

Variation in the Phenology of *Pygoscelis* Penguins

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*When you have seen one ant, one bird, one tree,
you have not seen them all.*

E. O. Wilson



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Declaration

I hereby declare that I conducted the work presented here under the supervision of Drs Tom Hart, Professor Alex Rogers, and Dr. Dora Biro. Contributions by others are acknowledged below and I have referenced any quotations or paraphrasing from other sources, including in tables and figures.

Chapter 1 is based on a paper published in Polar Biology in 2015 in which I am sole author.

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I hereby confirm that no part of my thesis has been accepted or is currently being submitted for any degree, diploma, or certificate or other qualification in this University or elsewhere.

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Abstract

Variation in phenology is linked to the timing of environmental variables and influences survival at both the individual and colony level. Therefore, understanding a species' annual cycle is vital to its ecology and conservation. By reviewing literature on *Pygoscelis* penguin phenology in Chapter 1, I identify major gaps, both spatially and temporally, in our knowledge of the timing of events in the three species (Adélie, *Pygoscelis adeliae*; chinstrap, and *Pygoscelis antarctica*; gentoo, *Pygoscelis papua*): particularly, 1) during the guard phase, 2) their behaviour in winter, 3) the phenology of colonies inhabiting locations away from scientific bases, and 4) the general phenology of chinstrap penguins. Chapter 2 assesses which time-lapse camera methods are most relevant to seabird research, highlighting the capabilities and limitations of cameras in past studies and how they may be best applied to future research. Chapter 3 examines the timing of the guard phase in gentoo penguins and how chick aggregation behaviours vary across several sites. Chapters 4 and 5 show variation in winter abundance at breeding sites in both gentoo and Adélie penguins related to abiotic factors and colony location. Lastly, Chapter 6 fills in gaps in the known timing and duration of phenology events in gentoo and chinstrap penguins across their full latitudinal ranges, while relating these timings to chick survival. In the conclusion, I summarize the main findings of the thesis, focusing on three major themes that were observed across the four data chapters and their implications: 1) behaviours are not consistent across colony locations 2) nor between years, and these behaviours depend on 3) local environmental conditions. I then synthesize these empirical findings from each of these chapters, discuss the implication of these findings to ecological theory and conservation policy, highlight some of the limitations of these studies, and recommend possibilities for future research.

CHAPTER ONE

A Comprehensive Review of the Phenology of *Pygoscelis* Penguins

1.1 Abstract

Phenology, the study of stages within the life cycles of plants and animals, has served as a proxy for weather and climate throughout human history, but has only recently become its own field of environmental science. Phenological constraints are particularly demanding in avian species because of the necessity of matching chick provisioning with high food abundance, while allocating time for migration. Within avian species, seabird phenology is of particular interest because many seabird species exhibit colonial breeding behaviour. Penguins, representing roughly 90% of the biomass in the Southern Ocean, are well studied in the context of population dynamics, prey abundance, and phenology. Here I review the annual cycles of *Pygoscelis* penguins, a genus including gentoo (*Pygoscelis papua*), chinstrap (*Pygoscelis antarctica*), and Adélie (*Pygoscelis adeliae*) penguins, to better understand what is known about their phenology, what causes known changes, and how their phenology influences fitness. Major differences exist between species, particularly in relation to winter migration, incubation shifts, and the timing of breeding. Even with the numerous studies examining phenology in *Pygoscelis* penguins, large gaps in our understanding of plasticity in the annual cycle remain. In particular, certain phases are neglected because they are logistically difficult to record or have erroneously been ignored. In addition, temporally, large gaps exist in our understanding of phenology, where studies have not been updated in over 20 years at a particular field site. Because phenology does vary greatly between years, depending on the colony, when

possible, researchers should strive to update phenological records by recording the dates of phases each year.

1.2 Introduction

Phenology, the study of stages within the life cycles of plants and animals, has served as a proxy for weather and climate throughout human history, but has only recently become its own field of environmental science. Phenological studies have helped to understand how wildlife respond to both local and global environmental changes and many studies, described in this review, have demonstrated long-term climate changes using phenological data. By interpreting phenology, how it changes over time, and its variation by region, we can better understand a species' ecology, including inter-species relationships, interactions with conspecifics, and their connection with biotic and abiotic factors.

Long-term studies have revealed widespread fluctuations in phenology in wildlife due to a changing climate. In particular, studies have demonstrated phenological advances in both the Northern (Beebee 1995, Fitter and Fitter 2002, Parmesan and Yohe 2003, Körner and Basler 2010, Menzelet al. 2006, Parmesan 2007) and Southern hemispheres (Chambers et al. 2013) with all studies pinpointing climate change as a major factor in these shifts in timing. Interpreting these trends proves difficult as broad shifts in phenology reveals either 1) the ability of most species to adapt to changes in climate over years, or 2) the extent to which climate change is influencing all aspects of species' life cycles, across taxa. One study argues

that a “yardstick” is necessary to measure how much a species must shift to adequately cope with environmental changes within their individual ecology and that this absolute measure should be food abundance at the most demanding time within a species’ annual cycle (Visser and Both 2005). However, rarely do studies measure both phenology and the timing and quality of food resources (Visser and Both 2005), particularly in the context of climate change, making the use of this particular “yardstick” difficult to interpret due to lack of data. Although it is crucial that species match food abundance to specific phases within their annual cycle, there are many other biotic and abiotic factors that may significantly influence different phenological measures and cause these trends associated with climate change.

Collectively, studies have identified the main drivers of phenology in a range of taxa, focusing on environmental, physiological, and genetic factors. Environmental variables influencing phenology include temperature, photoperiod, and precipitation, which all affect either food abundance or habitat availability, particularly during the critical breeding season (Forrest and Miller-Rushing 2010). In addition to ecological impacts, some studies have suggested that phenology may be linked with an individual’s genetics, as physical condition and age of maturity, both genetically linked in some species, are known influences of breeding timing (Hendry and Day 2005, Franks and Weis 2008, Metcalf and Mitchell-Olds 2009). Lastly, an individual’s physiology, particularly hormone control prior to and during breeding, influences when an individual either commences or ends particular phases within their annual cycle (Visser et al. 2010, Wilczek et al. 2010). The known causes of phenological

changes vary greatly between species and location and depend on each life history phase and, in most cases, multiple factors affect this timing (Parmesan 2006).

Phenological constraints are particularly demanding in avian species (Martin 1987) because of the necessity of matching chick provisioning with high food abundance (Durant et al. 2005), while allocating time for migration (Both et al. 2009). Birds have therefore become a focus of phenological studies, concentrating on two major phases in particular: breeding and migration. In response to recent climate change, researchers have identified large-scale shifts to earlier laying dates in many bird species (Crick and Sparks 1999, Liebezeit et al. 2014), while, overall, migration has shifted towards earlier departure dates in short-distance migratory birds and earlier arrival dates in long-distant migrants (Walther et al. 2002). Although climate change has clearly influenced phenology in many avian species, other species have shown no changes in the timing of their annual cycle or migration schedule (Chambers et al. 2013), suggesting that factors beyond climate dictate their phenology. Similar to other taxa, the timing of breeding and migration in birds is dictated by both ultimate and proximate factors. The ultimate factors include the favouring of genotypes, which match peak resource availability with the peak of chick provisioning demands (Lack 1954, Charnov and Krebs 1974); proximate factors include changes in photoperiod, climate, and the condition of resources (Wingfield et al. 1992, Lambrechts et al. 1997). Understanding these underlying causes of phenological changes in birds is essential to interpreting population dynamics (Reed et al. 2013a, Reed et al. 2013b), as phenology often dictates individual fitness.

Phenology in birds is known to influence reproductive success during the breeding season and survival during winter. For example, studies have provided evidence of earlier egg laying dates producing larger clutches (Winkler et al. 2002) and earlier commencement of breeding allowing for higher breeding success in a range of taxa (Perrins 1970, Dunn 2004). In addition, the timing of stopovers at particular sites during migration affects survival while departure and arrival dates influence condition in many migrants prior to the critical breeding season (Newton 2010). Because of these phenological consequences, which significantly impact an individual's fitness, understanding both the causes of timing shifts and the results of any changes is necessary to comprehend a species' role in their respective ecosystems.

Avian phenology also has consequences within the greater ecosystem, particularly in the context of predator-prey and inter-species relationships. As predators within their respective environments, many bird species must match the timing of certain phases within their annual cycle to the recruitment and life history cycles of their prey in what is known as the match/mismatch hypothesis (Cushing 1990). In other words, predators must choose a breeding site and the timing of breeding, which matches up with the timing of prey availability and abundance (Durant et al. 2007). However, when resource availability diminishes, birds must either 1) shift their breeding timing (Barbraud and Weimerskirch 2006), 2) cope with a disparity in prey availability by changing foraging behaviour or shifting prey types

(Croxall et al. 1999, Miller and Trivelpiece 2008, Nicol et al. 2008), or 3) skip the breeding season altogether (Drent and Daan 1980). Each of these outcomes consequently affects prey populations and other competitive species, as they must in turn adjust their own phenology.

Within avian species, seabird phenology is of particular interest because many seabird species exhibit colonial breeding behaviour. Coloniality dictates a constrained breeding strategy, which heavily influences phenology, as synchronicity with conspecifics improves individual fitness (Alcock 1993, Krebs and Davies 2009). Specifically, the origins of coloniality have been linked with lower predation risk, higher resource abundance, and quality nesting habitat, all of which dictate the timing of breeding in these species (Gaston 2004). Meta-analyses have identified trends in seabird breeding dates, suggesting that overall egg laying dates have advanced, although the results are highly dependent on species and region (Chambers et al. 2013, Liebezeit et al. 2014) with several seabird species in the southern ocean shifting towards later arrival and laying dates overall (Barbraud and Weimerskirch 2006). Of all seabirds in the southern hemisphere, penguins (*Sphenicidae*) are particularly well studied in the context of phenology (Ancel et al. 2013) and will be used here to interpret, in detail, variation in phenology on taxa in the Southern Ocean.

1.3 The Annual Cycle of Penguins

Penguins, representing roughly 90% of the seabird biomass in the Southern Ocean (Williams 1995), are well studied in the context of population dynamics, prey

abundance, and phenology. The order is composed of 20 species with taxa ranging from the Galapagos penguin (*Spheniscus mendiculus*), inhabiting the Galapagos islands near the equator in the Pacific Ocean, to the emperor penguin (*Aptenodytes forsteri*), which breeds as far south as 77.74° in latitude on the Antarctic continent (Borboroglu and Boersma 2013; Figure 1.4). Penguins are often considered a bellwether of environmental change in their respective ranges because of their status as top predators and distinct phenology as primarily colonial seabirds (Ainley 2002, Boersma 2008). Of the 18 species, under the International Union for Conservation of Nature (IUCN) 2013 Red List, 5 are endangered, 6 vulnerable, 2 near threatened, and 5 of least concern, which has changed dramatically in the past 20 years as only 5 were considered threatened in 1993 (IUCN 2014, Trathan et al. 2014). Because seabirds are the most threatened bird group, and penguins are the most threatened seabird taxa after albatrosses (Croxall et al. 2012), understanding their ecology is critical to their survival as species, and understanding their life history and its subsequent changes is a high research priority.

These documented population changes are likely related to recent shifts in the environment of the Southern Ocean and Antarctica. In particular, more frequent and intense storms, increased warm, wet conditions and consequent snowfall have all led to poorer breeding success in different species of penguins (Magellanic penguins, *Spheniscus magellanicus*, Boersma and Rebstock 2014; Southern rockhopper penguins, *Eudyptes chrysocome*, Crawford et al. 2008; Adélie penguins, *Pygoscelis adeliae*, Ducklow et al. 2007). Alternatively, some species and colonies have coped

with climate changes by either expanding their range southward (gentoo penguins, *Pygoscelis papua*, Lynch et al. 2012a) or expanding the size of colonies (Adélie penguins, LaRue et al. 2013) as nesting and foraging habitat have become available as a result of either glacier retreats or decreased spring sea ice extent. Although monitoring population changes to penguins is critical to our understanding of their ecology, research must also focus on species life history traits to understand what influences population dynamics at a proximate level (Jenouvrier 2013).

Phenology in penguins has been studied for the past century and, although patchy in its understanding, serves as an indicator of changes at a finer scale. The marine environment dictates much of the timing of phenology in penguins because of its dynamic nature, especially in and around the Antarctic continent. As colonial seabirds, most penguin species must synchronize their phenology within a narrow time frame to take advantage of high quality prey resources, lower predation risk, and availability of suitable nesting habitat during the critical breeding season (Gaston 2004). However, because of their broad and overlapping ranges, penguins have developed different breeding strategies to adapt to their niche environments. At one extreme, the emperor penguin (*Aptenodytes forsteri*) breeds during the harsh winter months on the Antarctic continent, while the king penguin (*Aptenodytes patagonicus*) breeds every two years, rearing chicks for 14-16 months, African penguins (*Spheniscus demersus*) breed throughout the year, while *Pygoscelis* penguins (gentoos, Adélies, and chinstraps, *Pygoscelis antarctica*) breed at the peak of the Antarctic summer (Borboroglu and Boersma 2013). However, even with these contrasting

breeding schedules, penguins have similar life history cycles, the timing of which is often influenced by the same proximate factors.

All penguins undergo similar life history patterns, although the timing and length of each stage varies by species (Ancel et al. 2013). This annual cycle, similar to that of other birds, includes a courtship, breeding, moult, and non-breeding period (Figure 1.1). In general, the courtship period includes the timing of return to the colony and a period in which partners court prior to laying eggs. During the breeding cycle, birds lay eggs, incubate, and, once the eggs hatch, guard the chicks at the nest during the “guard” period. Eventually, adults leave the chicks unattended but continue provisioning during the “post-guard” period. At the end of the breeding cycle, chicks moult their feathers and fledge, taking to the sea, ice, or land during the winter months, while adults stay near the colony or reside at stable offshore sea ice to moult their feathers after a period of intense foraging, known as hyperphagia. The adults then leave for winter migration or remain near the colony in non-migratory species. The timing and length of each of these phases varies between species, but is influenced by several proximate factors across taxa, including 1) photoperiod, 2) peak ocean productivity, and 3) sea surface and ambient temperature (Ancel et al. 2013). Although phenology is relatively well-studied, little is known about how physiology directly influences penguin phenology (Walker et al. 2005, Villanueva et al. 2012), and no studies to date have examined the genetic influence of individual physical condition and time to maturity on phenology in penguins, as has been found in other taxa (Ancel and Gilbert 2013).

When considering the phenology of penguins and both proximate and ultimate factors contributing to changes in timing, it is logical to focus on a few, well-studied, related species, which inhabit overlapping ranges. Here I examine the annual cycles of *Pygoscelis* penguins, a genus of species including gentoo, chinstrap, and Adélie penguins, to better understand what is known about their phenology, what causes known changes, and how their phenology influences fitness.

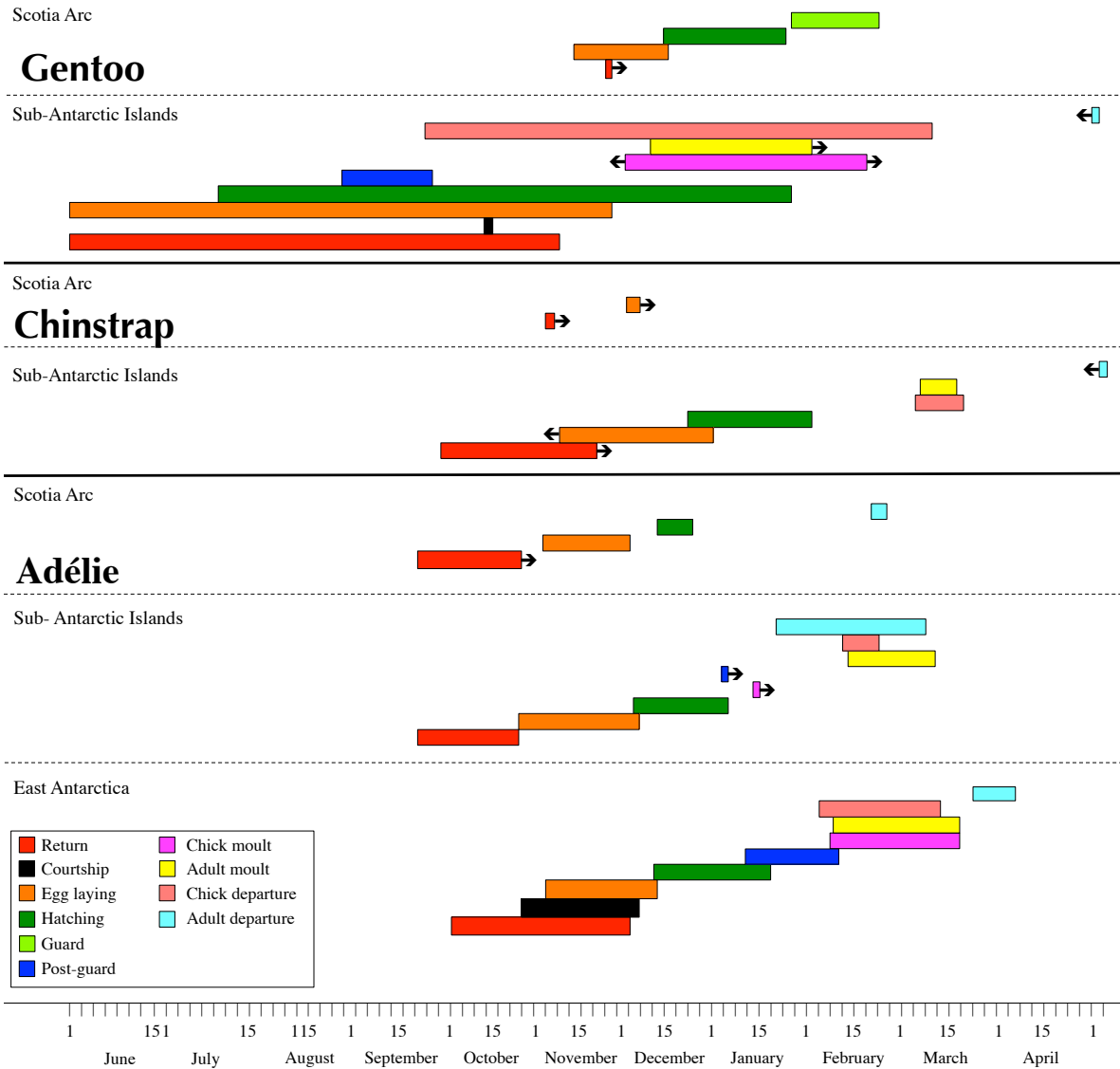


Figure 1.1. Gantt chart of known phenology dates for 1) gentoo (*Pygoscelis papua*), 2) chinstrap (*Pygoscelis antarctica*), and 3) Adélie penguins (*Pygoscelis adeliae*) within each of their respective regions. Each phase represents the range of known dates. Arrows indicate that either a start, end, or mean date was recorded but no further dates were published and the cycle therefore continues in the direction of the arrow. See Table 1.1 for exact dates, locations, and citations.

Table 1.1. Summary of phenology data available on *Pygoscelis* penguins. Table incorporates all available texts with dates included with some minor exceptions. See Appendix A.1 for definitions of each phase.

Species	Region	Location	Site	Latitude, Longitude	Annual Cycle Phase	Dates	Years Studied	Citation
Gentoo	Scotia Arc	Western Antarctic Peninsula	Petermann Island	65°10' S, 64°10' W	Return to colony	Start: November 18	1909	Gain 1914
					Egg laying	Start: November 9	2006	Chesalinet al. 2009
					Hatching	Start: December 19	2005	
			Port Lockroy	63°49' S, 63°30' W	Egg laying	November 22- December 6	1996- 1997	Cobley and Shears 1999
					Hatching	December 7- January 15		
					Guard	January 16- February 14		
			Cierva Point	64°09' S, 60°57' W	Hatching	December 10- 25	1991- 1996	Quintana and Cirelli 2000
			Waterboat Point	64°48' S, 62°43' W	Egg laying	December 2- 9	1921	Bagshawe 1938
					Hatching	January 8- 14	1922	
	Sub-Antarctic Islands	Argentina	Martillo Island	54°54' S, 67°23' W	Egg laying	October 29- November 2	2005- 2006	Ghyset al. 2008
					Hatching	December 5- 19		
		South Shetland Islands	King George Island	62°10' S, 58°30' W	Return to colony	October 7-25	1980	Jablonski 1987
					Egg laying	Start: November 5	1991-2009	Hinke et al. 2012
						1 st : October 16- November 24		
					Hatching	Start December 17	1980	Jablonski 1987

				December 10-25	1981- 1982	Trivelpiece and Volkman 1987
	Elephant Island	61°13' S, 55°11' W	Hatching	November 18- January 16	1976- 1977	Furse 1979
South Orkney Islands	Laurie Island	60°46' S, 44°42' W	Return to colony	September 25- November 5	1903	Clarke 1906
			Egg laying	Start: November 6		
			Chick moult	Start: February 11		
			Adult departure	End: April 25		
	Signy Island	60°43' S, 45°38' W	Return to colony	September 3- October 28	1947- 1987	Rootes 1988
			Egg laying	October 18- November 21		
			Hatching	November 17- December 27		
Falkland Islands	Volunteer Beach	51°29' S 57°50' W	Hatching	1 st : November 29- December 15	2001	Otley et al. 2005
				2 nd : November 30- December 12		
	Not specified	Not specified	Egg laying	Start: October 7	1858- 1860	Abbott 1860
South Georgia	Bird Island	54°00' S, 38°02' W	Egg laying	1 st : October 8- November 10	1986- 1988	Williams 1990
				Mean: October 30	1976	Croxall and Prince 1979
				Start: October 21	1936	Roberts 1940 ^a
			Hatching	Mean: December 3	1976	Croxall and Prince 1979

Prince Edward Islands	Marion Island	46°52' S, 37°51' E	Post-guard	Mean: December 31		
			Chick departure	Mean: February 28	1977	
			Return to colony	June 1- July 23	1994- 2003	Crawford et al. 2003
			Egg laying	Start: June 1- July 20 End: July 12- August 3		
				Start: June 16	1965- 1966	Zinderen Bakker et al. 1971 ^a
				Start: June 24	1974, 1976	Williams 1980
				Start: June 24	Not specified	Williams 1979
			Hatching	Start: July 16	1994- 2003	Crawford et al. 2003
			Post-guard	August 28- September 24	1951	Rand 1954
			Adult moult	Start: December 3	1994- 2003	Crawford et al. 2003
				End: March 22	1952	Rand 1955
			Chick departure	Start: September 18- October End: December 29	1994- 2003 1994- 2003	Crawford et al. 2003
			Replacement clutch	Egg laying: September 25- October 5 Hatching: October 30- November 9 Post guard end: December 5		

Crozet Archipelago	Possession Island	46°25' S, 51°44' E	Return to colony	June 28- July 10	1985	Bost and Jouventin 1991
			Egg laying	June 23- July 20		
				Start: June 29	1970	Despin 1972
				June 24- November 10	1984- 1987	Bost and Jouventin 1990b
			Hatching	August 18- December 18		
			Chick moult	End mean: November 22	1984- 1985	Bost and Jouventin 1991
			Chick departure	November 30- December 21	1984- 1985	
				January 20- February 17	1985	Bost and Jouventin 1990b
			Replacement clutch	August 10- 8	1984- 1987	
				1 st start: August 7- 17 1 st mean: September 9- 19 1nd: October 7- November 15	1984- 1985	Bost and Clobert 1992
Kerguelen Islands	Estacade	48°45' S, 68°45' E	Egg laying	August 14- September 24	1987, 2002, 2003	Lescroël et al. 2009
				Start: August 29	Unknown	Paulian 1953 ^b
			Hatching	September 20- October 24	1987, 2002, 2003	Lescroël et al. 2009
Macquarie Island	Macquarie Island	54°61' S, 158°85' E	Egg laying	Start: September 12	Unknown	Tulloch 1916 ^a
				Start: September 9	1949	Gwynn 1953
				Start: September 11- 18	1912- 1913	Falla 1937

					Adult moult	Start: January 2	1979	Reilly and Kerle 1981
					Courtship	Start: October 13	1949	Downes et al. Young 1959
					Egg laying	Start: October 22- 26	1949- 1950	Gwynn 1953
					Egg laying	October 15- 26	1949- 1953	Downes et al. 1959
					Hatching	Start: November 26- 30	1949- 1950	
						Start: November 30- December 1	1929	Falla 1937
Chinstrap	Sub-Antarctic Islands	South Shetland Islands	Deception Island	63°00' S, 60°40' W	Return to colony	Mean: October 26	Not specified	Conroy et al. 1975
					Egg laying	1 st Mean: November 4		
					Hatching	December 14- 27	1996- 1997	Moreno et al. 1998
						December 19- January 10	1994- 1995	Barbosa et al. 1997
						December 15- 31	1991- 1994	Viñuela et al. 1996
			Elephant Island	61°08' S, 55°07' W	Return to colony	Mean: November 8- 10	Not specified	Conroy et al. 1975
					Hatching	Start: December 15	1970- 1971	Conroy et al. 1975b
						End: December 27- January 1		
						December 16- January 4	1976- 1977	Furse 1979
			King George Island	62°10' S, 58°39' W	Return to colony	October 28- November 8	1980	Jablonski 1987

				Mean: November 8	1981- 1982	Trivelpiece and Volkman 1984
				November 2- 18	1977- 1981	Trivelpiece and Volkman
				Egg laying	Peak: November 27	1979
				Hatching	December 22- January 5	Trivelpiece and Volkman 1987
South Orkney Islands	Signy Island	60°43' S, 45°38' W	Return to colony	September 24- November 14	1947- 1987	Rootes 1988
				Start: November 5- 8	1981- 1981	Lishman 1985
			Egg laying	Start: November 1	1970- 1971	Conroy et al. 1975
				November 14- December 1	Prior to 1987	Rootes 1988
				November 28- December 20	1980-1982	Lishman 1985
				1 st : November 28- December 10 2 nd : December 2- 14	1973	Marchant and Higgins 1990
				1 st mean: November 25	1970- 1971	Conroy et al. 1975
			Hatching	December 24- January 11	Prior to 1987	Rootes 1988
				January 3- 24	1980-1981	Lishman 1985
			Chick departure	Start: December 26	1970- 1971	Conroy et al. 1975
				February 24- March 2	1981- 1982	Lishman 1985

						End: March 12	1970- 1971	Conroy et al. 1975				
					Adult moult	February 26- March 10						
					Laurie Island	60°46′ S, 44°42′ W	Return to colony	Start: November 2- 16	1995- 1998	Carlini et al. 2005		
								November 2- 14	1903- 1904	Clarke 1906		
					Egg laying	Peak: December 5- 17	1995- 1998		Carlini et al. 2005			
						Start: November 27	1904		Clarke 1906			
					Hatching	Start: January 7						
					Adult departure	End: April 28	1903- 1904					
					Scotia Arc	Western Antarctic Peninsula	Waterboat Point	64°48′ S, 62°43′ W	Return to colony	Start: November 1	1921	Bagshawe 1938
								Egg laying	Start: November 25- 29			
Adélie	East Antarctica	Queen Maud Land	Lützow-Holm Bay	69°10′ S, 37°30′ E	Return to colony	Mean: October 31- November 4	1990- 1991	Watanuki 1993				
					Return to colony	Start: October 1- 22	1990- 2006	Emmerson et al. 2011				
		Mac. Robertson Land	Béchervaise Island	67° 35′ S, 62° 49′ E		Mean: November 1						
						Start: October 20- 25	1974, 1980- 1981, 1988	Kerry et al. 1993				
						October 22- November 22	1990- 1992	Kerry et al. 1993				
					Egg laying	Mean: November 20	1990- 2006	Emmerson et al. 2011				
			November 11- December 5	1990- 1992	Kerry et al. 1993							

Wilkes Land				Hatching	Mean: December 25	1990- 2006	Emmerson et al. 2011
					December 19- January 10	1990- 1992	Kerry et al. 1993
				Post-guard	Mean: January 16	1990- 2006	Emmerson et al. 2011
					January 18- February 3	1990- 1992	Kerry et al. 1993
				Chick departure	February 10- March 6	1990- 2006	Emmerson et al. 2011
					February 18- March 5	1990- 1992	Kerry et al. 1993
	Mawson Station	67° 60' S, 62° 86' E	Return to colony	October 20- 22	1974, 1980, 1981, 1988, 1990		
	Prydz Bay	68°33' S, 77° 54' E	Return to colony	Start: October 7- 16	1981- 1984, 1986- 1987	Whitehead et al. 1990	
	Casey Station	66° 28' S, 110° 52' E	Return to colony	Mean: October 15	Unknown	Cowan 1979 ^a	
	Wilkes Station	66° 15' S, 110° 32' E	Chick moult	February 17- March 10	1958- 1960	Penney 1967 ^a	
			Adult moult	Mean: March 5			
	Haswell Island	66° 31' S, 93° 00' E	Return to colony	Start: October 14	1961- 1962	Pryor 1968	
				Start: October 19	1956	Korotkevich 1964 ^c	
				October 20	1958	Makushok 1959 ^c	
				Start: October 14- 19	1961- 1963	Nudel'man 1966 ^a	
			Courtship	Start: October 22	1961- 1962	Pryor 1968	
				October 30- November 30	1956	Korotkevich 1964 ^c	

			Egg laying	1st: November 12 2 nd : November 15	1961- 1962	Pryor 1968
				Start: November 8	1956	Korotkevich 1964 ^c
				Start: November 12	1958	Makushok 1959 ^c
			Hatching	Start: December 15	1961- 1962	Pryor 1968
				Start: December 15	1956	Korotkevich 1964 ^c
			Chick moult	January 31- February 28	1957	
			Adult moult	March 1- 10		
				Start: February 1	1958	Makushok 1959 ^c
			Adult departure	End: March 28	1961- 1962	Pryor 1968
				End: March 20	1957	Korotkevich 1964 ^c
				End: March 29	1958	Makushok 1959 ^c
Adélie Land	Dumont D'Urville Station	66° 40' S, 140°01' E	Return to colony	Start: October 22- 25	1995- 1996	Rodaryet al. 2000
			Egg laying	Start: November 12- 14		
				Mean: November 17	2006-2008	Beaulieu et al. 2010
			Hatching Hatching	Mean: December 23		
				Start: December 16- 18	1995- 1996	Rodary et al. 2000
			Post-guard	Start: January 9-16	1996- 1997	
	Port Martin	66°49' S, 141°24' E	Hatching	Start: December 13	1950	Sladen 1958

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George V Land	Cape Denison	67°00' S, 142°66' E	Return to colony	Start: October 12-17	1912-1913	Sladen 1958
				October 17	1913	Falla 1937
			Egg laying	Start: November 3-9	1912-1913	Sladen 1958
				Start: November 9	1913	Falla 1937
			Hatching	Start: December 17		Sladen 1958
	Cape Gray	66°51' S, 143°22' E		Start: December 17		Falla 1937
			Hatching	Start: December 17	1912	Falla 1937
Victoria Land	Cape Adare	71°28' S, 170°23' E	Return to colony	October 13	1921- 1922	Bagshawe 1938
				October 13- November 1	1910- 1913	Levick 1914
				Start: October 13- 14	1899, 1911	Sladen 1958
			Egg laying	Start: November 2-3		
			Hatching	Start: December 4-9		
	Cape Hallett	72°18' S, 170°12' E	Adult departure	March 14	1921- 1922	Bagshawe 1938
			Return to colony	Start: October 9- 13	1959- 1960	Reid 1964
			Egg laying	Start: October 30- November 3	1959- 1960	
			Hatching	December 5-7		

	Wood Bay	74°21' S 165°10' E	Return to colony	Median: October 30- November 12 End: November 10- 17	1994- 1999	Olmastroni et al. 2000
			Egg laying	November 6- 29		
				End: November 9 - 19	1999-2001, 2003	
			Hatching	December 16- 17		Olmastroni et al. 2004
				December 9- January 3	1994- 1999	
			Post-guard	Mean: January 8- 14	1999-2001, 2003	
			Post -guard	January 3- 22	1994- 1999	
			Chick departure	February 1- 21		
Princess Elizabeth Land	Davis Station	68°33' S, 78°15' E	Return to colony	October 4- 17	Unknown	Johnstone et al. 1973 ^a
Ross Island	Cape Bird	77° 13' S, 166° 28' E	Return to colony	Start: October 24	1977-1978	Davis 1982b
				1 st mean: November 11- 13	1967- 1970	Spurr 1975
				2 nd mean: November 15- 16s		
			Egg laying	Start: November 12	1977-1978	Davis and McCaffrey 1986
				November 6- December 1		Davis 1982b
				Mean: November 15	1967- 1971	Spurr 1975

		Chick departure	Start: January 28	1967- 1968	
Cape Crozier	77°50' S, 169°33' E	Return to colony	October 18- 25	1962, 1964, 1966- 1969, 1974- 1975	Ainley et al. 1983
			October 24- November 27	1974	Ainley 1978
			Start: October 20	1902	Sladen 1958
			Egg laying	Start: October 30- November 5	Ainley et al. 1983
		Hatching	Mean: November 18	1963- 1974	Ainley 2002
			Start: November 9	1902	Sladen 1958
Cape Royds	77°33' S, 166°09' E	Return to colony	December 8- January 9	1970- 1971	Oelke 1975
			October 22- 24	1968-1969	Ainley and Leresche 1973
		Egg laying	Start: October 26	1959- 1960	Taylor 1962
			End: November 16-20	1968-1969	Ainley and Leresche 1973
			November 4- December 4	1959-1960	Taylor 1962
			Start: November 7	1961	Stonehouse 1963
			1 st : November 9- 22 2 nd : November 11- 22	1965	Yeates 1971
		Hatching	1 st : December 15- 29 2 nd : December 16- 29		

				Post-guard	Start: January 9-20	1966	
				Adult moult	Start: February 1- 12 End: February 25	1959-1960	Taylor 1962
				Chick moult	Start: February 1		
				Chick departure	January 30- February 25		
					Start: January 25	Unknown	Yeates 1968
					End: February 20	1963- 1966	Spellerberg 1971
Scotia Arc	Western Antarctic Peninsula	Hope Bay	63°38' S, 56°98' W	Return to colony	Start: September 20- October 7	1945- 1948, 1952	Sladen 1958
					Start: October 17	1948- 1951	
				Egg laying	Start: November 1- 6	1945- 1948, 1952	
					Start: November 1	1948- 1951	
				Hatching	December 5- 16	1945- 1948, 1952	
					Start: December 8	1948- 1951	
				Chick moult	January 21- February 4		
		Booth Island	65°08' S, 64°00' W	Return to colony	Start: October 15	1904	
				Egg laying	Start: November 3		
		Paulet Island	63°58' S, 55°78' W	Return to colony	Start: October 12	1903	
		Arthur Harbour	64°46' S, 64°04' W	Return to colony	October 15- 16	1956	Holdgate 1963

				Egg laying	November 12- 23	1955- 1957			
				Adult departure	February 13- 16	1967			
				Petermann Island	65°10' S, 64°10' W	Return to colony	Start: October 22	1909	Sladen 1958
							Start: October 12		Gain 1914
				Egg laying	Mean: November 15	2004- 2008	Lynch et al. 2009		
					Start: November 9	1909	Sladen 1958		
Sub-Antarctic Islands	South Shetland Islands	King George Island	62°10' S, 58°30' W	Return to colony	Mean: October 8- 19	1981- 1983	Trivelpiece and Volkman 1984		
					Start: October 20	1977- 1978	Trivelpiece and Volkman 1979		
					September 28- October 18	1980	Jablonski 1987		
					Egg laying	Start: October 25- November 6	1991- 2009	Hinke et al. 2012	
						Peak: November 3 End: November 15	1977- 1979	Trivelpiece and Volkman 1979	
					Hatching	November 28- December 10	1981- 1982	Trivelpiece and Volkman 1987	
		Elephant Island	61°08' S, 55°07' W	Hatching	December 13- 27	1976- 1977	Furse 1979		
		South Orkney Islands	Signy Island	60°42' S, 45°36' W	Return to colony	September 26- October 22	2005	Dunn et al. 2011	
						Start: October 4- 8	1903, 1904, 1950, 1953	Sladen 1958	

Egg laying	Start: October 7	1948- 1951	
	Start: October 8	1950	Sladen 1953
	September 20- October 8	1947- 1987	Rootes 1988
	Start: September 21- 28	1980- 1982	Lishman 1985
	October 22- November 4	1947- 1987	Rootes 1988
	October 27- November 20	1980- 1982	Lishman 1985
	Start: October 27- November 2	1903, 1904, 1950, 1953	Sladen 1958
	Start: October 29	1948- 1951	
	November 2- 29		
	October 29- November 19	1950	Sladen 1953
Hatching	November 27- December 12	1947- 1987	Rootes 1988
	December 3- 17	1980-1982	Lishman 1985
	Start: December 4- 12	1903, 1904, 1950	Sladen 1958
	Start: December 4	1948- 1951	
	Start: December 4	1950	Sladen 1953
Post- guard	Start: December 23	1948- 1951	Sladen 1958
Chick departure	February 4- 15	1980-1982	Lishman 1985

		Adult moult	Start: February 7- March 3	2005	Dunn et al. 2011
		Adult departure	January 12- February 4	2005	
			End: March 1	1950	Sladen 1958
Laurie Island	60°46' S, 44°42' W	Return to colony	Start: September 27- October 7	1995- 1998	Carlini et al. 2005
			Start: October 7- 8	1903- 1904	Clarke 1906
		Egg laying	Peak: November 7- 17	1995- 1998	Carlini et al. 2005
			Start: October 29- November 2	1903- 1904	Clarke 1906
		Hatching	Start: December 6- 12		
		Chick moult	Start: January 7	1904	
		Adult departure	End: February 11	1904	

^aAs cited in Marchant and Higgins 1990

^b As cited in Williams 1979

^cAs cited in Pryor 1968

1.4 Phenology in *Pygoscelis* Penguins

The genus *Pygoscelis* includes three species: gentoo, chinstrap, and Adélie penguins. Also known as brush-tailed penguins because of their defining tail feathers, the three species inhabit the Antarctic continent and sub-Antarctic islands with overlapping ranges (Borboroglu and Boersma 2013). Recent studies have estimated roughly 3.79 million pairs of Adélie (Lynch and LaRue 2014), 387,000 pairs of gentoo (Borboroglu and Boersma 2013), and 8 million pairs of chinstrap penguins (Bird Life International 2014) within their respective ranges, collectively making up roughly 90% of Antarctic avian biomass (Williams 1995). Studies have revealed changes in the population between species, particularly along the Western Antarctic Peninsula (WAP), where the three species' ranges overlap and extreme warming is taking place, shifting the timing of sea ice establishment and retreat (Vaughan et al. 2003, Stammerjohn et al. 2008). These population changes include decreasing populations of Adélies around the Antarctic peninsula (Ducklow et al. 2007) but increasing Adélie populations in East Antarctica and the Ross Sea (Croxall et al. 2002, Lyver et al. 2014), while chinstraps are in decline throughout their range (Trivelpiece et al. 2011), and gentoo populations appear to be increasing (Lynch et al. 2008), although some colonies are stable, increasing, or decreasing for each of these species (see Borboroglu and Boersma 2013). *Pygoscelids* are well studied, with over 400 papers existing on Adélie penguins alone (Ancel et al. 2013) and their life history traits are well documented. In particular, their phenology has been a focus of study for the past

century, although large gaps exist both spatially and temporally in our understanding of their annual cycle.

Pygoscelids share similar traits within their individual breeding cycles and each phase of their phenology is relatively well defined because of synchronicity within colonies. For example, all three species typically lay a two-egg clutch (Borboroglu and Boersma 2013). Hatching dates tend to be synchronous within colonies (Ainley 2002), which holds true in many colonial seabirds (Gaston 2004). Pygoscelid parents take turns incubating and provisioning young, although there are variations in these patterns between species (Trivelpiece et al. 1987). In addition, chicks form aggregations during the post-guard period in all pygoscelids although the underlying mechanism of this behaviour is not well studied in gentoos (Wilson 2009).

Although variations exist in the timing of phases within the annual cycle of each of these three species, certain phenological traits appear to be consistent across their range and between years. For example, in gentoos, these intrinsic parameters include a two week nest attendance period prior to egg laying, a laying interval of approximately three days between eggs, an incubation period of 33-37 days, and general chick growth patterns (Bost and Jouventin 1991). While in Adélies, eggs are also laid roughly three days apart (Spurr 1975), incubation generally lasts 32- 34 days, and the guard period lasts about 22 days (Borboroglu and Boersma 2013). Similarly, in chinstraps, laying intervals are four days (Lishman 1985), incubation lasts 33- 36

days, and the guard period lasts approximately four weeks (Borboroglu and Boersma 2013).

Major differences also exist between species, particularly in relation to winter migration, incubation shifts, and the timing of breeding. During the winter, chinstrap and Adélie penguins are known to migrate long distances, often to common overwintering grounds (Clarke et al. 2003, Biuw et al. 2009, Hinke et al. 2015), while gentoos are known to stay resident near their breeding site, likely due to their near-shore foraging ecology (Bost and Jouventin 1990). In relation to incubation schedules, in chinstraps and gentoos, females always undergo incubation first (Lishman 1985, Watanuki 1993), while the opposite holds true with Adélies; males are always the first to incubate (Sladen 1958, Taylor 1962, Lishman 1985), except in rare cases of reverse incubation schedules (Ainley and Leresche 1973). In terms of breeding, when species overlap at colonies during the breeding season, Adélies are the first to arrive, followed by gentoos, and eventually chinstraps (Trivelpiece and Volkman 1987). Their delayed breeding timing, in relation to each other, reflects the competition between species for common foraging grounds and ideal nest sites and materials.

Given these similarities and differences, the genus varies substantially in phenology between sites and years (Table 1.1). Gentoos experience the most annual variation in phenology of the three pygoscelid species (Bost and Jouventin 1990, Lescroël et al. 2009), which is typical for species highly dependent on resources with inconsistent availability (Ashmole 1963, Boersma 1976, Potts et al. 1980, Croxall et al.

1988, Montevecchi 1993). Even between colonies located relatively close (< 5 km), the timing of breeding can be asynchronous up to two weeks on South Georgia Island (Williams 1990), with changes in local foraging condition providing the most plausible explanation for the variation (Bost and Jouventin 1990, Bost and Jouventin 1991). At a larger geographic scale, the Crozet and South Georgia gentoo colonies differ in mean laying dates by as much as three months, while laying dates in colonies of macaroni penguins at these same locations differ by only three weeks (Bost and Jouventin 1990). Farther south, laying periods are also shorter than northern colonies, differing by as many as 126 days, likely because of the common practice of laying second clutches in northern colonies (Bost and Jouventin 1990). However, within a colony, timing is often highly synchronous (Downes et al. 1959, Trivelpiece and Volkman 1987) and can depend on colony structure and nesting substrates (Williams 1990).

In contrast, Adélies have been known to exhibit relatively less annual variation in their breeding cycle, likely because of the link between the timing of sea ice extent and their phenology. However, substantial differences exist between the initiation of the annual cycle in Adélies in East Antarctica and the Scotia Arc and sub-Antarctic islands. In particular, phenology is advanced by 10-14 days at Signy Island in the South Orkney Islands compared to populations in the Ross Sea (Ainley 2002). Studies have linked these phenological changes within species to 1) an earlier increase in photoperiod around the Antarctic Peninsula, due to its lower latitude, and 2) earlier retreat of sea ice in the Antarctic Peninsula, which allows for a faster return to the

colony after the winter season (Ainley 2002). In addition, in Adélie penguins, the arrival, clutch initiation, and initial hatching dates are delayed with increasing latitude (Figure 1.2, Table 1.2), likely because of the same links between photoperiod, sea ice retreat, and the species' phenology.

Chinstrap, on the hand, are not as well studied in the context of spatial variation in phenology. All studies on chinstrap phenology, which provide dates and therefore variation in timing of particular phases, have been conducted on the South Orkney Islands and South Shetland Islands (with the exception of one one-year study at Waterboat Point on the WAP, Bagshawe 1938, Table 1.1), leaving gaps in our understanding of phenology of chinstraps inhabiting the Antarctic Peninsula and sub-Antarctic islands (Figure 1.3). However, given the known phenology of the species on the South Orkney and South Shetland Islands, there appears to be great variation in the return dates, and therefore subsequent breeding timing, with the return dates ranging from September 24 to November 16 (Rootes 1988, Carlini et al. 2005). However, considering the large gaps in our understanding of chinstrap phenology across their range, competition between Adélie and chinstrap penguins has been well documented and provides insight into how one's presence influences the other's phenology.

By examining inter-species competition between Adélies and chinstraps, we are able to better understand what dictates their phenology. When the two species overlap in breeding location, studies have found that Adélies breed on average 28

days earlier (Carlini et al. 2005). This asynchrony in breeding timing between the two species may allow for reduced competition for nest sites (Carlini et al. 2005) and for food during chick rearing periods (Trivelpiece and Volkman 1987). Chinstraps often displace Adélies by usurping nests during the incubation period, which decreases Adélie breeding performance (Carlini et al. 2005). This competitive behaviour may stem from the asynchrony in the breeding cycles of the two species; because Adélies return to the colony and begin the breeding process earlier, when established, larger chinstraps arrive, they are arriving fresh from foraging and able to compete with inexperienced Adélie adults who have been fasting for roughly three weeks (Trivelpiece et al. 1984). In relation to food resources, roughly 70% of the krill fed to chinstrap chicks is caught by parents after Adélie chicks fledge (Trivelpiece and Volkman 1987), suggesting that chinstraps with delayed breeding cycles benefit from reduced inter-species competition. Given these two factors, it appears that the asynchronous breeding in the two species stems from the need to offset competition for prey resources during peak chick provisioning times, while the timing of nesting is a consequence of this disparity at the detriment of Adélie fitness. Competition may become more frequent as pygoscelid populations expand their respective ranges and should become a focus of study between all three pygoscelid species.

The known causes of variation in each of the major phases of the annual cycle will be explored more in depth in the following section, to highlight the ecological significance of their phenology.

Table 1.2. The duration of recorded phases within the annual cycle of gentoo, chinstrap, and Adélie penguins. When available, ranges are included instead of means. See Figure A.1 for definitions of each phase.)

Species	Region	Location	Site	Latitude, Longitude	Annual Cycle Phase	Duration	Citation
Gentoo	Sub-Antarctic Islands	Argentina	Martillo Island	54°54' S, 67°23' W	Incubation	1st mean: 37 days	Ghys et al. 2008
					Incubation	36.5- 37 days	Otley et al. 2005
					Egg laying interval	3.2 days	Roberts 1940
		Falkland Islands	Volunteer Beach	51°29' S, 38°02' W	Incubation	Mean: 35.2- 35.3 days	Williams 1990
					Guard	Mean: 25.4- 29.9 days	
					Chick departure	75- 100 days old	
		South Georgia	Bird Island	54°00' S, 38°02' W	Incubation	Mean: 35.2- 35.3 days	Williams 1990
					Guard	Mean: 25.4- 29.9 days	
					Chick departure	75- 100 days old	
					Egg laying	125- 138 days	Bost and Jouventin 1990b
					Egg laying interval	3- 5 days	Despin 1972 ^a
						3.2 days	Bost and Jouventin 1991
					Incubation	1st: 34- 42 days	
						2nd: 32-41 days	
						33- 35 days	Despin 1972 ^a
					Hatching interval	0- 2 days	
					Post-guard	20 days old	
						20-37 days old	Bost and Jouventin 1991
					Chick moult	Start: 34- 47 days old	
						End: 74- 95 days old	
					Replacement Clutch	1st: 35- 40 days	

					Incubation	2nd: 33- 38 days	
	Kergulen Islands	Estacade	48°45' S, 68°45' E		Egg laying	26- 29 days	Lescroel et al. 2009
					Incubation	1st: mean: 36.0 days	
						2nd: mean: 33.8 days	
					Hatching interval	0-5 days	
	Prince Edward Islands	Marion Island	65°20' S, 37°51' E		Guard	End: 20- 33 days old	Williams 1980
					Chick departure	100- 105 days old	
	Heard and McDonald Islands	Macquarie Island	54°61' S, 158°85' E		Egg laying interval	3 days	Downes et al. 1959
						3- 4 days	Gwynn 1953
					Incubation	34- 35 days	
					Adult moult	15- 21 days	Reilly and Kerle 1981
	Scotia Arc	Western Antarctic Peninsula	Waterboat Point	64°48' S, 62°43' W	Incubation	Mean: 37 days	Bagshawe 1938
	Unknown	Unknown	Unknown	Unknown	Incubation	31- 35 days	Murphy 1936 ^b
					Chick departure	80- 105 days	Williams 1995 ^c
Chinstrap	Sub-Antarctic Islands	South Orkney Islands	Signy Island	60°42' S, 45°36' W	Nesting	10- 19 days	Lishman 1985
					Egg laying interval	3 days	
					Incubation	1st: 33- 39 days	
						2nd: 31- 38 days	
					Post-guard	19- 36 days old	
					Chick departure	48- 59 days old	
					Chick departure	Mean: 17.4- 22.1 days	Trivelpiece and Trivelpiece 1990

Adélie	East Antarctica	Mac. Roberston Land	Deception Island	63°00' S, 60°40' W	Post-guard	Mean: 22.3-24.6 days old	Vineula et al. 1996
					Chick departure	Mean: 53.1-57.4 days old	
		Queen Maud Land	Béchervaise Island	67°35' S, 62°49' E	Chick departure	56 days old	Kerry et al. 1993
		Ross Island	Lützow-Holm Bay	69°10' S, 37°30' E	Incubation	1st mean: 35.6 days 2nd mean: 33.9 days	Watanuki 1993
					Incubation	32- 38 days	
		Cape Hallett	Cape Royds	72°19' S, 170°16' E	Courtship	4- 14 days	Stonehouse 1963
					Egg laying interval	2- 4 days	
					Incubation	1st: 33- 39 days 2nd: 30- 37 days 33- 43 days	Taylor 1962
					Guard	1st chick: 16- 31 days 2nd chick: 14- 30 days 17-32 days	
					Adult moult	9- 17 days	Yeates 1968
					Chick departure	55 days old	
			Cape Bird	77° 13' S, 166° 28' E	Courtship	8-16 days	Davis 1982b
					Incubation	2nd: 32- 38 days 1st: 33- 37 days 2nd: 32-34 days	
					Guard	16- 34 days old	Spurr 1975
					Chick departure	46-55 days old	
			Cape Crozier	77°50' S,	Chick departure	46-55 days old	Ainley and

169°33' E				Schlatter 1972	
				Mean: 45.5-50 days old	Ainley et al. 1983
Victoria Land	Cape Adare	71°28' S, 170°23' E	Egg laying interval	2-3 days	Levick 1914
			Incubation	32 days	
Wilkes Land	Wilkes Station	66°15' S, 110°32' E	Egg laying interval	1- 4 days, Mean: 2.2 days	Penney et al. 1968
			Incubation	1st mean: 37.2 days	
				2nd mean: 34.6 days	
			Adult pre-moult	3- 7 days	Penney 1967
			Adult Moulting	6- 28.5 days	
			Adult post-moult	2- 4 days	
Scotia Arc	Western Antarctic Peninsula	Haswell Island	66°31' S, 93 00' E	Incubation	33- 36 days Pryor 1968
		Hope Bay	63°38' S, 56°98' W	Egg laying interval	3- 4 days, Mean: 3.0- 3.7 days
				Incubation	1st: 36- 38 days
					2nd: 35- 36 days
					Mean: 36 days Sladen 1953
Sub-Antarctic Islands	South Orkney Islands	Petermann Island	65°10' S, 64°10' W	Adult moult	20 days Gain 1914
		Signy Island	60°42' S, 45°36' W	Nesting	11- 27 days Lishman 1985
				Egg laying interval	3 days
					2- 4 days, Mean: 3.2 days
					Mean: 2.3- 3 days Marchant and Higgins 1990
				Incubation	1st: 33- 39 days Lishman 1985

					2nd: 32- 38 days	
					1st: 35- 37 days	Sladen 1958
					2nd: 33- 35 days	
					Guard	17- 28 days
					Post-guard	13- 28 days old
					Adult moult	15-22 days
					Chick departure	54- 64 days old
					Laurie Island	60°46' S, 44°42' W
					Incubation	31-33 days
					Chick departure	Mean: 21 days
						Trivelpiece and Trivelpiece 1990
						50-55 days old
						Volkman and Trivelpiece 1980
Unknown	Unknown	Unknown	Unknown	Incubation	33- 37 days	Sapin-Jaloustre and Bourliere 1951 ^b
					1st: 35- 38 days	Richdale 1957
					2nd: 33- 36	
					Adult moult	9- 16 days
						Cendron 1953 ^b

^aAs cited in (Marchant and Higgins 1990)^bAs cited in (Richdale 1957)^cAs cited in (Borboroglu and Boersma 2013)^dAs cited in (Ainley et al. 1983)

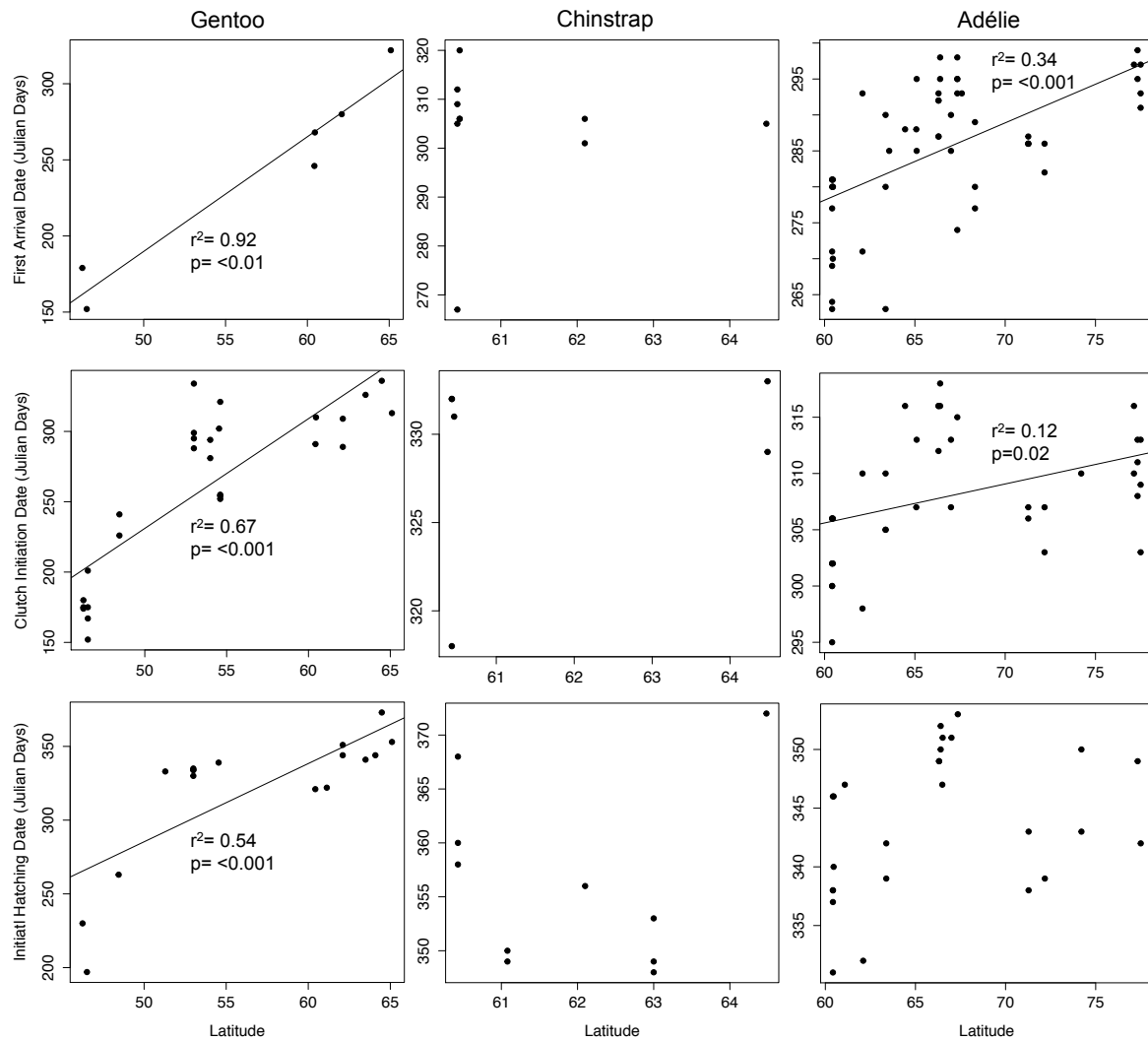


Figure 1.2. Linear models of 1) first arrival dates, 2) first clutch initiation dates, and 3) initial hatching dates vs. latitude (° S) of colony location for gentoo (*Pygoscelis papua*), chinstrap (*Pygoscelis Antarctica*), and Adélie penguins (*Pygoscelis adeliae*). Best-fit lines represent significant values ($P < 0.05$). All dates expressed as Julian days with the exception of dates in January and February where Julian day was added to 365 (eg. January 15 = 380). All data and citations found in Table 1.2.

1.5 Variations in the Annual Cycle

Beginning with the start of the breeding season, adults must time their return to the colony so that they arrive early enough to allow time for courtship, while still leaving substantial time to build condition and fat reserves during winter. Because adults must fast during courtship and the first incubation spell, before alleviated of nest duties by their partner, building fat reserves prior to arrival is necessary for the survival of both themselves and their young. Returning to the breeding site is likely dictated by a change in photoperiod, which triggers hormonal changes and hyperphagia (Ainley 2002). However, contrasting factors may limit the commencement of breeding, including the availability of snow-free nesting sites and competition for resources with other pygoscelid species (Gwynn 1953, Williams 1990). Males typically arrive first (Ainley 2002) and individuals that arrive earlier tend to be more experienced breeders (Trivelpiece and Volkman 1984), healthier (Moreno et al. 1998), and older in age (LeResche and Sladen 1970), and often have higher breeding success in the subsequent season (Spurr 1975, Bost and Jouventin 1984, 1991, Viñuela et al. 1996).

The timing of the next phase, courtship, is rarely studied but typically lasts 8-22 days in Adélies (Davis 1982b, Emmerson et al. 2001); no studies to date have examined variables that change the duration of this critical period within the life cycle of pygoscelids. However, one study found that pairs that nest either earlier or later

than the average are more likely to desert nests, suggesting that the timing of nest-building, as part of the courtship phase, may have fitness consequences (Davis 1982b).

The following phase, egg laying, is the most studied in the context of variations in timing. However, because changes in each phase within the annual cycle contribute to the timing of subsequent phases, the factors controlling egg laying dates are closely linked with those associated with arrival dates. Studies have consistently found year-to-year variation in laying and hatching dates (Bost and Jouventin 1990, Viñuela et al. 1996, Emmerson et al. 2011), due to two main factors; 1) variation in sea ice extent, especially prolonged pack ice, may delay a penguin's return to the breeding colony and subsequently alter the timing of later phases (Trivelpiece and Volkman 1987), and 2) annual changes in food availability may cause later breeding dates, as adults need longer to build up reserves and condition (Viñuela et al. 1996). Additional environmental factors, including wind conditions (Ainley and Leresche 1973) and sea surface (Bost and Jouventin 1990) and air temperatures (Lynch et al. 2012b), can also be influential in the timing of breeding. For example, mean October air temperatures have been shown to influence clutch initiation dates (CIDs) in all three pygoscelid species (Hinke et al. 2012, Lynch et al. 2012b), as ambient environmental conditions likely influence the availability of snow-free nesting sites.

The egg laying dates of gentoo penguins are particularly interesting because the species exhibits large year-to-year and spatial variation in the timing. In gentoos, significant differences in the timing of breeding are apparent between populations

inhabiting sub-Antarctic islands in the Indian and Pacific compared with those in the Scotia Arc (Bost and Jouventin 1990, Otley et al. 2005). The sub-Antarctic populations lay eggs substantially earlier in the winter and are known to frequently lay second clutches when nests fail at roughly the same time as the Scotia Arc populations are laying their first clutches in the spring (Trivelpiece and Volkman 1987, Bost and Clobert 1992). Subsequently, colonies located farther north are known to experience lower breeding success than their southern counterparts (Bost and Jouventin 1990, Williams 1990, Quintana and Cirelli 2000, Lescroël et al. 2009). This latitudinal variation and the common practice of laying second clutches later in the season is unique to gentoos within the pygoscelids and offers insight into fine scale environmental changes that may influence phenology in penguins.

After eggs are laid, incubation commences and parents must begin trading off nest duties by participating in “incubation spells” (Spurr 1975). At this time, partners must coordinate these spells meticulously so that they are in strong condition to raise their young. In Adélies, the male is usually the first to incubate once the first egg has been laid (Sladen 1958, Taylor 1962). However, in what Ainley and Leresche (1973) deemed a *reversed incubation schedule*, early arriving males may deplete fat reserves before eggs are laid and are therefore only successful in breeding if able to forage immediately, leaving the female on the nest, waiting to be alleviated from her duties. Increased foraging trip duration, as a result of different sea ice conditions between years, can decrease breeding success in Adélie penguins (Clarke et al. 2002), although the outcome differs between colony locations (Nicol et al. 2008, Beaulieu et al. 2010).

In particular, the timing of the first incubation spell, when the female first returns to relieve her partner from nest duty, seems to be particularly important, as a delay in return can lead to nest desertions (Davis 1982b). As a proximate explanation, hormones, specifically high corticosterone and low prolactin levels, which stimulate foraging and incubation behaviour, have led to nest abandonment as adults choose self-maintenance over breeding success during this period (Spée et al. 2010). This trade-off during incubation serves as an example of life history theory where an individual must consider its ability to reproduce in the future rather than the survival of its offspring at present (Stearns 1992).

Following incubation, eggs begin to hatch, and hatching dates have been known to vary due to colony size, nest location within a colony, the sex of chicks, and egg order, which affect key dates within a chick's life cycle later in life. In chinstraps, studies have found that larger colonies experience earlier hatching dates overall and nests located centrally within a sub colony hatch earlier than those at the periphery (Barbosa et al. 1997). In addition, isolated sub colonies have shown delayed hatching dates (Fargallo et al. 2006, Martín et al. 2006). One study found that male, second-hatched and large eggs exhibit a shorter hatching period when compared with female, first-hatched, small eggs in chinstraps (Fargallo et al. 2006). As hatching date is delayed, chicks then begin the post-guard period and fledge at a younger age (Viñuela et al. 1996), demonstrating the consequences one period has on later phases within the breeding cycle.

After chicks hatch, they are guarded by their parents in order to provide necessary thermoregulation (Taylor 1985) and protection from predators (Davis 1982a). During this period, known as the “guard phase,” chicks are demanding in their food requirements; therefore, food abundance dictates the timing and duration of this period. In polar ecosystems, sea ice extent and the timing of sea ice retreat influences annual primary productivity within the water column (Quetin and Ross 2001), particularly phytoplankton abundance (Hunt and Stabeno 2002). Because phytoplankton serve as the main diet of krill (*Euphausia superba*), and krill is an essential prey of many penguin species (Borboroglu and Boersma 2013), the timing of sea ice retreat may indirectly influence the timing of breeding (Ainley 2002), although evidence supports the idea that some species (eg. Adélies) are able to adjust foraging duration and prey species without adjusting phenology (Beaulieu et al. 2010). In Adélies, food requirements peak during the guard and post-guard periods, as adults must forage for themselves and their demanding chicks (Chappell et al. 1993). Within this period, foraging area and timing is limited, as chicks must be fed regularly (Angelier et al. 2008).

In order to keep up with provisioning demands, parents continue to undergo rotating nest duties. The timing of nest relief directly impacts breeding success as inadequate timing leads to chick mortality via starvation and nest desertions (Davis and McCaffrey 1986). In addition, a nest relief schedule must be synchronized between partners with precision so that the time chicks are unguarded is minimized to reduce time exposed to cold conditions and potential predation (Müller-Schwarze and

Müller-Schwarze 1980). The timing of these partner exchanges is influenced by sea ice extent and severe weather conditions (Olmastroni et al. 2004), which likely impacts foraging ability and therefore time needed to find adequate prey. In general, gentoos exhibit shorter nest relief patterns compared with other penguin species, which is likely due to their near shore foraging strategy (Lescroël et al. 2009). Because penguins are born in an altricial state, the timing of nest reliefs is critical to the survival of chicks and their growth.

As the chicks grow, parents begin leaving them unattended in order to keep up with their rising food demands and the post-guard phase begins. Some studies suggest that the decision to leave chicks unguarded and therefore commence the post-guard phase is likely made by adults, rather than chicks (Williams 1990) and adults in better condition or more experienced leave their chicks unguarded at a later age (Taylor 1962, Viñuela et al. 1996). Longer incubation periods can lead to parents leaving chicks unguarded, thus commencing their post-guard period when they are significantly younger (Vleck et al. 2000), which may decrease their chance of survival. During this stage, chicks cope with the lack of parental care by forming aggregations (aka. crèches) to better thermoregulate, increase vigilance against predators, and avoid aggressive advances from unrelated adults (Davis 1982a, Penteriani et al. 2003). It is well known that variation exists in the timing of this phase (Davis 1982a), and past studies have provided evidence that inter-annual environmental variation can delay the start date of the post-guard period (Olmastroni et al. 2004, Nicol et al. 2008, Beaulieu et al. 2010).

Following the post-guard period, chicks moult their feathers and begin the process of fledging, leaving their nest area and often the breeding site altogether. The timing of fledging in all pygoscelids is well-documented (Conroy et al. 1975a, Spurr 1975, Lishman 1985, Bost and Jouventin 1990, Kerry et al. 1993, Crawford et al. 2003, Olmastroni et al. 2004, Emmerson et al. 2011), yet studies rarely focus on variations in this timing and causes of changes to this critical life history stage (Viñuela et al. 1996). However, one study has shown that Adélie penguins fledge at a younger age when their hatching date is delayed (Viñuela et al. 1996). Fledging dates are often highly synchronous and late-hatching chicks may be forced to fledge at a younger age when the majority of the colony has already left the breeding site (Viñuela et al. 1996). This crucial period should be studied more in depth to determine what other proximate factors contribute to either an advanced or delayed mean chick departure date, or why some individuals are not able to synchronize with others within their colonies when fledging.

While the chicks begin the process of moulting and eventually fledging, adults begin their own moult, which is often triggered by changes in photoperiod (Ainley 2002) and hormone levels (Groscolas et al. 1986). The moult period involves another period of excessive feeding to build up fat reserves, as adults will not be able to forage while dropping their feathers. The changing of feathers is essential each year to ensure their waterproof abilities and insulating down (Penney 1967a, Taylor 1986). Adélies and chinstraps often begin winter migration, by departing the colony, before moult,

choosing to instead moult on solid pack ice rather than at the breeding colony (Penney 1967a, Marchant and Higgins 1990), while chinstraps and gentoos are known to moult exclusively before winter departure (Bost and Jouventin 1990, Viñuela et al. 1996). Adult moult, and the hyperphagia associated with this period, may restrict the time parents can spend guarding and provisioning chicks, likely dictating the timing for the post-guard period. Timing is most restricted at high latitudes as sea ice and daylight hours dictate foraging and therefore moult ability, which may explain the shortened breeding period of penguins at higher latitudes (Conroy et al. 1975a, Bost and Jouventin 1990, Croxall and Davis 1999). In addition, non-breeders begin their moult earlier in the season in Adélies (Penney and Emlen 1967b), likely because they are not restricted by parental duties.

Once finished moulting, or, in some Adélies, prior to moulting, adults depart their breeding grounds. The timing of adult departure has only been documented in Adélie and chinstrap penguins (Clarke 1906, Bagshawe 1938, Fraser and Trivelpiece 1996, Dunn et al. 2011) because of the logistical difficulties of noting dates towards the beginning of the harsh winter field season. However, some studies have documented winter migrations in Adélies (Davis et al. 1996, 2001, Clarke et al. 2003, Dunn et al. 2011) and chinstraps (Wilson et al. 1998, Biuw et al. 2009), or the lack of migrations in gentoos (Bost and Jouventin 1990), which provides insight into how pygoscelids spend their winter. Although the timing of departure and its variation is still a mystery in most colonies, researchers are beginning to better understand winter

behaviour due to developments in tracking techniques and will eventually be able to determine changes in the timing of departure at a range of sites.

In summary, variations in the phenology of pygoscelids provide insight into how both biotic and abiotic factors influence breeding and the great deviations that exist between colonies and species. Phenology directly influences breeding success in all three species and therefore population dynamics, allowing us to pinpoint why demographics change between years. Although the causes of variation in phenology are multifaceted due to the complexity of the dynamic Antarctic and sub-Antarctic ecosystems, this review has revealed five main causes of variation across the annual phases in all three species throughout their respective ranges: 1) temperatures, 2) weather conditions, 3) sea ice extent, 4) photoperiods, and 5) food abundance. Although much is known about pygoscelid phenology, there are clear gaps in our understanding of both specific dates of phases within colonies and inter-annual variation and its causes, which will be detailed in the following section.

1.6 Gaps in Our Understanding

Even with the numerous studies examining phenology in *Pygoscelis* penguins, large gaps in our understanding of plasticity in the annual cycle remain. In particular, certain phases are neglected because they are logistically difficult to record or have been ignored altogether. These phases include the courtship, guard, chick moult, and both adult and chick departure dates, making up over half of pygoscelid phenology on

land (Figure 1.1). In contrast, the egg laying (clutch initiation dates) and hatching periods have been studied in detail, acting as a yardstick in which to compare sites and years (Figure 1.1). Even though a well-studied phenology marker is necessary to understand variation, if possible, all phases within the annual cycle should be recorded to better understand what factors influence the plasticity of each individual phase and how they differ over time. In particular, as studied in other taxa, directional selection for either earlier or later dates due to mismatched peaks in prey availability and climate change may drive plasticity in the timing of breeding (Reed et al. 2013a), which may (Gienapp et al. 2013) or may not (Reed et al. 2013b) negatively influence population dynamics. Ultimately, a better understanding of each of these phases over both time and space and how each relates to individual fitness would provide insight into population dynamics and the importance of phenological plasticity in a changing climate. When comparing phenology in the three species, certain species have been studied in closer detail, especially Adélies. Because of their large range and improved access for more researchers to their sites, Adélie phenology has been well studied around scientific bases.

When moving away from these key sites, less is understood about their phenology and should therefore be studied in depth to see how the phenology compares to long-term studies. In contrast, little is known about chinstrap phenology, as only two regions, the South Shetland and South Orkney Islands, have been studied in depth (Figure 1.3). Given that only fourteen published studies exist on chinstrap phenology, which include dates, future research should focus on exploring this

species' annual cycle. Lastly, most research on gentoos has focused on the sub-Antarctic islands even though numerous unstudied colonies exist on the Western Antarctic Peninsula (WAP, Figure 1.3). The WAP has become a hot topic in light of climate change because of its accelerated warming; therefore studies should focus on colonies inhabiting this region and how warming trends may related to phenology, particularly in gentoos.

In addition, temporally, large gaps exist in our understanding of phenology, where studies have not been updated in over 20 years at a particular field site (Table 1.1). Because phenology does vary greatly between years, depending on the colony, when possible, researchers should strive to update phenological records by recording the dates of phases each year.

Lastly, studies examining inter-species competition and how this competition dictates phenology should be explored in more detail. Past research has demonstrated how chinstraps present at breeding grounds influences Adélie penguin phenology and survival (Trivelpiece and Volkman 1984, Trivelpiece and Volkman 1987, Carlini et al. 2005) yet only three studies to date have examined the relationship between gentoos and either of the two other pygoscelid species (Trivelpiece and Volkman 1987, Hinke et al. 2012, Lynch et al. 2012b). Because competition for resources, whether nesting sites or prey, clearly dictates the timing of key phases within the annual cycle, future research should explore inter-species relationships more in depth.

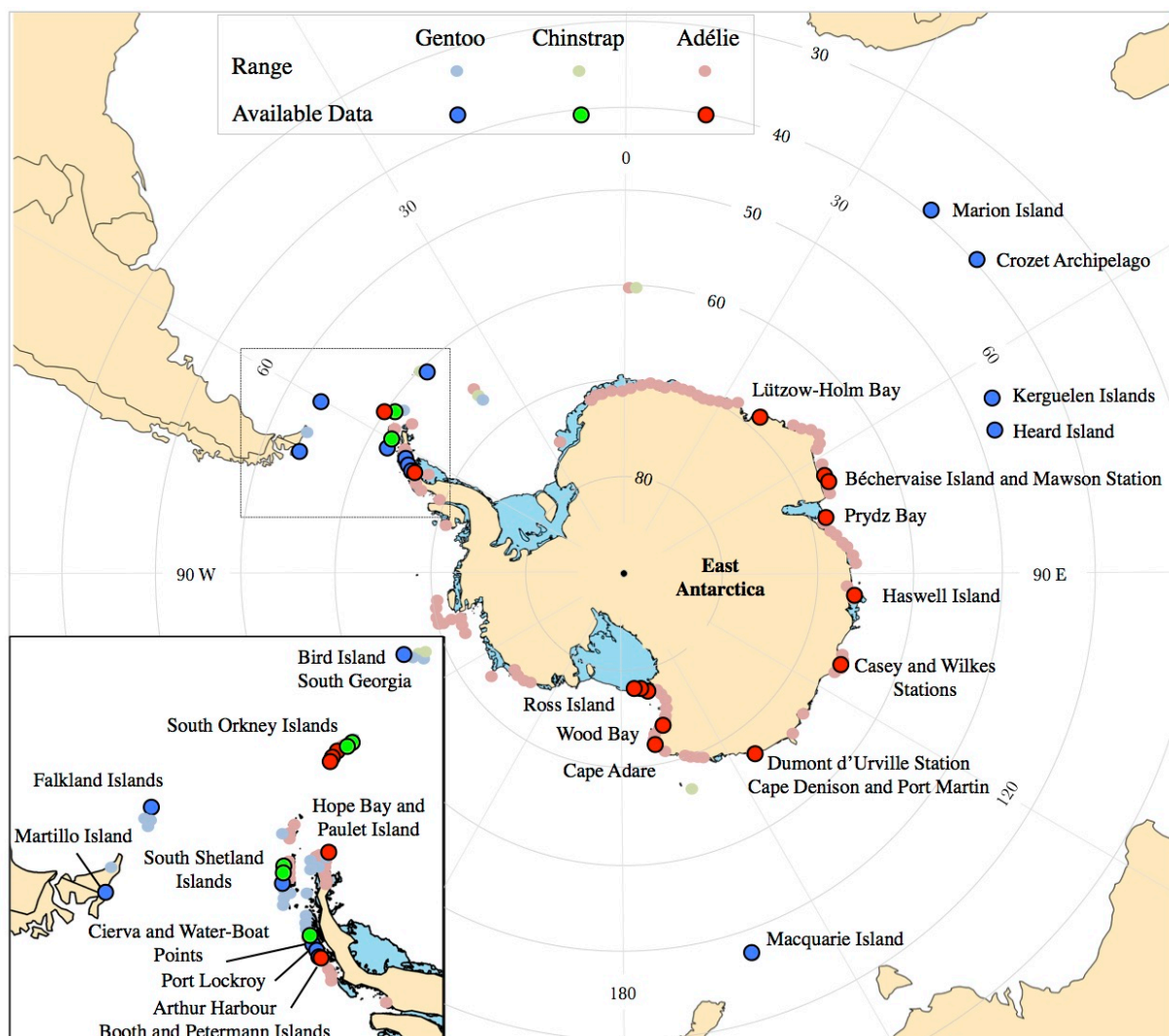


Figure 1.3. Map of sites with published phenology dates for all three *Pygoscelis* penguin species. Ranges adapted from Borboroglu and Boersma (2013) and Polito et al. (2011). See Table 1.1 for citations.

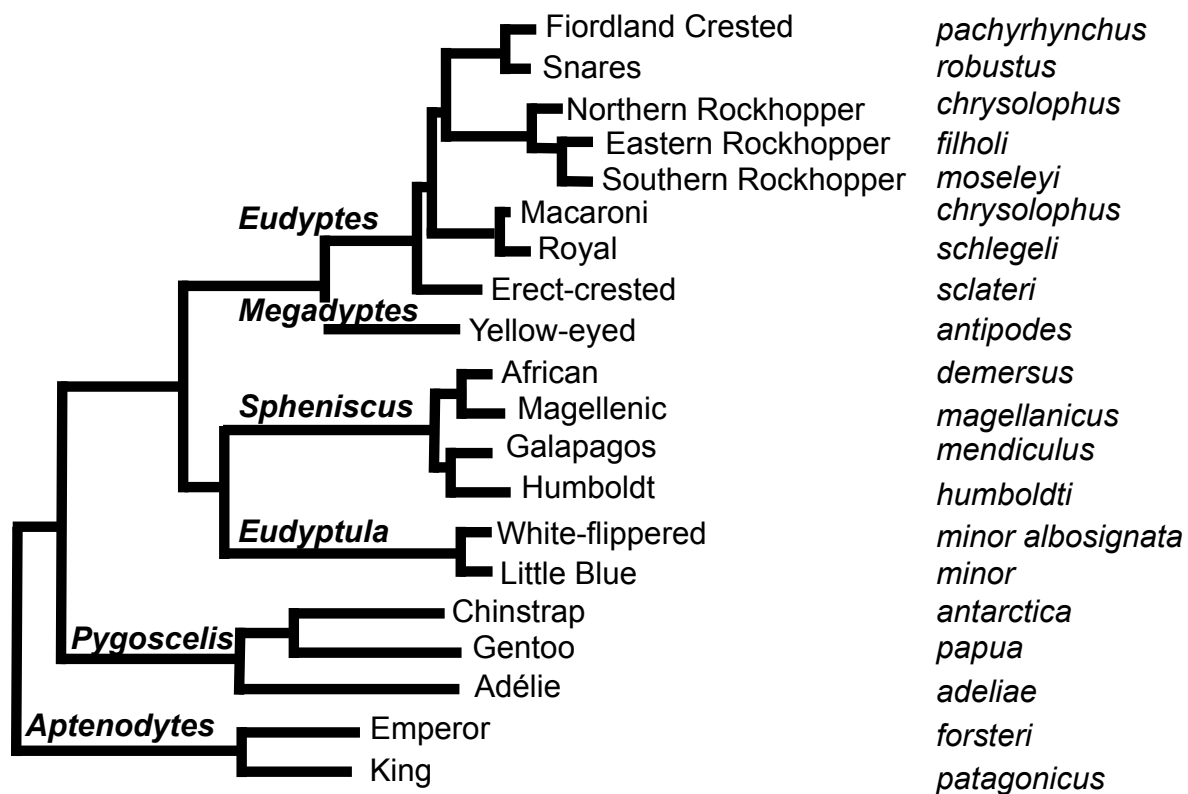


Figure 1.4. Phylogenetic tree showing the relationships between all 20 penguin (*Sphenicidae*) species. Tree based on figure from Baker et al. 2006.

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CHAPTER TWO

A Review of Time-Lapse Camera Capabilities and Limitations in Seabird Studies

2.1 Abstract

Ecological research has used remote techniques to monitor wildlife for much of its history; however, recent advances in technology have extended the possibilities of remote sensing methods, making camera systems more easily accessible, higher resolution, and more relevant to a larger range of research interests. Time-lapse photography is most applicable to study animals frequently present at a photographed location or to study frequently repeated behaviours. Therefore, time-lapse camera methods are particularly relevant to study colonial animals at fixed locations. Here, I review literature using time-lapse camera methods in the context of their application to seabirds, focusing on research aims. Cameras may remove observer biases and can be used to observe seabird behaviour in places or during times when human observation would be nearly impossible, including in remote locations, at night using infrared technology, and during harsh weather conditions. However, cameras are prone to mechanical failures and programming errors and need regular maintenance, depending on the frequency of photographs. Ultimately, the largest disadvantage of time-lapse cameras is also its biggest advantage; enormous amounts of data are produced, which need to be processed. Although many studies have used time-lapse camera techniques to understand seabird ecology, researchers can expand their study aims by examining how research on other taxa has used camera traps. In addition, as efficiency increases, demands for camera systems also increase; therefore, it is necessary to standardize data collection across sites and species to improve comparability across studies. Overall, for the study of colonial wildlife, time-lapse

photography proves to be a cost-effective, relatively non-invasive method, which can help researchers save time during fieldwork.

2.2 Introduction

Ecological research has used remote techniques to monitor wildlife for much of its history; however, recent advances in technology have extended the possibilities of remote sensing methods, making camera systems more easily accessible, higher resolution, and more relevant to a larger range of research interests (Bicknell et al. 2016). Traditionally, cameras have been used to focus on photographing one individual, identified by distinct markings, and either taking motion-triggered photographs or using hand-held devices to study an animal opportunistically (Cutler and Swann 1999). However, in cases where wildlife can be photographed in groups, alternative methods may prove more effective in terms of data output, time in the field, and expense. In particular, time-lapse cameras, camera systems installed at a field site and programmed to take an image at a set frequency, have recently become more accessible to researchers and provide numerous opportunities for the study of animals living in groups. To demonstrate these abilities and highlight possible limitations of time-lapse camera systems, here I review past uses of camera systems and how they may be applied or have been applied to the study of colonial wildlife, focusing on seabirds.

Cameras were first applied to the study of animal movement and the absence or presence of wildlife but, with technological advances, cameras were eventually capable of the remote monitoring of wildlife popular today. Beginning in the 19th century, photography was initially used to examine patterns in horse running movements (Guggisberg 1977) but was first applied to remotely observe wildlife ecology in the 1950s in studies on rodent habitat use (Pearson 1959) and prey types in birds (Royama 1959). Beginning in the 1970s, nest box photography became popular to study breeding birds and today remains one of the most widespread uses of camera technology in ecological research (Cutler and Swann 1999). Beginning in the 1980s, technological advances led to trigger-censor cameras encased in rugged, waterproof shells, which allows for autonomous remote monitoring of wildlife and use in harsh weather conditions (Swann et al. 2011). Today, these systems often include a time and date stamp and air temperature record watermarked on each image, which provides accurate records of the sequence and timing of events. Further improvements in camera systems eventually led to applications for time-lapse cameras in the field of ecology, which are relevant for a range of species and locations and even to track animal movement and the absence or presence of wildlife.

In contrast to motion-triggered cameras, which record individual, instantaneous events and are often deployed as networks, time-lapse cameras are most applicable to study animals frequently present at a photographed location or to study frequently repeated behaviours. Therefore, time-lapse camera methods are particularly relevant to study colonial animals such as seabirds and seals, breeding in

large groups. Here I review literature using time-lapse camera methods in the context of their application to seabirds and their potential for other colonial animals, focusing on distinct research aims. The range of cameras available, the constant advances in technology, and the availability of information on camera equipment types has been reviewed elsewhere and will therefore not be included in this review (Newbery and Southwell 2009, Swann et al. 2011).

2.3 Activity Budgets

Summarizing movement patterns serves as a fundamental use of time-lapse cameras, which allows researchers to better understand time-budgets. In particular, the postures (eg. sleeping, sitting, etc.) have been characterized in Adélie penguins (*Pygoscelis adeliae*, Derksen 1977), American oystercatchers (*Haematopus palliatus*, Pacheco and Castilla 2001), and great cormorants (*Phalacrocorax carbo*, Storch et al. 1999) using time-lapse cameras. However, the relevance of activity patterns to fitness or population dynamics is often difficult to test, so the majority of studies have focused instead on nest activity patterns as they relate to chick survival. Only a few studies to date have examined feeding rates or prey types in seabirds using time-lapse cameras. In particular, one study used cameras to identify seabird species feeding in aggregations on scallops discarded from commercial fishing activity in the Irish Sea (Veale et al. 2000). However, all other foraging-related seabird studies have focused on chick provisioning rates by parents, including in Caspian tern nests (*Hydroprogne caspia*, Oswald et al. 2013), northern royal albatrosses (*Diomedea sanfordi*, Sugishita

et al. 2015), and in common murre (*Uria aalge*, Roseneau et al. 1996), the latter of which used provisioning rates as a proxy to determine strength of the colony after the Exxon Valdez oil spill. These feeding rates can have direct effects on the survival of chicks, which serves as another major focus of seabird studies using time-lapse photography techniques.

2.4 Breeding Success and Survival

Time-lapse studies have proved to be particularly accurate in measuring breeding success when compared with direct observations (Adélie penguins, (Southwell and Emmerson 2015), providing researchers with an excellent alternative to measure fitness when time in the field is limited, expensive, or constrained by weather. Breeding success has been measured using time-lapse cameras in thick-billed murre (*Uria lomvia*, Lorentzen et al. 2010, Lorentzen et al. 2012, Merkel et al. 2015, Merkel et al. 2016), Atlantic petrels (*Pterodroma incerta*, Wanless et al. 2012), and Northern Rockhopper penguins (*Eudyptes c. moseleyi*, Crofts and Robson 2015) with great success. In addition, cameras methods have also been used to understand adult and chick survival in murre following the Exxon Valdez oil spill (Boersma et al. 1995, Dragoo et al. 1995, Boersma and Clark 2001) and after a large population decline (Harris and Wanless 1984), demonstrating how this technique can provide baseline information with which to measure change after devastating events. Furthermore, infrared time-lapse cameras have also been used to measure breeding success in burrowing species, including Atlantic petrels and great shearwaters

(*Puffinus gravis*, Wanless et al. 2007), which are otherwise particularly difficult to measure.

2.5 Phenology

Time-lapse cameras can also provide information on phenology and nest attendance, replacing the need for direct observation. One past study on Adélie penguins found that phenological dates obtained from cameras were accurate but slightly more variable than direct observations; however, the study captured only one image daily and highlighted the strength of photographing seabirds at a higher frequency when measuring phenology (Southwell and Emmerson 2015). Nest attendance patterns during either incubation or the guard period prove to be one of the most common uses of time-lapse cameras in seabird studies and have been utilized in the study of common terns (*Sterna hirundo*, Hatch and Hatch 1989, Zador and Piatt 1999, Arnold and Oswald 2013), common murrelets (Zador and Piatt 1999, Harding et al. 2007a, Harding et al. 2007b), thick-billed murrelets (Hatch and Hatch 1989), great cormorants (Gremillet et al. 2000), Horned puffins (*Fratercula corniculata*, Harding et al. 2005), black-legged kittiwakes (*Rissa tridactyla*, Heggøy et al. 2015), least terns (*Sternula antillarum*, Hillman 2012), and burrowing magenta petrels (*Pterodroma magenta*, Johnston et al. 2003). In addition, nest occupation has been observed in shy albatrosses (*Thalassarche cauta*) by stitching together images taken by multiple cameras simultaneously to create colony-wide panoramas (Lynch et al. 2015). Because nest attendance is linked to egg temperature, chick growth, and the survival

of fledglings (Deeming 2002), time-lapse cameras serve as a valuable method to better understand the health of a colony and individual fitness.

2.6 Population Dynamics

Estimating populations serves as the gold standard to understand how a colony or group of colonies is changing over both time and space. Counts should ideally take place at the peak of breeding to standardize data and remove bias across years and sites (Lynch et al. 2009). Time-lapse cameras have been used to examine temporal and spatial variation in the attendance of Adélie penguins at breeding sites to better understand the bias of direct counts (Southwell and Emmerson 2015) and when future counts should take place (Southwell et al. 2015). Colony attendance has also been observed in Atlantic puffins (*Fratercula arctica*, Harris 1980), horned puffins (Hatch 2002), parakeet auklets (*Aethia psittacula*, Hatch 2002), common murre (Murphy et al. 1985), thick-billed murre (Murphy et al. 1985, Mosbech et al. 2009, Huffeldt and Merkel 2013, Merkel et al. 2015), and least (*Aethia pusilla*) and crested auklets (*Aethia cristatella*, Piatt et al. 1990), using time-lapse cameras installed next to colonies. Additionally, population have been counted by attaching time-lapse cameras to either 1) kites in Adélie penguins (Fraser et al. 1999), Guanay cormorants (*Phalacrocorax bougainvillii*), macaroni penguins (*Eudyptes chrysolophus*), and king penguins (*Aptenodytes patagonicus*, Delord et al. 2015), or 2) unmanned aerial vehicles (UAVs) in gentoo penguins (*Pygoscelis papua*, Goebel et al. 2015, Ratcliffe et al. 2015). Satellites, taking images over time in a similar fashion to time-lapse cameras,

have also been used to count populations and identify locations of newly discovered colonies in Adélie (LaRue et al. 2014, LaRue and Knight 2014, Lynch and LaRue 2014) and emperor penguins (*Aptenodytes forsteri*, Barber-Meyer et al. 2007, Fretwell et al. 2012).

2.7 Predation

Time-lapse camera methods are also relevant in the study of predator-prey interactions and can identify causes of egg loss or chick fatality, while also helping researchers to understand habitat use and seabird ranges. Camera methods have successfully been installed to study chick predation in black-legged kittiwakes (*Rissa tridactyla*, Collins et al. 2014), little cormorants (*Microcarbo niger*, Powlesland et al. 2002), thick-billed murre (Merkel et al. 2015), Atlantic petrels (Wanless et al. 2012), and American oystercatchers (Sabine et al. 2005). Cameras have also been fixed on mussel farm buoys to understand how New Zealand king shags (*Phalacrocorax carunculatus*) use these buoys (Fisher and Boren 2012), serving as a unique example of how time-lapse cameras can be applied to the study of habitat use. In addition, recent technological advances have decreased the size and weight of cameras, allowing for time-lapse cameras to be mounted directly on individuals. One study used animal-borne time-lapse cameras to examine inter-species interactions and dive patterns in black-browed albatrosses (*Thalassarche melanophris*) in conjunction with depth data loggers (Sakamoto et al. 2009). Lastly, time-lapse cameras serve as an excellent tool to better understand site fidelity, particularly during the little-studied

non-breeding season, and has been applied the study of common murre, razorbills (*Alca torda*), black-legged kittiwakes, and northern fulmars (*Fulmarus glacialis*, Mudge et al. 1987).

2.8 Human Disturbance

Lastly, time-lapse cameras have been used as a tool to understand the effects of human disturbance and how scientists may be biasing their own datasets. The effects of both aircraft and recreational activity on least terns, common terns, gull-billed terns (*Gelochelidon nilotica*), and black skimmers (*Rynchops niger*, Hillman 2012) and direct human disturbance on Adélie penguins (Wilson et al. 1991) have been effectively studied using time-lapse cameras. In addition, to better understand whether scientific activities influence seabird behaviour, time-lapse cameras have been used to study how human presence during direct observations influences predation data on common murre (Parrish 1995) and the effects of stomach-retained temperature archival units (STAU) on chick feeding rates (Wilson et al. 1998). More in-depth studies are needed to establish whether cameras themselves alter seabird behaviour and bias data before researchers can ultimately consider this method non-invasive.

2.9 Capabilities

Time-lapse cameras have been applied to study a range of interests in seabird research and have major advantages over alternative methods. In particular, cameras may remove observer biases and can be used to observe seabird behaviour in places or during times when human observation would be nearly impossible, including in remote locations, at night using infrared, and during harsh weather conditions.

Photography also provides researchers with more accurate evidence for later identification of prey species, phenology events, and elusive behaviours, while also providing a time stamp for all events. Most notably, time-lapse cameras can allow researchers to save time and money spent on fieldwork, which is limited. Because cameras often provide more frequent observations, they are also able to observe more obscure behaviours or species, depending on their set frequency.

2.10 Limitations

Naturally, there are disadvantages to this technique, many of which may become irrelevant as technology progresses. Cameras are prone to mechanical failures and programming errors and need regular maintenance, depending on the frequency of photographs. In most cases, data cannot be obtained until a camera is maintained, which proves difficult in some remote regions, and there is the potential for cameras to provide inaccurate temperature readings, which has not yet been studied.

Depending on the system used, time-lapse cameras supply a large range of image

quality outputs and many affordable options provide low-quality data in terms of resolution. Also, depending on the study species, it may be difficult to study multiple burrows at once in ground-nesting seabirds and small seabirds may not be easily detected in the camera frame. As mentioned, studies have not fully yet addressed how cameras influence seabird behaviour, so there is a potential for nest disturbance, particularly abandonment (Cowie and Hinsley 1988), and either predator attraction or reduction (Richardson et al. 2009) to occur as a result of camera installation. In addition, if studying more elusive behaviours, such as predation events or species across a large geographic range, camera purchases and maintenance can become expensive and logistically difficult, as both batteries and computer memory are often limited.

2.11 Future Studies

Although many studies have used time-lapse camera techniques to understand seabird ecology, researchers can expand their study aims by examining how research on other taxa has used camera traps. For example, cameras methods can help us to understand social behaviour (eg. chick aggregations in gentoo penguins, Black et al. 2016) and environmental variables at study sites (eg. sea ice, glaciers, volcanoes, Harrison et al. 1992, Smith et al. 2003, Orr and Hoblitt 2008, Ahn and Box 2010, Overeem et al. 2011). In cases where individuals can be identified either by natural markings, as is the case in African penguins (Sherley et al. 2010), or by banding (Calvo and Furness 1992, Murray and Fuller 2000), researchers can use time-lapse

cameras to answer a larger range of questions. For example, by identifying individuals in images, researchers may be able to examine the physical condition of individuals (Kucera and Barrett 2011), a species range using time-lapse cameras along transects (Silveira et al. 2003), the parental investment of males compared to females, population structure (Ahumada et al. 2011, Hariyadi et al. 2011), and population estimates as an alternative to mark-recapture methods (Gardner et al. 2010). In addition, as infrared cameras become more cost-effective and durable, they can also be used to measure breeding parameters in burrowing species (e.g. Atlantic petrel and great shearwaters, Wanless et al. 2007) and nocturnal behaviours.

As technology advances, camera systems are becoming more powerful, relevant, and efficient, particularly when studying seabirds inhabiting remote locations. Battery life and storage capacity has increased, allowing for more time between servicing and lighter, smaller, more robust cameras. Researchers can also take advantage of solar panels and external, rechargeable batteries to reduce battery waste as well as satellites to obtain data more rapidly. However, as efficiency increases, demand for camera systems also increases; therefore, it is necessary to standardize data collection across sites and species to improve comparability across studies (eg. Commission for the Conservation of Antarctic Marine Living Resources, CCAMLR 2004, Join Nature Conservation Committee, Walsh et al. 1995). The research community would benefit from a data repository for camera data such as those found for tracking movements (Movebank, Kranstauber et al. 2011) and genetics (Genbank, Benson et al. 2008).

Ultimately, the largest disadvantage of time-lapse cameras is also its biggest advantage; enormous amounts of data are produced, which need to be processed. To speed up post-processing, the use of both citizen science (eg. Penguin Watch) and automation (eg. African penguins, Sherley et al. 2010; common guillemots, Dickinson et al. 2008, Dickinson et al. 2010, Gardner et al. 2010, Duyck et al. 2015) is necessary and these techniques must be refined and accessible to the research community.

2.12 Conclusion

Overall, for the study of colonial wildlife, time-lapse photography proves to be a cost-effective (Southwell and Emmerson 2015), relatively non-invasive method, which can help researchers save time during fieldwork when limited. Because of these advantages and the method's relative ease of use, time-lapse cameras can be used to expand our knowledge of both inter-specific and intra-specific behaviours and population dynamics over time and space in areas where studies were previously logistically impossible. Time-lapse cameras, implemented either alone or in conjunction with other methods, can effectively replace or improve other methods, including direct observation, tracking, surveys, and counts and is particularly efficient when studying elusive and nocturnal species as well as those sensitive to human presence. In addition, these methods can provide information on activity at night and during harsh weather conditions. However, researchers must budget time for

troubleshooting, maintenance, and post-processing. To date, there is little research on the potential effects of time-lapse or motion-trigger photography on animal behaviour and future research should focus on the extent that these techniques may be altering behaviour to prove the non-invasiveness of camera use.

2.11 References

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CHAPTER THREE

Why Huddle? Ecological Drivers of Chick Aggregations in Gentoo Penguins, *Pygoscelis papua*, Across Latitudes

3.1 Abstract

Aggregations of young animals are common in a range of endothermic and ectothermic species, yet the adaptive behaviour may depend on social circumstance and local conditions. In penguins, many species form aggregations (aka. crèches) for a variety of purposes, whilst others have never been observed exhibiting this behaviour. Those that do form aggregations do so for three known benefits: 1) reduced thermoregulatory requirements, 2) avoidance of unrelated-adult aggression, and 3) lower predation risk. In gentoo penguins, *Pygoscelis papua*, chick aggregations are known to form during the post-guard period, yet the cause of these aggregations is poorly understood. Here, for the first time, we study aggregation behaviour in gentoo penguins, examining four study sites along a latitudinal gradient using time-lapse cameras to examine the adaptive benefit of aggregations to chicks. Our results support the idea that aggregations of gentoo chicks decrease an individual's energetic expenditure when wet, cold conditions are present. However, we found significant differences in aggregation behaviour between the lowest latitude site Maiviken, South Georgia and two of the three higher latitude sites on the Antarctic Peninsula, suggesting this behaviour may be colony specific. We provide strong evidence that more chicks aggregate and a larger number of aggregations occur on South Georgia, while the opposite occurs at Petermann Island on the Antarctic Peninsula. Future studies should evaluate multiple seabird colonies within one species before generalizing behaviours based on one location, and past studies may need to be re-

evaluated to determine whether chick aggregation and other behaviours are in fact exhibited species-wide.

3.2 Introduction

Aggregations of young animals are common in a range of endothermic and ectothermic species, yet the behaviour's adaptive purposes depend on a species' social behaviours and local conditions. In avian species, crèching or aggregations of chicks may stem from ecological, morphological, or social adaptations (Gilbert et al. 2010). Ecologically, adverse weather conditions and lower than average ambient temperatures can cause chicks to aggregate more frequently or in more dense groups, for example in the common bushtit, (*Psaltriparus minimus*, Smith 1972), white pelican, (*Pelecanus erythrorhynchos*, Evans 1984), and house sparrow, (*Passer domesticus*, Beal 1978). Additionally, morphological restrictions, including poor insulation, may cause chicks of smaller species, or those with altricial young, to aggregate (Gilbert et al. 2010). Furthermore, sociality may contribute to the formation of chick aggregations in birds of the same or, rarely, different species (tree swallow, *Iridoprocne bicolor*, barn swallow, *Hirundo rustica*, and cliff swallow, *Petrochelidon pyrrhonota*; Meservey and Kraus 1976), although little research exists on this topic. Of all the bird families, penguins (*Spheniscidae*) are well known to exhibit aggregation behaviours during both the winter and summer months (Wilson 2009), and the purpose of aggregations is highly dependent on the species.

Many species of penguins form aggregations (e.g. emperor, *Aptenodytes forsteri*, Ancel et al. 1997; king, *Aptenodytes patagonicus*, Barré 1984, Le Bohec et al. 2005; chinstrap, *Pygoscelis antarcticus*, Penteriani et al. 2003, Martín et al. 2006; Adélie, *Pygoscelis adeliae*, Penney 1968, Davis 1982a, Lawless et al. 2001; African, *Spheniscus demersus*, Seddon and Van Heezik 1991, Seddon and van Heezik 1993), while others have never been observed exhibiting this behaviour (e.g. little, *Eudyptula minor*, yellow-eyed *Megadyptes antipodes*, Magellanic, *Spheniscus magellanicus*, Galapagos, *Spheniscus mendiculus*, and Humboldt penguins, *Spheniscus humboldti*, Wilson 2009). Those that do form aggregations (formally called 'crèches'; see Wilson 2009 for nomenclature) do so for three known benefits: 1) reduced thermoregulatory requirements, 2) avoidance of aggression from unrelated adults and 3) lower predation risk. Firstly, reduced energy requirements for thermoregulation may serve as the primary function of chick aggregations: in other words, that which served as the first evolutionary adaptation (Wilson 2009). In king and Adélie penguins, aggregations have increased either in size and compactness (Le Bohec et al. 2005) or have only occurred when colder, harsher weather conditions are present (Lawless et al. 2001); while in other species, such as the African penguin, aggregations have been observed even during warm temperature conditions (Seddon and van Heezik 1993). Therefore, only some species may form aggregations for thermoregulatory purposes, although the behaviour potentially varies between colonies, which, to our knowledge, has not yet been studied.

Secondly, chicks may form aggregations as a result of aggression from unrelated adults, where chicks are often corralled into one location by “floater” or nesting adults (Seddon and van Heezik 1993, de Leon et al. 2002). Chicks in aggregations are less disturbed by adults than individuals outside of aggregations (Seddon and van Heezik 1993). This behaviour is exhibited by chinstrap, rockhopper, Adélie, and African penguin species (Pettingill 1960, Penney 1968, Seddon and van Heezik 1993, de Leon et al. 2002, Penteriani et al. 2003) and serves as another explanation of the formation of chick aggregations.

Thirdly, in a classic example of both the group vigilance hypothesis and the predator dilution effect, chick aggregations may reduce predation risk by increasing the detection of predators while decreasing the chance of individual predation (Pulliam 1973). In Adélie penguins, fewer chicks are killed by predators when in large aggregations compared with those in smaller groups or not aggregating (Davis 1982a), while in other species (e.g. Adélies, rockhoppers, chinstraps), predation events only occur when individuals are not part of an aggregation (Pettingill 1960, Davis 1982a, Penteriani et al. 2003). There also may be an unexplained social benefit to aggregating as a chick, although no studies have yet provided evidence of sociality as a potential driver of aggregation.

In gentoo penguins, *Pygoscelis papua*, chick aggregations are known to form during the post-guard period, yet the cause of these aggregations is poorly understood (Wilson 2009). As a species which has a large spatial range, colonizing sub-Antarctic

islands and areas along the Antarctic Peninsula, it is possible that chick aggregation behaviour may stem from any of the three main drivers– thermoregulation, predation, or adult aggression– for different adaptive purposes. In addition, the principal driver may vary latitudinally with colony location. Because gentoo penguins are well known for their asynchronous breeding, dependent on the colony location (Williams and Croxall 1991), and the growth rate within colonies and post-guard period varies depending on breeding site (Bost and Jouventin 1990), there will likely be large differences in the timing of the post-guard phase between colonies and therefore the timing of aggregations. Here, for the first time, we examine the adaptive benefit of chick aggregation behaviour in gentoo penguins, using time-lapse cameras to measure the behaviour. To the best of our knowledge, we are the first to compare any chick aggregation behaviour at more than one colony, enabling us to examine whether this behaviour is generalizable across a species. To understand this behaviour in gentoo chicks, we formulated *a priori* hypotheses based on the three previously observed mechanisms behind chick aggregation behaviour in other penguin species:

1. If gentoo chicks form aggregations to lower thermoregulatory requirements, chicks will aggregate more 1) during cold, wet conditions, 2) when chicks are younger in age, and 3) the number of chick aggregations will change along a latitudinal gradient; colonies located farther north will form fewer aggregations due to decreased thermoregulatory output, while those located farther south will aggregate more often during harsher, colder conditions.

2. If chicks form aggregations due to aggressive advances from unrelated adults, then aggregations will occur more often 1) when more adults are present, and the adult to chick ratio is therefore higher, and 2) when fewer chicks are guarded by their parents.
3. Chicks will form larger aggregations, at a younger age, and a higher proportion of chicks will aggregate when predators are present, as a means of predator avoidance.

3.3 Methods

3.3.1 Study Sites

We deployed cameras at four study sites to study chick aggregations in gentoo penguins based on a latitudinal gradient: 1) Maiviken (-36.506, -54.246) on South Georgia, 2) Georges Point (-62.670, -64.669) on Ronge Island along the Western Antarctic Peninsula (WAP), 3) Port Lockroy (-63.484, -64.823) also along the WAP, and 4) Petermann Island (-64.142, -65.172) along the WAP (Figure 3.1). Petermann Island represents the southern breeding limit for gentoo penguins, located less than 11 km from the southernmost colony (Cape Tuxen, Lynch et al. 2008, 2009, Rider et al. 2009). Maiviken serves as a representation of gentoo penguins towards the more northern edge of their range (northern range ends on Crozet Island at a longitude of -45.83°; Bost and Jouventin 1991) and is infrequently studied. Port Lockroy, in the

well-studied Palmer Archipelago, consists of a gentoo colony, which is heavily visited by tourists and has thus been studied to define tourism related impacts on the species (Trathan et al. 2008). The Georges Point colony has been studied in the past (eg. (Barbosa et al. 2007, Barbosa et al. 2011); however, the phenology of the colony is not well defined.

Considering our three hypotheses, we must note that human visitation may affect our third hypothesis that a higher proportion of chicks will aggregate when predators are present, as a means of predator avoidance. At highly visited tourist sites (specifically Port Lockroy and Petermann Island), gentoos are habituated to human presence (Trathan et al. 2008), which may influence behaviours, including the likelihood of forming aggregations. In particular, gentoos at sites frequently visited by tourists may respond differently to predators than those at sites rarely visited, due to their acclimation to humans, which in turn may influence aggregation behaviour. However, the sub-colonies studied, including that at Port Lockroy and Petermann Island, are located away from tourist congregations and therefore less disturbed than other sub-colonies at the same sites, although gentoo chicks are mobile during the post-guard phase.

3.3.2 Camera system

One camera was deployed at each of our four gentoo colony study sites; each camera was installed roughly 10 meters from the perimeter of nesting sub-colonies. Cameras were installed using techniques similar to those described by Newbery and

Southwell (2009), with minor adjustments to the camera system (Appendix B). At each site, a Reconyx HC500 Hyperfire trail camera (Reconyx, Inc., Holmen, WI, USA) was mounted to a scaffold pole and anchored using a rock basket. The cameras were programmed in time-lapse mode to take nine hourly photographs daily, beginning at 9:00 and ending at 17:00 (GMT-2). Each camera captured images of 14-49 nests for the full 2012- 2013 breeding season (September 1- March 31, Figure B.2).

3.3.3 Annotations

Overall, the study period was defined as the post-guard period within a chick's annual cycle. Each site differed in the timing of this period (Figure 3.2), therefore, the commencement of the post-guard period was defined as the first image in which a chick was seen unguarded (see *Guarded and unguarded chicks* in Methods), and the period was defined as terminated when either all chicks had moulted to their fledgling feathers or, in cases where chicks departed the colony before the end of moult, all chicks had left the sub-colony site in view. Specifically, in the 2012-2013 breeding season, the post-guard period occurred during the following dates: 1) Maiviken (December 16- January 12), 2) Georges Point (February 1- March 1), 3) Port Lockroy (February 5- March 17), and 4) Petermann Island (January 22- March 3).

Counts of individuals were extracted from each image using software developed by Aytar (2012). In each image, a circle was centred over each visible individual to avoid counting individuals twice. The number of circles in each image

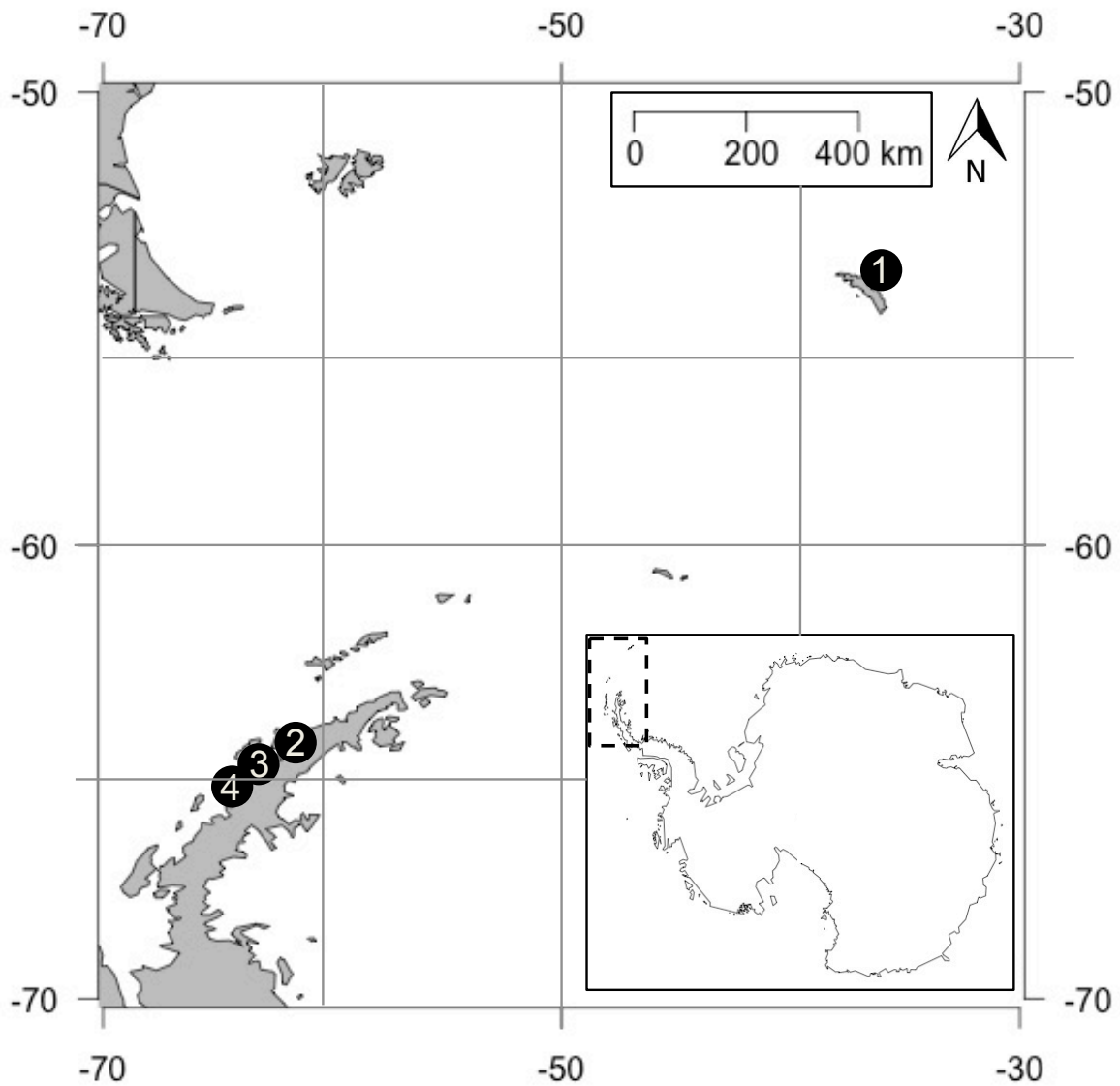


Figure 3.1. Map of studied gentoo penguin colony locations along a latitudinal gradient ranging from 1) Maiviken, South Georgia to 2) Georges Point, 3) Port Lockroy, and 4) Petermann Island on the Antarctic Peninsula.

was then extracted to determine counts. This process was used for counting both adults and chicks separately at each site in each image and all individuals at the edge of the image frame were included in our analysis. The adult to chick ratio was then determined for each image based on the counts of adults and chicks present within the camera frame.

3.3.3.2 Chick aggregations

Although many definitions exist for a chick aggregation in penguins (Wilson 2009), we chose to use the definition used for Adélie penguins in Davis (1982a). We defined a chick aggregation as a minimum of three chicks in close association, where the distance between individuals was less than 35 cm, approximately half the distance between nests, consistent with pecking distance. These distances were approximated in each image, not measured *in situ*. For each image, the total number of aggregations and the number of chicks in each aggregation was determined. Using these data we calculated: mean aggregation size, total number of chicks in aggregations, and ratio of aggregating chicks to total chicks, for each image.

3.3.3.3 Guarded and unguarded chicks

Guarded chicks were defined as being in close association with an adult and located one flipper length (~25 cm) or less from the brood patch of the nearby adult. In addition, any chicks involved in provisioning interactions or located directly on the nest with an adult were defined as guarded (aka. attended). All other chicks were

counted as unguarded. From this data, a ratio of guarded chicks to unguarded chicks was determined.

3.3.3.4 Weather conditions

Images were annotated for the presence or absence of wet conditions, defined as either snow cover, precipitation in the form of snow or rain, or conditions in which chick down feathers were noticeably wet. All weather conditions are presented here as binary data. In addition, ambient temperatures were extracted from an internal thermometer in the camera housing. Wind was not measured here, although it has been linked with aggregation behaviour in king penguins (Le Bohec et al. 2005).

3.3.3.5 Predators present

The presence of any pinnipeds or predatory birds was noted for each image and the species was determined using an identification guide (Lowen 2011). Using these data, the number of predators and scavengers was determined for each image.

3.3.3.6 Age of chicks

Because we were unable to determine the exact age of individuals and unable to differentiate between individuals from specific nests during the post-guard phase studied, we instead used the days from the start of the post-guard period (day 1= 1, day 2= 2, etc.) as a method to evaluate the effect of chicks aging, at a sub-colony level, in our analysis of aggregation behaviour.

3.3.4 Statistical Analysis

All analyses were conducted in R (v 3.0.3, R Core Development Team 2013) using the *stats* and *MASS* packages (Venables and Ripley 2002). To account for the known differences between the angle and view within each camera frame, which likely affect the explanatory variables, we counted the total number of nests on the first day of the post-guard period at each study site and used these nest counts as an offset term ($-\log(x)$) in each of our models, (*offset* function, *stats* package). To determine the relationship between each of our explanatory variables (Table 3.1) and the counts of the total number of aggregations in each image, we used a generalized linear model (GLM) with a Poisson error structure. We simplified this model by omitting insignificant coefficients, including time of day, the adult-to-chick ratio (square-root transformed), and temperature (ANOVA, $P=0.16$). Ultimately, for this first model, the GLM coefficients included an interaction between location and wet

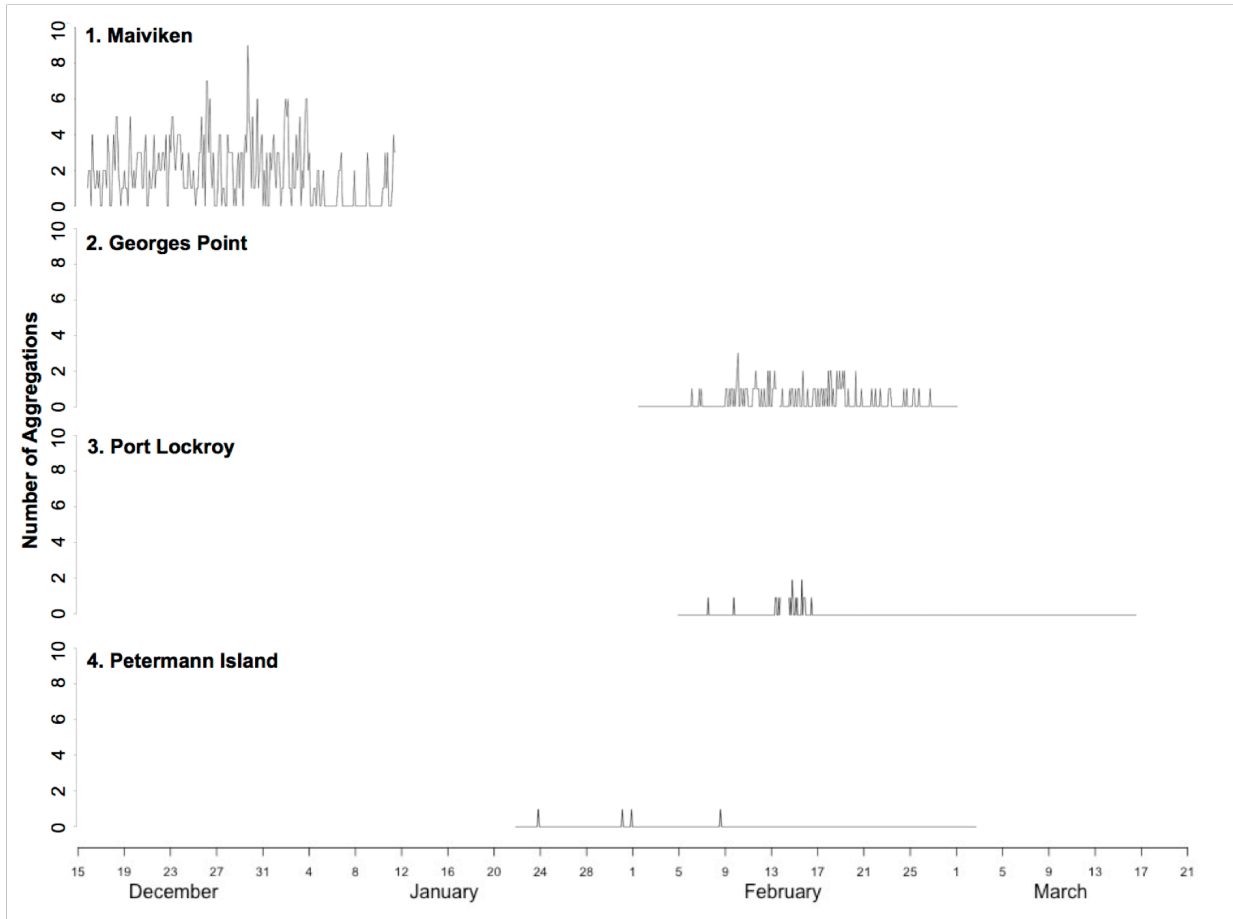


Figure 3.2. Time series demonstrating difference in the timing of the post-guard period and the number of aggregations over time at four sites: 1) Maiviken, 2) Georges Point, 3) Port Lockroy, and 4) Petermann Island.

conditions, the ratio of guarded to unguarded chicks (log transformed), and the day within the post-guard period (residual deviance: 232.61 on 426 degrees of freedom).

Due to overdispersion in both Poisson and quasi-Poisson GLMs, we used a negative binomial GLM (*glm.nb* function, *MASS* package) to determine interactions between each of the coefficients and the counts of aggregating chicks in each image. We also simplified our negative binomial GLM by omitting the time of day and the adult-to-chick ratio (square-root transformed, ANOVA, $P=0.07$). Our final model included the following coefficients: 1) interactions between location, temperature, and wet conditions, 2) the ratio of guarded to unguarded chicks (log transformed), and 3) the day within the post-guard period (residual deviance: 239.29 on 421 degrees of freedom). By examining both models with and without a correlation structure and the auto-correlation in the observed residuals (*acf* function, *stats* package), we determined that temporal autocorrelation did not occur in our data set and a correlation structure was therefore omitted from the model. We must note that our sample size for the number of predators present was small across the four sites ($n=8$) and was therefore not included in either model. Lastly, to understand relationships between coefficients, we examined contrasts by reordering the levels of factors (*relevel* function, *stats* package).

Table 3.1. Results from a negative binomial GLM on the number of gentoo penguin chicks aggregating (residual deviance: 239.29 on 421 degrees of freedom) and a Poisson GLM on the number of aggregations per nest unit (residual deviance: 232.61 on 426 degrees of freedom) for each coefficient included in the models. $p < 0.05$ and $** < 0.001$

Response variable	Coefficient		Estimate	SE	Z	P
Number of chicks aggregating	Location	Maiviken (intercept)	4.81	0.348	13.835	<0.001**
		Georges Pt.	-4.07	8.574	-4.743	<0.001**
		Port Lockroy	-0.35	<0.001	<0.001	0.999
		Petermann Isl.	-5.06	1.460	-3.466	<0.001**
	Wet		0.96	0.864	1.116	0.264
	Temperature		5.96	0.035	1.695	0.090
	Location: wet	Maiviken: wet	0.96	0.864	1.116	0.264
		Georges Pt.: wet	1.10	1.171	0.936	0.349
		Port Lockroy: wet	0.33	<0.001	<0.001	0.999
		Petermann Isl.: wet	4.92	2.097	2.344	0.019*
	Temperature: wet		-0.31	0.123	-2.523	0.012*
	Post-guard day		-0.05	0.025	-2.026	0.043*
	log(guarded chicks: unguarded chicks)		-0.61	0.116	-5.256	<0.001**
Number of aggregations	Location	Maiviken (intercept)	1.83	0.176	10.377	<0.001**
		Georges Pt.	-1.71	0.462	-3.696	<0.001**
		Port Lockroy	-18.58	825.6	-0.023	0.982
		Petermann Isl.	-4.60	1.016	-4.507	<0.001**
	Wet		-0.005	0.512	-0.010	0.992
	Location: wet	Maiviken: wet	-0.005	0.512	-0.010	0.992
		Georges Pt.: wet	0.29	0.702	0.412	0.681
		Port Lockroy: wet	14.63	825.6	0.018	0.986
		Petermann Isl.: wet	4.97	1.503	3.303	<0.001**
	Post-guard day		-0.07	0.017	-4.354	<0.001**
	log(guarded chicks: unguarded chicks)		-0.42	0.084	-4.955	<0.001**

3.4 Results

We found significant relationships between location, wet conditions, the ratio of guarded to unguarded chicks, and the age of chicks and each of our response variables: 1) the number of aggregations and 2) the number of chicks aggregating (3.1). Because nest counts were used to offset the data to account for the differences in the camera view and angle between each of our study sites, the following results indicate the relationship between each coefficient and our measures of aggregation behaviour per nest unit.

When examining the counts of aggregating chicks in each image, the Maiviken (South Georgia) chicks exhibited significantly more aggregation behaviour ($SE=0.35$, $P< 0.001$) than either the Georges Point (estimate= -4.07 , $P< 0.001$) or Petermann Island colonies (estimate= -5.06 , $P< 0.001$, Table 3.1). However, our model for the number of aggregations at each colony revealed that not only did chick aggregations increase significantly at Maiviken compared to Petermann Island (estimate= -4.60 , $P< 0.001$) and Georges Point (estimate= -1.71 , $P< 0.001$), but the number of aggregations exhibited by Petermann Island chicks also differed significantly from Georges Point (estimate= -2.87 , $P=0.008$, Table 3.1), with chicks at Petermann Island undergoing far fewer aggregations.

For both our measures of the number of chicks aggregating and the number of aggregations, we found negative relationships between our response variables and 1) the day within the post-guard period (estimate= -0.05, $P= 0.043$; estimate= -0.07, $P< 0.001$, respectively) and 2) the ratio of guarded chicks to unguarded chicks (estimate= -0.61, $P< 0.001$; SE= -0.42, $P< 0.001$, respectively, Table 3.1). In other words, the number of chicks aggregating and the total number of aggregations increased when chicks were younger and when more chicks were left unguarded by their parents.

We also found a relationship between the environmental variables of temperature and wet conditions present and the two measures of chick aggregations, although these conditions depended on the location of the colony. The number of aggregations and counts of chicks aggregating increased at Petermann Island when wet conditions were present at the colony (estimate= 4.92, $P=0.02$; estimate=4.97, $P<0.001$, respectively, Table 3.1). In addition, the number of aggregations at Petermann Island was significantly different from both the Georges Point (estimate= 2.87, $P=0.008$) and Maiviken colonies (SE=4.58, $P<0.001$, Table 3.1). We also found a significant negative relationship between temperature and wet conditions and the counts of chicks in aggregations across sites (estimate=-0.311, $P=0.01$, Table 3.1), but not between the total aggregation counts in each image. In other words, as temperature increased during wet conditions, the total counts of chicks in aggregations decreased.

Table 3.2. Summary of measures of variance (range, mean, and standard deviation) in three aggregation characteristics (1) average aggregation size, 2) total number of chicks in aggregations, and 3) total number of aggregations at each of our four study sites and in total across all four sites: Maiviken, Georges Point, Port Lockroy, and Petermann Island.

Aggregation measure	Measures of variance	Site				
		Maiviken	Georges Point	Port Lockroy	Petermann Island	All sites
Average aggregation size	Range	3- 73	3- 9	3- 10	3- 3	3- 73
	Mean	10.62	3.59	4.03	3	8.11
	<i>sd</i>	12.15	1.30	1.99	0	5.34
Total number of chicks in aggregations	Range	0- 105	0- 13	0- 10	0- 3	0- 105
	Mean	15.81	1.02	0.13	0.03	2.88
	<i>sd</i>	19.03	2.12	0.85	0.30	10.32
Percent of chicks aggregating	Range	0- 100	0- 52.53	0- 100	0- 37.5	0- 100
	Mean	27.62	3.99	1.28	0.16	5.92
	<i>sd</i>	27.93	8.25	8.53	2.15	16.28
Total number of aggregations	Range	0- 9	0- 3	0- 2	0- 1	0- 9
	Mean	3.59	0.28	0.03	0.01	0.37
	<i>sd</i>	1.30	0.55	0.20	0.10	1.00

3.5 Discussion

To the best of our knowledge, we are the first to study the adaptive significance of chick aggregation behaviour in gentoo penguins and the first to examine this behaviour at multiple colonies, covering a large geographic range, in any penguin species. Our results support the idea that aggregations occur to decrease an individual's energetic expenditure during wet, cold conditions. However, we found significant differences in aggregation behaviour across a latitudinal gradient, particularly between the Maiviken (South Georgia) site and two of the other three sites located in closer proximity on the Antarctic Peninsula, suggesting that this behaviour may be colony specific, and the result of a more complex set of interactions.

The timing of the post-guard phase varied notably between Maiviken, South Georgia and the three Antarctic Peninsula sites (Figure 3.2). The phenology of gentoo penguins has been shown to vary between years and locations, a relationship that is influenced by sea temperature and local resource availability (Bost and Jouventin 1990). Because aggregation behaviour is closely linked with the post-guard phase, the timing of this behaviour may be dictated by parental phenological constraints. Specifically, the timing of post-guard period may be dictated by the adult need to build up reserves prior to moult, and therefore leave chicks unguarded, while the formation of aggregations may be instead dictated by a chick's need to survive and thermoregulate without constant guard (Penteriani et al. 2003). In addition, certain colonies may be more synchronous than others (Williams et al. 1991) and asynchronicity may influence chick aggregation behaviour, as aggregations may be

smaller and less frequent when individuals enter the post-guard period at different times.

We found a significant link between temperature, increased wet conditions, and the age of chicks and our two measures of aggregation behaviour (Table 3.1), similar to past studies focusing on this behaviour in other penguin species (eg. Adélie penguins, Davis 1982a, Lawless et al. 2001; emperor penguins, Ancel et al. 1997; king penguins, Le Bohec et al. 2005). In particular, we found that a slight decrease in temperature when wet conditions were present correlated with an increased number of chicks aggregating (Table 3.2). In addition, chicks appear to aggregate earlier in the post-guard period when younger and therefore more vulnerable to cold, wet conditions. Although gentoo chicks are thought to fully self-regulate body temperature roughly 15 days after hatching (Taylor 1985), before the post-guard period, other evidence suggests that chicks may not be able to thermoregulate independently when wet conditions are present (Janes 1997). Our study supports harsh weather conditions potentially being as influential in chick aggregating behaviour as daily temperature variation.

Although our analysis revealed that, overall, aggregations are related to temperatures and wet conditions; we also found significant differences when examining each of our aggregation measures within sites (Table 3.1). In particular, the number of aggregations and chicks aggregating was significantly and positively related to wet conditions at the Petermann Island, Antarctic Peninsula study site, but not at

the other three sites. In addition, chicks at the two study sites located at either extreme of our latitudinal gradient, Maiviken and Petermann Island, underwent different degrees of aggregation behaviour: the Maiviken chicks aggregating significantly more while the Petermann Island chicks aggregated significantly less. It is possible that colonies may form aggregations using different mechanisms, depending on their location and the conditions present during the post-guard period. However, because our analysis across sites revealed general trends, it is more likely that aggregations form due to wet, cold conditions and that the differences in weather and the timing of the post-guard period between sites is driving aggregation extent.

Unlike in other penguin species (Adélie penguins, Davis 1982a; African penguins, Seddon and Van Heezik 1991; king penguins, Le Bohec et al. 2005) we did not find evidence to support either predator avoidance or aggregation from unrelated adults as a driver of chick aggregation formations in gentoo penguins (cf. African penguins, Seddon and van Heezik 1993; chinstrap penguins, Penteriani et al. 2003; king penguins, Le Bohec et al. 2005). However, the study of predator attendance was limited, as photographs were not taken frequently enough to consistently detect predation events or abundance ($n=8$). Therefore, we cannot reliably determine whether predation is an additional driver of this behaviour in gentoos. Likewise, gentoo chicks are particularly mobile when compared to conspecifics, so time-lapse images taken at a frequency of every hour, as is the case with this study, are limited in their ability to assess aggregation behaviour when chicks move outside the boundaries of the sub-colony.

In addition, the ratio of adults to chicks did not appear to influence our measures of chick aggregations, although we did find evidence that more chicks aggregated and more aggregations occurred across the species' range when fewer chicks were guarded by their parents (Table 3.2). However, the relationship between aggregations and the ratio of guarded to unguarded chicks likely suggests that chicks are aggregating more when adults are absent and thermoregulation is consequently more difficult, rather than because of aggressive advances from adults. Directly quantifying aggression events would be an obvious next step to confirm this finding. Nevertheless, because adult to chick ratio has been used to determine significant trends in this behaviour in the past (Penteriani et al. 2003), and we did not discover a relationship between this variable and aggregation measures, we believe that our results regarding unrelated adult aggression are likely accurate, even without direct observation.

We provide strong evidence that chick aggregations form more often and are larger in size at our northern-most colony on the island of South Georgia. The difference in aggregating behaviour between South Georgia and our three Antarctic Peninsula colonies provides evidence that this behaviour, although apparent in all four colonies, does not appear to be generalizable across the range of the species. Instead, we show that colonies exhibit distinct differences in their aggregating behaviour, which is likely due to differences in environmental conditions present and may be exaggerated by the difference in the timing of the post-guard phase. Studying

multiple sites within the species range is the first step in gaining a better understanding of the range of aggregation behaviours at a species level, demonstrating how colonies are related in their behaviours, and whether or not this behaviour is generalizable. Single colony studies, while useful, may lack this breadth of understanding. The significant differences in behaviours between colonies, as revealed by this study, demonstrate the necessity to examine colonies at multiple locations before generalizing results, which otherwise may be oversimplified when determining the drivers of observed behaviours.

Our results highlight the utility of time-lapse cameras to remotely monitor animal behaviour using scan sampling methods, without the need for *in situ* data collection (Newbery and Southwell 2009). The method allows for accurate measurement of the timing of behaviours and assures the standardization of sampling across multiple locations at the same time, while also limiting observer differences. We provide evidence of the strength of cameras as wide-scale behavioural sensors; however, the inability to routinely detect predation or events of adult aggression using time-lapse imagery also suggests some important limitations. Given the facility to study multiple colonies simultaneously, we were able to better understand how behaviours differ between colony locations in the same species. Future studies should evaluate multiple colonies before generalizing behaviours based on one location and past studies may need to be re-evaluated to determine whether chick aggregation and other behaviours are in fact exhibited species-wide.

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4

CHAPTER FOUR

Time-lapse Imagery of Adélie Penguins Reveals Differential Winter Strategies and Breeding Site Occupation

4.1 Abstract

Polar seabirds adopt different over-wintering strategies to survive and build condition during the critical winter period. Penguin species either reside at the colony during the winter months or migrate long distances. Tracking studies and survey methods have revealed differences in winter migration routes among penguin species and colonies, dependent on both biotic and abiotic factors present. However, scan sampling methods are rarely used to reveal non-breeding behaviours during winter and little is known about presence at the colony site over this period in Southern Ocean. Here we show that Adélie penguins on the Yalour Islands in the Western Antarctic Peninsula (WAP) are present year-round at the colony and undergo a mid-winter peak in abundance during winter. We found a negative relationship between daylight hours and penguin abundance when either open water or compact ice conditions were present, suggesting that penguins return to the breeding colony when darkness obstructs visibility during pelagic foraging and when either extreme low or high levels of sea ice exist offshore. In contrast, Adélie penguins breeding in East Antarctica were not observed at the colonies during winter, suggesting that Adélie penguins undergo differential winter strategies in the marginal ice zone on the WAP compared to those in East Antarctica. These results demonstrate that cameras can successfully monitor wildlife year-round in areas that are largely inaccessible during winter.

4.2 Introduction

Extreme seasonality in the Polar Regions has forced many animals to develop adaptations to cope with a dynamic habitat, including a constrained breeding period and resilience during the non-breeding season. At the end of summer, most polar wildlife species enter a non-breeding, winter period with harsh environmental conditions in which individuals must survive while also building condition immediately prior to the next breeding season. Penguins (*Spheniscidae*) represent a large biomass of seabirds in the Southern Ocean during winter (Croxall et al. 1979) but occupy different winter distributions (Culik et al. 1997, Pütz et al. 2002, Trivelpiece et al. 2007, Thiebot et al. 2011) and undergo a range of strategies, depending on the species and colony (Croxall et al. 1999). Emperor penguins (*Aptenodytes forsteri*) serve as an excellent example of an extreme overwintering strategy by breeding and raising their young during the winter months with severe time constraints and highly synchronous markers within their annual cycle (Borboroglu et al. 2013). In contrast, King penguins (*Aptenodytes patagonicus*) breed during the summer months, but raise each chick for fourteen months over winter, resulting in an overlap in incubation and chick rearing each summer (Olof 1996). Similarly, other Southern Ocean species (eg. Adélie penguins, *Pygoscelis adeliae*; chinstrap penguins, *Pygoscelis antarctica*; gentoo penguins, *Pygoscelis papua*; Macaroni penguin, *Eudyptes chrysolophus*; Southern Rockhopper Penguin, *Eudyptes chrysocome*) hatch and raise their chicks to fledglings during summer, yet adopt

various overwinter strategies to survive the non-breeding period and build condition prior to breeding the following summer.

These winter strategies include either long distance migrations (eg. chinstrap, Adélie, and Southern Rockhopper penguins) or residence at the colony site (eg. gentoo penguins, Borboroglu et al. 2013 and references therein) and depend on a complex relationship with sea ice (Ainley et al. 1993a, b, Forcada et al. 2006), the ocean bathymetry and currents present (Clarke et al. 2003, Erdmann et al. 2011), and prey availability (Stokes et al. 1998, Ribic et al. 2008, Thiebot et al. 2011). For those that do migrate, ranges vary between species and colonies and species are often associated with either pack ice (eg. Adélie penguins) or open water (eg. gentoo penguins) during winter, dependent on their frequency at the respective habitats and foraging strategies (Ainley et al. 1993a, Ainley et al. 1993b, Ribic et al. 2008, Ballerini et al. 2009, Emmerson and Southwell 2011).

The *Pygoscelis* genus of penguins includes two species that migrate long distances (chinstrap penguins, Trivelpiece et al. 2007, Biuw et al. 2009 and Adélie penguins, Davis et al. 1996, Davis et al. 2001, Hinke et al. 2015a, b) and one that stays predominantly at colony sites over winter (gentoo penguins, see Bost et al. 1990 and references therein), acting largely as a central place forager for the entire year. For those that do migrate, the duration and distance of migrations varies greatly by region, as colonies appear to winter in distinct regions to avoid an overlap in foraging areas (Trivelpiece et al. 2007, Ballard et al. 2010, Erdmann et al. 2011). An individual's condition during the winter period may have major consequences for both sedentary

and migratory species, affecting reproductive success during the following breeding period (Irvine et al. 2000, Clarke et al. 2002, Dugger et al. 2010, Lescroël et al. 2014). Subsequently, winter constraints, including a reduced photoperiod (Wilson et al. 1989, Fraser et al. 1996, Ainley 2002, Forcada et al. 2009), sudden changes in sea ice types and locations (Forcada et al. 2006), and dynamic prey movements (Tanton et al. 2004, Ribic et al. 2008), may influence whether an individual survives to return to breed in the summer (Wilson et al. 2001, Ainley 2002) and an individual's physical condition on return (Chappell et al. 1993, Trathan et al. 1996).

As an ice-obligate species during winter, recent evidence suggests that Adélie penguin populations have significantly declined along the Western Antarctic Peninsula (WAP) since 1980 (Forcada et al. 2006, Hinke et al. 2007, Lynch et al. 2012, Trathan et al. 2016), as their sea ice niche has decreased due to fewer frequent cold years (Fraser et al. 1992), while their populations have increased in East Antarctica where sea ice has remained relatively stable (Southwell et al. 2015). Consequently, monitoring Adélie populations is essential to understand changes in the population dynamics and behaviours of the species year-round. As roughly 15% of adult Adélie penguins do not survive the winter months (Ballerini et al. 2009 and references therein), it has been suggested that the non-breeding period serves as a critical time in the life history of the species, which likely dictates the stability of populations and recruitment rates within colonies (Trathan et al. 1996, Wilson et al. 2001, Ainley 2002, Hinke et al. 2007).

However, little is known about winter migrations and the presence or absence of individuals at breeding grounds during winter due to the difficulties of monitoring populations year-round on the Antarctic continent. What little information is published about Adélie overwintering behaviour has been determined primarily from tracking studies at isolated colonies along East Antarctica, the Ross Sea (Clarke et al. 2003, Ballard et al. 2010) and along the Antarctic Peninsula (Fraser et al. 1996, Dunn et al. 2011, Erdmann et al. 2011, Hinke et al. 2015a). From these studies, it appears that Adélie penguins in East Antarctica and the Ross Sea migrate large distances (~1400-17600 km, Davis et al. 1996, Clarke et al. 2003, Ballard et al. 2010), while studies along the WAP have found Adélies migrating more variable distances (Dunn et al. 2011, Erdmann et al. 2011, Hinke et al. 2015a) with anecdotal evidence that some individuals remain near the colony site over winter (Bagshawe 1938, Sladen 1958, Parmalee et al. 1977, Erdmann et al. 2011). Unfortunately, tracking devices are often expensive and difficult to deploy long-term (Bridge et al. 2011); therefore, small sample sizes are often produced (eg. Davis et al. 1996, Davis et al. 2001) without a complete winter season worth of information (eg. Davis et al. 1996).

To further enhance knowledge of the overwintering behaviour of Adélie penguins in the WAP and East Antarctica, we observed the presence of Adélie penguins at colony sites during the non-breeding period from camera images taken daily over winter in each of these regions. Cameras were deployed at the Yalour Islands along the WAP and at seven sites near Casey and Mawson stations in East Antarctica. Additionally, the cameras provided high-resolution data on sea ice extent

at the Yalour Islands site, allowing us to accurately measure near-shore sea ice and its influence on Adélie penguin presence or absence at the colony site over winter. Using this information, we aimed to determine 1) whether Adélie penguins are present at their breeding location on the Yalour Islands and colony sites near Casey and Mawson stations during winter and 2) whether the number of adults present increases as sea ice extent diminishes and daylight hours and daily air temperatures increase throughout the winter.

4.3 Methods

4.3.1 Study Sites

Our study sites included Adélie penguin breeding sites in the WAP and in East Antarctica (Figure 4.1). As of 2012, the Yalour Islands in the WAP (65°15'S, 64°17'W) were resident to roughly 2500 Adélie penguin breeding pairs (HJ Lynch, personal communication). The group of three islands is positioned within the year-round marginal ice zone (Lynch et al. 2012), which provides a variety of sea ice types throughout the year, dependent on local conditions. The study site is located on the northernmost main island and represents the species' southern edge of range on the WAP (Polito et al. 2011).

The east Antarctic study sites comprised seven Adélie penguin breeding sites near Mawson and Casey stations that currently hold around 75,000 breeding pairs: Blakeney Point (66°25' S, 110°53' E), Odbert Island (66°24' S, 110°58' E), Shirley

Island (66°28' S, 110°48' E), and Whitney Point (66°25' S, 110°53' E) near Casey Station as well as Petersen Island (67°57' S, 62°88' E), Verner Island (67°57' S, 62°88' E), and Welch Island (67°55' S, 62°91' E) near Mawson Station (Fig 1). These sites are on or close to (<2 km) the continental coastline where winter sea-ice can extend long distances northwards, winter pack-ice, in particular, can extend up to 1,000 km northwards in both areas (Clarke et al. 2003). Winter fast-ice, which can form a barrier to swimming, typically extends only short distances (2-10 km) northwards from the Casey sites, but can extend up to 80 km, northwards from the Mawson sites (NOAA National Ice Center 2015).

4.3.2 Camera System

The Yalour Islands camera overlooked three sub-colonies of Adélie penguins. The camera angle was set to view the maximum number of individuals possible while still allocating a large portion of the camera view to the near-shore sea ice. The camera was installed using the techniques described by Newbery and Southwell (2009) with minor adjustments to the camera system (Figure B.1). A Reconyx HC500 Hyperfire camera (Reconyx, Inc., Holmen, WI, USA) was installed and mounted to a scaffold pole and anchored using a rock basket. The camera was programmed in time-lapse mode to take eight photographs daily, beginning at 10:00 on March 1, 2012 and ending at 15:00 on January 6, 2014. The camera's batteries (lithium AA) and SD card were changed twice, but the camera and its angle were not changed.

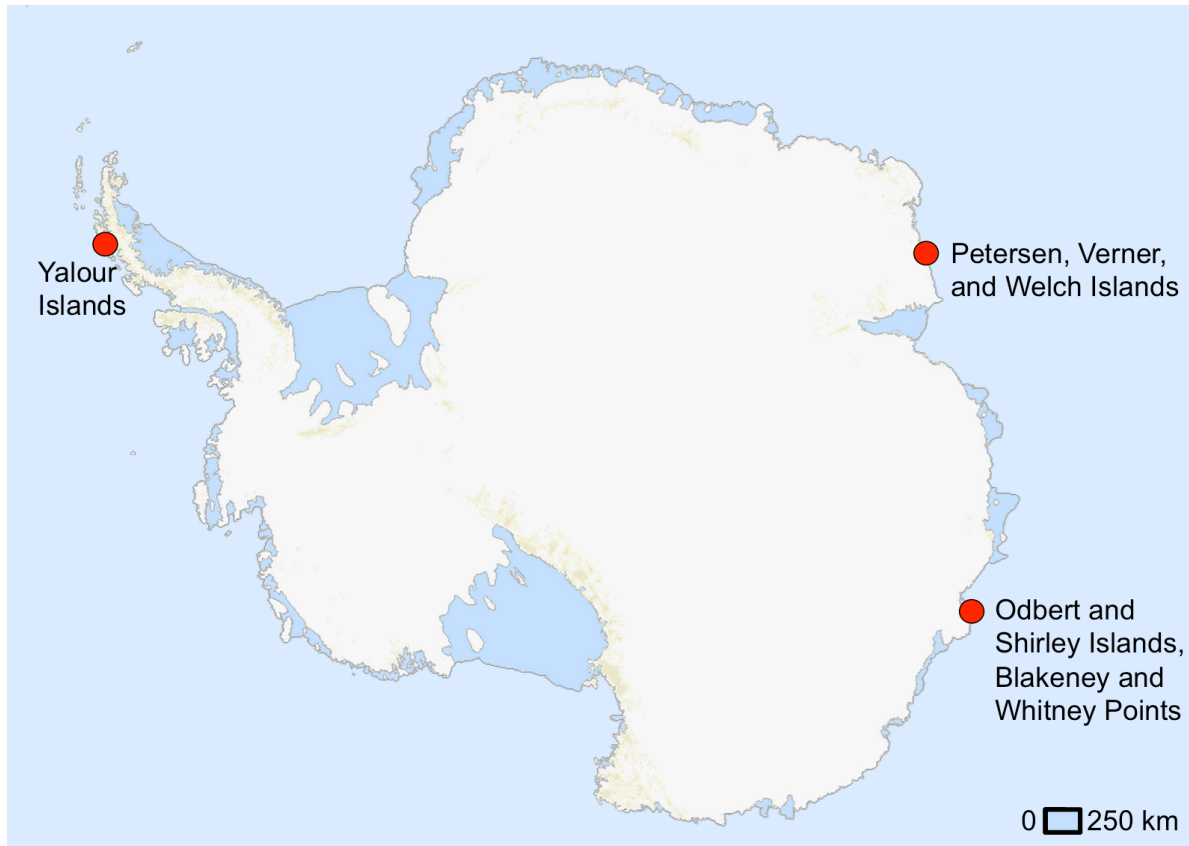


Figure 4.1. Map of our eight study sites, including 1) Yalour Islands on the Western Antarctic Peninsula, 2) Petersen Island, 3) Verner Island, 4) Welch Island, 5) Odbert Island, 6) Shirley Island, 7) Blakeney Point, and 8) Whitney Point in East Antarctica. Map adapted from USGS Antarctic Research Atlas.

Similarly, each of the seven cameras deployed in East Antarctica were installed using the methods described in Newbery and Southwell (2009). Each camera took one photo at solar midday each week (12:00 local time) from March 1 to September 27, 2013 and 2014 (31 total photos from each site per year). All cameras were deployed roughly 20-40 m from sub-colonies to include part of the breeding colony and four included the nearby coastline and ocean in the field of view. The SD cards were changed twice but the cameras' positions were not changed.

4.3.3 Data Extraction

Counts were extracted from each image using software developed by Aytar (2012). In each image, a circle was centred over each visible individual to avoid counting individuals twice (Fig S1). The number of circles in each image was then extracted, using the same software, to determine counts for each image date. For our study purposes, we defined winter as March 1- September 30 to provide a two-week buffer between the last departure date of fledglings from the previous breeding season and the first arrival date of adults the following spring. During the winter months, all birds were described as adults given the difficulty of confidently discerning adult and juvenile plumage due to the resolution (3.1 megapixels) of the images. The same individual (CB) annotated all images blind to date.

The Yalours camera on the WAP and four of the East Antarctica cameras (Odbert, Shirley, and Verner Islands and Whitney Point) overlooked the nearby marine environment enabling the extent and type of near-shore sea ice to be

determined. Sea ice extent was determined from the images using the guidelines described in *An Observer's Guide to Sea Ice* (Smith 2000), originally intended for the U.S. Sea Ice Reporting Agencies' observer reports forms. Sea ice in each image from all eight sites was ranked from 1-10 based off photographs provided in Smith (2000). Rankings of 1-6 indicate increasing concentrations of open drift, rankings of 7-9 indicate increasing concentrations of pack ice, and a ranking of 10 indicates compact ice (aka. fast ice). We defined compact ice, separate from pack ice, when sea ice did not appear to move over time (between images).

All the cameras automatically produced metadata on date and time of day, and the Yalours camera also produced temperature data throughout the study period. Daylight hours were extracted using the *sunalc* function in the *RAtmosphere* package of R (R Core Development Team 2013, Biavati 2014).

4.3.4 Statistical Analysis

We used generalized linear models (GLMs) to model penguin abundance at occupied colony sites in relation to environmental conditions. To avoid bias due to low daylight hours during winter, and therefore a lower volume of visible counts around the winter solstice, we used only those images taken at 12:00 (local time). All analyses were conducted in R (v 3.0.3) language for statistical computing using the *stats* package (R Core Development Team 2013), merging data from all years. Due to overdispersion in both poisson and quasi-poisson generalized linear models, we used a negative binomial GLM (*glm.nb* function, *MASS* package, Venables and Ripley

2002) to determine interactions between each of the coefficients and non-breeding (winter) Adélie counts. By examining the model with and without a correlation structure and the auto-correlation in the observed residuals (*acf* function, *stats* package), we determined that temporal autocorrelation did not occur in our data set and a correlation structure was therefore omitted from the model. Model selection was determined by choosing the model with the lowest ratio of residual deviance to degrees of freedom. Ultimately, the GLM independent variables included an interaction between sea ice type and both photoperiod (aka. daylight hours) and temperature (°C), year, and Julian date (residual deviance: 238.92 on 618 degrees of freedom). During model selection, the log of the sea ice score (1-10) coefficient was omitted (ANOVA, $P = 0.03$). Lastly, to understand relationships with environmental variables, we examined contrasts by reordering the levels of factors (*relevel* function, *stats* package).

4.4 Results

We observed considerable numbers of Adélies at the Yalour Islands colony site during the non-breeding (winter) period compared to those present during the breeding period. When birds were present during the non-breeding (winter) period, their abundance in the cameras' field of view ranged from 1 to 13 in 2012, 1 to 29 in 2013, and 1 to 9 in 2014.

Table 4.1. Results from a negative binomial GLM on Adélie penguin abundance during the non-breeding period at the Yalour Islands from 2012-2014 (residual deviance: 238.92 on 618 degrees of freedom). Reference level shown here is 2012 - Open water. * $P < 0.05$, ** $P < 0.01$, and *** $P \leq 0.001$

Coefficient		Estimate	SE	Z	P	
Sea ice type	Open water	2.65	0.918	2.881	0.004	**
	Pack	2.85	1.812	1.571	0.117	
	Compact	10.11	4.126	2.450	0.015	*
Year	2012	2.65	0.918	2.881	0.004	**
	2013	-0.28	0.360	-0.790	0.430	
	2014	-1.03	0.374	-2.755	0.006	**
Photoperiod: sea ice type	Photoperiod	-0.18	0.056	-3.260	0.001	**
	Photoperiod: pack	-0.34	0.232	-1.453	0.147	
	Photoperiod: compact	-1.09	0.476	-2.288	0.022	*
Air temperature (°C): sea ice type	Temperature	-0.09	0.050	-1.701	0.089	.
	Temperature: pack	0.15	0.148	1.025	0.306	
	Temperature: compact	0.86	0.299	2.866	0.004	**
						**
Julian date		-0.02	0.004	-4.718	0.000	*

Analysis of images from the East Antarctic sites revealed that Adélies were last seen in photographs at the seven sites between February 28 and March 29 in 2013 and between 4 February and 27 February in 2014. There were no further sightings of penguins at any of the sites until the following October at the beginning of the next breeding season in both years. We therefore considered Adélies as absent from all of the East Antarctic colony sites over the entire non-breeding, winter period.

Because all East Antarctic sites were unoccupied over winter, our analysis of relationships between abundance and environmental conditions was restricted to the Yalours site. We found significant relationships between the abundance of Adélie penguins during the non-breeding (winter) period and each of the environmental variables tested in Table 4.1. Adélies were significantly more abundant during compact ice conditions ($P = 0.015$) than open water conditions ($P < 0.001$), although both sea ice types exhibited a significant relationship with non-breeding (winter) abundance (Table 4.1). The relationship between non-breeding (winter) abundance and photoperiod when compact sea ice was present was significantly different from photoperiod when open water was present ($P < 0.001$, Table 4.1). However, both open water and compact ice photoperiods influenced penguin abundance in a clear negative relationship (Table 4.1). In other words, penguins were more abundant at the colony site during the non-breeding (winter) period when fewer daylight hours and either high compact or low open water levels of sea ice were present. In addition, temperature during specific sea ice types also influenced Adélie abundance; the effect

of temperature on penguin abundance when compact ice was present ($P = 0.009$) differed significantly from periods when open water ($P = 0.17$) or pack ice ($P = 0.385$) was present and exhibited a positive relationship with penguin abundance (Table 4.1). In other words, Adélie non-breeding (winter) abundance increased as temperature increased when compact ice was present.

In relation to date, over all three years, Adélies were significantly more abundant earlier in the non-breeding (winter) season ($P < 0.001$). We also found significant differences between years; penguins were significantly more abundant in 2012 ($P = 0.001$) than in 2014 ($P = 0.007$), although there was no significant difference between 2013 and the other two years ($P = 0.202$, Table 4.1).

4.5 Discussion

Here, we show that time-lapse cameras can successfully monitor colonial wildlife and near-shore sea ice conditions year-round, which will improve our understanding of winter behaviour at colonies in remote regions. By using cameras, we can monitor areas that are logistically difficult to access and increase the replication of monitored sites (Newbery et al. 2009). Until recently, research on Adélie penguins has focused primarily on measuring summer breeding parameters and remotely derived sea ice patterns, instead of winter behaviour and localized sea ice extent (Davis et al. 2001, Ballard et al. 2010). Moreover, winter ecology in the Southern Ocean has largely used methods of non-constant effort, such as those in

tracking studies (eg. Davis et al. 1996, Davis et al. 2001, Clarke et al. 2003, Erdmann et al. 2011) or species assemblage surveys (eg. Ainley et al. 1993a, b, Fraser et al. 1996, Ribic et al. 2008) in which survey efforts are much lower and more constrained in winter when compared with the summer months. Camera monitoring demonstrates the strong potential of image analysis as a method to monitor colonial species and abiotic activities year-round at a high-resolution scale, overcoming many- but not all- limitations of other survey methods. However, the inability to 1) distinguish between adults and juveniles, 2) describe behaviours at night, 3) examine individuals outside of the camera's range of view, and 4) know whether the individuals observed in winter at the Yalours also breed at the site serve as major limitations of this study's camera method until more affordable technology develops.

Substantial differences exist between East Antarctica and the Western Antarctic Peninsula (WAP) in terms of environmental drivers, particularly related to winter sea ice extent. In East Antarctica, widespread consolidated compact ice exists in many regions throughout the winter months (Gloersen et al. 1992, Stammerjohn et al. 1997, Stammerjohn et al. 2008, Fraser et al. 2012). The presence of such ice is likely to make it difficult for an Adélie penguin to journey to the colony site during the non-breeding (winter) period without extensive, energy-consuming travel across the ice (Ballerini et al. 2009), as has also been observed during the summer months (Emmerson and Southwell 2008). This may explain the winter absence of Adélie penguins from the Mawson colony sites, where winter fast-ice extends up to 1000 km from the coast (Clarke et al. 2003). Winter fast-ice extent is more limited at Casey, yet

pack-ice can consolidate into large, dense floes over extensive areas in winter and form a physical barrier to travel in a similar fashion to compact ice. In contrast, the WAP sea ice extent varies substantially throughout the winter months, undergoing periods of open water, pack ice, and compact ice, with large temporal fluctuations (Stammerjohn et al. 2008). Therefore, Adélies breeding on the WAP may either remain at their colony site during the winter period or choose to venture to other colony sites during this phase, without the limitations of seasonal compact sea ice extent.

Our results at the Yalours site support a strong association between winter sea ice and abundance; Adélies were present at the Yalour Islands during the non-breeding period when either compact sea ice or open water conditions were present (Table 4.1, Figure 4.2). Because Adélies are well-established pack ice inhabitants (Ainley 2002), they may not be able to exploit open-water areas as effectively due to adaptive restrictions (eg. diving behaviour, temperature regulation, Ainley et al. 1993a, b), which may explain their increased presence on land during periods of open-water habitat offshore. Likewise, Adélies are likely restricted in their foraging abilities during short periods of compact ice extent when the sea ice forms a solid barrier from the land to sea. Therefore, the timing of winter presence at the colony site may reflect periods when Adélies are temporarily limited in their foraging abilities yet need a place to rest. Future studies should also consider whether sea ice conditions at a larger temporal scale, beyond the sea ice extent found directly offshore, influence Adélie winter abundance at a colony site.

Our analysis on Adélies at the Yalours site also supported the idea that winter migrations may be linked with photoperiod. As daily daylight hours decreased throughout the winter, Adélie non-breeding abundance at the colony increased when either open water or compact sea ice conditions were present offshore. Presence at the colony site during decreased photoperiods may indicate that penguins are resting on land due to a lack of visual cues at sea needed to navigate, find prey offshore, and avoid predation during low light levels (Emlen et al. 1964, Penney et al. 1967, Wilson et al. 1993, Ainley and Ballard 2012). Adélie penguins at the Yalour Islands appear to peak in abundance once each non-breeding, winter period (Figure 4.2), which may reflect an individual's need to forage closer to shore, when the amount of daylight hours is diminished and extreme sea ice extents (eg. low, open water or high, compact ice) are also present.

Our study highlights the lack of understanding of winter ecology, even though the winter months serve as a critical period of survival. With novel methods of constant effort, we are able to reveal a new mid-winter phase in the annual cycle of a colony at the edge of the species' regional range, which would otherwise be limited by small sample sizes using survey efforts or tracking approaches. However, it is important to address that there is no way of knowing whether the birds in view during winter are the same as those in view over the summer months, yet it is assumed that many of the birds are present at both times of the year at the colony site based on anecdotal observations of other Adélie populations in the WAP (Erdmann et al. 2011)

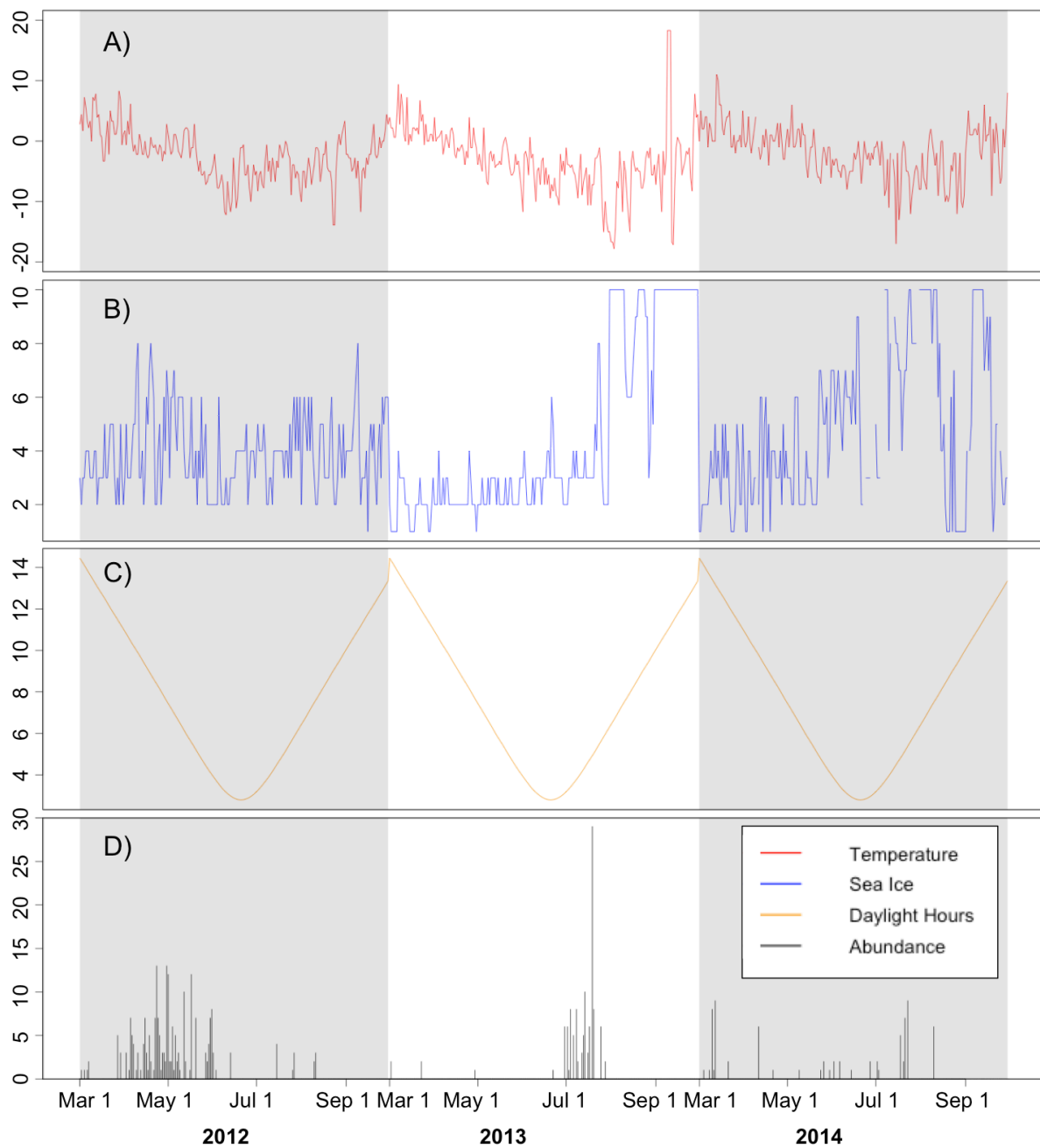


Figure 4.2. Winter (non-breeding) data at the Yalours site showing trends in (A) temperature, (B) sea ice rankings, (C) regional daylight hours, and (D) penguin abundance over time. Grey rectangles indicate the different study years: 2012, 2013, and 2014.

and personal observations from the images studied here in which Adélies engage in nesting or nest building behaviour during the non-breeding (winter) period. However, it is possible that many of those individuals seen overwintering at the colony site were first year fledglings. In addition, the observed individuals at the Yalour Islands, whether adult or juvenile, may have originated from other colonies and their presence may reflect anti-predatory behaviour, or prospection of alternate available colony sites in addition to the hypotheses discussed. It is likely that our results describe the relationship between environmental variables and Adélie non-breeding abundance at the Yalours from colonies throughout the WAP as well as juveniles, rather than solely from adults breeding at the Yalours during the summer months. Future research should explore the age dynamics of overwintering birds as their presence or absence from the colony site over winter may affect their survival and therefore the overall recruitment within the colony.

It has been proposed that changes in climate over the coming years will increase competition for resources and habitat among the *Pygoscelis* species along the WAP (Forcada et al. 2006). This increased competition will likely be most apparent at the edge of their respective ranges and within the marginal ice zone. Future studies should directly address the degree to which the environmental conditions present during winter, particularly along a species' edge of range, influence an individual's reproductive success in the following season. Understanding winter behaviour is essential to predicting population changes due to climate change in this rapidly

warming region and understanding how other threats, such as nearby fishing of prey resources, will affect individual survival year-round.

4.6 References

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CHAPTER FIVE

**Peeking into the Bleak Midwinter- Investigating
Non-Breeding Strategies of Gentoo Penguins using
a Camera Network**

5.1 Abstract

When monitoring species with extensive ranges in harsh climates, comprehensive studies across a species' range are both logistically and technically challenging and therefore rare. Such scarcity in data collection is particularly true in the Polar Regions where sea ice and weather constraints prevent widespread access to sites for much of the year, specifically during winter. Penguins (*Spheniscidae*) show large variations in winter strategies with many species migrating long distances while others are distinctly sedentary, remaining at the colony year-round. However, in some species, their attendance at the breeding site during the non-breeding winter period depends greatly on the colony location and environmental factors. Here we aim to examine fluctuations in winter attendance at the breeding site in gentoo penguins along a latitudinal gradient of seven sites, ranging from Martillo Island, a colony in Argentina, to Petermann Island, a colony located towards the species' southern edge of range on the Western Antarctic Peninsula. We use an established network of cameras to observe winter populations of penguins across a large latitudinal gradient. This study provides the first evidence of across year variation in gentoo non-breeding attendance at the breeding site. We found that both temporal and spatial factors drive winter attendance in this species with distinct patterns between years and colony locations, particularly at the edges of their range. Additionally, environmental and temporal factors, including sea ice extent directly offshore and photoperiod, appear to dictate gentoo winter attendance across their range. As experimental fisheries closures along the WAP may occur in the future (Hart et al. 2015), gentoos serve as ideal

subjects, in which to measure and detect pressures from fisheries year-round, which likely affect both adult survival and breeding success. Because gentoos are neither sedentary nor migratory during the non-breeding period, understanding patterns in winter site occupation across time and space provides insight into half of the species' annual cycle and has important implications in the face of changes in climate, direct human disturbance, and fisheries activities.

5.2 Introduction

When monitoring species with extensive ranges in harsh climates, comprehensive studies across a species' range are both logistically and technically challenging and therefore rare. Such scarcity in data collection is particularly true in the Polar Regions where sea ice and weather constraints prevent widespread access to sites for much of the year, specifically during winter. However, year-round studies across a species' complete range are especially relevant in polar environments because animals present during the summer breeding months may migrate, remain close to summer breeding sites, or adopt partial migration strategies during the non-breeding period, which is poorly understood (Chapter 1). Examining the mechanisms that govern these strategies is important in the face of climate change, changing fishing pressure, and increasing human visitation (Chown et al. 2015).

Penguins (*Spheniscidae*) show large variations in winter strategies with many species migrating long distances (eg. chinstrap *Pygoscelis antarctica*;

Magellanic, *Spheniscus magellanicus*), while others are distinctly sedentary, remaining at the colony year-round (eg. African, *Spheniscus demersus*; yellow-eyed, *Megadyptes antipodes*, Croxall and Davis 1999, Biuw et al. 2009). However, in some species (eg. Adélie *Pygoscelis adeliae*; gentoo *Pygoscelis papua*), their attendance at the breeding site during the non-breeding winter period depends greatly on the colony location (Bost and Jouventin 1990, Erdmann et al. 2011, Wilson et al. 1998). In addition, environmental factors, particularly sea ice extent, photoperiod, and food availability influence winter migration both temporally and spatially (eg. Clarke et al. 2003, Pütz et al. 2007, Ballard et al. 2010) and winter whereabouts can impact reproductive success, as individuals must build condition during the non-breeding period to successfully breed the subsequent summer (eg. Irvine et al. 2000, Clarke et al. 2002).

Gentoo penguins inhabit a large range in the Southern Ocean and Antarctic Peninsula and can therefore be used as an exemplar study species when examining behavioural changes along a latitudinal gradient. Gentoos are currently of interest in studies observing environmental change, as their populations are increasing at their Southern limit along the Western Antarctic Peninsula (WAP), while competitor populations (Adélie and chinstrap penguins) are declining (Lynch et al 2012, Trathan et al. 2016). Few studies have been conducted of non-breeding behaviour, examining either winter diet (LaCock et al. 1984, Williams 1991, Clausen and Pütz 2002) or winter locations using GPS or temperature loggers (Hindell 1989, Williams et al. 1992, Wilson et al. 1998, Tanton et al. 2004, Hinke and Trivelpiece 2011). Gentoos are known to remain present at breeding sites over winter in the sub-Antarctic islands

of South Georgia (Williams et al. 1992), the South Shetlands (Wilson et al. 1998, Hinke and Trivelpiece 2011) and Crozet Islands (see Bost and Jouventin 1990 and references therein), but there are large spatial gaps in our knowledge of their winter behaviour beyond these locations: particularly comparisons between behaviour at Sub-Antarctic islands and the southern edge of their range on the WAP.

Here we aim to examine fluctuations in winter attendance at the breeding site in gentoo penguins along a latitudinal gradient of seven sites, ranging from Martillo Island, a colony in Argentina, to Petermann Island, a colony located towards their southern edge of range on the WAP. Using time-lapse cameras, this study aims to determine inter-site and inter-annual variation in colony occupation during the non-breeding period. In particular, we aim to answer the following *a priori* hypotheses:

1. Attendance will increase as latitude decreases; colonies located farther north will increasingly remain sedentary at the breeding site.
2. Gentoo winter attendance on land will increase as the number of daylight hours decreases and will peak at the winter equinox, when minimal time is available to visually forage offshore.
3. Winter attendance will increase when open water conditions are found directly offshore because foraging conditions are optimal for this near-shore habitat-linked species and gentoos will therefore choose to rest on land close to their food source (Fraser et al. 1992, Wilson et al. 1998, Clausen and Pütz 2003, Tanton et al. 2004).

4. Winter attendance will change between years if attendance is closely associated with photoperiod.

5.3 Methods

5.3.1 Study Sites

We deployed cameras at seven sites to study winter attendance in gentoo penguins along a latitudinal gradient: 1) Martillo Island (-54.895, -67.401) in the Tierra del Fuego region of Argentina, 2) Maiviken (-54.505, -36.595) on South Georgia, and 3) Cuverville Island (-64.688, -62.622), 4) Danco Island (-64.734, -62.594), 5) Neko Harbour (-64.838, -62.532), 6) Port Lockroy (-64.823, -63.484), and 7) Petermann Island (-65.172, -64.142) along the WAP (Figure 5.1).

5.3.2 Camera System

Seven cameras were deployed, one at each of our seven study sites; each camera was installed roughly 10 meters from a nesting sub-colonies Appendix D). The cameras were installed using techniques similar to those described by Newbery and Southwell 2009 and Southwell and Emmerson 2015, with minor adjustments to the camera system (Appendix B). At each site, a Reconyx HC500 Hyperfire trail camera (Reconyx, Inc., Holmen, WI, USA) was mounted to a scaffold pole and anchored using a rock basket. The cameras were programmed in time-lapse mode to take between eight and fourteen photographs daily, beginning at 7:00 and ending at 20:00

(GMT-2), depending on the camera, and each camera captured images of 21-100 nests. To avoid bias due to low daylight hours during winter and therefore a lower volume of visible counts around the winter equinox and to keep our data consistent with the techniques described in Southwell & Emmerson (2015), we used only those images taken at 14:00 local time. Date, time of day, and temperature data were recorded by each camera in each image and extracted from the image metadata.

We must note that it is highly possible that individuals were present at the colony site during winter outside of the camera's range of view, which serves as a major limitation of this study. However, the camera was installed at the best possible location and angle to observe a large proportion of the colony (Figure D.1). Attendance during both the non-breeding and breeding phases has been noted (Figure 5.2, Table 5.1) to allow for comparisons between the two periods in what was observed by the cameras.

5.3.3 Data Extraction

Counts of individuals were extracted from each image using either a Zooniverse interface (www.penguinwatch.org), developed by our team for this specific purpose, or iTag, an open-sourced software for counting individual objects within images (Viquerat 2015). In both programs, in each image, a point was centred over each visible individual to avoid counting individuals twice (Figure D.1). The number of points in each image was then extracted to determine counts. This process

was used for counting adults at each site in each image and all individuals at the edge of the image frame were included in our analysis. One individual (CB) performed all counts. We analysed non-breeding data from each of our seven study sites beginning at the end of adult moult (last adult seen moulting) and ending one month prior to an initial peak in attendance during the breeding season (see Table 5.1 for dates). The

Danco Island, Neko Harbour, Port Lockroy, and Petermann Island cameras overlooked the nearby marine environment enabling the extent and type of near-shore sea ice to be determined. Sea ice extent was extracted from the images using the guidelines described in Smith (2000); sea ice in each image from these four sites was ranked from 1-10 and categorized as either open water, pack, or compact (aka. fast) ice based on photographs provided in Smith (2000). For the two sub-Antarctic colonies where sea ice is not present during the winter offshore (Martillo Island and Maiviken), the sea ice type was categorized as open water throughout the non-breeding period.

Date, time of day, and temperature data were extracted from the image metadata. Daylight hours were extracted using the *suncalc* function in the *RAtmosphere* package of R (Biavati 2014, R Core Development A 2013).

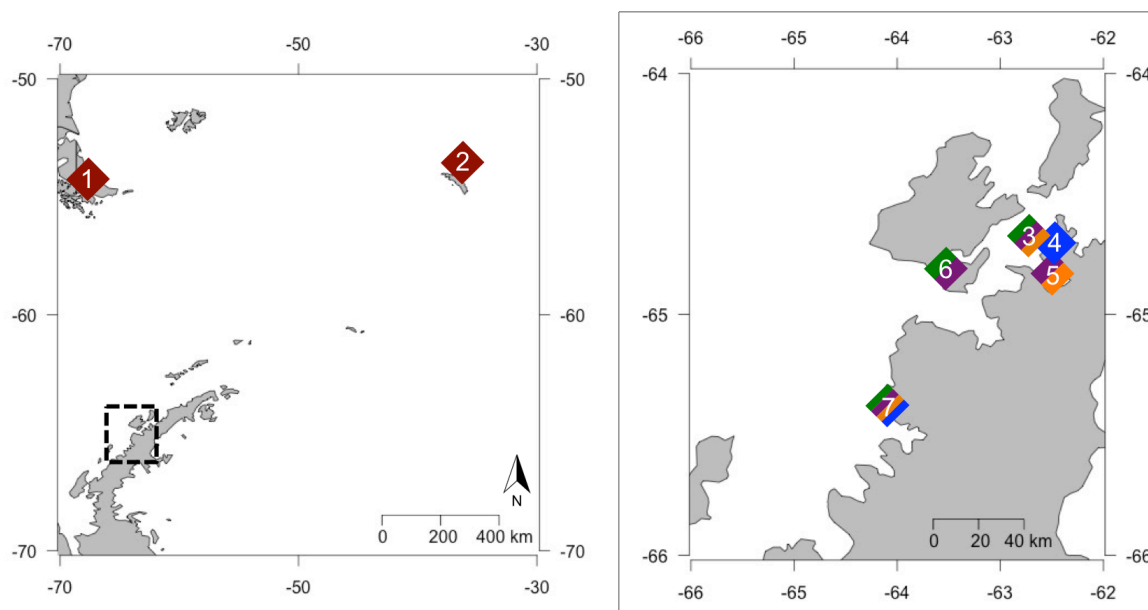


Figure 5.1. Map of seven study sites, including 1) Martillo Island, Argentina, 2) Maiviken, South Georgia, and 3) Cuverville Island, 4) Danco Island, 5) Neko Harbour, 6) Port Lockroy, and 7) Petermann Island on the Western Antarctic Peninsula. Similar colours indicate sites that are not significantly different in their counts of non-breeding presence when examining their orthogonal contrasts. The dashed box designates the region of study sites 3-7.

5.3.4 Statistical Analysis

All analyses were conducted in R (v 3.1.3) language for statistical computing using the *stats* package (R Core Development 2013). Variability in the rate of the Poisson process among individual birds was expected and, as anticipated, we found overdispersion in both Poisson and quasi-Poisson generalized linear models (GLMs). Variability among otherwise identical individuals is usually well accounted for by a Gamma distribution across the Poisson rate parameter and we therefore opted for fitting negative binomial GLMs (*glm.nb* function, *MASS* package; Venables & Ripley 2002) to understand relationships between each of our coefficients and the non-breeding counts at all seven study sites (Table 2). Our final model included the year, sea ice type, Julian date, and interactions between site location and both temperature and photoperiod as explanatory variables (Table 2). Interactions between sea ice type and both 1) year and 2) location were fitted but ultimately omitted during model simplification (ANOVA, $P=0.413$ and $P=0.862$, respectively).

To account for the differences between the angle and view within each camera frame, we counted the total number of nests at peak breeding in 2013 at each study site and used these nest counts as an offset term ($-\log(x)$) in each of our models (*offset* function, *stats* package). All models were first fitted with and without the inclusion of an auto-correlation structure; both autoregressive (AR) and autoregressive moving average (ARMA) models were used. There was no evidence of any temporal autocorrelation in any of our models and therefore our final models did not include

such structures. The final model resulted in a goodness-of-fit statistics with a p-value of 1; there was no evidence in favor of rejection of the model's fit.

Table 5.1. Summary of data at each study site, including the total number of images, non-breeding (N-B) dates, and both breeding (B) and non-breeding abundance means and ranges for 2012-2014. NA indicates data is not available.

Site	Total # of Images	Year												
		2012					2013					2014		
		N-B Dates	N-B Mean	N-B Range	B Mean	B Range	N-B Dates	N-B Mean	N-B Range	B Mean	B Range	N-B Dates	N-B Mean	N-B Range
Martillo	614	NA	NA	NA	NA	NA	Mar 25-Aug 30	5.67	0- 58	19.60	0- 55	Mar 29- Jul 29	10.76	0- 63
Maiviken	778	NA	NA	NA	14.70	0- 57	Apr 7-Sep 30	1.16	0- 42	15.83	0- 45	Apr 19-Sep 7	3.89	0- 49
Cuerville	1027	Apr 21-Sep 6	9.64	0- 85	35.63	0- 98	Apr 23-Oct 2	2.41	0- 49	73.56	0- 157	Apr 24-Oct 11	16.38	0- 134
Danco	729	NA	NA	NA	NA	NA	Apr 29-Oct 20	2.45	0- 43	48.75	0- 124	Apr 27-Oct 17	19.05	0- 87
Neko	1000	Apr 26-Sep 24	5.39	0- 61	40.84	0- 81	Apr 21-Oct 1	0.52	0- 11	57.10	0- 158	Apr 11-Oct 10	11.38	0- 110
Lockroy	1015	Apr 16-Aug 14	27.12	0- 159	87.31	0- 213	Apr 28-Oct 1	2.31	0- 94	78.53	0- 199	Apr 18-Aug 17	16.62	0- 101
Petermann	717	NA	NA	NA	12.04	0- 29	Apr 13-Oct 16	0.10	0- 8	11.06	0- 30	Apr 4-Oct 17	3.05	0- 23

5.4 Results

Analyses revealed relationships between year, sea ice type (compact, pack, or open water), time of year (Julian day), colony location, photoperiod (number of daylight hours daily), and temperature and non-breeding counts across seven study sites (Table 2). Our data, examining attendance only at 14:00 local time, may underestimate the number of individual at the breeding site because, as found in past studies (Williams et al. 1992, 1993, Tanton et al. 2004), gentoos are diurnal foragers, usually taking one trip daily, and may be foraging at the time the image was captured.

When examining temporal variation, we discovered significant differences between the three years across sites; penguin non-breeding attendance in 2014 ($SE= 3.79$, $P < 0.001$) was significantly greater than in 2013 ($SE= 1.90$, $P < 0.001$) and 2012 ($SE= 22.93$, $P < 0.001$) and attendance was also significantly greater in 2013 than in 2012 (Table 2; Figure 2).

We found that gentoo penguins were present at the breeding site in significantly higher numbers when either open water ($SE= 22.9$, $P < 0.001$) or pack ice ($SE= 23.0$, $P < 0.001$) was present, whereas gentoos were less present when compact (fast) ice was located directly offshore during winter ($SE= 0.498$, $P < 0.001$).

When examining variation in the timing of site occupation during the non-

breeding period, we found a significant negative relationship between Julian date and counts ($SE = 0.002$, $P < 0.001$). In other words, gentoos occupied the breeding site in larger numbers earlier in the non-breeding season (Table 2; Figure 2).

We also discovered a relationship between location and photoperiod and gentoo attendance. At our five WAP sites, gentoos increased in non-breeding counts as daylight hours increased (Table 2). However, at the two sub-Antarctic sites (Martillo Island and Maiviken), the opposite relationship was found; gentoos increased in winter attendance as daylight hours decreased.

We also found that temperature influenced gentoo non-breeding counts, but only at one site, Danco Island, located on the WAP ($SE = 0.046$, $P = 0.002$); as temperature increased, the Danco Island colony winter counts decreased.

Lastly, we found distinct patterns in gentoo occupation at the breeding site during the non-breeding period dependent on site location (Figure 1). Re-leveling our model revealed the following contrasts where letters indicate that sites are *not* significantly different in their overall winter counts: 1) Martillo Island (A), 2) Maiviken (B), 3) Cuverville Island (C, F), 4) Danco Island (D, F), 5) Neko Harbor (C, F), 6) Port Lockroy (E), and 7) Petermann Island (C, D, F, Figure 1). In other words, the colonies located at Maiviken (South Georgia), Martillo Island (Argentina), and Port Lockroy (WAP) occupied the breeding site during winter in significantly higher numbers than the other four WAP sites: Cuverville Island, Danco Island, Neko Harbour, and Petermann Island.

We cannot conclude that these relationships are due to site fidelity as individuals could not be discerned and were not marked in this study. However, gentoos on South Georgia and the Antarctic Peninsula were often seen sitting directly on the nest areas during the winter and even building or maintaining nests year-round, providing evidence that it is likely that many of the same individuals were present during both the breeding and non-breeding periods.

Table 5.2. Coefficients resulting from a negative binomial generalized linear model (GLM) of location, photoperiod, sea ice type, temperature, Julian date, and year at seven study sites related to gentoo penguin adult non-breeding abundance. Offsets of the $-\log(\text{nest counts})$ were used in both models to account for differences in the camera angle and view between sites; therefore, all estimates reflect the relationship between each coefficient and adult non-breeding abundance per nest unit. Significance is indicated as follows: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Coefficient		Estimate	SE	Z	P
Year	2012 (intercept)	8.08	0.733	11.03	<0.001***
	2013	-2.61	0.236	-11.08	<0.001***
	2014	-0.833	0.228	-3.66	<0.001***
Sea Ice Type	Open Water (intercept)	8.08	0.733	11.03	<0.001***
	Compact	-3.73	0.539	-6.92	<0.001***
	Pack	0.100	0.295	0.34	0.735
Julian Date		-0.011	0.002	-5.88	<0.001***
Location	Martillo Island	4.73	1.05	4.49	<0.001***
	Maiviken	7.95	1.50	5.28	<0.001***
	Cuerville Island	-4.98	0.819	-6.07	<0.001***
	Danco Island	-3.67	0.762	-4.82	<0.001***
	Neko Harbor	-5.63	0.823	-6.84	<0.001***
	Port Lockroy (intercept)	8.08	0.733	11.03	<0.001***
	Petermann Island	-4.69	1.08	-4.34	<0.001***
Location: Photoperiod	Martillo Island: Photoperiod	-0.728	0.127	-5.73	<0.001***
	Maiviken: Photoperiod	-1.43	0.198	-7.19	<0.001***
	Cuerville Island: Photoperiod	0.355	0.120	2.95	0.003 **
	Danco Island: Photoperiod	0.279	0.114	2.45	0.014 *
	Neko Harbor: Photoperiod	0.181	0.120	1.51	0.131
	Port Lockroy: Photoperiod	0.386	0.104	3.72	<0.001***
	Petermann Island: Photoperiod	0.020	0.141	0.14	0.887
Location: Temperature	Martillo Island: Temperature	-0.034	0.074	-0.46	0.643
	Maiviken: Temperature	-0.034	0.063	-0.53	0.594
	Cuerville Island: Temperature	-0.001	0.055	-0.03	0.979
	Danco Island: Temperature	-0.142	0.046	-3.09	0.002 **
	Neko Harbor: Temperature	-0.022	0.057	-0.39	0.697
	Port Lockroy: Temperature	0.142	0.046	3.09	0.002
	Petermann Island: Temperature	-0.112	0.072	-1.55	0.120

5.5 Discussion

By using a time-lapse camera system we have, for the first time, been able to show the pattern of attendance at gentoo breeding sites throughout the non-breeding period. This study provides the first evidence of across year variation in gentoo non-breeding attendance at the breeding site. We found that both temporal and spatial factors drive winter attendance in this species with distinct patterns between years and colony locations, particularly at the edges of their range. Additionally, environmental and temporal factors, including sea ice extent directly offshore, photoperiod, and temperature appear to dictate gentoo winter attendance across their range. As gentoos are neither sedentary nor migratory during the non-breeding period, understanding patterns in winter site occupation across time and space provides insight into half of the species' annual cycle and has important implications in the face of changes in climate, direct human disturbance, and fisheries activities (Chown et al. 2015).

The distinct patterns we found in gentoo winter attendance across the seven study sites separate site attendance into three spatial groups: the Falkland Islands, South Georgia, and the WAP. Gentoos inhabiting the sub-Antarctic sites (Martillo Island, Argentina and Maiviken, South Georgia) demonstrated consistently higher site occupation over the years studied when compared to the five WAP sites, representing gentoo behaviour at their northernmost edge of range (Figure 5.1). Considering that the Argentinian and South Georgia colonies are different sub-species (*Pygoscelis papua papua* in Argentina and *Pygoscelis papua elsworthii* in South Georgia, Levy et

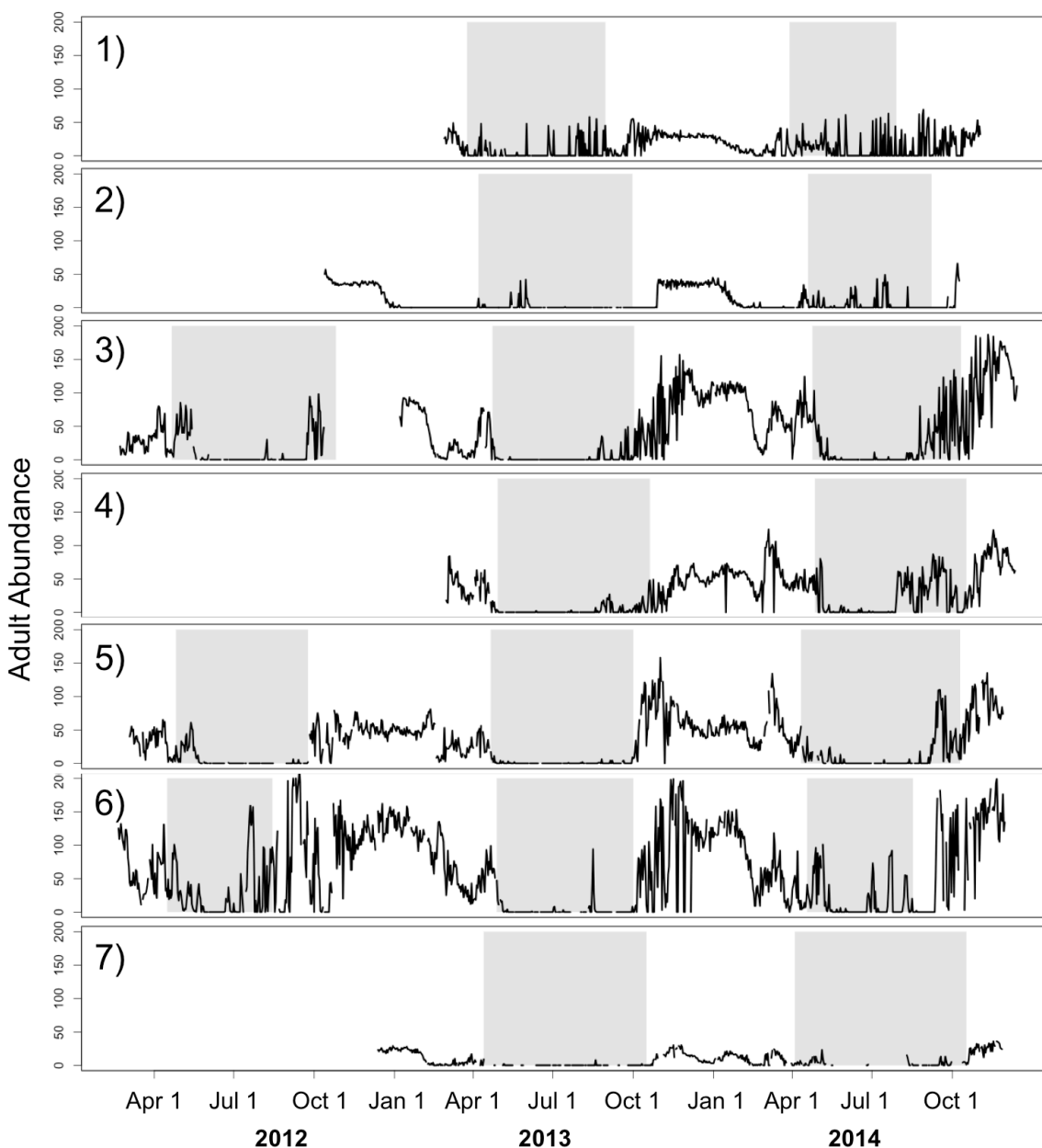


Figure 5.2. Time series of adult abundance from 2012-2014 at each of seven study sites, including 1) Martillo Island, 2) Maiviken, 3) Cuverville Island, 4) Danco Island, 5) Neko Harbour, 6) Port Lockroy, and 7) Petermann Island. Shaded areas indicate non-breeding period (see Table 5.1 for dates).

al. 2016) and separated by the polar front, the similarities in their winter site occupation highlight the importance of environmental and temporal factors, rather than genetics, on behaviours, as these sub-Antarctic colonies share more biotic and abiotic factors in common compared to those colonies located on the WAP. Past studies have provided evidence that birds in colonies located farther south are absent from the breeding site for longer periods over winter, often for over two months (see Bost and Jouventin 1990 and references therein), consistent with winter attendance studied here. However, we also found fine scale spatial variation across our five WAP sites with one site, Port Lockroy, emerging as statistically distinct from the other four sites (Figure 5.1, Table 5.2). These spatial patterns provide evidence that, although edge of range effects play a role in winter behaviour in this species, local environmental factors also dictate non-breeding attendance.

We found the same patterns in the relationship between photoperiod and winter counts as we did spatially across sites, separating the colonies into the same two distinct groups: the sub-Antarctic Islands and WAP colonies. Past studies have also found evidence that winter behaviour is dictated by photoperiod in other penguin species (Wilson et al. 1989, Fraser and Trivelpiece 1996, Ainley 2002, Forcada and Trathan 2009) and gentoos (Tanton et al. 2004), linking decreased daylight hours with reduced foraging ability as penguins are visual foragers and therefore need daylight to adequately navigate and feed (Emlen and Penney 1964, Penney and Emlen 1967, Wilson 1993). In addition, Hinke and Trivelpiece (2011) found that gentoos at the South Shetland Islands forage daily, are absent from the colony between 9 and 1500

(local time) throughout the winter, and lengthen their foraging trip duration as daily daylight hours also increase. However, this study is the first to show discrete differences in a response to photoperiod depending on the colony location.

Sub-Antarctic gentoo winter occupation increased as daylight hours diminished, while the opposite held true with our WAP gentoo colonies. The two spatial groups peak in winter attendance at opposite times in the non-breeding season, governed by a relationship with photoperiod, although other environmental factors, particularly sea ice in the WAP, which is not present to the same extent at the two sub-Antarctic sites, likely play a large role in winter attendance. In particular, individuals at the WAP colony sites may maximize foraging during shorter days by staying nearer to more optimal foraging areas, whether at other colony sites or on sea ice floes, when the colony sites studied are not at their optimal sea ice level for these near-shore foragers.

When examining the role of sea ice in winter attendance at four sites, where sea ice extent was measured directly offshore, using the time-lapse cameras, we found a clear relationship with open water and pack ice compared to compact ice conditions. Gentoos were significantly more abundant during the non-breeding period when open water or pack ice was present and significantly less abundant when compact ice appeared directly offshore. Past studies have indicated that gentoos are restricted to inshore foraging during the winter months to the same extent that they are during the breeding season (Williams et al. 1992, Tanton et al. 2004) and have similar

prey compositions during both periods (Williams 1991, Clausen and Pütz 2002). We provide evidence that gentoos on the WAP overwinter at breeding sites during periods when sea ice conditions are optimal for foraging directly inshore, using the breeding site as a resting area between foraging periods.

Lastly, we found considerable temporal variation in the counts of gentoos wintering at the breeding site; both year and the date within year influenced the extent of gentoo site occupation during the non-breeding period. Across the study sites, gentoos were more abundant in winter in 2014 than in 2013 or 2012 and in 2013 than in 2012. We also found that at all sites, with the exception of Danco Island, penguins were significantly more abundant earlier in the non-breeding season. To our knowledge, we are the first to examine differences in gentoo winter attendance between years across multiple sites, which provide critical insight into the plasticity of this behaviour.

The restraints associated with feeding and raising chicks are no longer present during the winter months, which may allow for greater flexibility in foraging extent and the timing when gentoos are found onshore. However, foraging is limited by the number of daylight hours (Tanton et al. 2004) and gentoos must rest ashore or on ice during the night, at the very least, to conserve energy (Bevan et al. 1995). Resting on land may allow gentoos to discover or maintain nest location, avoid predation at sea, or even aid in the exchange of information on prey quality and location (Ward and Zahavi 1973). Ultimately, we provide evidence that gentoos are found at the breeding

site over winter depending on the number of daylight hours daily and when sea ice conditions are ideal for foraging, although these relationships are highly dependent on the colony location. Gentoos are neither sedentary nor migratory during the non-breeding period, reflecting their large behavioural plasticity and ability to adapt to changing environmental conditions, which may have positive effects in the face of increasing threats, putting them at the competitive advantage to other penguin species inhabiting the same range. Gentoo winter attendance at colony sites also has large implications for fisheries management, particularly in the allocation of catch limits near breeding aggregations year round. As experimental fisheries closures along the WAP may occur in the future (Hart et al. 2015), gentoos serve as ideal subjects, in which to measure and detect pressures from fisheries year-round, which likely affect both adult survival and breeding success. Understanding winter behaviour provides critical information on local ecosystem effects, inter- and intra-species competition for resources, and best management practices in the face of increasing threats to polar species.

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CHAPTER SIX

Variation in the Phenology of *Pygoscelis* Penguins Across Two species' Latitudinal Range

6.1 Abstract

Inter-specific variation in the phenology of avian taxa has long been studied to understand a species' basic biology and how a species reacts to environmental changes over both space and time. Penguins (*Sphenicidae*) serve as an important example of how biotic and abiotic factors influence certain stages of seabird phenology because of their large ranges and the extreme conditions present in their Southern Ocean habitats. Here we examined the phenology of gentoo (*Pygoscelis papua*) and chinstrap penguins (*Pygoscelis antarctica*) to fill in gaps in our understanding of each of the dates within their annual cycles and to determine which phases are indeed intrinsic, or rather vary across a species range and between years. We found that latitude and season had a significant influence on the length in days of the nesting duration (first nesting activity to first egg laid), incubation duration (first egg laid to first chick hatched), and guard duration (first chick hatched to the last date both chicks seen guarded). The trend we observe here towards longer incubation times farther south, where ambient temperatures are colder, likely indicates that exposure to cold slows embryo growth within the egg. In addition, across species, in cases where loss or deaths occurred, colonies located farther south abandoned nests later and eggs or chicks were last seen in the nest at advanced dates in the breeding period. The variation in both space and time observed here in penguin phenology provides evidence that the duration of phases within the annual cycle of birds are not wholly intrinsic, or genetic, as previously understood.

6.2 Introduction

Inter-specific variation in the phenology of avian taxa has long been studied to understand a species' basic biology and how a species reacts to environmental changes over both space and time (Schwartz 2013). Variation mostly stems from an individual's requirement to match the peak in local resource quantity and quality to the peak of their own needs and the demands of their young (Visser and Both 2005). In turn, phenology impacts reproductive success by dictating clutch size, egg mass, chick growth, and the likelihood of predation, making it relevant to population dynamics and individual fitness (Schwartz 2013). Seabird phenology is particularly well studied because of their colonial nature and because the stages of seabird annual cycles are often highly constrained and synchronous (Gaston 2004). Penguins (*Sphenicidae*) serve as an important example of how biotic and abiotic factors influence certain stages of seabird phenology because of their large ranges and the extreme conditions present in their Southern Ocean habitats (Chapter 1).

In penguins, the variables dictating changes to the annual cycle differ significantly depending on the species and colony location. In particular, variation in sea ice extent, especially prolonged pack ice, can delay a penguin's return to the breeding colony and subsequently alter the timing of later breeding dates (Trivelpiece et al. 1987). Similarly, annual changes in food availability contribute to delayed breeding as adults must build up body condition and fat reserves prior to egg laying (Viñuela et al. 1996). Additional environmental factors, including wind conditions

(Ainley and Leresche 1973), sea surface temperature (Bost and Jouventin 1990), and ambient air temperatures (Lynch et al. 2012), can also impact the timing of breeding and the subsequent fitness of individuals. Likewise, abiotic factors, including the experience (Trivelpiece et al. 1984), health (Moreno et al. 1998), and age (LeResche and Sladen 1970) of adults, also dictate the breeding schedule. In addition, colony size (Barbosa et al. 1997), the sex of chicks (Fargallo et al. 2006), nest location within a colony (Fargallo et al. 2006, Martín and Soler 2006), and colony size (Barbosa et al. 1997), significantly influences hatching dates, one of the most well-studied periods in penguin phenology. Lastly, the timing of adult moult, which subsequently affects when chicks are left unguarded by their parents (Penteriani et al. 2003), is often triggered by changes in photoperiod (Ainley 2002) and hormone levels (Groscolas et al. 1986). Together, these variables, both environmental and individualistic, greatly affect certain stages of penguin phenology, yet many phases within the breeding cycle are considered fundamental (Borboroglu and Boersma 2013), without variability throughout a species range and between years.

Certain periods within the breeding season are thought to be intrinsic across a species range, ingrained within the biology of the species, rather than influenced by external variables. In gentoo penguins (*Pygoscelis papua*) these intrinsic parameters include a 2-week nest attendance period prior to egg laying, a laying interval of approximately 3 days between eggs, an incubation period of 33– 37 days, and general chick growth patterns (Bost and Jouventin 1991). Similarly, in chinstrap penguins

(*Pygoscelis antarctica*) laying intervals have been observed as 4 days (Lishman 1985), with incubation lasting 33–36 days, and the guard period taking approximately 4 weeks (Borboroglu and Boersma 2013). To date, no studies have yet, to our knowledge, found significant variability in any of these periods; however, past studies have not addressed why certain phases are plastic in their timing while others are ingrained in the biology of a species.

Here we examined the phenology of gentoo and chinstrap penguins to fill in gaps in our understanding of each of the dates within their annual cycles and to determine which phases are indeed intrinsic, or rather vary across a species range and between years. In particular, we aimed:

1. To establish the breeding phenology of two species of *Pygoscelis* penguins in the Southern Ocean, including all described phases (eg. incubation, guard, post-guard).
2. To determine how the timing and duration of individual phases changes along a latitudinal gradient and varies between years.
3. To understand how chick survival and nest abandonment rates are linked with phenology dates and durations to better comprehend the role phenology plays in individual fitness.

6.3 Methods

6.3.1 Study Sites

We monitored gentoo penguins at 13 sites and chinstrap penguins at 4 sites, ranging from the Falklands Islands, South Georgia, South Sandwich Islands, South Shetland Islands, and the Western Antarctic Peninsula (Figure 6.1). Study sites were chosen based on a nested design; we observed multiple breeding sites within a region and installed more than one camera at several breeding sites (Maiviken, Neko Harbour, Booth Island). Phenological dates had only been studied at 3 of the 17 study sites in the past (Bailey Head, Deception Island, Conroy et al. 1975b, Viñuela et al. 1996, Barbosa et al. 1997, Moreno et al. 1998, Port Lockroy, Copley and Shears 1999, and Petermann Island, Gain 1914). At one of the sites, where the two species nest directly next to each other (Booth Island), both chinstraps and gentoos were monitored by one of the two cameras.

6.3.2 Camera System

Twenty time-lapse cameras were deployed at 17 sites beginning on 12 October 2012 to 24 February 2016 (Table 5.1). Not all cameras photographed colonies during the same dates due to the logistical difficulties of setting up cameras on the same date across the two species' ranges (Table 5.1). Each camera was installed roughly three

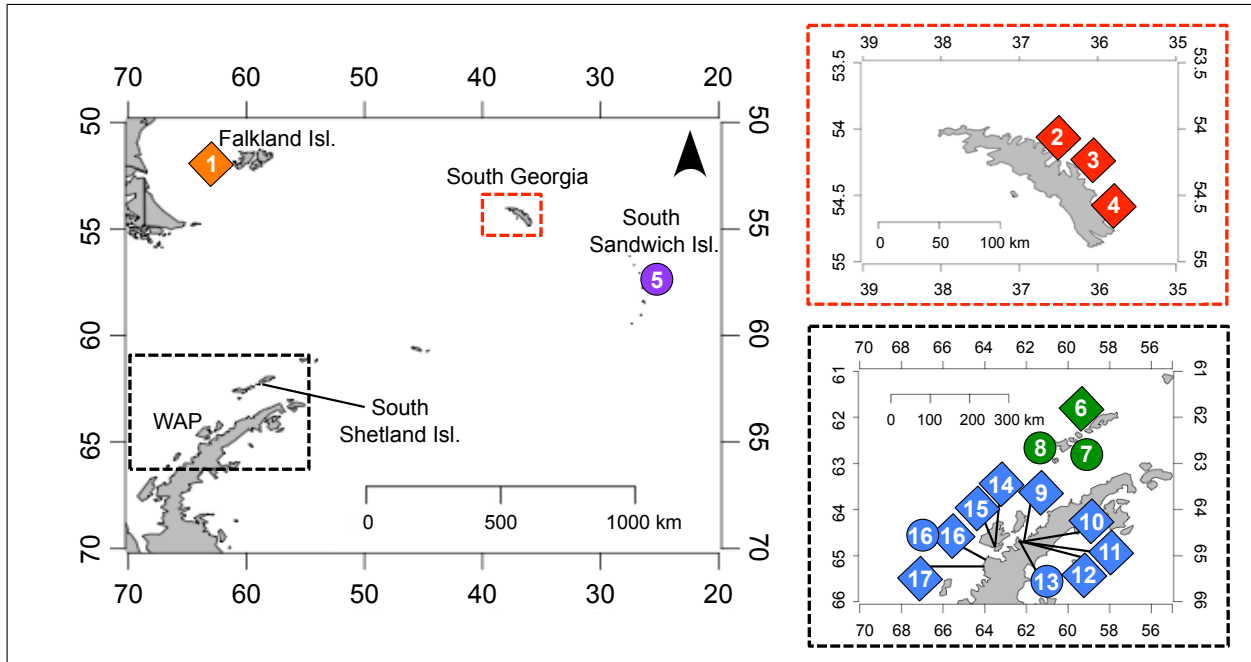


Figure 6.1. Map of 17 colony locations. Diamonds represent locations of gentoo penguin (*Pygoscelis papua*) colonies and circles represent locations of chinstrap penguin (*Pygoscelis antarctica*) colonies. The colonies are grouped by location from the Falklands Islands (orange), South Georgia (red), South Sandwich Islands (purple), South Shetland Islands (green) and the Western Antarctic Peninsula (blue). The numbers indicate each of the colonies specific location from 1) Beaver Island, 2) Maiviken, 3) Ocean Harbour, 4) Cooper Bay, 5) Saunders Island, 6) Aitcho Islands, 7) Half Moon Island, 8) Bailey Head, 9) Cuverville Island, 10) Georges Point, 11) Danco Island, 12) Spigot Peak, 13) Neko Harbour, 14) Damoy Point, 15) Port Lockroy, 16) Booth Island, and 17) Petermann Island.

meters from nesting sub-colonies at each of our study sites. The cameras were installed using techniques similar to those described by Newbery and Southwell 2009, Southwell and Emmerson 2015), with minor adjustments to the camera system (Figure B.1). At each site, a Reconyx HC500 Hyperfire trail camera (Reconyx, Inc., Holmen, WI, USA) was mounted to a scaffold pole and anchored using a rock basket (Antarctic Peninsula, South Shetland Islands, and South Sandwich Islands) or by being hammered into tussock grass or soil (Falklands Islands and South Georgia). The location of each camera was dictated by the distance from nearby nesting sites but also determined opportunistically by using locations with higher elevation, appropriate substrate (rock or tussock grass) for anchoring the camera system, and low snow accumulation (Southwell and Emmerson 2015). The cameras were programmed in time-lapse mode to take 6 photographs daily during year-long peak daylight hours at 1000, 1100, 1200, 1300, 1400, and 1500 local time, and each camera captured images of roughly 15 nests (Table E.1). Once installed, the cameras were maintained yearly to retrieve data from the previous year, check operations, and change the batteries. In a few cases, the camera angle did change year to year due to alterations in the location of nesting sub-colonies (Booth Island, Georges Point, Maiviken, and Petermann Island), which is common in gentoo penguins. In addition, to determine the accuracy of our methods using 6 images daily, we attached the same camera system to the same pole at 5 sites (Cooper Bay, Georges Point, Neko Harbour, Port Lockroy, and Booth Island) but changed the camera frequency setting to photograph the same nests every minute instead of every hour.

Table 6.1. A summary of the colony locations and data available for gentoo (*Pygoscelis papua*) and chinstrap penguins (*Pygoscelis antarctica*), including latitudes, longitudes, and dates of operation.

Species	Region	Site	Latitude, Longitude	Observation Dates for each camera
Gentoo	Falkland Isl.	Beaver Isl.	51°50' S, 61°16' W	7 Dec 2014- 6 Sep 2015
		South Georgia Isl.	54°48' S, 35°47' W	26 Dec 2014- 28 Oct 2015
	South Georgia Isl.	Maiviken	54°14' S, 36°29' W	12 Oct 2012- 2 Feb 2015
				15 Oct 2012-2 Jan 2015
		Ocean Harbour	54°20' S 36°16' W	31 Oct 2014- 12 Nov 2015
	South Shetland Isl.	Aitcho Isl.	62°23' S 59°46' W	9 Jan 2014- 5 Dec 2015
	Western Antarctic Peninsula	Booth Isl.	65°03' S, 64°01' W	3 Dec 2012- 29 Dec 2015
		Cuerville Isl.	64°41' S 62°38' W	10 Jan 2014- 6 Jan 2016
		Damoy Point	64°81' S, 63°53' W	26 Dec 2012-20 Nov 2014
		Danco Isl.	64°43' S, 62°35' W	5 Dec 2012- 6 Dec 2015
		Georges Point	64°40' S, 62°40' W	22 Dec 2012- 6 Jan 2016
		Neko Harbour	64°50' S, 62°31' W	3 Mar 2012- 6 Jan 2016
				14 Dec 2012- 6 Jan 2016
		Petermann Isl.	65°10' S, 64°08' W	12 Dec 2012- 8 Jan 2016
		Port Lockroy	64°49' S, 63°29' W	13 Dec 2012- 7 Jan 2016
Chinstrap	South Sandwich Isl.	Saunders Isl.	57°47' S, 26°27' W	12 Nov 2013- 24 Feb 2016
	South Shetland Isl.	Bailey Head	62°58' S, 60°30' W	20 Dec 2012- 20 Nov 2014
		Half Moon Isl.	62°59' S, 59°92' W	12 Dec 2012- 24 Dec 2015
				21 Dec 2012- 11 Dec 2015
	Western Antarctic Peninsula	Booth Isl.	65°03' S, 64°01' W	3 Dec 2012- 29 Dec 2015
		Spigot Peak	64°37' S, 62°33' W	25 Nov 2012- 9 Feb 2016

6.3.3 Phenological Dates

Each nest at each location was monitored from 12 October 2012 to 24 February 2016, where data were available (Table 6.1). For either each nest (nesting, laying of 1st egg aka. clutch initiation, laying of 2nd egg, hatching of 1st and 2nd eggs, guard and post-guard phases) or for the entire colony (arrival and departure dates, adult and chick moult dates), the following dates were recorded from images.

1. Arrival (colony wide): In chinstraps only, we noted the first day when individuals appear at the colony because individuals are not present at the colony continuously over winter. Because gentoo individuals are present year-round at the breeding site (Bost and Jouventin 1991, Chapter 5), we did not define arrival date.
2. Nesting (individual nests): At each nest, we noted the date when partners first began sitting on a nest continuously for a 24-hour period. The nesting duration began at the first nesting date and ended when the 1st egg is laid.
3. Laying of 1st egg (individual nests): At each nest, we noted the date when an egg was first observed.
4. Laying of 2nd egg (individual nests): At each nest, we noted the date when a 2nd egg was first observed.
5. Laying interval (individual nests). At each nest, we noted the number of days between the date when the 1st egg was laid and the 2nd egg was laid.
6. Incubation duration (individual nests): At each nest, the incubation duration began when the 1st egg was laid and ended when the 1st chick hatched.
7. Hatching of 1st chick (individual nests): At each nest, we noted the date when a 1st chick was first observed.
8. Hatching of 2nd chick (individual nests): At each nest, we noted the date when a 2nd chick was first observed.
9. Hatching interval (individual nests). At each nest, we noted the number of days between the date when the 1st chick hatched and the 2nd chick hatched.
10. Guard duration (individual nests): We considered the guard period to begin when the 1st chick was first observed (see #5) and end when the 1st chick left was left unguarded (see Chapter 1, Table A.1 for definition of parental guard) for 24 hours (aka. guard end date).
11. Adult moult (colony wide): We noted the first and last dates when adults were observed moulting with clearly displaced feathers.
12. Chick moult (colony wide): We noted the first date when chicks were viewed moulting. The end of chick moult was not noted because chicks fledged during moult.
13. Adult departure (colony wide): In chinstraps only, we noted the last date when adults were observed at the colony nesting site for a period of at least 15 days after moulting. Because gentoos individuals are present year-round at the breeding site (Bost and Jouventin 1991, Chapter 5), we did not define departure date.

6.3.4 Nest Survival Rates

Chick survival was monitored at each nest at each site during the study period. We noted whether individuals at each nest raised 0, 1, or 2 chicks to the end of the guard phase (see definition above, CCAMLR Standard Method A6B) of each year and, if fewer than 2 chicks survived to the beginning of the post-guard phase, we noted the dates when the last chick or egg was seen at the nest (aka. last seen date, Southwell and Emmerson 2015). In addition, we noted whether each individual nest laid 0, 1, or 2 eggs (eg. total eggs) and whether 0, 1, or 2 chicks hatched (eg. total chicks). We also noted if nests were abandoned and the date of abandonment; abandonment was defined as the last day a parent was seen on the nest prior to the end of the post-guard phase.

6.3.5 Statistical Analysis

All analyses were conducted in R (v 3.1.3) language for statistical computing (R Core Development Team 2013). Survival analysis was conducted using the *Surv* and *survreg* functions in the *survival* package (Therneau 2015). We chose the following parametric survival regression models instead of Cox proportional hazards regression models due to left censored data (when the start rather than end date is unknown) in four of our models (those with nest duration, laying interval, incubation duration, hatching interval, and guard duration as response variables), which are not possible

using Cox proportional hazards regression models. Initially, colony was added as a random effect to each of our survival models but latter removed because the random effect did not account for a large percent of the variation in the model and latitude was instead used as a substitute for colony location. The remaining 2 models (last seen date and nest abandonment) were right censored in our survival analysis. For each of the models, we fitted Weibull, exponential, Gaussian, logistic, log normal, and log logistic distributions and chose the distribution with the highest log-likelihood (Table 6.2). Due to a large number of missing values and to avoid over-fitting the model, nesting start date, nesting duration, and laying interval were not used as explanatory variables in any of the models (Table 6.2).

Next, to examine what influences whether a nest was abandoned, we fitted a binomial generalized linear mixed model (GLMM) using the *glmmPQL* function in the *MASS* package (Venables and Ripley 2002). The colony locations (eg. Aitcho Island) were considered a random effect in the model. The residuals of the model were then graphed using box-and-whisker plots to examine the differences in nest abandonment across colony locations. Due to a large number of missing values and to avoid over-fitting the model, nesting start date, nesting duration, first laying date, incubation duration, and laying interval were not used as explanatory variables in the following model (n= 426).

Nest abandonment (binary) ~ Species, Season, Chick total

To examine the variation and synchronicity of three particular dates (first laying, first hatching, and guard end dates) across all 17 colony sites, we graphed the 95% confidence intervals of each date at each site using the *plotCI* function in the *gplots* package (Warnes et al. 2013). In order to create this graph, we first transformed

Table 6.2. Summary of survival models used, including the distribution, log-likelihood, total observations in data set (n), and the variables removed.

Final model	Distribution	Log-likelihood	n	Model simplification
Nest duration ~ Species, Latitude, and Season	Weibull	-361	162	N/A
Laying interval ~ Season and Species	Weibull	-55.1	33	-Latitude (P=0.62) -Species (P=0.89)
Incubation duration ~ Species, Latitude, and Season	Gaussian	-433.1	334	N/A
Hatching interval ~ Species and Season	Weibull	-369.5	222	-Latitude (P=0.93) -Incubation duration (P=1)
Guard duration ~ Species, Latitude, Season, Hatching interval, Adult moult start date, and Chick moult start date	Log normal	-761.5	281	-Incubation duration (P=1)
Last seen date ~ Species and Latitude	Weibull	-417.6	186	-Season (P=0.59)
Nest abandonment date ~ Species, Latitude, Egg total, and Chick total	Weibull	-374.3	158	-Season (P=0.61)

all three dates by raising them to the power of 8 (after examining the skew of data to the power of 2 and 4) because, when plotting the density of each of the dates, the data were left skewed. We then adjusted the dates by season to account for seasonal variation within the colonies.

Lastly, to determine the accuracy of our methods, we compared the hatching dates obtained from cameras taking 6 photographs daily to those taking a photograph every minute at a subset of sites (Cooper Bay, Georges Point, Neko Harbour, and Booth Island). From the images taken every minute, we then obtained the 1st hatching dates, as described above, using the same methods. We compared the hatching dates obtained from the cameras taking 6 photographs daily to those taking photographs every minute using a paired samples t-test, using the *t.test* function in the *stats* package (R Core Development Team 2013).

6.4 Results

6.4.1 Phase Durations

When examining the duration of phases within the breeding period across sites and years in both gentoo and chinstrap penguins, we found that latitude and season influenced the length, in days, of the nesting duration (first nesting activity to first egg laid), incubation duration (first egg laid to first chick hatched), and guard duration (first chick hatched to the last date both chicks seen guarded, when applicable, Figure 6.2,

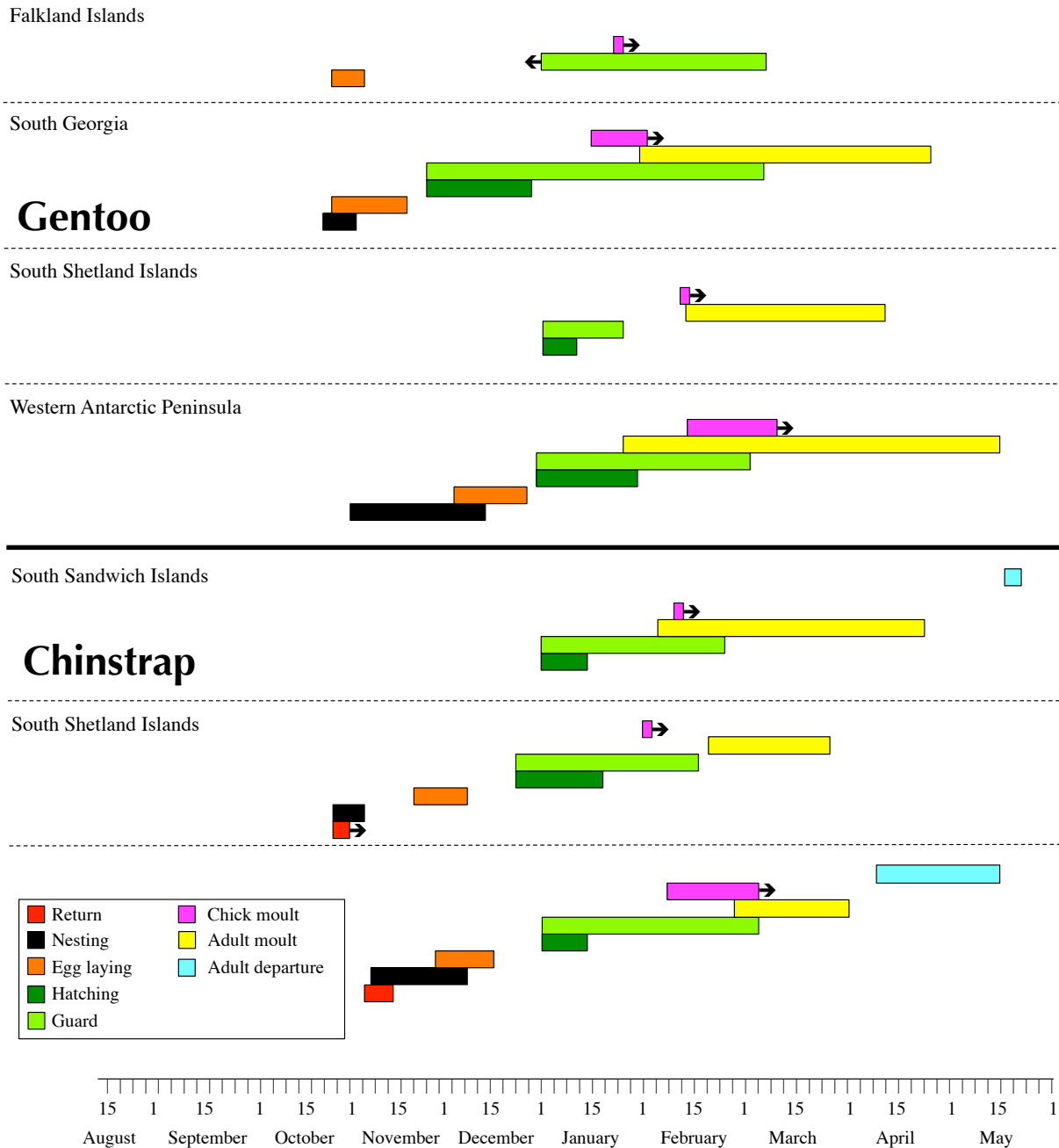


Figure 6.2. Gantt chart summarizing dates and duration of each phenological phase during the breeding period by location (Falkland Islands, South Georgia, South Sandwich Islands, South Shetland Islands, and the Western Antarctic Peninsula (WAP)) and species (gentoo, *Pygoscelis papua* and chinstrap, *Pygoscelis antarctica* penguins).

Table 6.3). In addition, in all models (with the exception of laying interval, where we did not find any significant variables in our model), species affected the duration (Table 6.3). Specifically, chinstraps exhibited longer nesting durations, hatching intervals, and guard durations than gentoo penguins, while the opposite held true with incubation duration (Table 6.3). Nest establishment duration increased as latitude decreased; in other words, colonies located farther north underwent more time between first nesting and laying eggs (Table 6.3). The opposite held true with incubation and guard durations; colonies located farther south incubated eggs longer and guarded their chicks for more days (Table 6.3). Lastly, the colony-wide start date of the adult moult significantly influenced the guard duration; when the adult moult started later, the guard duration was longer (Table 6.3).

Annual effects were significant ($P < 0.001$); longer nesting, incubation, and guard durations occurred in the 2014- 2015 season compared to the summer of 2013- 2014 (Table 6.3). However, hatching intervals were longer in the 2013- 2014 season than the 2014- 2015 season (Table 6.3).

6.4.2 Survival of Eggs and Chicks

Survival analysis on the dates when either an egg or chick was last seen in the nest before loss or death and the dates when parents abandoned their nests after eggs or chicks disappeared revealed distinct differences between species (Table 6.3). In

Table 6.3. Summary of model outputs as a result of survival analyses and a binomial generalized mixed model. Output from survival model of laying interval not included in table because results revealed no significant explanatory variables. ¹ Indicates reference level for each response variable. * $P < 0.04$, ** $P < 0.01$, *** $P < 0.001$.

Analysis	Response variable	Explanatory variable		Value	Standard error	p
Survival	Nesting duration	Species	¹ Chinstrap	2.065	1.181	0.08
			Gentoo	-0.776	0.112	$P < 0.001$ ***
		Latitude		-0.043	0.018	0.02*
		Season	2013- 2014	4.070	0.108	$P < 0.001$ ***
			2014- 2015	4.228	0.000	$P < 0.001$ ***
	Incubation duration	Species	¹ Chinstrap	-114.8	28.06	$P < 0.001$ ***
			Gentoo	20.37	3.658	$P < 0.001$ ***
		Latitude		1.72	0.435	$P < 0.001$ ***
		Season	2013- 2014	-1.54	3.233	0.64
			2014- 2015	15.71	3.435	$P < 0.001$ ***
	Laying interval	Season	¹ 2012- 2013	0.912	0.293	0.002**
			2013- 2014	0.112	0.410	0.785
			2014- 2015	0.629	0.332	0.058
	Hatching interval	Species	¹ Chinstrap	0.918	0.163	$P < 0.001$ ***
			Gentoo	-0.181	0.166	0.28
		Season	2013- 2014	0.590	0.172	$P < 0.001$ ***
			2014- 2015	0.233	0.183	0.20
	Guard duration	Species	¹ Chinstrap	1.099	0.581	0.06
			Gentoo	-0.176	0.041	$P < 0.001$ ***
		Latitude		0.012	0.004	$P < 0.01$ **
		Season	2013- 2014	0.177	0.036	$P < 0.001$ ***
			2014- 2015	0.189	0.045	$P < 0.001$ ***
		Adult moult start date		0.004	0.001	$P < 0.01$ **
	Last seen date	Species	¹ Chinstrap	5.633	0.055	$P < 0.001$ ***
			Gentoo	0.003	0.009	0.73
		Latitude		0.005	0.001	$P < 0.001$ ***
	Nest abandonment date	Species	¹ Chinstrap	5.546	0.068	$P < 0.001$ ***
			Gentoo	0.001	0.010	0.91
		Latitude		0.006	0.001	$P < 0.001$ ***
		Egg total		0.052	0.011	$P < 0.001$ ***
		Chick total		-0.014	0.007	0.04*
Binomial generalized mixed model	Nest abandonment (binary)	Species	¹ Chinstrap	1.505	1.116	0.18
			Gentoo	1.912	0.837	0.02*
		Season	2013- 2014	-1.898	0.421	$P < 0.001$ ***
			2014- 2015	0.036	0.567	0.95
		Chick total		1.336	0.191	$P < 0.001$ ***

addition, across species, colonies located farther south (higher latitudes) abandoned nests later and eggs or chicks were last seen in the nest at advanced dates in the breeding period (Table 6.3). Furthermore, as the total number of eggs laid in each nest increased, the date of abandonment advanced (Table 6.3).

6.4.3 Nest Abandonment

The binomial generalized mixed model on survival revealed that there were significantly fewer nests abandoned in the 2013- 2014 season than in the 2014- 2015 season and when more chicks were in the nests, parents were more likely to abandon the nest (Table 6.3). When examining the residuals of the random effect, colony, used in our model, we found that three colony locations were unique in their abandonment rates, all of which are inhabited by chinstrap penguins: 1) Saunders Island, South Sandwich Islands, 2) Half Moon Island, South Sandwich Islands, and 3) Booth Island, WAP (Figure E.1). Saunders and Booth Islands showed large variation in their abandonment rates with a slightly higher than average mean, while both cameras at Half Moon Island observed much lower than average abandonments rates (Figure E.1).

6.4.4 Phenology Dates

When observing the 95% confidence intervals at each site for the dates of first egg laying, first hatching, and the end of the guard period, we found differences between two distinct regions for each of these dates (Figure 6.3). For the first laying

and first hatching dates, South Georgia colonies laid and hatched eggs significantly earlier than those in the South Sandwich Islands, South Shetlands Islands, and WAP (Figure 6.3). For the end date of the guard period, the Falkland Island, South Georgia, and the South Shetland Island birds appeared to end the guard period earlier, albeit not significantly, than birds in the South Sandwich Islands and WAP (Figure 6.3).

6.4.5 Camera Accuracy

Lastly, our paired samples t-test of the first hatching dates as observed by cameras taking 6 photographs daily vs. cameras taking a photo every minute daily, showed no significant differences between the two groups ($t=-0.91$, d.f.= 16, $P=0.38$). In other words, increasing the frequency of photographs taken from 6 daily to every minute did not significantly influences the dates observed.

6.4.6 Anecdotes

Anecdotally, one replacement clutch occurred at Neko Harbour during the 2014- 2015 season, although neither egg hatched. In addition, in one nest at Half Moon Island during the 2014- 2015 season, three eggs were laid and all eggs hatched; however, all three chicks eventually died.

6.5 Discussion

We provide evidence that the duration of key phases, thought to be intrinsic within these two species (Lishman 1985, Bost and Jouventin 1991, Borboroglu and Boersma 2013), are instead highly plastic between years and vary along a latitudinal gradient. Most surprisingly, for the first time in any avian taxa documented *in situ*, we found that individuals nesting farther south incubated their eggs longer. In addition, individuals nesting in colonies farther south exhibited shorter nesting periods prior to egg laying but guarded their chicks longer. We also found latitudinal differences in the timing of nest abandonment, demonstrating how these phenology shifts may influence fitness at the breeding sites studied. By examining numerous sites across the two species' ranges, documenting a large sample size of individual nests (427 gentoo and 148 chinstrap nests), and analysing variation across multiple seasons, we provide evidence that avian phenology has more trade-offs between breeding stages, years, and species than previously recognized.

It is well established that clutch size and nest attentiveness can vary with latitude (Deeming 2002), yet, to our knowledge, we are the first to discover inter-specific variability in incubation duration in avian taxa using field-based methods. A past study, taking eggs from sub-species at two locations (temperate, *Troglodytes aedon aedon*, and tropical, *Troglodytes aedon musculus*, house wrens) and incubating them in a lab, found that chicks from eggs located farther south hatched on average 1.2 days later than the other, more equatorial sub-species (Robinson et al. 2008). Both

meta-analyses, examining intra-specific relationships in incubation duration (Martin et al. 2007, Martin and Schwabl 2008), and lab experiments, exposing eggs to a variety of conditions (Olson et al. 2006), have found that when eggs are exposed to colder temperatures, chicks consequently take longer to hatch and adults produce larger eggs (Martin 2008). The gentoo colonies studied here nest on a variety of substrates (eg. bare soil in the Falkland Islands, Tussock grass in South Georgia, and rocks in all other locations), which may explain differences in exposure to ambient temperature and therefore the spatial variation observed; however, the chinstrap colonies we studied nest exclusively on rocks at all study sites yet also varied significantly in the length of incubation across a latitudinal gradient. Lab-based experiments have also provided evidence that increased daylight hours can speed up embryo growth within an egg, shortening the length of incubation (Shutze et al. 1962, Isakson et al. 1970, Cooper et al. 2011). The trend we observe here, in penguins, towards longer incubation times farther south, where air temperatures are colder and summer daylight hours during the breeding period are longer, likely indicates that exposure to cold temperatures outweighs any photoacceleration in these two species. Additional studies on intra-specific variation in incubation duration have also revealed that high predation, small body size, and high quality food resources may speed up incubation times, which may also explain some of the variation seen here in the pygoscelids (Worth 1940, Nice 1954, Lack 1968, Ricklefs 1968, Perrins 1976, Boersma 1982, Krebs and Avery 1984, Bosque and Bosque 1995). Future studies should focus on responses to these variables *in situ* within one species.

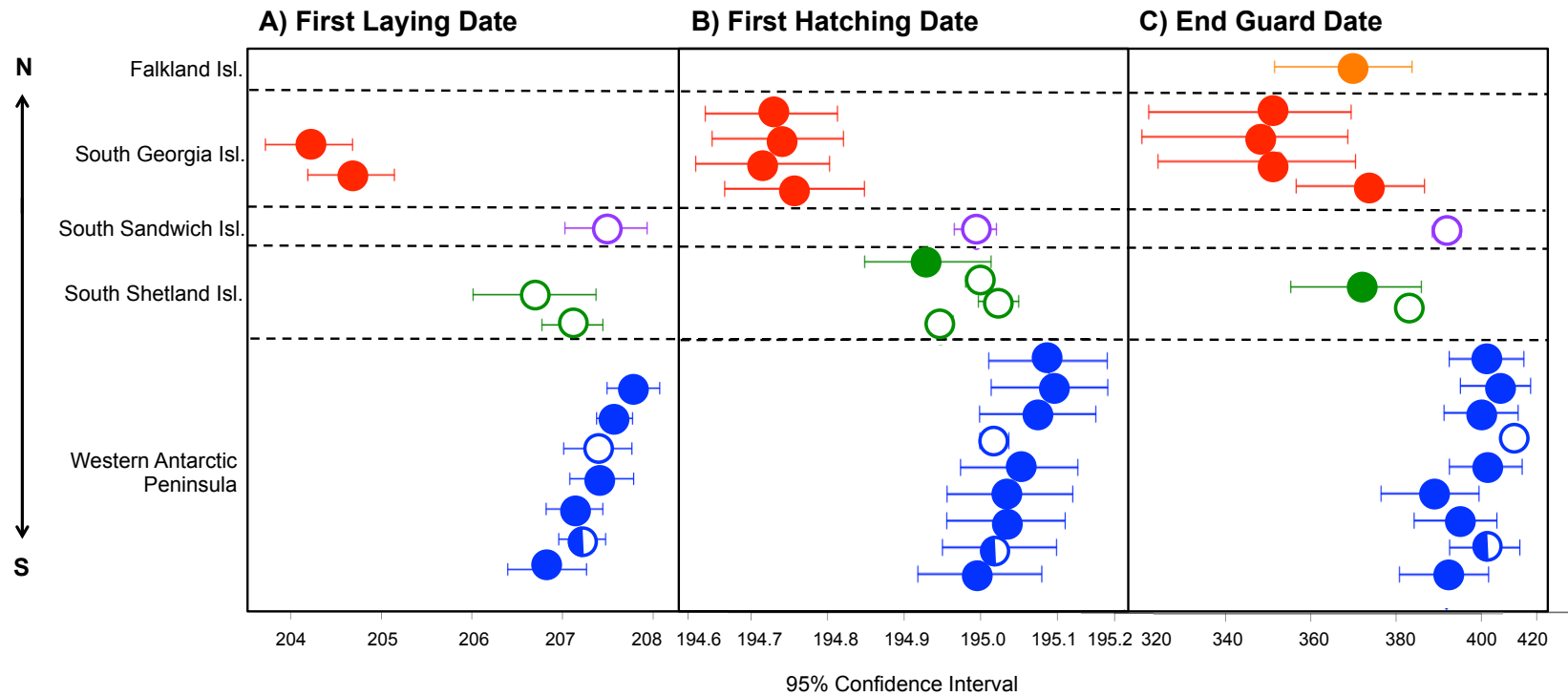


Figure 6.3. 95% confidence interval plots of a) first laying date, b) first hatching date, and c) guard end date at 17 colony locations for gentoo and chinstrap penguins. Colours indicate the following colony location: 1) Falkland Islands (orange), 2) South Georgia (red), 3) South Sandwich Islands (purple), 4) South Shetland Islands (green), and 5) Western Antarctic Peninsula (blue). Closed circles indicate sites where only gentoo penguins were observed, open circles indicate sites where only chinstrap penguins were observed, and the half-closed circles indicates the site where both gentoos and chinstraps were observed. Latitude increases from top to bottom. Adjusted R^2 values and d.f. included a) $R^2=0.99$, d.f.= 143, b) $R^2 = 0.99$, d.f.= 313, and c) $R^2 = 0.99$, d.f.= 331.

Colonies located farther south also exhibited significantly shorter nesting periods but guarded their chicks longer. The shift toward laying eggs shortly after beginning to build a nest at the breeding site may be a result of colonies shifting their phenology to provide maximum time for embryo growth within eggs in areas where cold exposure may stunt the growth rate. In both species, the date when adults moult influences how long the chicks are guarded, as parents must trade off the need to build up energy reserves prior to moult (known as hyperphagia) while continuing to care for their young (Penteriani et al. 2003). The longer guard durations observed farther south may result from adults beginning their moult at later dates. Future studies should track individual moult times (rather than colony-wide, as done here) to better understand latitudinal trends in moult and guard duration.

In addition, across species, in cases where loss or deaths occurred, colonies located farther south abandoned nests later and eggs or chicks were last seen in the nest at advanced dates in the breeding period (Table 6.3). This delay in egg or chick loss and nest abandonment may also be linked to the longer incubation durations observed farther south; as eggs take longer to fully develop before hatching, the chance of the egg succumbing to predation or spoiling in a flooded nest increases, leading to later abandonments and deaths. In addition, we found that when chinstraps abandon nests, the eggs or chicks are more advanced in age. We also discovered that three colony locations exhibited unique trends in their abandonment rates, all of which are inhabited by chinstrap penguins: 1) Saunders Island, South Sandwich

Islands, 2) Half Moon Island, South Shetland Islands, and 3) Booth Island, WAP (Figure E.1). We provide further evidence of variability in chinstrap populations (Trivelpiece et al. 2011), where some colonies exhibit low nest abandonment (Half Moon Island, South Shetland Islands) while others show large deviations in how likely an individual's nest will fail (Saunders Island, South Sandwich Islands and Booth Island, WAP).

The variation in both space and time observed here in penguin phenology provides evidence that the duration of phases within the annual cycle of birds is not intrinsic, or genetic, as previously understood. Here, we have successfully filled in gaps in the phenological dates of the two species to better understand their basic biology, particularly during the guard period and adult and chick moult (Figure 6.2, 6.3). Furthermore, we have shown the applications of non-invasive time-lapse cameras to the study of phenology and that even as few as 6 photographs daily can provide enough information to observe accurate dates at both colony and individual levels and examine spatial and temporal trends. Future research can improve upon these methods by observing more years and gaining information on the ages and experience of individuals.

6.6 References

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7

CHAPTER SEVEN

Concluding Remarks

7.1 Introduction

Variation in phenology is linked to the timing of environmental variables and influences survival at both the individual and colony level (Forrest and Miller-Rushing 2010). Therefore, understanding a species' annual cycle is vital to studying their ecology and conservation. By reviewing literature on *Pygoscelis* penguin phenology in Chapter 1, I identified major gaps, both spatially and temporally, in our knowledge of the timing of events in these three species: particularly, 1) during the guard phase, 2) their behaviour in winter, 3) the phenology of colonies inhabiting locations away from scientific bases, and 4) the phenology of chinstrap penguins. Chapter 2 assessed which camera methods are most relevant to seabird research, highlighting the capabilities and limitations of cameras in past studies and how they may be best applied to future research. Chapter 3 examined the timing of the guard phase in gentoo penguins and how chick aggregation behaviours vary across several sites. Chapters 4 and 5 showed variation in winter abundance at breeding sites in both gentoo and Adélie penguins related to abiotic factors and colony location. Lastly, Chapter 6 filled in gaps in the known timing and duration of phenology events in gentoo and chinstrap penguins across their full latitudinal ranges, while relating these timings to chick survival. Here, I hope to further synthesize the empirical findings from each of these chapters, discuss the implication of these findings to ecology and conservation policy, highlight some of the limitations of these studies, and recommend possibilities for future research.

7.2 Empirical Findings

By summarizing the main findings of this thesis, I aim to illustrate the three major themes that were observed across the four data chapters and their implications: 1) behaviours are *not* consistent across colony locations 2) nor between years, and these behaviours depend on 3) local environmental conditions.

In particular, the studies provide further evidence that behaviours differ significantly between three separate regions: 1) East Antarctica, 2) The Western Antarctic Peninsula (WAP) and South Shetland Islands, and 3) sub-Antarctic Islands (Falkland Islands, South Georgia, and South Sandwich Islands) and Argentina (Bost and Jouventin 1990, Borboroglu and Boersma 2013). In addition, many of the gentoo and chinstrap behaviours studied varied considerably along a latitudinal gradient. Gentoo chicks in South Georgia aggregated in larger groups and more frequently than the three colonies studied on the WAP, while chicks at the southernmost site on the WAP, Petermann Island, aggregated significantly less frequently and in smaller numbers. Likewise, gentoo penguins inhabiting sub-Antarctic sites (Argentina and South Georgia) demonstrated consistently higher breeding site occupation during winter when compared to the five WAP sites studied. In gentoo penguins, the first laying and first hatching dates of colonies in South Georgia differed significantly from the South Shetlands Islands and the WAP. In both gentoos and chinstraps, colonies located farther north also experienced longer nesting durations and shorter incubation and guard durations.

Unsurprisingly, we also found significant differences between Adélie presence at the breeding site overwinter in East Antarctica, where they were absent during winter, compared to the WAP, where they peaked in presence once each winter.

The thesis also revealed yearly variation in behaviours, many of which are typically studied over one season. Adélies were more abundant at the Yalours site during the non-breeding period in 2012 than in 2014 while gentoo winter abundance was greater in 2014 than in 2013 or 2012. In addition, gentoos and chinstraps took longer to nest, incubate eggs, and guard chicks in the 2014- 2015 breeding season than during the summer of 2013- 2014. Chinstrap penguins abandoned the nest significantly later and their eggs or chicks were last seen later in the breeding season than gentoo penguins.

Lastly, local conditions, including sea ice directly offshore annotated from images, temperature measured by gauges located on the cameras, and photoperiods influenced many of the behaviours evaluated. For example, gentoo chicks aggregated more when wet, cold conditions were present. In East Antarctica, Adélies were absent from the breeding site in winter at all 7 colonies studied, likely due to the compact (fast) ice present consistently throughout the winter (Gloersen et al. 1992, Stammerjohn et al. 1997, Stammerjohn et al. 2008, Fraser et al 2012). However, at the southern edge of their range in the marginal ice zone on the WAP, Adélies were found at a breeding site year-round, particularly when either compact sea ice or open water was present, when temperatures increased and compact ice was present offshore, and when daily daylight hours diminished. Conversely, gentoos were significantly more abundant at a

breeding site during the non-breeding period when open water or pack ice was present and significantly less abundant when compact ice appeared directly offshore. Interestingly, gentoos at sub-Antarctic sites (South Georgia and Argentina) increased in abundance in winter as daylight hours decreased while the opposite held true on the WAP, demonstrating how a colony's response to abiotic variables can vary depending on the colony location.

7.3 Ecological Implications

The differences observed here between colony locations and years highlight the importance of examining behaviours at multiple sites and in several years before generalizing a behaviour for a whole species. Although useful, studies in which a behaviour is studied within one colony or year (Davis 1982, Lishman 1985, Clausen and Pütz 2003, Tanton et al. 2004, Le Bohec et al. 2005, Dunn et al. 2011) should not simplify the complexities of behaviours across a species range and instead serve as an excellent starting point to further examine variation in behaviours. In addition, a species' basic biology, once considered to be intrinsic, or genetic, (Deeming 2002, Borboroglu and Boersma 2013) may instead differ significantly along a latitudinal gradient; this was the case with the incubation and guard durations in gentoo and chinstrap penguins studied here. Overall, generalization of behaviours should be avoided, particularly in species inhabiting large geographic ranges. In addition, colonies located at the edges of a species range, such as the gentoo colonies studied here in Argentina and Petermann Island on the WAP, when put into a broader geographic context, serve as interesting

examples of the extremes of this variation.

7.4 Policy Implications

Understanding the degree of variation in behaviours across both space and time can also help to identify vulnerable or at risk colonies. For example, by examining nest abandonment, we have identified that chinstraps have larger variation than gentoos in whether or not a nest is abandoned and have pinpointed colonies which may be most vulnerable: Saunders Island, the South Sandwich Islands and Booth Island, WAP. In addition, we have also produced colony survival rates over several years, which can be used to track the strength of colonies, unproductive years, and therefore larger areas of concern. Changes in climate over the coming years may increase competition for resources and habitat among the *Pygoscelis* species along the WAP (Forcada et al. 2006) and has likely already influenced the distribution of these three species (Lynch et al. 2012).

Understanding both breeding and non-breeding behaviour is essential to predicting population changes due to climate change in this rapidly warming region and deciphering how other threats, such as nearby fishing of prey resources (Chown et al. 2015), will affect individual survival year-round.

7.5 Limitations

One major limitation of studying phenology is the lack of consistency in how dates and durations are measured. Because phenology in pygoscelids has

been noted since 1899 (Sladen 1958) and has been studied by hundreds of researchers to date (Chapter 1), a unified method is needed to compare phenology results conducted by different research groups. Although the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR) has suggested methods for measuring phenology (CCAMLR 2004) researchers examining sub-Antarctic pygoscelid colonies may choose different methods of measurement. I hope that by expressing how I defined each of the stages here and providing others with an extensive list of past phenological dates and citations, these methods may be better unified in the future.

In addition, the less invasive time-lapse camera system has provided its own limitations. Unfortunately, in pygoscelids, like most seabirds, it is currently difficult to identify individuals in images without marking birds. Therefore, the types of studies that can be conducted on pygoscelids using time-lapse cameras are limited. Our inability to track individuals limited the information available when examining winter abundance, as we were unable to determine whether the individuals seen in winter were the same individuals observed breeding at the site during the summer months. However, by combining time-lapse cameras techniques with the use of GPS tracking units, temperature loggers, paint markings (Calvo and Furness 1992, Murray and Fuller 2000), stable isotopes (Polito et al. 2011), weigh bridges (eg. Kerry et al. 1993), or audio recordings (Lengagne et al. 1997, Aubin & Jouventin 2002) researchers can obtain considerably more information than using any one of these methods alone.

Furthermore, by choosing non-invasive methods, we were unable to measure the body size or age of individuals, which may have provided insight into the studied behaviours (Worth 1940, Nice 1954, Lack 1968, Ricklefs 1968, Perrins 1976, Boersma 1982, Krebs and Avery 1984, Bosque and Bosque 1995).

Furthermore, cameras must be set at a greater frequency (more than once every hour) to capture more discrete behaviours such as predator presence and aggressive advances between individuals. However, time-lapse cameras can serve as an excellent way to standardize a phenology method across research groups and sites, taking measurements at precisely the same time while also encouraging less invasive research.

7.6 Recommendations for Future Research

Future studies should focus on how each of the phenology timings studied is influenced by biotic variables and additional abiotic factors. The addition of local environmental measurement devices to each camera system, such as wind and snow gauges, would enhance phenology studies while also providing information relevant to a broader array of scientific interests. The addition of data on local prey abundance and quality as well as fine-scale nesting terrain would further build on the phenology data provided and improve our understanding of the plasticity of certain colonies and species when adjusting their phenology. Additional information on fisheries locations and localized catch year-round combined with standardized phenology data would greatly improve our awareness of how fishing influences the timing of breeding, survival of individuals, and winter

attendance.

Although using time-lapse cameras can limit the ability to answer certain research questions, this thesis provides evidence of the immense capabilities of the method and the method should be used in future research when applicable.

Because of the remote nature and harsh conditions present at many study sites and because cameras are less invasive and likely produce more accurate results on wild behaviours when compared with *in situ* observation, I encourage researchers to conduct future studies using the technique described. As research using time-lapse cameras expands, the approach serves as a consistent method of constant effort in which questions can be answered more easily between years and across study sites when compared with other behavioural ecology techniques.

Furthermore, future studies should focus on the goal of establishing long-term research projects using time-lapse cameras to better understand behaviours as time series. In addition, future research should determine whether non-invasive individual identification is possible in pygoscelids as has been found in African penguins (*Spheniscus demersus*, Sherley et al. 2010). In the future, by comparing data obtained by time-lapse cameras to data collected using traditional tracking methods on the same individuals, we should also be able to better understand how these methods can best be combined and optimize both quality of data collection and non-invasiveness of methods. Lastly, as cameras become smaller, more durable, and less expensive, the use of thermal cameras in field biology has immense application in providing more information on individuals, such as temperature (Kastberger and Stachl 2003, McCafferty et al. 2011, McCafferty et al. 2013) and perhaps individual identification and biometrics, and

will likely become a popular ecology methods when coupled with visible-spectrum cameras.

7.7 References

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APPENDICES

Appendix A

Supplementary Material for Chapter 1

A1. Terminology for each phase within the annual cycle of *Pygoscelis* penguins.

Return to colony: The date in which the first adult is seen returning to the rookery. The phase is sometimes expressed as a range of dates beginning when the first individual returns and ending when the majority of birds are present at the colony.

Courtship: The time period when copulations are noted at the breeding site.

Egg laying: The start of the egg laying period is often referred to as the clutch initiation date (CID) and the majority of studies have measured this date, or the mean of these dates, when examining phenology. This phase ends when the second clutch is laid or, in the case of northern sub-Antarctic gentoo populations, when the two-egg clutch is re-laid. The phase is sometimes expressed as a range of dates.

Incubation: the time period in which the eggs are incubated, beginning when the second egg is laid, and partners alternate incubation shifts. The phase ends when the first egg hatches.

Hatching: The hatching period begins when the first egg hatches and ends when the second egg hatches. Studies often only measure the beginning of this phase; in other words, the date in which the first egg hatches.

Guard: The period in which chicks are guarded by their parents and stay within the nest boundaries. The phase begins when the second egg hatches and ends when the first chick is unguarded by parents, leaving the nest.

Post-guard: This phase commences when the first chick leaves the nest area and is considered unguarded by a parent and ends when chicks depart the colony.

Chick moult: The time period in which chicks moult their down feathers, beginning with the first visible moulting individual and ending with the last.

Adult moult: The time period in which adults moult their feathers, beginning with the first visible moulting individual and ending with the last.

Chick Departure: The date or series of dates when chicks depart the colony, beginning with the first individual departing to sea and ending with the last.

Adult Departure: The date or series of dates when adults depart the colony, beginning with the first individual departing to sea and ending with the last

Appendix B

Supplementary Material for Chapter 3

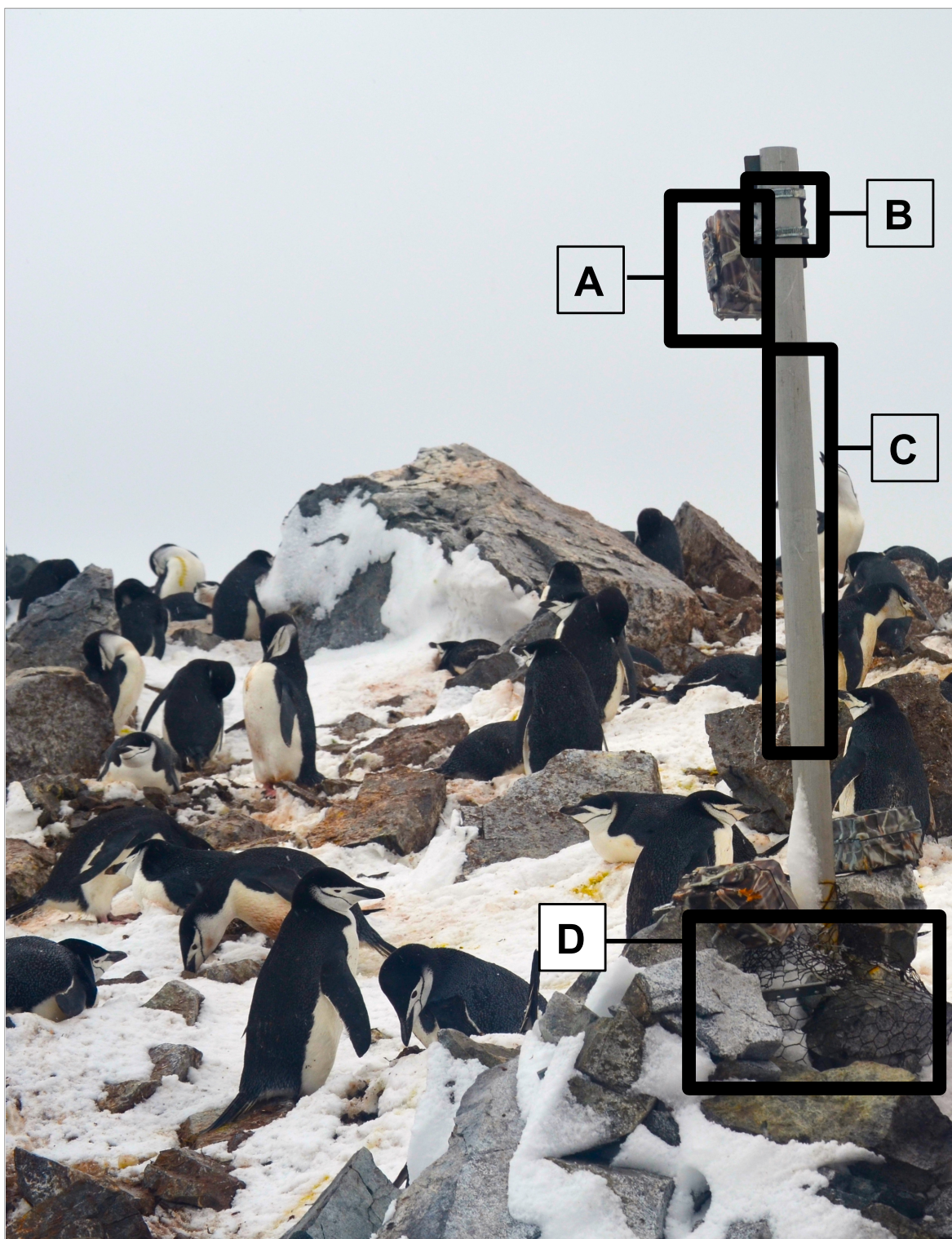


Figure B.1. Example of camera system installed at Orne Harbour overlooking chinstrap penguins (*Pygoscelis antarctica*): comprised of a A) Reconyx Hyperfire HC500 trail camera (Reconyx, Inc., Holmen, WI, USA) set to time-lapse mode, B) mounting apparatus, C) steel or carbon fibre pole, and D) rock basket.

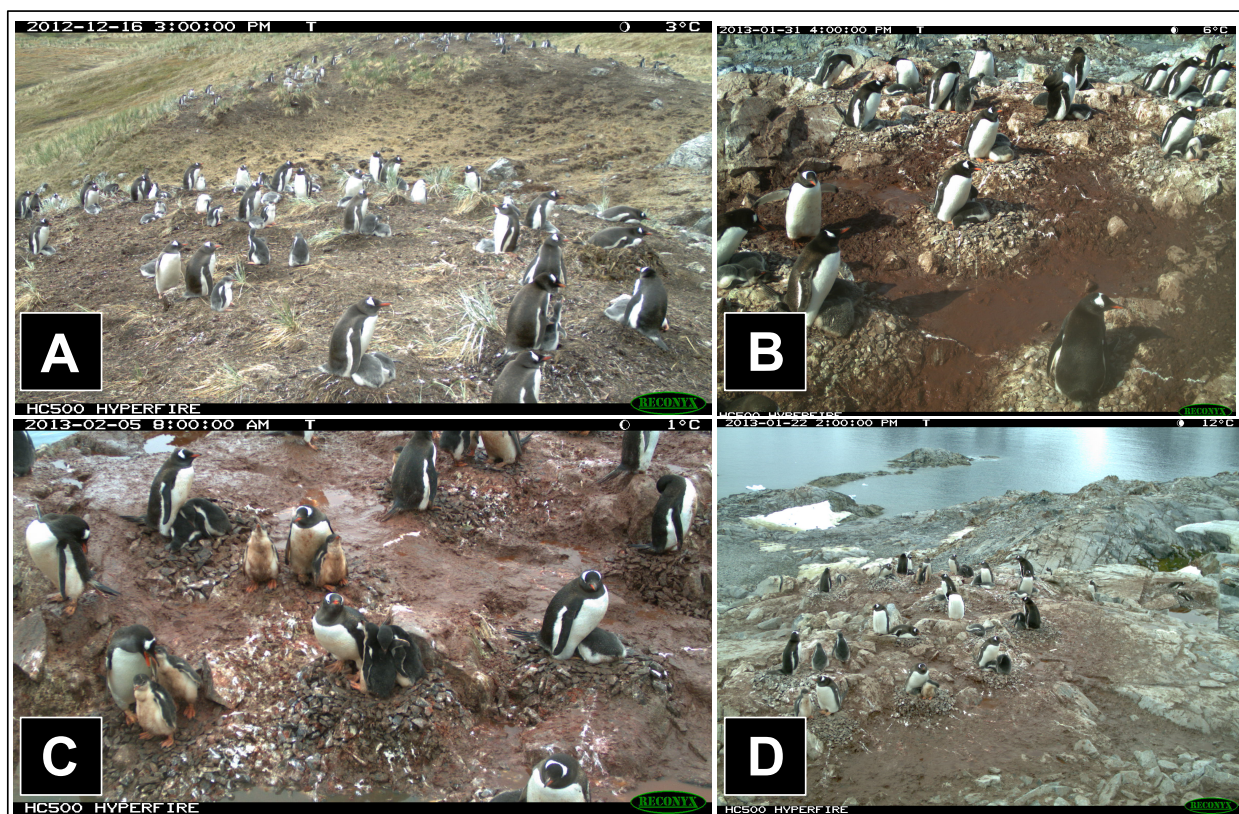


Figure B.2. Images from the first day of the post-guard period in gentoo penguins (*Pygoscelis papua*) during the 2012- 2013 breeding season at each of the four study sites examined in Chapter 3: A) Maiviken, B) Georges Point, C) Port Lockroy, and D) Petermann Island.

Appendix C

Supplementary Material for Chapter 4



Figure C.1. Annotated image from the Yalours Island site, demonstrating how counts were extracted from each photograph. Purple and yellow circles each represent 1 penguin individual.

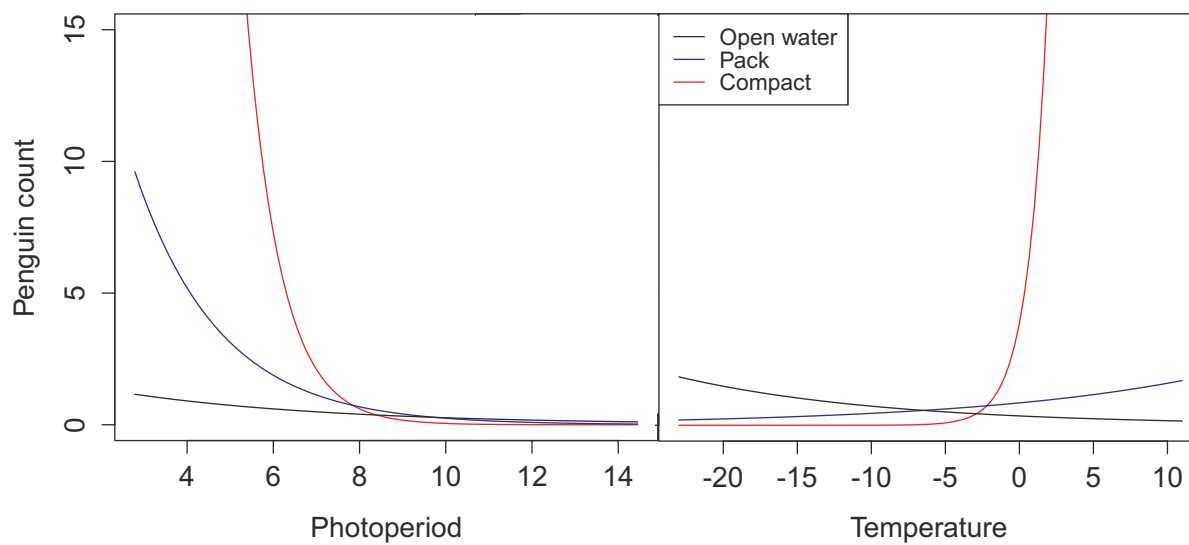


Figure C.2. Penguin counts for median photoperiod and temperature during each sea ice type (open water, pack ice, and compact ice).

Appendix D

Supplementary Material for Chapter 5

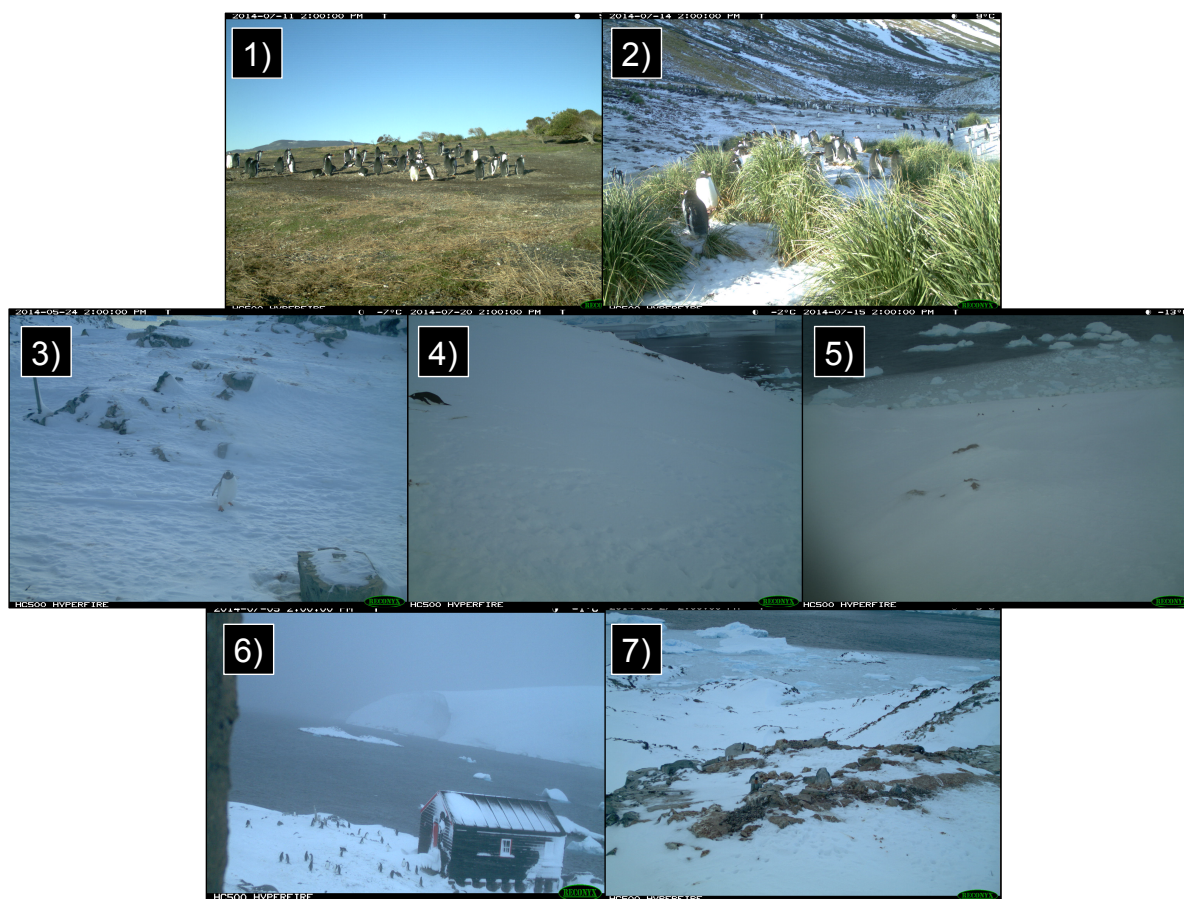


Figure D.1. Example images taken during the non-breeding period of 2014 at 1) Martillo Island, 2) Maiviken, 3) Cuverville Island, 4) Danco Island, 5) Neko Harbour), 6) Port Lockroy, and 7) Petermann Island.

Appendix E

Supplementary Material for Chapter 6

Table E.1. Table summarizing phenology dates and duration at each gentoo (*Pygoscelis papua*) and chinstrap (*Pygoscelis antarctica*) colony locations studied. See 6.3.3 for definition of dates and durations.

Follow the following website address for direct access to the table:

https://docs.google.com/spreadsheets/d/1sM49cluCjIZn6K9RRrVXkWRibM_KxfY-kqWV5Ns--ME/edit?usp=sharing

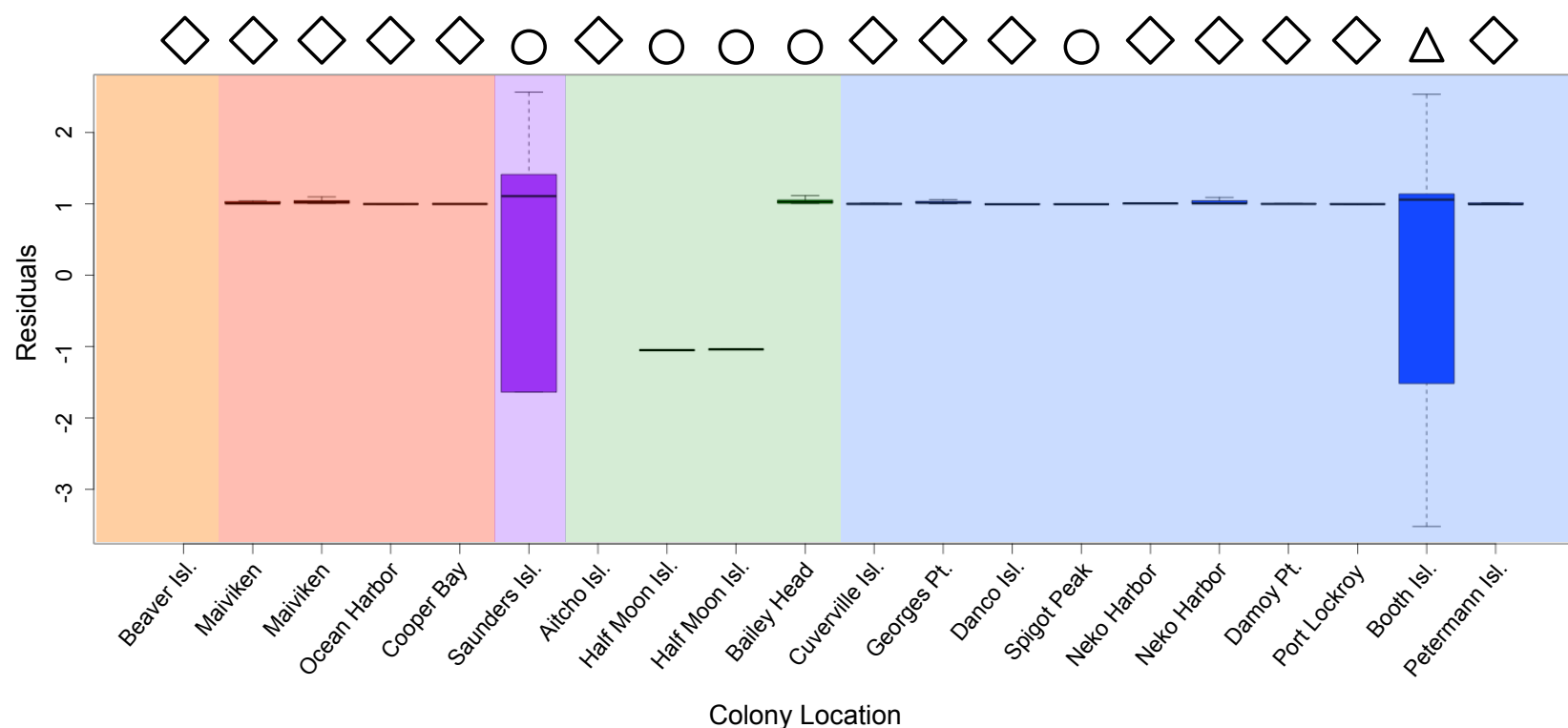


Figure E.1. Box-and-whisker plots of residuals resulting from binomial generalized mixed model of nest abandonment, showing difference in nest abandonment as a binary variable across 20 sub-colonies at 17 locations. Colours indicate the following colony location: 1) Falkland Islands (orange), 2) South Georgia (red), 3) South Sandwich Islands (purple), 4) South Shetland Islands (green), and 5) Western Antarctic Peninsula (blue). Diamonds indicate sites where only gentoo penguins were observed, circles indicate sites where only chinstrap penguins were observed, and the triangle indicates the site where both gentoos and chinstraps were observed. Latitude increases from left to right.

Appendix F

First-authored Papers Published During the Course of the DPhil

Black C (2015). Phenology of *Pygoscelis* penguins: A comprehensive review of the phenology of *Pygoscelis* penguins. *Polar Biology*, 39:405.

Black C, Collen B, Johnston D, Hart T (2016). Why huddle? Ecological drivers of chick aggregations in gentoo penguins across latitudes. *Plos ONE*, 11:2.

Black C, Raya Rey A, Hart T (accepted February 2017). Peeking into the bleak mid-winter: investigating non-breeding strategies of gentoo penguins using a camera network. *The Auk*.