

A comprehensive review of the phenology of *Pygoscelis* penguins

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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.

Keywords Phenology · *Pygoscelis* · Annual cycle · Chinstrap penguin · Adélie penguin · Gentoo penguin

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 changing climate. In particular, studies have demonstrated phenological advances in both the northern (Beebee 1995; Fitter and Fitter 2002; Parmesan and Yohe 2003; Menzel et al. 2006; Parmesan 2007; Körner and Basler 2010) 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

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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 influence different phenological measures significantly and cause these trends to be 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 in egg laying dates as earlier 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), whereas proximate factors exist, including 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, b), 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 is necessary for an individual's 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 (Spheniscidae) 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.

The annual cycle of penguins

Penguins, representing roughly 90 % of the seabird biomass in the Southern Ocean (Williams 1990), are well studied in the context of population dynamics, prey abundance, and phenology. The order is composed of 18 species with taxa ranging from the Galapagos penguin, inhabiting the Galapagos Islands near the equator in the Pacific Ocean, to the emperor penguin, which breeds as far south as 77.74° in latitude on the Antarctic continent (Borboroglu and Boersma 2013). 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, five are endangered, six vulnerable, two near threatened, and five of least concern, which has changed dramatically in the past 20 years as only five were considered threatened in 1993 (Trathan et al. 2014; IUCN 2015). 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); and 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 with 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 polar 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 2 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 (Fig. 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

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 2015) within their respective ranges, collectively making up roughly 90 % of Antarctic avian biomass (Williams 1990). 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 Adélie 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 turn 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 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). While in Adélie, eggs are also laid roughly 3 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 4 days (Lishman 1985), incubation lasts

33–36 days, and the guard period lasts approximately 4 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), while gentoos are known to stay resident near their breeding site, likely due to their near-shore foraging ecology (Bost and Jouventin 1990a). In relation to incubation schedules, in chinstraps and gentoos, females always undergo incubation first (Lishman 1985; Watanuki 1993), while the opposite holds true with Adélie where 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, Adélie are the first to arrive, followed by gentoos, and eventually chinstraps (Trivelpiece et al. 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). Gentoos experience the most annual variation in phenology of the three pygoscelid species (Bost and Jouventin 1990a; 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 2 weeks on South Georgia Island (Williams 1990), with changes in local foraging condition providing the most plausible explanation for the variation (Bost and Jouventin 1990a; 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 3 months, while laying dates in colonies of macaroni penguins at these same locations differ by only 3 weeks (Bost and Jouventin 1990a). 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 1990a). However, within a colony, timing is often highly synchronous (Downes et al. 1959; Trivelpiece et al. 1987) and can depend on colony structure and nesting substrates (Williams 1990).

In contrast, Adélie 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 Adélie in East Antarctica and the Scotia Arc and sub-Antarctic islands. In

Table 1 Summary of phenology data available on *Pygoscelis* penguins

Species	Region	Location	Site	Latitude, longitude	Annual cycle phase	Dates	Years studied	References
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	Chesalin et 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		
	Sub-Antarctic Islands	Argentina	Martillo Island	54°54'S, 67°23'W	Guard	January 16–February 14		
					Hatching	December 10–25	1991–1996	Quintana and Cirelli (2000)
					Egg laying	December 2–9	1921	Bagshawe (1938)
		South Shetland Islands	King George Island	62°10'S, 58°30'W	Hatching	January 8–14	1922	
					Egg laying	October 29–November 2	2005–2006	Ghys et al. (2008)
	South Orkney Islands	Elephant Island	Laurie Island	61°13'S, 55°11'W	Return to colony	October 7–25	1980	Jablonski (1987)
					Egg laying	Start: November 5		
					Hatching	Start December 17	1980	Jablonski (1987)
					Hatching	December 10–25	1981–1982	Trivelpiece et al. (1987)
					Hatching	November 18–January 16	1976–1977	Furse (1979)
South Orkney Islands	Signy Island	60°43'S, 45°38'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				
			Return to colony	September 3–October 28	1947–1987	Rootes (1988)		
			Egg laying	October 18–November 21				
			Hatching	November 17–December 27				

Table 1 continued

Species	Region	Location	Site	Latitude, longitude	Annual cycle phase	Dates	Years studied	References
		Falkland Islands	Volunteer Beach	51°29'S, 57°50'W	Hatching	1st: November 29– December 15 2nd: November 30– December 12	2001	Otley et al. (2005)
			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	1st: October 8–November 10 Mean: October 30	1986–1988 1976	Williams (1990) Croxall and Prince (1979)
					Hatching	Start: October 21 Mean: December 3	1936 1976	Roberts (1940) ^a Croxall and Prince (1979)
					Post-guard Chick departure	Mean: December 31 Mean: February 28	1977	
		Prince Edward Islands	Marion Island	46°52'S, 37°51'E	Return to colony Egg laying	June 1–July 23 Start: June 1–July 20 End: July 12–August 3 Start: June 16	1994–2003 1965–1966	Crawford et al. (2003) Zinderen Bakker et al. (1971) ^a
						Start: June 24 Start: June 24	1974, 1976 Not specified	Williams (1980) 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 End: March 22	1994–2003 1952	Crawford et al. (2003) 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		

Table 1 continued

Species	Region	Location	Site	Latitude, longitude	Annual cycle phase	Dates	Years studied	References
		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	
						1st start: August 7–17	1984–1985	Bost and Clobert (1992)
		1st mean: September 9–19						
		1st: October 7–November 15						
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
Macquarie Island		Macquarie Island		54°61'S, 158°85'E	Hatching	September 20–October 24	1987, 2002, 2003	Lescroël et al. (2009)
					Egg laying	Start: September 12	Unknown	Tulloch (1916) ^a
Heard and McDonald Islands		Heard Island		53°00'S, 73°50'E		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. (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)					

Table 1 continued

Species	Region	Location	Site	Latitude, longitude	Annual cycle phase	Dates	Years studied	References		
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. (1975b)		
					Egg laying	1st Mean: November 4				
					Hatching	December 14–27			1996–1997	Moreno et al. (1998)
			Elephant Island		61°08'S, 55°07'W	Return to colony	December 19–January 10	1994–1995	Barbosa et al. (1997)	
							Hatching	December 15–31	1991–1994	Viñuela et al. (1996)
							Mean: November 8–10	Not specified	Conroy et al. (1975b)	
		King George Island	62°10'S, 58°39'W	Return to colony	Hatching	Start: December 15	1970–1971	Conroy et al. (1975b)		
					End: December 27–January 1					
					December 16–January 4	1976–1977	Furse (1979)			
					October 28–November 8	1980	Jablonski (1987)			
					Mean: November 8	1981–1982	Trivelpiece et al. (1984)			
		South Orkney Islands	Signy Island	60°43'S, 45°38'W	Return to colony	November 2–18	1977–1981	Trivelpiece and Volkman (1979)		
						Egg laying	Peak: November 27	1977–1982		
						Hatching	December 22–January 5	1981–1982	Trivelpiece et al. (1987)	
						September 24–November 14	1947–1987	Rootes (1988)		
						Start: November 5–8	1981–1981	Lishman (1985)		
						Start: November 1	1970–1971	Conroy et al. (1975b)		
Egg laying	November 14–December 1	November 28–December 20	Return to colony	Prior to 1987	1980–1982	Rootes (1988)				
				1980–1982	Lishman (1985)					
				1st: November 28–December 10	1973	Marchant and Higgins (1990)				
				2nd: December 2–14						
				1st mean: November 25	1970–1971	Conroy et al. (1975b)				
				Hatching	December 24–January 11	Prior to 1987	Rootes (1988)			
				January 3–24	1980–1981	Lishman (1985)				
				Start: December 26	1970–1971	Conroy et al. (1975b)				
				Chick departure	February 24–March 2	1981–1982	Lishman (1985)			
				End: March 12	1970–1971	Conroy et al. (1975b)				
Adult moult	February 26–March 10									

Table 1 continued

Species	Region	Location	Site	Latitude, longitude	Annual cycle phase	Dates	Years studied	References
Adélie	Scotia Arc	Western Antarctic Peninsula	Water-Boat Point	60°46'S, 44°42'W	Return to colony	Start: November 2–16	1995–1998	Carlini et al. (2005)
					Egg laying	November 2–14	1903–1904	Clarke (1906)
	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	Return to colony	Mean: November 1	1974, 1980–1981, 1988	Kerry et al. (1993)
					Egg laying	Start: October 20–25	1990–1992	Kerry et al. (1993)
					Egg laying	Mean: November 20	1990–2006	Emmerson et al. (2011)
					Egg laying	November 11–December 5	1990–1992	Kerry et al. (1993)
					Hatching	Mean: December 25	1990–2006	Emmerson et al. (2011)
					Hatching	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)					
Wilkes Land	Mawson Station	67° 60'S, 62° 86'E	Return to colony	October 20–22	1974, 1980, 1981, 1988, 1990			
			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		
			Chick moult	February 17–March 10	1958–1960	Penney (1968)		
	Haswell Island	66° 31'S, 93° 00'E	Adult moult	Mean: March 5				
Return to colony	Start: October 14	1961–1962	Pryor (1968)					

Table 1 continued

Species	Region	Location	Site	Latitude, longitude	Annual cycle phase	Dates	Years studied	References
						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	1961–1962	Pryor (1968)
						2nd: November 15		
						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	Rodary et al. (2000)
					Egg laying	Start: November 12–14		
						Mean: November 17	2006–2008	Beaulieu et al. (2010)
					Hatching	Mean: December 23		
					Hatching			
						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)
		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)
						Start: December 17		Falla (1937)

Table 1 continued

Species	Region	Location	Site	Latitude, longitude	Annual cycle phase	Dates	Years studied	References
			Cape Gray	66°51'S, 143°22'E	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		
					Adult departure	March 14	1921–1922	Bagshawe (1938)
			Cape Hallett	72°18'S, 170°12'E	Return to colony	Start: October 9–13	1959–1960	Reid (1964)
							1959–1960	
					Egg laying	Start: October 30– November 3		
					Hatching	December 5–7		
			Wood Bay	74°21'S 165°10'E	Return to colony	Median: October 30– November 12	1994–1999	Olmastroni et al. (2000)
						End: November 10–17		
					Egg laying	November 6–29		
						End: November 9–19	1999–2001, 2003	Olmastroni et al. (2004)
					Hatching	December 16–17		
						December 9–January 3	1994–1999	Olmastroni et al. (2000)
					Post-guard	Mean: January 8–14	1999–2001, 2003	Olmastroni et al. (2004)
					Post-guard			
						January 3–22	1994–1999	Olmastroni et al. (2000)
					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)
						1st mean: November 11–13	1967–1970	Spurr (1975)
						2nd mean: November 15– 16 s		

Table 1 continued

Species	Region	Location	Site	Latitude, longitude	Annual cycle phase	Dates	Years studied	References
					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	1964–1969, 1974–1975	Ainley et al. (1983)
						Mean: November 18	1963–1974	Ainley (2002)
						Start: November 9	1902	Sladen (1958)
			Cape Royds	77°33'S, 166°09'E	Hatching	December 8–January 9	1970–1971	Oelke (1975)
					Return to colony	October 22–24	1968–1969	Ainley and Leresche (1973)
						Start: October 26	1959–1960	Taylor (1962)
					Egg laying	End: November 16–20	1968–1969	Ainley and Leresche (1973)
						November 4–December 4	1959–1960	Taylor (1962)
						Start: November 7	1961	Stonehouse (1963)
						1st: November 9–22	1965	Yeates (1971)
						2nd: November 11–22		
					Hatching	1st: December 15–29		
						2nd: December 16–29		
					Post-guard	Start: January 9–20	1966	
					Adult moult	Start: February 1–12	1959–1960	Taylor (1962)
						End: February 25		
					Chick moult	Start: February 1		
					Chick departure	January 30–February 25		
						Start: January 25	Unknown	Yeates (1968)
						End: February 20	1963–1966	Spellerberg (1971)

Table 1 continued

Species	Region	Location	Site	Latitude, longitude	Annual cycle phase	Dates	Years studied	References			
	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
					Booth Island	65°08'S, 64°00'W	Hatching	December 5–16	1945–1948, 1952		
									Start: December 8		1948–1951
							Chick moult	January 21–February 4			
							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)	
	Sub-Antarctic Islands	South Shetland Islands	King George Island	62°10'S, 58°30'W	Return to colony	Start: November 9	1909	Sladen (1958)			
								Mean: October 8–19	1981–1983	Trivelpiece et al. (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	1977–1979	Trivelpiece and Volkman (1979)
					End: November 15						
					Hatching	November 28–December 10	1981–1982	Trivelpiece et al. (1987)			

Table 1 continued

Species	Region	Location	Site	Latitude, longitude	Annual cycle phase	Dates	Years studied	References
			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)
					Egg laying	Start: October 4–8	1903, 1904, 1950, 1953	Sladen (1958)
						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)
							2005	
					Adult departure	January 12–February 4		
						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)

Table 1 continued

Species	Region	Location	Site	Latitude, longitude	Annual cycle phase	Dates	Years studied	References
						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	

Table incorporates all available texts with dates included with some minor exceptions. See “Appendix” for definitions of each phase

^a As cited in Marchant and Higgins (1990)

^b As cited in Williams (1979)

^c As cited in Pryor (1968)

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 (Fig. 2; Table 1), likely because of the same links between photoperiod, sea ice retreat, and the species’ phenology.

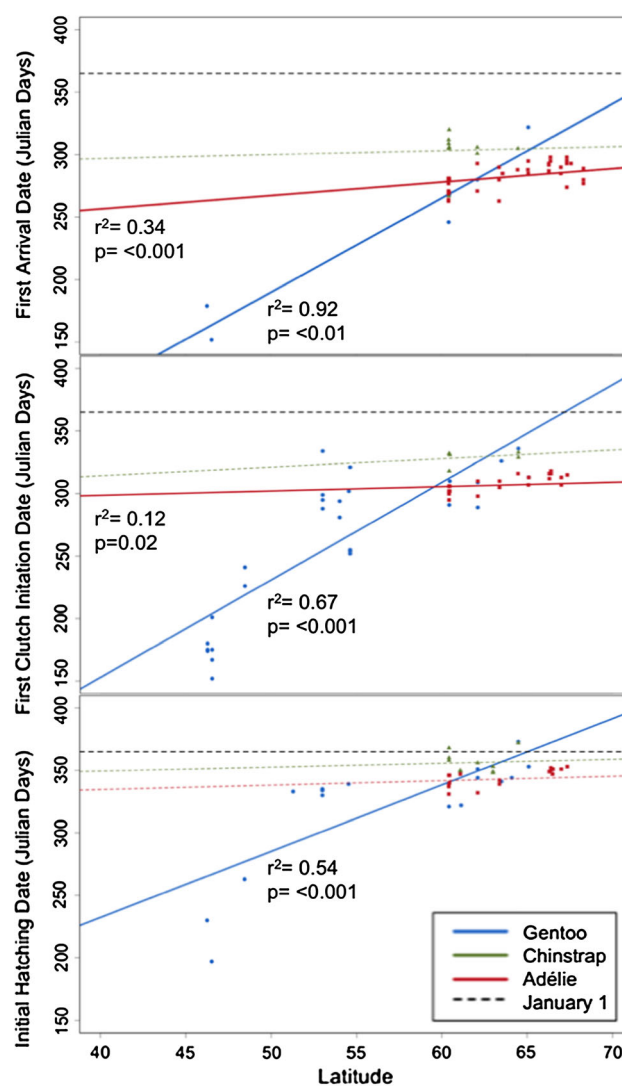


Fig. 2 Linear model of (1) first arrival dates, (2) first clutch initiation dates, and (3) initial hatching dates versus latitude of colony location for gentoo (*Pygoscelis papua*), chinstrap (*Pygoscelis Antarctica*), and Adélie penguins (*Pygoscelis adeliae*). Un-perforated lines represent significant values ($p < 0.05$) and dashed lines represent insignificant values. All dates expressed as Julian days with the exception of dates in January and February where Julian day was added to 365 (e.g. January 15 = 380). All data and citations found in Table 2

Table 2 The duration of recorded phases within the annual cycle of gentoo, chinstrap, and Adélie penguins

Species	Region	Location	Site	Latitude, longitude	Annual cycle phase	Duration	References
Gentoo	Sub-Antarctic Islands	Argentina	Martillo Island	54°54'S, 67°23'W	Incubation	1st mean: 37 days	Ghys et al. (2008)
		Falkland Islands	Volunteer Beach	51°29'S, 38°02'W	Incubation	36.5–37 days	Otley et al. (2005)
		South Georgia	Bird Island	54°00'S, 38°02'W	Egg laying interval	3.2 days	Roberts (1940)
					Incubation	Mean: 35.2–35.3 days	Williams (1990)
					Guard	Mean: 25.4–29.9 days	
					Chick departure	75–100 days old	
		Crozet Archipelago	Possession Island	46°25'S, 51°44'E	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)	
	Kergulen Islands	Estacade	48°45'S, 68°45'E	Chick moult	Start: 34–47 days old End: 74–95 days old		
				Replacement Clutch Incubation	1st: 35–40 days 2nd: 33–38 days		
				Egg laying	26–29 days	Lescroël et al. (2009)	
				Incubation	1st: mean: 36.0 days 2nd: mean: 33.8 days		
	Prince Edward Islands	Marion Island	65°20 S, 37° 51'E	Hatching interval	0–5 days		
				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	Water-Boat Point	64°48'S, 62°43'W	Incubation	Mean: 37 days	Bagshawe (1938)	
Unknown	Unknown	Unknown	Unknown	Incubation	31–35 days	Murphy (1936) ^b	

Table 2 continued

Species	Region	Location	Site	Latitude, longitude	Annual cycle phase	Duration	References
Chinstrap	Sub-Antarctic Islands	South Orkney Islands	Signy Island	60°42'S, 45°36'W	Chick departure	80–105 days	Williams (1990) ^c
					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	
		South Shetland Islands	King George Island	62°10'S, 58°39'W	Chick departure	48–59 days old	
					Chick departure	Mean: 17.4–22.1 days	Trivelpiece and Trivelpiece (1990)
			Deception Island	63°00'S, 60°40'W	Post-guard	Mean: 22.3–24.6 days old	Viñuela et al. (1996)
					Chick departure	Mean: 53.1–57.4 days old	
			Adélie	East Antarctica	Mac. Roberston Land	Béchervaise Island	67°35'S, 62°49'E
Queen Maud Land	Lützw-Holm Bay	69°10'S, 37°30'E					
					Ross Island	Cape Hallett	72°19'S, 170°16'E
Cape Royds	77°33'S, 166°09'E	Courtship				4–14 days	Stonehouse (1963)
Cape Bird	77° 13'S, 166° 28'E	Egg laying interval			2–4 days		
					Incubation	1st: 33–39 days 2nd: 30–37 days	Taylor (1962)
						33–43 days	Yeates (1968)
					Guard	1st chick: 16–31 days 2nd chick: 14–30 days	Yeates (1971)
		17–32 days				Taylor (1962)	
		Adult moult			9–17 days		
			Chick departure	55 days old			
			Courtship	8–16 days	Davis (1982b)		
Incubation	2nd: 32–38 days 1st: 33–37 days			Spurr (1975)			
	Cape Crozier	77°50'S, 169°33'E	Guard	16–34 days old	Davis (1982b)		
Chick departure				46–55 days old	Ainley and Schlatter (1972)		
	Victoria Land	Cape Adare	71°28'S, 170°23'E	Egg laying interval	2–3 days	Ainley et al. (1983)	
Wilkes Land					Wilkes Station	66°15'S, 110°32'E	Incubation
	Egg laying interval	1–4 days, Mean: 2.2 days	Penney (1968)				

Table 2 continued

Species	Region	Location	Site	Latitude, longitude	Annual cycle phase	Duration	References
					Incubation	1st mean: 37.2 days 2nd mean: 34.6 days	
					Adult pre-moult	3–7 days	Penney and Emlen (1967)
					Adult Moult	6–28.5 days	
					Adult post-moult	2–4 days	
			Haswell Island	66°31'S, 93°00'E	Incubation	33–36 days	Pryor (1968)
	Scotia Arc	Western Antarctic Peninsula	Hope Bay	63°38'S, 56°98'W	Egg laying interval	3–4 days, Mean: 3.0–3.7 days	Sladen (1958)
					Incubation	1st: 36–38 days 2nd: 35–36 days Mean: 36 days	Sladen (1953)
			Petermann Island	65°10'S, 64°10'W	Adult moult	20 days	Gain (1914)
	Sub-Antarctic Islands	South Orkney Islands	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	Sladen (1958) Marchant and Higgins (1990)
					Incubation	1st: 33–39 days 2nd: 32–38 days	Lishman (1985)
						1st: 35–37 days 2nd: 33–35 days	Sladen (1958)
					Guard	17–28 days	
					Post-guard	13–28 days old	Lishman (1985)
					Adult moult	15–22 days	Dunn et al. (2011)
					Chick departure	54–64 days old	Lishman (1985)
			Laurie Island	60°46'S, 44°42'W	Incubation	31–33 days	Clarke (1906)
		South Shetland Islands	King George Island	62°10'S, 58°39'W	Chick departure	Mean: 21 days 50–55 days old	Trivelpiece and Trivelpiece (1990) Volkman and Trivelpiece (1980)
	Unknown	Unknown	Unknown	Unknown	Incubation	33–37 days 1st: 35–38 days 2nd: 33–36	Sapin-Jaloustre and Bourlière (1952) ^p Richdale (1957)
					Adult moult	9–16 days	Cendron (1953) ^b

When available, ranges are included instead of means. See “Appendix” for definitions of each phase

^a As cited in (Marchant and Higgins 1990)

^b As cited in (Richdale 1957)

^c As cited in (Borboroglu and Boersma 2013)

^d As cited in (Ainley et al. 1983)

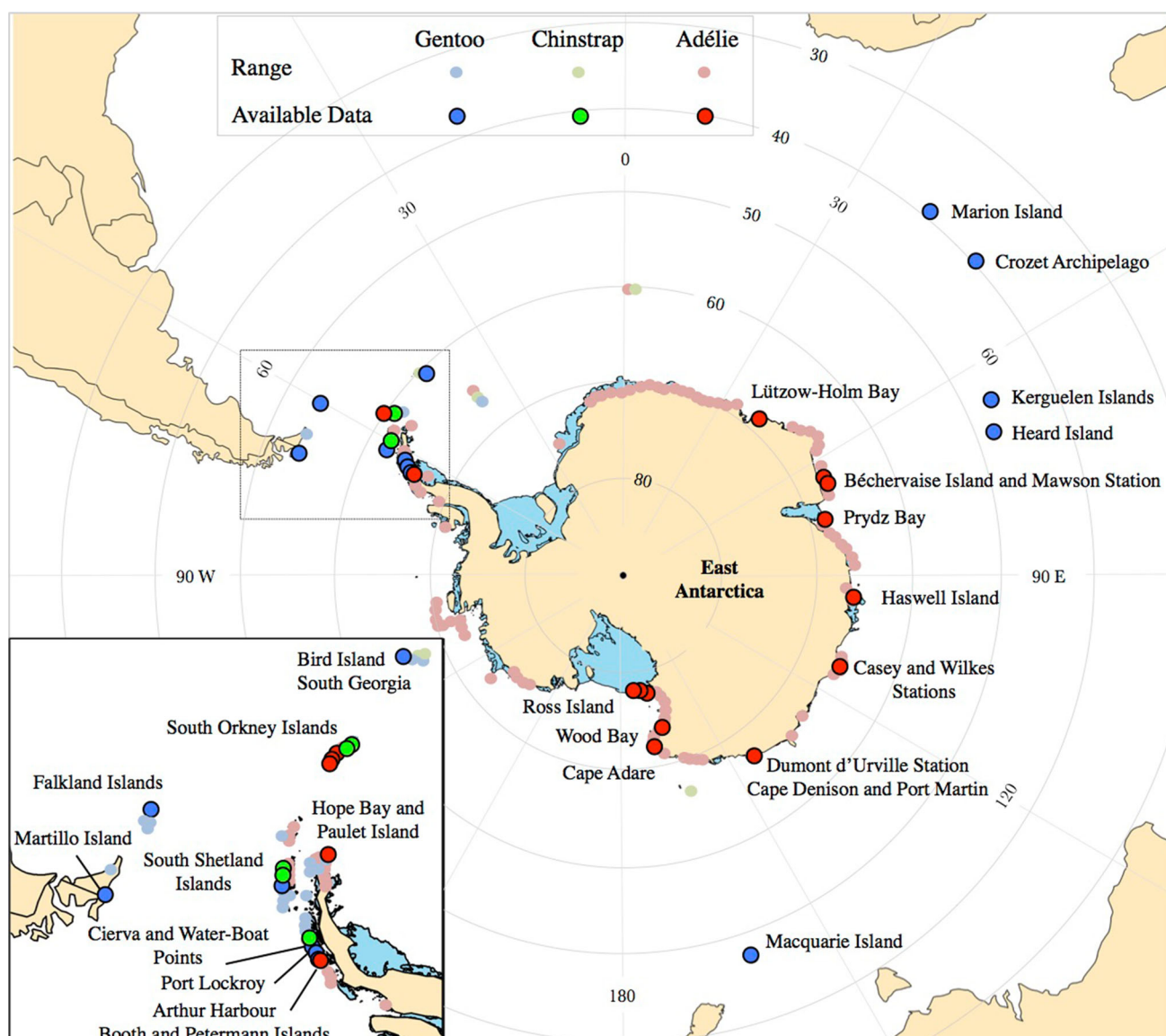


Fig. 3 Map of sites with published phenology dates for all three *Pygoscelis* penguin species. Ranges adapted from (Borboroglu and Boersma 2013) and (Polito et al. 2011). See Table 1 for citations

Chinstraps, 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 1-year study at Water-boat point on the WAP; Bagshawe 1938; Table 1), leaving gaps in our understanding of phenology of chinstraps inhabiting the Antarctic Peninsula and sub-Antarctic islands (Fig. 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 et al. 1987). Chinstraps often displace Adélie 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 Adélie return to the colony and begin the breeding process earlier, and 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 3 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 et al. 1987), suggesting that chinstraps with delayed breeding cycles benefit from reduced interspecies 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.

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 et al. 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; 1991; Viñuela et al. 1996).

The timing of the next phase, courtship, is rarely studied but typically lasts 8–22 days in Adélie (Davis 1982b;

Emmerson et al. 2011); 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 1990a; 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 et al. 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 1990a) 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 1990a; 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 et al. 1987; Bost and Clobert 1992). Subsequently, colonies located farther north are known to experience lower breeding success than their southern counterparts (Williams 1990; Bost and Jouventin 1990a; 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 Adélie, 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 a classic 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 influence 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 (e.g. Adélie) are able to adjust foraging duration and prey species without adjusting phenology (Beaulieu et al. 2010). In Adélie, 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 (Spurr 1975; Conroy et al. 1975a; Lishman 1985; Bost and Jouventin 1990a; 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 1968; 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 1968; Marchant and Higgins 1990), while chinstraps and gentoos are known to moult exclusively before winter departure (Bost and Jouventin 1990a; 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 1990a; Croxall and Davis 1999). In addition, non-breeders begin their moult earlier in the season in Adélies (Penney and Emlen 1967), 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 and Boersma 1996; Davis et al. 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 1990a), 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.

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 (Fig. 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 (Fig. 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 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 Adélie. 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 (Fig. 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, Fig. 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 be 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). 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 et al. 1984; Trivelpiece et al. 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 et al. 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.

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Appendix 1: Terminology for each phase within the annual cycle of *Pygoscelis* penguins. See below for citations supporting these definitions

1. 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.
2. Courtship: The time period when copulations are noted at the breeding site.
3. 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. These phases end when the second clutch is laid or, in the case of northern sub-Antarctic gentoo populations, when the two-egg clutch is relaid. The phase is sometimes expressed as a range of dates.
4. 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.
5. 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.
6. 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.
7. 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.
8. Chick moult: The time period in which chicks moult their down feathers, beginning with the first visible moulting individual and ending with the last.
9. Adult moult: The time period in which adults moult their feathers, beginning with the first visible moulting individual and ending with the last.
10. 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.
11. 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.

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