexible reproductive timing can buffer reproductive success of Pygoscelis spp. Penguins in the Antarctic Peninsula region. *Marine Ecology Progress Series*, *454*, 91–104. https://doi.org/10.3354/meps09633

Hinke, J. T., Barbosa, A., Emmerson, L. M., Hart, T., Juáres, M. A., Korczak-Abshire, M., Milinevsky, G., Santos, M., Trathan, P. N., Watters, G. M., & Southwell, C. (2018). Estimating nest-level phenology and reproductive success of colonial seabirds using time-lapse cameras. *Methods in Ecology and Evolution*, *9*(8), 1853–1863. https://doi.org/10.1111/2041-210X.13015

Hinke, J. T., Salwicka, K., Trivelpiece, S. G., Watters, G. M., & Trivelpiece, W. Z. (2007). Divergent responses of Pygoscelis penguins reveal a common environmental driver. *Oecologia*, *153*(4), 845–855. https://doi.org/10.1007/s00442-007-0781-4

Hinke, J. T., Santos, M. M., Korczak-Abshire, M., Milinevsky, G., & Watters, G. M. (2019). Individual variation in migratory movements of Chinstrap penguins leads to widespread occupancy of ice-free winter habitats over the continental shelf and deep ocean basins of the Southern Ocean. *PLOS ONE*, *14*(12), e0226207. https://doi.org/10.1371/journal.pone.0226207

Humphries, G. R. W., Naveen, R., Schwaller, M., Che-Castaldo, C., McDowall, P., Schrimpf, M., & Lynch, H. J. (2017). Mapping Application for Penguin Populations and Projected Dynamics (MAPPPD): Data and

tools for dynamic management and decision support. *Polar Record*, *53*(2), 160–166. https://doi.org/10.1017/S0032247417000055

Inouye, B. D., Ehrlén, J., & Underwood, N. (2019). Phenology as a process rather than an event: From individual reaction norms to community metrics. *Ecological Monographs*, *89*(2), e01352. https://doi.org/10.1002/ecm.1352

Jones, F. M., Allen, C., Arteta, C., Arthur, J., Black, C., Emmerson, L. M., Freeman, R., Hines, G., Lintott, C. J., Macháčková, Z., Miller, G., Simpson, R., Southwell, C., Torsey, H. R., Zisserman, A., & Hart, T. (2018). Time-lapse imagery and volunteer classifications from the Zooniverse Penguin Watch project. *Scientific Data*, *5*(1), Article 1. https://doi.org/10.1038/sdata.2018.124

Keogan, K., Daunt, F., Wanless, S., Phillips, R. A., Walling, C. A., Agnew, P., Ainley, D. G., Anker-Nilssen, T., Ballard, G., Barrett, R. T., Barton, K. J., Bech, C., Becker, P., Berglund, P.-A., Bollache, L., Bond, A. L., Bouwhuis, S., Bradley, R. W., Burr, Z. M., … Lewis, S. (2018). Global phenological insensitivity to shifting ocean temperatures among seabirds. *Nature Climate Change*, *8*(4), Article 4. https://doi.org/10.1038/s41558-018-0115-z

Kooyman, G. L., Ainley, D. G., Ballard, G., & Ponganis, P. J. (2007). Effects of giant icebergs on two emperor penguin colonies in the Ross Sea, Antarctica. *Antarctic Science*, *19*(1), 31–38. https://doi.org/10.1017/S0954102007000065

Korczak-Abshire, M., Hinke, J. T., Milinevsky, G., Juáres, M. A., & Watters, G. M. (2021). Coastal regions of the northern Antarctic Peninsula are key for Gentoo populations. *Biology Letters*, *17*(1), 20200708. https://doi.org/10.1098/rsbl.2020.0708

Kriegler, E., Hall, J. W., Held, H., Dawson, R., & Schellnhuber, H. J. (2009). Imprecise probability assessment of tipping points in the climate system. *Proceedings of the National Academy of Sciences*, *106*(13), 5041–5046.

Kumar, A., Yadav, J., & Mohan, R. (2021). Seasonal sea-ice variability and its trend in the Weddell Sea sector of West Antarctica. *Environmental Research Letters*. https://doi.org/10.1088/1748-9326/abdc88

Lynch, H., Fagan, W., Naveen, R., Trivelpiece, S., & Trivelpiece, W. (2012). Differential advancement of breeding phenology in response to climate may alter staggered breeding among sympatric pygoscelid penguins. *Marine Ecology Progress Series*, *454*, 135–145. https://doi.org/10.3354/meps09252

Lynch, H. J., Naveen, R., Trathan, P. N., & Fagan, W. F. (2012). Spatially integrated assessment reveals widespread changes in penguin populations on the Antarctic Peninsula. *Ecology*, *93*(6), 1367–1377. https://doi.org/10.1890/11-1588.1

Lynch, H. J., White, R., Black, A. D., & Naveen, R. (2012). Detection, differentiation, and abundance estimation of penguin species by high-resolution satellite imagery. *Polar Biology*, *35*(6), 963–968. https://doi.org/10.1007/s00300-011-1138-3

Lynnes, A. S., Reid, K., & Croxall, J. P. (2004). Diet and reproductive success of Adélie and Chinstrap penguins: Linking response of predators to prey population dynamics. *Polar Biology*, *27*(9), 544–554. https://doi.org/10.1007/s00300-004-0617-1

Madsen, J., Tamstorf, M., Klaassen, M., Eide, N., Glahder, C., Rigét, F., Nyegaard, H., & Cottaar, F. (2007). Effects of snow cover on the timing and success of reproduction in high-Arctic pink-footed geese Anser brachyrhynchus. *Polar Biology*, *30*(11), 1363–1372. https://doi.org/10.1007/s00300-007-0296-9

Matthysen, E., Adriaensen, F., & Dhondt, A. A. (2011). Multiple responses to increasing spring temperatures in the breeding cycle of blue and great tits (Cyanistes caeruleus, Parus major). *Global Change Biology*, *17*(1), 1–16. https://doi.org/10.1111/j.1365-2486.2010.02213.x

McCormack, S. A., Melbourne-Thomas, J., Trebilco, R., Blanchard, J. L., Raymond, B., & Constable, A. (2021). Decades of dietary data demonstrate regional food web structures in the Southern Ocean. *Ecology and Evolution*, *11*(1), 227–241. https://doi.org/10.1002/ece3.7017

McDowall, P. S., & Lynch, H. J. (2019). When the "selfish herd" becomes the "frozen herd": Spatial dynamics and population persistence in a colonial seabird. *Ecology*, *100*(10), e02823. https://doi.org/10.1002/ecy.2823

McGrath, L. J., Iii, C. van R., & Fontaine, J. J. (2022). *Flower Power: Tree Flowering Phenology as a Settlement Cue for Migrating Birds*. 10.

McMahon, K. W., Michelson, C. I., Hart, T., McCarthy, M. D., Patterson, W. P., & Polito, M. J. (2019). Divergent trophic responses of sympatric penguin species to historic anthropogenic exploitation and recent climate change. *Proceedings of the National Academy of Sciences*, *116*(51), 25721–25727. https://doi.org/10.1073/pnas.1913093116

Meredith, M., Sommerkorn, M., Cassotta, S., Derksen, C., Ekaykin, A., Hollowed, A., Kofinas, G., Mackintosh, A., Melbourne-Thomas, J., & Muelbert, M. M. C. (2019). *Polar Regions. Chapter 3, IPCC Special Report on the Ocean and Cryosphere in a Changing Climate*.

Miller, A. K., Kappes, M. A., Trivelpiece, S. G., & Trivelpiece, W. Z. (2010). Foraging-Niche Separation of Breeding Gentoo and Chinstrap Penguins, South Shetland Islands, Antarctica. *The Condor*, *112*(4), 683–695. https://doi.org/10.1525/cond.2010.090221

Miller, A. K., Karnovsky, N. J., & Trivelpiece, W. Z. (2009). Flexible foraging strategies of Gentoo penguins Pygoscelis papua over 5 years in the South Shetland Islands, Antarctica. *Mar Biol*, 11.

Morley, S. A., Barnes, D. K. A., & Dunn, M. J. (2019). Predicting Which Species Succeed in Climate-Forced Polar Seas. *Frontiers in Marine Science*, *5*. https://www.frontiersin.org/articles/10.3389/fmars.2018.00507

Nicol, S. (2006). Krill, Currents, and Sea Ice: Euphausia superba and Its Changing Environment. *BioScience*, *56*(2), 111–120. https://doi.org/10.1641/0006-3568(2006)056[0111:KCASIE]2.0.CO;2

Parmesan, C. (2006). Ecological and Evolutionary Responses to Recent Climate Change. *Annual Review of Ecology, Evolution, and Systematics*, *37*(1), 637–669. https://doi.org/10.1146/annurev.ecolsys.37.091305.110100

Perrins, C. M. (2008). THE TIMING OF BIRDS' BREEDING SEASONS. *Ibis*, *112*(2), 242–255. https://doi.org/10.1111/j.1474-919X.1970.tb00096.x

Pfeifer, C., Barbosa, A., Mustafa, O., Peter, H.-U., Rümmler, M.-C., & Brenning, A. (2019). *Using Fixed-Wing UAV for Detecting and Mapping the Distribution and Abundance of Penguins on the South Shetlands Islands, Antarctica*. 22.

Polar Data Centre, U. K, Convey, P., Geissler, P., Jobson, M., & Newsham, K. (2021). *Microclimate data from Jane Col, 2007-2016 [Version 2.0]*. NERC EDS UK Polar Data Centre. https://doi.org/10.5285/1BF0CFE7-A2E6-4C82-A0CD-D913876B6854

Regehr, H. M., & Rodway, M. S. (1999). Seabird Breeding Performance during Two Years of Delayed Capelin Arrival in the Northwest Atlantic: A Multi-Species Comparison. *Waterbirds: The International Journal of Waterbird Biology*, *22*(1), 60. https://doi.org/10.2307/1521994

Romano, A., Garamszegi, L. Z., Rubolini, D., & Ambrosini, R. (2022). Temporal shifts in avian phenology across the circannual cycle in a rapidly changing climate: A global meta-analysis. *Ecological Monographs*, *n/a*(n/a), e1552. https://doi.org/10.1002/ecm.1552

Rubenstein, D. R., & Wikelski, M. (2003). SEASONAL CHANGES IN FOOD QUALITY: A PROXIMATE CUE FOR REPRODUCTIVE TIMING IN MARINE IGUANAS. *Ecology*, *84*(11), 3013–3023. https://doi.org/10.1890/02-0354

Saba, G. K., Fraser, W. R., Saba, V. S., Iannuzzi, R. A., Coleman, K. E., Doney, S. C., Ducklow, H. W., Martinson, D. G., Miles, T. N., Patterson-Fraser, D. L., Stammerjohn, S. E., Steinberg, D. K., & Schofield, O. M. (2014). Winter and spring controls on the summer food web of the coastal West Antarctic Peninsula. *Nature Communications*, *5*(1), 4318. https://doi.org/10.1038/ncomms5318

Samplonius, J. M., Atkinson, A., Hassall, C., Keogan, K., Thackeray, S. J., Assmann, J. J., Burgess, M. D., Johansson, J., Macphie, K. H., Pearce-Higgins, J. W., Simmonds, E. G., Varpe, Ø., Weir, J. C., Childs, D. Z., Cole, E. F., Daunt, F., Hart, T., Lewis, O. T., Pettorelli, N., … Phillimore, A. B. (2021). Strengthening the evidence base for temperature-mediated phenological asynchrony and its impacts. *Nature Ecology & Evolution*, *5*(2), 155–164. https://doi.org/10.1038/s41559-020-01357-0

Santora, J. A., LaRue, M. A., & Ainley, D. G. (2020). Geographic structuring of Antarctic penguin populations. *Global Ecology and Biogeography*, *29*(10), 1716–1728. https://doi.org/10.1111/geb.13144

Sergio, F., Blas, J., Forero, M. G., Donázar, J. A., & Hiraldo, F. (2007). Sequential settlement and site dependence in a migratory raptor. *Behavioral Ecology*, *18*(5), 811–821. https://doi.org/10.1093/beheco/arm052

Shoji, A., Aris-Brosou, S., Culina, A., Fayet, A., Kirk, H., Padget, O., Juarez-Martinez, I., Boyle, D., Nakata, T., Perrins, C. M., & Guilford, T. (2015). Breeding phenology and winter activity predict subsequent breeding success in a trans-global migratory seabird. *Biology Letters*, *11*(10), 20150671. https://doi.org/10.1098/rsbl.2015.0671

Southwell, C., & Emmerson, L. (2015). Remotely-operating camera network expands Antarctic seabird observations of key breeding parameters for ecosystem monitoring and management. *Journal for Nature Conservation*, *23*, 1–8. https://doi.org/10.1016/j.jnc.2014.11.002

Spurr, E. B. (2008). BREEDING OF THE ADÉLIE PENGUIN PYGOSCELIS ADELIAE AT CAPE BIRD. *Ibis*, *117*(3), 324–338. https://doi.org/10.1111/j.1474-919X.1975.tb04220.x

Stammerjohn, S. E., Martinson, D. G., Smith, R. C., & Iannuzzi, R. A. (2008). Sea ice in the western Antarctic Peninsula region: Spatio-temporal variability from ecological and climate change perspectives. *Deep Sea Research Part II: Topical Studies in Oceanography*, *55*(18), 2041–2058. https://doi.org/10.1016/j.dsr2.2008.04.026

Stenson, G. B., & Hammill, M. O. (n.d.). *Can ice breeding seals adapt to habitat loss in a time of climate change?*10.

Strycker, N., Wethington, M., Borowicz, A., Forrest, S., Witharana, C., Hart, T., & Lynch, H. J. (2020). A global population assessment of the Chinstrap penguin (Pygoscelis antarctica). *Scientific Reports*, *10*(1), Article 1. https://doi.org/10.1038/s41598-020-76479-3

Thackeray, S. J., Henrys, P. A., Hemming, D., Bell, J. R., Botham, M. S., Burthe, S., Helaouet, P., Johns, D. G., Jones, I. D., Leech, D. I., Mackay, E. B., Massimino, D., Atkinson, S., Bacon, P. J., Brereton, T. M., Carvalho, L., Clutton-Brock, T. H., Duck, C., Edwards, M., … Wanless, S. (2016). Phenological sensitivity to climate across taxa and trophic levels. *Nature*, *535*(7611), Article 7611. https://doi.org/10.1038/nature18608

Thackeray, S. J., Sparks, T. H., Frederiksen, M., Burthe, S., Bacon, P. J., Bell, J. R., Botham, M. S., Brereton, T. M., Bright, P. W., Carvalho, L., Clutton-Brock, T., Dawson, A., Edwards, M., Elliott, J. M., Harrington, R., Johns, D., Jones, I. D., Jones, J. T., Leech, D. I., … Wanless, S. (2010). Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments: PHENOLOGICAL CHANGE ACROSS MAJOR ENVIRONMENTS. *Global Change Biology*, *16*(12), 3304–3313. https://doi.org/10.1111/j.1365-2486.2010.02165.x

Trivelpiece, W. Z., Hinke, J. T., Miller, A. K., Reiss, C. S., Trivelpiece, S. G., & Watters, G. M. (2011). Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. *Proceedings of the National Academy of Sciences*, *108*(18), 7625–7628. https://doi.org/10.1073/pnas.1016560108

Trivelpiece, W. Z., Trivelpiece, S. G., Geupel, G. R., Kjelmyr, J., & Volkman, N. J. (1990). Adélie and Chinstrap Penguins: Their Potential as Monitors of the Southern Ocean Marine Ecosystem. In K. R. Kerry & G. Hempel (Eds.), *Antarctic Ecosystems* (pp. 191–202). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-84074-6_20

Trivelpiece, W. Z., Trivelpiece, S. G., & Volkman, N. J. (1987). Ecological Segregation of Adélie, Gentoo, and Chinstrap Penguins at King George Island, Antarctica. *Ecology*, *68*(2), 351–361. https://doi.org/10.2307/1939266

V, S., & V, L. (1995). Recruitment of Antarctic krill Euphausia superba and possible causes for its variability. *Marine Ecology Progress Series*, *123*, 45–56. https://doi.org/10.3354/meps123045

Vaughan, D. G., Marshall, G. J., Connolley, W. M., Parkinson, C., Mulvaney, R., Hodgson, D. A., King, J. C., Pudsey, C. J., & Turner, J. (2003). Recent Rapid Regional Climate Warming on the Antarctic Peninsula. *Climatic Change*, *60*(3), 243–274. https://doi.org/10.1023/A:1026021217991

Verhulst, S., & Nilsson, J.-A. (2008). *The timing of birds' breeding seasons: A review of experiments that manipulated timing of breeding*. https://doi.org/10.1098/rstb.2007.2146

Visser, M. E., & Both, C. (2005). Shifts in phenology due to global climate change: The need for a yardstick. *Proceedings of the Royal Society B: Biological Sciences*, *272*(1581), 2561–2569. https://doi.org/10.1098/rspb.2005.3356

Visser, M. E., te Marvelde, L., & Lof, M. E. (2012). Adaptive phenological mismatches of birds and their food in a warming world. *Journal of Ornithology*, *153*(1), 75–84. https://doi.org/10.1007/s10336-011-0770-6

Vleck, C. M., & Vleck, D. (2002). Physiological Condition and Reproductive Consequences in Adélie Penguins. *Integrative and Comparative Biology*, *42*(1), 76–83. https://doi.org/10.1093/icb/42.1.76

Walsh, J., Reiss, C., & Watters, G. (2020). Flexibility in Antarctic krill Euphausia superba decouples diet and recruitment from overwinter sea-ice conditions in the northern Antarctic Peninsula. *Marine Ecology Progress Series*, *642*, 1–19. https://doi.org/10.3354/meps13325

Wethington, M., Flynn, C., Borowicz, A., & Lynch, H. J. (2023). Adélie penguins north and east of the 'Adélie gap' continue to thrive in the face of dramatic declines elsewhere in the Antarctic Peninsula region. *Scientific Reports*, *13*(1), Article 1. https://doi.org/10.1038/s41598-023-29465-4

Whelan, S., Hatch, S. A., Gaston, A. J., Gilchrist, H. G., & Elliott, K. H. (2022). Opposite, but insufficient, phenological responses to climate in two circumpolar seabirds: Relative roles of phenotypic plasticity and selection. *Functional Ecology*, *36*(7), 1782–1795. https://doi.org/10.1111/1365-2435.14064

Williams, T. D. (1995). *The Penguins: Spheniscidae*. Oxford University Press.

Williams, T. D., & Rodwell, S. (1992). Annual Variation in Return Rate, Mate and Nest-Site Fidelity in Breeding Gentoo and Macaroni Penguins. *The Condor*, *94*(3), 636–645. https://doi.org/10.2307/1369249

Winkler, D. W., Jørgensen, C., Both, C., Houston, A. I., McNamara, J. M., Levey, D. J., Partecke, J., Fudickar, A., Kacelnik, A., Roshier, D., & Piersma, T. (2014). Cues, strategies, and outcomes: How migrating vertebrates track environmental change. *Movement Ecology*, *2*(1), 10. https://doi.org/10.1186/2051-3933-2-10

Youngflesh, C., Jenouvrier, S., Hinke, J. T., DuBois, L., St. Leger, J., Trivelpiece, W. Z., Trivelpiece, S. G., & Lynch, H. J. (2018). Rethinking "normal": The role of stochasticity in the phenology of a synchronously breeding seabird. *Journal of Animal Ecology*, *87*(3), 682–690. https://doi.org/10.1111/1365-2656.12790

Youngflesh, C., Jenouvrier, S., Li, Y., Ji, R., Ainley, D. G., Ballard, G., Barbraud, C., Delord, K., Dugger, K. M., Emmerson, L. M., Fraser, W. R., Hinke, J. T., Lyver, P. O., Olmastroni, S., Southwell, C. J., Trivelpiece, S. G., Trivelpiece, W. Z., & Lynch, H. J. (2017). Circumpolar analysis of the Adélie Penguin reveals the importance of environmental variability in phenological mismatch. *Ecology*, *98*(4), 940–951. https://doi.org/10.1002/ecy.1749

3

Chapter 3

Building a tool to extract breeding parameters nest-by-nest

Abstract.

Previous work showed all three species of Pygoscelid penguins advancing their breeding seasons in response to warming temperatures on the Antarctic Peninsula. To further understand any impacts of this change on penguin populations, I need other measures such as breeding success as well as dates of further breeding milestones. In this chapter, I develop and validate a nest-tracking tool capable of using volunteer annotations of time-lapse camera images to semi-automatically produce nest-by-nest estimates of breeding success, hatching phenology, crèching phenology and dates of chick loss. This tool accommodates several different sources of variability including inconsistencies in data curation, camera movement, volunteer inaccuracies and natural variability in the penguin's breeding cycle. To test this tool I used it on eight seasons of timelapse imagery of Gentoo penguins (*Pygoscelis papua*) breeding on George's Point, Rongé Island, Antarctica. The tool proved accurate but time-consuming and future filtering processes and tools might be needed to make the tool time-efficient. Nonetheless, the results of this pilot analysis resulted in a nest-by-nest time series of breeding phenology and breeding success that will be key to study the factors influencing breeding success in Chapter 4.

Introduction.

My next aim is to understand whether the record phenological changes observed in Chapter 2 are affecting the three species' breeding success. I expect this data to be helpful at understanding whether those shifts are being forced upon the penguins by climate change or, on the contrary, they are a way for penguins to adapt to it.

In order to do this I used time-lapse images from the PenguinWatch camera network as previous studies achieved accurate manual estimates of breeding success and phenology from time-lapse imagery (Hinke et al., 2018). In this study, I built a tool with the ambition of extracting breeding success and phenology data from the whole network of 87 cameras, so it was necessary to automate as many processes as possible in order to analyse as many cameras as possible.

Previous work in automating chick detection used volunteer annotated data from the PenguinWatch project (www.penguinwatch.org) on the Zooniverse Citizen-Science platform (www.zooniverse.org) to extract chick presence from time-lapse images (Jones et al., 2018, 2020). This was only possible to achieve for those seasons where camera view it is stable throughout the season, however, it is relatively frequent for the field of view to move, changing the identity and amount of nests that appear in frame. In order to compensate for this and extract breeding success data from as many colonies and seasons possible it will be necessary to compensate for that by tracking individual nests throughout the whole season.

In this chapter, I built a nest-tracking tool capable of accommodating these sources of variability plus those derived from the natural variability of the penguins and their environment, the long-term nature of our dataset and the inaccuracies of volunteer annotations. Once these peculiarities have been taken into account this tool is capable of reliably estimating the date of chick hatching and crèching, the date for chick mortality and consequently breeding success. This will become helpful to study the causes of chick mortality, derive survivorship curves, estimate colony synchronicity, estimate guard duration and determine the effect on phenology and breeding behaviour of early and late breeding nest by nest in Chapter 4.

Methods.

In order to test the possibilities of the nest-tracking tool I analysed time-lapse imagery data from GEORa, a PenguinWatch camera overlooking a colony of Gentoo penguins (*Pygoscelis papua*) located on George's Point, Antarctica (-64.669, -62.6698). I chose this camera because it provides a continuous time series (seasons 12-13 to 20-21) and it tracks 15-30 nests per year, all relatively close to the camera. These images were analysed by thousands of volunteers using the PenguinWatch project on the Zooniverse platform (www.penguinwatch.org), who were instructed to annotate the positions of Adults, Chicks and Eggs on a selection of images from the breeding season. Each image was annotated by nine different volunteers before it was withdrawn from the pool. I used these annotations of chick presence in order to estimate breeding success as well as phenology.

I estimate colony breeding success as the number of chicks that survive up to the point of crèche per amount of nest attempts in a particular field of view (Moreno, 2010). Nest attempts were calculated as those nests with continuous adult presence for more than 10 days. Studies in chick mortality indicate that chick loss happens predominantly during incubation and early guard stage (Clarke et al., 2002; Davis & McCaffrey, 1986). Considering that it is unlikely to see chicks from cameras in their first 7-10 days, chick survival was estimated here as the number of chicks that are seen alive at each nest by the end of the second week after their initial detection.

Building the nest-tracking tool

I built a nest-tracking tool in order to semi-automate the extraction of adult, egg and chick presence from volunteer annotation data in each image, nest per nest throughout the season. Presence data was transformed into breeding success if the chicks live long enough but also informs us of hatching and crèching phenology, season length, and the exact dates for egg/chick loss. For a schematic description of the processes involved in the nest-tracking tool, please refer to Figure 1.

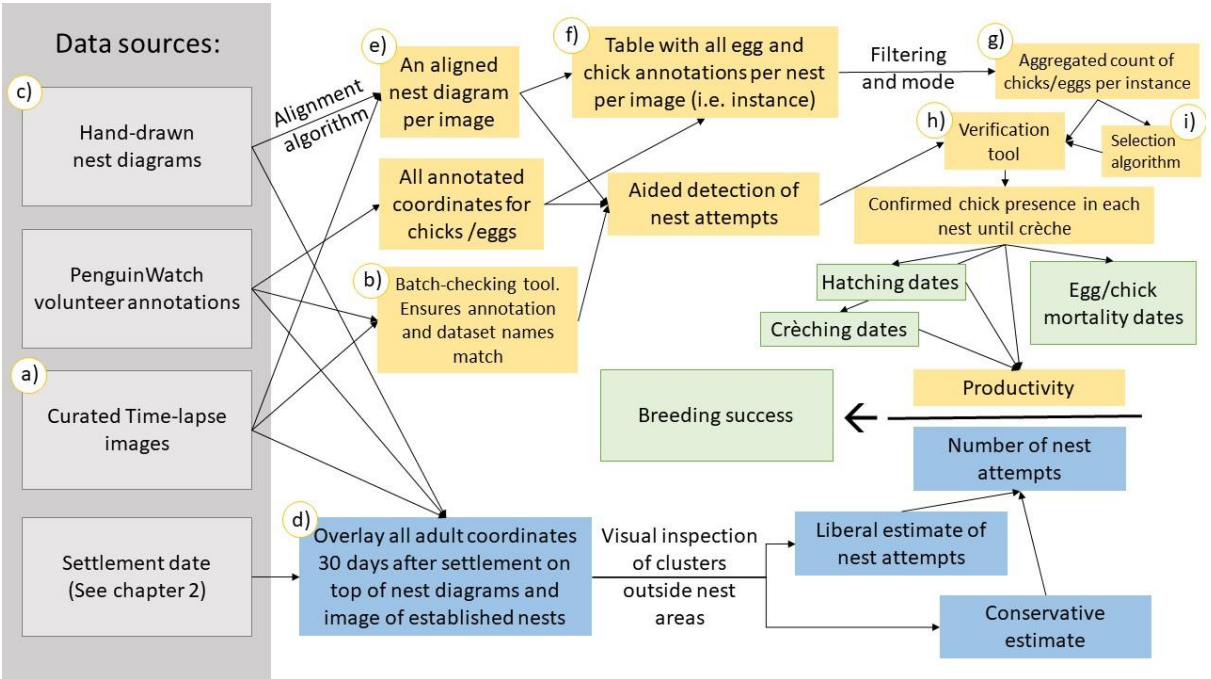


Figure 1: Schematic description of the processes involved in the nest-tracking tool. Original data sources are coloured grey. Yellow boxes indicate the path to obtain chick presence data and blue boxes indicate the path to obtain the number of nest attempts in the season. Green boxes show the different results of extracting chick presence from time-lapse images.

Data Curation

The first step in the nest tracking tool was to make sure the image labelling in the volunteer annotations downloaded from the zooniverse matched the current image names. Over the years, multiple researchers curated the Penguin Watch time-lapse image dataset for different partial projects, but this is the first time that I have enough data to establish a longer time series. Upon gathering all available timelapse data I found 2531 image folders, mostly duplicated and sometimes saved under multiple (up to 5) different names. Duplicated folders were unified under a unique consensus label/name in order to establish the current dataset (Figure 1a). In order to make sure previous annotations corresponded to current folder and image labels I built a batch-checking tool to groundtruth every batch of images uploaded to the PenguinWatch project in the zooniverse platform (Figure 1b).

I used the adult annotations as they can be automatically groundtruthed against the output of the pengbot3000, an AI algorithm built previously for our lab (Arteta et al., 2016). This is a particular type of algorithm that estimates adult presence in an image by scoring each pixel with a value of "*penguinness*" (Figure 2a). After running all our newly-labelled images through the algorithm, it retuned a matrix/heatmap marking the location of penguins in each image. I then chose a random selection of images in each batch uploaded to the Zooniverse and queried the heatmap matrix for its *penguinness* values at the coordinates of the annotations. Finally, I treated those values as a sample extracted from a population; all the pixels in the corresponding heat map, modelled as a normal distribution of mean μ and standard deviation σ. If the annotations did coincide with penguin locations, their coordinates would not be random and their values would be higher and lie further away from the mean. Following the usual threshold in frequentist statistics I chose a value of two standard deviations (2σ) away from the mean (μ) to mark non-randomness and therefore the validity of the annotations (Figure 2b).

In order to easily visualise the adequacy of each batch the tool presents the researcher with a panel including the aforementioned *penguinness* deviation metric for each batch (Figure 2b) as well as a selection of annotations from each batch (Figures 2c and 2d). The tool's output iss a panel for every batch of every folder ever uploaded to the Zooniverse platform, including the four worst-scoring annotations, two with an intermediate score and two with the best score (Figures S1 and S2 Appendix S3.1). This allows the researcherto quickly detect low scores and at the same time visualise whether those were due to poor annotations by the volunteers, poor light conditions or batch misnaming. As a result, 3 percent of the batches used in this study were suspected to be misnamed ($n = 120$) and were removed from the study.

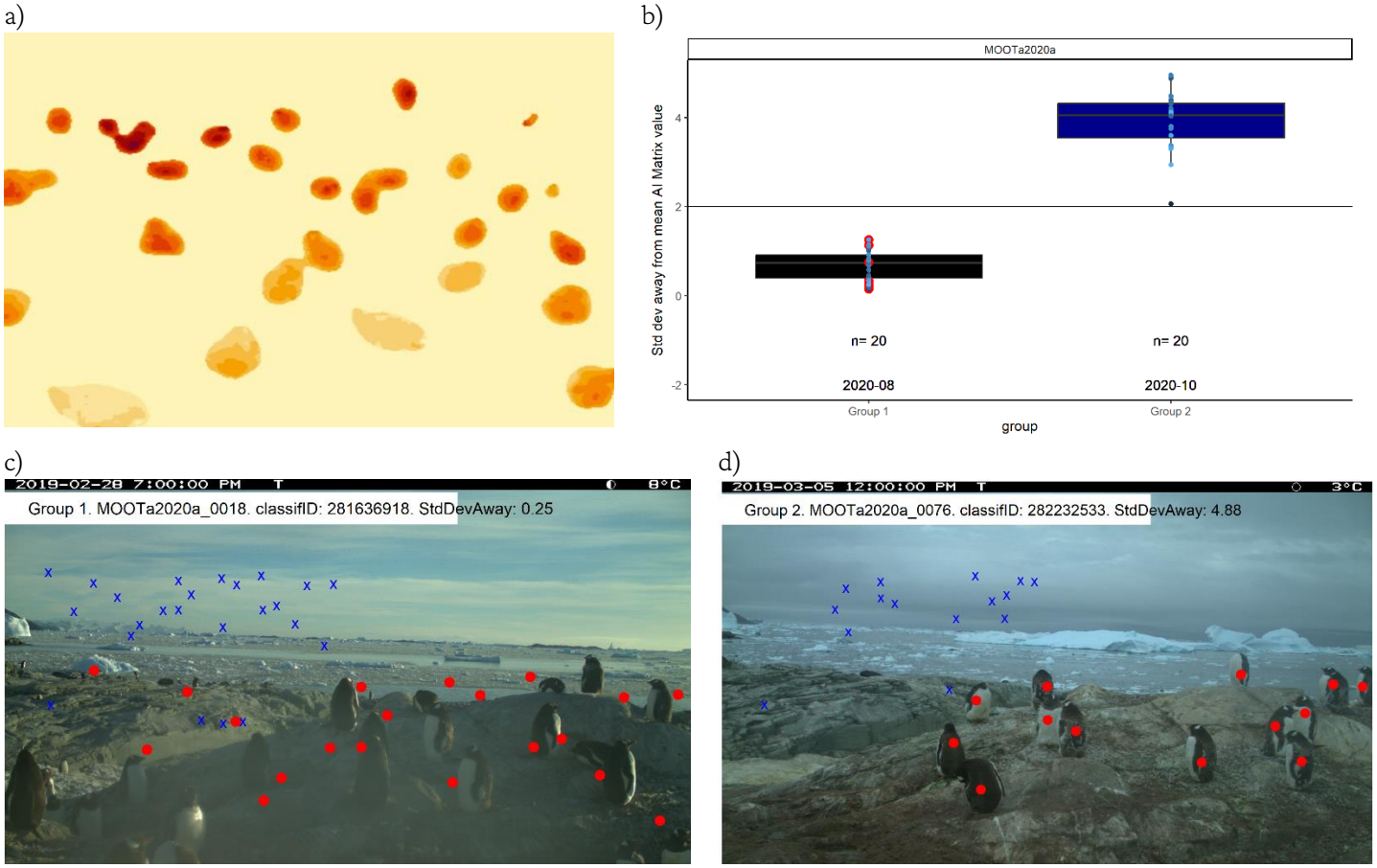


Figure 2: a) Output matrix from the pengbot3000 AI algorithm (Arteta et al., 2016). Matrix values plotted in false colour in order to show penguin presence, location and shape in a given timelapse image. b) Diagnostic plot part of the batch-checking tool's output to ground-truth if image labels in volunteer annotations correspond to current image labels for the two batches uploaded under the folder name MOOTa2020a. To do this I extracted the values from the corresponding AI matrix at the position of the volunteer-annotated coordinates. This was done for a random selection of 20 images per group/batch. The tool compares the values at those points with the overall distribution of values in the whole matrix (assumed normal) and express the difference as Standard Deviations. High values indicate non-randomness and adequacy of the labelling. Both Figures c) and d) show two different types of annotations. This is the tool's system to check for resizing errors. Before uploading images to the Zooniverse I downsized them to 1000 pixels wide in order to save space in the online server. Blue crosses show the coordinates as extracted directly from the Zooniverse and correspond to volunteer annotations in the downsized image. Red dots show the same coordinate annotations after upsizing them back to the original image dimensions. Both were plotted in order to verify the reverse resizing process had been performed successfully and the annotations did match the fully-sized images I am working on. c) One of the randomly selected volunteer classifications from Batch 1 (uploaded August 2020) as folder MOOTa2020a. None of the images in this batch showed great scores in the diagnostic plot (Figure 2b). The annotations were not correctly on the penguins despite being in the correct overall area of the image (Appendix S3.1), so this batch was considered mislabelled, probably from the same colony but in a different year. d) One of the randomly-selected volunteer classifications from Batch 2 (uploaded October 2020) as folder MOOTa2020a. All the images in the batch show acceptable scores and a general agreement on penguin location (Appendix S3.1) and was therefore considered a correctly-labelled batch.

Nest identification

For the nest-tracking tool to follow the presence of annotated adult chick and egg coordinates in individual nests I manually drew a 'nest diagram' using paint.NET (www.getpaint.net) to identify the territory of each nest during each season with a unique colour (Figures 1c and 3). paint.NET is an open access tool that allows overlaying of several layers (nest diagram and timelapse images) and changing their opacity so it is possible to draw nest territories while seeing the original images. Normally it was necessary to redraw nest territories each season as they change their position slightly from season to season. Often nest diagrams also needed to

be redrawn within a season if the camera view moves due to wind, terrain subsidence (due to thawing) or if the view changes when cameras are serviced halfway through a season.



Figure 3: Nest diagrams for a) Chinstrap and b) Gentoo penguins overlayed on top of the same image of the 17-18 season for camera BOOTc.

Using nest diagrams has two main advantages: it allows avoiding an otherwise problematic clustering process as well as allowing telling species apart when two of them are in frame. Clustering annotations is a standard procedure to deal with multiple volunteer annotations of one individual image in Citizen Science data that deals good results regarding adults (Jones et al., 2018, 2020). However, it is unusual for more than one or two volunteers to click on a particular chick unless they are already big and/or belong to the closest nests to the camera. For this reason, I decided to mark nest areas and extract the mode for each nest between those volunteers that annotated any chicks.

In order to make sure no nest attempts were missed, I plotted the coordinates of the first month after settlement (As defined in Chapter 2) on top of the nest diagrams in order to visually aid the detection of nests and check that none were missed (Figures 1d and 4).



Figure 4: Image of the early season of camera AITCb overlaid with the nest diagrams drawn for that season and overlayed with all annotations for the first month after settlement. Annotations are coloured by day in order to better spot places where penguins spend more than one day. Smaller dots indicate adult annotations, greater dots indicate chick and egg annotations.

An alignment algorithm to compensate camera movement

There can be minor and major changes to the field of view of the camera throughout the season. Major changes can be quite drastic and can completely remove particular nests from view resulting in a broken time series. This usually results in several nests being removed from the dataset but in the worst case scenarios it is necessary to remove the whole season. Minor camera movements throughout the season (caused by wind, tripod instability, etc) shift the relative position of the nests in the image and would cause individuals to be assigned to the wrong nest, especially in busy colony areas. In order to account for these small shifts I developed a bespoke aligner algorithm (Figure 1e and Figure 5). This algorithm compares the reference image on which the nest diagram has been drawn to all other images from that season. This algorithm needed to be built specifically for this purpose because standard alignment algorithms pick up the contrasted black and white of any penguins and return nonsensical results. The other source of data I used was an AI-generated density map of penguins per pixel that allows the automatic detection of adults in every image analysed (Arteta et al., 2016). For a technical description of the workings of the alignment algorithm, refer to appendix S3.2.

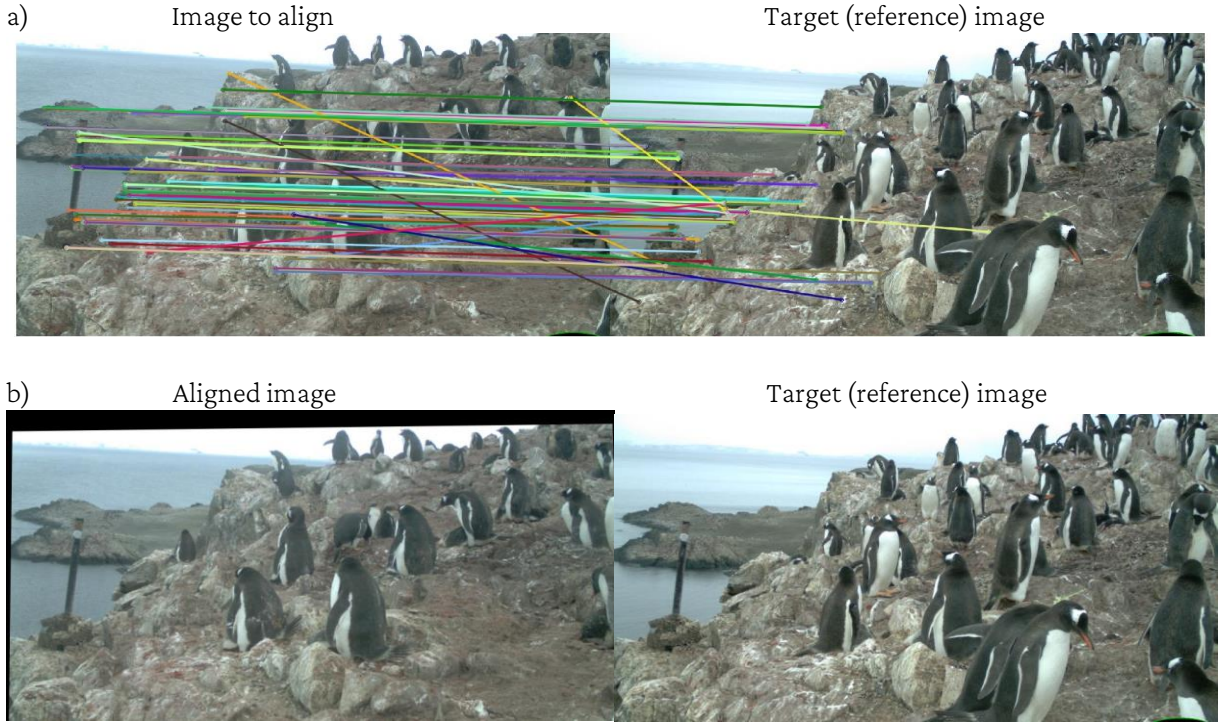


Figure 5: Workings of the Alignment algorithm on two consecutive images where a minor misalignment has occurred between them. a) match-making stage, notice how the matches ignore all adult penguins despite their contrasted colours. Adult penguins have been filtered out previously thanks to an AI developed previously in our lab (Arteta et al., 2016). Most matchlines have a similar slope and they are mostly distributed all over the image allowing for accurate warping and rescaling of the image throughout its surface, not just rotating and repositioning. b) Successful result of the alignment. Notice the coastline position and the rocks along the bottom of the image. Alignment images by Carlos Arteta.

Extracting data for each nest area

Once this was done the tool returns a nest diagram specifically realigned for every image in the season. I used this as a map allowing us to know which pixels in each image corresponds to which nest (Figure 1e). Then, it was possible to simply overlay all adult, chick, and egg coordinates in the volunteer annotations on top of the nest diagrams to obtain a count of how many annotations in each category did each volunteer annotate eachin each nest at every image during the season (Figure 1f). The final number of adults, chicks and eggs is the mode among all the volunteers that annotated that image and nest (Figure 1g). However, I only considered instances in which at least two volunteers have annotated a certain category within a given nest area (Adults, chicks or eggs).

Filtering, selecting and verifying annotations

In practice, volunteers' annotations proved to have a number of inaccuracies, especially for chicks and eggs, resulting in distorted chick survival estimates. I noticed several types of frequent false positives, as summarised below. See appendix S3.3 for further examples and a more detailed description:

- Great amount of egg and chick annotations in moments where it is biologically impossible for an egg or a chick to be in the image. It is most common for adults to be identified as chicks or eggs in the early season where volunteers have no chick or egg presence to compare. Chicks and eggs were also ocassionally mistaken for rocks, mounds of snow or other animals like giant petrels.

- Far away adult penguins annotated as chicks. This is again more common in the early season but happens frequently throughout the season in those nests that are further away and look smaller in the image. Normally this is just done by one volunteer out of the ten that review each image.

- Annotations of chicks and eggs when all that is present in the image is incubating adults. It is very frequent for volunteers to annotate two chicks or two eggs on an incubating adult, assuming what could be underneath it despite the contents of the nest are not visible at all.

As a result, I built a filtering process (Figure 1g) to remove annotations based on the mode (at least two volunteers are required to mark a chick or an egg inside a nest area) and on the time of year (any chick annotations before settlement are discarded).

In addition, I included an optional verification tool (Figures 1h and 6) that allows the researcher to visualize each nest, image by image and corroborate or correct the number of individuals inside the nest area (Figure 6). The researcher can verify, dismiss, and correct the number of adults, chicks and eggs annotated by the volunteers. The tool also allows the researcher to flexibly establish an early and late season boundaries, to zoom in and to clear the image of any overlaid nest diagrams and other diagnostic marks. To make this corroboration task more efficient and present the researcher with the minimum number of images I built a bespoke selection algorithm (Figure 1i). This algorithm organises the images in chronological order until the first true positive of two chicks is achieved (or until the researcher is convinced there is only one chick). This finding determined the first chick detection in each nest and the beginning of the count towards the breeding success estimate. The researcher can then reverse the order to work back through the images to reliably determine the time of crèche. If there has been a chick or egg loss during any of these periods the researcher can keep working in reverse chronological order until finding the point in which that egg or chick was lost.

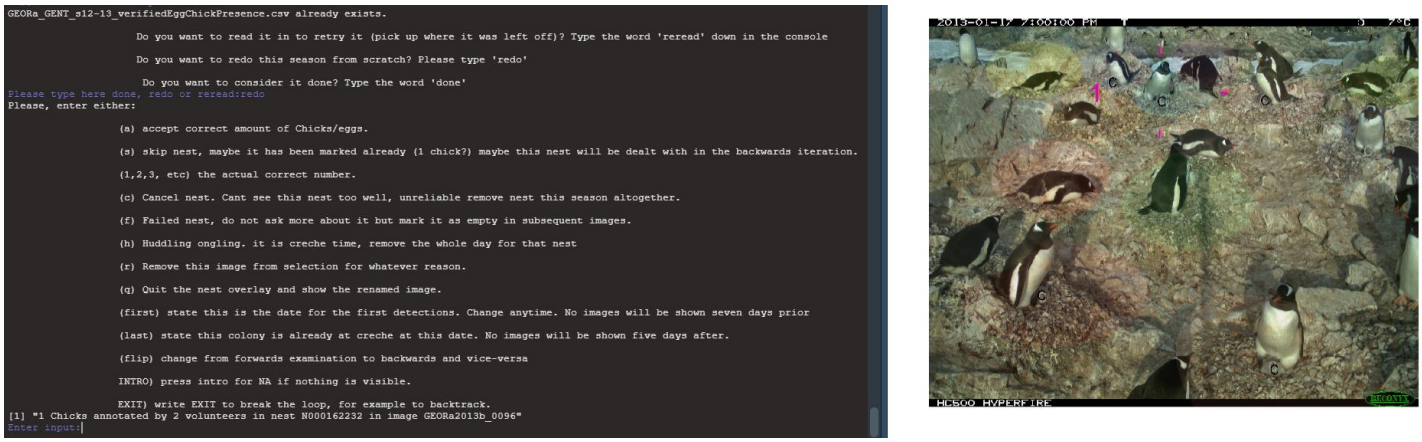


Figure 6: Interface of the verification tool, an optional task within the nest tracking tool. The researcher is presented with an image where the target nest is shown overlaid with the estimated number of individuals in the nest overlaid over the nest diagram and its respective timelapse image. The researcher is prompted to choose one of the following actions to perform: To accept the volunteers' estimate, to skip the image, to manually introduce the number of individuals in view, to withdraw the nest or the image from the dataset, to mark the nest as failed, to remove all overlaid images and show only the renamed image while zooming in into the target nest and to establish early and late season time boundaries for each nest (i.e. filtering by date).

Results.

The filtering process (See appendix S3.3) and the selection algorithm maximise the number of annotations verified (Table 1c) while using minimum input (Table 1e). Only between 1 and 30% of the total volunteer annotations are presented to the researcher for validation (Table 1f) and that is enough to verify between 24 to 58% of each season's dataset (Table 1c).

Despite the good performance of the filtering process, the overall number of annotations that need to be verified was still too high for the present purposes: between 482 and 1148 annotations (Table 1f). This is too many, considering I am monitoring between 15 and 31 nests (Table 1a) and made the process excessively time-consuming (Table 1g).

This is mostly due to the low number of true positives in most seasons (Table 1d and 1e). The real percentage of true positives is likely higher as in this study I were not focusing on late season annotations, when chicks are bigger and easier to detect. It is worth pointing out the disproportionate number of false positives in the last two seasons analysed (Table 1d and 1e).

Table 1: Amount of annotations for all the seasons of study at George's Point (Camera GEORa). The table shows (a) the number of nests in study each season (b) the total number of annotations provided by volunteers and (c) the number of annotations after the various levels of filtering (See Appendix S3.3). The table also shows the number of true positives: the number of annotations that (d) correctly detect the presence of chicks and (e) correctly detect the number of chicks. Percentages in d) and e) are calculated against the filtered data (c), since those are the annotations that could be verified by an expert, the percentage of true positives is likely to be higher. f) Number of inputs that the expert needed to verify all nests in each season and reliably derive all metrics. Percentage calculated as a fraction of the total of annotations. g) Time it took the researcher to verify each season. In season s13-14 I barely had annotations for an unknown reason. In season s18-19 the low amount of annotations is due to the permanence of snow until very late in the season, resulting in only 1 nest managing a single chick.

GEORa	S12-13	S13-14	S14-15	S15-16	S16-17	S17-18	S18-19	S19-10	S20-21
a) Number of nests monitored	15	15	20	23	27	31	17	16	16
b) Number of chick annotations	5711	71	3674	29994	4714	5420	218	45244	39021
c) Annotations verified after filtering by date, mode and selection algorithm	2128 (37%)	2	2142 (58.3%)	9624 (32%)	1622 (34%)	1923 (35%)	36 (16.5%)	10938 (24%)	16649 (42%)
d) Correct detection of chicks on nests	567 (26.6%)	0	1142 (53%)	1037 (10.7%)	463 (28.5%)	654 (34%)	0 (0%)	535 (4.8%)	883 (5.3%)
e) Correct estimation of the amount of chicks on nests	394 (18.5%)	0	901 (42%)	756 (7.8%)	334 (20.5%)	501 (26%)	0 (0%)	339 (3%)	680 (4%)
f) Number of verification inputs	572 (10%)	2	1148 (31.2%)	1051 (3.5%)	482 (10.2%)	666 (12%)	13 (5.9%)	543 (1.2%)	918 (2.3%)
g) Hours of verification	4.2	0.01	5.3	4.1	2.8	3.0	0.05	6.1	6.7

It was not possible within the time-frame of the thesis to extract breeding success and phenology data from more colonies using the nest tracking-tool. With such a high amount of false positives verification became necessary and the time needed in the verification process made including other colonies in the analysis impossible. I opted to proceed with a hand annotation of the breeding success at all the other colonies discussed in Chapter 4. Still, data for GEORa is used to showcase the possible contributions to breeding success analyses that the nest tracking tool could provide, once it is possible to achievea more efficient way to filter out false positives (Chapter 4).

Validation of the nest-tracking tool

The nest-tracking tool estimates of breeding success were very simmilar to the manual estimates (Figure 7) estimated by the researcher (IJM). The average difference between techniques is of 0.15 chicks/nest and the overall trends and year-to-year changes were generally coincident. In both estimations it wass possible to observe two dips in breeding success in seasons s15-16 and s18-19, due to late thawing of snow (See Chapter 4).

The nest tracking tool generally overestimated breeding success as measured by hand. These differences were not due to a difference in the number of chicks detected but on the number of nest attempts considered. Visual inspection of whole seasons allows the consideration of more nest attempts that can be overlooked by the volunteers, since they are not seeing nest occupation synchronously. This is especially true for nest locations further from the cameras.

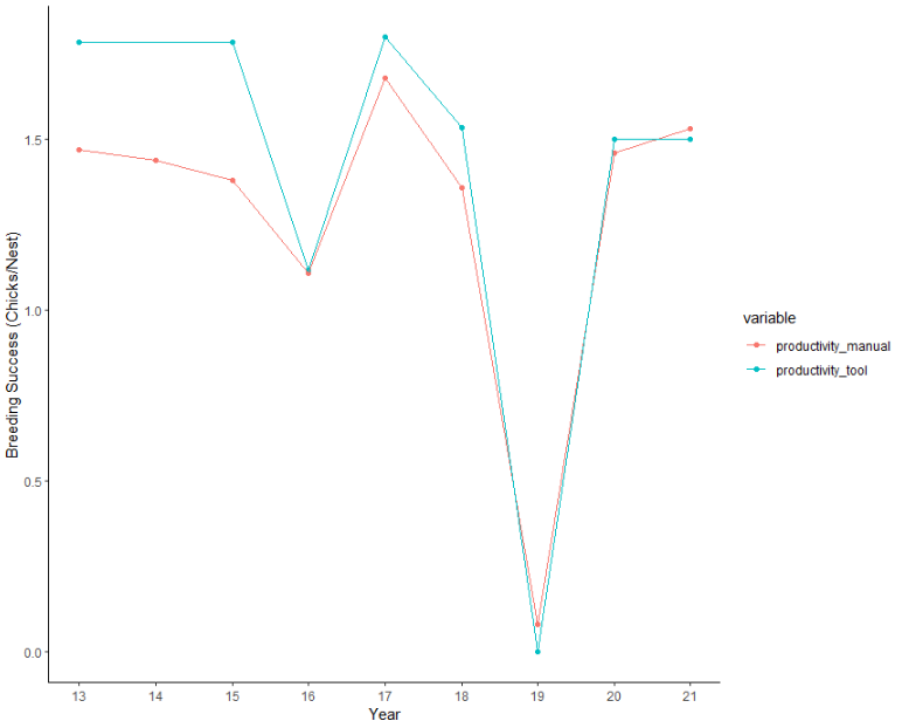


Figure 7: Comparison of manual and nest-tracking tool estimates of Breeding Success. All data corresponds to timelapse images from camera GEORa, monitoring Gentoo penguins on George's point.

Regarding phenology,the visual detection of the first chick by an expert rendered a slightly earlier estimate of hatching than any of the automated nest tracking tools, despite annotation data being verified nest by nest by IJM, the same expert (Figure 8). On average, the first chick is detected by volunteers 2.3 days later than through visual exploration by the expert. This is possibly due to the inherent difficulty of detecting days-old chicks. Possibly this is exacerbated by our filtering process that only considered chicks annotated by more one volunteer in order to filter out false positives. Only in one season (s19-20) did the volunteers detect a chick earlier than the researcher (Figure 8).

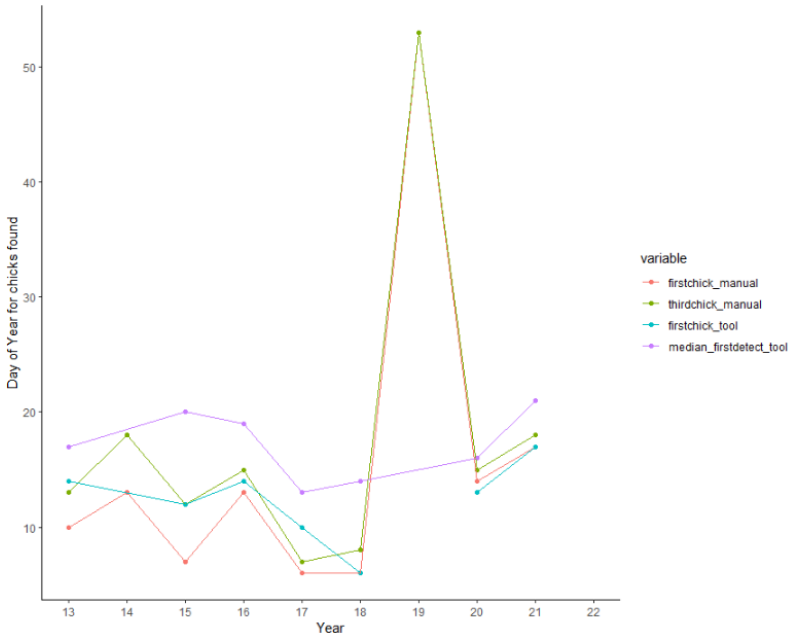


Figure 8: Comparison of manual and nest-tracking tool estimates of hatching phenology. All data corresponds to timelapse images from camera GEORa, monitoring Gentoo penguins on George's point.

Discussion.

Main findings

This chapters results can be summarised as:

- A curated dataset
- A curated annotation database thanks to the development of a batch-checking tool
- An alignment tool
- verification tool with a selection algorithm to minimise researcher input
- An estimate of Adult chick, and egg presence in every nest area in every image throughout each season.
- The resulting estimates of both phenology and breeding success were accurate, however, very time consuming to acquire.

Building a Nest-Tracking tool

Building a tool capable of following the number of chicks in each nest throughout the season continues to be a very desirable and promising idea, but in practice it proved to require much more researcher input than initially expected. This is due to various sources of variability and uncertainty:

The first source of variability is due to the study being conducted in a natural setting:

- Penguin breeding seasons are highly variable in timing and duration of life-history events within and across colonies, species and seasons. This required us to check manually what images are to be uploaded to the Zooniverse not to get volunteers bored by watching many empty images.
- This is also the reason behind the aided verification of nest attempts, since there is a varied occurrence of causes causing nesting interruption.
- Cameras being exposed to weather events mean that the framing of the image moves frequently, which required us to build a bespoke image aligner that also requires a small degree of verification to check whether it is working properly.

Another source of variability is due to the long-term nature of the study and the dataset analysed.

- The long-term nature of this study also required us to build a number of exceptions that could accommodate for changes in camera make, model, scheduling, image size resolution and position between seasons.
- The dataset that has been partially analysed by other researchers resulting in minor inconsistencies in data curation. This required us to verify that the images to which the volunteer annotation coordinates refer indeed correspond to the images being aligned and verified.

Finally, image analysis using citizen science annotations.

- Volunteers have varying levels of experience, knowledge and commitment. This required us to accommodate the different sources of false positives by building a verification tool into the process.
- The great amount of false positives further required us to introduce several steps of data filtering and the construction of a selection algorithm to alleviate the number of images that needed verification.

All these sources of variation required the researcher's input in various points during the analysis of the dataset and made it impossible for us to build a fully automated nest-tracking tool. I had to build various safeguards and checkpoints in order to accommodate and minimise the many sources of variability that concur in the final dataset, finally achieving a semi-automated tool. Most of them were fairly quick to apply with the researchers mostly needing to inspect some plots and graphs in order to check things are alright as in the batch-checking tool. However, the low number of true positives in the guard stage make the verification stage too long and hence impractical. The following were the greatest sources of false positives:

- Annotation of faraway adults as chicks. These false positives possibly indicate that those volunteers did not have an accurate image of the appearance of chicks. Their comparatively smaller size may lead them to think they are indeed smaller individuals and hence they get annotated as chicks.

- Annotation of chicks and eggs in times of the season and the breeding cycle where it is biologically impossible. These false positives possibly indicate a lack of understanding of the breeding cycle and the times at which they occur in the year.

- Annotation of chicks and eggs in nests despite they are not visible. These annotations possibly indicate a lack of understanding of the task, as chicks and eggs should not be marked unless visible.

- It is noticeable that the error in false positives is much greater in time-lapse images acquired more recently (Table 1). There are two possible (non-exclusive) explanations for this.

    - Our newest cameras (Reconyx Ultrafire) have a wide angle lens that can capture a great number of nests in good quality images, due to its wide angle lens and greater resolution (2048x968). However, the process of resizing the images before uploading them to the zooniverse downsizes the image to 1000x500 in order to save space. The result is that the nests are much more crammed and the chances of getting clicks in an unintended nest are greater. This could be the reason behind the greater number of false positives in GEORa s20-21, s21-22 and AITCb s21-22.

    - Another possibility worth exploring is the change in volunteer attendance our project had after the 2020 pandemic. For example, since 2020 our citizen science project got lots of attention from the Duke of Edinburgh programme. This programme is aimed at teenagers that take part in a volunteering project for a certain number of hours in order to obtain a qualification. To overcome this it may be necessary to establish a performance test for volunteers before their data is considered. In order to test this idea it would be possible to use their user ID numbers to (individually but anonymously) check their performance. This could be easily done with the Batch checking tool that compares adult annotations to the AI matrix of penguin presence.

The greater number of false positives in chick annotations had been noted by previous studies (Jones et al., 2018, 2020). They found that the greatest source of error were images where there were no chicks. They reported that the number of chicks on average deviated from an expert-annotated dataset between 1.18 to 3.17 chicks/image. That is quite a good result considering those studies were looking at overall chick count in the image. However, that sort of error looking at productivity nest by nest distort breeding success and phenology metrics greatly.

This large number of false positives made data analysis with the verification tool impractical despite of the filters and the use of a selection algorithm that minimises minimise the number of images for verification. For this reason, for the present study I took the pragmatic decision of replacing volunteers' estimates of breeding success by our own (Chapter 4), even after a very time consuming process of improvement of the filtering procedures. This work has not been in vain, as the prospect of using the automatic tool once that a better volunteer filtering system is implemented remains attractive. Here are some ideas:

- Finding new ways of filtering the dataset. For example, I could delve deeper into the dataset and explore the percentage of true and false positives as I increase the threshold of volunteers marking chicks in a nest.
- Given the low detectability of early chicks (Figure 8) any threshold of volunteer annotations above 1 will result in loss of early chick detections. However, maintaining a threshold of 1 will preserve false positives. In order to compensate for this, I could selectively show images corresponding to the early chick stage to a greater number of volunteers and then use a threshold above 1.
- Another possibility is to filter by user. I could use the batch-checking tool (Figure 2) to score individual users. Even if the tool only compares adult annotations this could give us an idea of reliability. I could even study annotation accuracy over time and filter out chick annotations of users below a certain threshold of annotations.
- Building a chick AI. This is quite a difficult task due to the variety of shapes, sizes and degrees of dirt of the chicks and would require a large expert-verified dataset.
- Currently the largest images obtained with *ultrafire* cameras (resolution 2040x968 pixels) are resized down to 1000x500 pixels. I could stop resizing them and split them in four images of roughly 1000x500 pixels. This would make the observed image less crowded and make it easier for volunteers to see into the nests. These images would need a further post-processing step to stitch them back together.

Also, several other options could be tested in order to reduce the percentage of false positives in future annotations:

- Edit the workflow questions. The current workflow includes the following question for volunteers to annotate: "For each penguin in the image select 'adult' or 'chick' from the list. Please also label any penguin 'eggs' and 'other' animals". It is possible that this question is too open and induces volunteers to think that the presence of chicks and eggs is to be expected and that might create a bias that would favour the current amount of false positives, especially in the early and late season, where there are no egs or chicks in frame to compare with adults. Before changing the workflow it would be worth analysing the "Easter-egg hunt" a temporary workflow that I put together to look for nest contents only (chicks and eggs).
- Include images of adults chicks and eggs in the main annotation page. A tutorial and field guide exists and is only one click away as part of the annotation workflow. However, given the great amount of false positives for chicks it might be worth placing some images of chicks in their various stages in the main page of the workflow.
- I could also put together a better tutorial, for example a video where I take volunteers through the annotation process while I explain the various differences in chicks and eggs as well as the timing at which they can be expected.
- Building two sepparate workflows: A limited workflow with training images that new volunteers need to train on before they are allowed to annotate the real research images.

Estimates of Breeding success, Hatching and Crèching Phenology:

After the process of verifying multiple seasons at GEORa, the nest tracking tool rendered similar estimations of breeding success to those obtained by an expert (Figure 6). Hatching and crèching phenology estimates from the nest-tracking tool are also similar to those derived directly from expert hand annotation. In all but one season the researcher was able to find the respective phenological milestone before the volunteers. On average, the researcher detected the presence of chicks 2.3 days before the volunteers did. Detecting very small chicks is really difficult not only for their size but because they are mostly covered by the adult as they cannot thermoregulate by themselves. For an experienced researcher it is easy to recognise a tiny flipper or head as a chick but I do not think it is fair to expect such degree of detection from untrained volunteers. However it might be worth increasing the amount of volunteers annotating this image in order to increase accuracy.

Despite the error this delay is overall quite consistent and allows for the detection of year-to-year changes in phenology and the correct determination of overall trends. It would be worth seeing if this error is maintained in other colonies, species and years but for now it is possible to say this is a promising result and a fair estimate of penguin phenology.

Other Considerations

In the current study I have ignored egg metrics due to the great error associated with egg annotations because of the great difficulty egg detection. This means I am missing an estimate of egg-laying phenology, a very important landmark of the breeding success. I suggest it would be very valuable information to acquire in future iterations of the nest tracking tool. Laying could possibly be estimated by building a tool to estimate penguin position in order to find the period with the greatest amount of images of the nest occupant laying down. This could be done using our bespoke AI pengbot3000 to estimate penguin position or other general tools like optic flow or even a simple machine learning algorithm.

In future studies it would be worth developing new tools to estimate laying date. For example, I could use pengbot3000, the AI penguin detection algorithm (Arteta et al., 2016) to spot penguin posture (Figure 2a). A period of more than 15 days of penguin laying down could be an indicator that they are in incubation. Other tools like optic flow, which detects the changes in pixel content between consecutive images could also be a possibility to detect lack of movement through lack of changes in the images. If all these fail, I could always estimate a nest by nest metric of settlement (See chapter 2) that could serve as an indicator of each nest's relative position in that season's phenology.

Once I have an estimated laying date per nest I might be able to get more accurate effects of early breeding that include failed attempts (See chapter 4). These would be useful in determining nest by nest whether early breeders do have greater breeding success. In addition, that would allow us to study whether it is the same nests that are earlier consistently and whether that has a consistent effect on breeding success. This would be particularly interesting in relation to snow and to when nesting sites become available.

Conclusions.

The nest-tracking tool proved useful at accommodating all other types of variability in the dataset and proved capable of following individual nests and produced good estimates for a number of biologically-meaningful metrics including: hatching and crèching phenology, breeding success and mortality dates. This dataset will be used in the next chapter (Chapter 4) to showcase the possibilities that this tool can offer when studying multiple aspects of breeding behaviour (including breeding phenology estimates) and breeding success. This includes studies on: changes in breeding success over time and across the Antarctic Peninsula, effects of environmental conditions, synchronicity, carry-over effects, in-season effects, human visitation and the differential effect of early and late breeding. I hope to overcome these teething problems to prepare a semi-automated analysis with the whole set of colonies in the near future.

References.

Arteta, C., Lempitsky, V., & Zisserman, A. (2016). Counting in the Wild. In B. Leibe, J. Matas, N. Sebe, & M. Welling (Eds.), *Computer Vision – ECCV 2016* (pp. 483–498). Springer International Publishing. https://doi.org/10.1007/978-3-319-46478-7_30

Clarke, J., Kerry, K., Irvine, L., & Phillips, B. (2002). Chick provisioning and breeding success of Adélie penguins at Béchervaise Island over eight successive seasons. *Polar Biology*, *25*(1), 21–30. https://doi.org/10.1007/s003000100307

Davis, L. S., & McCaffrey, F. T. (1986). Survival analysis of eggs and chicks of Adélie penguins (Pygoscelis adeliae). *The Auk*, *103*(2), 379–388.

Hinke, J. T., Barbosa, A., Emmerson, L. M., Hart, T., Juáres, M. A., Korczak-Abshire, M., Milinevsky, G., Santos, M., Trathan, P. N., Watters, G. M., & Southwell, C. (2018). Estimating nest-level phenology and reproductive success of colonial seabirds using time-lapse cameras. *Methods in Ecology and Evolution*, *9*(8), 1853–1863. https://doi.org/10.1111/2041-210X.13015

Jones, F. M., Allen, C., Arteta, C., Arthur, J., Black, C., Emmerson, L. M., Freeman, R., Hines, G., Lintott, C. J., Macháčková, Z., Miller, G., Simpson, R., Southwell, C., Torsey, H. R., Zisserman, A., & Hart, T. (2018). Time-lapse imagery and volunteer classifications from the Zooniverse Penguin Watch project. *Scientific Data*, *5*(1), Article 1. https://doi.org/10.1038/sdata.2018.124

Jones, F. M., Arteta, C., Zisserman, A., Lempitsky, V., Lintott, C. J., & Hart, T. (2020). Processing citizen science- and machine-annotated time-lapse imagery for biologically meaningful metrics. *Scientific Data*, *7*(1), Article 1. https://doi.org/10.1038/s41597-020-0442-6

Moreno, J. (2010). Reproductive Success. In M. D. Breed & J. Moore (Eds.), *Encyclopedia of Animal Behavior* (pp. 64–69). Academic Press. https://doi.org/10.1016/B978-0-08-045337-8.00119-4

4

Chapter 4

Factors affecting Pygoscelid breeding success in space and time

Abstract.

The three species of pygoscelid penguins are undergoing some of the fastest changes in phenology ever recorded. These changes are directly related to warming in the Antarctic Peninsula, possibly via mechanisms such as food availability in the early season. In this chapter I study whether those phenological changes are impacting the breeding success of these three species or, alternatively, whether this change is a way for these species to adapt to climate change. In order to do this I manually estimate breeding success over ten years in a sample of 11 colonies throughout the Antarctic Peninsula using PenguinWatch time-lapse imagery. I also used the more detailed nest-by-nest estimates of breeding success and breeding phenology in George's Point obtained in Chapter 3. Using these two data sources I find the record phenological change observed in Chapter 2 does not seem to be impacting breeding success over the period of study. However, I found a negative effect of snow presence in the colony that is greater in later years. I also investigate the effects of various other aspects in breeding success including: changes over time and across locations in the various species, effects synchronicity, carry-over effects, in-season effects, human visitation and timing (Early vs late breeders).

Introduction.

Climate Change and Phenological advance

Penguins in the Antarctic Peninsula (AP) are experiencing some of the fastest environmental changes on the planet. The rate of temperature increase is the second fastest after the North Atlantic (Meredith et al., 2019). The AP is currently warming at +0.32°C/decade (Carrasco et al., 2021) and reaching 0.42 ± 0.15 °C/decade at Vernadsky Research Station, in the Argentine Islands (Turner et al., 2020). The temperature increase is especially impactful for penguins, because they select ice free, relatively dry areas on which to establish their colonies. Data from this camera network shows that my colonies of study are warming nearly an order of magnitude faster than the AP average (0.34 ± 0.07 °C/year; Appendix S2.3).

Temperature increase is causing rapid change of the physical environment including glacial melt (Baumhoer et al., 2018), ice-shelve retreat (Flexas et al., 2022) and a rapid disappearance of sea-ice especially since 2016 (Eayrs et al., 2021). The most important change is possibly the loss of sea ice, as this implies a loss of ice-algae, the main primary producer of the region and on which the whole Antarctic food chain depends. This loss is especially significant for mesopredators, including penguins, seals and whales (Suprenand & Ainsworth, 2017).

In Chapter 2 I have already documented a record phenological shift on the three pygoscelid penguin species: the Adélie penguin (*Pygoscelis adeliae*), the Chinstrap penguin (*Pygoscelis antarctica*) and the Gentoo penguin (*Pygoscelis papua*). In this chapter, I investigate whether this is affecting their breeding success or, on the contrary, the phenological shift is an adaptation that succeeds in compensating or exploiting the new environmental conditions derived from climate change.

Breeding success

Breeding or reproductive success is defined here as the number of independent offspring produced per breeding attempt (Moreno, 2010) to the point of crèche. After that chicks become mobile and survival is impossible to monitor. Studies in chick mortality indicate that chick loss happens predominantly during incubation and early guard stage (Clarke et al., 2002; Davis & McCaffrey, 1986) so success up to crèching is likely to be a good proxy for overall breeding success. For pygoscelid penguins, our measure of breeding success encapsulates adult pair performance from arrival through to laying (2 eggs), egg survival until hatching and chick survival until crèching (Figure 1). This estimate (0, 1 or 2 surviving chicks per nest) sums up the realised breeding capabilities of a pair to raise offspring while taking into consideration the environmental conditions of a particular season. It also makes it easy to compare between nests and colonies.

Breeding success is one of the most important parameters to determine demographic fluctuations in any population (Johnston et al., 2019). Breeding success is a precondition for recruitment in the following years and is a key component of productivity and fitness. Here I refer to productivity as the total number of new individuals produced by a population in a given season (Ricklefs & Bloom, 1977), while fitness is the contribution of a given individual to the breeding population. The latter only includes the individuals successfully recruited after their juvenile years (Moreno, 2010).

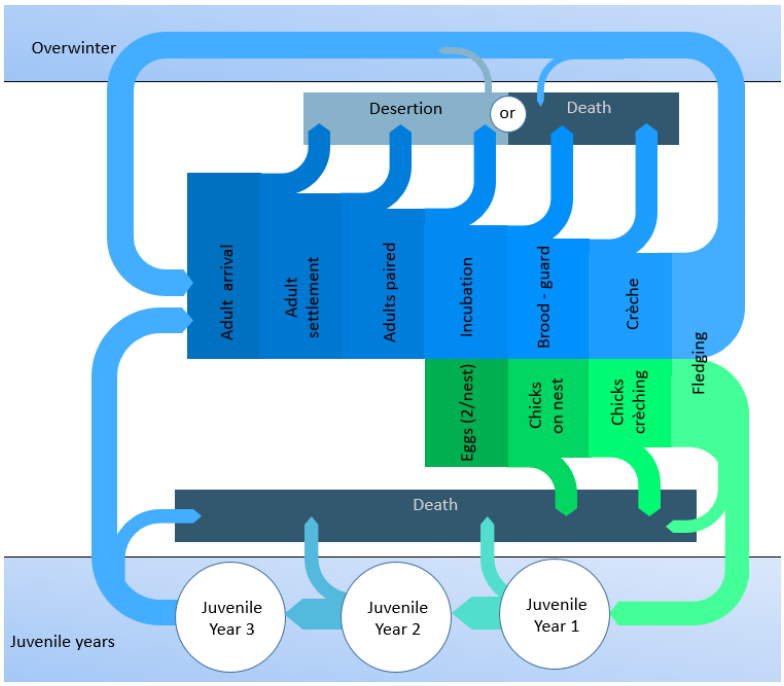


Figure 1: Schematic representation of the life cycle of pygoscelid penguins and their chicks.

An individual's potential breeding success depends on a number of traits determined by genetics and upbringing (e.g. "silver spoon effects"). However, this potential is limited by the individual condition and the season's environmental conditions. The fitness and life-long breeding success of an individual depends on both the number of breeding attempts and the breeding success in them (Joly et al., 2023). However, the impossibility of sustaining top performance throughout lifetime leads to trade-offs between investing in present adult survival and investment in current or future reproduction attempts (Shoji et al., 2015). Each individual is constantly affected by the cost-benefit of their participation and investment in the current/coming seasons against the benefits of possible subsequent seasons (Vleck & Vleck, 2002). These depend on individual decisions that can be translated into discrete behavioural choices, for example the choice to skip breeding (Shoji et al., 2015), minimise provisioning for self-preservation (Weimerskirch et al., 2001) or even desert before the end of the season (Numata et al., 2000) in order to gain better chances on the next. The trade-off between survival and breeding can also translate into a change in reproductive effort. For example, animals tend to increase their reproductive effort if future reproduction is uncertain due to old age (terminal investment) or unfavourable environmental conditions making survival unlikely until the next reproductive opportunity (Duffield et al., 2017).

FACTORS KNOWN TO AFFECT BREEDING SUCCESS

To the best of our knowledge there are no studies linking individual characteristics and greater breeding success repeatedly across many seasons (Joly et al., 2023). This is partly due to the difficulty of studying life-long breeding success in long-lived animals. However, in given seasons several individual characteristics have been related to greater breeding success if found in the group of best performing individuals. These are not necessarily intrinsic characteristics of the individual, as they might change season to season, but they help to explain what are the factors affecting the potentiality of breeding success in an individual.

Perhaps the most studied is body condition, usually measured as body mass divided by a skeletal measure (Johnson et al., 1985; Labocha & Hayes, 2012), which in penguins is generally flipper length (Numata et al., 2000; Robinson et al., 2005). This measure can inform us of the physiological status of an animal in a particular moment, by estimating how much fat and muscle reserves does the individual have while accounting for the build of that particular animal. This is important in birds in order to undertake the great effort that is reproduction and especially so in penguins, where prolonged fasting periods are a key part of the incubation and guard periods (Williams, 1995).

Body condition specifically at the beginning of a season is probably the best estimate of the potentiality for breeding success of the individual (Labocha et al., 2014) as it is the result of the aggregation of a lot of individual, environmental and life-history parameters up to that moment in time. Its correlation with breeding success is very strong (Vleck & Vleck, 2002). As such, it is used frequently by females to select a partner during the mating season (Marks et al., 2010) and by scientists to study the effects that multiple parameters can have on penguins as a proxy for the effects on its breeding potentiality (Vleck & Vleck, 2002).

Age and experience are also factors limiting breeding success in penguins, although their relationship is not straightforward. Breeding success increases with age (Saraux & Chiaradia, 2022) but just up to a point where it starts decreasing, the phenomenon known as senescence. Part of the effect of experience comes from their capability to adapt to their partner and establish nest relief patterns that are as stable and short as possible (Croxall & Davis, 1999; Nisbet & Dann, 2009).

Breeding success can also be affected by previous events in the life-history of the individual, normally during the previous season or even the previous winter. For example, the decision to skip a year can have carry-over effects by improving survivability and future breeding success (Shoji et al., 2015) and can contribute to greater life-long breeding success despite of completely missing one season (Joly et al., 2023). Breeding attempts themselves come at a short-term survival cost for the individual, especially if they finish late. Finishing time is doubly important for Pygoscelids, as they first have a post-breeding full-body moult before they migrate (Adélies and Chinstraps). Failing to finish a season in time can result in a mismatch with food resources in the pre-moult fattening period or missing favourable opportunities for migration. Either of this could make the winter season more risky, and make it more difficult to reach the following season in good condition.

The decision on when to breed is of great importance for maximising breeding success. As discussed in chapter 2, penguins try to time their breeding so that the period of maximum growth (and food demand) of the chicks matches the time of maximum food availability. Failure to do so results in a phenological mismatch that puts the season's breeding output at risk, or imposes greater reproductive efforts this season, that can have carry over effects into the next (Visser et al., 2012).

When and where to breed might be influenced by other animals' choices, because synchronicity in breeding brings many advantages in exploiting high-quality food resources, choosing suitable habitat and affecting predator avoidance (Gaston et al., 2009; Ims, 1990b). On one hand, breeding at a joint place and time facilitates the active defense of a colony from aerial predators together with neighbours (Young, 1994). On the other hand, it "swamps" predators by concentrating all available prey (only eggs and chicks up to a certain age are attacked) in the smallest possible time window (Ims, 1990a). Outliers from that window would therefore be so disproportionally affected by predation that some models suggest synchronicity is even more important than matching favourable environmental conditions (Youngflesh et al., 2018). Despite the need for synchronicity in colonial breeders it is well established that greater breeding success is associated to early breeders compared to late-breeders within a colony (Ahola et al., 2007; Bennett et al., 2022).

Apart from the internal factors of the individual, the resulting breeding success is known to be greatly influenced by seasonal environmental conditions. This is particularly true in polar species where snow and ice are responsible for conditioning the very physical appearance and disappearance of the breeding grounds and therefore affecting all possible decisions regarding the choices of whether or not to breed but also on when to do so. Even once the decision has started yearly environmental conditions have a great effect on breeding success through Food availability (amount and food type)(Crawford et al., 2006; Pütz et al., 2001)

Finally other effects like human visitation have demonstrated various effects of human disturbance on penguins. Disturbances include a range of effects from very short-term behavioural changes (Holmes, 2007) to long term effects on penguins' health. The latter include the presence of heavy metals in bones, erythrocytic nuclear abnormalities and greater levels of stress hormones in feathers (Barbosa et al., 2013). In very few studies it was possible to establish a link between human presence and Breeding success and whenever possible the results were mixed. Breeding next to a human research station could potentially have positive effects, possibly due to the greater protection from shy aerial predators (Holmes et al., 2006; Woehler et al., 1994). The effects of colony visitation (by scientists or tourists) overall seems to be a negligible (Carlini et al., 2005; Lynch et al., 2010) to negative effect on breeding success, either directly (Giese, 1996), or indirectly

(Patterson, 2001; Trathan et al., 2008). Most studies suggest visitation could impact populations through impairing recruitment through the disturbance of prospecting juveniles (Trathan et al., 2008; Woehler et al., 1994).

Aims

There has been general discussion on what is the main driver of population decline for Chinstraps and Adélies in the Antarctic Peninsula. On one hand it has been proposed that these declines are happening during winter, especially for immature birds that would find it increasingly difficult to make it to breeding age in this changing world. This would be especially difficult for these two species who are migratory and spend their winters out in the ocean, while Gentoos stay in the vicinity of their colony. Another (non-exclusive) option is that the decline comes from mortality during the breeding season, because parents are not managing to raise enough chicks.

In this chapter I attempt to answer this last possibility by building a Breeding Success dataset capable of tracking the fluctuations of breeding success in the three pygoscelid species in several colonies across the Antarctic Peninsula over the last 10 years. I also use this dataset to test various sources of variability in Breeding success including environmental conditions, human visitation, synchronicity, within-season and across season (carry-over) effects and early breeding.

Methods.

DATA SOURCES

All data is derived from the images taken by the PenguinWatch camera network in Antarctica for 11 colonies during the period 2012-2022. Time-lapse images for all colonies and seasons shown in Table 1 were manually reviewed in order to estimate breeding success.

Table 1: Table containing all the colonies of study as well as their locations, including all cameras, species and seasons.

Colony code	Colony name	Latitude	Longitude	Camera code	Species	First season	Last season
ARDL	Ardley Island	-62.2136	-58.9337	ARDLb	ADEL	22-23	22-23
				ARDLc	GENT	22-23	22-23
BAIL	Bailey Head	-62.964	-60.504	BAILa	CHIN	12-13	22-23
BROW	Brown Bluff	-63.522	-56.889	BROWc	GENT	15-16	21-22
GAST	Gaston Island	-64.4877	-61.8358	GASTa	CHIN	15-16	21-22
SPIG	Spigot Peak	-64.631	-62.555	SPIGa	CHIN	12-13	15-16
GEOR	Geroge´s point	-64.669	-62.6698	GEORa	GENT	12-13	20-21
DAMO	Damoy Point	-64.8175	-63.519	DAMOa	GENT	13-14	20-21
JOUG	Jougla Point	-64.826	-63.493	JOUGa	GENT	14-15	19-20
BOOT	Booth Island	-65.0665	-64.0235	BOOTc	CHIN	16-17	21-22
					GENT	16-17	21-22
PETE	Petermann Island	-65.171	-64.137	PETEc	ADEL	12-13	21-22
				PETEe	GENT		
YALO	Yalour Islands	-65.235	-64.158	YALOa	ADEL	12-13	20-21

I only considered seasons containing at least two months of data including both hatching and crèche stages. Some of the shorter seasons with just over two months of data may be biased towards inflated breeding success estimates. Missing images in the early season underestimate nest attempts, while late in the season could miss mortality events in late guard. Breeding success in such cases can be considered a maximum estimate, and werebe flagged as incomplete.

I estimate colony breeding success as the number of chicks that survive up to the point of crèche per number of nest attempts in a particular field of view (Moreno, 2010). Nest attempts were calculated as those nests with continuous adult presence for more than 10 days. Studies in chick mortality indicate that chick loss happens predominantly during incubation and early guard stage (Clarke et al., 2002; Davis & McCaffrey, 1986). Considering that it is unlikely to see chicks from cameras in their first 7-10 days, chick survival is estimated here as the number of chicks that are seen alive at each nest by the end of their third week after their initial detection.

Manual Estimation of Breeding Success, hatching and crèching phenology.

Due to a large number of false positives in the volunteer annotations, the verification process of the data was much more time-consuming than initially expected (See chapter 3). Because of the time-constraints of this thesis it was not possible to study more colonies using the nest-tracking tool or to endeavour in the process of finding more efficient tools to refine volunteer annotations. For present purposes, it was pragmatically preferable to resort to manual estimation of breeding success for this study. Manual breeding success estimation from time-lapse cameras has been tested before against ground counts and resulted successful (J. T. Hinke et al., 2018).In the future, I expect to be able to establish further filters earlier in the process that can allow us to use the dataset of volunteer annotations. In addition, I expect these manual counts couldserve as a gold standard against which to compare these results (both the chick output and the number of nesting attempts) to the results from further iterations of the nest-tracking tool.

Upon visual inspection of the early season images, I realised that identification of nesting attempts proved insufficiently reliable, so I estimated numbers through two different nest-counting procedures. The first one counts all those instances in which a nest is continuously occupied in one location continuously for at least 10 days after settlement (as in the nest-tracking tool). The second one, more conservative, requires the penguin to also amass nest material (i.e. stones) and to have been seen next to a partner in the nest area. In case, an egg is spotted in a penguin nest, that is considered as a nest attempt regardless of the fulfilment of any of the above conditions. In the few cases, that the same spot is unoccupied and reoccupied (often by different species) those is considered as two separate nesting attempts.

Regarding the manual estimation of hatching and crèching phenology, I derived two measures for each of these two life-history milestones. For the manual estimation of both the hatching and the crèching date, it was not feasible to extract the occurrence of each of those milestones in each nest across the nine seasons. I derived two estimates for each metric (Hatching and crèche) from the visual inspection of each season. The first one is the first instance of the milestone. This is, the first chick or the first time a chick stepped out of their nest area. This is an easy and common metric in phenology but very prone to outliers (Inouye et al., 2019). I decided to also estimate these milestones as the date for the third nest with a chick to be seen or the third nest to be seen with a chick outside of the nest area (For hatching and creching respectively). I believe that this measure is more representative of the colony and has less chances of being an outlier and therefore to oscillate excessively across seasons.

Other data

Apart from this, I extracted number of days of snow persistence from the time-lapse images. After the visual inspection of the various seasons, it became apparent that prolonged snow persistence in the early season as well as big snowfall in the midseason may be clear drivers of chick mortality. While trying to detect snow presence in the images was very time consuming, detectingthe thawing of the winter snow was a really apparent event when observing the luminosity of the images (See Appendix S4.1 Figure S1). Using this detection of spring thaw I estimated the persistence of snow in each season as the number of days between the settlement of penguins (See chapter 2) and the spring thaw (Figure 5c).

Results.

Breeding successs in Pygoscelid Penguins

On average breeding success, as estimated from hand-annotated data, was 1.37 ± 0.25 (mean chicks/nest ± s.d.) for Adélies, 1.28 ± 0.43 for Chinstraps and 1.07 ± 0.48 for Gentoos. In none of the three species there is a statistically significant trend in breeding success change during the period of study (t-values for mixed models using colony as a random factor are -1.1, -0.3 and -0.1 for Adelies, Chinstraps and gentoos respectively; Figure 2).

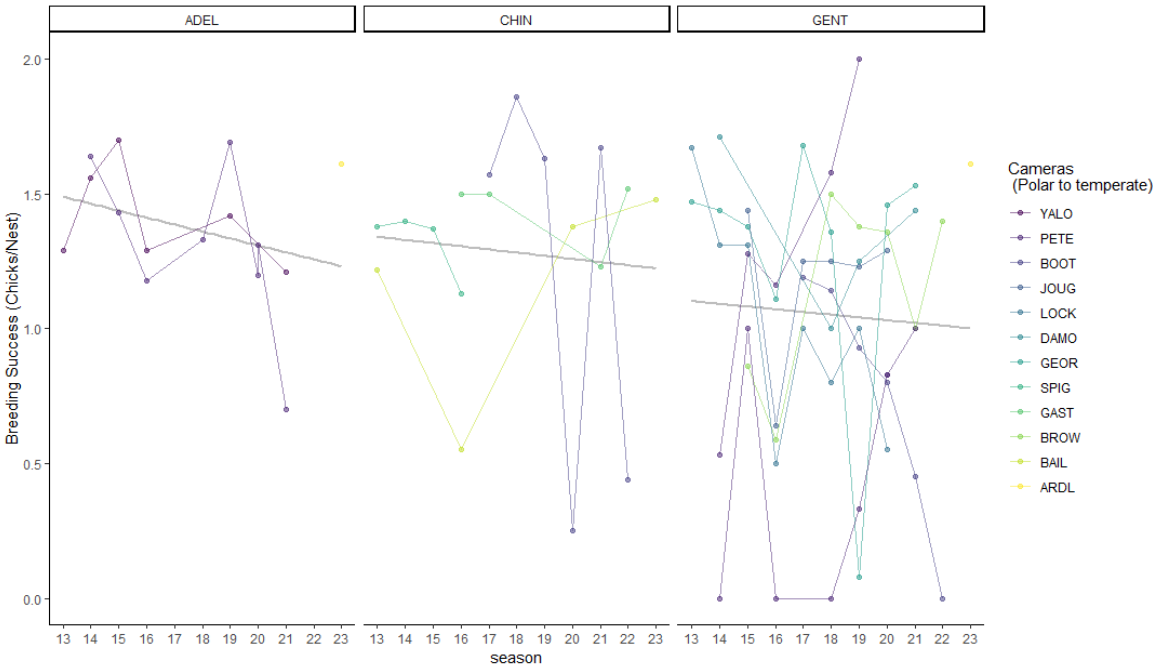


Figure 2: Time-series of breeding success per colony in the various colonies selected for study. All estimates of breeding success are hand-annotated from time-lapse imagery.

Breeding success throughout the area of study

Breeding success in Adélies and Chinstraps is almost always consistently well above 1 chick per nest, with few exceptions. In Gentoos, breeding success is generally lower and there is greater variability, mainly colony-dependent (Figure 3). Gentoos only achieve equivalent levels of breeding success to Adélies and Chinstraps in some colonies at the centre of their range (Figure 3). It is very likely that this is due to an edge-of-range effect, as both the northernmost colony (BROW) and the southernmost colonies (PETE and BOOT) are in areas of great sea-ice concentration. Breeding success estimates from camera PETEc falls out of the latitudinal gradient that could be indicative of an edge-of-range effect on Figure 3. This is possibly because PETEc is a newly established sub-colony with few nests and is growing year after year.

Considering all localities where there are two species living in the same colony it is possible to see the breeding success trends are not colony-specific but species-specific (Figure 4). While breeding success declines for Adélie penguins in Petermann Island (PETE), it increases for Gentoo penguins. In Booth Island (BOOT), relatively close to Petermann, the situation is the opposite with Gentoos showing a very clear downward trend while Chinstraps maintain their breeding success high in all but two years (Figure 4).

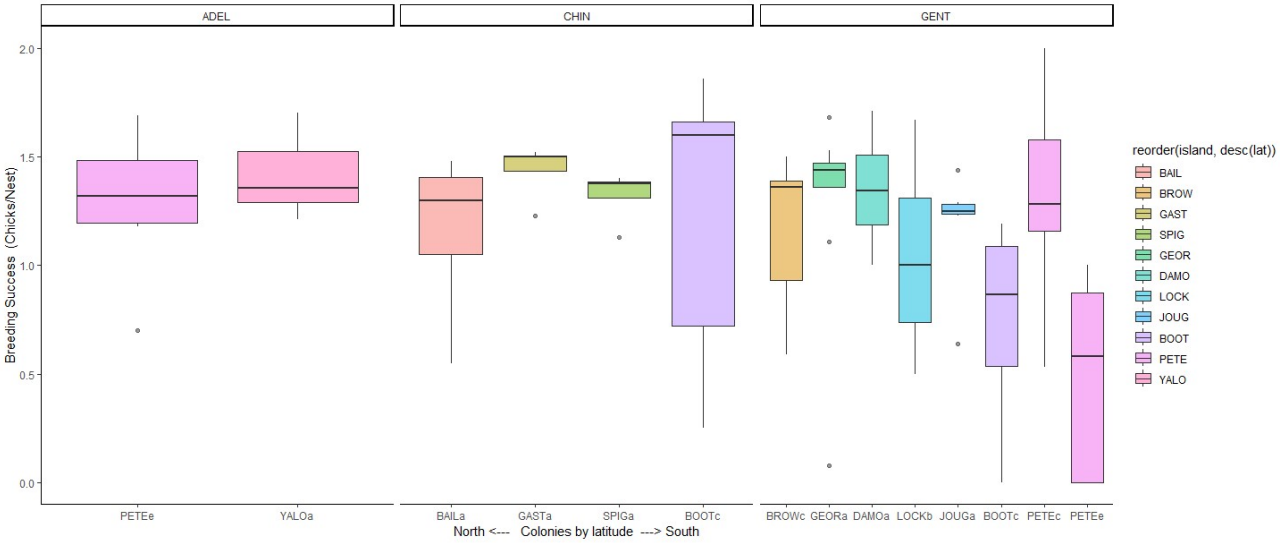


Figure 3: Boxplots showing the estimates in breeding success values at each colony for the three species of study. Colonies are ordered North (Left) to South (right) in the x-axis to show the effects of latitudinal variation. All estimates of breeding success are hand-annotated from time-lapse imagery.

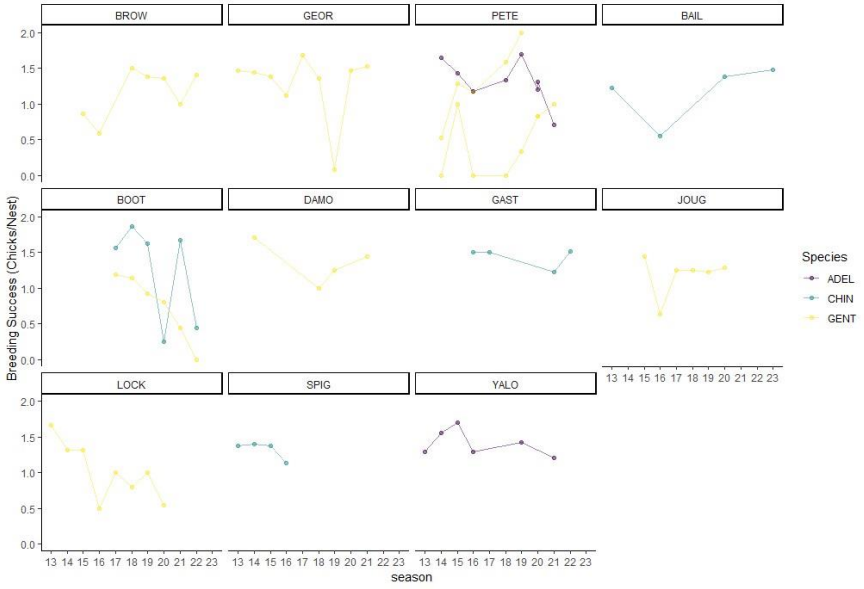


Figure 4: Manually estimated breeding success in the different colonies of study throughout the period of study of Penguin Watch.

The only significant changes throughout the observation period happen for Gentoos in Booth Island, Port Lockroy and one of the cameras in Petermann as listed on Table 2.

Table 2: Summary of model statistics for breeding success over time for species and colonies that have shown a statistically significant change throughout the monitoring period. All models are linear models that use Breeding success as response variable and year as an independent variable.

Camera	Species	Estimate	Std. Error	t-value	p-value
BOOTc	Gentoo	-0.23286	0.03468	-6.714	0.00256
LOCKb	Gentoo	-0.12405	0.04386	-2.828	0.03004
PETEc	Gentoo	0.24419	0.05485	4.452	0.0211

Extreme weather events

In the last seasons of fieldwork in the Antarctic Peninsula it has become apparent that snow persistence in the colonies has increased considerably. I tested the effect of snow on reproductive success. I counted all days with snow presence in George's point (camera GEORa) since settlement, and compared it to breeding success. The result was a clear negative effect of the amount of days of snow on breeding success (linear model with p-value = 0.01; Figure 5a). Counting days of snow was again very time consuming so I attempted an automatic detection of snow in the images by way of detecting luminosity, which was not possible. The analysis of luminosity, however, showed a very clear signal of the spring thaw (See appendix S4.1, Figures S1 and S2). This made it possible to estimate a measure of snow permanence in the colony from the date of settlement and study its evolution through the study period (Figure 5b) and its relationship with Breeding Success across the various colonies I monitor in the AP (Figure 5c).

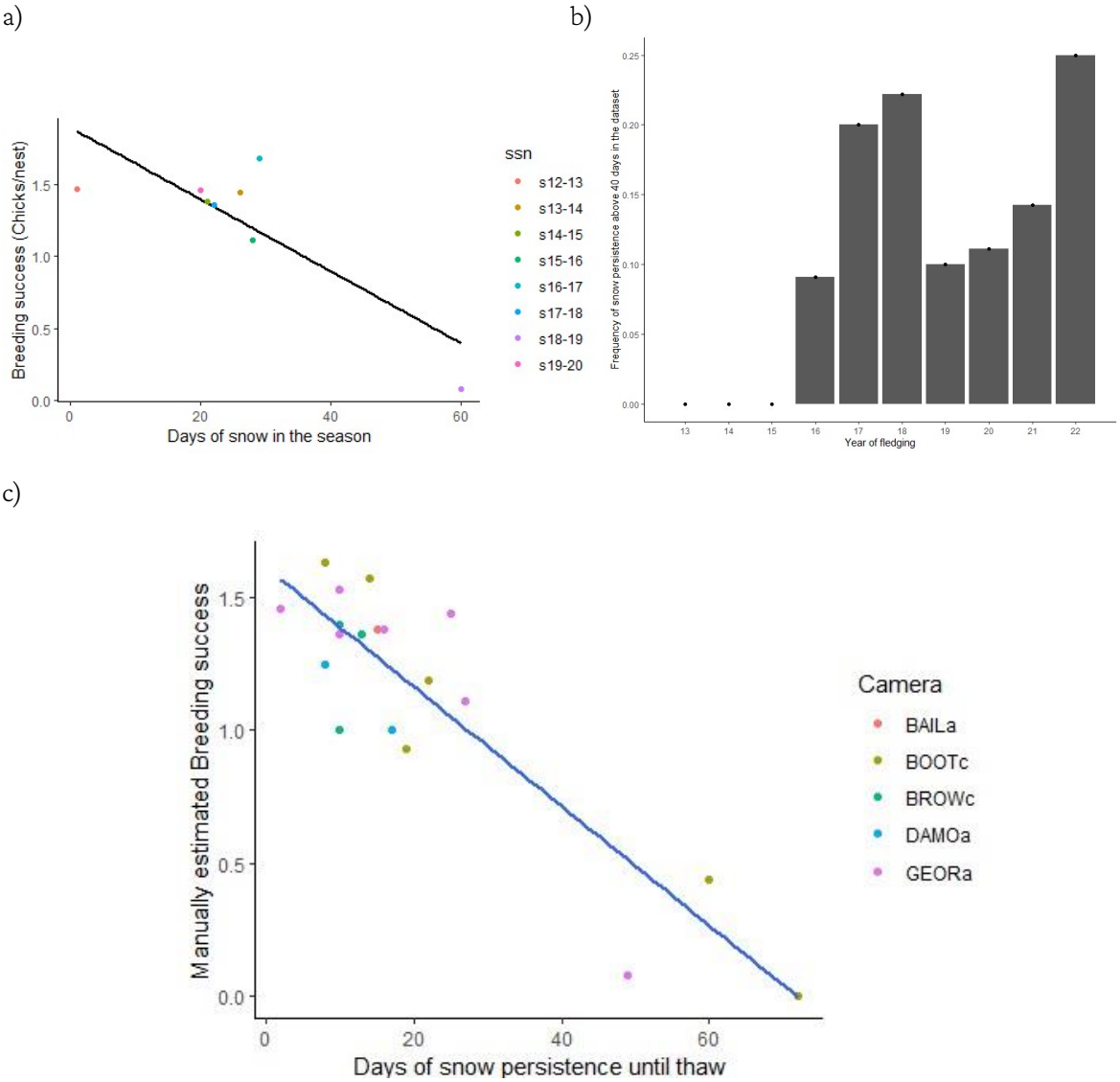


Figure 5: a) Effect of the amount of days of snow in George's Point (camera GEORa) on breeding success. b) Increase over time in the frequency of seasons with more than 40 days of snow presence . In order to increase the sample size for this analysis I interpolated the settlement date using a linear model, since phenological advance over the last 10 years can be approximated linearly (See Figure 2 in Chapter 2). c) Effect of the estimated amount of days of snow between settlement and the thawing date (See Aappendix S4.1 Figures S1, S2 and S3) on manually-estimated breeding success. This study includes both Chinstrap and Gentoo colonies. Several colonies are missing because they miss sufficient images from the early season to estimate settlement date. Refer to Table 1 for details on the cameras of study.

I found a negative effect of snow persistence in breeding success (t value = 7.5; using mixed models with colony and species as a random effect) for both Chinstraps and Gentoos. No relationship could be found for either Adélie colony, as there were not enough seasons for which I had all three estimates necessary to run the analysis: settlement, thaw date and breeding success. Finally, it is worth noting that snow persistence increased significantly during the nine years of study (linear model with p-val = 0.01; Figure 5b).

Synchronicity

Synchronicity (measured here as the standard deviation of hatching or crèching dates for individual nests) has a negative correlation with breeding success (Figure 6). Seasons where the colony is more synchronous in hatching dates are those with the greater breeding success (linear model with p-val = 0.0112; Figure 6a). No significant relationship could be established for synchronicity in crèching date (Figure 6b).

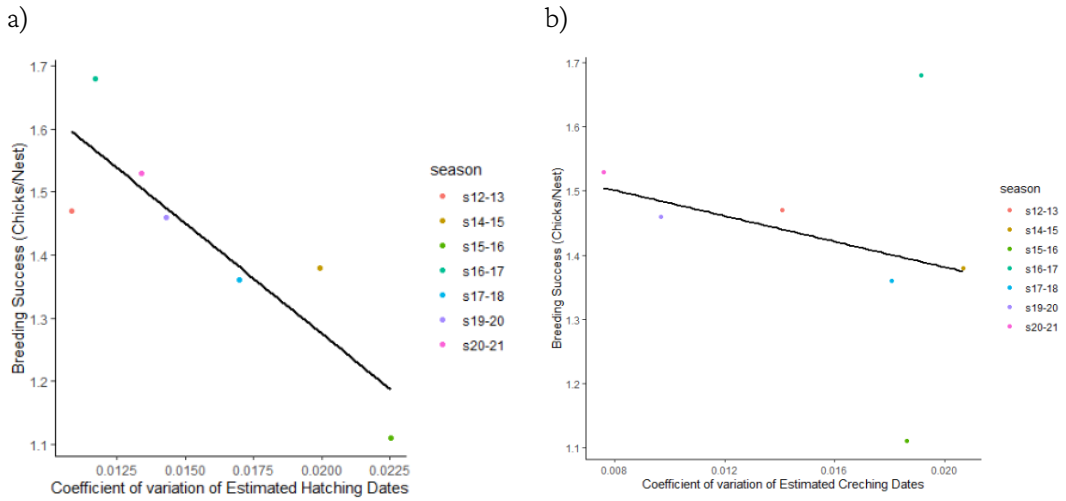


Figure 6: Effect of synchronicity on breeding success in the different seasons. Both (a) Hatching dates and (b) crèching dates as well as breeding success are estimated using the Nest-tracking tool. Only the relationship between seasona variation in Hatching date and Breeding success (a) is significant (linear model; p-val = 0.0112). All data corresponds to timelapse images from camera GEORa, monitoring Gentoo penguins on Geroge's point. The imagery was annotated by Zooniverse volunteers and extracted using the Nest-tracking tool.

Human visitation

To test the effects of human visitation I compared breeding success in Gentoos between Damoy and Jougla Point and Port Lockroy (50% more visits), all located within 2 km (Figure 7). It is possible to see that LOCK is the colony with the lowest breeding success consistently throughout the monitoring period. When tested statistically the breeding success for LOCK is significantly lower (|t-val|>2), despite the fact that season takes up most of the variance of the model (Table 3).

Table 3: Linear mixed model explaining breeding success in three Gentoo penguin colonies located within port Lockroy bay: Port Lockroy, Damoy Point and Jougla Point. This model includes colony as the only independent variable and season as the only random effect. Most of the variance is explained by the season as a random effect and LOCK shows a statistically significant lower breeding success that the other two colonies.

Breeding success in Port Lockroy Bay Fixed Effect: Colony (DAMO, JOUG, LOCK) Random Effect: Season		Variable (Random)	Variance explained
		Season	0.11841 (83.5%)
		Residual	0.02303 (16.4%)
Variable (Fixed)	Estimate	Std. Error	T-value
Intercept	1.31159	0.14608	8.978
Colony: JOUG	0.03028	0.12029	0.252
Colony: LOCK	-0.28065	0.11211	-2.503

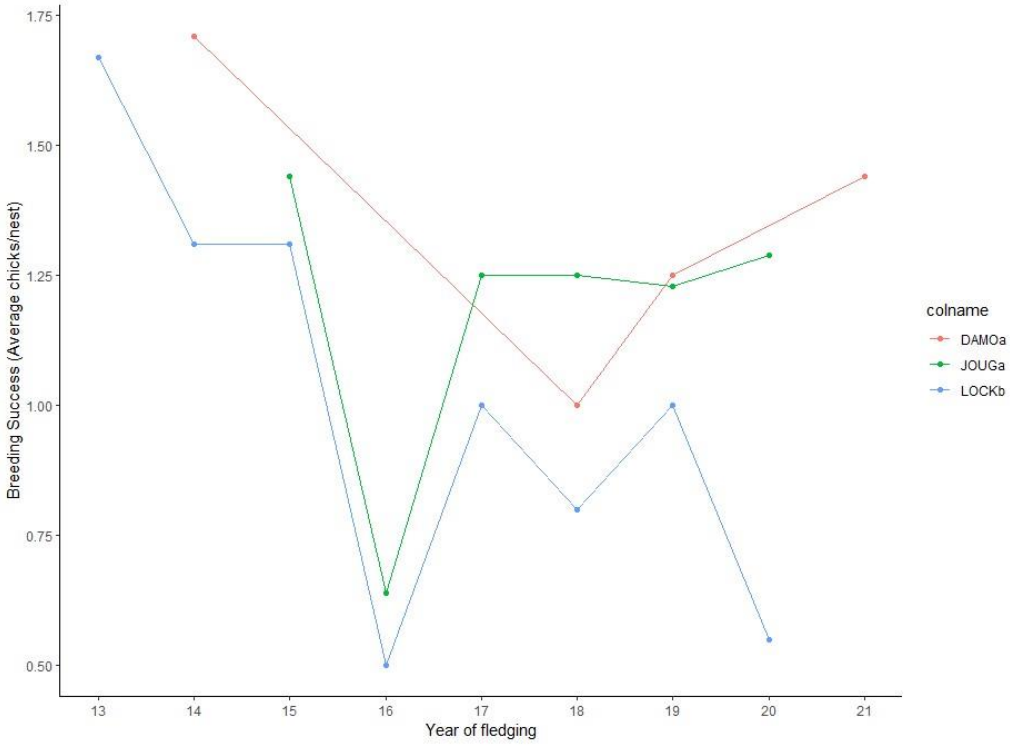


Figure 7: Time series of manually-estimated breeding success in three colonies located inside Port Lockroy Bay: Port Lockroy, Damoy Point and Jougla Point.

Within-season effects on breeding success

I analysed one within-season effect, the effect of rearing length on breeding success. Since incubation is fairly constant, I used the duration of the chick-guard period (from the first detection of a chick to the first time the chick abandons the nest) to estimate rearing length. The results are different across species (Figure 8) with Adélies showing greater success in shorter seasons and Chinstraps in longer seasons. In Gentoos this relationship is colony dependent. This data could only be estimated for some colonies and more estimates would be needed before reaching further conclusions.

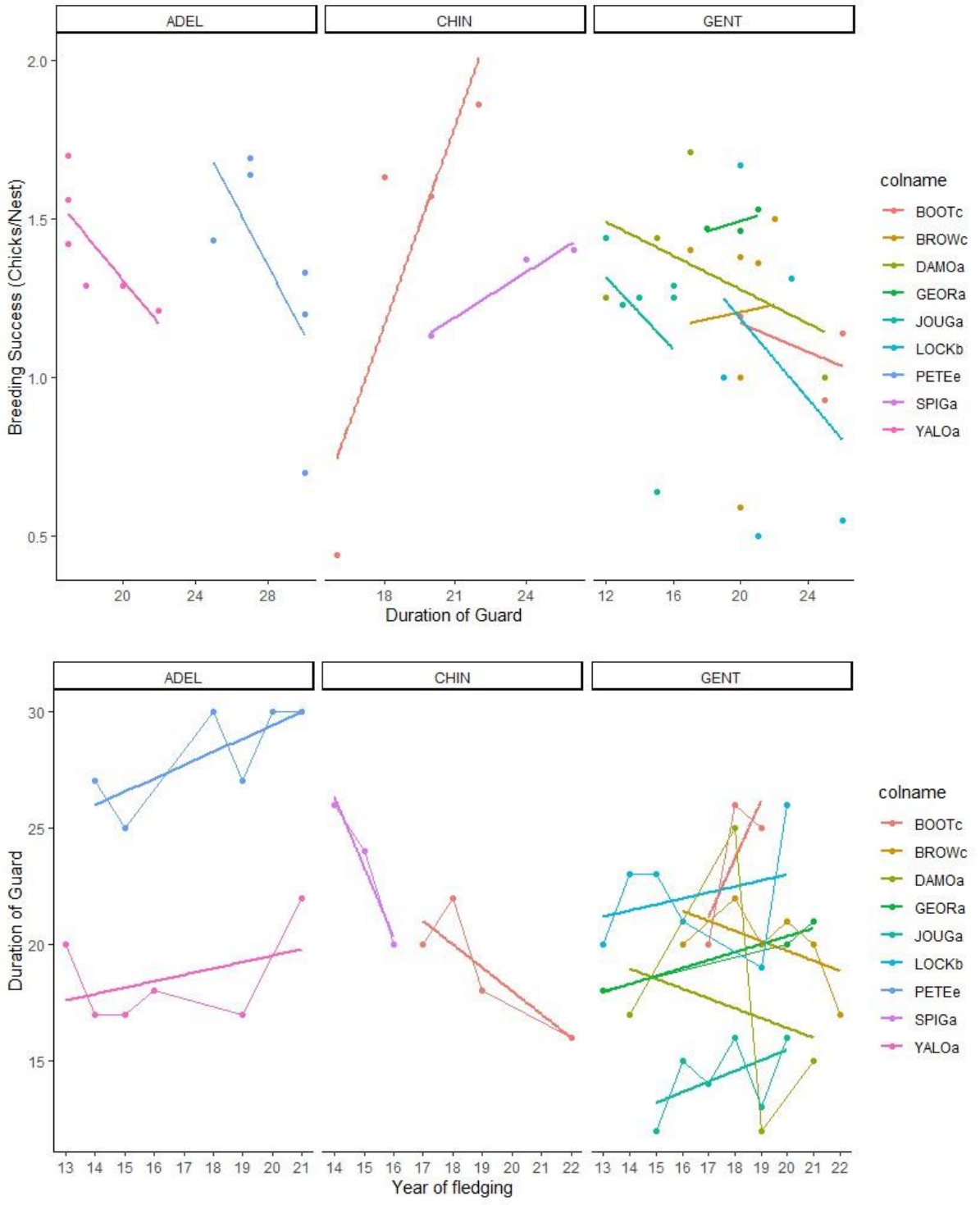


Figure 8: a) Effect of guard length (days) on estimated breeding success across colonies for the three different species of study. b) Evolution of guard length during the years of monitoring.

Across seasons (Carry-over) effects

I used data obtained from the nest tracking tool in GEORa to study two common types of carry-over effects that can have impacts on breeding success across successive seasons. Despite the data was extracted nest-by-nest, the analysis is run using the colony's yearly average as it is not possible to be sure the same individuals occupy the same nest year to year. First is breeding success itself, as great effort in one season can impact performance in the next (Figure 9a). The second is the impact of guard length – also used here as a measure of effort – on the following season's breeding success (Figure 9b). Neither relationship is statistically significant but both point towards a colony-level negative effect of breeding effort on the following season. This is for now anecdotal evidence; I expect further improvements of the nest-tracking tool will allow the extension of this research in order to achieve more statistically results and to expand this to other species, colonies and seasons.

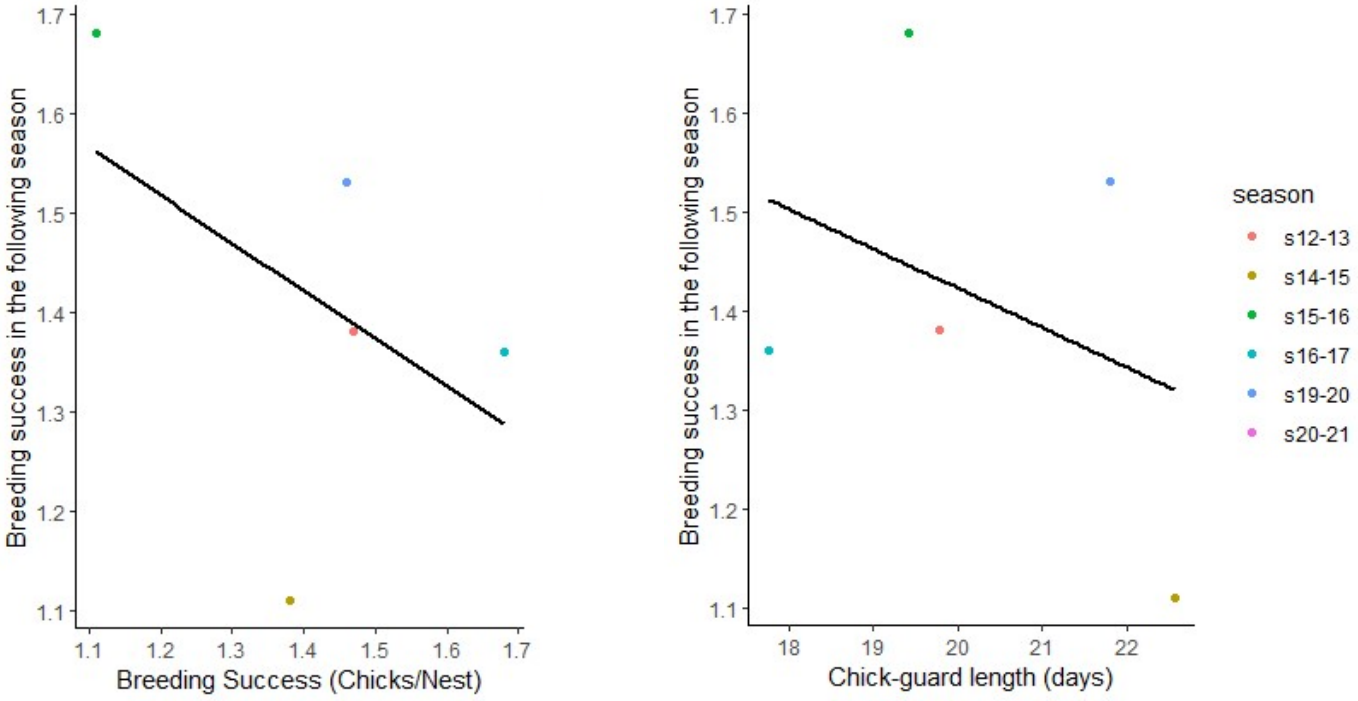


Figure 9: Analyses of potential carry-over effects on Breeding success. a) effect of breeding success on the following season's breeding success. b) effect of season length (from guard length) on breeding success in the following season. None of the relationships is statistically significant. All data corresponds to timelapse images from camera GEORa, monitoring Gentoo penguins on George's point. The imagery was annotated by Zooniverse volunteers and extracted using the Nest-tracking tool.

Early vs late breeders

It is usually the case in penguins that early breeders have a greater breeding success (Morrison et al. 2019). In this study, I did not find that early breeders had a statistically significant different nest output in any of the seasons of study (Figure 10). It is worth noting that complete breeding failure (both eggs/chicks) happened before hatching, so no nests with zero output could be included in this study.

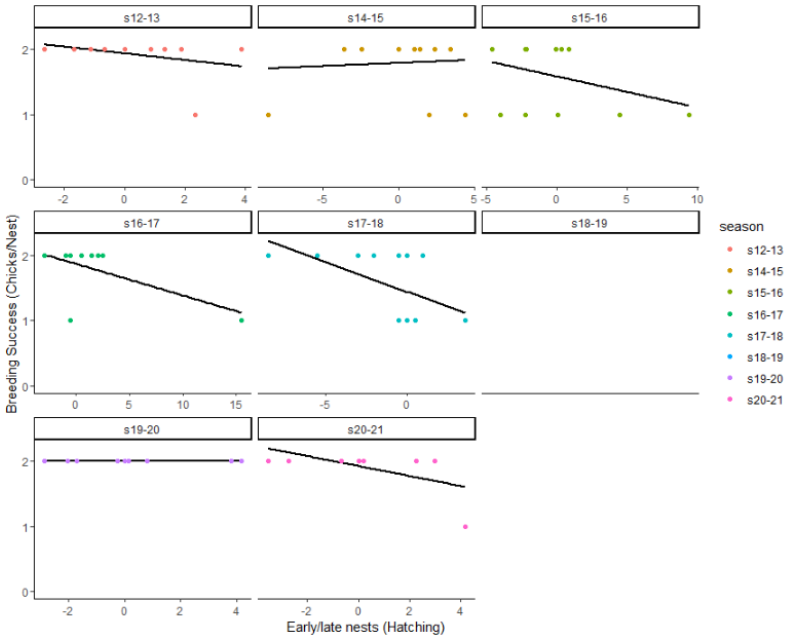


Figure 10: Effect of early and late hatching on breeding success per season of study. All data corresponds to timelapse images from camera GEORa, monitoring Gentoo penguins on Geroge's point. The imagery was annotated by Zooniverse volunteers and extracted using the Nest-tracking tool. None of the relationships were significant using linear models nor a mixed-effect model including season as a random effect.

Chick Mortality

Using the data for chick mortality provided by the nest-tracking tool I could build the mortatily curves for George's Point Colony (Camera GEORa) during eight seasons of study (Figure 11). These curves showed that most of the mortality happened before the hatching (estimated as first detection) of the chicks.

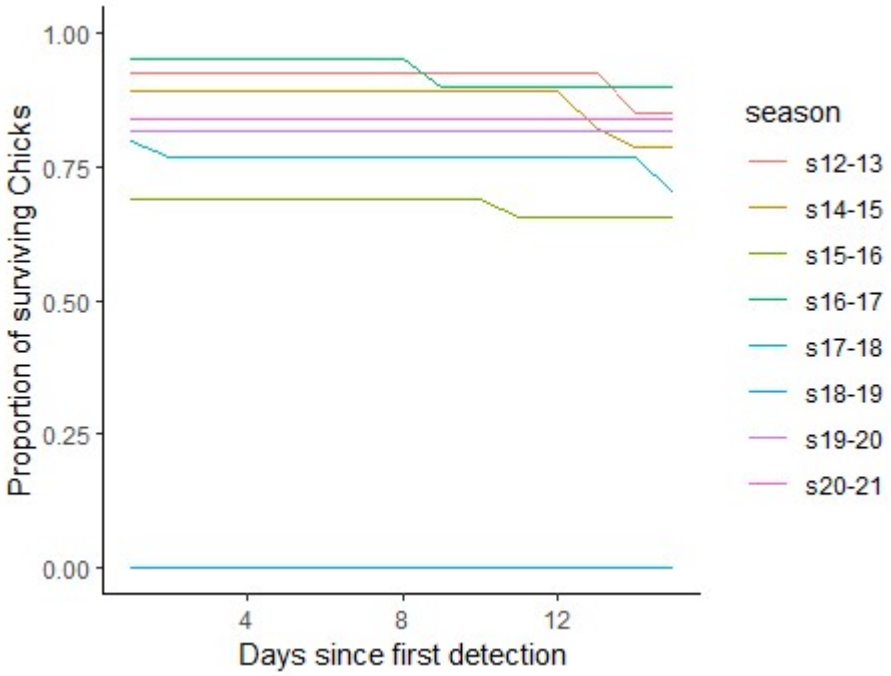


Figure 11: Mortality curves for chicks in George's Point (as seen from camera GEORa). Proportion of surviving chicks for each day after each chick's first detection.

PHENOLOGY ESTIMATION

The nest tracking tool allows us to access breeding data but also an estimate of the phenology of hatching and creching (Figure 12). These two are clearly influenced by the estimated setlement date. Despite the lag the overall trend in hatching phenology is preserved with an overall advance in hatching phenology until season s17-18 and showing a clear delay from s19-20 onwards.

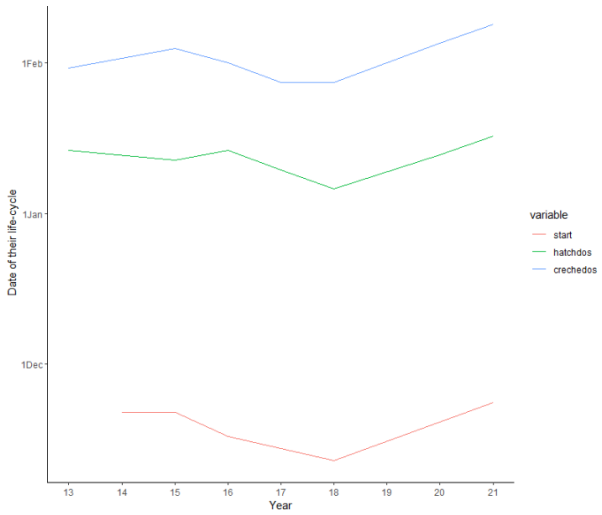


Figure 12: Phenological landmarks over multiple seasons of study in GEORa. Settlement is estimated as described in Chapter 2, while hatching and crèching dates are estimated using the nest tracking tool.

Discussion.

Main findings

- Breeding success has not significantly changed over our period of study. In these ten years Adelie and Chinstrap have shown a greater average breeding success than Gentoos (Figure 2).
- For adelies and Chinstraps Breeding success is simmilar throughout their breeding range, however for gentoos there is a very clear edge of range effect (Figure 3).
- Snow persistence (From settlement to thawing) is a major factor affecting breeding success to the point of frequently causing catastrophic breeding failure (Figure 5). At the same time snow persistence has been increasing significantly over the last ten years.
- My preliminary analysis on synchronicity shows greater breeding success is negatively related with hatching synchronicity within a colony (Figure 6). That is not the case for creching success.
- Human visitation shows a significant negative effect on the most visited colony (Port Lockroy) in comparison with two of its neighbouring colonies: Jougla Point and Damoy Point (Figure 7).
- A preliminary analysis shows season length might have be some species-distinct within-season effect on breeding success. This potential should be studied using more colonies (Figure 8). However, no significant carry-over effects were detected between seasons (Figure 9) nor any effects on the relative timing of breeding of each nest within the colony (Figure 10).

The Breeding Success of Pygoscelid Penguins

The values for Breeding Success that I find in our study broadly match the upper end of previous studies estimating reproductive success using different methods. Our estimates of breeding success for Adélies are similar to those found on the low disturbance areas in Esperanza/Hope bay (Carlini et al., 2007) and on King George Island (J. Hinke et al., 2012). At the same time our estimates are much higher than those in high disturbance areas of Hope Bay (Carlini et al., 2007) and in those measured in heavily-studied individuals at Bechervaise Island between 1990 and 1999 (Clarke et al., 2002).

Breeding success values for Chinstraps are largely in line with those found previously at Deception island (Barbosa et al., 1997). Our measurements are also much greater than those of other penguins including African Penguins (Crawford et al., 2006 and references within), Rockhopper Penguins (Pütz et al., 2001) and Magellanic Penguins (Pütz et al., 2001).

Gentoo's breeding success values are overall lower than that of their congeners, but in line with previous studies in King George Island (Hinke et al., 2012) and the Falkland/Malvinas (Pütz et al., 2001). Their Breeding Success may be lower because of a possible edge of range effect as Gentoo colonies at both the northern and southern edge of the Antarctic Peninsula have a lower breeding success. Both edges are areas of great sea-ice concentrations and have not had presence of Gentoo penguins until recent decades. In later years Gentoo breeding success is improving only in those colonies that are at the edge of their range (BROW, PETE) which could be evidence of the establishment of the species in new areas.

In this study it is possible to see that these estimates (Figure 3) and their trends (Figure 4) are specific to the combination of colony and species with markedly different trends between species even when nesting side by side (Figure 4). For these reasons it would be interesting to include more colonies into the latitudinal gradient and more multi-species colonies in future studies.

It is worth noting that our method is likely to render lower values for breeding success compared to traditional monitoring methods established by the Comission for the Conservation of Antarctic Marine Living Resources (CCAMLR, 2014). CCAMLR estimates rely on a single visit to estimate nest numbers after 95% of nests have laid their clutches and another one to count chicks after hatching has ended. Timelapse camera monitoring allows us to observe the early season where some nests are lost before even reaching incubation, especially due to the flooding of nests due to rain or snow thawing. This might result in slightly lower estimates using our method, even compared to previous studies using time-lapse imagery where they did not go back to check

the early season (Hinke et al., 2018). This gap might increase as early nest loss is becoming more common in the latter years due to the greater amount of precipitation (pers. obs. after reviewing 54 seasons from 11 colonies) and snow persistence in the early season (Figure 5b).

Despite our likely underestimate, our estimates of breeding success are among the highest in the literature. On one hand, this is likely to be due to our colonies being less visited by tourists and scientists (Barbosa et al., 2013; Carlini et al., 2007). On the other, the occurrence of high breeding success across species and colonies indicates that very likely the phenological changes observed in chapter 2 should be indeed part of these penguins' adaptation to climate change. Phenological plasticity had previously been found to buffer the impact of changing environmental conditions to breeding success (Hinke et al., 2012). However, this is the first time that this has been observed as a sustained time series and in multiple colonies. Also this is the first time such a study has been conducted in Chinstraps.

These estimates of breeding success show the reverse pattern of current population trends for the three penguin species. Adélies and Chinstraps are both declining throughout the Antarctic Peninsula (Lyver et al., 2014; Strycker et al., 2020), however their Breeding Success is the highest in this study and greater than in most studies of this and other species. Gentoos, on the other hand, are expanding throughout the Antarctic Peninsula and increasing their populations in already-established colonies (Dunn et al., 2019) but their breeding success is generally much lower.

This study indicates that these widespread population changes are unlikely to be driven by breeding success in the summer season. It is then likely that the demographic trends of the three species are related to the events happening outside of the breeding season, during the juvenile years and/or winter season (Figure 1). In this sense the greatest difference is Adélies and Chinstraps are migratory and spend their winters off at sea, while Gentoos are winter residents that stay at and around the colony. This is an indication that the increasingly warmer winters can be creating more difficult conditions for the first two migratory species: for example decreasing the amount of food availability or reducing the amount of ice floes they need to rest on. Concurrently, Gentoos could be benefitting from a reduced amount of sea-ice at and around their colonies that would make it easier for them to overwinter at and around the colonies. In order to test this in future studies it would be interesting to test winter colony attendance of Gentoos from time-lapse imagery against sea-ice extent derived from satellite imagery. The change in sea-ice has been so marked in the last ten years that it should be possible to track these changes within our time series.

It would also be interesting to explore the possibility that these species have a big floating population as a consequence of the increasing number of nests attempts aborted in the early season (Figure 11) due to snow (Figure 5) and rain (Pers. obs.). This could greatly alter the nest counts as many fail before or early after laying, so they will not be counted in standard manual or drone surveys that happen after the incubation peak. The extent of the loss of nests might be lesser for Gentoo penguins as these are capable of relaying a clutch. Maybe a camera-based estimate of nest loss in the early season could be a useful tool to complement drone surveys and in order to get a better estimate of breeding-adult numbers in the population.

Early nest loss due to environmental effects (Figure 5) could also alter the population dynamics as Adélies and Chinstraps would have a forced year off due to their inability to lay a replacement clutch. Their season is over before they have invested too much on it, meaning they would reach the following season free of carry-over effect. Their individual breeding success would therefore be higher, despite of the number of breeding pairs being lost and the subsequent loss of productivity. The capability of Gentoos to relay a clutch might be helping them compensate for early-season failure, although the effect of snow permanence seems to be very similar to that of Chinstraps (Figure 5).

Environmental effects

I found snow permanence to have a very significant negative effect on breeding success in Chinstraps and Gentoos (Figure 5c). It has not been possible to test this hypothesis in Adélies because of the lack of seasons with all three parameters necessary for this analysis (Breeding success, and settlement and thaw dates). It would be very interesting to expand this study to other colonies and years (especially Adélies) in order to achieve a better understanding of the different effects that snow can has on the different species or whether this is a latitude-dependent effect. Adding more datapoints would also help determine the shape of the relationship between snow presence and breeding success. With only a few datapoints it is impossible to

establish whether the relationship is linear, sigmoid or exponential, despite the good fit of the linear relationship I have established (Figure 5).

This negative effect of snow on breeding success is very worrying given the current trend towards greater amount of snow in the breeding season, especially in the Antarctic Peninsula region (Figure 5b). It is unlikely that this occurrence is behind Chinstrap and Adélie population decline in the AP over the last two decades, since the amount of great snow seasons started in 2018 according to our dataset (Figure 5b). However it is behind the recent loss of breeding success in some Gentoo colonies like BOOT (Figure 4) and maybe it is the reason stalling in the increase of Gentoo numbers (Heather Lynch, pers. comm.) as they are comparatively not accustomed to big snows.

In the future it would be worth exploring the construction of a tool capable of detecting snow in the images. The current tool (See appendix S4.1) can only detect thaw date, however it would be interesting to explore the development of AI or an algorithm that could detect snow in single images, which the current algorithm fails to do. This would be relevant as melt from single snow events can also affect chicks. This would allow us to detect the moments of chick development where snows are more deleterious. A similar tool should be developed for rain in the south Shetland islands as that was an important contributing factor to nest failure in Chinstraps in Baily Head (BAILa) in the later years (pers. obs. of time-lapse images).

Human visitation

To examine human impact, I compared three nearby Gentoo colonies. One of them, Port Lockroy, is one of the most visited colonies in the Antarctic Peninsula with 15000 visitors/year on average over the last two decades (Flynn et al., 2023). This is due to the presence of a historic hut and the world's southernmost post office. The other two colonies –Damoy Point and Jougla Point– are located within two kilometres of Port Lockroy, but are not visited nearly as often (on average 5000 and 7500 visitors/year respectively). Our results indicate that in port Lockroy the breeding success has been lower than in the other two consistently throughout the last decade (Figure 7, Table 3).

Our results are in line with other studies that use a similar method to link breeding success or demographic trends with visitation over a longer time series (Lynch et al., 2010). However, our findings are not consistent with a previous study conducted in the same area where no effect on breeding success was found (Trathan et al., 2008). Reasons for the lack of agreement could include a temporal mismatch as the previous study was conducted during the previous decade, when tourism was less prevalent.

It would be interesting in future studies to extend this analysis to other groups of colonies within a close area but with very different levels of visitation. It would be interesting as well to carry out some behavioural studies that could shed some light into the mechanisms linking visitation to this possible impact on breeding success.

Synchronicity

Hatching synchronicity has been previously described as a strong phenomenon within penguin colonies (Ainley, 2002; Ims, 1990a; Youngflesh et al., 2018). In this study I find different seasons to have different levels of synchronicity and this is significantly related to breeding success (Figure 6a). This has been hypothesised before using other types of data (Youngflesh et al., 2017, 2018) and has been generally explained as a predator avoidance mechanism (Young, 1994). Given the great changes in extreme weather events observed in the area of study it would be worth considering in future studies whether synchronicity is causal, or could be a consequence of other (e.g. environmental) factors. It would also be interesting to expand this study to other colonies in order to understand if this relationship holds true for other species and whether within species the advantages of synchronicity hold throughout the latitudinal range. Using Citizen Science data, I could also access already-annotated predator presence annotations in order to test the predator avoidance assumption.

Carry-over effects

I found negative –albeit non-significant– relationships between breeding success in a given season and breeding success and guard length in the previous season (Figures 9a and 9b). Both of these variables are related to the reproductive effort that the particular colony has dedicated in a given season, so these results indicate that effort has a negative effect in the next season's output. This has been found true in many other species of seabirds, including blue penguins (Joly et al., 2023). To the best of our knowledge this is the first time that guard duration (as an approximation of season duration) has been used to study carry-over effects. Guard duration could be an important metric as slower chick growth is related to lack of food availability (McKinnon et al., 2012), so season length could become an indicator of foraging effort if I see this in a general trend throughout the nests of a colony (easy to do using the nest tracking tool). It would be interesting to study if this relationship were true for penguins too, as I could see how food scarcity can have knock-on effects in the following season.

It would be interesting to include more years of data in the analyses in order to test if the observed relationships are significant and there are indeed carry-over effects as a result of reproductive effort. This would be especially interesting to do in relation to foraging effort as there are growing concerns about krill depletion in our area of study (Klein et al., 2018; Salmerón et al., 2023).

In further studies it would also be very interesting to expand this research to other species and test whether they are affected differentially. This would be especially interesting to do in multiple colonies along the latitudinal gradient of the Antarctic Peninsula to test whether each species is affected differently under different environmental conditions. Southern (more polar) colonies within each species have a narrower environmental window for reproduction and carry-over effects could play a different role on life history decisions like whether or not to breed and on breeding success. I can hypothesise that the impact of carry-over effects on breeding success could be smaller in Southern colonies if their winter season is longer and have more time to recover from the previous season. Alternatively, Southern Colonies might suffer a greater proportion of individuals skipping seasons and/or deserting nests if they have not recovered from the winter season but understand they have a narrower window for reproduction. Again, this might affect the three pygoscelid species differently, especially as Adélies and Chinstraps perform great migrations, while Gentoos are non-migratory. Gentoo's ability to recover from the breeding season overwinter might be different (they are less mobile and have fewer hours of sunlight) and also might be differentially affected by climate change. I expect a better understanding of carry-over effects and their consequences on life-history decisions and subsequent breeding success can contribute to a better understanding of their capability to respond to threats and to modelling of their demography.

Early vs late breeders

I did not find early breeders to have greater breeding success in any of the seasons of study (Figure 10). While hatching date is a reliable indicator of the overall phenology of the season (Figure 12), all the nests that failed completely did so before hatching so I cannot with this data confirm if those missing are early or late layers. I desisted on attempting to estimate laying using the nest tracking tool because of the overall difficulty to detect eggs and the unreliability of volunteer annotations. It is worth exploring laying-related metrics of phenology (See discussion in Chapter 3) before concluding whether there is indeed no relationship and synchronicity (Figure 6a) is more important than early breeding (Youngflesh et al., 2018).

Finally it would be interesting to study the possible conflict early breeding presents in the later years, where there is an increased amount of nest loss in the early season due to growing snow persistence (Figure 5b). Usually early breeding is related to greater breeding success but in the later seasons snow is melting later and early breeders are more likely to be affected by the greater persistence of snow as well as by the increased amount of water on the ground of the colony ground due to both precipitation and thawing. The conventional idea that early breeders have an advantage (Morrison et al. 2019). may be inappropriate for a time of climate change if their hormonal cycles evolved under stable conditions are resulting in females laying at inconvenient times. This change of conditions could be related to the phenological delay observed from 2020 onwards (Figure 12). This would be especially interesting regarding Gentoos, that are capable of laying replacement clutches.

Chick Mortality

Our mortality curves do not resemble those in previous reports, in which the greatest chick mortality happens in the first few weeks of chick life (Clarke et al., 2002; Davis & McCaffrey, 1986). Most of the mortality in the colonies of study happens before the chicks are detected (Figure 11). This could be due early nest loss as there is a great amount of observed nest losses in the early season before hatching (pers. obs. through cameras). This could also be due to worse chick detection in the first week of the chick's life, however chicks are on average only detected by volunteers 2.3 days after experts do (Figure 7b).

Conclusions.

Breeding success is quite high overall with Adélie and Chinstrap seeing the greatest estimates. Gentoo penguins only reach similar values to their congeners in the centre of their latitudinal gradient, possibly indicating an ice-mediated edge-of-range effect. However these values of breeding success are opposed to the overall population trends for the three species, indicating that possibly the reasons behind the great changes in population do not occur within the breeding season but outside of it. It is worth investigating the post-breeding moult period and the winter season.

On top of that, the breeding output for the three species has been affected by a variety of factors during the last decade. In this chapter I saw that snow permanence, lack of synchronicity and possibly human visitation are all negatively affecting penguin breeding success. It would be worth expanding this study in order to understand how these three threats are affecting each species specifically and whether these effects are related to the latitudinal gradient throughout their respective breeding ranges and how. For now all it is possible to say is that the three species of penguins are facing a compound of threats that is worth further research.

References.

Ainley, D. G. (2002). *The Adélie Penguin: Bellwether of Climate Change*. Columbia University Press.

Barbosa, A., de Mas, E., Benzal, J., Diaz, J. I., Motas, M., Jerez, S., Pertierra, L., Benayas, J., Justel, A., Lauzurica, P., Garcia-Peña, F. J., & Serrano, T. (2013). Pollution and physiological variability in Gentoo penguins at two rookeries with different levels of human visitation. *Antarctic Science*, *25*(2), 329–338. https://doi.org/10.1017/S0954102012000739

Barbosa, A., Moreno, J., Potti, J., & Merino, S. (1997). Breeding group size, nest position and breeding success in the Chinstrap penguin. *Polar Biology*, *18*, 410–414.

Baumhoer, C. A., Dietz, A. J., Dech, S., & Kuenzer, C. (2018). Remote sensing of Antarctic glacier and ice-shelf front dynamics—A review. *Remote Sensing*, *10*(9), 1445.

Carlini, A. R., Coria, N. R., Santos, M. M., & Buján, S. M. (2005). *The effect of Chinstrap penguins on the breeding performance of Adèlie penguins*. 12.

Carlini, A. R., Coria, N. R., Santos, M. M., Libertelli, M. M., & Donini, G. (2007). Breeding success and population trends in Adélie penguins in areas with low and high levels of human disturbance. *Polar Biology*, *30*(7), 917–924. https://doi.org/10.1007/s00300-006-0251-1

Carrasco, J. F., Bozkurt, D., & Cordero, R. R. (2021). A review of the observed air temperature in the Antarctic Peninsula. Did the warming trend come back after the early 21st hiatus? *Polar Science*, *28*, 100653. https://doi.org/10.1016/j.polar.2021.100653

CCAMLR. (2014). *CCAMLR Ecosystem Monitoring Program*. www.ccamlr.org

Clarke, J., Kerry, K., Irvine, L., & Phillips, B. (2002). Chick provisioning and breeding success of Adélie penguins at Béchervaise Island over eight successive seasons. *Polar Biology*, *25*(1), 21–30. https://doi.org/10.1007/s003000100307

Crawford, R. J., Barham, P. J., Underhill, L. G., Shannon, L. J., Coetzee, J. C., Dyer, B. M., Leshoro, T. M., & Upfold, L. (2006). The influence of food availability on breeding success of African penguins Spheniscus demersus at Robben Island, South Africa. *Biological Conservation*, *132*(1), 119–125.

Croxall, J. P., & Davis, L. S. (1999). Penguins: Paradoxes and patterns. *Marine Ornithology*, *27*, 1–12.

Davis, L. S., & McCaffrey, F. T. (1986). Survival analysis of eggs and chicks of Adélie penguins (Pygoscelis adeliae). *The Auk*, *103*(2), 379–388.

Duffield, K. R., Bowers, E. K., Sakaluk, S. K., & Sadd, B. M. (2017). A dynamic threshold model for terminal investment. *Behavioral Ecology and Sociobiology*, *71*(12), 185. https://doi.org/10.1007/s00265-017-2416-z

Dunn, M. J., Forcada, J., Jackson, J. A., Waluda, C. M., Nichol, C., & Trathan, P. N. (2019). A long-term study of Gentoo penguin (Pygoscelis papua) population trends at a major Antarctic tourist site, Goudier Island, Port Lockroy. *Biodiversity and Conservation*, *28*(1), 37–53. https://doi.org/10.1007/s10531-018-1635-6

Eayrs, C., Li, X., Raphael, M. N., & Holland, D. M. (2021). Rapid decline in Antarctic sea ice in recent years hints at future change. *Nature Geoscience*, *14*(7), Article 7. https://doi.org/10.1038/s41561-021-00768-3

Flexas, M. M., Thompson, A. F., Schodlok, M. P., Zhang, H., & Speer, K. (2022). Antarctic Peninsula warming triggers enhanced basal melt rates throughout West Antarctica. *Science Advances*, *8*(31), eabj9134.

Flynn, C. M., Hart, T., Clucas, G. V., & Lynch, H. J. (2023). Penguins in the anthropause: COVID-19 closures drive Gentoo penguin movement among breeding colonies. *Biological Conservation*, *286*, 110318.

Gaston, A. J., Gilchrist, H. G., Mallory, M. L., & Smith, P. A. (2009). Changes in seasonal events, peak food availability, and consequent breeding adjustment in a marine bird: A case of progressive mismatching. *The Condor*, *111*(1), 111–119.

Giese, M. (1996). Effects of human activity on Adélie penguin Pygoscelis adeliae breeding success. *Biological Conservation*, *75*(2), 157–164. https://doi.org/10.1016/0006-3207(95)00060-7

Hinke, J., Polito, M., Reiss, C., Trivelpiece, S., & Trivelpiece, W. (2012). Flexible reproductive timing can buffer reproductive success of Pygoscelis spp. Penguins in the Antarctic Peninsula region. *Marine Ecology Progress Series*, *454*, 91–104. https://doi.org/10.3354/meps09633

Hinke, J. T., Barbosa, A., Emmerson, L. M., Hart, T., Juáres, M. A., Korczak-Abshire, M., Milinevsky, G., Santos, M., Trathan, P. N., Watters, G. M., & Southwell, C. (2018). Estimating nest-level phenology and reproductive success of colonial seabirds using time-lapse cameras. *Methods in Ecology and Evolution*, *9*(8), 1853–1863. https://doi.org/10.1111/2041-210X.13015

Holmes, N. D. (2007). Comparing King, Gentoo, and Royal Penguin Responses to Pedestrian Visitation. *The Journal of Wildlife Management*, *71*(8), 2575–2582. https://doi.org/10.2193/2005-715

Holmes, N. D., Giese, M., Achurch, H., Robinson, S., & Kriwoken, L. K. (2006). Behaviour and breeding success of Gentoo penguins Pygoscelis papua in areas of low and high human activity. *Polar Biology*, *29*(5), 399–412. https://doi.org/10.1007/s00300-005-0070-9

Ims, R. A. (1990a). On the Adaptive Value of Reproductive Synchrony as a Predator-Swamping Strategy. *The American Naturalist*, *136*(4), 485–498. https://doi.org/10.1086/285109

Ims, R. A. (1990b). The ecology and evolution of reproductive synchrony. *Trends in Ecology & Evolution*, *5*(5), 135–140.

Johnson, D. H., Krapu, G. L., Reinecke, K. J., & Jorde, D. G. (1985). An evaluation of condition indices for birds. *The Journal of Wildlife Management*, 569–575.

Johnston, A. S. A., Boyd, R. J., Watson, J. W., Paul, A., Evans, L. C., Gardner, E. L., & Boult, V. L. (2019). Predicting population responses to environmental change from individual-level mechanisms: Towards a standardized mechanistic approach. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1913), 20191916. https://doi.org/10.1098/rspb.2019.1916

Joly, N., Chiaradia, A., Georges, J.-Y., & Saraux, C. (2023). Unpacking the lifelong secrets of little penguins: Individual quality, energy allocation, and stochasticity in defining fitness. *Evolution*, *77*(9), 2056–2067.

Klein, E. S., Hill, S. L., Hinke, J. T., Phillips, T., & Watters, G. M. (2018). Impacts of rising sea temperature on krill increase risks for predators in the Scotia Sea. *PLOS ONE*, *13*(1), e0191011. https://doi.org/10.1371/journal.pone.0191011

Labocha, M. K., & Hayes, J. P. (2012). Morphometric indices of body condition in birds: A review. *Journal of Ornithology*, *153*(1), 1–22. https://doi.org/10.1007/s10336-011-0706-1

Labocha, M. K., Schutz, H., & Hayes, J. P. (2014). Which body condition index is best? *Oikos*, *123*(1), 111–119. https://doi.org/10.1111/j.1600-0706.2013.00755.x

Lynch, H. J., Fagan, W. F., & Naveen, R. (2010). Population trends and reproductive success at a frequently visited penguin colony on the western Antarctic Peninsula. *Polar Biology*, *33*(4), 493–503. https://doi.org/10.1007/s00300-009-0726-y

Lyver, P. O., Barron, M., Barton, K. J., Ainley, D. G., Pollard, A., Gordon, S., McNeill, S., Ballard, G., & Wilson, P. R. (2014). Trends in the Breeding Population of Adélie Penguins in the Ross Sea, 1981–2012: A Coincidence of Climate and Resource Extraction Effects. *PLoS ONE*, *9*(3), e91188. https://doi.org/10.1371/journal.pone.0091188

Marks, E. (first), Rodrigo, A., & Brunton, Dianne. (2010). Ecstatic display calls of the Adélie penguin honestly predict male condition and breeding success. *Behaviour*, *147*(2), 165–184. https://doi.org/10.1163/000579509X12512863752751

McKinnon, L., Picotin, M., Bolduc, E., Juillet, C., & Bêty, J. (2012). Timing of breeding, peak food availability, and effects of mismatch on chick growth in birds nesting in the High Arctic. *Canadian Journal of Zoology*, *90*(8), 961–971. https://doi.org/10.1139/z2012-064

Meredith, M., Sommerkorn, M., Cassotta, S., Derksen, C., Ekaykin, A., Hollowed, A., Kofinas, G., Mackintosh, A., Melbourne-Thomas, J., & Muelbert, M. M. C. (2019). *Polar Regions. Chapter 3, IPCC Special Report on the Ocean and Cryosphere in a Changing Climate*.

Moreno, J. (2010). Reproductive Success. In M. D. Breed & J. Moore (Eds.), *Encyclopedia of Animal Behavior* (pp. 64–69). Academic Press. https://doi.org/10.1016/B978-0-08-045337-8.00119-4

Nisbet, I. C. T., & Dann, P. (2009). Reproductive performance of little penguins *Eudyptula minor* in relation to year, age, pair-bond duration, breeding date and individual quality. *Journal of Avian Biology*, *40*(3), 296–308. https://doi.org/10.1111/j.1600-048X.2008.04563.x

Numata, M., Davis, L. S., & Renner, M. (2000). Prolonged foraging trips and egg desertion in little penguins (*Eudyptula minor*). *New Zealand Journal of Zoology*, *27*(4), 277–289. https://doi.org/10.1080/03014223.2000.9518236

Patterson, D. L. (2001). *The effects of human activity and environmental variability on long-term changes in Adélie penguin populations at Palmer Station, Antarctica* [PhD Thesis, Montana State University-Bozeman, College of Letters & Science]. https://scholarworks.montana.edu/xmlui/bitstream/handle/1/8056/31762103446934.pdf?sequence=1

Pütz, K., Ingham, R., Smith, J., & Croxall, J. (2001). Population trends, breeding success and diet composition of Gentoo Pygoscelis papua , magellanic Spheniscus magellanicus and rockhopper Eudyptes chrysocome penguins in the Falkland Islands. A review. *Polar Biology*, *24*(11), 793–807. https://doi.org/10.1007/s003000100293

Ricklefs, R. E., & Bloom, G. (1977). Components of Avian Breeding Productivity. *The Auk*, *94*(1), 86–96.

Robinson, S., Chiaradia, A., & Hindell, M. A. (2005). The effect of body condition on the timing and success of breeding in Little Penguins Eudyptula minor. *Ibis*, *147*(3), 483–489. https://doi.org/10.1111/j.1474-919x.2005.00431.x

Salmerón, N., Belle, S., Cruz, F. S., Alegria, N., Finger, J. V. G., Corá, D. H., Petry, M. V., Hernández, C., Cárdenas, C. A., & Krüger, L. (2023). Contrasting environmental conditions precluded lower availability of Antarctic krill affecting breeding Chinstrap penguins in the Antarctic Peninsula. *Scientific Reports*, *13*(1), Article 1. https://doi.org/10.1038/s41598-023-32352-7

Saraux, C., & Chiaradia, A. (2022). Age-related breeding success in little penguins: A result of selection and ontogenetic changes in foraging and phenology. *Ecological Monographs*, *92*(1), e01495. https://doi.org/10.1002/ecm.1495

Shoji, A., Aris-Brosou, S., Culina, A., Fayet, A., Kirk, H., Padget, O., Juarez-Martinez, I., Boyle, D., Nakata, T., Perrins, C. M., & Guilford, T. (2015). Breeding phenology and winter activity predict subsequent breeding success in a trans-global migratory seabird. *Biology Letters*, *11*(10), 20150671. https://doi.org/10.1098/rsbl.2015.0671

Strycker, N., Wethington, M., Borowicz, A., Forrest, S., Witharana, C., Hart, T., & Lynch, H. J. (2020). A global population assessment of the Chinstrap penguin (Pygoscelis antarctica). *Scientific Reports*, *10*(1), Article 1. https://doi.org/10.1038/s41598-020-76479-3

Suprenand, P., & Ainsworth, C. (2017). Trophodynamic effects of climate change-induced alterations to primary production along the western Antarctic Peninsula. *Marine Ecology Progress Series*, *569*, 37–54. https://doi.org/10.3354/meps12100

Trathan, P. N., Forcada, J., Atkinson, R., Downie, R. H., & Shears, J. R. (2008). Population assessments of Gentoo penguins (Pygoscelis papua) breeding at an important Antarctic tourist site, Goudier Island, Port Lockroy, Palmer Archipelago, Antarctica. *Biological Conservation*, *141*(12), 3019–3028. https://doi.org/10.1016/j.biocon.2008.09.006

Turner, J., Marshall, G. J., Clem, K., Colwell, S., Phillips, T., & Lu, H. (2020). Antarctic temperature variability and change from station data. *International Journal of Climatology*, *40*(6), 2986–3007. https://doi.org/10.1002/joc.6378

Visser, M. E., te Marvelde, L., & Lof, M. E. (2012). Adaptive phenological mismatches of birds and their food in a warming world. *Journal of Ornithology*, *153*(1), 75–84. https://doi.org/10.1007/s10336-011-0770-6

Vleck, C. M., & Vleck, D. (2002). Physiological Condition and Reproductive Consequences in Adélie Penguins1. *Integrative and Comparative Biology*, *42*(1), 76–83. https://doi.org/10.1093/icb/42.1.76

Weimerskirch, H., Zimmermann, L., & Prince, P. A. (2001). Influence of environmental variability on breeding effort in a long-lived seabird, the yellow-nosed albatross. *Behavioral Ecology*, *12*(1), 22–30.

Williams, T. D. (1995). *The Penguins: Spheniscidae*. Oxford University Press.

Woehler, E. J., Penney, R. L., Creet, S. M., & Burton, H. R. (1994). Impacts of human visitors on breeding success and long-term population trends in Adélie Penguins at Casey, Antarctica. *Polar Biology*, *14*(4), 269–274. https://doi.org/10.1007/BF00239175

Young, E. (1994). Skua and penguin: Predator and prey. https://cir.nii.ac.jp/crid/1130000794942172928

Youngflesh, C., Jenouvrier, S., Hinke, J. T., DuBois, L., St. Leger, J., Trivelpiece, W. Z., Trivelpiece, S. G., & Lynch, H. J. (2018). Rethinking "normal": The role of stochasticity in the phenology of a synchronously breeding seabird. *Journal of Animal Ecology*, *87*(3), 682–690. https://doi.org/10.1111/1365-2656.12790

Youngflesh, C., Jenouvrier, S., Li, Y., Ji, R., Ainley, D. G., Ballard, G., Barbraud, C., Delord, K., Dugger, K. M., Emmerson, L. M., Fraser, W. R., Hinke, J. T., Lyver, P. O., Olmastroni, S., Southwell, C. J., Trivelpiece, S. G., Trivelpiece, W. Z., & Lynch, H. J. (2017). Circumpolar analysis of the Adélie Penguin reveals the importance of environmental variability in phenological mismatch. *Ecology*, *98*(4), 940–951. https://doi.org/10.1002/ecy.1749

5

Chapter 5

Event cameras, a novel tool for studying behaviour
Pilot study monitoring Ecstatic Display on wild penguins

• Abstract •

The ecstatic display (ED) is common in various penguin species, and has been known for long, but its function and quantitative details in Chinstrap penguins (*Pygoscelis antarcticus*) remains unknown. During ED, the penguin points its head up and emits a loud call while beating its wings, often starting a display outburst among nearby individuals. Because this behaviour influences -and is influenced by- surrounding animals it requires study in the time dimension as well. In this chapter I pilot the use of a novel technology: event (or neuromorphic) cameras to characterise and quantify ED during two weeks within the chick-guard period at Deception Island, Antarctica. Event camera sensors are completely different from frame-based devices as they record changes in light intensity pixel by pixel whenever they occur (emulating retinal receptors). This change-based recording system plus their inherent microsecond time resolution and extensive dynamic range make these devices ideal for capturing movement. Detected events (per-pixel changes in light intensity) produced by a specific behaviour can be easily stacked up to show the shape of each behaviour. These shapes can be used to train a machine-learning algorithm. I use this approach to produce a complete ethogram for 16 nests spanning 93 hours . Ground-truthing the technique against a human analyst shows an estimated 95% accuracy. I use this dataset to characterise Ecstatic Display for the first time in Chinstrap Penguins, study its occurrence, its contagiousness and differences between individuals. Ecstatic Display is performed by every individual in the study regardless of date, sex, time of day or day within the observation period. This behaviour is greatly influenced by weather, neighbouring nests performing ED and by the amount of hours an individual has been in the nest after a changeover. I hypothesise that this behaviour could have a dynamic territorial function, possibly to avoid neighbours stealing nesting material. This may explain its patterns of occurrence and transmissibility around the colony. This pilot study proves that event cameras can produce a precise quantitative description of behaviour in a relatively efficient, automated and non-invasive way.

• Introduction •

Ecstatic display

Displays are stereotyped sequences of movements used to communicate between conspecifics. In penguins, they are widespread and are used for a variety of purposes including mate choice and pair bonding.

Many displays are typically accompanied by vocalizations known to be distinctive between individuals or pairs, allowing both mate and chick recognition in most penguin species: Adélie Penguins (*Pygoscelis adeliae*; Speirs & Davis, 1991)), Gentoo Penguins (*P. papua*; Jouventin & Aubin, 2002) Rockhopper Penguins (*Eudyptes chrysocome*; Searby & Jouventin, 2005), African Penguins (*Spheniscus demersus*; Favaro et al., 2015), Magellanic Penguins (*S. magellanicus*; Clark et al., 2006), and Macaroni Penguins (*E. chrysolophus*; Searby et al., 2004).

Ecstatic Display (ED) is one of the most common displays in Pygoscelids, however, there is an almost complete lack of information regarding the displays of Chinstrap Penguins. The only exceptions are a mention in a recent general essay on penguin communication (Jouventin & Dobson, 2017) and a study on the Ecstatic Display Call (Bustamante & Marquez, 1996). As such, the information I currently have to understand this behaviour comes from a handful of studies on Chinstrap's sister species (Adélie and Gentoo penguins) as well as personal observations.

During the ecstatic display, penguins stand fully erect on their nests with their stretched neck and bill pointing upward. They move their outstretched flippers back and forth in fast beats (0.61 beats per second in Adélies; Penney, 1964) while emitting loud rasps that make their chest vibrate synchronously. These rasps, known as the Ecstatic Display Call (EDC), are normally emitted in pairs of syllables made up of a short inhale followed by a long and loud exhale (Bustamante & Marquez, 1996), similar to the mutual display call (Penney, 1964).

In Adélies, ED has been described to be performed mostly by males during the mating and early incubation period, declining in frequency as the breeding season advances (Derksen, 1977). Following literature on bird vocal signalling, two functions have been suggested for this behaviour, given that the call is performed from the nest (Penney, 1964) and overwhelmingly produced by males during the early season (Derksen, 1977; Penney, 1964). These functions are, firstly, to assert their claim over their nest and, secondly, to attract potential mates (Lynch & Lynch, 2017; Marks et al., 2010; Penney, 1964; Sladen, 1958). This does not fully align with my personal observation as I have witnessed Adélie penguins perform ED in the late chick guard season at Petermann Island on the 15th of January 2024. I have not observed this behaviour in Gentoo penguins so late in the season.

This interpretation has been supported by a variety of studies describing the Adélie EDC as an honest display signal that can accurately convey body condition information to females (Davis & Darby, 2012; Lynch & Lynch, 2017; Marks et al., 2010). Lower frequencies in the EDC have been associated with greater success in attracting partners (Davis & Darby, 2012) while Marks et al. (2010) found a strong correlation between a lower frequency of the call in the early season and better body condition, early arrival, and better overall breeding outcome. Marks et al. (2010) did not find, however, a correlation between call frequency and the likelihood of pairing.

Their hypothesis suggests that it is impossible for females to choose a partner based on visual cues due to Pygoscelid phenotypic similarity (Davis & Darby, 2012). Instead, lower call frequency can be used by females to ascertain male body condition, since these can only be achieved by bigger (fatter) individuals (Penney 1964). Fatter individuals, in turn, would be in better condition to withstand the significantly longer fasting periods males face during breeding season (Chappell et al., 1993; Davis & Darby, 2012). Furthermore, the frequency of each individual's call shift as they lose body mass throughout the season (Marks et al., 2010).

Ecstatic displays in Adélies were not found to have any particular daily rhythms although cameras in their study (Penney, 1964) did not collect data beyond 18:00 hours. ED were also observed to be inhibited by the presence of females and, if attempted, would develop into a mutual display or at least stop ED from reaching its climax (Penney, 1964). Finally, ED were inhibited in windy days with a subsequent increase in the amount of displays during the hours or days following a storm (Penney, 1964).

These displays are not exclusive to the early breeding season and are not always performed to attract a female. Penney (1964) describes "Ecstatic display outbursts by males over eggs or chicks were usually initiated by the displaying of a lone bird or by some other disturbance in the colony. Ecstatic outbursts often followed fighting or nest relief ceremonies. Even a human's nearness to a colony induced ecstatic displays in certain individuals. […] Males in defensive situations, immediately after being defeated in territorial disputes, sometimes gave the ecstatic display. Males were never known to give the ecstatic [display] when acting aggressively toward another bird". This was interpreted by Penney (1964) as a displacement activity (Tinbergen, 1952), but of course, this is a proximate rather than a functional hypothesis.

One common occurrence is for ecstatic displays to be "contagious" (Derksen, 1977; Penney, 1964) and when one individual display, it is common for nearby penguins to engage in the same display creating a sort of "Mexican-wave" through sections of a colony. This was interpreted by Penney (1964) as an example of mimetic behaviour (Armstrong, 1951).

In general, there is support for ED in Adélies being an honest signal towards unpaired females. However, many of the observations that are true for Adélies might not be extended to Chinstrap Penguins. Indeed, Chinstraps frequently perform ED outside of the mating season, usually in the absence of a mate and without obvious provocation. In these situations, its function remains unexplained even in Adélies (Lynch & Lynch, 2017). In this paper, I aim to investigate ED in Chinstraps, explore differences between Pygoscelid species, and its main function in Chinstrap Penguins.

Event cameras

Event (or *neuromorphic*) cameras are a relatively novel technology, acquiring data in a fundamentally different way to conventional cameras. Common "frame-based" video recording logs a reading of all pixels in the sensor several dozen times per second in order to capture movement. In event cameras, every pixel works independently, each of them logging relative changes in light intensity only whenever they occur. Each of these changes is an 'event' and it is solely recorded with its corresponding pixel location (x and y in the sensor), timestamp t and polarity p. When a subject moves within the field of view of the camera, it sequentially triggers contiguous pixels resulting in a lightweight and schematic description of that movement.

The idea dates back to a silicon retina (Mahowald et al. 1994) and has gained increasing interest in research and industry since the first usable camera sensors (Lichtsteiner et al. 2008) were developed. This interest is fuelled by the realisation that acquiring a series of images might not be the best way to capture dynamic scenes. Indeed, this unique technology has particular advantages for the study of animal behaviour:

- High dynamic range: Frame-based cameras ability to capture light is limited by their exposure time, aperture and sensor sensitivity, which are the same for all pixels. In event cameras, as each pixels work independently, they can simultaneously record changes in both very bright and very dark areas of the image. This results in a significantly higher dynamic range (140dB versus 60dB) making them useful in contrasting and challenging lighting conditions.
- Extreme temporal resolution: The pixels have a time resolution of µs as opposed to frame-based cameras which usually have ms resolution at best.
- Low power consumption: event camera chips need less energy than their frame-based counterparts.

Aims

To the best of our knowledge, event cameras have never been deployed in wildlife settings, nor have they been used for animal behavioural monitoring. Here I put their advantages to use, investigating an understudied behaviour in wild Chinstrap Penguins (*Pygoscelis antarcticus*), the Ecstatic Display (ED).

Our aims are to describe the occurrence and function of the elusive ED behaviour, to obtain insight into why it occurs, and 2) to investigate the potential of event cameras for behavioural monitoring.

• Materials and methods •

Data acquisition

I co-deployed two cameras framing the same group of 16 nests at the Punta Descubierta/Vapour Col colony (62°59'S 60°44'W) on Deception Island, South Shetland Islands, Antarctica. The first camera was a traditional camera trap (Reconyx Ultrafire 2), set in time-lapse mode (one picture per minute during the observation period). The second camera was a DAVIS 346 Event Camera (Taverni et al. 2018). This camera continuously recorded events and stored them in ten-minute-sequences as well as taking black and white still frames every 8 seconds (a special feature of this model). For the camera to record automatically, it was connected to a Raspberry Pi 4 (https://www.raspberrypi.org), which recorded both events and stills to an SSD hard-drive. The system was powered by Li-ion batteries.

a)



b)



c)



Figure 1: a) Camera setup showing the timelapse camera and the waterproofed event camera at the top of the tripod and the rest of the camera setup (batteries, CPU and SSD) further down the pole. b) Field of view for the reconyx timelapse camera (image taken at 1-minute intervals) and c) Field of view of the event camera taken at the same moment as Figure 1b. This equivalence between event frames and timelapse cameras was used to synchronise both sources of data.

The event and time lapse cameras were affixed to the top of an aluminium tripod 1.8m tall (Figure 1). The event camera was insulated in a watertight sealed container and fitted with a Nikon 32mm UV filter to provide a clear view. The rest of the elements (Battery, CPU and SSD) were kept in a separate watertight container further down the pole to reduce sail effect and facilitate daily battery changes. These three elements were attached to the sides of the container Velcro™ to avoid rattling against eachother because of the wind.

The event camera was deployed from the 5th - 27th January 2022. With our setup the camera could record continuously for up to 16 hours. However, several data gaps were introduced due to adverse weather conditions preventing battery changes. I also removed from the analyses those ten-minute sequences that were unusable due to a muddy lens or to camera movement in high winds. It was not possible to study ED beyond the 16th of January due to the chicks becoming mobile and leaving the nest. In total I retained 560 ten-minute sequences resulting in 93 hours of recording over 11 days.

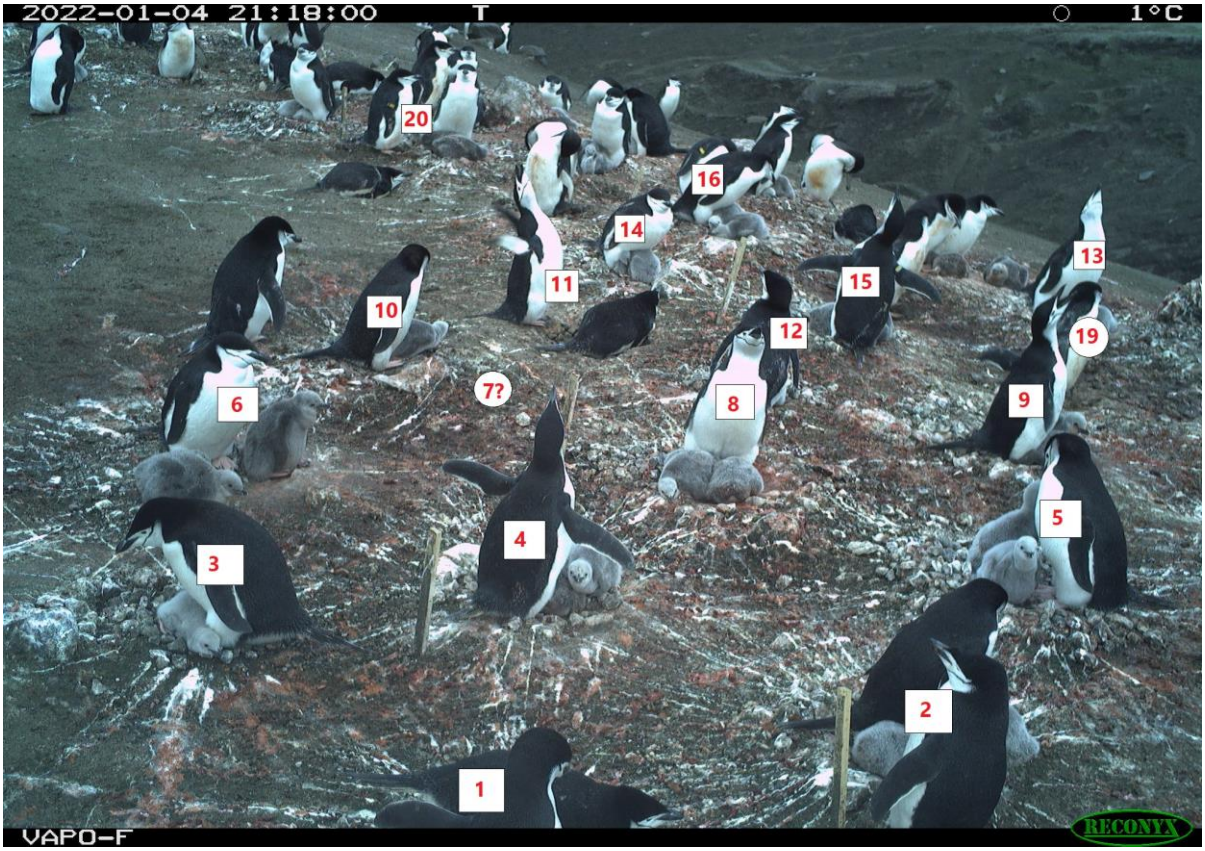
Timestamps of both cameras were manually aligned since the event camera setup lacked an internal clock and the timestamp for recording initiation needed to be recorded manually. Timestamps were corrected using a time offset since time drift was existent but negligible. To manually establish that offset, I checked for the timing of arrival/departure of banded individuals from their nests in both timelapse imagery and the black and white event frames. Simultaneous images were selected by checking the overall positions of all individuals in frame and selecting the images with most similar positions (Figures 1b and 1c).

To study the at-nest behaviours, I chose 16 nest areas (i.e. Regions of Interest) that remained in clear view for both cameras throughout the observation period (Figure 2a and 2b). These areas needed to be redrawn three times as the camera view moved slightly within the deployment time. These areas allow us to isolate the pixels corresponding to each nest regarding the detection of behaviours using an AI. Adding/stacking up all of the pixels in each of the nest areas results in distinct behaviour profiles for each type of behaviour allowing for machine learning algorithms to discriminate different behaviours and detect their occurrence and duration (Figure 2c).

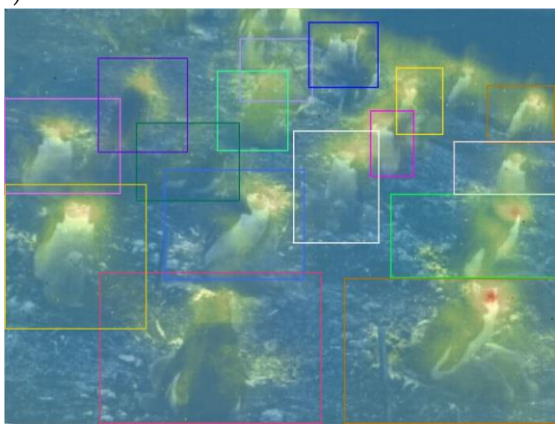
It was possible to determine the identity of the adult(s) present at each nest throughout the observation period by manually annotating changeovers in the 1-min timelapse imagery. In six nests changeovers could be doubtlessly identified (N02, N04, N08, N15, N16, N20) as each one of the partners was temporarily marked with a yellow band in the right flipper for another study. In other two nests (N01 and N09), it was possible to reliably identify one of the members of the pair due to persistent marks on their flippers (Figure 3). From observing these eight marked nests, it is possible to be certain that changeovers under the 1 min timelapse frequency are rare (n = 1; 0.1% of total changeovers in marked pairs). Therefore, it is possible to keep track of the adult present at nest at a given time in the other nests by monitoring changeovers. I draw additional assurance by observing the unique pattern and amount of dirt on each member of the pair as well as observing the incoming adult feeding the chicks. I also individually reviewed the longest stints (those over 900min or 15hrs) to further make sure no changeover was missed.

14 out of sixteen nests were breeding. One other nest was occupied by a pair of juveniles (N11) and another one was occupied by a lone juvenile (N07). This was assumed because of the lack of chicks or eggs, lack of nesting materials and the erratic patterns of attendance to the colony. It is unlikely that these were failed breeders, as these usually vacate the colony after failing the attempt.

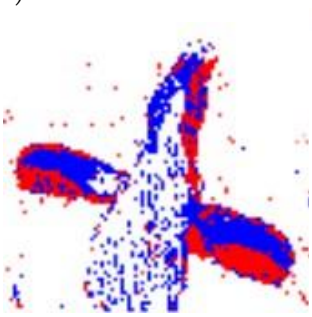
a)



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c)



Ecstatic Display



Adult flapping its wings

Figure 2: a) Map showing the location of each nest within the frame of the image as seen from the timelapse camera. Nests 19 and 20 were not considered in the final study; N19 failed and left before the start of the monitoring with the event camera and nest N20 was not visible from the event camera. Conversely N07 arrived and established itself some time later. b) Examples of Regions of interest or Nest Areas used for calculating nest activity as well as detecting Ecstatic displays. In order to draw them I overlayed a heatmap showing the frequency of events in each pixel over one example event camera frame. These areas needed to be drawn four different times due to three fortuitous shifts in the camera view. c) Appearance of two different behaviours (Ecstatic display and adult flapping) as seen through sum of events captured with the event camera over a short period of time. Stacking all the events in a time frame while the penguins stays put on the nest allows for the visualization of distinct shapes for different types of behaviour. Blue and red events (dots) represent respectively an increase and a decrease of light intensity at that pixel position.

Other data

Other sources of data include: 1) Genetic sex (N02 and N16), behavioural sex (pairs from observed mating, N10 and N11); 2) meteorological data from the AEMET (Spanish Meteorological service) meteorological station located 5 Km away on the Gabriel de Castilla Research station, also on Deception Island.

a)



b)



c)



Figure 3: a) The two members of nest N08 during a changeover showing their right flippers with and without the yellow band. b) Both adults in N01 during a changeover with one of them showing the white mark above its right flipper that allows individual detection of the individuals within the pair. c) Individual N09B Showing three pale marks in their right flipper at the beginning, middle and towards the end of the observation period (see chick size differences).

Data analysis

Ecstatic display instances and their duration were extracted using machine learning as described by Hamann et al. (2023). A computer vision training dataset was constructed using twenty-eight 10-minute sequences (including all hours of the day) totalling 10 night and 18 day sequences. Both the nest areas and the ecstatic display behaviours were annotated by a penguin expert (myself) and confirmed by two further researchers using the platform www.CVAT.ai. In this chapter I performed an extra filtering process in order to increase the proportion of true positive predictions (i.e. detections) from the dataset provided by the machine-learning algorithm up to 94% true positives (Appendix S5.1).

• Results I: ED Behaviour Description •

I present ED occurrence here as rate of Ecstatic Displays per hour, to account for differences in monitoring times between nests and individuals (especially due to camera movement cropping N03, N06 and N10 for two days). This also overcomes problems with adults moving out of the nest (N06 and N14), the erratic presence patterns of the non-breeders (N07 and N11) and occasional snow and mud occlusion. In cases where adults were sexed behaviourally, this information was occasionally lost when snow occlusion prevented continual observation.

Within nests, the amount of time in frame for each individual also varies greatly, partly because it was impossible to track the identity of non-banded individuals after one big snow that obscured the lens for almost a day. This caused the initial pair identities A-B to be renamed as C-D after the snow in unbanded individuals. If the pair could be sexed (behaviourally or genetically), their identities will be presented as M-F. When the Two members of any pair are in the nest, the identity will be marked as T (Two). Finally, in nest N07, there is generally one individual but it is impossible to know if it is the same individual throughout the observation period because there are no changeovers or similar happening. For this reason, individuals in this nest will be marked as 0, 1 or 2 depending on the number of individuals in the nest at any given time.

General occurrence of ED in Chinstrap Penguins

Ecstatic Display was present in all 16 nests monitored and in all of them was performed by both members of the pair (Figure 4a), paired juveniles (N11) and unpaired individuals (N07). There is great variability between nests, with N11 displaying three times as often as N06.

There also was large individual variability (Figure 4b). ED frequency does not look like it is idiosyncratic of each individual as it is possible to see differences in frequency within individuals, for example those labelled A-B before the snow and as C-D after it (N05, N12, N13 and N14 in Figure 4b). Individuals in the first half of the observation period (A and B) show similar values of ED frequency and lower than those same individuals after the big snow (marked as C and D). In most nests the frequency of ED is lower or null when both members of the pair are in the nest (identified as T, Figure 4b).

Ecstatic Displays were performed every day throughout the study, with frequency increasing towards the end of the observation period (Figure 4c), and were performed during every hour of the day (Figure 4d). Due to the great noise-to-signal ratio in night recordings with the event camera it was impossible to derive ED predictions from the machine learning algorithm during night hours. From the hand annotations it is possible to estimate that ED are similarly frequent at night, but this cannot be quantified because only 8 night sequences were annotated (Figure S1 in Appendix S5.2). It is noteworthy however that the other two behaviours annotated as possible confounders (Chick and adults flapping) are barely present at night.

The frequency of the display was slightly greater in females throughout the observation period (Figure 4e). Females performed more ED in three out of the four sexed nests (Figures 4a and 4b) but with only four sexed nests this is for now just an indication.

Looking at the evolution of ED frequency per nest throughout the observation period it is possible to see the great variation within nests and across days (Figure 4f). Most nests mostly follow the same trends which is possibly what explains the growth in ED frequency in all nests with individuals identified as A-B as well as C-D as discussed above (Figure 4b). However, since our nests were within view of each other, and EDs are contagious, these cannot be considered independent observations.

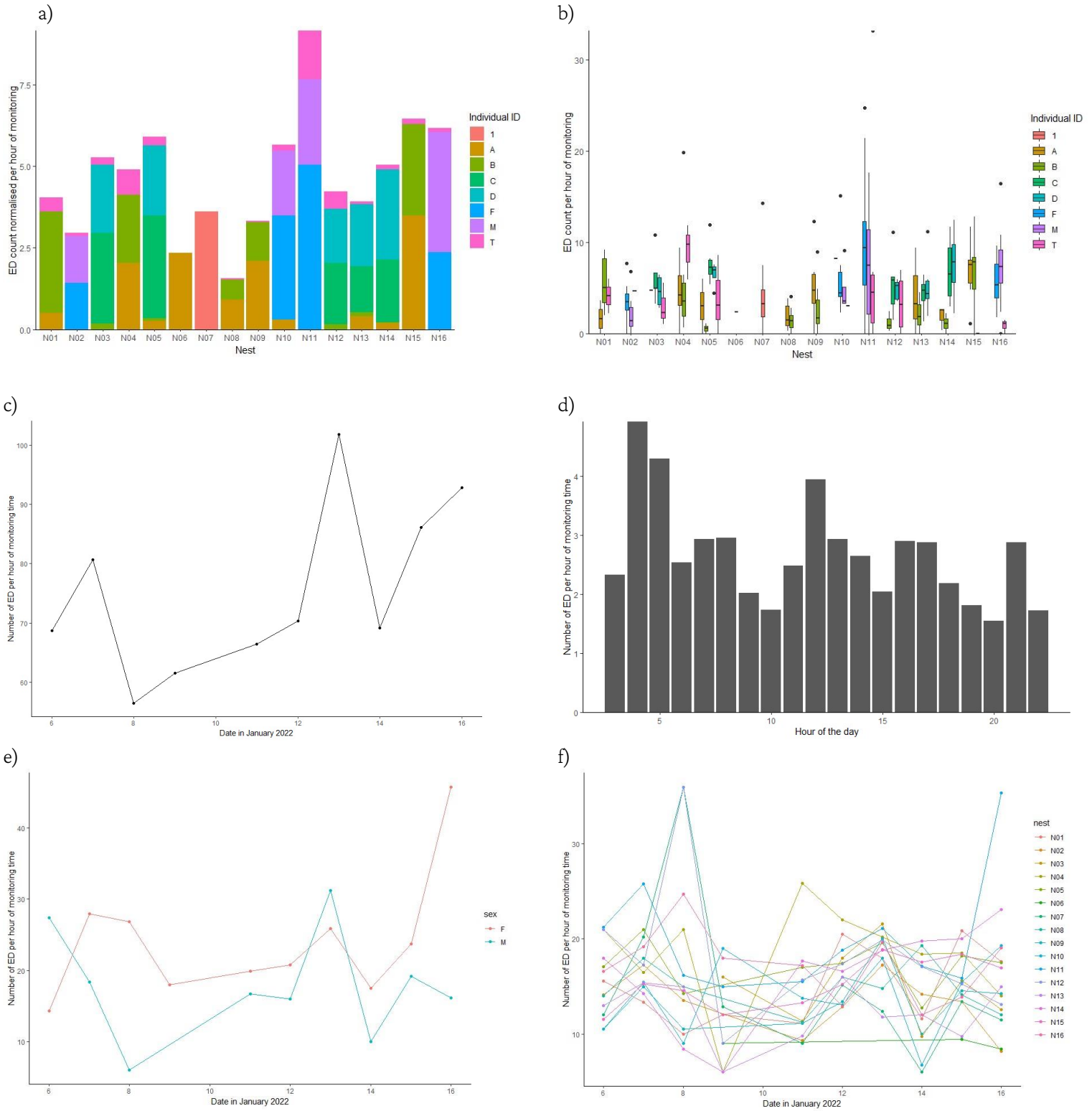


Figure 4: Quantification of ED occurrence during the study period. a) Overall ED frequency per nest for the whole monitoring period. b) frequency of ED per stint for each individual; Identities with less than 3 hours of total monitoring time are not shown. c) ED frequency per day of observation. d) ED frequency in each hour of an individual's stint. e) ED frequency in males and females per day and f) ED frequency per nest each day. In all figures frequency is the ED count per amount of time monitored for each particular nest, individual, or day of study.

ED duration

The mean duration of Ecstatic displays was 11.5 seconds and the mode was 13 seconds (Figure 5a). ED duration was fairly constant with no great differences between nests and individuals (Figure 5b). There does not seem to be great differences throughout the observation period (Figure 5b) nor throughout the day (Figure 5c). Note, as a caveat, that EDs less than 5s were filtered out to remove false positives (Appendix S5.1).

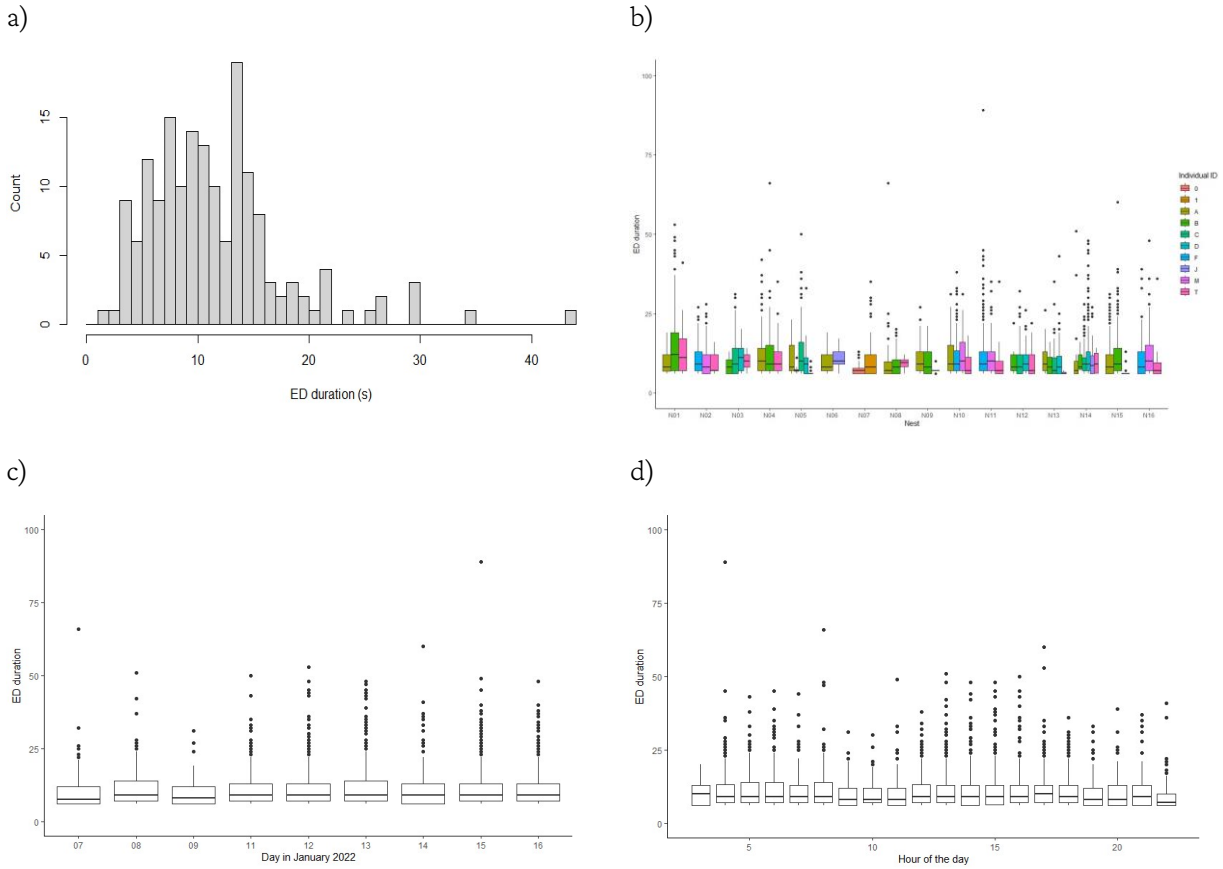


Figure 5: ED duration: a) Distribution of ED duration. This histogram only shows the duration of manually annotated ED since the main dataset is derived from predictions that have been filtered precisely because of their duration (>5s). ED duration as estimated by the ML detector b) per nest and individual c) per day of the season and d) per hour of day.

Transmissibility of ED behaviour

One of the aims of the study is to understand how ED is transmitted throughout a colony since it is very common for one individual's ED to trigger the same behaviour in one or more individuals. This sometimes results in multiple nests displaying after eachother and creating a wave of display that can spread through the colony. To follow this line, I analysed each instance of ED to determine whether it was unprompted (labelled a "Leader") or if instead started when another individual was already (previously but overlapping in time) displaying ("Follower"). To account for the level of precision in ED delimitation by the Machine-learning algorithm I also classify a relationship as Leader-Follower if two EDs occurred within a five-second difference. Using this classification, 45.7% (n = 3090) of EDs in the dataset are Leaders, while 54.2% (n = 3658) are followers.

Most nests show similar proportions, with a greater number of following EDs over leading ED; the only exceptions being N13 and N16, which have a greater frequency of leading EDs (Figure 6a). Those are the nests where individually both members of the pair have a greater frequency of leading displays (Figure 6c). There does not seem to be sex-specific differences as three out of four sexed nests show females performing more

as leaders (N02, N11 and N16), and that is also true for males (N02, N10 and N16), but no such differences appear in unsexed nests. Looking at those individuals first marked as A-B and later as C-D (for nests N05, N12, N13 and N14 the original A and B adult identities were lost through the study because of a snowtorm) it is possible to see that there does not seem to be individual idiosyncrasy in how much do they perform through time. When together in the nest (labelled T, Figure 6c) most pairs tend to lead more than they follow (N04, N05, N10, N14, N16) and some do the opposite (N01, N02, N03 and N12). Keep in mind that much of the T sequences are removed due to filtering out of any stints shorter than one hour, for the equivalent plot using all the data see Figure 2 in appendix S5.2 Finally there are differences in duration between ED types (Figure 6b) with Following ED being slightly longer (mean = 11.49s) than leading ED (mean = 9.4s).

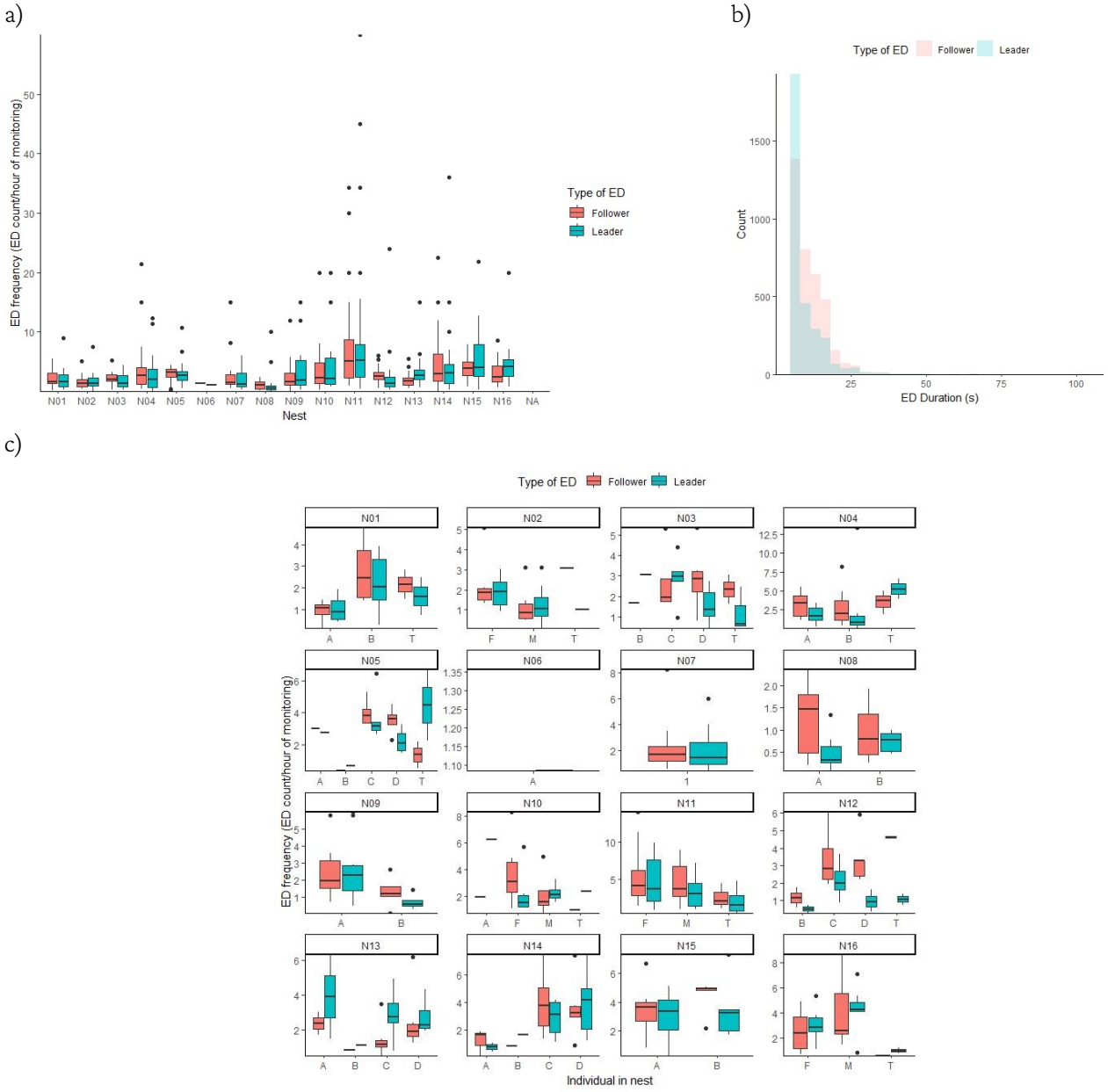


Figure 6: Occurrence of leading and following ED. a) ED frequency per nest b) Histogram of ED duration and c) ED frequencies per individual. For figure 6c only stints with at least an hour of monitoring time were included for the full dataset please refer to figure 2 in appendix S5.2. Nest identities are as follows: Adults in each nest are originally labelled A and B, however in nests N05, N12, N13 and N14 the original A and B adult identities were lost through the study because of a snowstorm and after they were relabelled as C and D. Whenever the individual could be sexed (Genetically or behaviourally) it is labelled as M and F. Perids when both members of the pair are in the nest are labelled T (Two). On nest N07 the labels refer to the number of individuals at the nest as it is impossible to know if the individual(s) is/are consistently the same one(s).

ED in relation to stints

ED frequency changes noticeably during a stint and it does so differently for breeders and non-breeding individuals (Figure 7a). While breeding pairs increase their frequency of ED throughout each stint, non-breeders perform much more in the early hours of the stint and then fall quiet with the exception of some bursts at some points during some very long stints that breeder do not endure (Figure 7a). ED duration does not seem to change much regardless of the moment of the stint the individual is in (Figure 7b).

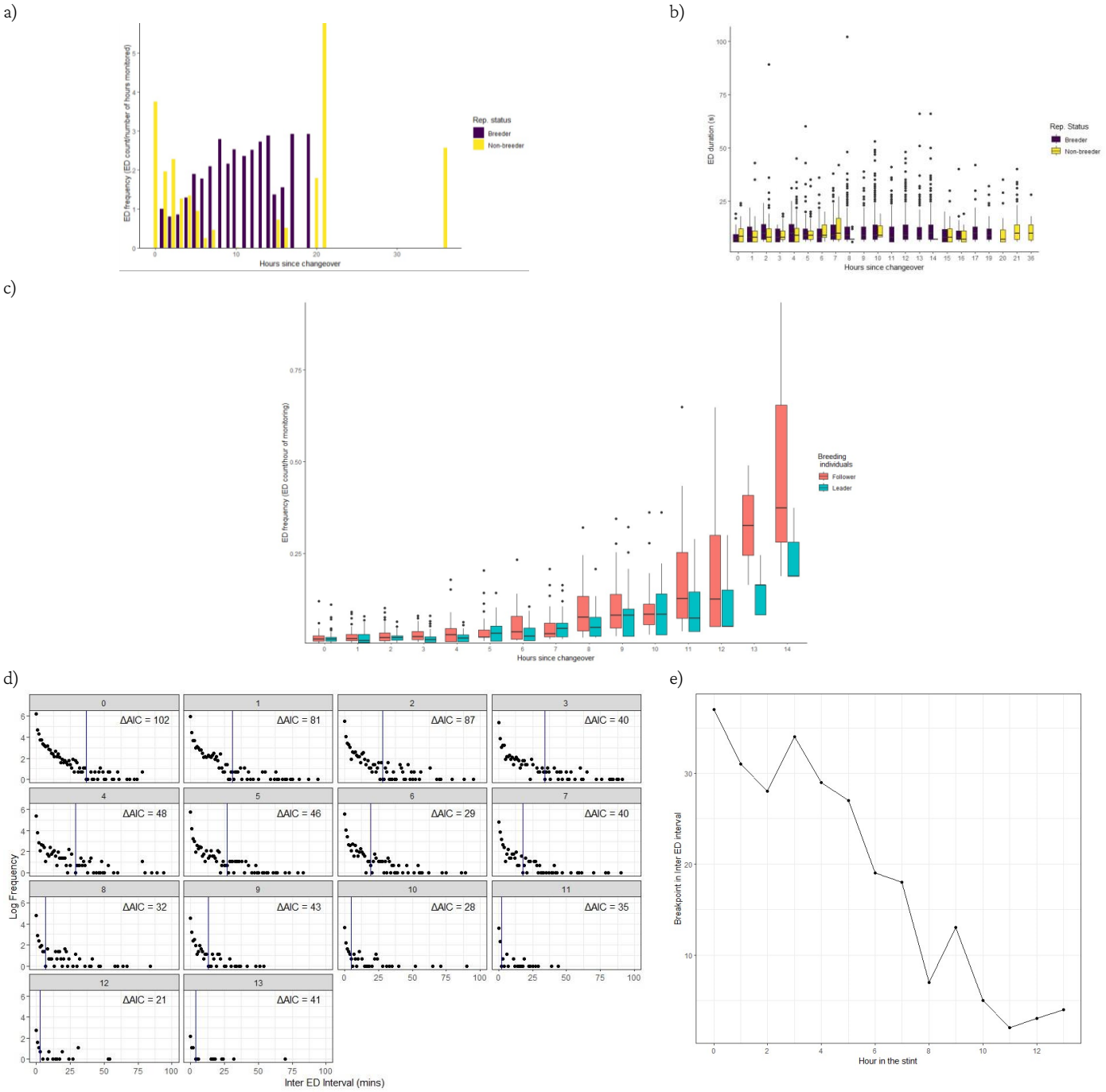


Figure 7: Changes in ED throughout a stint, starting when an individual is left alone after a changeover. a) Frequency of ED and b) ED duration in each hour of the stint since changeover. c) Changes in leading and following through a stint in breeding individuals. d) LogFrequency plots (Sibly et al., 1990) in order to find the whether there are bouts in each hour of the stint across nests. Hour of the stint is indicated in the header of each panel. All bout aggregations were statistically significant as shown in the ΔAIC comparing a linear to a broken stick model (calculated using *chngpt* package). Breakpoints derived from the broken stick model are shown as vertical blue line. e) Breakpoints of the previous broken-stick models for every hour in the stint showing bouts become shorter later in the stint.

There is an increase in the frequencies of both leaders and followers as the stint progresses (p = 1.20e-05; linear model).

I also conducted an analysis testing whether this behaviour is structured in bouts (Sibly et al., 1990) and whether this changes as the stint progresses. The analysis shows ED is structured in bouts at every hour during the stint (AIC > 2 for every hour of the stint; figure 7d). The analysis also shows how ED are more concentrated within the bouts as the stint progresses (Figure 7e). It is relevant how both the first statistically significant increase in ED frequence (Figure 7c) and the greatest drop in inter-ED interval (Figure 7e) happens between hours 6 and 8. This is potentially related to the median stint duration being 6.5 hours.

EDs occur in waves

Ecstatic display behaviour is clustered in periods (waves) where multiple nests perform ED interspersed with periods where no ED is observed (Figure 8a). In each of those ED waves only some nests take part but they will do so frequently throughout the duration of that wave. Testing the occurrence of ED at every minute during the observation period it is possible to confirm ED behaviour is far from a stochastic occurrence (using the Wald-Wolfowitz Runs Test; p-val = 10^{-10}).

In this chapter, I will define a wave as a consecutive period of time where there are at least two ED per minute. This means there can be multiple leaders in a wave as it is possible for the same or different penguins to display within the same 1-minute period without overlap. I decided on the establishment of waves as discrete units because I think these periods serve as discrete units as each wave is participated by a discrete group of individuals that participate often and is different from the groups that participate in the neighbouring waves. Waves were typically 7.5 minutes long in duration but ranged from 1 to 52 minutes long.

Looking at the chain of contagiousness in more detail, it was possible to establish the position of each ED in the chain of the wave. Lone performers were identified as those individuals that perform the ED independently from any other individual. This is, its ED is unprompted and at the same time it does not lead any other individuals into performing it. If one individual starts performing ED while another individual is also performing, I labelled these "follower" and "leader" respectively. Frequently individuals performing an ED trigger each other, often reciprocally, creating a wave of ED that can move throughout the sub-colony. In order to study the transmission phenomenon I differentiated between proximate leaders (those performing immediately before) and ultimate leaders (the first individual to start the wave).

Of all leading EDs in the dataset (n = 3090) most were performed without any followers (lone performers; n = 2061) while the remaining 33.3% (n = 1029) were actually followed by at least another individual. In those occasions that an ED was followed, it was most commonly followed by just one other individual (n = 500). Of all following EDs, most happen both preceded and followed by ED in other nests (31.9%; n = 2405) while the ultimate leaders (15.6%; n = 1047) and the ultimate followers (17.5%; n = 1173) were a minority of the total of ED in study.

There seems to be no differences in the individual's sequential positions they take within the wave. The amount of ED performed by each nest does not seem to show any particular preference for any of the positions. The same was true for the individuals in each nest as the proportions of ED performed by each individual are similar (Figures 3 and 4 in appendix S5.2). This is also true for sex differences in nests where sex wasknown or inferred.

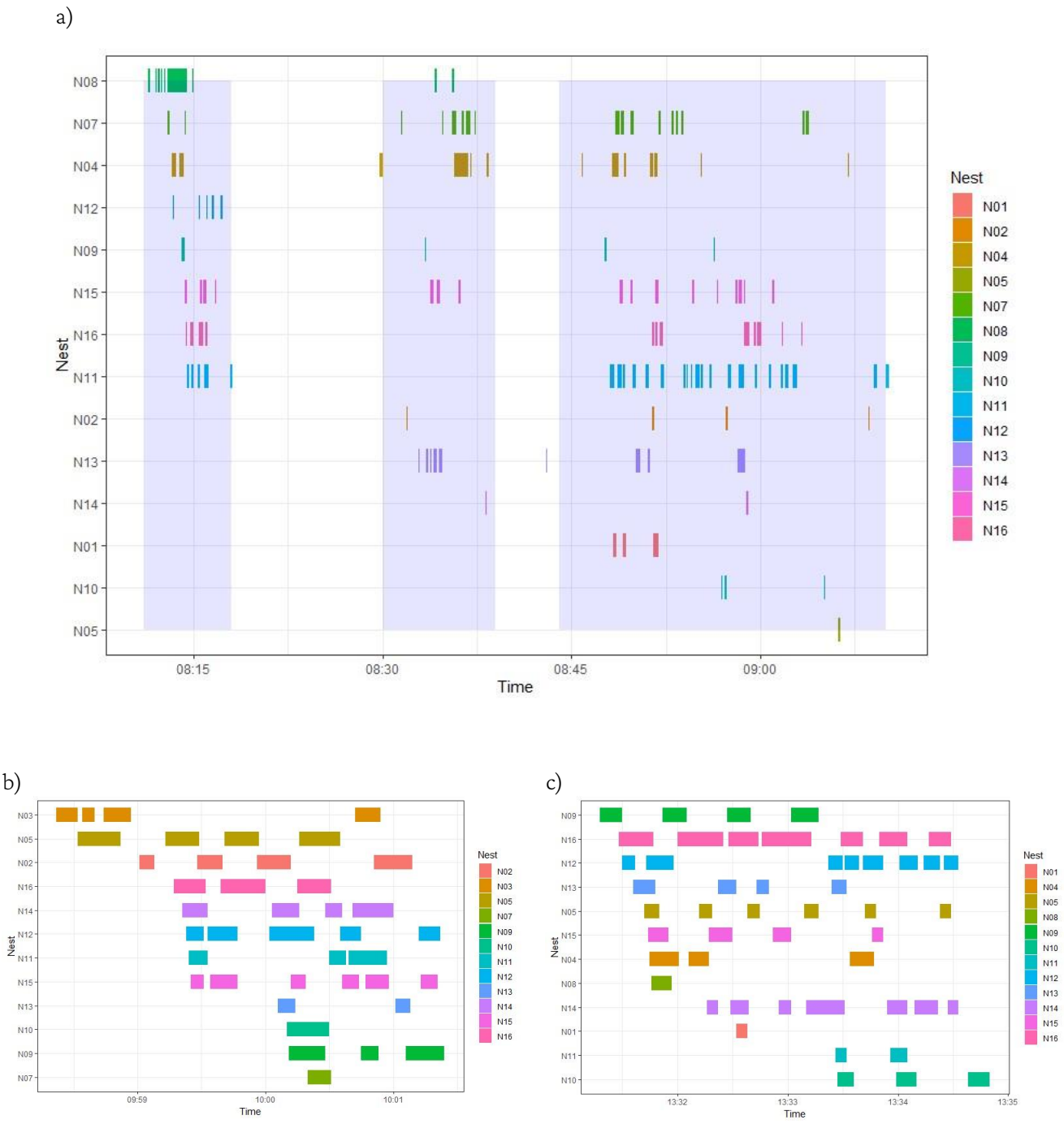


Figure 8: a) Example of ED occurrence during one hour of monitoring showing three waves of ED occurrence (blue background). b) Wave 4880 and c) wave 15781, two of the busiest ED waves in the dataset.

Influence of neighbouring nests

Visual analysis suggests that there are two groups of nests that trigger each other frequently without a clear leader-follower relationship between them (Figure 9): the group of nests N01 to N05 (with N02 being triggered almost exclusively by N01 and N05) and the group of nests N10 to N16 (with N13 being triggered almost exclusively by N15, its closest nest). In particular, the pairs of nests N11/N14 and N12/N15 both seem to trigger each other frequently. There are not any particular leader-follower relationship other than by proximity.

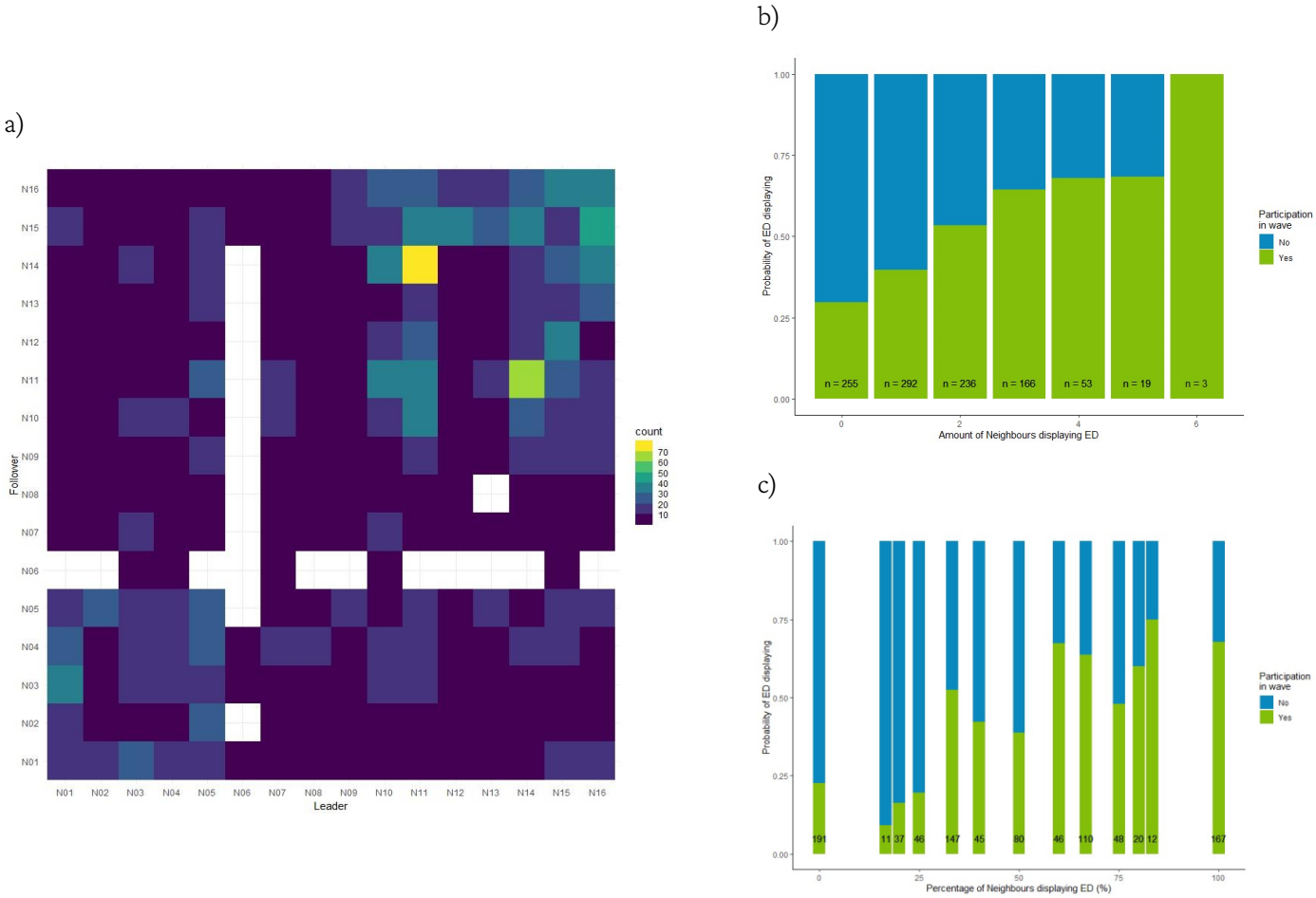


Figure 9: Influence of neighbours. a) 2D matrix counting the times that a particular nest (Follower) has started their ED display in response to any of the other nests (Leaders). b) Probability of displaying ED in a wave based on the number of neighbours displaying. c) Probability of displaying ED in a wave based on the percentage of neighbours displaying.

Weather

Weather has an effect on the occurrence of ecstatic display. Windspeed inhibited ED occurrence at as low as windspeeds of 1m/s ($p = 0.038$; Figure 10a). ED frequency was not significantly related to temperature (Figure 10b) or humidity (Figure 10c). Only once the temperature was adjusted for wind-chill (including both windspeed and humidity) does the weather seem to have a significant continuous effect inhibiting ED ($p = 0.0182$; figure 10d).

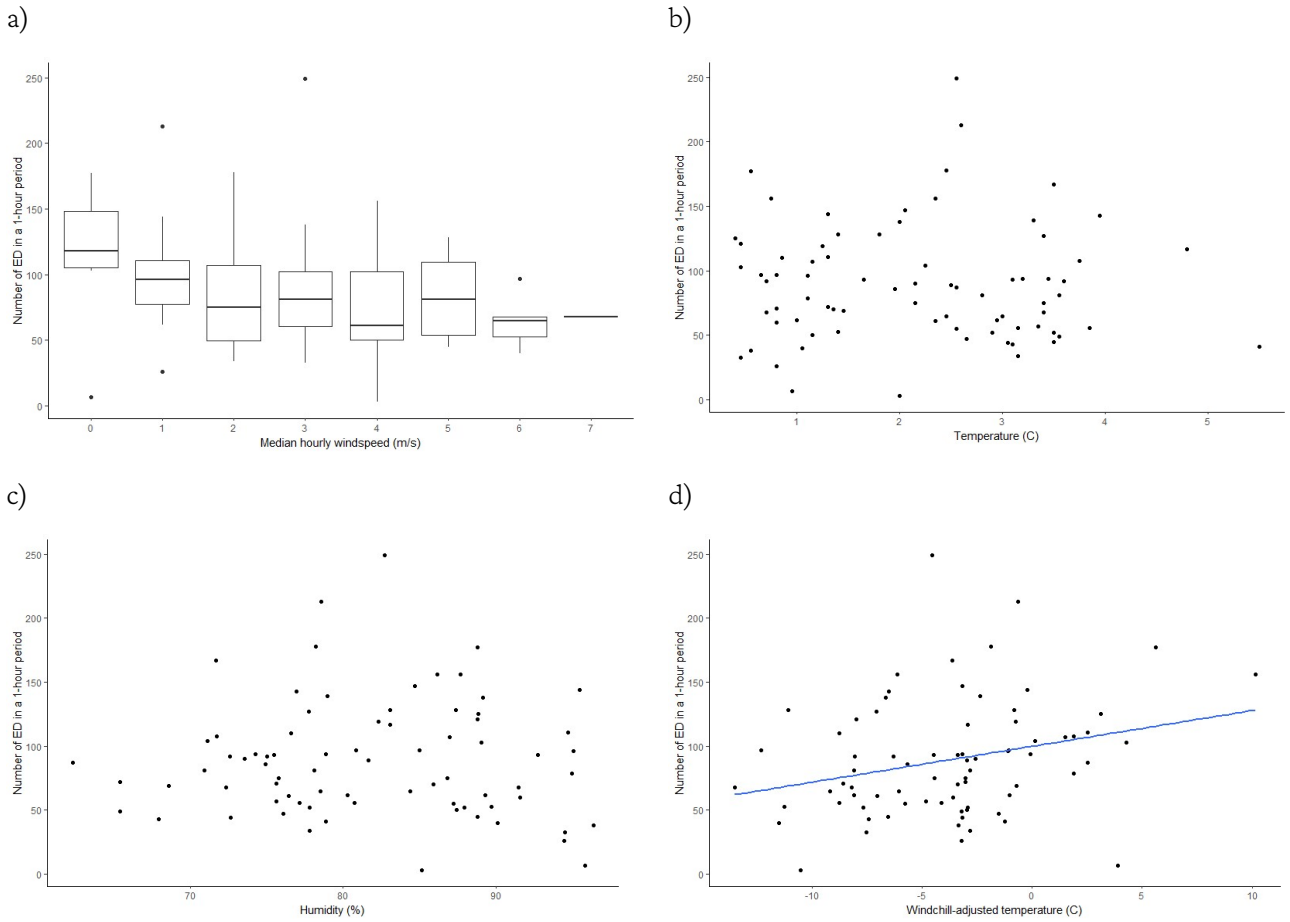


Figure 10: Effect of weather on the hourly frequency of ED. a) Wind, b) Temperature, c) Humidity and d) temperature adjusted to wind-chill.

• Results II: Understanding ED Behaviour •

In this section, I used the knowledge from the previous section in order to build different models that can explain the different aspects of ecstatic display behaviour.. For a more detailed description of variable construction and model selection please refer to Appendix S5.3.

Model 1: What influences the occurrence of ED behaviour at colony level?

In this model I evaluated the overall amount of ED for every complete hour of the observation period where all 16 nests were in view (n = 85). I decided to include the following variables in the analysis: Day of the month (Figure 4c), Hour of the day (4d), amount of nests with more than 6 hours after changeover (Figure 7c), mean hours at the nest after changeover across nests (Figure 7c) and weather (windchill-adjusted temperature; Figure 10). I also decided to include the number of changeovers to test whether newcomers induce ED either by triggering a territorial response on the colony or simply by moving through the colony. This analysis only includes breeding nests.

The only three variables left in the best fitting model according to AIC values (See Table S1 in appendix S5.3) are weather, Day of the month (as continuous variable, not factor) and number of changeovers in that hour.

Table 1: Model explaining ED occurrence at colony level. The linear model that best explains the amount of ED detected at each hour during the observation period includes the three variables shown below. The overall p-value of the model is 0.0057. For model selection, refer to Table 1 in appendix S5.3.

Response variable: ED amount per hour during the observation period				
Explanatory variables	Estimate	Std. Error	t-value	p-value
(Intercept)	48.709	29.649	1.643	0.1048
Hourly mean Windchill-adjusted Temperature (C)	2.331	1.094	2.131	0.0365 *
Day of the month (Continuous)	4.911	2.184	2.249	0.0276 *
Number of changeovers per hour	-6.946	3.493	-1.989	0.0505 .

Note first that weather does have a significant effect, with warmer temperatures allowing greater amounts of ED. This is possibly due to the incompatibility of ED with the need for the parents to cover and protect chicks from adverse conditions. This could also be behind the increase of the probability of ED increasing continuously with the days of the month, since every day there are more chicks able to thermoregulate and they can do so better. Finally, the number of changeovers per hour is an inhibiting factor, this is possibly because this variable also captures the amount of pairs at the nest per hour and that is an inhibitor of ED (Figure 4b) as well as the presence of first hours since the changeover, seen to have a reduced amount of ED (Figure 7c).

Model 2: What factors influence an individual's participation in a particular wave?

Considering that in sister species this has been previously described as a territorial behaviour I included some variables to test the influence of other members of the colony in an individual's decision to take part. To test this, I also included the amount of both neighbours and non neighbours that took part in the wave (Figure 7b). I also wanted to test the internal predisposition so I included some variables that could convey some readiness to engage in ED. These are: Minutes since the last performed ED, the Amount of ED performed in the previous hour and hours at the nest after changeover (Figure 7c). I also included two variables to test whether the development of the wave itself influences how many penguins decide to join it. To test this I included length of the wave and overall frequency on ED/minute of the wave. Finally, I also included windchill-adjusted temperature (Figure 10) and the day of the month since they have been proven to have an influence on ED display in Model 1.

Table 2: Model explaining factors influencing whether individuals take part in a certain wave. The generalized linear model that best explains the participation of a nest in a given wave includes the five variables shown below. For model selection, refer to Table S2 in appendix S5.3. R^2= 0.198.

Response variable: Participation of a nest in a wave (Binary)				
Explanatory variables	Estimate	Std. Error	t-value	p-value
(Intercept)	0.067662	0.050890	1.330	0.184060
Amount of ED in the previous hour (count)	0.014398	0.003296	4.368	1.43e-05 ***
Hours since the last changeover	-0.013215	0.004701	-2.811	0.005062 **
Duration of the current wave (min)	0.017774	0.002603	6.828	1.76e-11 ***
ED frequency in the current wave (ED/min)	0.057392	0.015152	3.788	0.000164 ***
Amount of neighbours performing ED	0.064668	0.014852	4.354	1.52e-05 ***

Note that neither non-neighbours, day of the month nor temperature have a significant influence over whether an individual joins the wave or not. For an individual to take part in a certain wave there seems to be two overall drivers. The first one is related to the internal state of the penguin as reflected by the influence of Amount of ED in the previous hour and hours since changeover. The second driver relates to the behaviour of

the rest of the members of the colony; the number of neighbours directly next to the nest as well as the number of others displaying in the wave and the overall length of the wave itself are related to a greater chance of an individual joining in.

Model 3: Once an individual participates, what factors affect amount of display?

In order to test this I chose several variables aimed at capturing the individual's inner state. These are: Minutes since the last performed ED, amount of ED performed in the previous hour, and hours at the nest after changeover (Figure 7c). To capture the internal dynamic of the wave I included the minute at which each individual joined the wave. In order to include the surrounding colony environment I included the amount of neighbours and non-neighbours performing ED for each nest. Finally I also included windchill-adjusted temperature (Figure 10) and day of the month as they have influence the overall amount of ED.

Table 3: Model explaining factors influencing how much do individuals display ED once they take part in a certain wave. The linear mixed effects model that best explains the number of ED detected in each wave for each of the nests participating in itincludes the five variables shown below. All models include nest as a random-effect model. For model selection, refer to Table 3 in appendix S5.3.

Response variable: number of ED displays in a wave (only for participating individuals)			
Explanatory variables	Estimate	Std. Error	t-value
(Intercept)	1.62287	0.37653	4.310
Hours since the last changeover	0.08319	0.04169	2.040
Amount of neighbours performing ED	0.77881	0.12286	6.339
Amount of non-neighbours performing ED	0.29307	0.05025	5.832
Windchill-adjusted Temperature (C)	0.11069	0.03172	3.489
Minutes between the start of the wave and start of the ED	-0.08828	0.03283	-2.689

The amount of ED performed by an individual once they become part of a wave is partially influenced by their internal state, with individuals performing more the greater the time since they relieved their partners. There seems to be an element of peer pressure as the number of both neighbours and non-neighbours performing ED also stimulates ED performance in an individual. Temperature also plays a role with greater displaying in warmer conditions. Finally, the minute of joining the wave is correlate with fewer ED. This correlation might not explain a biological process, but it possibly is due to for individuals joining later having less time to display before the wave dies.

Model 4: Factors affecting each nest's sequential position within a wave

In this analysis I intend to understand if there are any factors that facilitate follower nests (2^{nd} to the n^{th}) to join in a wave. In order to understand this analysis it is worth noting that lower wave position values mean earlier joining (as the first nests to display get lower numbers), so a positive parameter estimate is related to later displaying. I included several inner state variables like time since last ED, amount of ED in the previous hour and hours since changeover. I also included several variables to inform about the broader situation in the colony like overall amount and percentage of neighbours and non-neighbours displaying in the current wave.

Table 4: Model explaining factors influencing each nest's position within a certain wave. The linear mixed effects model that best explains each nest's position in a wave they participate inincludes the three variables shown below. All models include nest as a random-effect model. For model selection, refer to Table 4 in appendix S5.3.

Response variable: Nest's position in a wave they participate in			
Explanatory variables	Estimate	Std. Error	t-value
(Intercept)	3.03501	0.24793	12.241
Time since the last ED (mins)	0.013109	0.006790	1.931
Percentage of neighbouring nests involved in the current wave (%)	0.025771	0.005022	5.132
Hours since the changeover	0.073729	0.047082	1.566

Note that having displayed more recently is related to earlier sequential positions in the wave. The amount of hours since changeover wave as well as the percentage of neighbours performing ED correlate with later positions in the wave.

A possible explanation of this is that individuals that are already active displaying ED are more easily triggered to perform ED. At the same time those that have spent more time in the nest are more difficult to bring into the wave and possibly need peer pressure from more nests in order to start displaying ED.

Model 5: Factors affecting leading behaviour

In this analysis I included variables relating to the amount of ED performed by each nest previously to one of the nests deciding to perform a leading ED. Some refer to the amount of ED performed by the nest in question: Time since the last ED and Amount of ED in the previous hour. Specifically I included time since the last leading ED and time since the last leading ED that was actually followed by another nest. I also included some variables that show how much ED have the neighbours performed in the previous minute, ten minutes and hour periods. Finally I also included hours since the changeover and nest identity to test whether some nests are more prone to this behaviour than others.

Table 5: Model explaining factors influencing why does an individual decide to engage in leading behaviour. The generalized linear model that best relates the variables to one nest displaying unprompted includes the four variables shown below. For clarity only nests showing a significant difference are shown in the table. For model selection refer to Table 5 in appendix S5.3.

Response variable: Number of leading ED per hour per nest				
Explanatory variables	Estimate	Std. Error	t-value	p-value
(Intercept)	6.244e-02	5.931e-03	10.527	< 2e-16 ***
Amount of ED in previous hour (count)	4.831e-04	1.152e-04	4.192	2.77e-05 ***
Time since leading some other penguin	-4.821e-06	2.000e-06	-2.411	0.01591 *
Hours since changeover	-1.792e-03	3.493e-04	-5.129	2.93e-07 ***
Nest08	-3.418e-02	7.831e-03	-4.364	1.28e-05 ***
Nest13	2.089e-02	7.814e-03	2.673	0.00753 **
Nest14	2.376e-02	7.847e-03	3.028	0.00247 **
Nest15	4.925e-02	7.929e-03	6.212	5.32e-10 ***
Nest16	5.528e-02	7.874e-03	7.021	2.26e-12 ***

First, it is worth noting that none of the variables capturing ED activity in other nests (neither neighbouring nor non-neighbouring) made it to the final model, pointing that leading is driven only by the inner state of the individual. There are two variables related to an increase in ED activity prior to the leading ED: the amount of ED performed in the previous hour and the time since the last leading ED that was actually followed by

another nest. Both point that leading EDs are more common whenever there has been previous ED activity recently. The time since changeover indicates that Leading ED are less common in the late hours of a stint, in line with figure 7c.

Finally, the factor nest shows some nests tend to lead more frequently than others. In particular four nests (N13, N14, N15, N16) lead significantly more than the others are nests while Nest 08 performs Leading EDs much less frequently than any other nest.

Model 6: Factors affecting when a following ED is triggered in other nests.

For this model I included whether the follower is a neighbour to the leader. I also included several variables relating to the inner state of the follower, including: time since the last ED, total amount of ED in the previous hour, total amount of leading ED in the previous hour and hours since the changeover. I also included some variables that show how much ED have the neighbours performed in the previous minute, ten minutes and hour periods. Finally I also included hours since the changeover and nest identity.

Table 6: Model explaining factors influencing when does an individual decide to respond to a leading ED. The generalized linear model that best relates the variables to one nest displaying unprompted includes the six variables shown below. For clarity only nests showing a significant difference are shown in the table. For model selection refer to Table 6 in appendix S5.3.

Response variable: Potential follower nest responds or not to a leading ED (Binary)				
Explanatory variables	Estimate	Std. Error	t-value	p-value
(Intercept)	0.1285993	0.0215434	5.969	2.47e-09 ***
The follower is neighbour to the leader	0.0240475	0.0084934	2.831	0.00465 **
Neighbours displaying ED in the prev. minute (count)	0.2459974	0.0057272	42.952	< 2e-16 ***
Time since the last ED (Min)	-0.0003625	0.0001301	-2.786	0.00535 **
Time since leading (Min)	0.0095415	0.0019989	4.773	1.84e-06 ***
Hours since changeover	-0.0021421	0. 0009787	-2.189	0.02864 *
Nest04	0.0405376	0.0180321	2.248	0.02459 *
Nest05	0.0454548	0.0172931	2.628	0.00859 **
Nest08	-0.0454741	0.0205925	-2.208	0.02725 *
Nest14	0.0346585	0.0176574	1.963	0.04970 *
Nest15	0.0447063	0.0187579	2.383	0.01718 *

There is a clear influence of direct neighbours in triggering a following ED. While amount of nests displaying in the previous minute or hours did not made it into the model there are two variables relationg to Neighbour displays that correlate with greater chances of displaying. The two are: whether the leader is indeed a Neighbour and second is the amount of neighbours performing ED in the minute prior to following. Time since the last ED and time since leading are also correlated but in opposite directions. While having displayed recently enhances the chances of following ED, specifically having performed a leading ED is inversely correlated to performing a following ED. Finally, the amount of Following ED is greater in some specific nests. Except for N08, all other nests are those that are completely surrounded by other nests, which would make sense considering how much do neighbours influence the Following ED.

• Discussion •

Main findings

- Ecstatic Display is displayed by all individuals regardless of various factors like the time of day, the day within the observation period, their reproductive status or their sex (Figure 4).
- ED duration does not seem to be affected by any of the factors studied in this chapter (Figures 5, 6 and 8) other than stint hour (Figure 7).
- ED frequency is inhibited by the presence of a partner at the nest (Figure 6, Table 1) and it increases during breeding individuals' stints at the colony (Figure 7 and Tables 3, 4, 5, 6). The time within a stint also changes the structure of the display, with ED bouts becoming more concentrated and further away as the stint progresses (Figure 7).
- ED is transmissible within a colony with some ED (leaders) triggering this behaviour in other nests (followers). Generally neighbours are most likely to respond in this way to any given ED display (Figures 8, 9 and tables 4 and 6).
- ED is organised in waves (Figure 8) in which a group of nests participate repeatedly but distinct from previous and subsequent waves.
- Weather (windchill-adjusted temperature) has a major effect inhibiting ED (Figure 10 and table 1).

Ecstatic Display in Chinstrap Penguins

In Chinstraps, I recorded ED being performed by all nesting individuals. This includes males, females as well as non-breeding individuals (Figure 4a). ED was performed continuously throughout the whole observation period , which corresponds to the chick-guard stage of the breeding season, more than a month after the mating season. This is, Ecstatic display in Chinstrap penguins is different to the ED previously described in Adélie Penguins. In Adélies, ED is performed solely by males on the nest at the beginning of the season, possibly with territorial and mate attraction functions.

I have found no consistent differences between individuals, nests or between males and females (the latter might be due to the small (n= 4) amount of sexed individuals). ED frequency (number of ED/hour; Figure 4e) and leading/following proportions (Figure 6) remained roughly constant during the observation period. There were some differences regarding nest location (Figure 4a and 6c). The most notable one is the greatest proportion of Leading ED shown in nests located at the top of a ridge (N13, N14, N15 and N16 (Table 5)). This is the area of the colony that first becomes free of snow and accessible in the early season, and individuals in those nests are generally associated with better individual quality and greater breeding experience (Morrison et al., 2019; Smiley & Emmerson, 2016).

Regarding an overall driver of ED, there is onlyone variable that remains common to all models:the number of hours since changeover (Tables 2 to 6). Hours since changeover are linked to greater ED frequency (Table 3 and Figure 7c), however, it seems more difficult for penguins to engage in ED. Hours since changeover is related to a reduced chance to engage in ED in multiple ways: It inhibits participating in a wave (table 2), taking a more leading position in it (Table 4) or at performing leading (Table 5) and following EDs (table 6). At the same time, The explanation of this apparent contradiction comes through the structuring of ED in bouts and the changes in bout structure that happen throughout a stint (Figure 7d).

As a penguin stays in the nest, its displaying bouts become tighter (inter display interval becomes shorter; figure 7e) but the time between bouts remains roughly similar (Figure 7d). This is possibly due to save energy with increasing the periods without activity and concentrating the increase in ED frequency throughout the stint (Figure 7c) in denser bouts. It is worth noting that the greatest change in ED behaviour happens between hours 6 and 8 of a stint. At that time is when both the first significant increase in ED happens (Figure 7c) and the inter display interval drops, precisely around the mean (7.2) and median (7) stint duration. The

behavioural change may occur when the probability that the partner fails to return increases. This is not yet a functional explanation, but it may provide a route to search for one.

The increase in ED frequency during a stint is consistent with the group of variables relating to the amount of ED performed previously and the time since the last ED. These variables are present in all models and in all of them they point in the same direction: the chances of ED are greater the greater the previous amount of ED. ED has greater chances of being triggered the greater the amount of ED in the previous hour (positive estimates in models 2 and 5) and, conversely, the shortest the time since the last ED (Negative estimates in Tables 4, 5 and 6).

Regarding the transmissibility of ED behaviour, its "contagiousness" is clearly influenced (Tables 2 to 6) by the behaviour of the neighbours (Figure 9b). It is the performance of first-degree neighbours within pecking distance that influences an individual's participation in a wave (Table 2), their sequential position in which they join waves (Table 3), how much do they display once joined (Table 2) as well as their chances of performing a following ED in response to a leader. The number of non-neighbouring penguins performing also seems to affect the amount of display once the penguin has started its display (Table 2).

So far, it is not possible to say that there are hierarchical relationships between nests. Leader-follower relationships are mainly dominated by proximity (Figure 9a) and the greater amount of leading ED performed in nests at the top of the ridge only provides weak evidence that those could be occupied by birds in better condition (Table 5).

Weather has a major effect inhibiting Ecstatic Display (Figure 10, Table 1), as it was already observed in Adélies (Marks et al., 2010). This is very possibly because in colder conditions adults cannot physically perform as they tend to cover chicks, laying down on them when they are smaller and standing windwards of them when they are bigger (pers. obs.). This would also explain why ED is more frequent later in the season (Table 1) as chicks start thermoregulating by themselves. Weather does not appear to affect the decision of whether to join a wave (Table 2), leading (Table 5) or following (Table 6) but it appears to affect how much ED is performed once they start a bout (Table 3).

Hypotheses on the function of ED in Chinstrap penguins

A display is a mean of communication among conspecifics to convey specific messages. In Adélies the Ecstatic display has been described to perform a territorial function between males, but it has also been claimed to be used for mate attraction towards females. There are a few considerations that can help us understand the reasons behind ED.

First, ED in Chinstraps during the chick-guard stage of the breeding season (the period of study) is performed by both sexes. ED frequency is reduced when both members of the pair are at the nest (Figure 6c, Table 1).

Secondly, the fact that EDs are performed by all nests (Figure 4a), by both members of each pair (Figure 4b), at all times of the day (Figure 4d), every day of the season and throughout each whole guarding stint (Figure 7c) suggests that the behaviour is functionally important, but its adaptive significance remains obscure.

Finally, it is remarkable that ED frequency increases after 7 hours of a changeover (Figure 7c), the average duration of a shift, as if it represented intention movements anticipating the partner's return. ED is probably energetically costly, and increasing its frequency is a telling choice. However, this increase in ED is carried out in a way that saves energy, by concentrating them in denser bouts and maintaining an inter-bout period of reduced activity.

I examine three non-exclusive hypotheses about the reasons behind performing Ecstatic Display:

The first hypothesis is that this behaviour serves a territorial function. Instances of whole nests being taken over by neighbours once the season is underway are uncommon (unheard of, to the best of my knowledge).

However it is a very common occurrence for individuals to steal from other nests the pebbles that this species uses as nesting material. Stones are the only nesting material available in Antarctica and it is very valuable as it allows to raise the nest surface above the meltwater that often trickles down the colony slopes. Nestas are therefore very important for saving eggs and chicks from a likely hypothermia (Moreno et al., 1999). Nest maintenance is a costly effort and indeed nest size is related to the parents' health status and provisioning capacity (Fargallo et al., 2001). The size of choice of these stones is very specific and penguins generally choose to steal them from neighbouring nests than gathering them from the ground (Carrascal et al., 1995).

The Ecstatic Display Call has been proven to honestly convey information about body condition, attract females, and deter males during Adélies' mating season (Davis & Darby, 2012; Lynch & Lynch, 2017; Marks et al., 2010). In Chinstraps it could convey readiness to defend their nest-territory (especially their valuable nest stones) in a way that avoids escalation into physical confrontation and potential damage. This is a common function of signals in animals from deer to songbirds (Clutton-Brock and Albon, 1979). Loud, salient and costly signalling may be expected behaviour to have in a colonial situation, especially where nest size is linked to breeding success and stone theft is frequent and triggers fights (Moreno et al., 1999).

This territorial hypothesis would explain why ED is performed by every penguin under every condition and time, as the readiness to defend the nest stones would need to be revalidated periodically. This would also explain its transmissibility, especially why both joining a wave and following an ED are stimulated by first degree neighbouring nests and not by the nests from the rest of the colony. ED would signal the readiness/capability to fight and would need to be met with a similar response by the potential nests involved. It would also explain why females tend to display more as females are generally more stolen from then males (Fargallo et al., 2001).

Territorial defence could also explain why ED frequency is reduced during the changeover, when both members of the pair are at the nest (Figure 6c, Table 1). In the presence of both members of the couple ED could a) be avoided in order to not perform an aggressive behaviour towards the partner and/or b) not be necessary as the presence of two adults *per se* could be strong advertising of resource holding potential.

Under this hypothesis the increase in ED throughout the stint would be a way to reinforce the territorial claim in front of neighbours that may become bolder as the absence of the missing partner is prolonged. The sharp increase in behaviour occurs after about 7 hours, when partners come back on average. At that point a hypothetical time-keeping neighbour could attempt to take advantage if they perceive increased exhaustion or greater probability of desertion by the missing partner.

The change in bout structure concentrates the increase of ED frequency in tighter bouts as the stint progresses (Figure 7d) and could serve as a way to save energy. The more concentrated bout structure would allow starving penguins to maintain longer periods without activity despite an increase in ED frequency throughout the stint (Figure 7c). Should this indeed be a strategy to save energy , it would explain why stint hour correlates negatively with ED initiation (Tables 2 and 5) and why it is related to taking later positions once joining a wave (Table 4). The birds would be trying to save energy and with every hour that passes it would take an ever greater amount of peer pressure either to join a wave (Table 3) or to respond to a leading ED (Table 6). This would also explain why most of the growth in ED frequency corresponds to Following EDs (Figure 7c).

Another possibility is that ED may have a warm-up function for adults that have been stationary for longer and anticipate the imminence of a foraging trip after being relieved. This hypothesis has several difficulties: it does not explain why ED frequency is stimulated by neighbour performances (Tables 3 and 6) or why the increase in ED through a stint is mainly driven by following ED (Figure 7c). It also fails to explain why displaying is only ever observed at nests and why ED frequency decreases in colder conditions (Figure 10d).

It is of course possible that I missing a totally different adaptive significance, or even that EDs, being so taxonomically widespread, is just a phylogenetic relict of a once functional behaviour in an ancestral species. As usual such non-functional hypotheses cannot be rejected outright, but do not provide any useful guidance

to immediate continuing research. ED could still be a territorial behaviour (or not) but its increase could be driven by their psychological anticipation for the changeover to come. There would therefore be a component of ED being an intention movement (Tinbergen, 1960) purely or partially driven by the psychological expectation of a hungry individual to be relieved and move on to sea.

To conclude, it is worth keeping in mind that, while all the models presented above are statistically significant, they only explain 20% of variance. There are likely other variables like age, experience, carry-over effects and many more that might be at play but I did not have access to them in this non-invasive study. Including them in further studies would surely paint a more complete and complex picture and could be helpful at explaining for example the different ED baselines for the different nests.

On the Pilot use of event cameras for behavioural studies

The deployment of only one event camera and one timelapse camera have provided a rich and detailed dataset of behaviour occurrence on 85 hours of monitoring at 16 nests/regions of interest simultaneously and independently. This just required annotating 29 ten-minute sequences, roughly 0.5% of the whole dataset, and building a lightweight machine-learning algorithm (Hamann et al., 2023). Considering the expert annotation task required two weeks' work, it means that acquiring this dataset would have been impossible in practice using traditional video annotation techniques.

The result is a very accurate (94% true positives; Appendix S5.1) ethogram for each individual showing occurrence and duration of ED (Figure 8 and Figure 5 in Appendix 5.2). These three pieces of information have allowed differences in occurrence and duration during the observation period , diel rhythms, individual idiosyncrasies, differences between males, females and non-breeding individuals, transmissibility of the behaviour, effects of changeovers, etc.

This dataset even allows for further analyses that have not been pursued in this chapter. For example, I could have pursued the study of raw event rates (overall changes in intensity) in order to study the activity patterns in each nest throughout the observation period (Figure 6 in Appendix S5.2). Another option that fell out of the chapter was the study of spectrograms generated from the oscillation of the wingbeats (Figure 7 in Appendix S5.2). This could possibly become a finer way of filtering ED from chick and adult flaps in the dataset over the hard filtering using ED duration (Appendix S5.1). Studying differences in frequency throughout the observation period , in diel rhythms, between individuals, sexes, throughout a stint would also have been interesting questions that will need to be addressed in another paper. Finally, this very dataset could have also served to study other behaviours apart from ED. I could have already focused on adults and chicks flapping as I have already annotated the occurrence of these behaviours because of their possible confusion with ED (Figure 1 in Appendix S5.2). Possibly it would be interesting to look into the changeovers and annotate/detect feeding behaviour and test whether bouts of parents feeding chicks could be a way to estimate food provisioning. Acquiring such data uninvasively would be valuable for penguin conservation research.

Despite the wealth and quality of data, this pilot study has encountered several difficulties that should be addressed in future studies with event cameras. This deployment was intended as a pilot study, and gaps in the data make many of the analyses difficult, especially those related to tracking an individual over a long period of time like the study of changeovers. This is mostly due to the limitations that I had on battery life, which could be fixed in future studies. I would lose data whenever the weather would not allow us to reach the colony first thing in the morning or not at all during specific days. This has resulted in really irregular amounts of the hours of monitoring for different nests and individuals.

A similar situation occurred during the night hours. Despite having monitored many night hours I was not able to use any of these sequences due to a combination of the camera reading becoming much noisier and

the wind conditions becoming stronger. Despite I could annotate ED in night sequences by eye it was not possible to build a ML model that would extract these behaviours reliably.

I also missed parts of the day sequences due to camera movement. This was unavoidable, because even the sturdiest tripod will shake in 120Km/h winds, and algorithms may mistake such movement for subject movement. In this sense it is worth noting how useful it was to leave a little area showing an unchanging mountain face without wildlife (Figure 1c, triangle shaped at the top right corner). Activity in that triangle would serve as an easy and reliable way to find wind gusts and filter them out, discarding the minimum amount of data possible. Strong winds also caused the whole tripod to get covered in mud and guano, obscuring the lens of the event camera and causing data loss. A similar situation occurred for the time-lapse camera when it got obscured mid-deployment, which resulted in us losing track of individuals in non-banded nests halfway through the observation period . Both cameras were looking westwards, the most common wind direction. Further deployments will have to take this into account. Inability to follow individuals if they left the frame could be overcome by individual markings.

Another problem of this pilot study was the CPU controlling the camera did not have a built-in clock. This resulted in the need for a very tedious alignment process comparing scenes between the time-lapse images where I annotated the changeovers (Figure 1b) and the frames provided by the event camera (Figure 1c). This was time-consuming and added unnecessary uncertainty about the boundaries between different identities of the individual(s) at the nest.

In conclusion, event cameras provide a non-invasive and easy-to-deploy technique for behaviour monitoring in the wild. The quality and wealth of data acquired is extraordinary despite the complexity that the data gaps impose in its analysis. The only caveats being the current difficulty to power (and to record) continuously as well as the need to use Machine Learning to extract further data beyond that annotated by hand.

• References •

Armstrong, E. A. (1951). The nature and function of animal mimesis. *Bulletin of Animal Behavior*, *10*, 46–49.

Bustamante, J., & Marquez, R. (1996). Vocalizations of the Chinstrap Penguin Pygoscelis antarctica. *Colonial Waterbirds*, *19*(1), 101. https://doi.org/10.2307/1521812

Carrascal, L. M., Moreno, J., & Amat, J. A. (1995). Nest maintenance and stone theft in the Chinstrap penguin (Pygoscelis antarctica) 2. Effects of breeding group size. Polar Biology, 15, 541-545.

Chappell, MarkA., Janes, DonaldN., Shoemaker, VaughanH., Bucher, TheresaL., & Maloney, ShaneK. (1993). Reproductive effort in Adélie penguins. *Behavioral Ecology and Sociobiology*, *33*(3), 173–182. https://doi.org/10.1007/BF00216598

Clark, J. A., Boersma, P. D., & Olmsted, D. M. (2006). Name that tune: Call discrimination and individual recognition in Magellanic penguins. *Animal Behaviour*, *72*(5), 1141–1148. https://doi.org/10.1016/j.anbehav.2006.04.002

Clutton-Brock, T. H., & Albon, S. D. (1979). The roaring of red deer and the evolution of honest advertisement. Behaviour, 69(3-4), 145-170.

Davis, L. S., & Darby, J. T. (2012). *Penguin Biology*. Elsevier.

Derksen, D. V. (1977). *A Quantitative Analysis of the Incubation Behavior of the Adélie Penguin*. 16.

Favaro, L., Gamba, M., Alfieri, C., Pessani, D., & McElligott, A. G. (2015). Vocal individuality cues in the African penguin (Spheniscus demersus): A source-filter theory approach. *Scientific Reports*, *5*(1), Article 1. https://doi.org/10.1038/srep17255

Fargallo, J. A., De León, A., & Potti, J. (2001). Nest-maintenance effort and health status in chinstrap penguins, Pygoscelis antarctica: the functional significance of stone-provisioning behaviour. Behavioral Ecology and Sociobiology, 50, 141-150.

Hamann, F., Ghosh, S., Martinez, I. J., Hart, T., Kacelnik, A., & Gallego, G. (2023, December 6). *Low-power, Continuous Remote Behavioral Localization with Event Cameras*. ArXiv.Org. https://arxiv.org/abs/2312.03799v1

Jouventin, P., & Aubin, T. (2002). Acoustic systems are adapted to breeding ecologies: Individual recognition in nesting penguins. *Animal Behaviour*, *64*(5), 747–757. https://doi.org/10.1006/anbe.2002.4002

Jouventin, P., & Dobson, F. S. (2017). *Why Penguins Communicate: The Evolution of Visual and Vocal Signals*. Academic Press.

Mahowald, M. (1994). An analog VLSI system for stereoscopic vision (Vol. 265). Springer Science & Business Media.

Lichtsteiner, P., Posch, C., & Delbruck, T. (2008). A 128$\times $128 120 dB 15$\mu $ s latency asynchronous temporal contrast vision sensor. IEEE journal of solid-state circuits, 43(2), 566-576.

Lynch, M. A., & Lynch, H. J. (2017). Variation in the ecstatic display call of the Gentoo Penguin (Pygoscelis papua) across regional geographic scales. *The Auk*, *134*(4), 894–902. https://doi.org/10.1642/AUK-17-4.1

Marks, E. (first), Rodrigo, A., & Brunton, Dianne. (2010). Ecstatic display calls of the Adélie penguin honestly predict male condition and breeding success. *Behaviour*, *147*(2), 165–184. https://doi.org/10.1163/000579509X12512863752751

Morrison, C. A., Alves, J. A., Gunnarsson, T. G., Þórisson, B., & Gill, J. A. (2019). Why do earlier-arriving migratory birds have better breeding success? *Ecology and Evolution*, *9*(15), 8856–8864. https://doi.org/10.1002/ece3.5441

Moreno, E., Moreno, J., & De Leon, A. (1999). The effect of nest size on stone-gathering behaviour in the chinstrap penguin. Polar Biology, 22, 90-92.

Penney, R. L. (1964). *TERRITORIAL BEHAVIOR AND SOCIAL INTERACTIONS.BY THE ADÉLIE PENGUIN*.

Searby, A., & Jouventin, P. (2005). The double vocal signature of crested penguins: Is the identity coding system of rockhopper penguins Eudyptes chrysocome due to phylogeny or ecology? *Journal of Avian Biology*, *36*(5), 449–460. https://doi.org/10.1111/j.0908-8857.2005.03416.x

Searby, A., Jouventin, P., & Aubin, T. (2004). Acoustic recognition in macaroni penguins: An original signature system. *Animal Behaviour*, *67*(4), 615–625. https://doi.org/10.1016/j.anbehav.2003.03.012

Sibly, R. M., Nott, H. M. R., & Fletcher, D. J. (1990). Splitting behaviour into bouts. *Animal Behaviour*, *39*(1), 63–69.

Sladen, W. J. (1958). *The Pygoscelid penguins: I. Methods of study. II. The Adélie penguin*.

Smiley, K., & Emmerson, L. (2016). A matter of timing: Adélie penguin reproductive success in a seasonally varying environment. *Marine Ecology Progress Series*, *542*, 235–249. https://doi.org/10.3354/meps11536

Speirs, E. A. H., & Davis, L. S. (1991). Discrimination by Adélie penguins, Pygoscelis adeliae, between the loud mutual calls of mates, neighbours and strangers. *Animal Behaviour*, *41*(6), 937–944. https://doi.org/10.1016/S0003-3472(05)80631-1

Taverni, G., Moeys, D. P., Li, C., Cavaco, C., Motsnyi, V., Bello, D. S. S., & Delbruck, T. (2018). Front and back illuminated dynamic and active pixel vision sensors comparison. IEEE Transactions on Circuits and Systems II: Express Briefs, 65(5), 677-681.

Tinbergen, N. (1952). 'Derived' Activities; Their Causation, Biological Significance, Origin, and Emancipation During Evolution. *The Quarterly Review of Biology*, *27*(1), 1–32. https://doi.org/10.1086/398642

Tinbergen, N. (1960). Comparative Studies of the Behaviour of Gulls (Laridae): A Progress Report1). *Behaviour*, *15*(1–2), 1–69. https://doi.org/10.1163/156853960X00098

6

Chapter 6

General Conclusions

Pygoscelid penguins change with their climate

The three species of Antarctic Penguins studied in this thesis are demonstrating a remarkable capability for adaptation. As seen in chapter 2, all three are advancing their breeding season in response to some record warming conditions (Appendix 2.3) in the area and they are doing so at record speeds. This may in fact result in an adaptation to climate change' as breeding success has been overall high (Chapter 4) despite the warming of the last decade. The absence of records of reproductive success in earlier periods makes it impossible at the moment to conclude whether the observed reproductive performance is comparable to that of a pre-warming world. It is very likely that no mismatch has happened during the breeding season so the steep declines in Chinstrap and Adélie populations that have been observed throughout the Antarctic Peninsula (Che-Castaldo et al., 2017; Strycker et al., 2020) should be the result of an impact outside the breeding season. I suggest these impacts could be affecting the winter season or the yearly pre-winter moult.

Currently the greatest rate of warming occurs during the colder winter months (Carrasco et al., 2021). Possibly this is affecting Adélies and Chinstraps differentially as they are migratory species that spend their winters in the high seas on the edge of the ice-shelf, while Gentoos spend their winter months close to their breeding colonies. The decline of Adélies and Chinstraps could be affected by the current loss of sea-ice in the area (Eayrs et al., 2021; Gross, 2005), needed for resting during the many night-hours; Hinke et al., 2019). It would also be possible that the loss of sea ice impacts their survival by way of changes in food availability (Flores et al., 2012; Lascara et al., 1999; Meyer, 2012). Both possibilities are worth investigating as there are very few

studies in either and they are not mutually exclusive. Gentoos, on the other hand, could benefit from the milder winter conditions and the reduced amount of winter sea-ice (Black et al., 2017; Hinke & Trivelpiece, 2011); this could explain their expansion to new areas of the Antarctic Peninsula in the last decade (Carpenter-Kling et al., 2019).

It would be worth investigating the possibility that these three species might be impacted during their yearly pre-winter moult. All three species undergo a full-body moult after their chicks fledge; this sees them lose their waterproof abilities and keeps them out of the water for 2-3 weeks (Williams, 1995). In order to prepare for that fasting period all adults endeavour in a pre-moult exodus, sometimes quite far from the colony (Warwick-Evans et al., 2019). In Chapter 4 I showed season length has been changing significantly and differently for the three species, while breeding success is generally greater in the shorter seasons and longer seasons might have an impact on Breeding Success. I suggest there are two main ways in which longer seasons could affect future breeding success. First is because these species might simply have less time to recover from the breeding season. This could affect Adélies and Chinstraps especially because they need to travel to their wintering grounds. The second is because these changes in schedule might result in a trophic mismatch during the pre-moult trip or a greater overlap with krill fisheries, which typically are more active Feb-May (CCAMLR Fishery Report 2022: *Euphausia Superba* in Area 48). Our data may make it possible to test if seasons with longer guard stages actually show longer pre-moult trips (not visible in all cameras) and whether this happens in years with greater fishing activity. For Adélies and Chinstraps a mismatched moult further risks starting migration late with a loss of favourable migrating conditions or simply a loss of time at the wintering areas.

PYGOSCELID PENGUINS FACE COMPOUND THREATS

This thesis raises several questions about potential effects that can affect the breeding cycle of these species and have potential problems for their conservation.

In Chapter 2, I show the loss of freezing days is working against the phenological advance of Chinstraps and Adélies. Considering that the phenological advance is likely the result of the penguin's adaptation to climate change (as it is not affecting their breeding success; Chapter 4) the loss of freezing days is hampering penguins' adaptation to climate change. It would be worth investigating whether the loss of freezing days is indeed related to krill-loss in the early season as hypothesised in Chapter 2.

The study on Breeding Success in Chapter 4 still raises interesting questions about the effects of climate change on Pygoscelid penguins during the breeding season. The main concern is regarding snow permanence in the colonies and its negative effect on breeding success, given our finding that snow persistence has increased significantly during our monitoring period. This is possibly due to the progressive weakening of the polar vortex above Antarctica due to the widespread warming of the region lessening the temperature difference with the surrounding temperate air masses (Zuev et al., 2020). A weak polar vortex (not too cold comparatively to the temperate air around it) is characterised by low speed winds (Zuev & Savelieva, 2022) and lets warmer and moist air further into Antarctica, increasing precipitation (Zuev et al., 2020). Given that Pygoscelids nest over naked rock, increasing snow cover, especially after laying has started, may be a serious negative influence. This could have major impacts on the population by causing early-season failure, something that is likely to affect Adélies and Chinstrap disproportionately as these species are incapable of relaying a clutch.

This is something that affects Chinstraps and Gentoos equally, although it would be better to include further colonies and several Adélie colonies in future studies in order to gain a broader picture. It would also be good to broaden this study to include other sources of precipitation as in the more temperate South Shetland Islands it has been rain that stopped the breeding of penguins in the early season (pers. obs. of time-lapse images).

The impact of snow in the early season can have further consequences if earlier breeders (usually those with better body condition and greater breeding success) are those most affected by precipitation (be this rain or

snow). Choosing a time to breed implies a gamble against the elements as breeding early can be advantageous in earlier years but under the new circumstances, it can result in a season aborted early. These changes should be studied also with relation to breeding synchronicity, that has been found to be more important than early breeding in influencing breeding success, both in Chapter 4 and other studies (Youngflesh et al., 2018).

Early monitoring is key for effective conservation

Monitoring needs to go beyond population numbers and start including behavioural responses into the process for more effective management (Heller & Zavaleta, 2009). In long-lived species such as penguins, using demographic collapse in sentinel species (Croxall et al., 2012) as an signal for ecosystem change means allowing years of unsuccessful breeding before realising things are going wrong (Cerini et al., 2023). This also means the decline will be well underway before researchers can establish a baseline of what "normal" means and the causes of the decline and it is possible to take any mitigating action. It is necessary therefore to start including behavioural monitoring on top of population monitoring in order to detect early warning signs based on behavioural changes. The use of these techniques does not necessarily need to stop at the monitoring stage as they can be useful too during the implementation of conservation actions like Marine Protected Areas (Wilson et al. 2021).

In chapters 2 to 5 I show that both time-lapse as well as event cameras are suitable non-invasive tools to monitor breeding behaviour in the wild. Both can provide behavioural metrics that can serve as early warnings of population change prior to demographic declines and all their data can be reanalysed once new questions arise or new techniques become available. Time-lapse cameras are cheaper and easier to deploy and can serve a role for monitoring remote locations for extensive periods of time. Event cameras need maintenance more frequently but are capable of fulfilling intensive monitoring of specific behaviours that can be detected using AI. Their extremely high temporal resolution makes them preferable for monitoring behaviour.

The behavioural parameters that can more efficiently be extracted from event cameras can be easily compared with environmental conditions in order to understand the source of behavioural changes and to signal the causes of possible threats. Both techniques could be further coupled with methods like GPS or guano samples in order to study other aspects like foraging ecology. Time lapse cameras are especially easy to deploy and service even in remote locations that can only be accessed during a limited period of time, making it easier to cover a lot of ground while making the study replicable between colonies and species as well as across years. This opens the door to demographic, conservation and behavioural landscape-scale studies like those in chapters 2 and 4

I hope the studies derived from this thesis encourage the use of time-lapse imagery and event data as effective, cheap, and non-invasive technologies to monitor behaviour with conservation purposes.

On the use of technology for environmental research

Both time-lapse and event cameras make large-scale data acquisition very easy. However, extracting biologically meaningful information from such data requires a good amount of technical development. To start, in every chapter I have needed to either adapt existing biologically-meaningful metrics for a fixed camera view setup (e.g. Breeding success in Chapter 4) or to develop new metrics altogether (e.g. 'colony settlement' in Chapter 2 or thaw date in chapter 4). These have required a trial-and-error process where each step required the coding and ground-truthing of new tools.

It is obviously desirable to automate as much of the process as possible, as this sort of technology amasses huge volumes of data. The Penguin Watch project currently has 8.2 million time-lapse images from the Penguinwatch network, over 35 million volunteer classifications by 120000 volunteers resulting in 340 million single annotations on the Penguinwatch citizen science platform. This amount of data requires to

automate as many parts of the analysis process as possible but this is not easy. For example, for this thesis I have needed to write over 12,000 lines of code, and there is still plenty of room to add subroutines that could improve the filtering and interpretation of data.

Another consequence of dealing with increasingly rich technologies that yield vast datasets is that collaborating is becoming more necessary than ever. In Chapter 5, I used an altogether new type of camera (the event camera) and in Chapter 4 I needed external help to build an alignment algorithm. Both needed to be done in collaboration with AI experts from the Technical University of Berlin and from Oxford University respectively. It would not have been possible for a team of biologists to effect all the necessary engineering in order to implement event cameras and produce the necessary AI, nor for engineers to dominate the biology necessary to understand the meaningful aspects of the natural processes of study.

Despite the intensive attempts at automating the processing of time-lapse and event data, and the collaboration with world experts in outside disciplines, the great inherent natural complexity of the problems made it impossible to fully automate data collection or data processing. This means that –for the moment and probably for a very long time– there is still the need for a (human) scientist in the loop.

The final consequence of accessing these immense amounts of data is that question-driven research is more necessary than ever, even if it is just not to get lost in the data. In preparing the chapter on the event data, the real problem was to choose what not to present, since presenting the fine scale of the data and all of the relationships within it can risk losing the thread of the research question.

References.

Black, C., Rey, A. R., & Hart, T. (2017). Peeking into the bleak midwinter: Investigating nonbreeding strategies of Gentoo Penguins using a camera network. *The Auk*, *134*(3), 520–529. https://doi.org/10.1642/AUK-16-69.1

Carpenter-Kling, T., Handley, J. M., Connan, M., Crawford, R. J. M., Makhado, A. B., Dyer, B. M., Froneman, W., Lamont, T., Wolfaardt, A. C., Landman, M., Sigqala, M., & Pistorius, P. A. (2019). Gentoo penguins as sentinels of climate change at the sub-Antarctic Prince Edward Archipelago, Southern Ocean. *Ecological Indicators*, *101*, 163–172. https://doi.org/10.1016/j.ecolind.2019.01.008

Carrasco, J. F., Bozkurt, D., & Cordero, R. R. (2021). A review of the observed air temperature in the Antarctic Peninsula. Did the warming trend come back after the early 21st hiatus? *Polar Science*, *28*, 100653. https://doi.org/10.1016/j.polar.2021.100653

Cerini, F., Childs, D. Z., & Clements, C. F. (2023). A predictive timeline of wildlife population collapse. *Nature Ecology & Evolution*, *7*(3), Article 3. https://doi.org/10.1038/s41559-023-01985-2

Che-Castaldo, C., Jenouvrier, S., Youngflesh, C., Shoemaker, K. T., Humphries, G., McDowall, P., Landrum, L., Holland, M. M., Li, Y., Ji, R., & Lynch, H. J. (2017). Pan-Antarctic analysis aggregating spatial estimates of Adélie penguin abundance reveals robust dynamics despite stochastic noise. *Nature Communications*, *8*(1), 832. https://doi.org/10.1038/s41467-017-00890-0

Croxall, J. P., Butchart, S. H. M., Lascelles, B., Stattersfield, A. J., Sullivan, B., Symes, A., & Taylor, P. (2012). Seabird conservation status, threats and priority actions: A global assessment. *Bird Conservation International*, *22*(1), 1–34. https://doi.org/10.1017/S0959270912000020

Eayrs, C., Li, X., Raphael, M. N., & Holland, D. M. (2021). Rapid decline in Antarctic sea ice in recent years hints at future change. *Nature Geoscience*, *14*(7), Article 7. https://doi.org/10.1038/s41561-021-00768-3

Fishery Report 2022: Euphausia superba in Area 48. (n.d.).

Flores, H., Van Franeker, J. A., Siegel, V., Haraldsson, M., Strass, V., Meesters, E. H., Bathmann, U., & Wolff, W. J. (2012). The association of Antarctic krill Euphausia superba with the under-ice habitat. *PloS One*, *7*(2), e31775.

Gross, L. (2005). As the Antarctic Ice Pack Recedes, a Fragile Ecosystem Hangs in the Balance. *PLOS Biology*, *3*(4), e127. https://doi.org/10.1371/journal.pbio.0030127

Heller, N. E., & Zavaleta, E. S. (2009). Biodiversity management in the face of climate change: A review of 22 years of recommendations. *Biological Conservation*, *142*(1), 14–32.

Hinke, J. T., Santos, M. M., Korczak-Abshire, M., Milinevsky, G., & Watters, G. M. (2019). Individual variation in migratory movements of Chinstrap penguins leads to widespread occupancy of ice-free winter habitats over the continental shelf and deep ocean basins of the Southern Ocean. *PLOS ONE*, *14*(12), e0226207. https://doi.org/10.1371/journal.pone.0226207

Hinke, J. T., & Trivelpiece, W. Z. (2011). Daily activity and minimum food requirements during winter for Gentoo penguins (Pygoscelis papua) in the South Shetland Islands, Antarctica. *Polar Biology*, *34*(10), 1579–1590. https://doi.org/10.1007/s00300-011-1018-x

Lascara, C. M., Hofmann, E. E., Ross, R. M., & Quetin, L. B. (1999). Seasonal variability in the distribution of Antarctic krill, Euphausia superba, west of the Antarctic Peninsula. *Deep Sea Research Part I: Oceanographic Research Papers*, *46*(6), 951–984.

Meyer, B. (2012). The overwintering of Antarctic krill, Euphausia superba, from an ecophysiological perspective. *Polar Biology*, *35*(1), 15–37. https://doi.org/10.1007/s00300-011-1120-0

Strycker, N., Wethington, M., Borowicz, A., Forrest, S., Witharana, C., Hart, T., & Lynch, H. J. (2020). A global population assessment of the Chinstrap penguin (Pygoscelis antarctica). *Scientific Reports*, *10*(1), Article 1. https://doi.org/10.1038/s41598-020-76479-3

Warwick-Evans, V., Downie, R., Santos, M., & Trathan, P. N. (2019). Habitat preferences of Adélie Pygoscelis adeliae and Chinstrap Penguins Pygoscelis antarctica during pre-moult in the Weddell Sea (Southern Ocean). *Polar Biology*, *42*(4), 703–714. https://doi.org/10.1007/s00300-019-02465-9

Williams, T. D. (1995). *The Penguins: Spheniscidae*. Oxford University Press.

Youngflesh, C., Jenouvrier, S., Hinke, J. T., DuBois, L., St. Leger, J., Trivelpiece, W. Z., Trivelpiece, S. G., & Lynch, H. J. (2018). Rethinking "normal": The role of stochasticity in the phenology of a synchronously breeding seabird. *Journal of Animal Ecology*, *87*(3), 682–690. https://doi.org/10.1111/1365-2656.12790

Zuev, V. V., Borovko, I. V., Krupchatnikov, V. N., & Savelieva, E. S. (2020). Influence of the Temperature of the Lower Subtropical Stratosphere on Antarctic Polar Vortex Dynamics. *Atmospheric and Oceanic Optics*, *33*(6), 708–711. https://doi.org/10.1134/S1024856020060160

Zuev, V. V., & Savelieva, E. (2022). Antarctic Polar Vortex Dynamics Depending on Wind Speed Along the Vortex Edge. *Pure and Applied Geophysics*, *179*(6–7), 2609–2616. https://doi.org/10.1007/s00024-022-03054-4

Appendices.

Appendix 2.1.

Camera locations

Table S.2.1.1: Details on the camera codes used on this study (including location, season and number of images available) for each species. The camera codes used here are in compliance with those used by the MAPPPD project (www.penguinmap.com; Humphries et al., 2017). Abbreviations A.P (Antarctic Peninsula), F./M. (Falklands/Malvinas), S.G. (South Gerogia), S.Sh. (South Shetland Islands), W.S. (Weddell Sea)

Species	Camera code	Colony name	Latitude	Longitude	Number of images	First season studied	Last season studied
Adélie	BROWb	Brown Bluff, A.P.	-63.521	-56.889	13729	s14-15	s19-20
	HEROa	Heroina Island, W.S.	-63.4	-54.6	6956	s15-16	s17-18
	LLANc	Copacabana/Llano Point, South Shetland Islands	-62.1763	-58.4485	17111	s14-15	s19-20
	LLANd		-62.1763	-58.4485	8551	s17-18	s19-20
	LLANe		-62.1768	-58.4489	18887	s13-14	s18-19
	LLANf		-62.1768	-58.4489	11617	s13-14	s19-20
	LLANm		-62.1768	-58.4489	8547	s16-17	s19-20
	LLANp		-62.1759	-58.4461	17185	s14-15	s18-19
	LLANq		-62.1749	-58.4457	19617	s14-15	s19-20
	MADDa	Madder Cliffs, W.S.	-63.3	-56.48	4218	s16-17	s18-19
	PAULa	Paulet Island, W.S.	-63.58	-55.78	23676	s17-18	s20-21
	PETEd	Petermann Island, A.P.	-65.172	-64.136	36044	s12-13	s18-19
	SIGNb	Signy Island, South Orkney	-60.737	-45.657	8781	s15-16	s20-21
	SSISc	Saunders, S. Sandwich Is.	-57.805	-26.42	878	s14-15	s14-15
	YALOa	Yalour Islands, A.P.	-65.235	-64.158	28082	s11-12	S21-22
Adélie & Chinstrap	SIGNa	Signy Island, South Orkney	-60.737	-45.657	9731	s10-11	s20-21
Adélie & Gentoo	PETEe	Petermann Island, A.P.	-65.172	-64.136	27668	s12-13	s17-18
Chinstrap	AITCd	Aitcho Barrientos Is., S.Sh.	-62.406	-59.74	20402	s14-15	s19-20
	BAILa	Bailey Head, S.Sh.	-62.964	-60.504	18721	s12-13	s20-21
	BAILb	Bailey Head, S.Sh.	-62.964	-60.504	12005	s16-17	s20-21
	EMELa	Emeline Island, S.Sh.	-62.3918	-59.7928	172	s19-20	s19-20
	GASTa	Gaston Island, A.P.	-64.4877	-61.8358	10523	s14-15	s19-20
	GEORd	Georges Point, A.P.	-64.67	-62.621	18586	s15-16	s17-18
	GEORe	Georges Point, A.P.	-64.669	-62.6698	1842	s18-19	s19-20
	HALFa	Half Moon Island, S.Sh.	-62.595	-59.899	2135	s10-11	s11-12
	HALFb	Half Moon Island, S.Sh.	-62.595	-59.899	16861	s12-13	s20-21

	HALFc	Half Moon Island, S.Sh.	-62.596	-59.898	30794	s12-13	s19-20
	PTWIa	Point Wild, S.Sh.	-61.099	-54.859	2850	s13-14	s14-15
	PTWIb	Point Wild, S.Sh.	-61.099	-54.859	4277	s14-15	s15-16
	SIGNc	Signy Island, South Orkney	-60.737	-45.657	7858	s15-16	s20-21
	SPIGa	Orne Harbour, A.P.	-64.631	-62.555	27667	s12-13	s19-20
	SSISa	Saunders, S. Sandwich Is.	-57.808	-26.398	8729	s13-14	s15-16
	SSISb	Saunders, S. Sandwich Is.	-57.808	-26.398	7182	s13-14	s16-17
	TETRa	Tetrad Islands, A.P.	-63.9166	-60.733	5976	s16-17	s19-20
Chinstrap & Gentoo	BOOTc	Booth Island, A.P.	-65.0665	-64.0235	15799	s14-15	s18-19
Gentoo	AITCb	Aitcho Barrientos Is., S.Sh.	-62.4057	-59.7451	9968	s13-14	s18-19
	AITCc	Aitcho Barrientos Is., S.Sh.	-62.4078	-59.747	23328	s13-14	s19-20
	BEAVa	Beaver Island, F./M.	-51.8389	-61.2777	14404	s14-15	s16-17
	BLEAb	Bleaker Island, F./M.	-52.2	-58.85	17240	s17-18	s17-18
	BOOTa	Booth Island, A.P.	-65.067	-64.037	18189	s11-12	s20-21
	BOOTb	Booth Island, A.P.	-65.067	-64.022	23824	s12-13	s19-20
	BROWa	Brown Bluff, W.S.	-63.522	-56.889	2973	s10-11	s14-15
	BROWc	Brown Bluff, W.S.	-63.52	-56.893	4419	s14-15	s18-19
	BRYDa	Bryde Island East, A.P.	-64.889	-62.927	7379	s15-16	s19-20
	COOPc	Cooper Bay, S.G.	-54.783	-35.802	12073	s14-15	s19-20
	CUVEa	Cuverville, A.P.	-64.682	-62.621	34098	s11-12	s20-21
	CUVEb	Cuverville, A.P.	-64.682	-62.621	14135	s12-13	s18-19
	DAMOa	Damoy Point, A.P.	-64.8175	-63.519	12960	s13-14	s19-20
	DANCa	Danco Island, A.P.	-64.728	-62.5965	11666	s11-12	s20-21
	DANCb	Danco Island, A.P.	-64.728	-62.5965	14576	s12-13	s15-16
	GEORa	Georges Point, A.P.	-64.67	-62.669	27085	s12-13	s19-20
	GEORb	Georges Point, A.P.	-64.669	-62.6698	17671	s13-14	s19-20
	GODTa	Godthul, S.G.	-54.2	-36.3	11886	s15-16	s18-19
	GODTb	Godthul, S.G.	-54.2	-36.3	98382	s15-16	s15-16
	JOUGa	Jougla Point, A.P.	-64.826	-63.493	19345	s14-15	s19-20
	LLANa	Copacabana/Llano Point, South Shetland Islands	-62.1771	-58.4461	23764	s13-14	s19-20
	LLANb		-62.1771	-58.4461	22589	s13-14	s19-20
	LLANg		-62.1751	-58.4483	21503	s14-15	s19-20

	LLANh		-62.1751	-58.4483	8524	s17-18	s19-20
	LLANi		-62.1742	-58.4471	23742	s13-14	s19-20
	LLANj		-62.1742	-58.4471	22949	s13-14	s19-20
	LOCKa	Port Lockroy, A.P.	-64.8268	-63.4929	20681	s11-12	s19-20
	LOCKb	Port Lockroy, A.P.	-64.825	-63.492	39286	s12-13	s19-20
	MAIVa	Maiviken, S.G.	-54.249	-36.49	207	s14-15	s14-15
	MAIVb	Maiviken, S.G.	-54.249	-36.49	4675	s12-13	s13-14
	MAIVc	Maiviken, S.G.	-54.249	-36.49	37489	s12-13	s19-20
	MARTf	Isla Martillo, Patagonia	-54.9067	-67.3872	57589	s12-13	s17-18
	MIKKa	Mikkelsen Harbour	-63.902	-60.79	12010	s14-15	s19-20
	MOOTa	Moot Point, A.P.	-65.204	-64.075	3674	s14-15	s18-19
	NEKOa	Neko Harbour, A.P.	-64.844	-62.529	23161	s11-12	s19-20
	NEKOb	Neko Harbour, A.P.	-64.8448	-62.5296	6449	s11-12	s12-13
	NEKOc	Neko Harbour, A.P.	-64.843	-62.528	17573	s12-13	s19-20
	OCEAa	Ocean Harbour, S.G.	-54.3414	-36.2474	6783	s14-15	s15-16
	PETEa	Petermann Island, A.P.	-65.172	-64.137	29303	s11-12	s20-21
	PETEc	Petermann Island, A.P.	-65.171	-64.137	25926	s12-13	s18-19
	SANDa	Sandebugten, S.G.	-54.324	-36.34	6785	s14-15	s15-16
	SAUNa	Saunders, the Neck, F./M.	-51.306	-60.241	14181	s12-13	s19-20

References:

Humphries, G. R. W., Naveen, R., Schwaller, M., Che-Castaldo, C., McDowall, P., Schrimpf, M., & Lynch, H. J. (2017). Mapping Application for Penguin Populations and Projected Dynamics (MAPPPD): Data and tools for dynamic management and decision support. *Polar Record*, *53*(2), 160–166. https://doi.org/10.1017/S0032247417000055

Appendix 2.2.

Temperature validation.

Before using the temperature data from the in-built camera temperature logger I conducted several analyses to validate the accuracy and bias of our dataset against the temperature readings of a nearby meteorological station. I ground-truthed data from timelapse (TL) cameras SIGNa to SIGNe located on Signy Island (Appendix S2.1) against their corresponding measures from the meteorological station located at the British Antarctic Survey (BAS) research base on Signy Island (Polar Data Centre, U. K et al., 2021). It is worth noting that the camera readings correspond only to the 11AM 12AM and 1PM measurements, since those are the only measurements common to all cameras and years.

First I tested our dataset to determine if it is unbiased. To do this I derived several daily parameters (Mean, median, maximum temperature) in both datasets and tested them against each other. I plotted these daily values for a visual interpretation (plots S2.2.1, .2 and .3) as well as running linear models using the *lm* function in R (Table S2.2.1). In an ideal scenario of no bias across the temperature range the slope of the model should be 1 and the intercept zero.

Observing plots S2.2.1, .2 and .3 it is possible to see TL camera temperature estimates are biased across the range of temperatures. Mean and median temperature data derived from the camera is 1.8 and 1.6 degrees warmer than that of BAS logs (plots S2.2.1 and S2.2.2; Table S2.2.1). This is partly due to the TL dataset logging only midday temperatures rather than to a consistent bias across the temperature range since when I compare maximum temperatures the difference between datasets is reduced to 1 degree (plot S2.2.3; Table S2.2.1). That means the cameras I use are on average 1 degree warmer than the BAS readings. On the plus side.this bias is consistent thoughout the temperature range. This can be observed in S2.2.1, .2 and .3 and is confirmed by the slopes of the linear models, all of them very close to 1 (Table S2.2.1).

Table S2.2.1: Table showing the slope and Intercept of the three linear models ran to assess the bias of our timelapse camera dataset (from cameras SIGNa to SIGNe) compared to a professionally measured air temperature from the nearest British Antarctic Survey (BAS) meteorological station.

Plot	Dependent variable (y)	Independent variable (x)	Slope	Intercept
2.1	Daily Mean temperature SIGN	Daily Mean temperature BAS	0.999	1.807
2.2	Daily Median temperature SIGN	Daily Median temperature BAS	0.979	1.621
2.3	Daily Maximum temperature SIGN	Daily Maximum temperature BAS	1.009	1.050

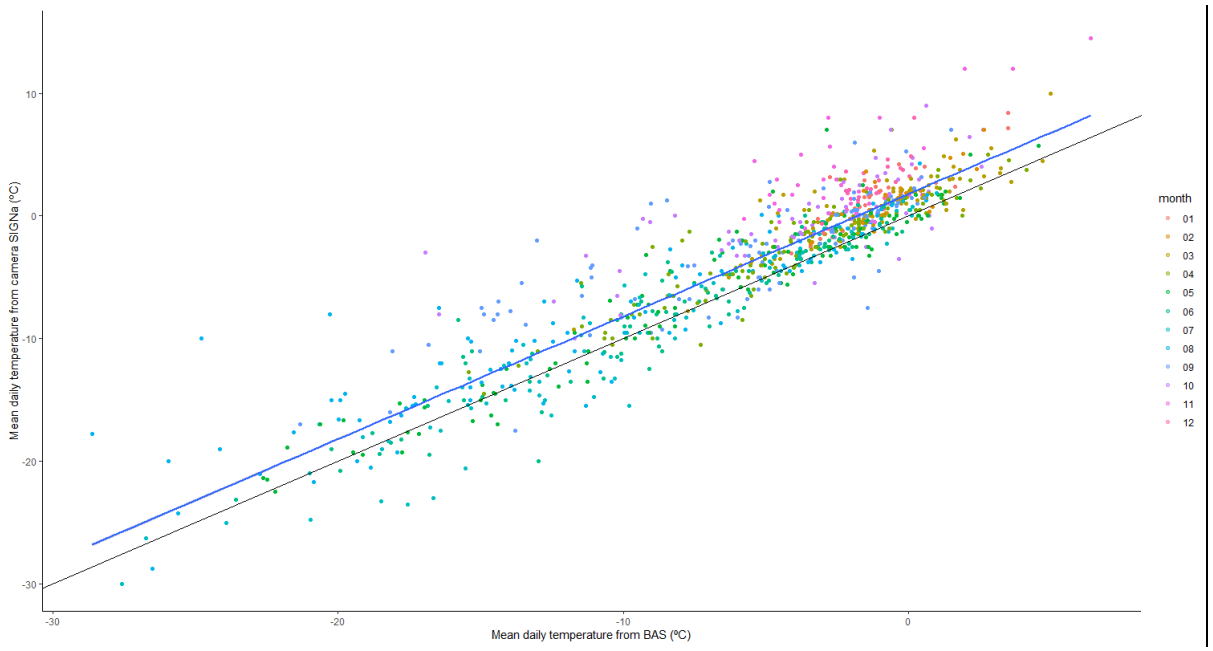


Figure S2.2.1: Daily mean temperature values from our camera at Signy Island (SIGNa) are plotted against equivalent readings from the meteorological station at the British Antarctic Survey (BAS) station on Signy Island. Each datapoint is coloured according to the month they were measured in. A blue line showing the linear model fil is plotted in the foreground. A black line with 0 intercept and slope 1 representing perfect equivalence between both datasets is plotted in the background for reference.

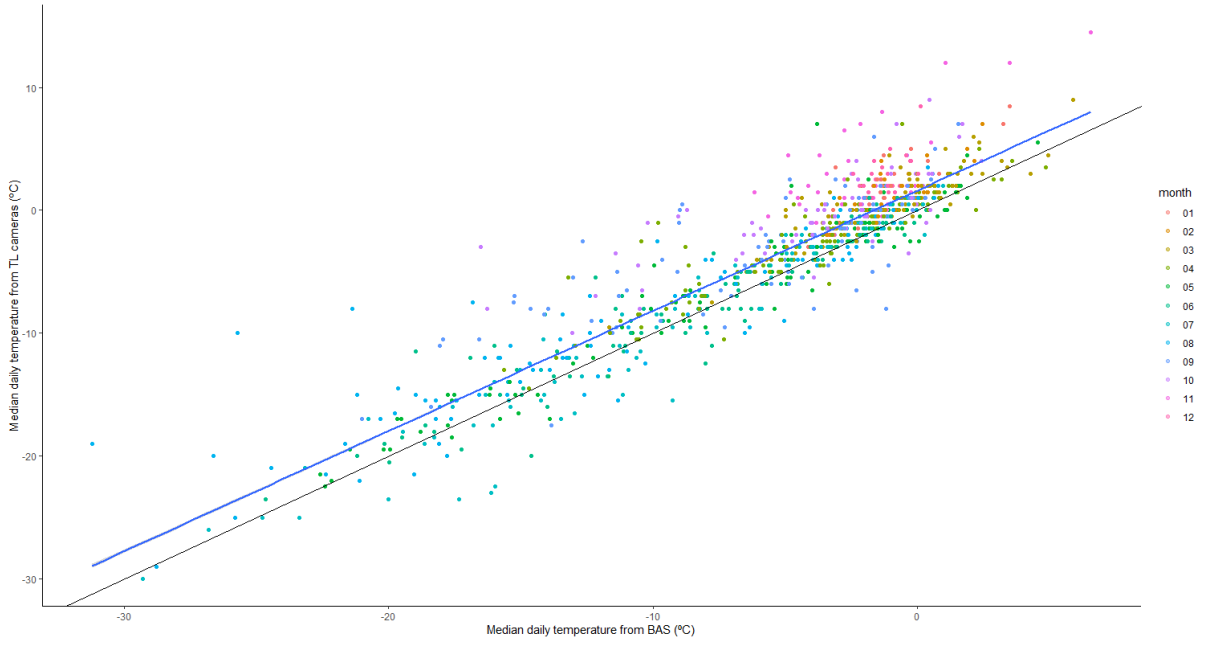


Figure S2.2.2: Daily median temperature values from our camera at Signy Island (SIGNa) are plotted against equivalent readings from the meteorological station at the British Antarctic Survey (BAS) station on Signy Island. Each datapoint is coloured according to the month they were measured in. A blue line showing the linear model fil is plotted in the foreground. A black line with 0 intercept and slope 1 representing perfect equivalence between both datasets is plotted in the background for reference.

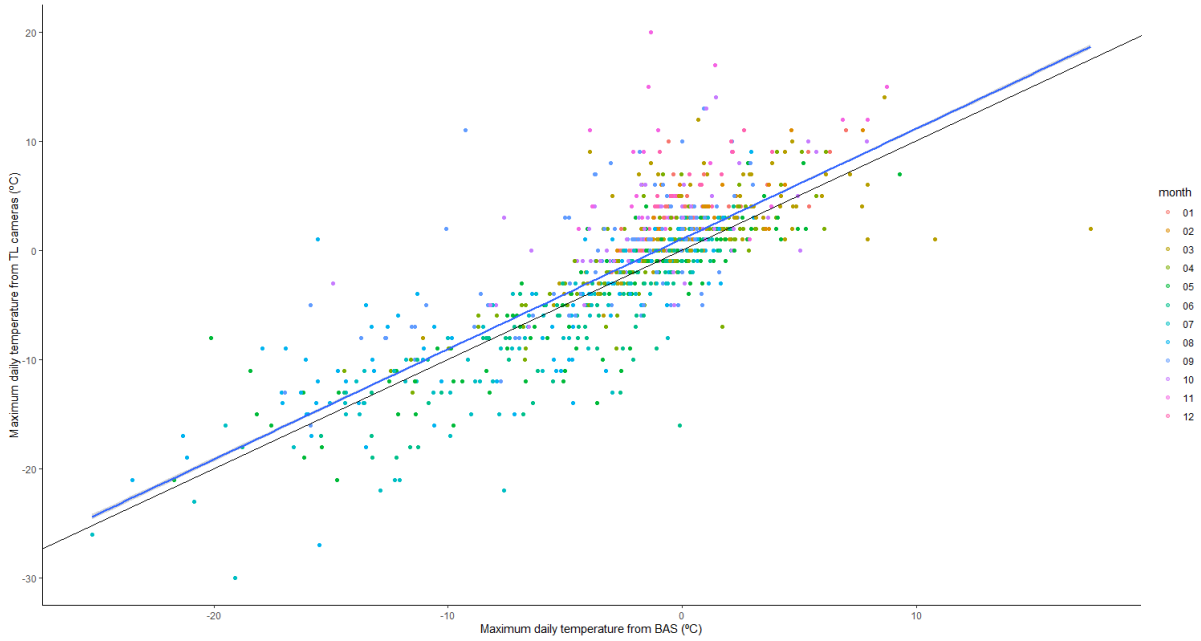


Figure S2.2.3: Daily maximum temperature values from our camera at Signy Island (SIGNa) are plotted against equivalent readings from the meteorological station at the British Antarctic Survey (BAS) station on Signy Island. Each datapoint is coloured according to the month they were measured in. A blue line showing the linear model fil is plotted in the foreground. A black line with 0 intercept and slope 1 representing an ideal equivalence between both datasets is plotted in the background for reference.

To test for accuracy I used both the monthly mean and median temperatures (Figures S2.2.4 and S2.2.5) since it is aggregated values I am going to be using in the phenology models. I calculated the average difference between measured TL values and those predicted by the model using the predict function in base R. The average deviation of the observed from the fitted values in the models are 1.427 for the median temperature and 1.455 for the mean temperature.

It is also worth noting that monthly means in warmer months are further biased in the warmer months as compared to the colder months (Figure S2.2.4). This is possibly due to the greater sensitivity of the mean to outliers compared to that of the median. I speculate the camera could have overheated on sunny days and contributed to increased temperature readings. In any case mean monthly averages are not consistently biased and therefore I will use the median monthly temperatures instead of the mean when conducting our analyses.

In conclusion, our temperature measurements can be used, with two caveats. First, our daily readings are 1.6 to 1.8 degrees warmer depending on whether I use the median or mean (respectively). Second, the accuracy is limited and any changes below ~1.4 degrees are within the measuring error of the camera.

References

Polar Data Centre, U. K, Convey, P., Geissler, P., Jobson, M., & Newsham, K. (2021). *Microclimate data from Jane Col, 2007-2016 [Version 2.0]*. NERC EDS UK Polar Data Centre. https://doi.org/10.5285/1BF0CFE7-A2E6-4C82-A0CD-D913876B6854

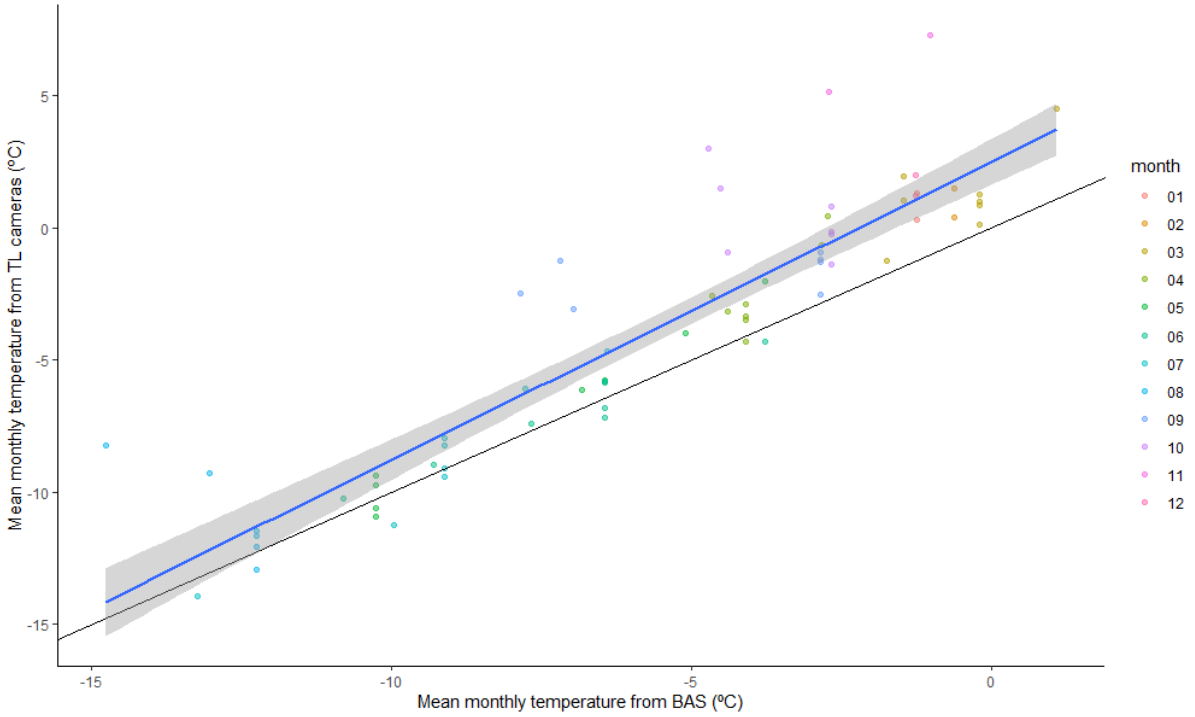


Figure 2.4: Monthly median temperature values from our camera at Signy Island (SIGNa) are plotted against the equivalent mean from the meteorological station at the British Antarctic Survey (BAS) station on Signy Island. Each datapoint is coloured according to the month they were measured in. A blue line showing the linear model fit is plotted in the foreground with its corresponding confidence interval. A black line with 0 intercept and slope 1 representing an ideal equivalence between both datasets is plotted in the background for reference.

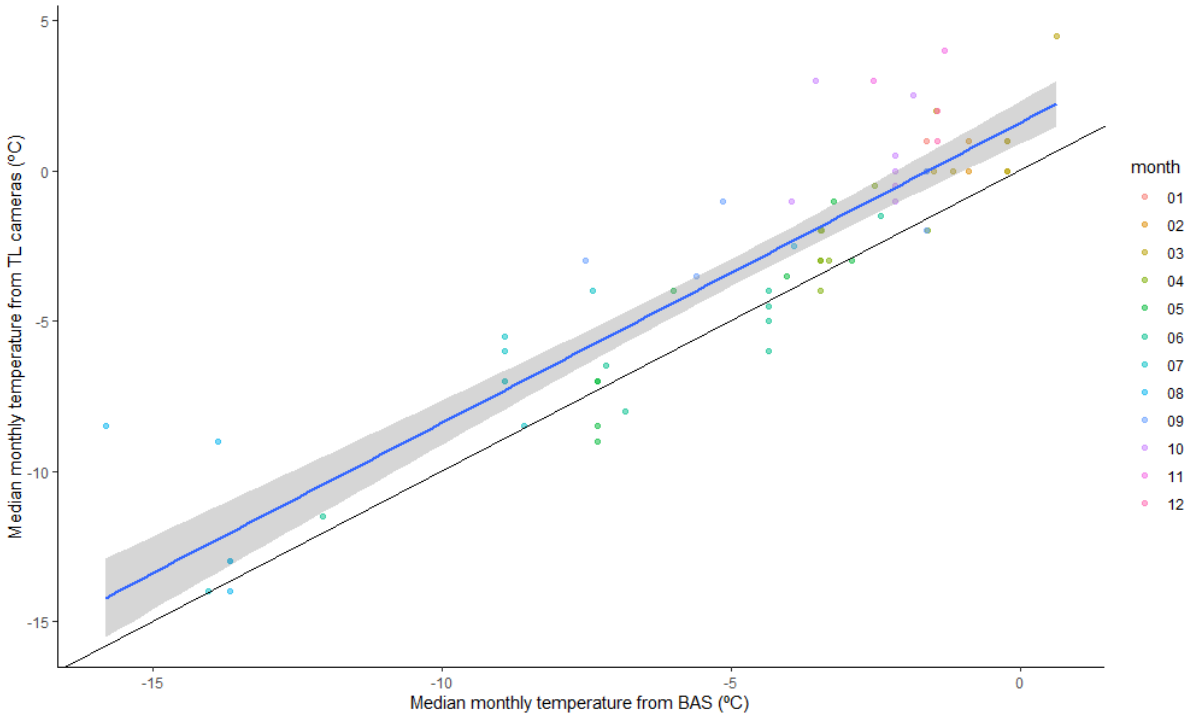


Figure 2.5: Monthly median temperature values from our camera at Signy Island (SIGNa) are plotted against the equivalent mean from the meteorological station at the British Antarctic Survey (BAS) station on Signy Island. Each datapoint is coloured according to the month they were measured in. A blue line showing the linear model fit is plotted in the foreground with its corresponding confidence interval. A black line with 0 intercept and slope 1 representing an ideal equivalence between both datasets is plotted in the background for reference.

Appendix 2.3.

Model selection.

A) Models for overall phenological shift

Table S2.3.1: Mixed models used to calculate rate of change rate in settlement date for each species over the last decade (Negative slope meaning shift to earlier dates). Models were performed using the *lmer* function within the *lme4* package in R. Settlement dates were tested against the continuous time variable year using camera position as a random effect. See Figure 2 in the main text for individual colony datapoints used in this model and their slopes.

Mixed models: Species settlement date ~ year. Random Effect: Colony			
Month	Slope (days/year)	Std. Error	t-value
Adelie (AP)	-1.020	0.207	-4.925
Chinstrap (AP)	-1.042	0.158	-6.578
Gentoo (AP)	-1.296	0.446	-2.692
Gentoo (Scotia Sea)	-2.024	1.183	-1.710

B) Models of temperature increase in the region

Table S2.3.2: Mixed models of monthly temperature increase over the last decade used to calculate warming rate in the study area. Models were performed using the *lme* function within the *nlme* package in R. Average midday temperature data for each month was tested against the continuous time variable year using camera position as a random effect. See figure 3 for individual colony slopes and Figure S2.2.2 for the monthly temperature datapoints used in these models.

Mixed models: Mean spring temperature ~ year. Random Effect: Colony				
Period	Slope (°C/year)	Std. Error	t-value	p-value
August	0.3764	0.05582	6.7428	<2e-16
September	0.4095	0.0857	4.778345	<2e-16
October	0.2038	0.05467	3.727369	3e-04
November	0.4474	0.04484	9.978066	<2e-16
Yearly	0.3407	0.07249	4.700722	<2e-16

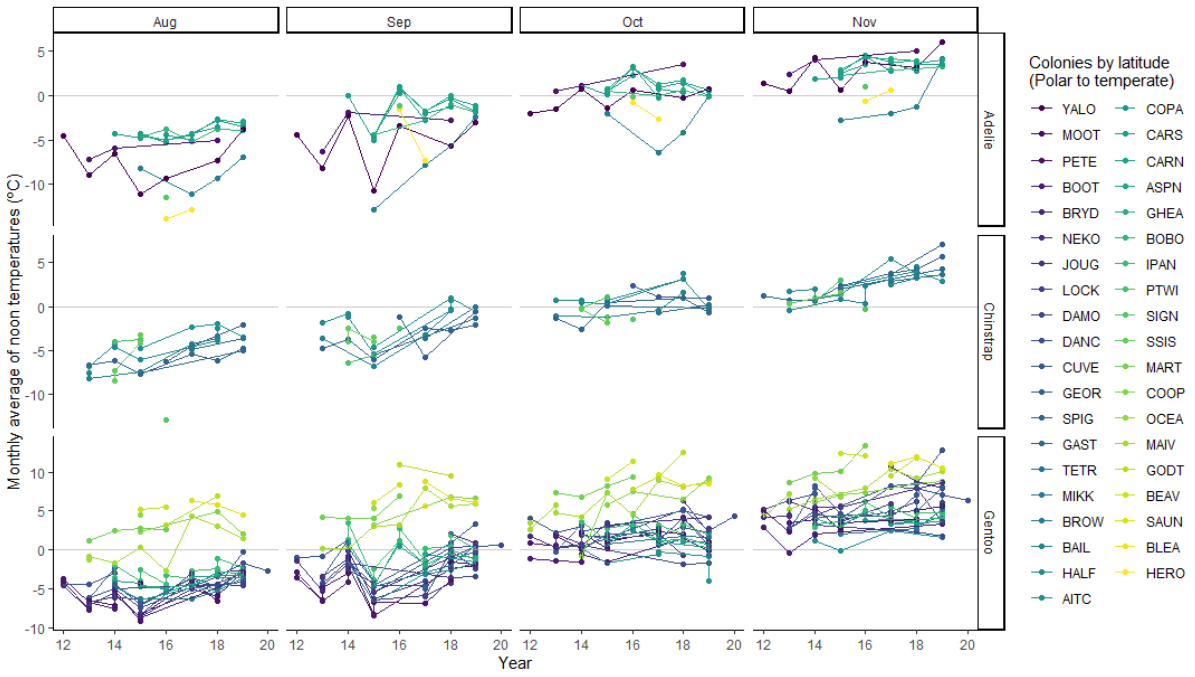


Figure S2.3.1: Monthly average estimates of direct temperature measurements from in-built camera thermometers by year. Data from each colony is joined by a line and coloured according to the latitude of the colony (Darker meaning more southern/polar).

C) Model selection for environmental variables related to phenological advance.

In order to select the best fit I ran all models containing latitude plus two environmental variables extracted from the in-built camera temperature loggers: *Median spring air temperature* and *proportion of days above zero in October*. It is worth noting that spring is considered September to November, the period during which penguins are arriving and settling at the colonies.

Days above zero in October will be calculated as the proportion of days in which the temperature reaches above 1.8 degrees (due to camera bias See Appendix S2.2 and Table S2.2.1 inside) at least at one point during the day. I chose October as the month of reference since it was the only of the three spring months with enough variability in all colonies, since southern colonies had most of their September at 100% freezing days and vice versa for November.

Models were built using only colonies at the Antarctic Peninsula since they are the only ones belonging to the latitudinal gradient (Figure 3 in main article). I computed the models using the lmer function of the lme4 package and they were compared using the *compare_performance* function in the *performance* package in R.

Models were selected by means of their AIC. If two models were within 2 points of AIC were considered to be equally explanatory, in such case the model with the fewer explanatory variables was selected.

Every selected model was tested for variable collinearity using the function *check_collinearity* and for normality using *check_model* in the *performance* package. The resulting models for these three species are robust regarding collinearity, normality of residuals and normality of random effects. All these models tested significantly better than their respective null models and all explain a sizable proportion of the variance as measured by the marginal and conditional R-squares of the three selected models.

Table S2.3.3: Adelie Penguin Model selection. Model selection was conducted including all variables of interest and dropping them off sequentially. Models are compared using AIC values although marginal and conditional R squared values are also shown to indicate the proportion of variance explained. If two models were within 2 points of AIC were considered to be equally explanatory.

Fixed effects			Random effects	AIC	Marg. Rsq	Cond Rsq
Median Spring Temp	September days above 0°C	Latitude	Colony	388.93	0.599	0.907
	September days above 0°C	Latitude	Colony	395.088	-	-
Median Spring Temp		Latitude	Colony	393.135	-	-
		Latitude	Colony	395.357	-	-
Null model (No fixed effects)			Colony	404.660	-	-

Table S2.3.4 Chinstrap Penguin model selection. Model selection was conducted including all variables of interest and dropping them off sequentially. Models are compared using AIC values although marginal and conditional R squared values are also shown to indicate the proportion of variance explained. If two models were within 2 points of AIC were considered to be equally explanatory.

Fixed effects			Random effects	AIC	Marg. Rsq	Cond Rsq
Median Spring Temp	September days above 0°C	Latitude	Colony	212.144	0.662	0.752
	September days above 0°C	Latitude	Colony	225.826	-	-
Median Spring Temp		Latitude	Colony	214.287	-	-
		Latitude	Colony	224.537	-	-
Null model (No fixed effects)			Colony	236.461	-	-

Table S2.3.5: Antarctic Gentoo Penguin model selection: Model selection was conducted including all variables of interest and dropping them off sequentially. Models are compared using AIC values although marginal and conditional R squared values are also shown to indicate the proportion of variance explained. This only includes Gentoo colonies below latitude 60S.

Fixed effects			Random effects	AIC	Marg. Rsq	Cond Rsq
Median Spring Temp	September days above 0°C	Latitude	Colony	1041.907	-	-
	October days above 0°C	Latitude	Colony	1040.397	0.481	0.692
Median Spring Temp		Latitude	Colony	1041.690	-	-
		Latitude	Colony	1049.174	-	-
Null model (No fixed effects)			Colony	1064.216	-	-

Appendix 2.4.
Colonies around the Scotia Sea.

Equivalent graphs to the Antarctic Peninsula plots on the main article. Figure S2.4.1 depicts the variation in settlement date across the years of study and figure S2.4.2 shows their variation regarding median spring air temperature.

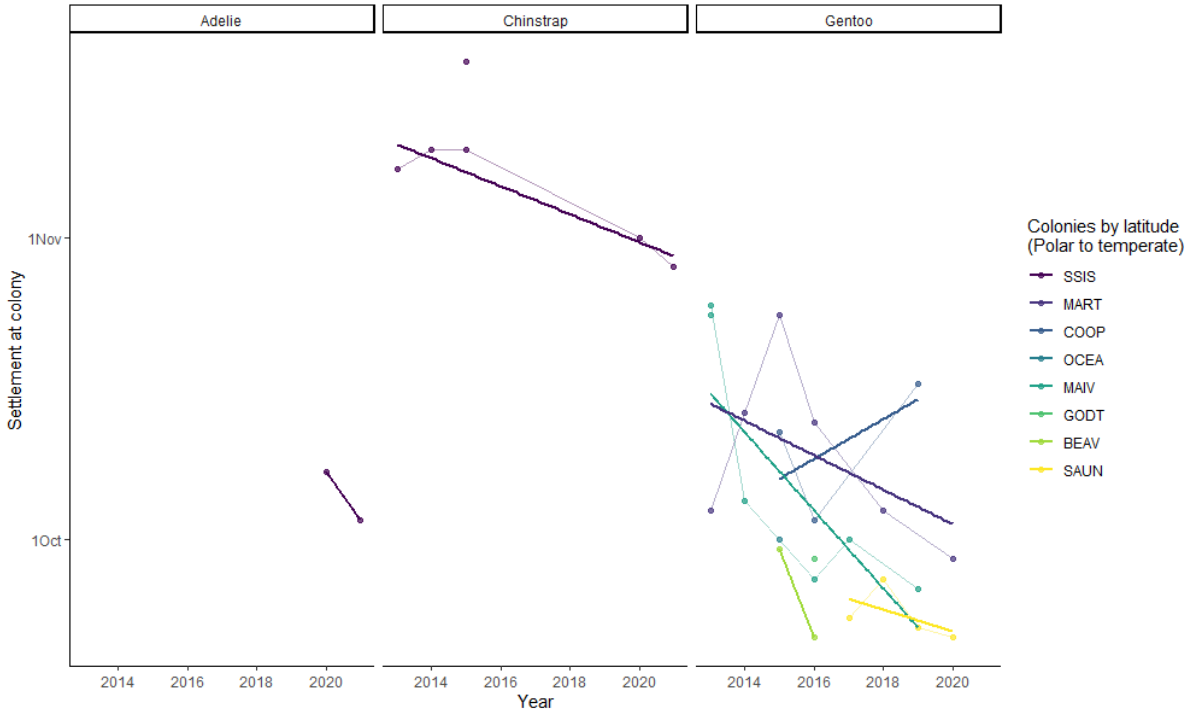


Figure S2.4.1: Time series for the settlement date as estimated from Antarctic monitoring cameras for each species through the period of study. Settlement data for each camera is overlaid with their respective regression lines to ease interpretation and coloured according to their latitude from higher -more polar- latitudes (darker) to lower -more temperate- latitudes (brighter).

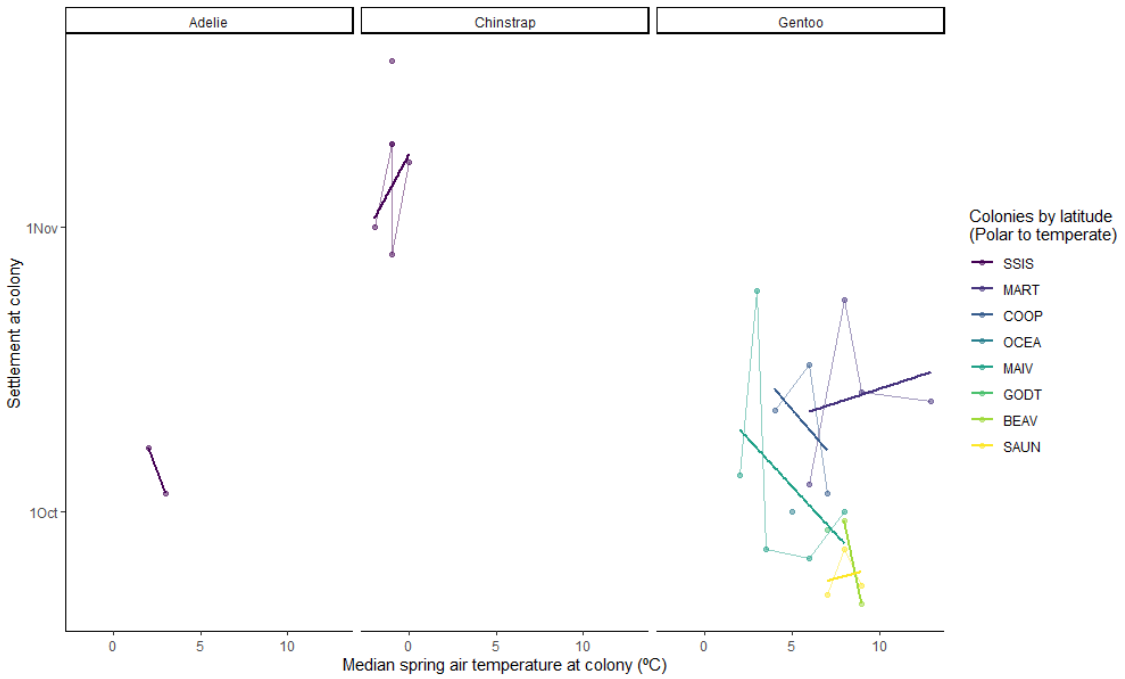


Figure S2.4.2: Estimated settlement date by median spring air temperature for all cameras present at colonies around the Scotia Sea. Points belonging to the same camera are linked together and a linear regression is shown for each colony

to ease interpretation. Regressions as well as linked datapoints are coloured by colony according to their latitude from more polar (darker) to more temperate (brighter).

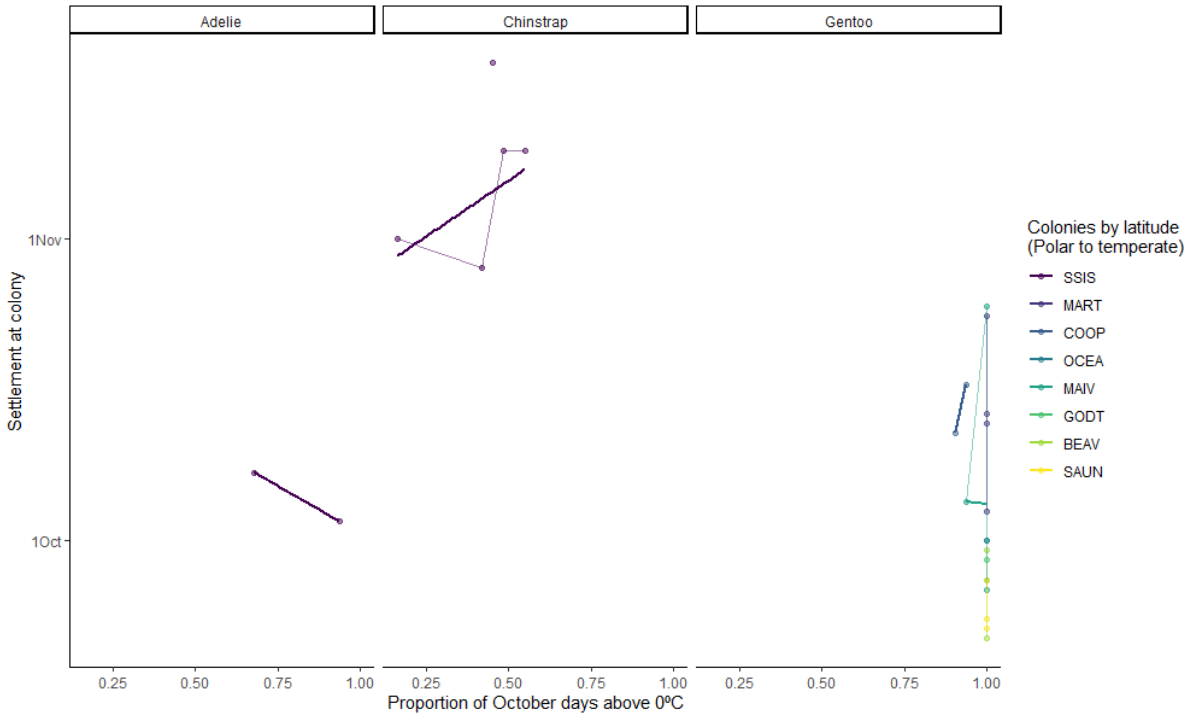


Figure S2.4.3: Estimated settlement date in relation to the amount of freezing days in October for all cameras present at colonies around the Scotia Sea. Points belonging to the same camera are linked together and a linear regression is shown for each colony to ease interpretation. Regressions as well as linked datapoints are coloured by colony according to their latitude from more polar (darker) to more temperate (brighter).

Appendix 2.5.
Population trends

Nest count for Adelie (Figure S2.5.1), Chinstrap (Figure S2.5.2) and Gentoo Penguins (Figure S2.5.3). Data extracted from the MAPPPD database is shown for all the colonies whose phenology is studied in the main paper.

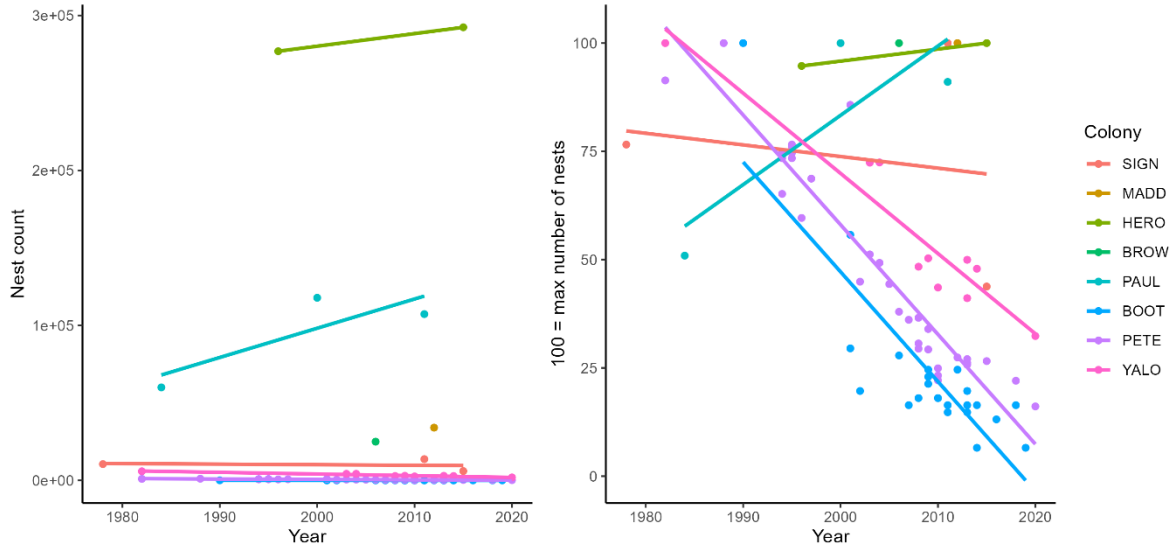


Figure S2.5.1: Left) Total nest count for all Adelie colonies in this study present in the MAPPPD database. Right) Same nest count data standardized to visualize trends.

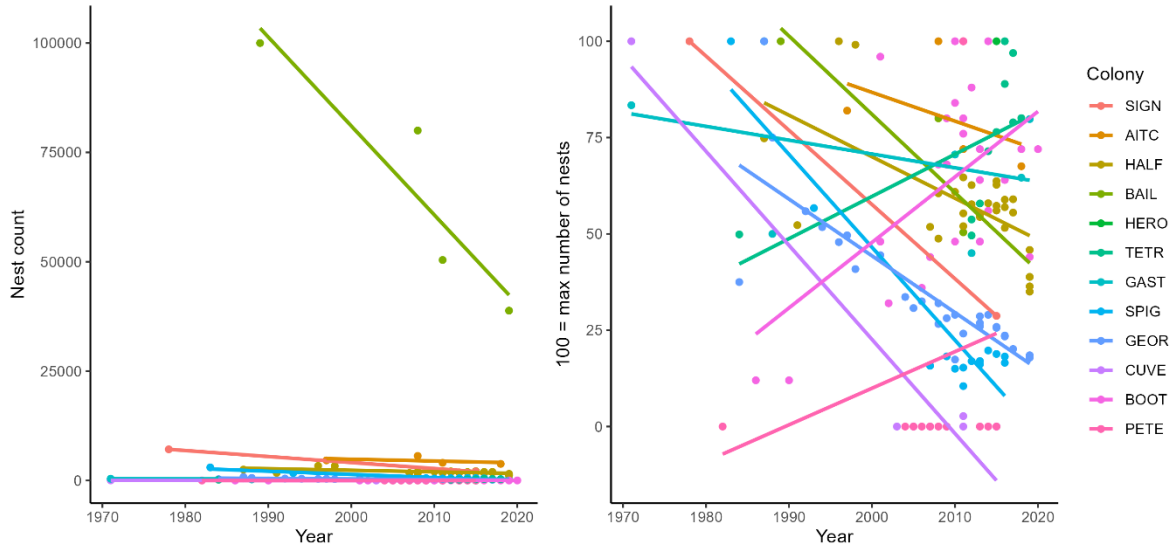


Figure S2.5.2: Left) Total nest count for all Chinstrap colonies in this study present in the MAPPPD database. Right) Same nest count data standardized to visualize trends.

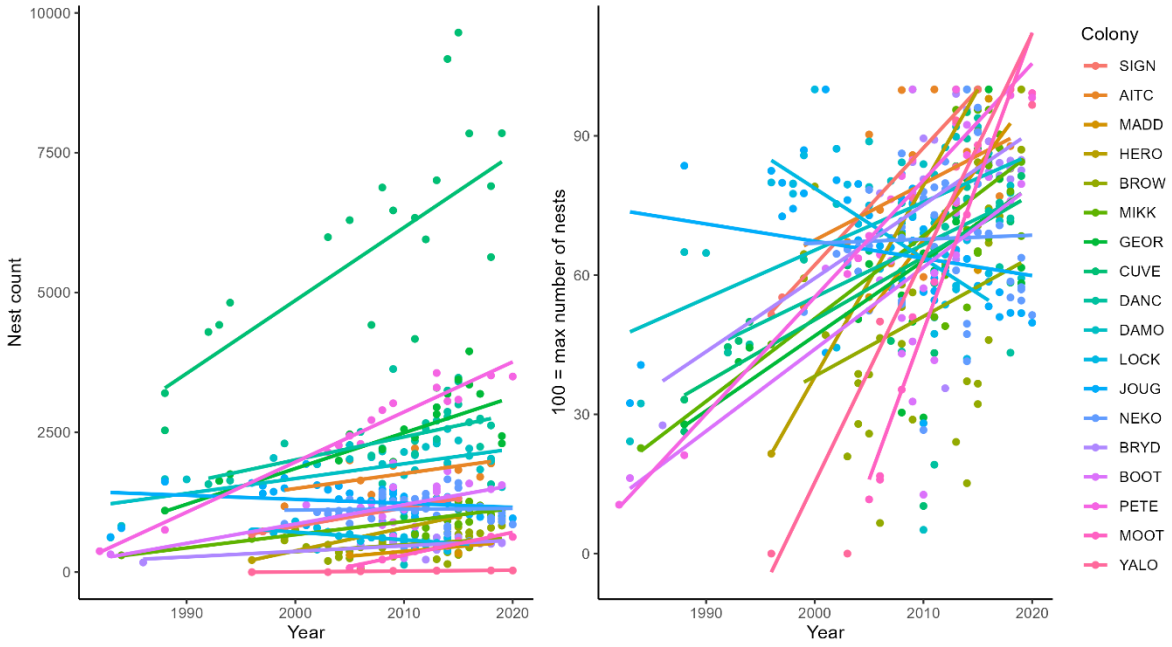


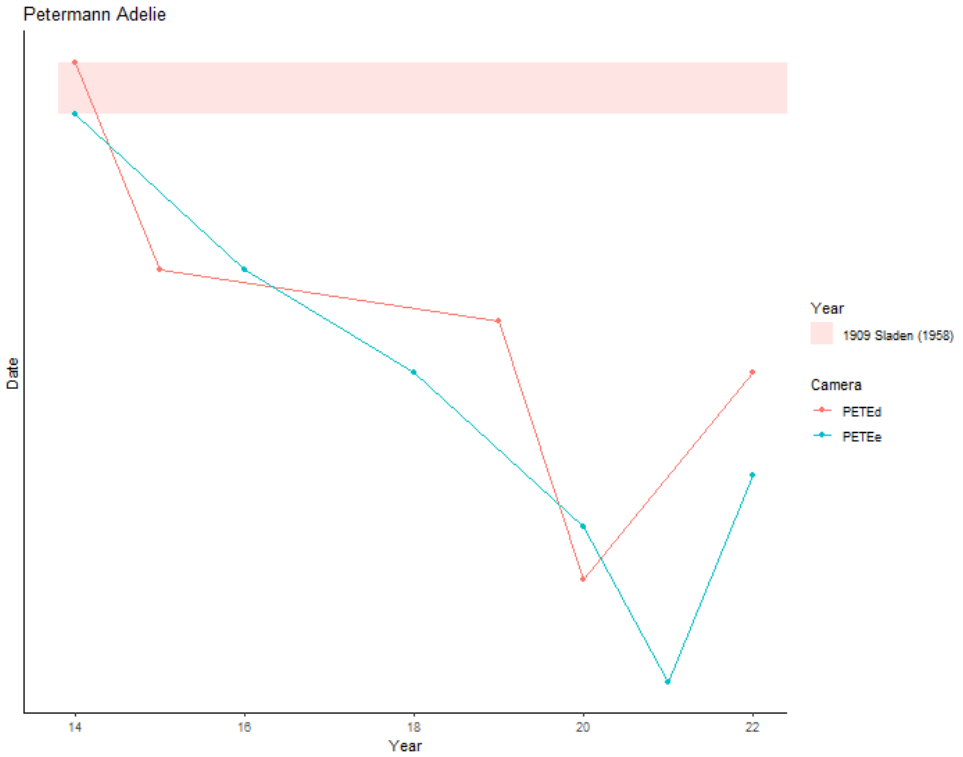
Figure S2.5.3: Left) Total nest count for all Gentoo colonies in this study present in the MAPPPD database. Right) Same nest count data standardized to visualize trends.

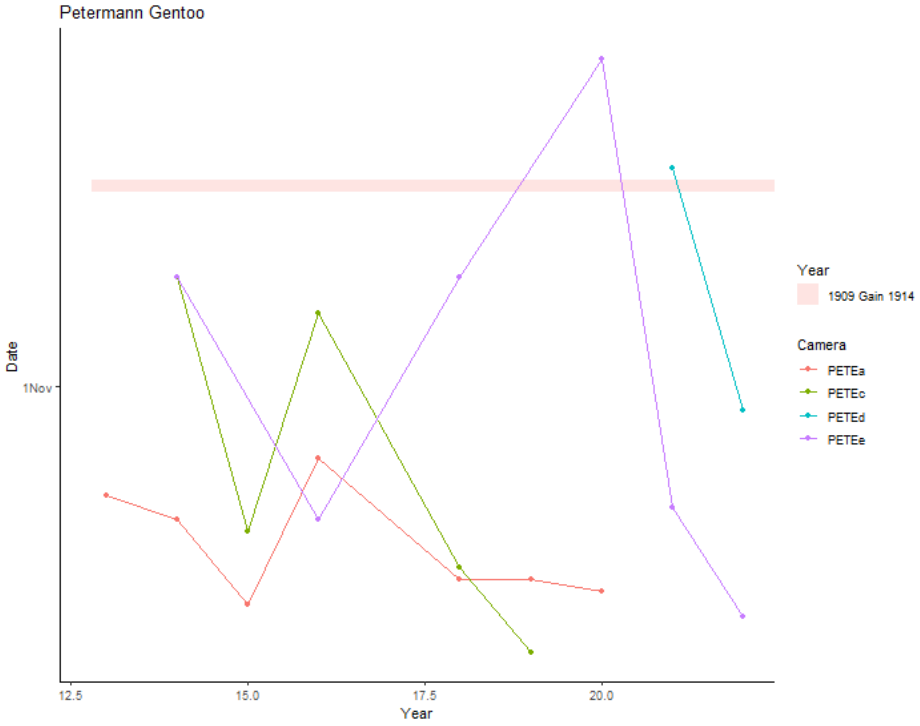
Appendix 2.6.
Settlement compared to historical arrival data

This appendix contains a comparison of our settlement data to all historical data regarding "return to the colony" as reviewed by Black (2016). There are not many records of arrival data in the bibliography and many of them do not coincide with our colonies and species of study. This has left us with a handful of comparisons per species, enough for an indicative overview on how this data compares to historical observations. In order to keep two more comparisons we have compared historical data from Laurie Island to our cameras at Signy and historical data for Chinstraps at King George to our settlement data at the Aitcho Islands.

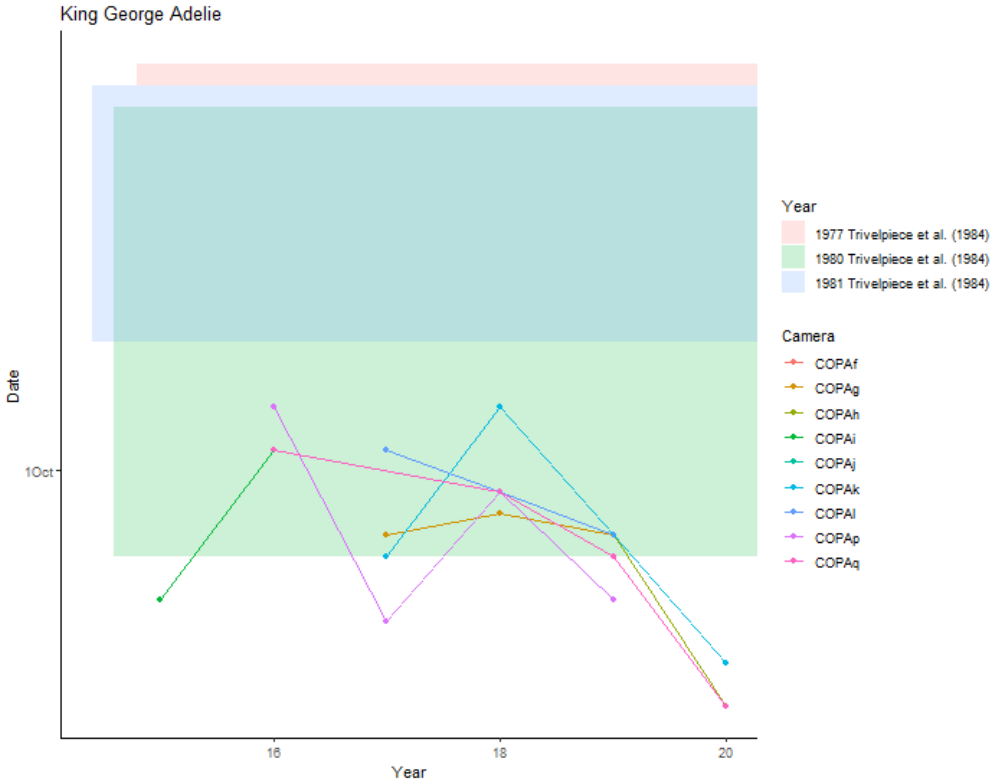
In all plots, settlement data used in this study is represented as dots joined by a line. Historical data is represented as tiles in the background covering the dates (y-axis) for which arrival has been described in the bibliography in that colony. The left-hand side of these tiles has been offset in order to allow better differentiation of periods and sources of data when there are several overlaid.

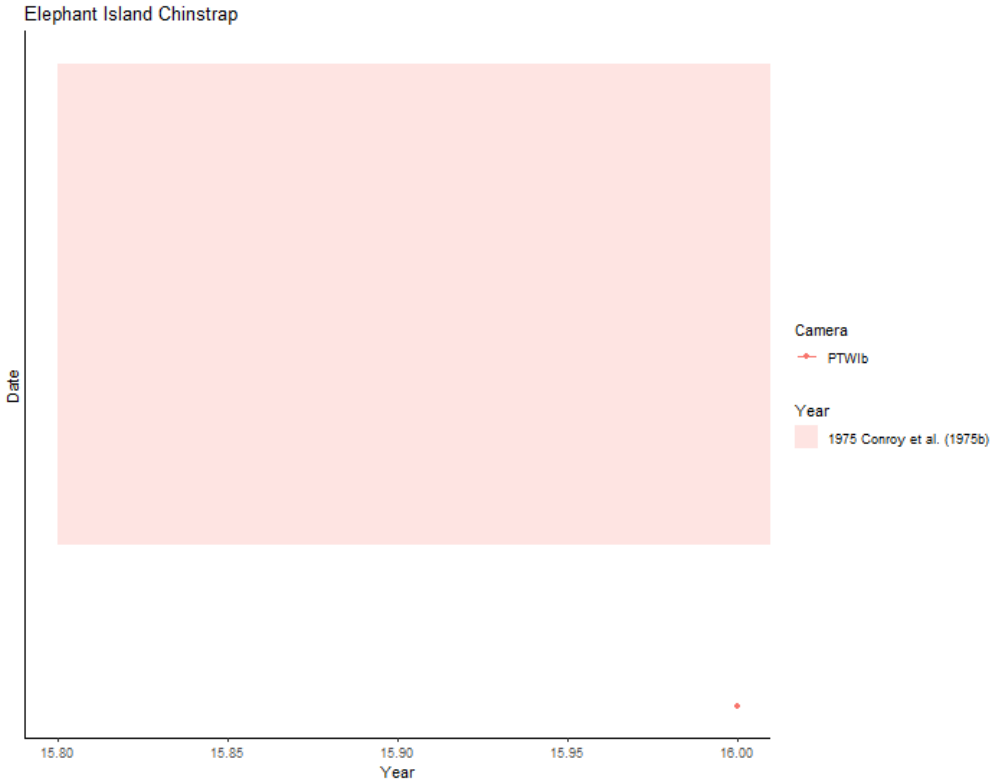
Western Antarctic Peninsula

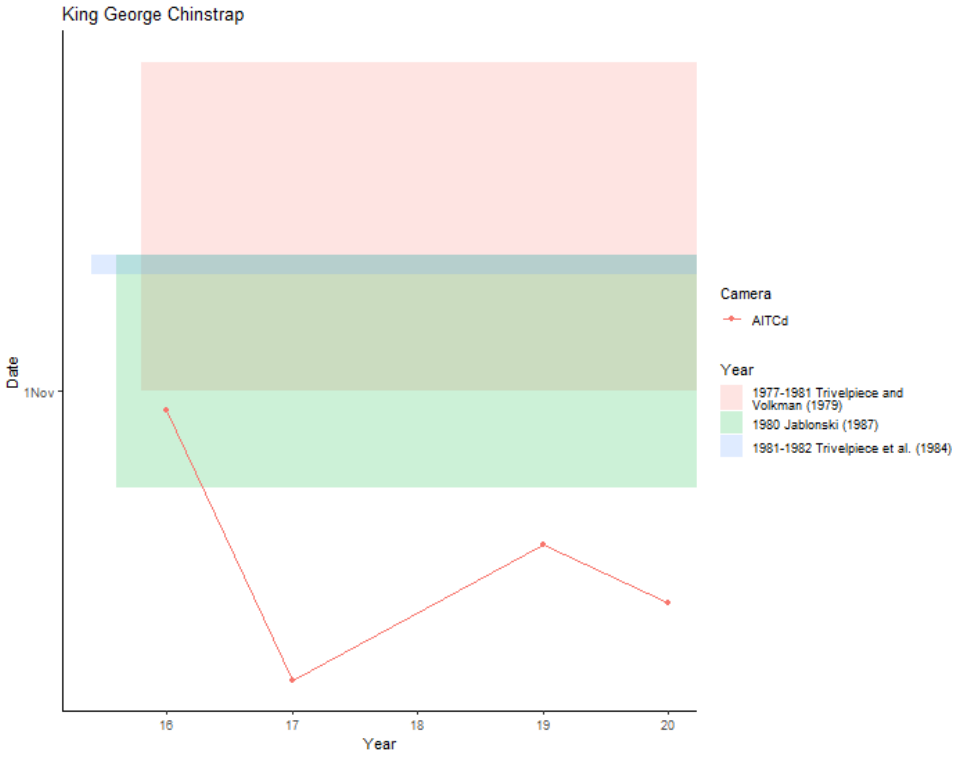


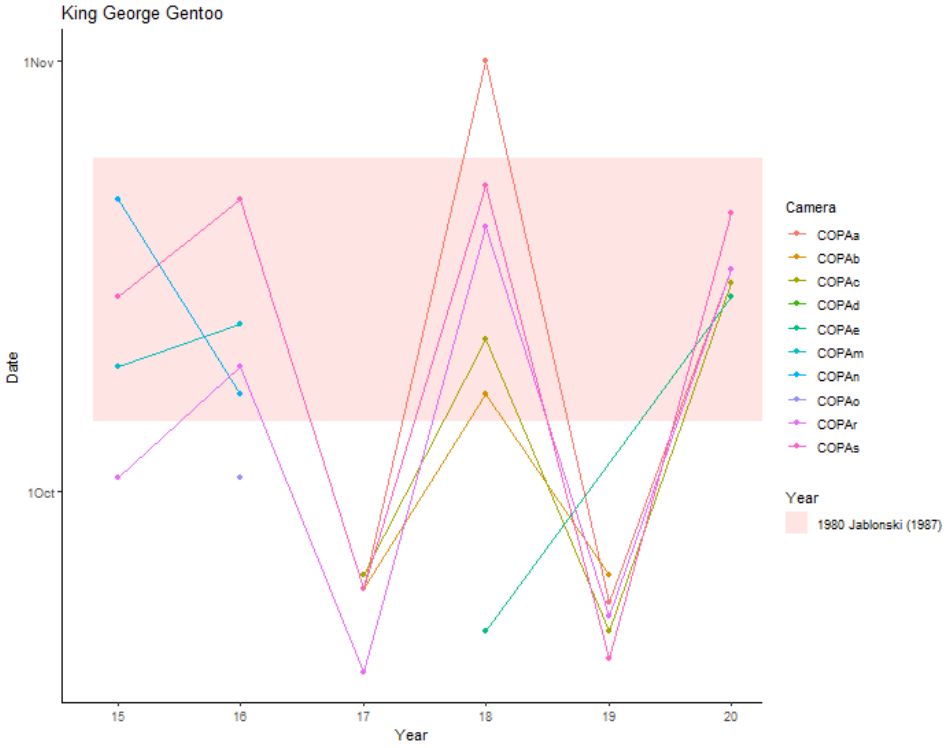


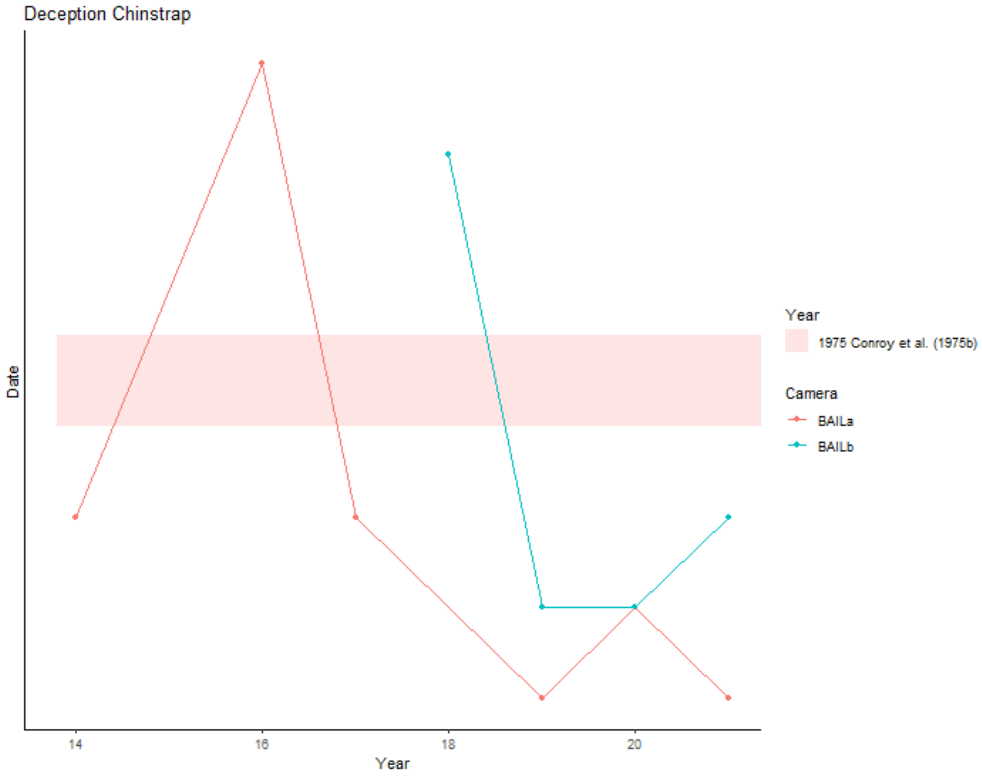
South Shetlands



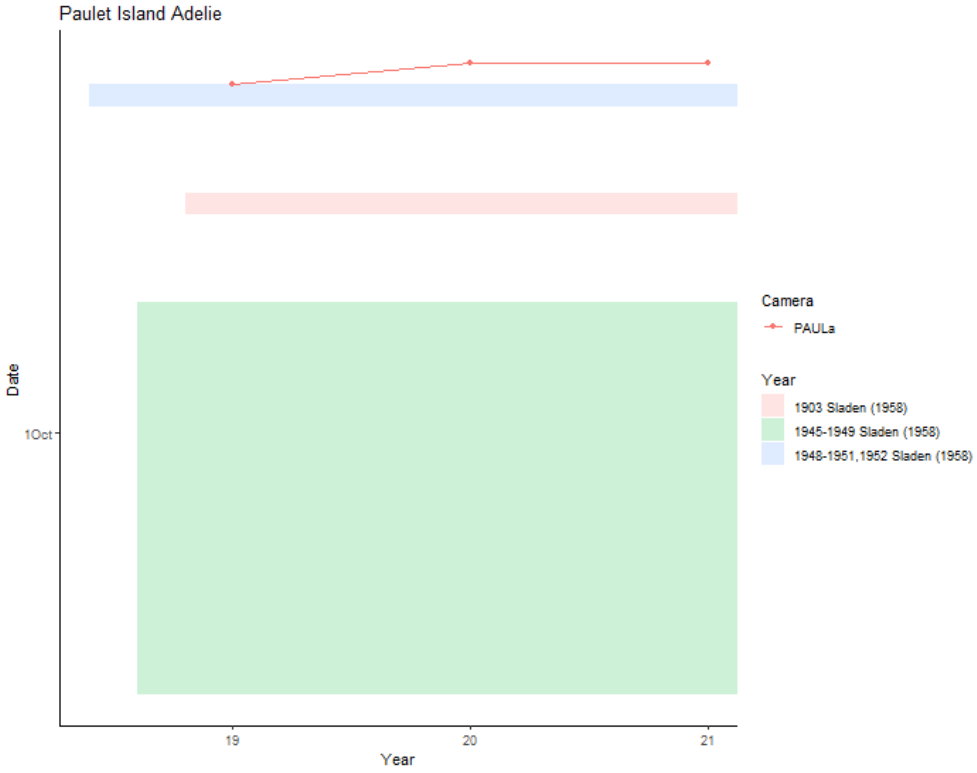

Elephant Island Chinstrap
Date
15.80
15.85
15.90
15.95
16.00
Year
Camera
PTWIb
Year
1975 Conroy et al. (1975b)


King George Chinstrap
Date
1Nov
16
17
18
19
20
Year
Camera
AITCd
Year
1977-1981 Trivelpiece and Volkman (1979)
1980 Jablonski (1987)
1981-1982 Trivelpiece et al. (1984)

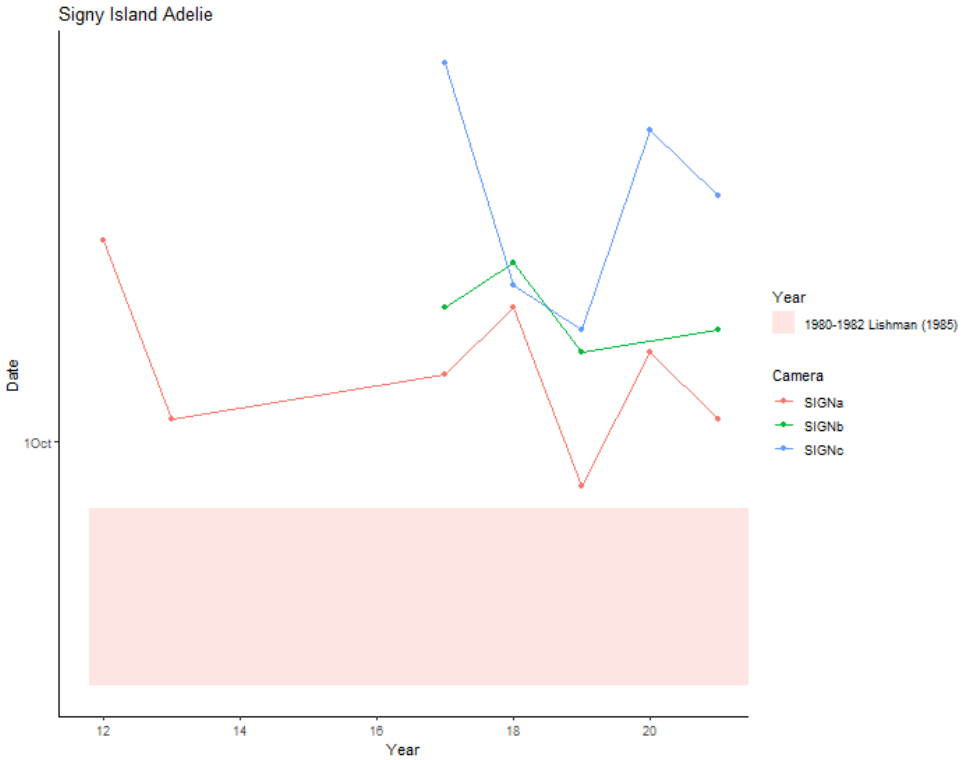

King George Gentoo
1Nov
1Oct
Date
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16
17
18
19
20
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COPAb
COPAc
COPAd
COPAe
COPAm
COPAn
COPAo
COPAr
COPAs
Year
1980 Jablonski (1987)

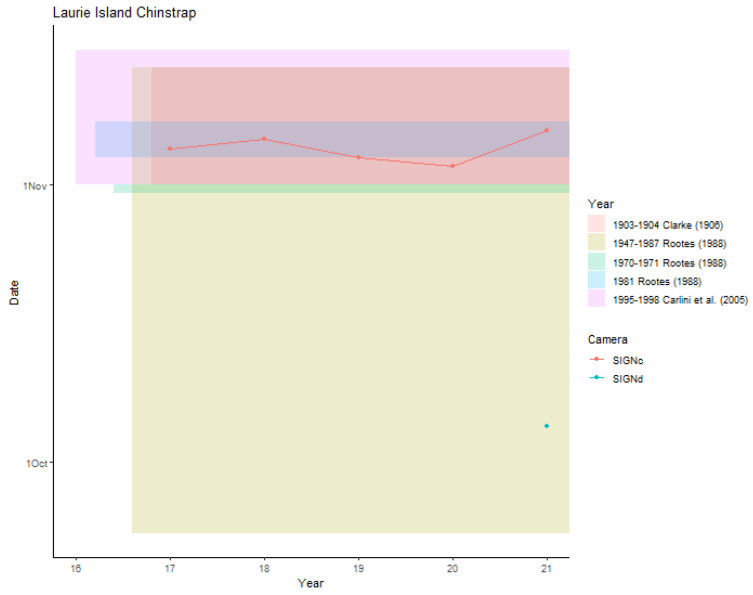

Deception Chinstrap
Date
14
16
18
20
Year
Year
1975 Conroy et al. (1975b)
Camera
BAILa
BAILb

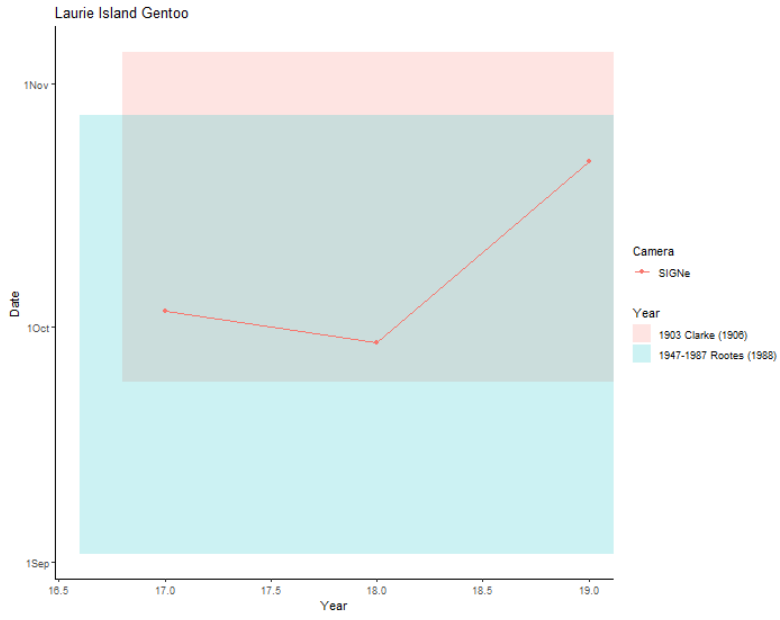
Weddell Sea



South Orkney







References:

Black, C. E. (2016). A comprehensive review of the phenology of Pygoscelis penguins. *Polar Biol*, 29.

Appendix 3.1. Data curation and Batch-checking tool

Figures S3.1.1 and S3.1.2 in the following pages showcase the use of the batch-checking tool built as part of the nest-tracking tool. Its purpose it is to verify whether curated colony codes are indeed those of the images previously uploaded to the zooniverse. The tool is intended to allow the researcher to perform this task quickly, in one gaze of the resulting plot. Each batch or group of images uploaded together for each folder name will result in a separate diagnostic plot (Figures S3.1.1 and S3.1.2). Each of these diagnostic plots are made up of 9 panes. The first seven panes show a random selection of images of different scorings of accuracy (comparing zooniverse coordinates with pengbot3000 AI estimation of '*penguiness*'). These images are overlayed with blue crosses (showcasing the location of raw coordinates annotated by volunteers) and red dots (the resized coordinates). The purpose of showing both coordinates is to check wether the images in each batch were indeed resized before uploading them to the zooniverse.

The eigth pane is a boxplot showing the scorings of accuracy of a selection of up to 20 images in that group/batch. The ninth pane shows the same data as a comparison between the overall pixel values in the output matrix of the model and the values at the volunteer-annotated coordinates.

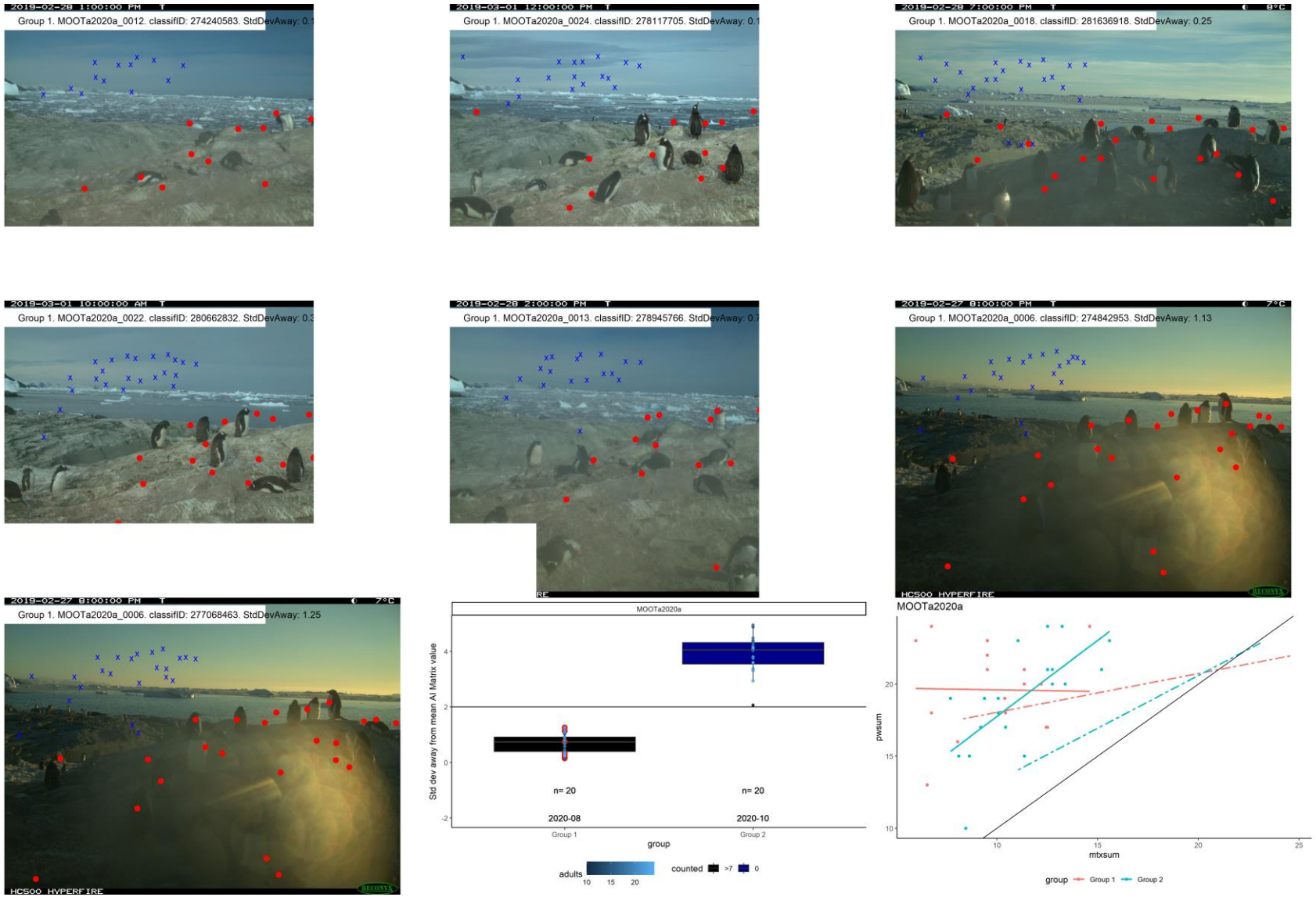


Figure S3.1.1: Diagnostic plot, output of the Batch-checking tool for the first batch of images uploaded as MOOTa 2020a to the Zooniverse on August 2020. Neither the raw coordinates nor the resized coordinates seem to correspond with the penguins in the images so probably this batch belongs toa misnamed folder of the same colony.

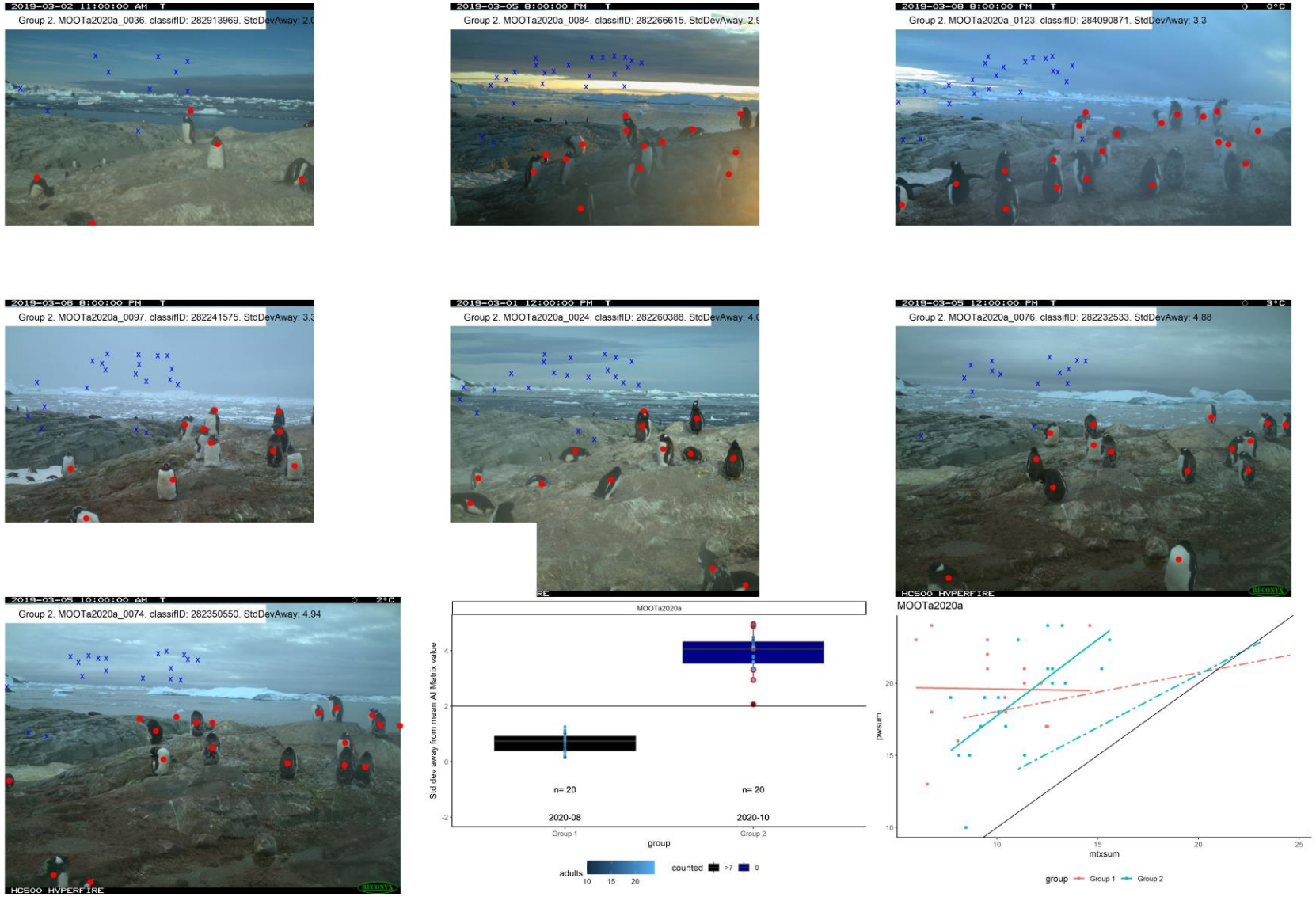


Figure S3.1.2: Diagnostic plot, output of the Batch-checking tool for the second batch of images uploaded as MOOTa 2020a to the Zooniverse on October 2020. Resized coordinate match adult locations quite well in the image, indicating this is the correct batch and that the correct coordinate are the resized ones (Red)

Appendix 3.2. Alignment Algorithm

The Alignment Algoritm was built in its entirety by Carlos Arteta. Here is his description of the Alignment process:

Given two image frames f_0 and f_1, typically of the same camera taken at different times, the goal of the image aligner is to compute a homography matrix H_01 that allows mapping frame f_1 onto f_0 such that any pixel in them corresponds to the same spatial location. This is achieved with the following steps:
1 - Determine points of interest in each frame, for example salient parts of the frames that may preserve their distinctive appearance under image changes such as illumination. The keypoint extraction is done using the feature extractor ORB (Rublee et al., 2011).
2 - Discard points of interest that correspond to penguins, which are expected to move significantly between frames and cannot be considered reference points between images. Penguin keypoints are discarded using the penguin density maps. That is, any keypoint extracted from an image region where the penguin density is greater than 0 is discarded.
3 - Each keypoint extracted is processed to compute a keypoint descriptor, a vector that encodes the appearance of the image location. This step is also done with ORB (Rublee et al., 2011), known as an integrated keypoint detection and description.
4 - The set of keypoints from each frame is matched to establish correspondences between the images. The process of matching is done using the RANSAC algorithm (Fischler & Bolles, 1981), a robust method to find the parameters of a mathematical model (homography in this case) based on data that may have outliers (i.e. keypoints that matched incorrectly). To find the homography, RANSAC iteratively samples a subset of the keypoints and finds a homography based on those. Then, it evaluates the set of keypoint matches that supports such a homography. By repeating this process, RANSAC determines the homography that has the largest support on the data and discards outliers.

Once the homography H_01 is computed, it can be used to align any two locations in the frames. This includes taking a nest diagram drawn in either of the frames, and projecting it onto the other frame.

References:

Fischler, M. A., & Bolles, R. C. (1981). Random sample consensus: A paradigm for model fitting with applications to image analysis and automated cartography. *Communications of the ACM*, *24*(6), 381–395.

Rublee, E., Rabaud, V., Konolige, K., & Bradski, G. (2011). ORB: An efficient alternative to SIFT or SURF. *2011 International Conference on Computer Vision*, 2564–2571. https://ieeexplore.ieee.org/abstract/document/6126544/

Appendix 3.3. Rationale for filtering annotations

I realised that false positives are most often due to only one of the volunteers annotating the picture incorrectly (Figure S3.3.1). In order to account for this I introduced a filter that requires at least two different volunteers to mark a chick or an egg in a particular instance order for that instance to be considered for verification.



Figure S3.3.1: Examples of four images where one volunteer has incorrectly annotated multiple adults as chicks (Marked with a C) or eggs (Marked with an E) in the early season at George's Point. The different colours of the E and C marks indicate volunteer ID within the annotations of each image.

Unfortunately, this filtering process eliminates true positives, especially in the first days after chicks hatch, when they are smaller and much more difficult to detect (Figure S3.3.2).



Figure S3.3.2: Examples of two images where some valid annotations have been lost due to the filtering requirement for two volunteers to annotate within the nest area. Chick annotation marks (Marked with a C) and egg marks (Marked with an E) are displayed in different colours to indicate volunteer ID within the annotations of each image.

Another common source of false positives is the early season. The most common occurrence is for volunteers to annotate adults as chicks if they look smaller because they are further away (Figure S3.3.3). I decided to filter out any annotations ocurring before settlement (See chapter 2).



Figure S3.3.3: Examples of two images where various volunteers have incorrectly annotated the presence of chicks (Marked with a C) and eggs (Marked with an E) in the early season at George's Point. The different colours of the E and C marks indicate volunteer ID within the annotations of each image.

Mistaking far away penguins for chicks is a common mistake throughout the season, unfortunately it is not possible to do much about that without dropping the top nests. I did not do this in this study in order to maintain a bigger sample size (Figure S3.3.4).



Figure S3.3.4: Examples of two images where various volunteers have incorrectly annotated far-away adults as chicks (Marked with a C) in the mid season at George's Point. The different colours of the E (mark for eggs) and C marks indicate volunteer ID within the annotations of each image.

Other common source of false positives is for volunteers to annotate chicks and eggs on adult individuals that are tightly on their nests despite no chicks or eggs are visible (Figure S3.3.5). This is a common ocurrece during egg laying. Since out-of-nest adults are not marked as chicks or eggs I understand that volunteers are marking what they think it is below those adults. To accommodate this I built an option within the verification tool to include a lower and an upper date limit to reliable annotations in each season. The researcher can include and change these boundary dates as they see fit in order to view the images during the verification process.. This possibly indicates the need to emphasise the tutorials.



Figure S3.3.5: Examples of two images where various volunteers have annotated adults on nests as chicks (Marked with a C) or eggs (Marked with an E) at George's Point. It is likely they are marking what they think it is underneath the adults since they have only marked the adults whenever they are on nests. In the Right image the volunteer has annotated two chicks on each nest, possibly because they know these penguins have two chicks per nest. In the left image the volunteer has annotated as chicks all adults standing and as eggs all adults laying down. The different colours of the E and C marks indicate volunteer ID within the annotations of each image.

Appendix 4.1. Snow detection.

In order to extract amount of snow from the images I derived three metrics of pixel values from each image throughout the whole season: Median, mean and mode. I do this for six different sections of the image: whole image, mid and lower third of the image as well as the left, mid and right third of the image. For each combination of region and metrics I calculate a smoothed quadratic spline (using the *smooth.spline* function from the 'stats' package in R).

The original intention was to try to find a metric for snow presence but that resulted impossible. Instead I could only find a clear consistent signal across colonies and seasons, a clear drop in pixel value after the winter snow thaws in spring/summer. This is because after all the snow melts the soil stays wet (and therefore darkened) for many days before drying up and progressively regain luminosity (Figure S4.1.1). I will then use this estimated thaw date to calculate the amount of days of snow persistence since the penguins settled.

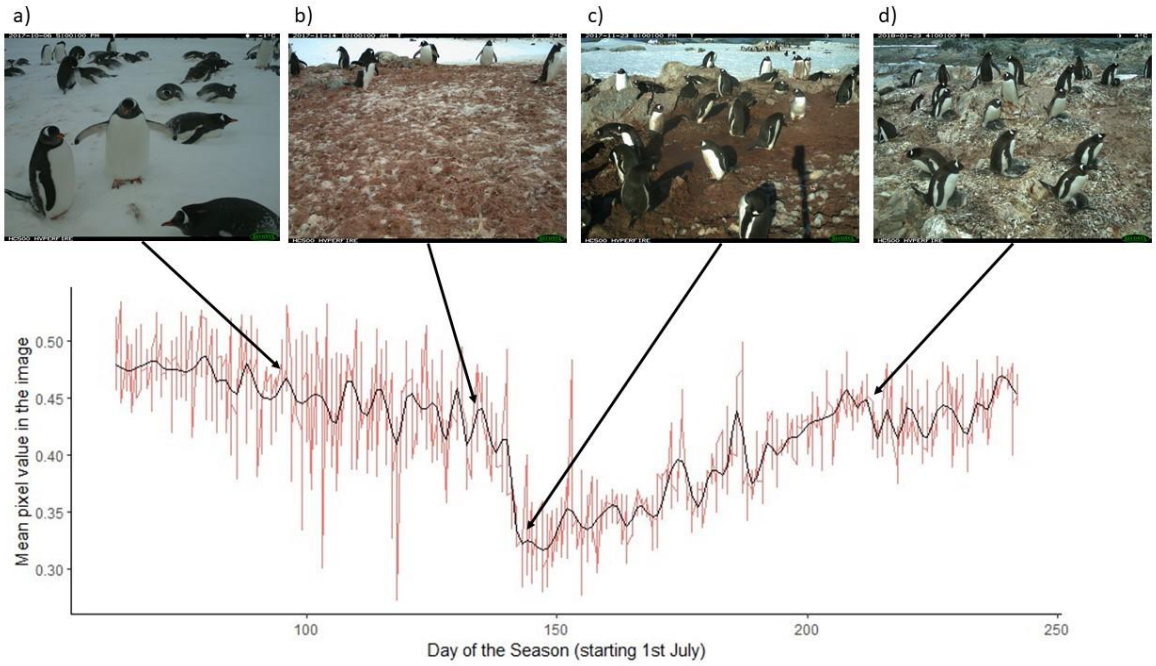


Figure S4.1.1: Example of one of the metrics (mean) used to estimate the winter snow thaw of the season. In this example I show the mean pixel value for the whole image in the 14-15 season as seen from camera GEORa at George's Point. a) Penguins arrive at the beginning of the season and stand on the winter snow. B) Penguins defecate on the snow helping its thawing, making the snow progressively darker. c) Thawing after winter leaves the ground wet (and dark) for many days. After the snow has molten, they can start building their nests and laying eggs. d) As the ground dries the mean pixel value rises steadily.

After comparing all combinations of metrics and areas of the image in multiple seasons and colonies I saw that none of the combinations of metrics and areas was consistently reliable at finding the main thaw date (Figure S4.1.2). It is very common that two of these estimates do achieve a close estimate to the hand-annotated thaw date (Figure S4.1.2) so I decided the most reliable estimate was the composite the median of all of those estimations (Figure S4.1.3).

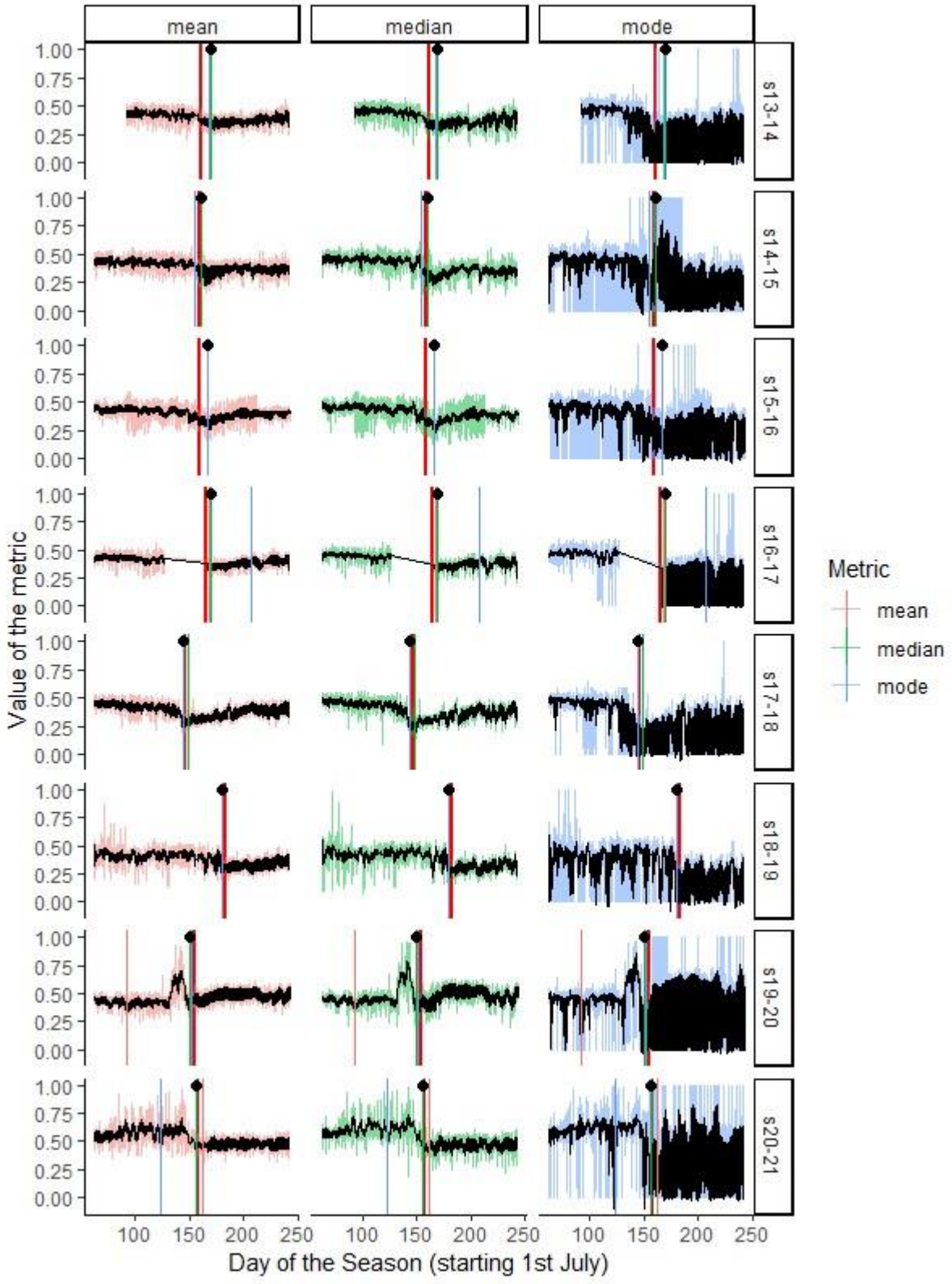


Figure S4.1.2: Mean, median and mode metrics of pixel value for the whole image calculated for each of the seasons recorded at George's Point (camera GEORa). Mean, median and mode metrics are coloured red, green and blue and their corresponding smoothing splines are overlayed in black colour. Mean, median and mode estimates of thaw date are represented as vertical lines in their respective colours. Hand annotated thaw date is represented as a vertical thick red line. The median of all three estimates (Mean, mode and median is represented as a black spot).

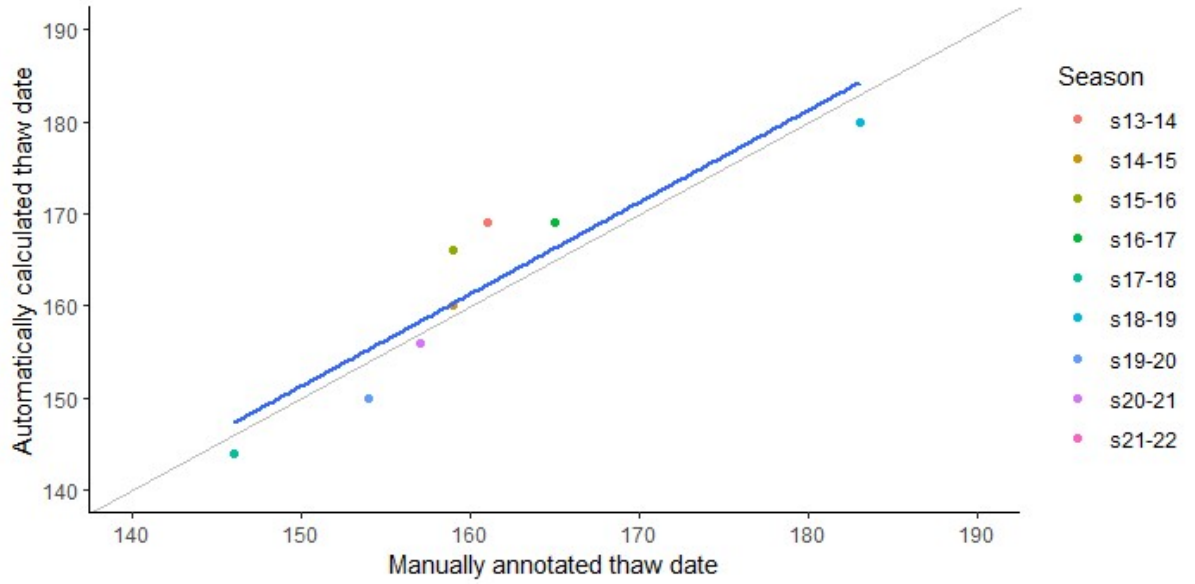


Figure S4.1.3: Correlation between manually annotated thaw date and the estimated thaw date at George's Point (camera GEORa). The latter is derived from the median of the three thaw date estimates obtained with the three different metrics (Mean, mode and median). The thick blue line represents the regression for this correlation and the thin grey line represents the perfect correlation (i.e. slope = 1, intercept = 0).

Appendix 5.1. Validating the Machine Learning method

In order to assess the strengths and weaknesses of the Machine Learning Method I am going to compare its results to the annotations of an expert. There were 307 instances of ED suggested by the Machine Learning detector that fall into expert-annotated sequences, which allow us to classify them into true and false positive and negative detections (Table S5.1.1).

Table S5.1.1: Types of ML detections for 307 manually annotated ED instances.

True Positives	True Negatives	False Positives	False Negatives
149	92	47	19
48.8%	29.9%	15.3%	6%

Of all instances eventually presented by the detector, (i.e. all positives considered), 76% of them are correct identifications of ED behaviour. Since detections are made every third of a second it is also possible to study the precision regarding the duration of these ED instances. The median difference in duration between annotated and detected EDs is 1.77 seconds with a Standard Deviation of 3.35 seconds (Figure S5.1.1).

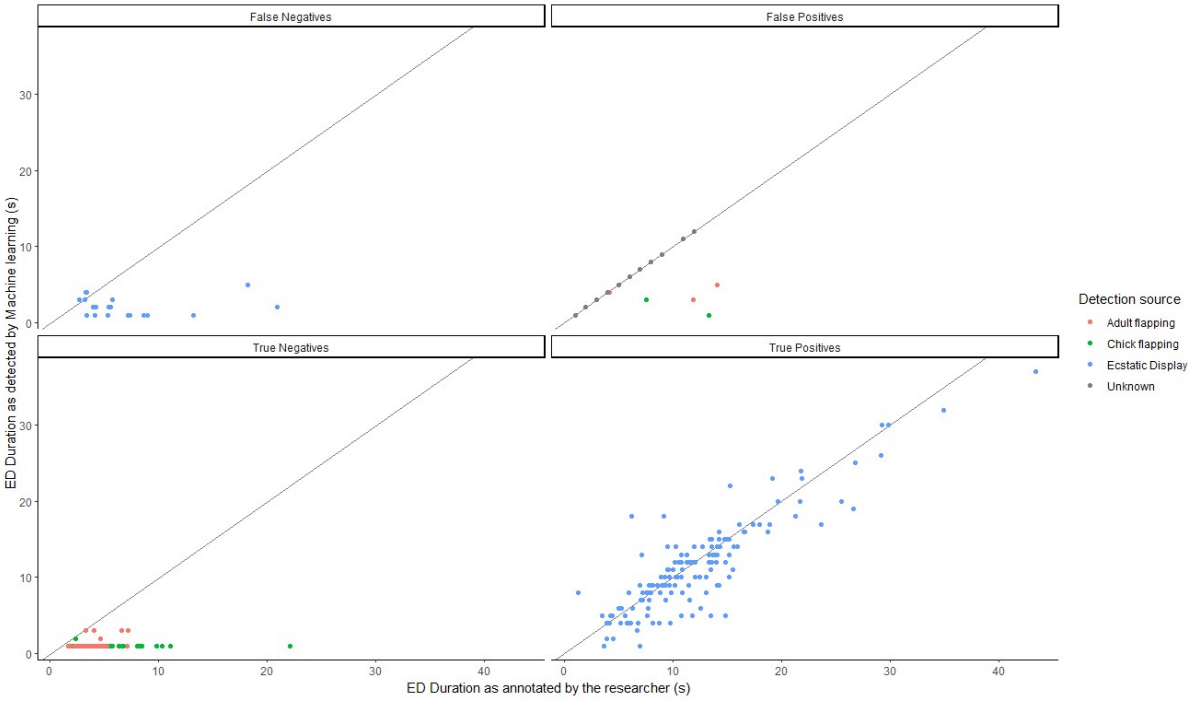


Figure S5.1.1: Relationship between calculated and annotated duration of all 307 instances of ED presented by the ML algorithm of which I have expert-annotations for. These are presented in four panes depending on the type of data (true and false positives and negatives) and coloured by the known or unknown origin of the detection.

Firstly, it is possible to see the detector is not picking up some instances of ED (False negatives, Figure S5.1.1). Most of them are detected as very short behaviours (<5 seconds) despite half of them are annotated longer than that. This does not amount to big numbers of instances but it seems to affect more to those nests near the border of the frame (N01, N02, N06) and N10 a nest with a very mobile adult (Figure S5.1.2a). Perhaps these failed detections are due to the individual not fitting properly into the nest area while performing the ED.

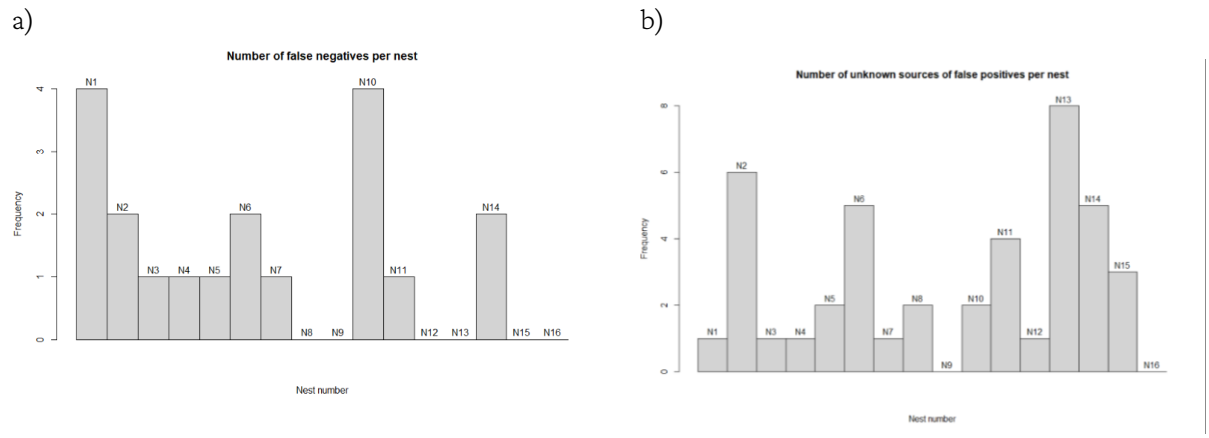


Figure S5.1.2: Histograms of the amount of a) false negatives and b) unknown sources of false positives per nest.

Regarding false positives (Figure S5.1.1), there are some instances that can be explained by adults and chicks flapping their wings but most of them are instances of unknown origin. These false instances occur mainly in those nests further away from the camera and with greater overlap in their nest areas with their neighbours (Figure S5.1.2b). It would also be worth looking into the possibility for these EDs to be detected by mistake from a neighbour with an overlapping nest area.

Most of the instances of Adults and Chicks flapping that were marked as possible confounders are not identified as ED by the detector and are classified as true negatives (Figure S5.1.1). Finally, it is possible to see that the true positives are quite well distributed along the bisector line, showing the detector also does a good job at detecting their length. If anything, detector durations are slightly shorter.

Filtering results

In order to increase the proportion of true ED detections in the dataset I filtered the ED instances by their duration. It is possible to remove 82% of false positives by removing all ED instances calculated to be 5 or less seconds long (Figure S5.1.3).

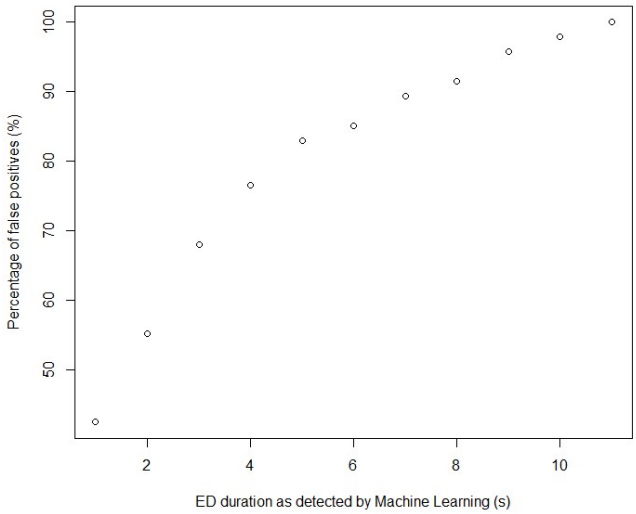


Figure S5.1.3: Cumulative sum of False Positives per ED duration as calculated by the Machine Learning Detector. Expressed as a percentage of the total proportion of false positives in the annotated sample.

If I filter out those ED instances greater than 5 seconds, the pattern of detection changes. This is because I am turning some true positives (n = 16) into false negatives in order to turn some false positives (n = 39) into true negatives. The type of detections in the remaining dataset would remain as shown in Table S5.1.2.

Table S5.1.2: Types of detections depending on their accuracy for 307 instances of annotated ED after filtering out instances of ED equal or under 5 seconds.

True Positives	True Negatives	False Positives	False Negatives
124	131	8	35
43.3%	42.6%	2%	11.4%

This means that the remaining instances provided by the detector (i.e. true and false positives) after filtering are 93.93% true positives and 6.06% false positives. The median difference in ED duration after this filtering process would be 1.4 seconds with a standard deviation of 2.9 seconds. When visualizing this filtering process it is possible to see that this method effectively leaves out all Adult and Chicks flapping behaviours and most of the false positives of unknown origin at the cost of removing 10.7% (n = 16) of the true positives (Figure S5.1.4).

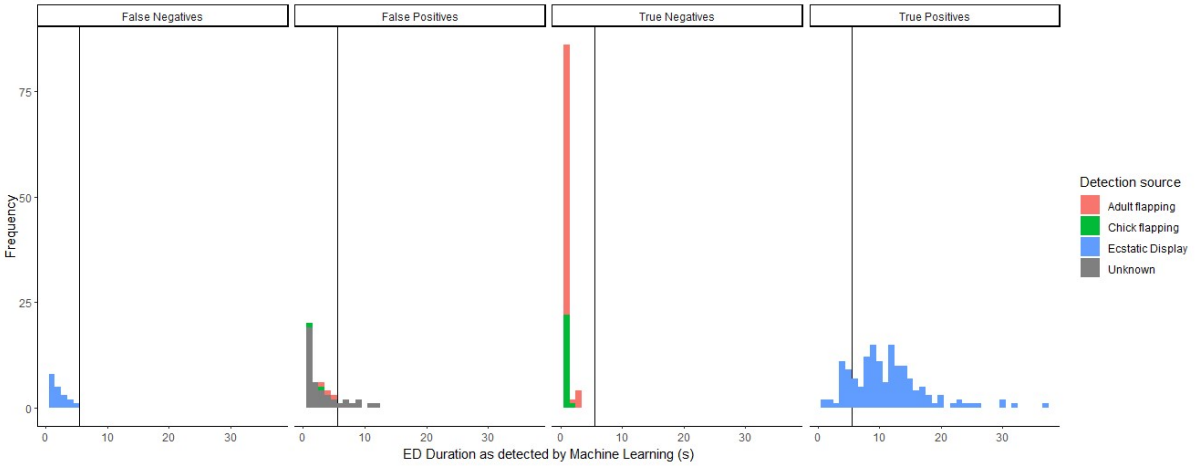


Figure S5.1.4: Histograms showing the frequency of ED instances based on their duration as detected by Machine Learning. The figure is divided in four panes by the type of data (true and false positives and negatives) and coloured depending on whether the source of the detection is known. The black vertical lines represent the 5 second threshold that has been used as a cut-off to filter ED instances.

This simple filtering method therefore raises the amount of true positives from 76% to 94%, however at the price of removing 10% of the true positives. I think it is worth raising the final amount of positives in order to gain certainty that or dataset is an accurate representation of the ED occurred during the study.

Appendix 5.2. Other plots

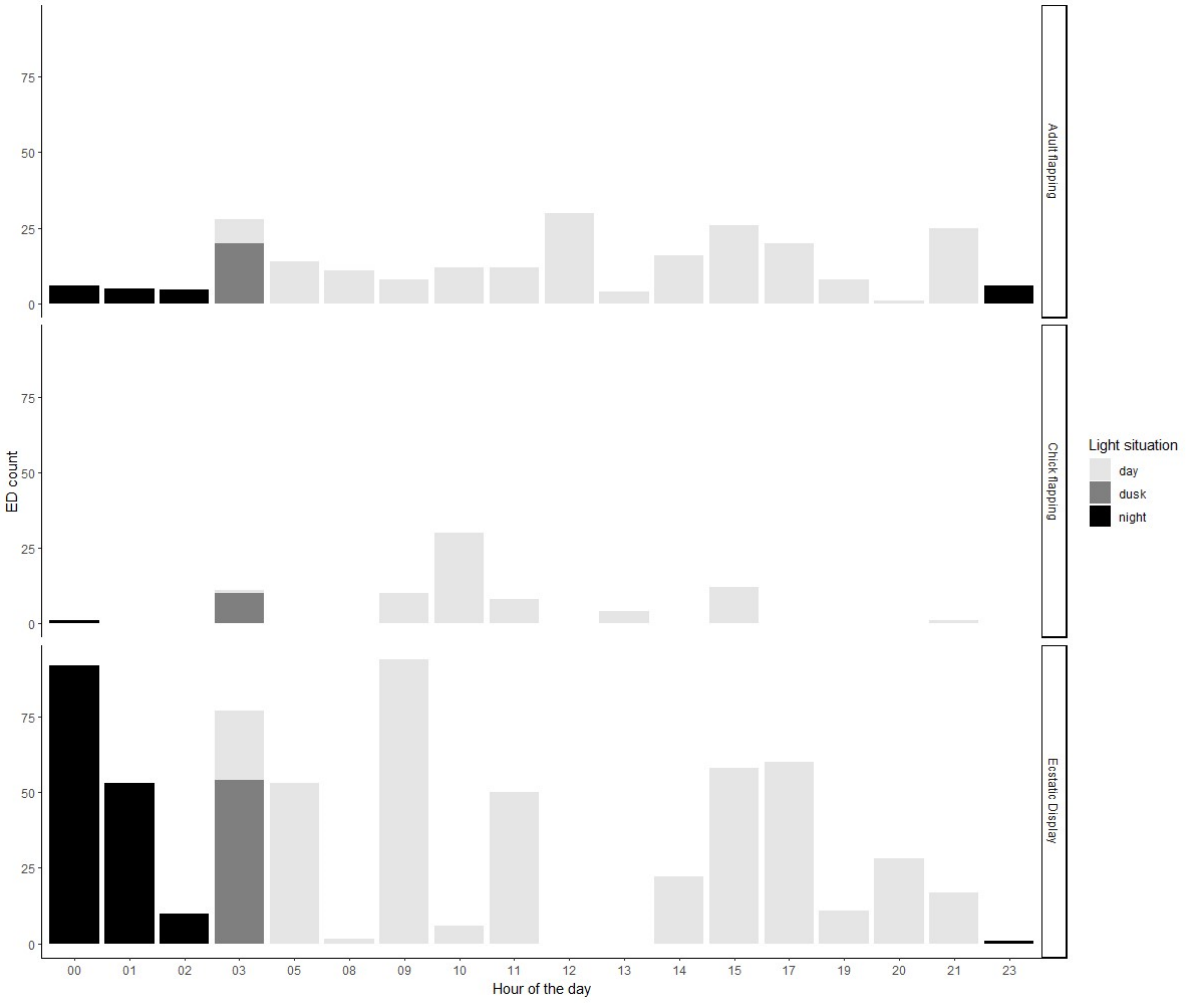


Figure S5.2.1: ED count of each of the three behaviours annotated by an expert per ten-minute sequence. Counts are coloured by the light situation: day, dusk and night.

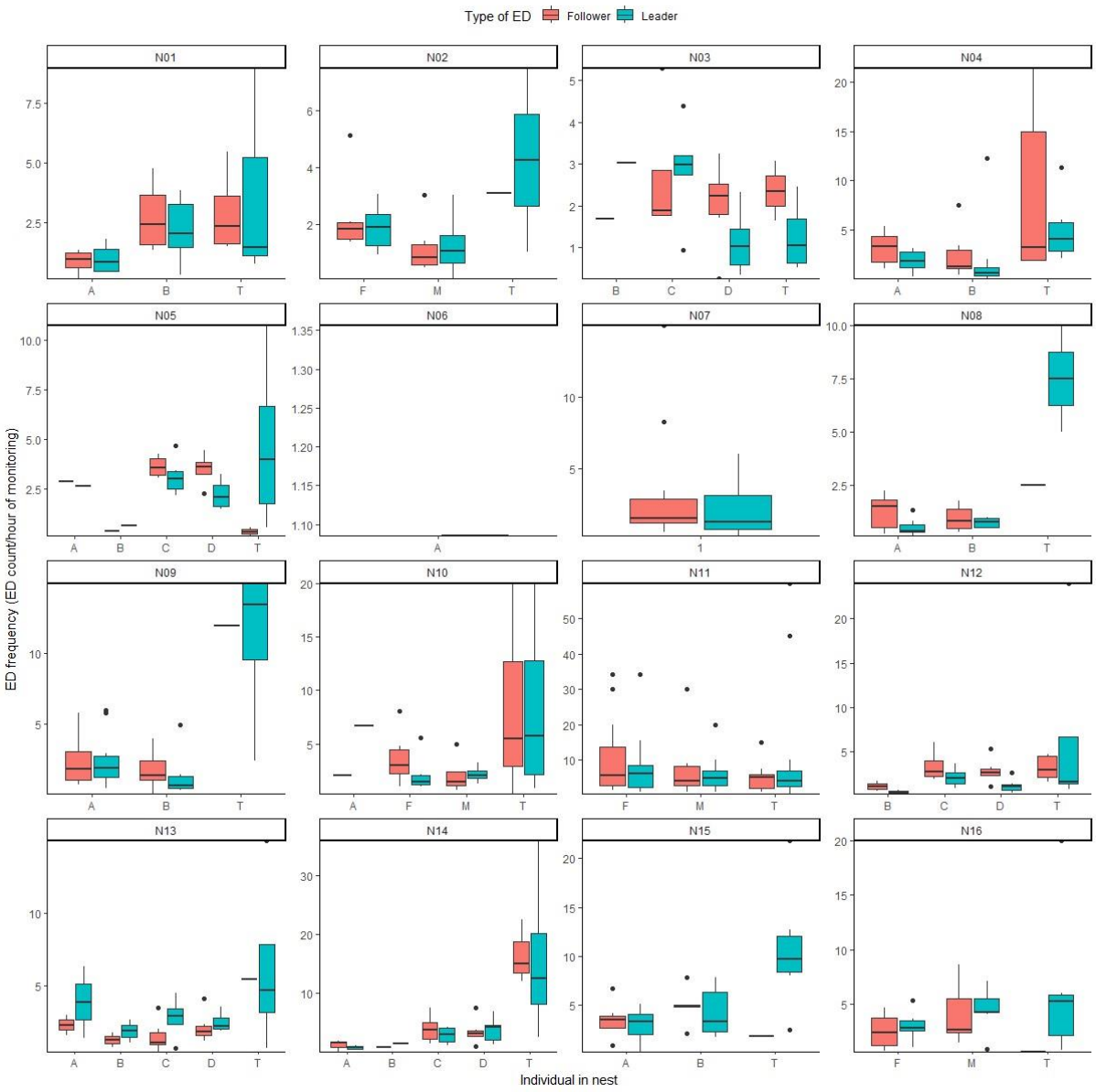


Figure S5.2.2: ED frequencies per individual all stints considered. For the filtered dataset please refer to figure 6 in the main body of Chapter 5.

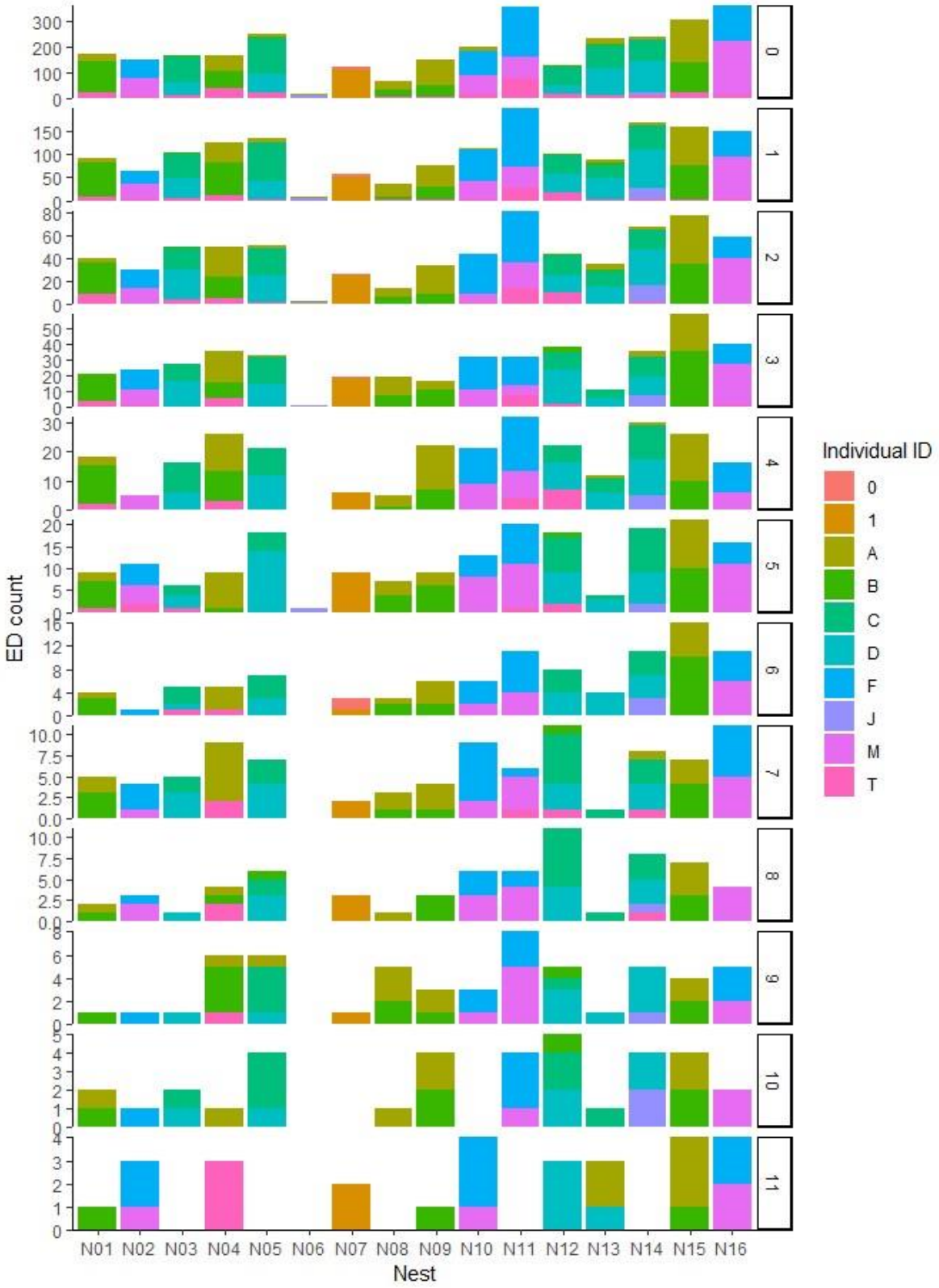


Figure S5.2.3: Counts of the number of ED per nest and individual (colour) in each numeric sequential position in a wave. It is possible to observe there are not nests or individuals that take any preferential position within the wave.

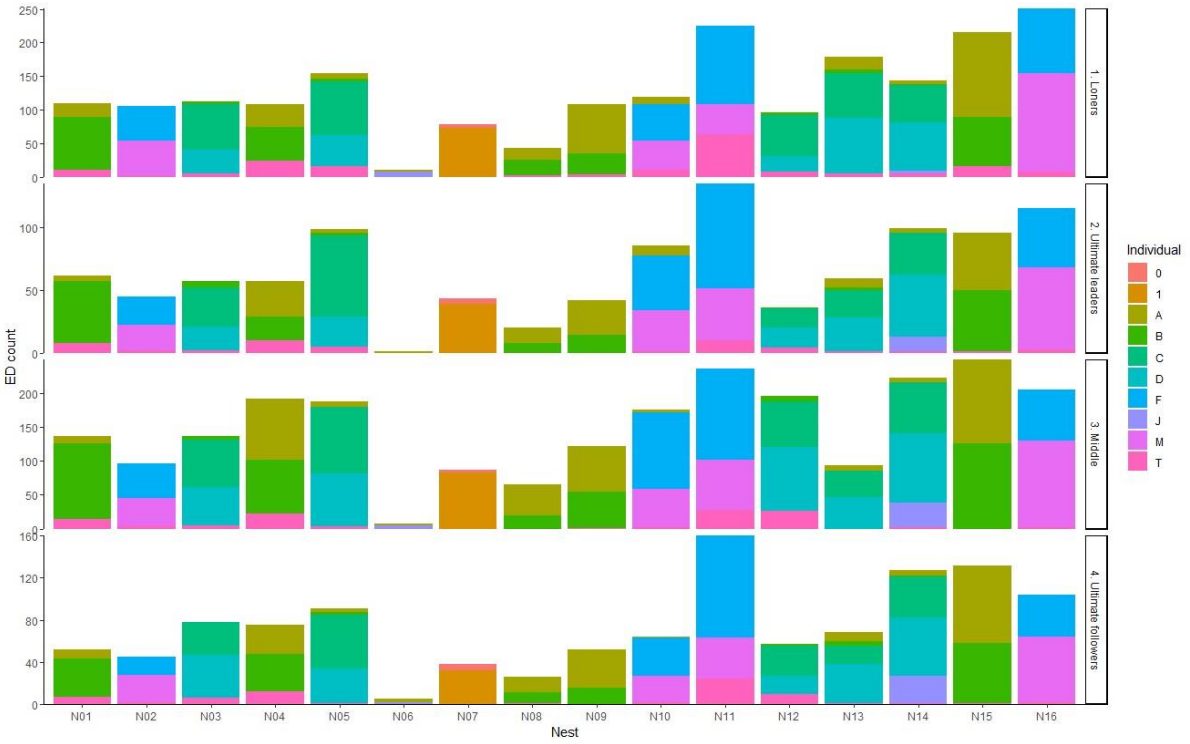


Figure S5.2.4: Counts of the number of ED per nest and individual (colour) in each categorical sequential position in a wave. It is possible to observe there are not nests or individuals that take any preferential position within the wave.

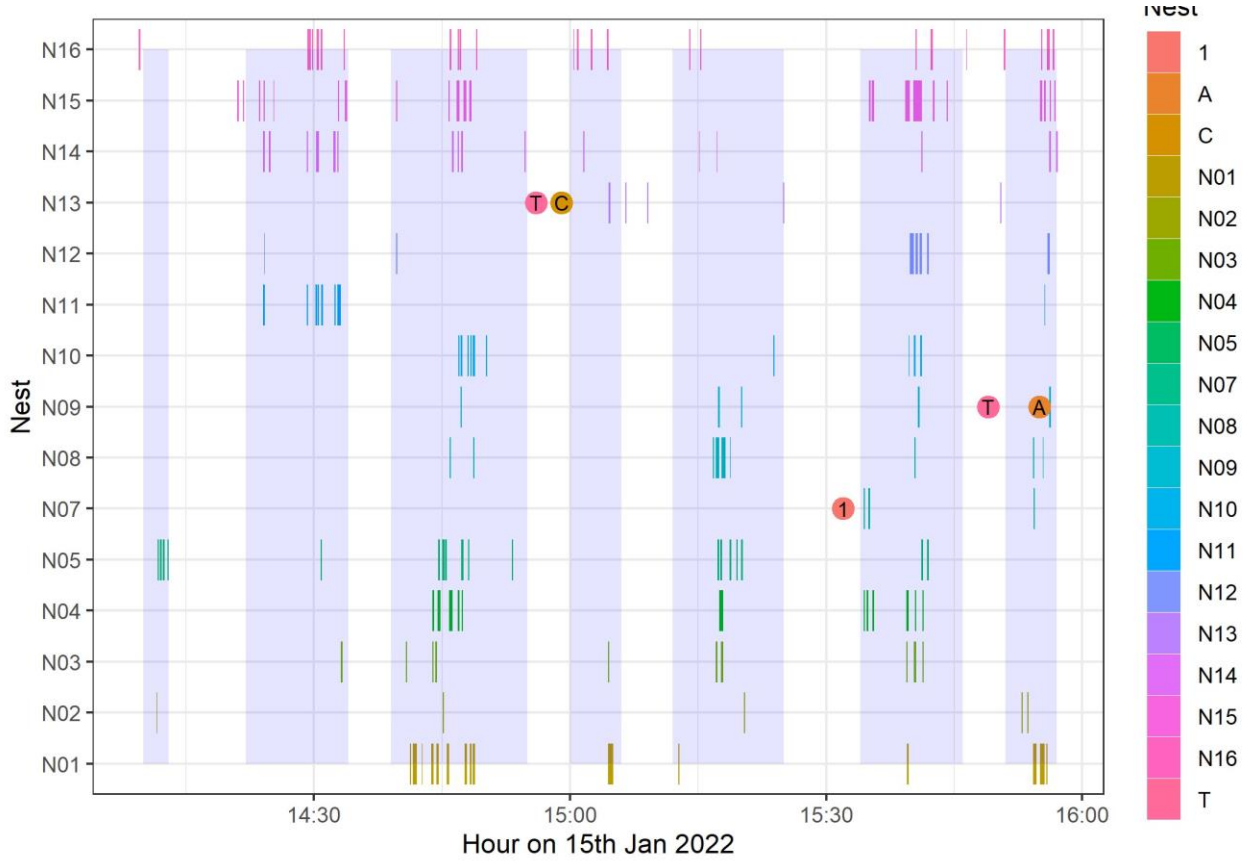


Figure S5.2.5: Example of a 1-hour long ethogram showing all ED predictions and their duration for all 16 nests in study. These predictions are overlaid with blue rectangles showing the duration of their respective waves. On top letters and numbers show the change of identity of the individual on each nest: Adults A and C, T for two adults on the nest (Changeover starts) and 1 meaning 1 penguin showed up in that nest, previously empty.

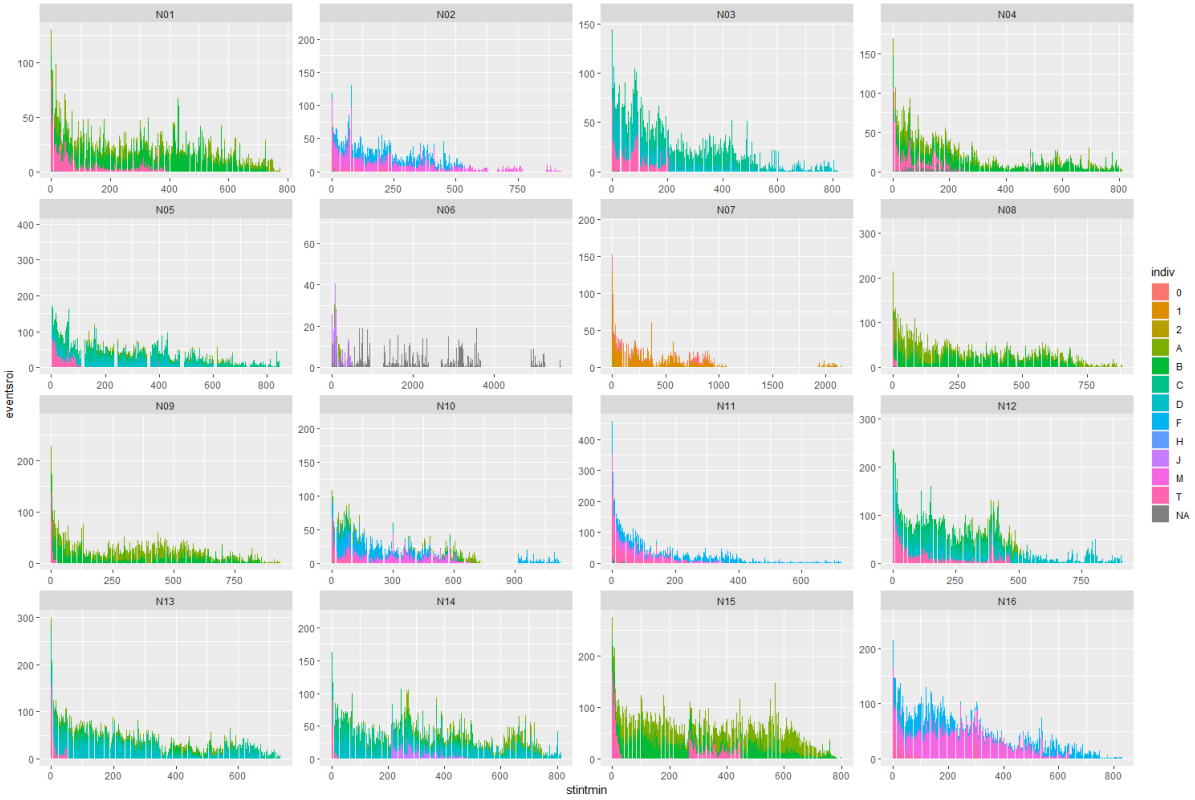


Figure S5.2.6: Example analysis of raw event rate. Y-axis indicates percentage of the pixels in the nest area/region of interest triggered per minute. X-axis shows the minutes into a stint for each individual.

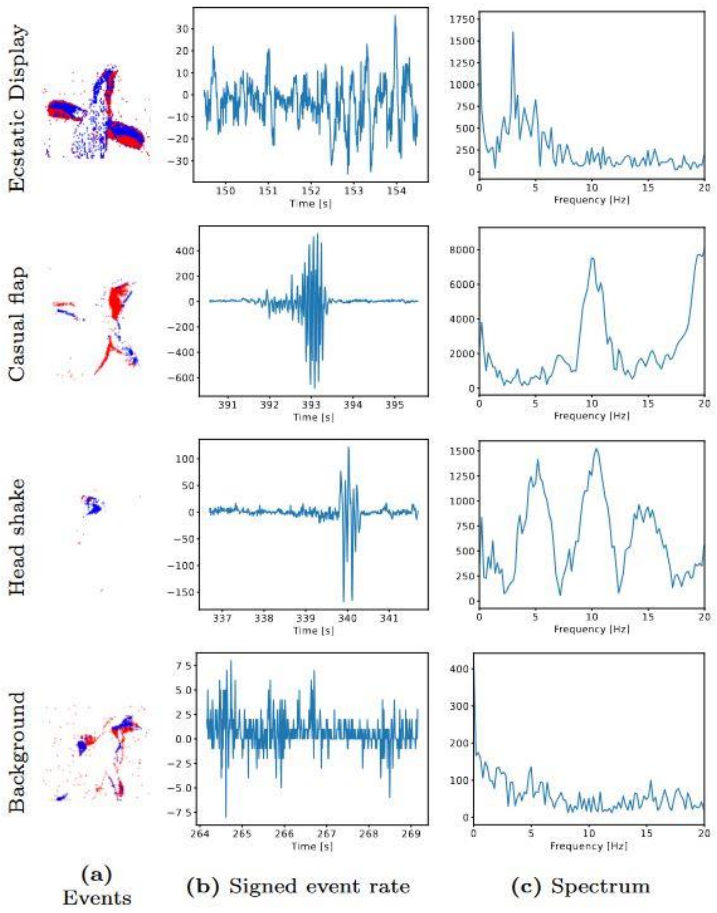


Figure S5.2.7: Example of a spectrogram analysis that can be performed treating the beating of the wings as a wave. In future studies I could use a fourier transformation in order to detect ED, Adult (casual) flaps or head shakes. This could also be extended to other oscillatory behaviours including chick flaps, snaking (used in pair recognition), head bowing and food-provisioning. Data analyses and image provided by Suman Ghosh and Friedhem Hamann.

Appendix 5.3. Model building and Model Selection

In order to build the models I started with a selection of variables that I found appropriate (rationale described in the main body of the paper) considering the results arising from the Results I section and the existing bibliography on ED from other species. In order to build these models I started building a model with all variables of interest and start dropping them one by one based on AIC criterion until dropping variables did not cause a significant change in AIC (ΔAIC >2). I finally selected the model which had the lowest AIC (within 2 points of ΔAIC) with the least amount of variables (more parsimonious). Unless stated otherwise all models have been fitted to only breeding nests.

Here is a description of all the variables uses to build the models:

Variables used to describe the overall state of the colony:

- Windchill-adjusted temperature. Abbreviated in the model selection tables as windchill. Calculated as 33 + (0.474 + 0.454*sqrt(Windspeed(m/s)) -0.0454*Windspeed(m/s)) * (Temperature(C)- 33)
- Day of the month. Abbreviated as dom.
- Hour of the day. Abbreviated as hod.
- Number of changeovers in a one hour period. Abbreviated as numchangeo.

Variables used to capture the inner state of an individual penguin

- Hours since changeover. Calculated from the first minute that the individual is left alone by their partner (7c), I abbreviated it as hourssincho. In model 1 where the response variable is overall ED/hour I turned this variable two possible variables that could capture its effect. First into a sum of all of the hours each bird in view was at (abbreviated as cumhourscho) and into the amount of individuals that had been at the nest for more than 6 hours, the median changeover time (abbreviated as bighours).
- ED in previous hour. A count of the number of ED displayed by one particular nest in the hour previous to the start of a wave, a leading or the first ED of a following bout. Abbreviated as edinprevhour.
- Time since the last ED. Complementary to the last one I also calculated the time in minutes since the last ED performed by that same individual (abbreviated as timesinceed). Simmilarly I built variables that describe the time since that individual performed a leading ED (timesincelead) and time since a leading ED successfully triggered another penguin (timesinceleadsbdy)

Variables used to capture the status of other nests in the colony

- Amount of ED in neighbouring nests in the previous minute (nghbprevmin), ten minutes (nghbprevtenmin) and hour (nghbprevhour).
- When studying following ED I use relationtoleader to mark whether the leading nest is a neighbour to the nest of study or not.
- Amount of contiguous (Neighbouring, within pecking sitance) nests that perform ED display in a wave (count). Amount of nests that display ED in a particular wave. Abbreviated as amountcontig.
- Amount of non-contiguous nests that perform ED in a particular wave (Count). Abbreviated as amountnoncontig.

When considering waves I built two variables describing each wave.

- Wave duration (min). Abbreviated as wavelength.
- Wave ED density (ED/min). This is the overall amount of ED in the wave divided by wave duration. Abbreviated as wavedensity. Waves with less than 3 EDs are kept out of the analysis.
- Minutes since the start of the wave. How long did it take a certain nest to join a wave after it started. Abbreviated as timeinwave.

Table S5.3.1: Model selection for the linear model explaining amount of ED performed in each of the hours monitored during the observation period . Only fully monitored hours were considered (n = 76). Variable names have been abbreviated as follows: numchangeo (Number of changeovers in each 1 hour period), cumhourscho (Cumulative hours since changeover across all nests), bighours (How many nests have individuals that have been on the nest for more than 6 hours, i.e. the average changeover time), windchill (windchill-adjusted temperature in degrees centigrades), dom (day of the month) and hod (Hour of day).

Independent variables in each model	d.f.	AIC	p-value
numchangeo + cumhourscho + windchill + bighours + dom + hod	8	795.9879	
numchangeo + windchill + bighours + dom + hod	7	794.1415	
numchangeo + windchill + cumhourscho + dom + hod	7	794.0589	
bighours + windchill + cumhourscho + dom + hod	7	796.8282	
numchangeo + cumhourscho + windchill + bighours + dom	7	795.0074	
bighours + windchill + dom + hod	6	795.3133	
bighours + numchangeo + dom + hod	6	794.4237	
windchill + numchangeo + dom + hod	6	792.1501	
cumhourscho + windchill + dom + hod	6	794.9342	
cumhourscho + numchangeo + dom + hod	6	794.1734	
bighours + windchill+ dom	5	795.1292	
bighours + numchangeo + dom	5	795.5304	
windchill + numchangeo + dom	5	791.5686	0.005774
cumhourscho + windchill+ dom	5	794.2487	
cumhourscho + numchangeo + dom	5	794.5406	
windchill + dom	4	793.6322	
numchangeo + dom	4	794.2163	
numchangeo + windchill	4	794.7295	
windchill	3	796.3334	
dom	3	795.6684	
numchangeo	3	797.7028	
Null model	2	798.7044	

Table S5.3.2: Model selection for the generalized linear models aiming to understand the factors influencing whether a certain individual take part in a certain wave or not.

Independent variables in each model	d.f.	AIC
timesinceed + edinprevhour + wavelength + wavedensity + hourssincho + amountcontig + amountnoncontig + aparente + dom	11	969.7
timesinceed + edinprevhour + wavelength + wavedensity + hourssincho + amountcontig + amountnoncontig + aparente	10	967.7
timesinceed + edinprevhour + wavelength + wavedensity + hourssincho + amountcontig + aparente	9	966.6859
edinprevhour + aparente + wavelength + wavedensity + hourssincho + amountcontig	8	966.1875
timesinceed + aparente + wavelength + wavedensity + hourssincho + amountcontig	8	974.9972
timesinceed + edinprevhour + wavelength + wavedensity + hourssincho + amountcontig	8	965.1632
timesinceed + edinprevhour + aparente + wavedensity + hourssincho + amountcontig	8	1010.9954
timesinceed + edinprevhour + aparente + wavelength + hourssincho + amountcontig	8	979.2911
timesinceed + edinprevhour + aparente + wavelength + wavedensity + amountcontig	8	971.2453
timesinceed + edinprevhour + aparente + wavelength + wavedensity + hourssincho	8	982.2342
edinprevhour + wavelength + wavedensity + hourssincho + amountcontig	7	964.7354
timesinceed + wavelength + wavedensity + hourssincho + amountcontig	7	973.0922
timesinceed + edinprevhour + wavedensity + hourssincho + amountcontig	7	1009.0035
timesinceed + edinprevhour + wavelength + hourssincho + amountcontig	7	977.2920
timesinceed + edinprevhour + wavelength + wavedensity + amountcontig	7	970.5019
timesinceed + edinprevhour + wavelength + wavedensity + hourssincho	7	981.1693
wavelength + wavedensity + hourssincho + amountcontig	6	981.7277
edinprevhour + wavedensity + hourssincho + amountcontig	6	1008.3406
edinprevhour + wavelength + hourssincho + amountcontig	6	977.0604
edinprevhour + wavelength + wavedensity + amountcontig	6	970.6595
edinprevhour + wavelength + wavedensity + hourssincho	6	981.6092
Null Model	2	1301.4

Table S5.3.3: Model selection for the linear mixed models aiming to understand the factors influencing the amount of ED once a certain individual decides to take part in a certain wave. All models use nest as a random effect variable.

Independent variables in each model	d.f.	AIC
dom + timesinceed + edinprevhour + timeinwave + hourssincho + amountcontig + aparente + amountnoncontig + (1|nest)	11	1805.0
timesinceed + edinprevhour + timeinwave + hourssincho + amountcontig + aparente + amountnoncontig + (1|nest)	10	1805.3
dom + edinprevhour + timeinwave + hourssincho + amountcontig + aparente + amountnoncontig + (1|nest)	10	1803.1
dom + timesinceed + timeinwave + hourssincho + amountcontig + aparente + amountnoncontig + (1|nest)	10	1803.0
dom + timesinceed + edinprevhour + timeinwave + amountcontig + aparente + amountnoncontig + (1|nest)	10	1806.8
dom + timesinceed + edinprevhour + timeinwave + hourssincho + aparente + amountnoncontig + (1|nest)	10	1824.1
dom + timesinceed + edinprevhour + timeinwave + hourssincho + amountcontig + amountnoncontig + (1|nest)	10	1812.2
dom + timesinceed + edinprevhour + timeinwave + hourssincho + amountcontig + aparente + (1|nest)	10	1835.7
dom + timeinwave + hourssincho + amountcontig + aparente + amountnoncontig + (1|nest)	9	1801.1
timeinwave + hourssincho + amountcontig + aparente + amountnoncontig + (1|nest)	8	1801.5
hourssincho + amountcontig + aparente + amountnoncontig + (1|nest)	7	1817.0
timeinwave + amountcontig + aparente + amountnoncontig + (1|nest)	7	1803.8
timeinwave + hourssincho + aparente + amountnoncontig + (1|nest)	7	1820.8
timeinwave + hourssincho + amountcontig + amountnoncontig + (1|nest)	7	1808.4
timeinwave + hourssincho + amountcontig + aparente + (1|nest)	7	1831.8
Null model	2	1883.3

Table S5.3.4: Model selection for the linear mixed models aiming to understand the factors influencing the position in which different individuals take part in a certain wave. All models use nest as a random effect variable.

Independent variables in each model	d.f.	AIC
timesinceed + edinprevhour + hourssincho + amountcontig + perccontig + (1|nest)	8	1660.9
edinprevhour + hourssincho + amountcontig + perccontig + (1|nest)	7	1661.8
timesinceed + hourssincho + amountcontig + perccontig + (1|nest)	7	1658.9
timesinceed + edinprevhour + amountcontig + perccontig + (1|nest)	7	1661.1
timesinceed + edinprevhour + hourssincho + perccontig + (1|nest)	7	1660.3
timesinceed + edinprevhour + hourssincho + amountcontig + (1|nest)	7	1666.4
hourssincho + amountcontig + perccontig + (1|nest)	6	1660.4
timesinceed + amountcontig + perccontig + (1|nest)	6	1659.9
timesinceed + hourssincho + perccontig + (1|nest)	6	1658.3
timesinceed + hourssincho + amountcontig + (1|nest)	6	1664.7
hourssincho + perccontig + (1|nest)	5	1660.0
timesinceed + perccontig + (1|nest)	5	1681.9
timesinceed + hourssincho + (1|nest)	5	1682.7
Null model	2	1686.8

Table S5.3.5: Model selection for the linear mixed models aiming to understand the factors influencing the position in which different individuals take part in a certain wave. All models use nest as a random effect variable.

Independent variables in each model	d.f.	AIC
timesinceed + edinprevhour + timesinceleading + timesinceleadingsbdy + hourssincho + nghbprevmin + nghbprevtenmin + nghbprevhour + nest	11	1375.0
timesinceed + timesinceleading + timesinceleadingsbdy + hourssincho + nghbprevmin + nghbprevtenmin + nghbprevhour + nest	10	1373.0
timesinceed + edinprevhour + timesinceleadingsbdy + hourssincho + nghbprevmin + nghbprevtenmin + nghbprevhour + nest	10	1373.0
timesinceed + edinprevhour + timesinceleading + hourssincho + nghbprevmin + nghbprevtenmin + nghbprevhour + nest	10	1375.6
timesinceed + edinprevhour + timesinceleading + timesinceleadingsbdy + hourssincho + nghbprevtenmin + nghbprevhour + nest	10	1375.3
timesinceed + edinprevhour + timesinceleading + timesinceleadingsbdy + hourssincho + nghbprevmin + nghbprevhour + nest	10	1376.2

timesinceed + edinprevhour + timesinceleading + timesinceleadingsbdy + hourssincho + nghbprevmin + nghbprevtenmin + nest	10	1374.0
timesinceed + edinprevhour + timesinceleading + timesinceleadingsbdy + hourssincho + nghbprevmin + nghbprevtenmin + nghbprevhour	10	1439.9
edinprevhour + timesinceleading + timesinceleadingsbdy + hourssincho + nghbprevmin + nghbprevtenmin + nest	9	1371.0
timesinceed + timesinceleading + timesinceleadingsbdy + hourssincho + nghbprevmin + nghbprevtenmin + nest	9	1373.6
timesinceed + edinprevhour + timesinceleadingsbdy + hourssincho + nghbprevmin + nghbprevtenmin + nest	9	1373.4
timesinceed + edinprevhour + timesinceleading + hourssincho + nghbprevmin + nghbprevtenmin + nest	9	1374.4
timesinceed + edinprevhour + timesinceleading + timesinceleadingsbdy + hourssincho + nghbprevtenmin + nest	9	1372.2
timesinceed + edinprevhour + timesinceleading + timesinceleadingsbdy + hourssincho + nghbprevmin + nest	9	1418.0
edinprevhour + timesinceleading + timesinceleadingsbdy + hourssincho + nest	7	1371.7
timesinceed + edinprevhour + timesinceleadingsbdy + hourssincho + nest	7	1371.4
timesinceed + edinprevhour + timesinceleading + hourssincho + nest	7	1372.4
timesinceed + edinprevhour + timesinceleading + timesinceleadingsbdy + nest	7	1370.2
timesinceed + edinprevhour + timesinceleading+ nest	6	1444.9
edinprevhour + timesinceleadingsbdy + hourssincho + nest	6	1370.6
timesinceleadingsbdy + hourssincho + nest	5	1416.8
edinprevhour + hourssincho + nest	5	1440.9
edinprevhour + timesinceleadingsbdy + nest	5	1381.4
edinprevhour + timesinceleadingsbdy + hourssincho	5	1372.6
Null model	2	1487.2

All analyses were finished from a ship in Antarctica in December 2023.

The final text arrived on the 5th Jan 2024, the day before the deadline (as is custom),

in Punta Arenas. Hours before boarding another ship for Antarctica.

All corrections were finished in Oxford, April 2024.

The final nicer version was submitted for deposit from Madrid in April 2025.

This thesis has been all over the place.