Plasticity and partitioning of foraging behaviours among and within sympatric *Pygoscelis* penguin populations

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Abstract

Central-place foragers, such as breeding seabirds, need to adjust their foraging behaviours in response to the growth and development of their offspring. As a result, they need to return to their nests regularly. These breeding constraints limit their foraging ranges. In the Southern Ocean, sympatrically breeding penguin species often have overlapping foraging ranges and niches that may lead to competition. Interspecific (between species) and intraspecific (within species) competition are important processes that may shape the foraging behaviours of penguins. However, competition pressure may vary with changes in environmental conditions across several scales (e.g. between years or within breeding seasons as a function of fluctuating central-place foraging constraints).

This dissertation aimed to determine how the foraging behaviour of two closely related and co-occurring seabird species - chinstrap (*Pygoscelis antarcticus*) and gentoo (*P. papua*) penguins – differ among and within populations. I analysed high-resolution location (GPS) and dive data from 221 individuals breeding at two sites (Nelson Island and Kopaitic Island) in the West Antarctic Peninsula during the 2018/19 austral summer. These sites are characterised by different environmental conditions and penguin population sizes, two factors that may influence foraging behaviours and niche partitioning. The first chapter includes a general background of the study and the dissertation's aims and objectives. In the second chapter, I investigated intraspecific phenotypic plasticity of foraging behaviours among and within these penguin populations. In a subsequent chapter, I quantified foraging niche separation and identified factors that modify interspecific niche separation between chinstrap and gentoo penguins at the two sites.

To test whether penguins exhibited phenotypic plasticity in foraging trip distances and duration, and to partition diving behaviours (e.g. maximum dive depth) among and within populations, I fitted a series of generalized linear mixed-effects models with species, site, breeding stage (incubation, brood and crèche) and environmental variables as covariates. In addition to comparing foraging behaviours between populations, my analysis quantified how individuals differed in their average behavioural expression using a repeatability index. I used an autocorrelated kernel density estimate approach to quantify space use and overlap between species as breeding transitioned from incubation to brood and crèche.

Sites greatly influenced both species' foraging behaviours, with the Kopaitic Island environment being a colder, saltier environment which may be more suitable for foraging. Chinstrap penguins, which prey almost exclusively on Antarctic krill *(Euphausia superba)*, along with gentoo penguins (dietary generalists) showed plasticity in foraging trip and dive behaviours between sites and breeding stages. During brood and crèche, chinstrap penguins contracted their foraging ranges and dived deeper, increasing niche overlap and opportunity for interspecific competition with gentoo penguins. Foraging niche overlap was influenced by site-specific environmental conditions. For example, warmer sea-surface temperatures (which correlate with increased diving depths) and shallower bathymetry (which limits diving depth) at Nelson Island reduced opportunity for niche separation between the two species, especially during the brood and crèche stages of the breeding season.

My results show that chinstrap and gentoo penguin foraging behaviours are plastic depending on site and breeding stage. Furthermore, my results show that seasonal changes in central-place foraging constraints and environmental conditions can modulate niche separation between these co-occurring species. A continuation in climate change (e.g. further warming sea temperatures) in this region of the Southern Ocean is expected to impact penguin prey distribution, which will likely lead to changes in foraging behaviour and niche overlap of chinstrap and gentoo penguins. While chinstrap and gentoo penguins may adjust their foraging behaviour to adapt to changing environmental conditions, these changes may have consequences for population dynamics and the future distribution and abundance of these species.

Keywords

Antarctic Peninsula, bio-logging, central-place foraging, diving, foraging behaviours, intraspecific competition, interspecific competition, individual repeatability, niche partitioning, phenotypic plasticity, penguins, sympatric, seabirds

Disclaimer

Each of the research chapters in this dissertation was structured and written with a scientific publication in mind. The chapters are, therefore, written concisely and independently presented. For this reason, some repetition of information related to method sections and references occurs. References are listed at the end of each chapter. Supplementary materials for Chapter 2 and Chapter 3 are given at the end of the document.

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Plagiarism Declaration

I, … Leandri de Kock … understand the meaning of plagiarism and declare that all of the work in the dissertation is my own. Each contribution in this dissertation from the works of other researchers has been cited and referenced.

Signature

Date Signed by candidate

10 April 2024

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Chapter 1: General Introduction

1. Southern Ocean and climate change

Global ocean sea surface temperatures (SST) increased during the 20th century and are predicted to rise further due to ongoing climate change, increasing overall climate variability (Constable et al. 2014; IPCC 2022). Physical oceanographic changes due to climate change are particularly pronounced in the Southern Ocean, especially the Antarctic Peninsula region (Stammerjohn et al. 2008; Kerr et al. 2018). For example, near-surface temperatures in west Antarctica have increased by 2.4℃ since 1958 (Vaughan et al. 2003; Bromwich et al. 2013). SST determine primary productivity and the current warming of global oceans can decrease ocean productivity (Behrenfeld et al. 2006). Over the last two decades, phytoplankton have declined in the Antarctic Peninsula region (Montes-Hugo et al. 2009), along with regional fluctuation in the biomass of a keystone species, Antarctic krill (*Euphausia superba*; hereafter krill) (Atkinson et al. 2019; but see Cox et al. 2019; Krafft et al. 2021). Around 70% of krill stocks occur in the Southwest Atlantic sector of the Southern Ocean (Atkinson et al. 2009), one of the regions most affected by climate change (Rogers et al. 2020). Krill survive in temperatures ranging from -1.8°C to 5.5 °C (Tarling 2020), but optimal growth occurs at temperatures between 0.5 to 1.0 °C (Michael et al. 2021). Climate change, ocean warming and changes in ocean productivity may therefore change the abundance, distribution and community composition of lower trophic level species, such as krill, that may affect where, when and how marine predators such as fish, seabirds and mammals forage (Frederiksen et al. 2006; Durant et al. 2007; Cook et al. 2012).

2. Individual variation in foraging behaviours

Changes in climate and environmental conditions are not the only drivers leading to variation in the foraging behaviours of marine predators. Species' foraging distributions can be directly affected by competitive interactions. Competition is a symbiotic interaction for limited resources (in the form of food, territory, mates etc.) to survive. Competition may occur among individuals from the same species (intraspecific competition) or between different species (interspecific competition) (Pianka 1981).

Intraspecific competition is density-dependent meaning that population size will influence access to resources such as prey (Ballance et al. 2009). Assuming similar resource availability, at low population densities (small colonies), intraspecific competition for resources is low, but as population densities increase (colonies become larger) per capita resource availability decreases leading to higher competition for resources between conspecifics. Intraspecific competition may have significant impacts on resource availability, which could lead to differences in foraging behaviours at the individual- and population levels (Ceia and Ramos 2015). Intraspecific competition occurring between populations (e.g. at different sites) may be reduced when individuals from each population make use of site-specific foraging behaviours (e.g. Baylis et al. 2008; Masello et al. 2010; Wakefield et al. 2013; Baylis et al. 2018). Furthermore, individuals often exhibit different foraging behaviours within their colony to limit intraspecific competition (e.g. Bolnick et al. 2003; Ceia and Ramos 2015; Michelot et al. 2021). For example, biologging data from sea lions (*Zalophus wollebaeki*) indicated that individuals from the same colony exhibited three different diving strategies (deep, intermediate and shallow diving) to reduce competition between conspecifics (Villegas-Amtmann et al. 2013).

Individual variation in marine predators' foraging strategies have been poorly studied until recently (e.g. (Lowther et al. 2012; Patrick et al. 2014; Potier et al. 2015; Wakefield et al. 2015; Hertel et al. 2020; Schwarz et al. 2021). Repeated measures taken over time may show that individuals can differ in their average expression of a behaviour (Dingemanse et al. 2010; Dingemanse and Dochtermann 2013) (Figure 1). When behaviours between individuals differ, it is because an individual only expresses a limited range of behaviours that is present in the population, often referred to as an individual's 'behavioural type' or 'personality' (Dall et al. 2004; Bell et al. 2009). Behavioural types vary between individuals in the population (Figure 1a). An individual's foraging behaviour type will then determine how narrow an individual's foraging niche is compared to their population's foraging niche (Figure 1a). 'Repeatability' estimates can be calculated to quantify the extent of individual variation of behaviours within a population (Bell et al. 2009). Quantifying variation in foraging behaviours at the individual level is important because the individual behaviours might determine a species' population-level response to changes within their environment (e.g. change in food availability) (Bolnick et al. 2003; Dingemanse and Wolf 2013). Detection of individual or site-specific specialisations in marine predators has potential implications for the understanding of the ecological and evolutionary processes (Mitchell et al. 2021) and is thus useful for conservation management programs.

3. Geographic variation in foraging behaviours

Individual variation in foraging behaviour is common between populations of the same species that forage in contrasting environmental conditions (e.g. Patrick et al. 2014). Geographically separate animal populations often experience markedly different environmental conditions (e.g. temperatures) that may lead to inter-population variation in resource use (e.g. Tremblay and Cherel 2003; Hückstädt et al. 2016; Handley et al. 2017; Howells et al. 2017; Bolton et al. 2019; Patterson et al. 2022). Many studies assume that behaviours will be similar between populations (Foster 1999) and behavioural variations over geographic regions are often not explicitly considered. Often, foraging behaviour and habitat use variations within species are quantified for a single population or among populations that are relatively close to each other (e.g. Hinke et al. 2007; Kokubun et al. 2010; Ito et al. 2021) and are assumed to be the same for all populations of the species. This is a problematic assumption to make because the available foraging habitat will often vary between populations.

It is thus important to study how marine predators specialise their behaviours within their unique foraging areas to predict variations in their responses to environmental changes. Some marine predators, for example, exhibit varying site-specific foraging strategies in contrasting marine environments (e.g. Baylis et al. 2018; Olmastroni et al. 2020; Elley et al. 2022). Inter-population variation in foraging behaviours (e.g. site-specific responses) reflects phenotypic plasticity: the ability of a genotype to express diverse phenotypes in response to different environmental conditions (Houston and McNamara 1992) (Figure 1b). Phenotypic plasticity in foraging behaviours is an important trait which allows species to adapt to the varying environments they encounter across their distributional range (Grémillet and Charmantier 2010), to increase fitness over short and long time scales (Vedder et al. 2013) (Figure 1b). Site-specific foraging behaviours enable species to respond to changes in their environment that occur due to the potential effects of climate change and fisheries (e.g. Michelot et al. 2021). A better understanding of how the foraging behaviours differ between populations that occupy varying environments may help to predict responses to continuing anthropogenic-driven changes in the environment. In contrast, failure to account for phenotypic plasticity would likely result in inconsistent behavioural predictions of a species.

Figure from O’Dea et al. 2022:
Unifying individual differences in personality, predictability and plasticity: A practical guide.

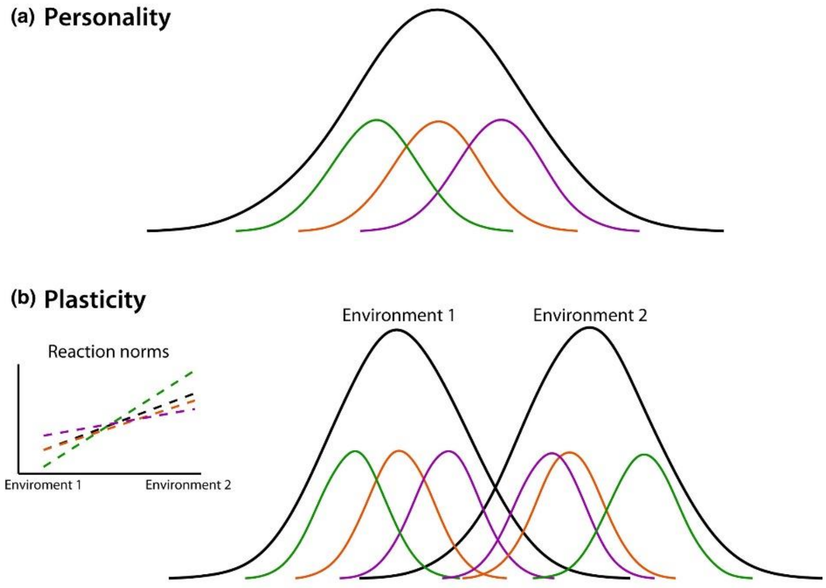

Figure 1. An illustration of two types of individual differences for a behavioural trait. The black curve represents the normal distribution of behaviour in a population. The smaller coloured curves represent the distribution of behaviour expressed by an individual within the population. (A) ‘Personality’ (also known as behavioural type) represents differences in the mean behavioural expression within an individual. B) ‘Plasticity’ represents how individual behavioural expressions differ between individuals due to changes in the environment. As the environments change from 1 to environment 2, the average behavioural expression of the population (shown by the black curve) shifts to the right. Additionally, individual averages (shown by the coloured curves) also shift to the right with varying extents (varying slopes in reaction norms). This figure was extracted from O’Dea et al. 2022.

4. Seabirds show variability in their foraging behaviour

Seabirds that occur in the polar regions show high geographical variability in their foraging behaviours (Tremblay and Cherel 2003; Meyer et al. 2017). Seabirds need to cope with highly variable conditions at both their nesting sites and their foraging areas (Forcada and Trathan 2009). Furthermore, foraging behaviours within seabird populations may differ between breeding stages as a function of central-place foraging constraints (Jessopp et al. 2020). Central-place foraging adults need to adjust their foraging behaviours according to the needs of their eggs and chicks (Ydenberg et al. 1994). During incubation, one parent fasts and keeps the eggs safe and warm, while the other forages. After a few days, parents switch incubation roles. During the brood and crèche (i.e. chick-rearing) stages, adults need to meet the increased energetic demands of their growing chicks while attempting to maintain their body condition (Ricklefs 1983; Bevan et al. 2002; Ropert-Coudert et al. 2004).

Seabirds have different mechanisms to balance their own energy needs with those of their chicks. During the chick-rearing stage, seabirds increase their foraging efforts to meet the increasing demands of their chicks (Ratcliffe et al. 2018). For example, seabirds perform shorter foraging trips (Ichii et al. 2007; Poupart et al. 2017) or alternate between long and short foraging trips (Saraux et al. 2011), modify their diving behaviour (Booth et al. 2018; Ito et al. 2021), switch to a more energy-dense prey diet (Handley et al. 2017), and are more active at night (Charrassin et al. 1998). As soon as chicks are large enough to be left alone on their nest (e.g. albatross chicks) or stay together in groups (e.g. crèche stage in penguins), both parents forage simultaneously to supply their chicks with an adequate amount of food to grow.

5. Interspecific competition between sympatric seabirds

In the Southern Ocean, sympatrically breeding seabird species (with similar life histories) often have overlapping foraging ranges and niches that may lead to interspecific competition (Lee et al. 2021; Fromant et al. 2022). Interspecific competition is a form of competition between different species for limited resources (e.g. food or shelter). Competition is an important process that may shape species foraging behaviours and has become important to understand in a climate change context (Urban et al. 2016). This is because climate change alters the physical environment, which directly affects how species and prey are distributed (Harley et al. 2006). When resources become limited, competition may further lead to breeding failure and population decline (Begon et al. 2009).

Neighbouring colonies of seabirds who depend on similar prey resources are likely to have overlapping foraging ranges that may lead to interspecific competition (Masello et al. 2010). Sympatric seabird species can only co-occur at breeding sites if their foraging behaviours are in different niche axes (Pianka 1981). Niche theory suggests that predators separate their foraging in space, time and diet composition to reduce competition (e.g. Navarro et al. 2013; Quillfeldt et al. 2020). Seabirds often partition their trophic niches: through slight differences in their breeding phenology (Clewlow et al. 2019), by adjusting their diets with supplements of other prey types (Petalas et al. 2021), by foraging at different times of the day (Wilson 2010), and by foraging at different depths (Cimino et al. 2016).

The extent of niche partitioning and the potential for interspecific competition may vary with changes in environmental conditions across several scales. For example, in land breeding seabirds, niche overlap may intensify as foraging areas of several sympatric seabirds contract during the breeding season, and moderate during non-breeding periods (e.g. winter) when many of these seabirds migrate away from the breeding colonies and increase their foraging ranges (Bost, et al. 2009b; McCutcheon et al. 2011). Changing environmental conditions that affect prey availability (e.g. primary and secondary productivity) may also alter the degree of niche separation across seasons, years or sites (Saba et al. 2014; Steinberg et al. 2015; Bonnet-Lebrun et al. 2021; Narvestad et al. 2022). At a finer scale, niche partitioning can vary between breeding stages as a function of central-place foraging constraints (Fromant et al. 2022). The foraging ranges of seabirds often differ between breeding stages as adults adjust their foraging behaviours (e.g. trip distances and duration) according to the needs of their offspring (Ydenberg et al. 1994; Shaffer et al. 2003). Breeding adults typically increase their provisioning rate as chicks grow older. Consequently, foraging trips become shorter during the chick-rearing stages (Ichii et al. 2007; Poupart et al. 2017). Thus, increased spatial overlap during the chick-rearing stages may lead to more competitive interactions between species as they compete for similar resources in smaller foraging areas (Kappes et al. 2015).

6. Pygoscelid penguins – the brush-tailed penguins

Brush-tailed penguins (genus *Pygoscelis*) are good examples of central-place foraging seabirds whose foraging range and behaviours depend on their breeding stage (Ropert-Coudert et al. 2004; Phillips et al. 2021). All *Pygoscelis* penguins include Antarctic krill in their diets (Volkman et al. 1980; Trivelpiece et al. 1987) and thus their foraging behaviours are highly dependent on krill distribution. In the Antarctic Peninsula region, Adélie penguins (*Pygoscelis adeliae*), Chinstrap penguins (*Pygoscelis antarcticus*) and Gentoo penguins (*Pygoscelis papua*) coexist on numerous islands. Studies have shown that these species partition their trophic niches along multiple dimensions by having slight differences in their body shape and size (Gorman et al. 2014), their breeding phenology (Clewlow et al. 2019), space use (horizontal- Wilson 2010 and vertical- Cimino et al. 2016), diet (e.g. gentoo penguins supplement their krill diet with fish and other prey; Kokubun et al. 2010; Polito et al. 2015) and temporal behaviours (Miller et al. 2010) to avoid competition.

The diet-niche overlap between *Pygoscelis* penguins has been extensively studied as it could lead to interspecific competition where species breed sympatrically. *Pygoscelis* penguin population trends (especially chinstrap penguins) may be driven by krill availability in the Antarctic Peninsula (Herman et al. 2017; Youngflesh et al. 2017). Krill biomass is affected by climate change (Flores et al. 2012), increased krill fishing (Trathan et al. 2018) and the recovery of seal and whale populations which in turn will affect penguin dynamics (Trivelpiece et al. 2011; Hinke et al. 2017). Recent estimates of *Pygoscelis* penguin abundance in the Antarctic Peninsula and South Shetland Island region revealed roughly 795,900 pairs of Adélie (Lynch and LaRue 2014), 2.1 million pairs of Chinstrap (Strycker et al. 2020) and 127,320 pairs of Gentoo penguins (Herman et al. 2020). However, many of the estimates in the region were done decades ago and may have changed over recent years (Humphries et al. 2017).

In this study, I focus on the foraging behaviours of Chinstrap and Gentoo penguins. Both are species of 'least concern' in terms of global conservation assessments (Birdlife International 2019; Birdlife International 2020). Even so, their population dynamics remain uncertain with studies highlighting possible population increases or decreases at monitored sites (Sander et al. 2007; Lynch et al. 2012; Naveen et al. 2012). During the last two decades, Chinstrap penguin population numbers have decreased while the Gentoo penguin population has increased regionally (in breeding colonies near the Antarctic Peninsula and the South Shetland Islands) (Forcada et al. 2006; Hinke et al. 2007; Carlini et al. 2009; Lynch et al. 2012; Strycker et al. 2020). A comparison of the foraging behaviours among and within both species in these regions may help explain their contrasting population trends.

6.1. Chinstrap penguins

Most Chinstrap penguin (hereafter chinstrap[s]) (Figure 2) breeding colonies are situated in the Antarctic Peninsula region, including the South Orkney-, South Sandwich- and South Georgia islands where krill is abundant. Several small chinstrap colonies are located in the Antarctic Peninsula region (Strycker et al. 2020) which is within CCAMLR Subarea 48.1 (see Figure 1, Meyer et al. 2020,). Here, chinstrap populations are declining while population trends in other regions (e.g. South Sandwich Islands) are stable (Lynch et al. 2012; Strycker et al. 2020).

Chinstraps are foraging specialists, feeding almost exclusively on krill (Kokubun et al. 2010; Miller et al. 2010). Chinstraps prefer to forage in open waters off the shelf where the bathymetry is deeper than 200 m (Kokubun et al. 2010; Miller et al. 2010). Most chinstraps in the Antarctic Peninsula and South Shetland Island regions show directed movement towards the shelf break where krill availability may be high (Warwick-Evans et al. 2022). Foraging trips can last anywhere between 3 hours to 7 days travelling up to 250 km away from the colony depending on the location and breeding stage (Lishman 1985; Trivelpiece et al. 1987; Warwick-Evans et al. 2018). Depending on their breeding stage, a common strategy for chinstraps is to have short daytime trips close to shore and long overnight trips to the shelf edge (Ichii et al. 2007; Miller et al. 2010). Chinstraps often forage in the pelagic zone, diving to midwater depths between 15 to 30 m (Wilson and Peters 1999; Miller and Trivelpiece 2008; Kokubun et al. 2010; Wilson 2010). Dives at these midwater depths lead to higher foraging efficiencies than shallower or deeper dives (Kokubun et al. 2010; Wilson 2010).

Figure 2. Chinstrap penguins can be identified by the narrow black stripe on their chin, their pink feet and black soles. Photo: Chris Oosthuizen.

6.2. Gentoo penguins

Gentoo penguins (hereafter gentoo[s]) (Figure 3) have a circumpolar distribution with breeding colonies located from the northern sub-Antarctic islands to the Antarctic Peninsula (Herman et al. 2020). The global population of gentoos is estimated to be approximately 432,144 breeding pairs (Herman et al. 2020). The gentoo population has increased by an estimated 23% along the West Antarctic Peninsula (WAP) since 2013 and now accounts for about 30% of the global population (Herman et al. 2020). In the WAP, gentoos often breed sympatrically with chinstraps and/or Adélie penguins (Woehler and Croxall 1997; Hinke et al. 2007; Wilson 2010).

Gentoos often restrict their foraging ranges to within 25 km of the colony during the breeding season (Kokubun et al. 2010; Wilson 2010). Because they forage close to shore, their travelling distances are often very similar between sites (Miller et al. 2010). Gentoos also restrict their feeding to mostly daylight hours (Wilson et al. 1996) and mean trip durations are between 7 to 12 hours (Miller et al. 2009). Gentoos are generalist predators feeding on a variety of prey types such as krill, fish and squid (Camprasse et al. 2017). Gentoo foraging strategies are known to vary temporally and geographically often depending on local conditions (Miller et al. 2009; Polito et al. 2015). In the WAP, gentoos feed mostly on krill with some supplementing their diet with fish (e.g. South Shetland Islands, Kokubun et al. 2010; Miller et al. 2010). Gentoos perform both benthic and pelagic dives, diving to mean depths of 30 to 90 m (Lescroël and Bost 2005; Miller et al. 2009; Kokubun et al. 2010). Gentoo penguins prefer to forage in on-shelf areas where bathymetry is < 200 m deep (Kokubun et al. 2010). Gentoos dive more efficiently when diving to the bottom (i.e. benthically) (Kokubun et al. 2010; Wilson 2010) where prey (e.g. benthic fish) are spatially predictable.

Figure 3. Gentoo penguin and chick. Gentoo penguins can be identified by the wide, white stripe that expands from their eyes to the top of their head and the orange-red bill. Photo: Chris Oosthuizen.

7. Studying penguin foraging behaviours in a changing environment

Penguins are viewed as 'sentinels' of the Southern Ocean because their foraging behaviours change with fluctuations in environmental conditions and prey availability (Frederiksen et al. 2007; Hazen et al. 2019; Handley et al. 2021). Similarly, brush-tailed penguins are vulnerable krill predators that are most sensitive to changes in krill availability and growth (as a result of climate change) (Klein et al. 2018). Climate change could create mismatches between predators and prey if predators cannot adapt their foraging behaviours quickly as prey availability and distribution change.

Seasonality effects (changes in environmental conditions within a breeding season) may modify niche partitioning between species depending on the breeding stage and therefore increase the opportunity for interspecific competition. The chinstrap and gentoo breeding season occurs during the austral summer (December to February) when sea ice decreases (Haas et al. 2001) and solar radiation increases causing nearshore waters to undergo major physical changes. Understanding the effects that environmental variability may have on penguin foraging behaviour is important (Burrows et al. 2011). Physical oceanographic parameters such as currents (Bost, et al. 2009a), bathymetry (Chiaradia et al. 2007) and sea ice (Watanuki et al. 1997) may further restrict penguin foraging ranges during the breeding season. For example, changes in SST (due to increased solar radiation or weather storms) within a breeding season may affect krill distribution leading to changes in chinstraps foraging behaviour (e.g. Salmerón et al. 2023). Bathymetry is an important predictor which describes the preferred habitats of seabirds (Soanes et al. 2016), especially chinstrap penguins (Warwick-Evans et al. 2018). Thus, the environmental characteristics of a site may have a large influence on how species interact with each other near the colony. But changes in environmental conditions may also lead to changes in the distribution of prey (Pelletier et al. 2012), which ultimately influences the distribution and diving behaviours (e.g. diving depths) of predators (Le Guen et al. 2018; Salmerón et al. 2023). For example, the amount of solar light available may change within the breeding season influencing krill availability and the at-sea distribution and dive behaviours of penguins (Trathan and Hill 2016). Antarctic krill exhibit diel vertical migration patterns that can be closely linked to fluctuating insolation (Friedlaender et al. 2013).

Recent developments in biologging instruments led to GPS-depth data loggers that can provide information on the at-sea foraging habits of marine predators (Ryan et al. 2004; Ropert-Coudert et al. 2012). Penguins who often have small foraging ranges can now easily be tracked using these devices. Additionally, diving depth is also measured with these instruments allowing researchers to quantify dive behaviour in diving marine predators (e.g. Mattern et al. 2007). These advances allow researchers to measure a range of foraging behaviour parameters (e.g. trip duration, maximum distance from the colony, maximum dive depth and dive duration) simultaneously at finer scales in space and time for individuals and populations (Hussey et al. 2015).

With chinstraps and gentoos sharing similar diets in the Antarctic Peninsula, I would expect that these species utilize similar depth ranges to forage on krill which may lead to overlapping foraging niches. High-resolution location (GPS) and dive data from 221 breeding individuals were collected during the 2018/19 austral summer. It is easy to deploy biologging devices on penguins during the breeding season because they regularly travel between foraging in the ocean and their nests on land (Orians and Pearson 1979). Penguins nest in large colonies and thus it is easy to collect data from multiple individuals to study inter-individual variation in behaviours because all individuals are exposed to the same environmental conditions and have access to the same resources (Ceia and Ramos 2015; Camprasse et al. 2017).

8. Study area- foraging in the Antarctic Peninsula

The high-resolution location and dive data were collected at two sites (Nelson Island and Kopaitic Island) in the WAP where chinstraps and gentoos breed sympatrically (Figure 4). Nelson Island (part of the South Shetland Island group) and Kopaitic Island (part of the Duroch Island group) are approximately 131 km apart, on opposite sides of the Bransfield Strait (Figure 4). Both study sites are within the CCAMLR Subarea 48.1 (Antarctic Peninsula and the South Shetland Islands), which includes suitable habitat for breeding krill predators who forage on krill during the summer months (Trathan and Hill 2016; Warwick-Evans et al. 2022). The water masses of the WAP region are nutrient-rich, promoting primary production and supporting large numbers of krill predators (seals, whales and seabirds) and krill stocks in summer (Ducklow et al. 2006). Nelson Island, for example, is part of a recognized Antarctic Specially Protected Area (ASPA 133) due to the abundance of seabird species, including one of the largest chinstrap colonies in Antarctica.

The Bransfield Strait is a relatively deep channel that separates the South Shetland Islands from the tip of the Antarctic Peninsula. The waters in the Bransfield Strait are important spawning and nursery grounds for krill (Atkinson et al. 2004). Relatively warm, fresh water from the Antarctic Circumpolar Current flows into the northern Bransfield Strait from the Bellinghausen Sea and Drake Passage, circulating the South Shetland Islands (where Nelson Island is situated, Figure 4) (Renner et al. 2012; Ruiz-Barlett et al. 2018). In contrast, cold, saline water flows into the Bransfield Strait from the continental shelf of the Weddell Sea near the tip of the Antarctic Peninsula (where Kopaitic Island is situated, Figure 4) (Sangrà, et al. 2011; Renner et al. 2012; Ruiz-Barlett et al. 2018). The contrasting hydrographic conditions around each island generate physical gradients across the Bransfield Strait, which may lead to plasticity in the foraging behaviour of penguins.

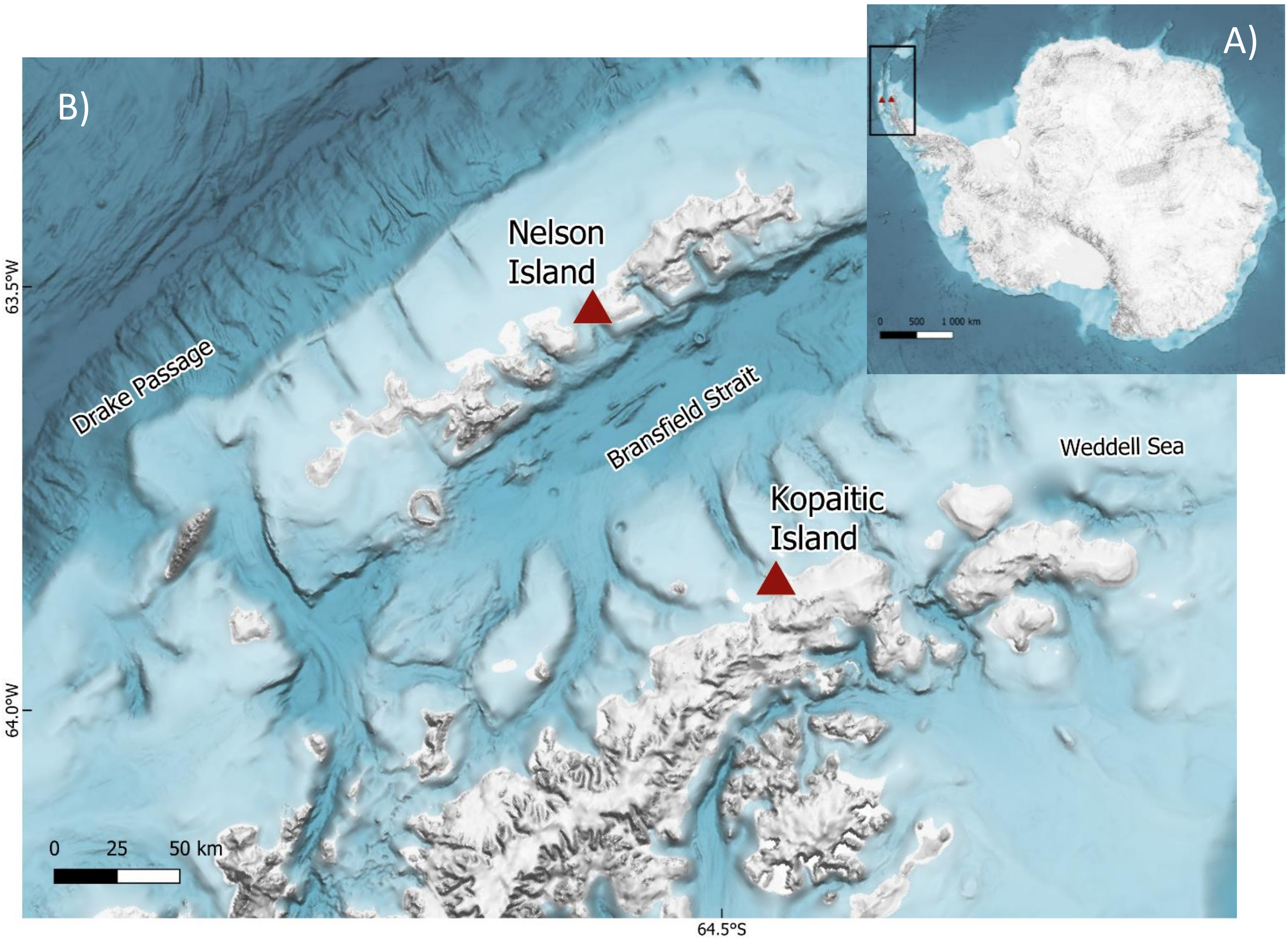

Figure 4. Study area. A) Location of the West Antarctic Peninsula (WAP) (black box) relative to Antarctica. B) Island locations (red triangles) where tags were deployed on both chinstrap and gentoo penguins.

My study sites have differing environmental conditions and penguin population sizes, two factors that may influence foraging behaviours and niche partitioning among and within populations. The most recent population estimates report 3347 gentoo breeding pairs and 89685 chinstrap breeding pairs at Nelson Island while at Kopaitic Island some 3400 gentoos and 9400 chinstraps pairs breed each year (Woehler 1993; Silva et al. 1998). Thus, the chinstrap breeding population size differs tenfold between the two sites which may lead to differences in foraging behaviours among chinstrap populations (e.g. as in northern gannet, *Morus bassanus*, colonies; Wakefield et al. 2013). Furthermore, spatial and behavioural information from chinstrap and gentoo penguins has been widely recommended to be used for conservation management practices to define potentially important bird and biodiversity areas in Antarctica (Handley et al. 2021).

Following an extensive literature review, I have identified gaps in the literature that I aim to address in this study. While studies have highlighted temporal variations in the foraging behaviour of penguins at a single location, few have concurrently investigated the geographic variation in foraging behaviour across distant populations to determine how foraging behaviour may vary at large spatial scales where environmental conditions differ. Even fewer studies have focused on quantifying and comparing the individual variation of foraging behaviours among and within populations of the same species. Several studies have compared foraging behaviours between sympatrically breeding chinstraps and gentoos (i.e. related to interspecific competition), but few have compared this relationship between sites simultaneously during one breeding season. Furthermore, few studies have investigated the effects of environmental changes and life-history constraints on niche partitioning. Previous studies investigating niche partitioning between chinstraps and gentoos have only focused on diet and horizontal space use (e.g. overlapping foraging areas), ignoring dive behaviour, a critical component of their foraging behaviour given that penguins are diving predators.

9. Dissertation aims and objectives

This dissertation aims to determine how the foraging behaviour of two closely related and co-occurring seabird species – chinstrap and gentoo penguins - differ among and within populations. In the first research chapter, I investigate the phenotypic plasticity of foraging behaviours among and within these penguin populations. The objectives for this chapter include (1) characterising the environmental space (i.e. habitat characteristics) used by chinstrap and gentoo penguins during the breeding season at both islands and comparing (2) foraging trip- and (3) diving behaviours among- and within populations of chinstraps and gentoos, respectively. I also investigate (4) how breeding stage and time of day influence their foraging behaviours. By combining foraging trip- and dive behaviours, I tested whether site-specific foraging behaviours exist within species.

In a subsequent chapter, I quantify foraging niche partitioning and identify the factors that modify niche partitioning between chinstrap and gentoo penguins. The specific aims were to (1) quantify how spatial overlap changes as the breeding season progresses from incubation to brood and crèche, and (2) assess how central-place foraging constraints and seasonal changes in environmental conditions can modify niche separation between these species. I address these aims by (1) describing changes in the spatial distribution of foraging penguins over the breeding season and (2) modelling foraging dive depth as a function of breeding stage and environmental covariates.

10. References

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Chapter 2: Phenotypic plasticity of foraging behaviours in chinstrap and gentoo penguins in the Antarctic Peninsula

1. Abstract

Geographically separate conspecifics often experience markedly different ecological conditions that may lead to inter-population variation in resource use, reflecting phenotypic plasticity. Furthermore, intraspecific competition may have impacts on resource availability, leading to differences in foraging behaviours at the individual- and population levels. In this chapter, I compared phenotypic plasticity of foraging behaviours among and within populations of two closely related and co-occurring seabird species - chinstrap (*Pygoscelis antarcticus*) and gentoo (*P. papua*) penguins. I analysed location (GPS) and dive data from 221 individuals breeding at two sites (Nelson Island and Kopaitic Island) on opposite sides of the Bransfield Strait, West Antarctic Peninsula. I fitted a series of linear mixed-effects models to test whether species exhibited plasticity in their foraging trip- and diving behaviours. Fitted models included individual identity as a random effect and my analysis also estimated a repeatability index to quantify individual variation in behaviour. Environmental differences at the study sites (e.g. colder, saltier water around Kopaitic Island) were associated with plasticity in both species' foraging behaviours. Chinstrap penguins generally performed longer foraging trips at Nelson Island, which decreased during chick-rearing. Chinstrap penguin diving followed a diel pattern at both sites, but individuals generally dived deeper at Kopaitic Island. Gentoo penguins at Kopaitic Island foraged further, dived deeper and showed more plasticity between dives than at Nelson Island. My results emphasize that multiple sites need to be included when studying the foraging behaviour of penguin populations to account for phenotypic plasticity in various environmental conditions.

Keywords

Diving, environmental space, foraging behaviours, individual repeatability, phenotypic plasticity

2. Introduction

The foraging behaviours of marine predators influence prey population dynamics and ecological interactions (Carroll et al. 2017). Geographically separate conspecifics often experience markedly different ecological conditions that may lead to inter-population variation in resource use (Bolton et al. 2019; Patterson et al. 2022). Inter-population variation in foraging behaviours reflects phenotypic plasticity: the ability of a genotype to express diverse phenotypes in response to different environmental conditions (Houston and McNamara 1992). Phenotypic plasticity in foraging behaviours is an important trait allowing species to adapt to the varying environments they encounter across their distributional range (Grémillet and Charmantier 2010), to increase fitness over short and long time scales (Vedder et al. 2013). Having a better understanding of how foraging behaviours differ among populations that occupy diverse environments is crucial for predicting their responses to the ongoing anthropogenic-driven changes in the environment. In contrast, failure to consider phenotypic plasticity is likely to result in inconsistent behavioural predictions of a species.

Environmental conditions and phenotypic plasticity are not the only drivers leading to variation in foraging behaviours. Intraspecific competition (i.e., competition among members of the population) may also have significant impacts on resource availability, which could lead to differences in foraging behaviours at the individual- and population levels (Ceia and Ramos 2015). Individuals often exhibit variations in foraging behaviours (i.e. differ in their average expression of a behaviour) to reduce intraspecific competition within their colony (Bolnick et al. 2003; Dingemanse et al. 2010; Dingemanse and Dochtermann 2013). For example, biologging data from sea lions (*Zalophus wollebaeki*) indicate that individuals from the same colony exhibit three different diving strategies (deep, intermediate and shallow diving) to reduce competition between conspecifics (Villegas-Amtmann et al. 2013). Individual differences usually occur because an individual only expresses a limited range of a behaviour that is present within the population, often referred to as an individual's 'behavioural type' (Dall et al. 2004; Bell et al. 2009). An individual's behavioural type then varies from other individuals in the population (O'Dea et al. 2022). Inter-individual variation in foraging strategies has been poorly studied until recently (e.g. Lowther et al. 2012; Patrick et al. 2014; Potier et al. 2015; Wakefield et al. 2015; Hertel et al. 2020; Schwarz et al. 2021).

Central place foraging marine predators (e.g. seabirds) are perfect for studying population- and individual- variation in foraging behaviour and habitat use because their foraging trips are limited as they regularly need to return to a central place (e.g. their nest) during the breeding season. The marine habitats associated with the short foraging ranges of breeding seabirds may differ between colonies. For example, seabirds that occur in the highly variable Southern Ocean often show high geographical variability in their foraging behaviours (Tremblay and Cherel 2003; Pinaud and Weimerskirch 2007; Grémillet and Charmantier 2010; Sala et al. 2014). Consequently, seabirds are often considered to be indicator species of the environment because their foraging behaviours change with fluctuations in the environment and prey availability across a variable habitat (Bestley et al. 2020).

Penguins, who show phenotypic plasticity in their foraging behaviours, are especially sensitive to changes in climate and prey distributions (e.g. Dehnhard et al. 2016; Camprasse, et al. 2017b; Michelot et al. 2021). Brush-tailed penguins (genus *Pygoscelis*) breeding in colonies distributed across the Antarctic Peninsula are good models to study the effect of environmental variations on the plasticity of foraging behaviours among and within populations. Their diet is heavily dependent on Antarctic krill (*Euphausia superba,* hereafter krill) (Hinke et al. 2007; Panasiuk et al. 2020) which are sensitive to changes in environmental conditions (Hill et al. 2013; Atkinson et al. 2019). In this study, I focus on chinstrap penguins (*Pygoscelis antarcticus,* hereafter chinstraps) and gentoo penguins (*Pygoscelis papua,* hereafter gentoos) who have contrasting population trends (Lynch, et al. 2012b). During the last two decades, population trends show that chinstrap populations are declining while gentoo populations are increasing around the Western Antarctic Peninsula (WAP) (Lynch et al. 2012b). Both species are of 'least concern' in terms of specific global conservation assessments (Birdlife International 2019; Birdlife International 2020). Even so, their population dynamics remain uncertain and predictions on how environmental changes may affect their future behaviour and survival, will be important for conservation actions.

Chinstraps are specialist predators feeding almost exclusively on krill (Kokubun et al. 2010; Miller et al. 2010). Chinstraps mostly breed on islands in the Antarctic Peninsula region where krill is abundant (approximately 2.1 million breeding pairs; Strycker et al. 2020). Chinstraps tend to forage off-shelf in open waters where the bathymetry is deeper than 200 m (Kokubun et al. 2010). Their foraging efficiency (foraging success depending on total foraging time) is highest at midwater depths (typically between 15 to 30 m) where they perform pelagic dives (Miller and Trivelpiece 2008; Kokubun et al. 2010; Wilson 2010). In contrast, gentoos are generalist predators that exhibit plastic foraging behaviours when feeding on different prey types (krill, fish and squid; Lescroël et al. 2004) in different regions (Camprasse, et al. 2017a). Gentoos have a circumpolar breeding distribution with breeding colonies located from the northern sub-Antarctic islands to the Antarctic Peninsula (approximately 432,144 breeding pairs; Herman et al. 2020). Gentoos often restrict their foraging ranges to within 25 km of the colony during the breeding season (Kokubun et al. 2010; Wilson 2010). They prefer to forage in areas where bathymetry is shallower than 200 m and often perform benthic and pelagic dives, diving to mean depths of 30 to 90 m (Lescroël and Bost 2005; Miller et al. 2009; Kokubun et al. 2010).

In this study, I compare plasticity in the foraging behaviour of chinstrap and gentoo populations at two islands in the WAP (Figure 1). My study took place at Nelson Island (part of the South Shetland Island group) and Kopaitic Island (part of the Duroch Island group) which are approximately 131 km apart, on opposite sides of the Bransfield Strait. The Bransfield Strait is a relatively deep channel that separates the South Shetland Islands from the tip of the Antarctic Peninsula. Relatively warm, fresh water flows into the northern Bransfield Strait from the Bellinghausen Sea and Drake Passage, circulating the South Shetland Islands (where Nelson Island is situated) (Renner et al. 2012). In contrast, cold, saline water flows into the Bransfield Strait from the continental shelf of the Weddell Sea near the tip of the Antarctic Peninsula (where Kopaitic Island is situated) (Sangrà et al. 2011; Ruiz-Barlett et al. 2018). The contrasting hydrographic conditions around each island generate physical gradients across the Bransfield Strait, which may lead to plasticity in the foraging behaviour of marine predators such as penguins.

The main aim of this chapter was to investigate whether chinstraps and gentoos breeding at Nelson Island and Kopaitic Island exhibit phenotypic plasticity of foraging behaviours among and within populations. To achieve this, habitat use and foraging trip- and dive behaviours of both species were characterised using biologging data. Few studies have focused on quantifying and comparing the individual variation of foraging behaviours within a species at multiple sites over the same breeding season. To study inter-individual phenotypic plasticity, I estimated the repeatability in foraging trip- and dive behaviours. My specific goals were to 1) characterise the environmental space (i.e. habitat characteristics) used by chinstrap and gentoo penguins during the breeding season at both islands and compare 2) foraging trip- and 3) diving behaviours among- and within populations of chinstraps and gentoos, respectively. I also investigated 4) how breeding stage and time of day influence their foraging behaviours. I hypothesized that krill specialists (chinstraps) and dietary generalists (gentoos), will show contrasting levels of behavioural plasticity in foraging stages, with specialists displaying less plasticity.

3. Methods

3.1 Tag deployments

Axy-Trek Marine tags (https://www.technosmart.eu) with integrated GPS, pressure (depth) and temperature sensors were deployed on adult breeding chinstrap and gentoo penguins through all stages (incubation, brood and crèche; December 2018 to February 2019) of the breeding season at Kopaitic Island and Nelson Island in the WAP, Antarctica (Figure 1) (Supplement 1). At Kopaitic Island, tags were deployed on the north-eastern aspect of the island (where all breeding colonies are located). At Nelson Island, deployments were made in colonies on the northern, western and southern aspects of Harmony Point, to capture potential variation in preferred foraging regions.

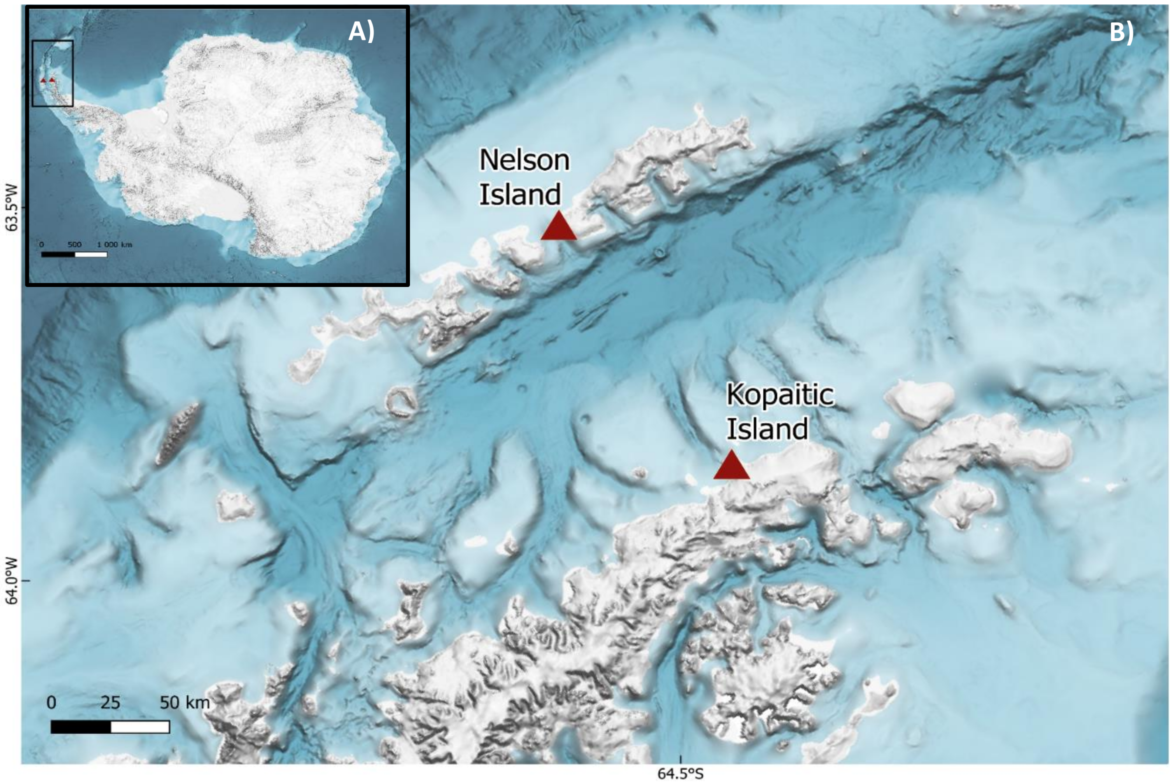

Figure 1. Study area. A) The West Antarctic Peninsula (black box). B) Island locations (red triangles) where tags were deployed on both chinstraps and gentoos.

Adult penguins who switched incubation or chick-rearing (brood and crèche) duties with their partners and were about to leave the colony on a foraging trip were caught (either by hand or net), weighed and briefly restrained (less than 10 minutes) for tag deployment. Tags were attached to the central dorsal region of the back using Tesa tape and cyanoacrylate glue (Loctite 401®) (Wilson et al. 1997). Penguins were tracked for 5.7 ± 2.5 days (mean ± standard deviation), on average, before tags were retrieved. Given the short deployment duration and small size of the tags (40 x 20 x 8 mm), I expect that any potential negative effects from tag attachment will be minor and of short duration (Evans et al. 2020).

3.2 Tag data processing

Tag data were processed and analysed in R version 4.2.1 (R Core Team 2022). Please see my GitHub repository (https://github.com/Leandri3/PhenotypicPenguins) for examples of all the R scripts used in the data analysis. Tags were programmed to record GPS locations every four minutes at Nelson Island and every second at Kopaitic Island which were subsequently resampled to 30-second intervals to reduce computing time. All tags recorded temperature and depth every second.

I obtained 221 data sets with location and dive data at sea (Chinstraps: Kopaitic = 62, Nelson = 93; Gentoos = Kopaitic = 35, Nelson = 31) (Supplement 1). I split GPS tracks into separate foraging trips using diving profiles and distance to colony plots. Foraging trips started when a penguin first dived and ended when diving stopped, and the penguin was near the colony of deployment. GPS locations on land near the breeding colony were removed so that only the at-sea locations could be used for subsequent analyses. To remove sporadic location errors, locations were filtered based on speed, distance and angle using the 'trip' package (Sumner et al. 2011), assuming a maximum travel speed of 15 km/h. For each foraging trip, I calculated trip duration (hr), distance travelled (km) and maximum distance from the colony (km) with the 'geosphere' package (Hijmans et al. 2017).

Dive data were analysed using the 'diveMove' package (Luque 2007). The 'calibrateDepth' function in the 'diveMove' package takes the TDR recorded observations, automatically detects dives, and assigns dive activities and -phases according to criteria such as time and speed. A depth threshold of 5m was used to define dives and to exclude surface and near-surface behaviours. The dive data were zero-offset-calibrated using the 'filter' function in 'diveMove'. Zero-offset calibration corrects for drifts in TDR device pressure and noise in depth measurements. The 'filter' function implements a smoothing/filtering mechanism where running quantiles can be recursively applied to depth measurements (Luque and Fried 2011). Dive phases are then assigned depending on changes in vertical rate and depth. For each dive, the function 'diveStats' was used to calculate various summary statistics such as maximum depth, bottom time and dive duration. Dive duration included the total time of all the phases of a dive, while bottom time was calculated based on the duration of the bottom phase of the dive. The maximum dive depth of each dive was also recorded. Dives with durations longer than 10 minutes were removed as I considered these to be infrequent recording errors.

I used the '*crawlWrap*' function from the 'MomentuHMM' package (McClintock and Michelot 2018) to predict the location of each dive from the irregularly spaced GPS locations. This function calculates the step lengths and turning angles made by an animal and fits a continuous-time correlated random walk (CTCRW) model (Johnson et al. 2008), whereafter locations at specific time steps (the start point of each dive) were predicted. In the CTCRW model, I specified location errors around GPS points by assuming a 50 m isotropic error ellipse (McClintock and Michelot 2018).

For each predicted dive location, the solar elevation angle (degrees above the horizon) at the start of a dive was calculated using the 'maptools' package (Bivand et al. 2022). The time-of-day of each dive was then defined as either day (solar elevation > 0°) or twilight (solar elevation between 0° and -12°). No dives occurred during astronomical twilight (solar elevations between -12° and -18°) or at 'night' (solar elevations <-18°).

3.3 Utilisation distributions

I calculated utilisation distributions (UDs) from dive locations to quantify the extent of space use of chinstraps and gentoos and to characterise the environmental space that penguins from Kopaitic- and Nelson Islands encountered. I calculated 50% kernel UDs (representing core foraging areas) and 95% kernel UDs (representing home ranges) using the 'adehabitatHR' package (Calenge 2011). The kernel smoothing parameter (*h)* was set to 7 km. This was the average spatial scale at which area-restricted search behaviours occurred according to first passage time analysis (I used the '*findScale'* function in the 'Track2KBA' package; Lascelles et al. 2016; Beal et al. 2021) (Supplement 2). UDs were calculated separately for the incubation and chick-rearing stages of the breeding season for each island and species.

3.4 Classification of diving behaviour

I assumed that penguin diving behaviours could be classified into three different classes: 'foraging dives' and deep or shallow 'non-foraging dives'. Prey are often pursued and captured during the bottom phase of a dive (Bost et al. 2007; Phillips et al. 2021). Therefore, dives were grouped based on similarities in bottom time, maximum depth and dive residuals (Bestley et al. 2015) (Supplement 3) using an Expectation Maximization (EM) algorithm (Dempster et al. 1977; McLachlan and Krishnan 1997; Chimienti et al. 2016). This unsupervised, non-hierarchical clustering method fits Gaussian mixture models and calculates estimates with maximum likelihood from diving characteristics in two steps (E and M-step). The EM analysis was performed using the 'RMixMod' package (Lebret et al. 2015). The resulting clusters were visually checked and associated with a dive class which best represented my a priori expectations of dive behaviours (Supplement 3). I then limited subsequent analyses to foraging dives only. It should be kept in mind that even 'non-foraging' dives could contain important foraging information. However, the probability of foraging during such dives is lower. Penguins probably performed other activities such as travelling, exploring and searching for prey patches during such dives.

3.5 Characterising environmental space

Several variables that might affect the foraging behaviour of penguins in the Antarctic Peninsula were used to characterize and compare the environmental space in the home range of each population. I used a 1 km resolution raster to extract environmental variables from the 95% UD of each population during incubation and chick-rearing. For static covariates (bathymetry, slope and distance to shelf edge), values were extracted for each overlaying cell of the 95% polygon. For time-varying covariates (sea surface temperature, salinity, horizontal- and vertical geostrophic currents) that change over the breeding season, I extracted the mean value of every overlaying cell in each breeding stage. See Supplement 4 for details on the environmental variables used. I used a principal component analysis (PCA) to identify the most important environmental variables that characterise each foraging distribution. Additionally, the dominant water masses occurring in each foraging distribution were identified using temperature-salinity plots created in Ocean Data Viewer 5.6.2 (ODV) (Schlitzer 2022).

3.6 Comparing foraging behaviours between populations and individuals

3.6.1 Foraging trip behaviours

I compared 1) foraging trip duration and 2) maximum trip distance from the colony between populations using linear mixed-effects models with a Gaussian error distribution. I tested the effects of site (Kopaitic Island or Nelson Island) and breeding stage (distinguishing either two categories (Incubation/Chick-rearing) or three (Incubation/Brood/Crèche) on the trip behaviours.

3.6.2 Foraging diving behaviours

I used generalized linear mixed models (GLMMs) to test the effects of site, breeding stage, and time-of-day (as categorical variable 'temporal' (Day or Twilight) or as a continuous covariate, 'solar elevation') as fixed effects on two different response variables. Firstly, I used maximum dive depth (obtained from the 'diveMove' analysis) as a response. Models of maximum dive depth were fitted using a gamma error distribution with a log link function to ensure that the predicted estimates were positive.

Second, I determined whether there was phenotypic plasticity in the foraging dive type (benthic or pelagic foraging). To determine dive type, I extracted the bathymetric depth at each dive location and calculated the proportion of the water column used in a dive, with dives classified as 'benthic' (0) if the dive exploited more than 80% of the water column. If maximum dive depth was less than 80% of the water column, the dive was classified as 'pelagic' (1). Models of foraging dive type were fitted with a binomial error distribution and a logit link function.

3.6.3 Model fitting

Linear mixed models were fitted using the 'lme4' package (Bates et al. 2015), and GLMMs were fitted using the 'glmmTMB' package (Brooks et al. 2017). All foraging trip and diving mixed-effects models included individual identity as random effect, allowing individuals' mean foraging behaviours to deviate from the population mean. In the GLMMs, an Ornstein-Uhlenbeck time-varying covariance structure was used to account for temporal autocorrelation between dives performed by an individual (Brooks et al. 2017). Models were fitted separately by species.

All models were fitted using maximum likelihood estimation (Zuur et al. 2009). Model selection was based on Akaike Information Criterion (AIC) scores. The model with the lowest AIC score represented the most parsimonious model in the set. When multiple models had similar support (ΔAIC < 2; though this is not a strict cut-off value), the model with the fewest parameters was selected (Burnham et al. 2011). I had few explanatory variables and therefore used an all-combinations model selection strategy (Doherty et al. 2012) via the '*dredge'* function in the 'MuMin' package (Bartoń 2022). Different representations of the same environmental variable (e.g., time-of-day as a categorical or continuous covariate) were never fitted in the same model. Inference was based on the most parsimonious models identified, refitted with Restricted maximum likelihood estimation to provide more reliable estimates of the variance components (Zuur et al. 2009). Linear mixed model fit was assessed using the 'performance' package (Lüdecke et al. 2021) and GLMM model fit was evaluated using the 'DHARMa' package (Hartig 2017). Models did not violate model fit assumptions. The total amount of variance explained was summarised with marginal (only fixed effects) and conditional (fixed and random effects) R^2 values (Nakagawa and Schielzeth 2013; Nakagawa et al. 2017).

3.6.4 Repeatability analysis

The random intercept of individual identity in mixed-effects models decomposed the variance of the response into between- and within-individual components (Dingemanse and Dochtermann 2013). Thus, in addition to comparing foraging behaviours between sites, my analysis quantified how individuals differed in their average behavioural expression (i.e. 'behavioural type') (Bell et al. 2009). I calculated 'repeatability' *(R)*, an index that measures the proportion of variation in behaviour that can be attributed to individual differences (i.e. the variance explained by animal identity divided by the total phenotypic variance) (Bell et al. 2009; Nakagawa and Schielzeth 2010). Trip and dive repeatability estimates were calculated with the 'performance' package (Lüdecke et al. 2021). Repeatability estimates range from 0 to 1. Repeatability scores close to 0 indicate either low inter-individual variation (i.e. little plasticity of behaviour between individuals) or high within-individual variation (high plasticity of individual behaviour) (Nakagawa and Schielzeth 2010). Following Michelot et al. 2021, repeatability was classified into three categories: low ($R < 0.25$), moderate ($0.25 < R < 0.5$) and high ($R > 0.5$). I report the adjusted repeatability ($R_{(adjusted)}$) which is calculated with the models including the fixed and random effects.

4. Results

4.1 Spatial distribution

Chinstraps at Nelson Island foraged in the Drake Passage and Bransfield Strait, while conspecifics at Kopaitic Island were limited to the Bransfield Strait (Figure 2A & B). Incubating chinstraps ranged over an area 14 times larger at Nelson Island than at Kopaitic Island (Figure 2A, Supplement 2). During chick-rearing, the home range sizes of both chinstrap populations decreased (Figure 2B, Supplement 2). This trend was not observed in gentoos, which foraged close to their breeding colonies at both sites with similar-sized home ranges during incubation and chick-rearing (Figure 2C & D; Supplement 2).

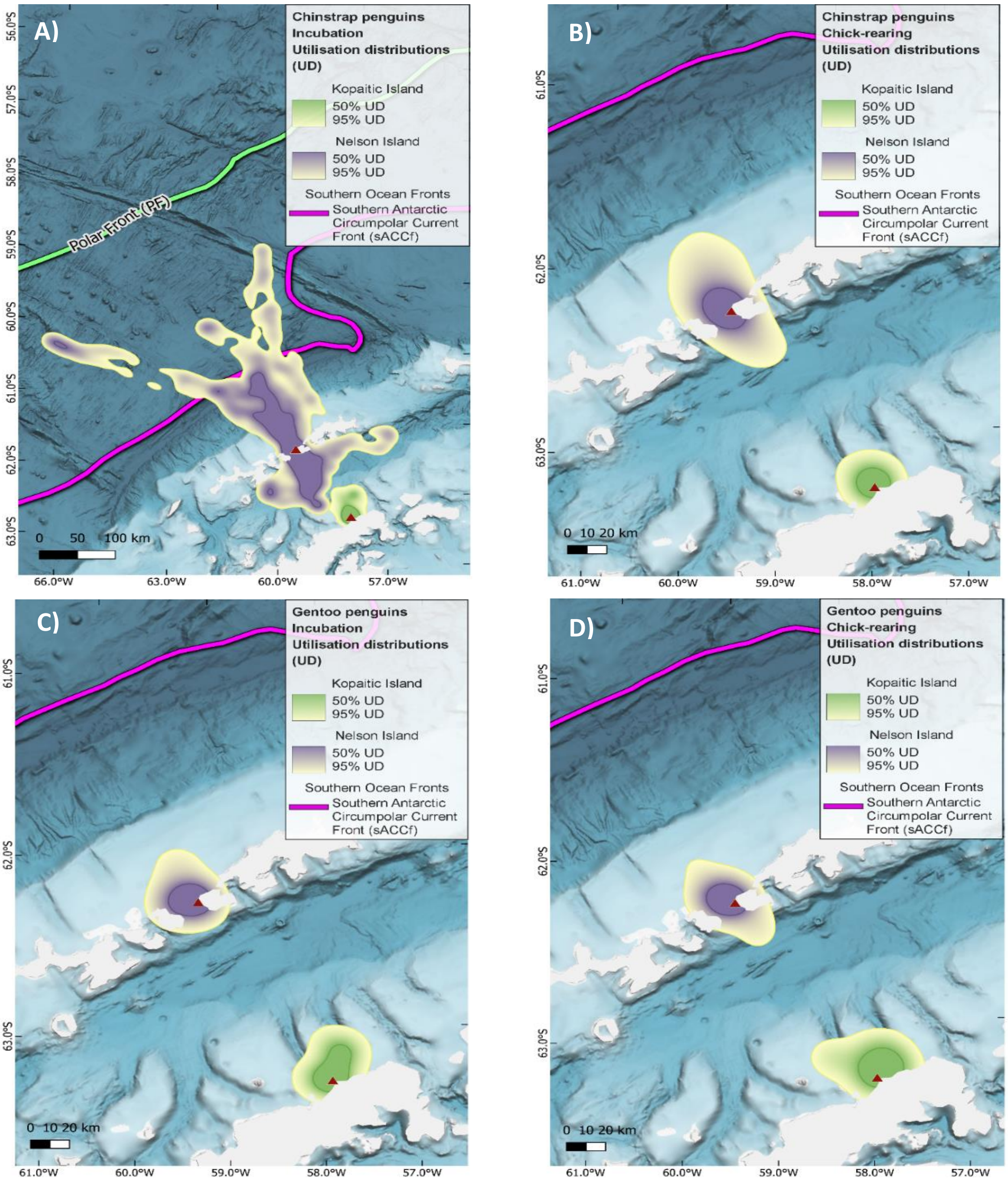

Figure 2. Spatial distribution of breeding chinstraps (A & B) and gentoo penguins (C & D) at Nelson Island (purple) and Kopaitic Island (green) between December 2018 and February 2019. A&B) 50% kernel (coloured line) and 95% kernel (yellow outline) utilisation distribution (UD) of chinstraps at Nelson Island (n = 93) and Kopaitic Island (n = 62) during A) incubation and B) chick-rearing stages. C&D) 50% kernel (coloured line) and 95% kernel (yellow outline) UDS of gentoos at Nelson Island (n = 31) and Kopaitic Island (n = 35) during C) incubation and D) chick-rearing stages. Bathymetry obtained from IBCSO v2 (Dorschel et al. 2022) is shown in the background. The solid pink line indicates the Southern Antarctic Circumpolar Current Front. The figure was prepared in QGIS v3.28 using Quantarctica3.2 software (Matsuoka et al. 2021).

4.2 Classification of diving behaviours

The EM algorithm clustered dives into three groups based on bottom time, maximum depth, and dive residuals (see Supplement 3 for the EM classification output). I assumed that dives with long bottom times, shallow to deep maximum depths and positive dive residuals corresponded to ‘foraging’ dives (Table 1). Approximately 45% of chinstrap dives and 66% of gentoo dives were classified as foraging dives (Table 1).

Table 1. Mean estimates (± standard deviation) of bottom time, dive residuals and maximum depth within the foraging and non-foraging diving behaviour groups for chinstrap and gentoo penguins breeding at Kopaitic- and Nelson Islands, respectively.

Chinstrap penguins				
Kopaitic Island				
Diving behaviour	Bottom time (s)	Dive residuals	Maximum depth (m)	Number of dives
Foraging	17.38 ± 9.96	0.1 ± 0.39	48.71 ± 22.82	12090 (45.55%)
Non-foraging - deep	0.47 ± 0.50	-0.03 ± 0.39	43.58 ± 23.89	12530 (47.21%)
Non-foraging - shallow	4.75 ± 5.63	-0.45 ± 0.30	7.03 ± 1.60	1921 (7.24%)
Total dives				26543
Nelson Island				
Diving behaviour	Bottom time (s)	Dive residuals	Maximum depth (m)	Number of dives
Foraging	18.98 ± 10.93	0.03 ± 0.44	36.49 ± 22.84	69332 (49.84%)
Non-foraging - deep	0.53 ± 0.50	0.04 ± 0.46	44.73 ± 21.75	49648 (35.69%)
Non-foraging - shallow	0.34 ± 0.49	-0.22 ± 0.41	8.45 ± 2.66	20129 (14.47%)
Total dives				139109

Gentoo penguins				
Kopaitic Island				
Diving behaviour	Bottom time (s)	Dive residuals	Maximum depth (m)	Number of dives
Foraging	40.77 ± 24.63	0.08 ± 0.36	66.48 ± 43.86	9051 (67.85%)
Non-foraging - deep	0.7 ± 0.49	-0.11 ± 0.38	70.33 ± 43.73	2563 (19.21%)
Non-foraging - shallow	0.29 ± 0.47	-0.25 ± 0.22	6.75 ± 1.44	1726 (12.94%)
Total dives				13340
Nelson Island				
Diving behaviour	Bottom time (s)	Dive residuals	Maximum depth (m)	Number of dives
Foraging	35.71 ± 19.57	0.11 ± 0.50	53.18 ± 23.02	18907 (66.91%)
Non-foraging - deep	0.61 ± 0.50	-0.14 ± 0.54	51.03 ± 29.53	6849 (24.24%)
Non-foraging - shallow	4.3 ± 5.86	-0.52 ± 0.30	6.59 ± 1.30	2501 (8.85%)
Total dives				28257

4.3. Environmental space of each island

Temperature-salinity plots showed clear differences in the predominant water masses encountered by penguins at each island. At Kopaitic Island, the dominant water mass in the upper 150 m (the part of the water column where most penguins forage) was Winter Water (Figure 3A). At Nelson Island, the dominant water mass in the upper 150 m was Antarctic Surface Water (Figure 3B).

Principal component analysis showed that sea surface temperature (SST) and salinity were the most important covariates to explain variability between the Kopaitic Island and Nelson Island environments. Both these covariates were negatively correlated and clearly separated the environmental spaces of each island during incubation and chick-rearing for both species (Figure 3). Chinstraps and gentoos breeding at Kopaitic Island foraged in colder (mean SST = -0.19 ± 0.29 °C) and saltier (mean salinity = 34.3 ± 0.03 PSU) water compared to those at Nelson Island (mean SST = 0.67 ± 0.32°C, mean salinity = 34.1 ± 0.20 PSU) (Figures 3C & D, see Supplement 4 for salinity results). As the breeding season progressed, SST gradually warmed (particularly at Nelson Island) due to an increase in solar radiation (Supplement 4). Gentoos foraged on and off the shelf at both islands while chinstraps mainly foraged off-shelf (where bathymetry was deeper than 200 m), particularly in incubation (Supplement 4). Supplement 4 provides additional PCA results and information on the evolution of the dominant water masses over the breeding season at each island.

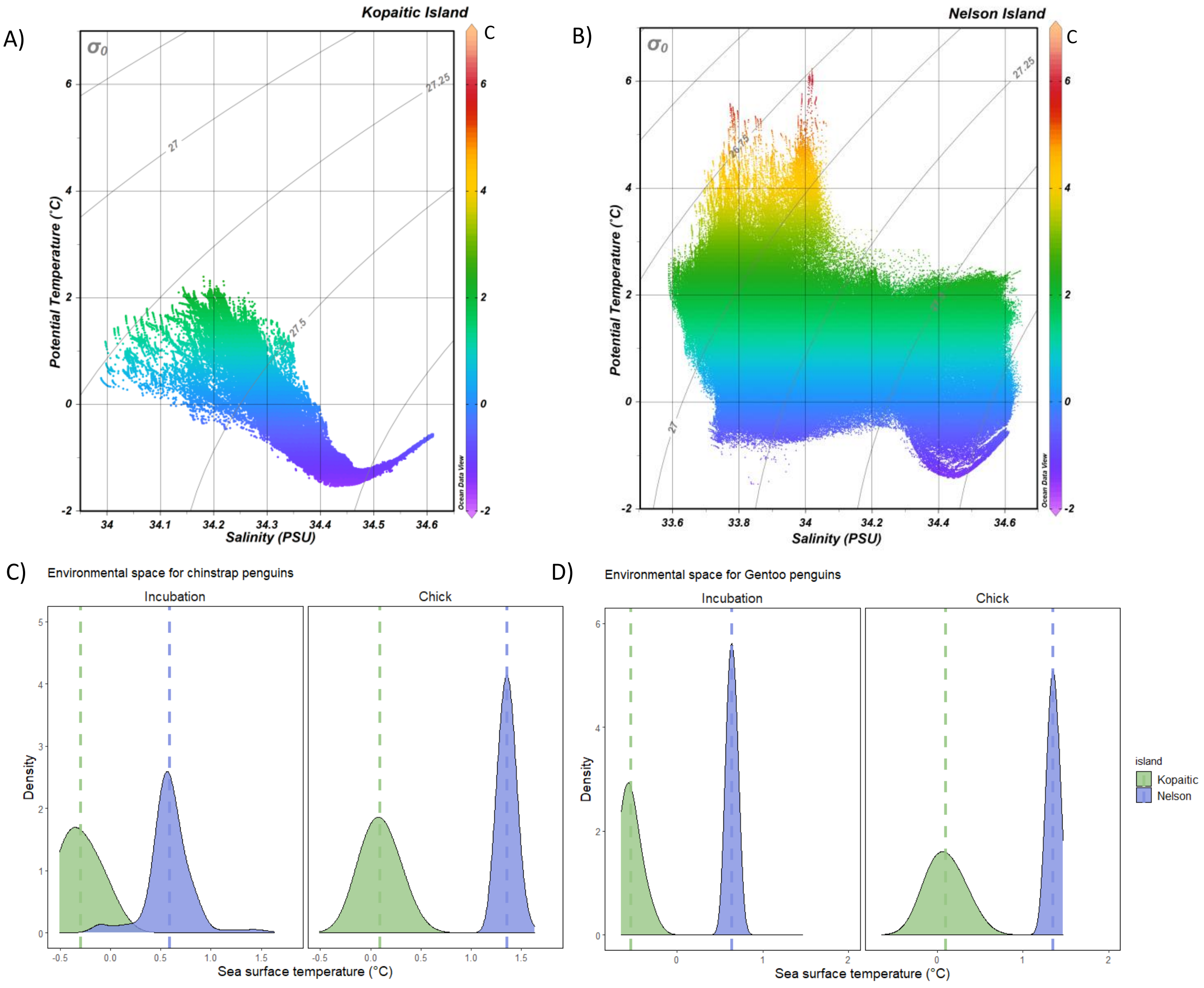

Figure 3. Characterising the environmental space in the home ranges of chinstrap and gentoo penguins breeding at Kopaitic and Nelson Island. A&B) Temperature-salinity plots for the upper 150 m of the water column around A) Kopaitic Island and B) Nelson Island based on the extracted salinity and potential temperature values from the home ranges of both species. The distinct water mass around A) Kopaitic Island was Winter Water (potential temperatures below 0°C and salinities between 34.0 and 34.44 g/kg; Jenkins and Jacobs 2008; Cape et al. 2019). B) At Nelson Island, Antarctic Surface Water was dominant (potential temperatures above 0°C and salinities between 33.7 to 34.5 g/kg; Cape et al. 2019). Points are coloured according to the potential temperatures measured. Vertical grey lines represent isopycnals which indicate the density of a layer. C&D) Sea surface temperature (SST) (˚C) differences at Kopaitic Island (green) and Nelson Island (blue). SST was highlighted as the most important environmental variable characterising the environment of C) chinstrap and D) gentoo penguins. The SST at Kopaitic Island was colder than the temperatures experienced at Nelson Island. The dashed lines represent the mean SST value measured for each site.

4.4. Chinstrap penguin foraging behaviour

Table 2. Summary of trip and dive parameters for chinstrap penguins tracked at Kopaitic- and Nelson Islands during the incubation and chick-rearing stages. Values are given as mean ± sd.

Chinstrap penguins				
Trip parameters	Incubation		Chick-rearing	
	Kopaitic (n = 28)	Nelson (n = 57)	Kopaitic (n = 198)	Nelson (n = 459)
Trip duration (hours)	17.76 ± 14.7	52.38 ± 51.8	5.01 ± 2.63	10.75 ± 6.34
Maximum distance (km)	11.3 ± 15.4	69.5 ± 80.9	5.25 ± 4.73	13.1 ± 26.5
Number of trips per individual*	1.57 ± 0.69	2.00 ± 1.25	2.97 ± 1.71	4.28 ± 2.48
Dive parameters (Foraging dives > 5m)	Incubation		Chick-rearing	
	Kopaitic (n=2991)	Nelson (n=21681)	Kopaitic (n=8833)	Nelson (n=46557)
Bottom time (s)	17.6 ± 9.78	18.5 ± 10.8	17.8 ± 9.78	19.7 ± 10.7
Dive duration (s)	78.4 ± 20.5	69.9 ± 28.6	86.1 ± 24	80.8 ± 28.2
Maximum depth (m)	39.7 ± 17.8	27.5 ± 20.1	51.9 ± 23.3	40.7 ± 22.9
Percentage of pelagic dives (%)	78.44	97.08	67.17	70.9

**The number of trips per individual is a function of trip duration and deployment duration*

4.4.1. Trip behaviours

Variation in foraging trip behaviours (n = 741) was best explained by an interaction of the fixed effects breeding stage (incubation/chick-rearing) and island (model selection results given in Supplement 5). Chinstraps from Nelson Island made longer foraging trips (duration and distance travelled) compared to those at Kopaitic Island (Table 2). These differences were most pronounced during incubation, when the foraging trips from Nelson Island were 46.88 hours longer and 72.59 km further, on average than at Kopaitic Island (Figure 4A). During chick-rearing, trip durations were similar between sites (lasting between ± 5 to 25 hours) (Figure 4A & B).

Together with the individual random effect, these variables explained a large part of the variation in trip duration ($R^2_{(conditional)}$ = 85.5%) and maximum distance ($R^2_{(conditional)}$ = 71.7%). The repeatability estimate of trip duration was high ($R_{(adjusted)}$ = 0.77) indicating low-within individual variation in foraging trip durations (Figure 4B). The foraging trip parameters were highly correlated (ρ = 0.79) and thus only results for trip duration are shown (see Supplement 5 for results of maximum distance).

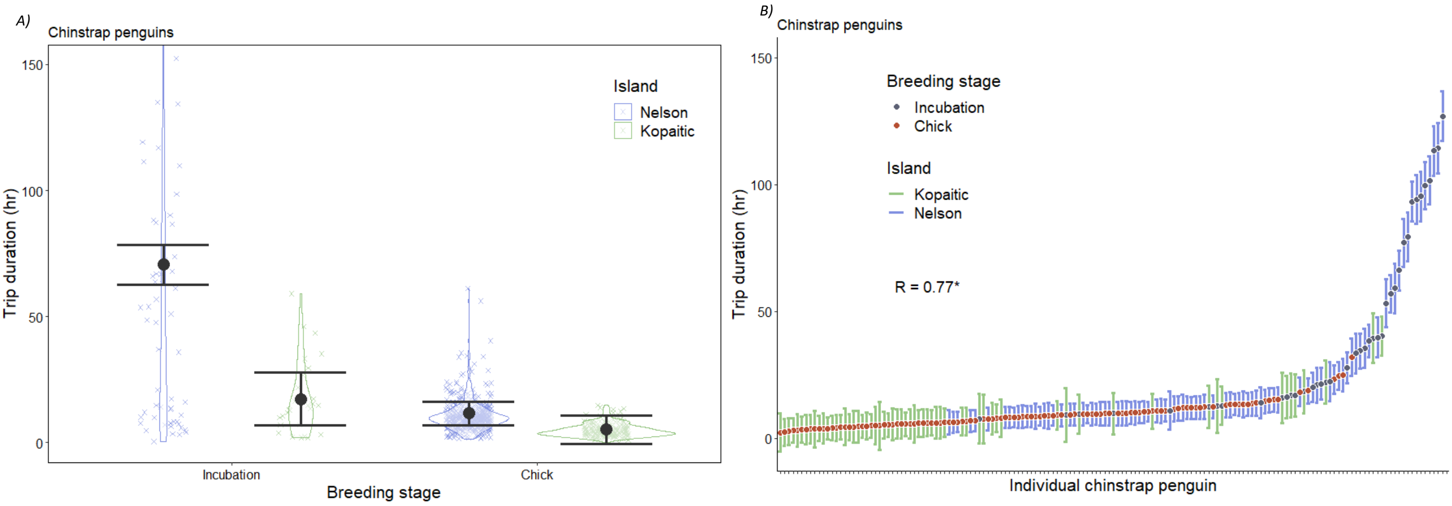

*Figure 4. A) Predicted mean foraging trip duration in hours (hr) for chinstraps breeding at Nelson Island (blue) and Kopaitic Island (green) during incubation and chick-rearing. The mean model estimates and 95% confidence intervals are shown in black. The observed data and violin plots that show the spread of the data are coloured by island. B) Plot of the individual behavioural types (i.e. random effects) of trip duration. The mean model estimates are coloured according to breeding stage (incubation = grey, chick-rearing = red), and 95% confidence intervals are coloured according to island. *R = Repeatability estimate.*

4.4.2. Dive behaviours

The mean maximum depth of chinstrap foraging dives varied by site, across breeding stages (incubation/brood/crèche) and according to the solar elevation ($R^2_{(conditional)}$ = 40.3%, model selection results in Supplement 5). The predicted mean maximum dive depths generally became deeper as solar elevation increased, except during crèche at Kopaitic Island where chinstrap dive depths became shallower as solar elevation increased (Figure 5A).

Differences in maximum depth were evident between stages. Chinstraps dived shallower during incubation compared to brood and crèche (Figures 5A & B). Interestingly, during brood, both populations concentrated their foraging dives at two different depths (Kopaitic Island: around ± 45 and 75 m, Nelson Island: around ± 10 and 50 m) (Figure 5A). Differences in maximum dive depth between sites may not be clear at the population level (Figure 5A) but at the individual level (Figure 5B) sites clustered to show that Kopaitic Island individuals dived deeper than Nelson Island individuals during each breeding stage even though there was a large overlap in mean depths. The repeatability estimate of maximum depth was low ($R_{(adjusted)}$ = 0.07) which indicates high within-individual variance (i.e. low consistency) in maximum diving depths relative to the between-individual variation (Figure 5B). Plasticity in maximum dive depths was therefore large within individuals (i.e. between dives). Even so, individual behavioural types for mean maximum dive depths were evident, ranging from 15 m to 40 m (Supplement 5).

The best model of foraging dive type (benthic/pelagic) included an interaction between the breeding stage (incubation/brood/crèche) and time-of-day (day, twilight) and an interaction between breeding stage and island as fixed effects ($R^2_{(conditional)}$ = 80.4%, Supplement 5). Chinstraps performed mostly pelagic foraging dives (> 67% of all dives) at both sites (Table 2), especially during twilight phases (Supplement 5). Predicting foraging dive type was more variable during daylight. Incubating chinstraps nearly always dived pelagically during the day at Nelson Island, but the probability of a daytime pelagic dive was lower at Kopaitic Island and during brood and crèche at Nelson Island (Supplement 5). The repeatability estimate for the foraging dive type models was high (*R(adjusted)* = 0.72) because individuals consistently performed pelagic dives (i.e. low within-individual variation in dive type) (Supplement 5).

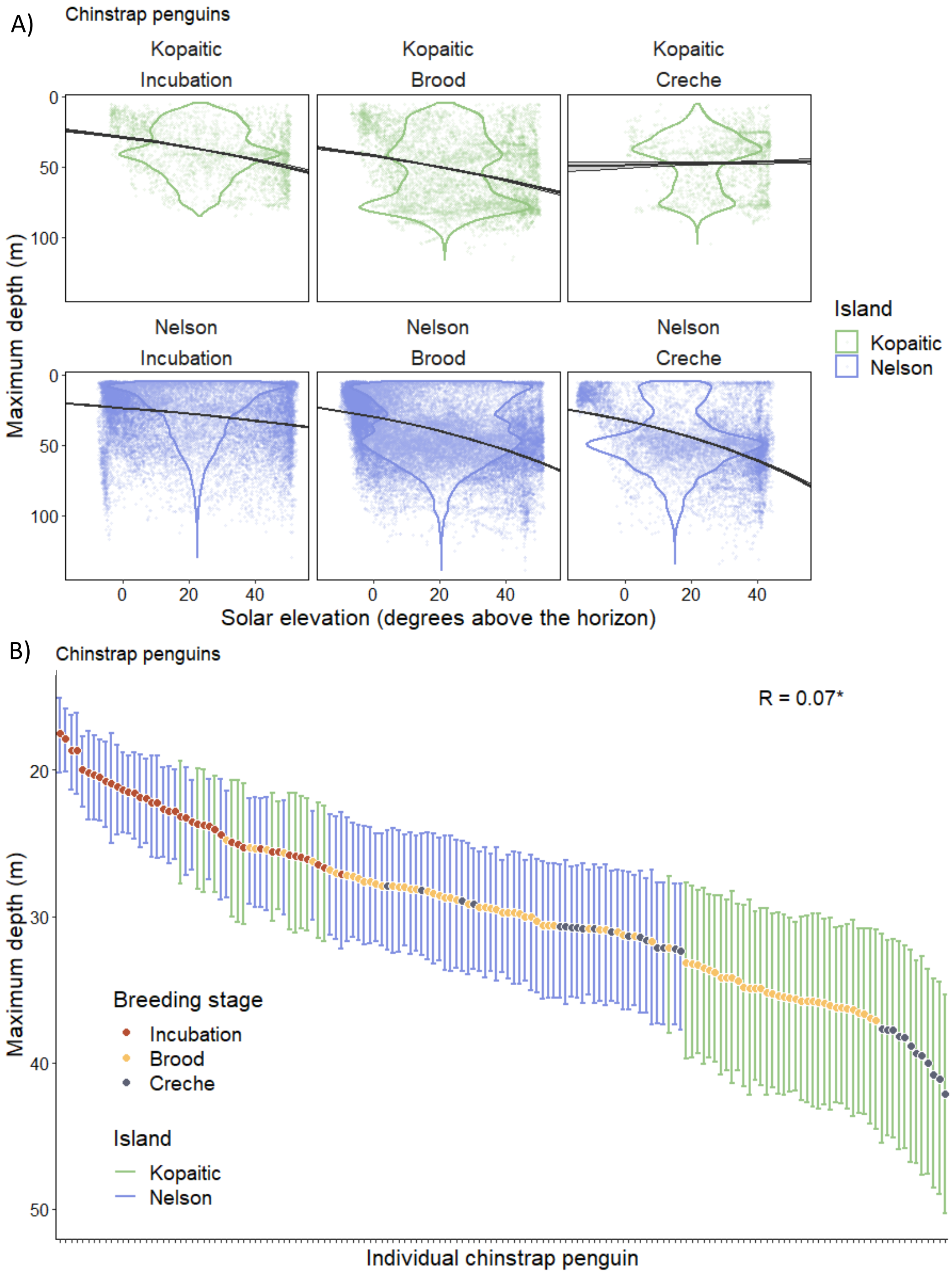

*Figure 5. A) Maximum dive depth of chinstrap penguins breeding at Kopaitic Island (green) and Nelson Island (blue) across all breeding stages. The mean model estimates and 95% confidence intervals are shown in black. The observed data and violin plots that show the spread of the data are coloured by island. B) Plot of the individual behavioural types (i.e. random effects) in maximum dive depth (m) for chinstrap penguins breeding at Kopaitic Island and Nelson Island. The mean model estimates are coloured according to breeding stage (incubation = red, brood = yellow and crèche = grey). The 95% confidence intervals are coloured by island populations. *R = Repeatability estimate*

4.5. Gentoo foraging behaviour

Table 3. Summary of trip and dive parameters for gentoo penguins tracked at Kopaitic Island and Nelson Islands during the incubation and chick-rearing stages. Values are given as mean ± sd.

Gentoo penguins				
Trip parameters	Incubation		Chick-rearing	
	Kopaitic (n = 13)	Nelson (n = 62)	Kopaitic (n = 97)	Nelson (n = 162)
Trip duration (hours)	10.91 ± 4.09	18.70 ± 26.4	9.24 ± 4.15	9.12 ± 4.33
Maximum distance (km)	10.2 ± 8.97	14.5 ± 29.9	18.4 ± 37.7	10.2 ± 7.22
Number of trips per individual*	1.92 ± 0.95	4.18 ± 2.81	2.38 ± 1.24	4.42 ± 2.58
Dive parameters (Foraging dives > 5m)	Incubation		Chick-rearing	
	Kopaitic (n = 1284)	Nelson (n = 7077)	Kopaitic (n = 7676)	Nelson (n = 11660)
Bottom time (s)	38.2 ± 22.2	36.3 ± 19.8	41.7 ± 24.7	35.8 ± 19.2
Dive duration (s)	139 ± 56.5	114 ± 36.6	133 ± 57.7	121 ± 29.1
Maximum depth (m)	78.7 ± 48	46.6 ± 22.8	64.7 ± 42.8	57.3 ± 22.1
Percentage of benthic dives (%)	30.45	58.06	50.98	57.26

**The number of trips per individual is a function of trip duration and deployment duration.*

4.5.1 Trip behaviours

Gentoos performed short foraging trips during incubation and chick-rearing at both sites (distances <18 km and <24 hours, on average; Table 3). However, model selection indicated that maximum trip distance varied by island ($R^2_{(conditional)}$ = 30%, Supplement 6). On average, conspecifics from Kopaitic Island travelled 4.11 km further from their colonies than those from Nelson Island (Figure 6A). Differences between sites were clear from the individual behavioural types for maximum trip distance (ranging from 6 to 20 km) where sites mostly clustered together (Figure 6B). The repeatability estimate was moderate ($R_{(adjusted)}$ = 0.26) indicating that variance in maximum trip distances was moderate within individuals.

An interaction between breeding stage (incubation/chick-rearing) and island best explained the variation in trip duration ($R^2_{(conditional)}$ = 66.5%, Supplement 6). Predicted mean trip durations were 8.58 hours longer at Nelson Island during incubation but were similar between populations during chick-rearing (Supplement 6). Repeatability of foraging trip duration was high within gentoo individuals (i.e. low within-individual variation) ($R_{(adjusted)}$ = 0.58) (Supplement 6). The trip parameters were positively correlated (ρ = 0.96) and only results for maximum distance are shown (see Supplement 6 for trip duration results).

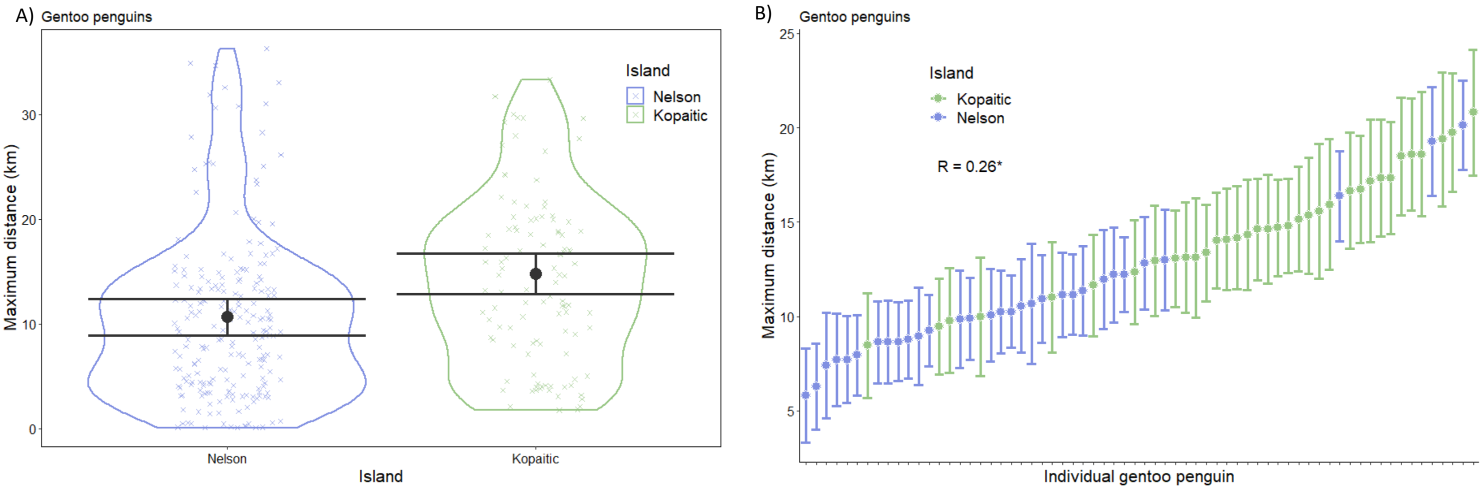

*Figure 6. A) Predicted mean foraging trip maximum distance (km) from the colony for gentoo penguins breeding at Nelson Island (blue) and Kopaitic Island (green). The mean model outputs and 95% confidence intervals are shown in black. The observed data and violin plots that show the spread of the data are coloured by island. B) Plot of the individual behavioural types (i.e. random effects) in maximum trip distance. The mean model estimates and 95% confidence intervals are coloured according to island. *R = Repeatability estimate.*

4.5.2. Dive behaviours

The mean maximum dive depths of gentoos varied by site, according to solar elevation and across breeding stages (incubation/brood/crèche) ($R^2_{(conditional)}$ = 43.9%, model selection results in Supplement 6). Gentoos at Nelson Island and Kopaitic Island mostly dived to maximum depths of 40-60 m and 50-100m, respectively, with individuals at Kopaitic Island generally diving deeper when solar elevation increased (Figure 7A). The repeatability in the diving depth behaviour of gentoos was moderately low ($R_{(adjusted)}$ = 0.29; Supplement 6). The moderately low repeatability estimate indicates moderate within-individual variance with plasticity in maximum diving depths being more evident for individuals from Kopaitic Island (who dived deeper) compared to those from Nelson Island (Supplement 6).

Gentoos adjusted their dive types according to their surrounding environments (site and solar elevation) and breeding stage. For example, during incubation, Kopaitic Island gentoos performed more pelagic foraging dives (>69% of all dives) compared to Nelson Island conspecifics at the same stage (>58% of all dives classified as benthic) (Table 3). Foraging dive type depended on separate two-way interactions between breeding stage (incubation/brood/crèche), island and solar elevation ($R^2_{(conditional)}$ = 67.3%, Supplement 6). At Nelson Island, the probability of benthic dives decreased as solar elevation increased (Figure 7B). Thus, at midday, Nelson Island gentoos were performing both benthic and pelagic foraging dives. The opposite trend was observed at Kopaitic Island, where penguins predominantly made pelagic dives during low solar elevations and benthic dives as solar elevation increased (Figure 7B). Overall, for most of the breeding season, individuals from Nelson Island were more likely to make benthic dives compared to Kopaitic Island individuals (Figure 7B). As the breeding season progressed, gentoos at Kopaitic Island changed their foraging dive strategy to include more benthic dives (Figure 7B). Dive-type behaviours of individuals were highly repeatable (i.e. low within-individual variation) ($R_{(adjusted)}$ = 0.65, Supplement 6) indicating that individuals continually used the same dive-type strategy when foraging.

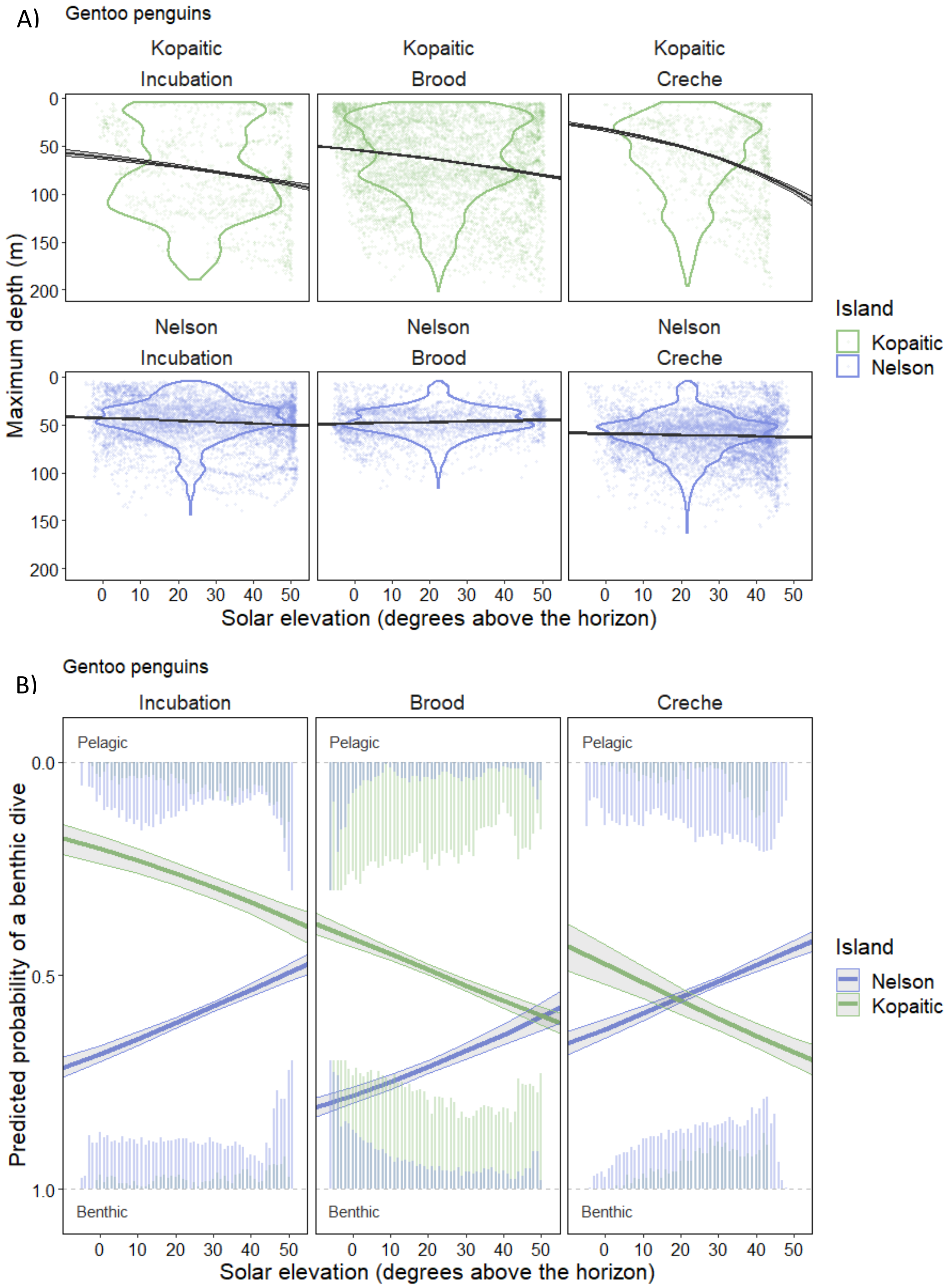

Figure 7. A) Maximum dive depth of gentoo penguins breeding at Kopaitic Island (green) and Nelson Island (blue) across all breeding stages. The mean model estimates and 95% confidence intervals are shown in black. The observed data and violin plots that show the spread of the data are coloured by island. B) Predicted probability of gentoos performing benthic foraging dives as the day progresses at Kopaitic Island and Nelson Island across all breeding stages. The mean model estimates ± 95% confidence intervals are coloured by island. The observed data are plotted as histograms (density divided into solar elevation bins) in the background to show the spread of the data.

5. Discussion

Both species showed between and within population phenotypic plasticity in different facets of their foraging behaviour. The degree of phenotypic plasticity depended on species, site, solar elevation and breeding stage. Sites greatly influenced species' foraging behaviours, with the Kopaitic Island environment being a colder, saltier environment which may be more suitable for foraging. Krill specialists (chinstraps), showed phenotypic plasticity in their foraging trip behaviours while dietary generalists (gentoos), showed phenotypic plasticity in both their foraging trip and dive behaviours between sites and breeding stages.

5.1 Two islands, two different environments

The environmental variables extracted from penguin foraging ranges showed clear differences in the physical characteristics of the water column (and therefore presumably in foraging conditions) around Kopaitic Island and Nelson Island. Around Nelson Island, the exploited habitat was dominated by a fresh, warm Antarctic Surface Water mass compared to the saline, cold Winter Water mass around Kopaitic Island. My results are consistent with what has been reported previously in the WAP (Sangrà et al. 2011; Renner et al. 2012; Ruiz-Barlett et al. 2018): cold water from the Weddell Sea dominates the southern part of the Bransfield Strait while warm and fresher water from the Bellinghausen Sea and the Drake Passage dominates the northern part of the Bransfield Strait and South Shetland Island region.

From the start of the breeding season, waters surrounding Nelson Island were warmer than at Kopaitic Island, and it kept getting warmer (up to 4℃) as the breeding season progressed (Supplement 4). Sea surface temperature is projected to become even warmer in the WAP due to projected climate change (Vaughan et al. 2003; Constable et al. 2014). The Antarctic Peninsula region is undergoing some of the fastest and strongest warming trends (Clarke et al. 2006; Schofield et al. 2010) which have a direct impact on the local marine fauna's breeding success and distribution (e.g. penguin species; Forcada et al. 2006; Lynch, et al. 2012a). SST-level changes affect the distribution and abundance of prey organisms such as fish, krill and squid (Bost et al. 2009) which are primary prey resources of gentoos and chinstraps. In areas of warm freshwater such as Nelson Island, krill tend to occur in smaller sizes and abundances (Lascara et al. 1999). Krill are especially sensitive to changes in SST levels with a narrow optimal growth temperature range between 0.5 and 1.0℃ (Atkinson et al. 2006; Michael et al. 2021). The SST conditions of a habitat would therefore influence prey availability (Behrenfeld et al. 2006) and thus the foraging behaviours of krill predators such as chinstraps and gentoos (Durant et al. 2007). Similarly, salinity differences have a substantial influence on the physiology, growth and distribution of marine organisms such as krill (Zhu et al. 2019).

Kopaitic Island might provide more suitable foraging conditions for penguins. The cold conditions of Kopaitic Island are optimal for krill growth (Michael et al. 2021) and are often associated with higher primary productivity (Arrigo et al. 2008) which results in improved foraging conditions for predators and thus requires shorter foraging distances. In my study, Kopaitic Island chinstraps travelled much shorter foraging distances than their conspecifics at Nelson Island even during incubation (when not physiologically constrained to stay close) which indicates that suitable foraging conditions were close by. In contrast, at Nelson Island, foraging conditions might not be ideal because penguins had increased foraging efforts (e.g. chinstraps and gentoos made longer foraging trips) to find enough food.

Another important environmental feature that influences the distribution of krill and other marine organisms is bathymetry (Guinet et al. 2001; Yen et al. 2004; Meyer et al. 2017). The bathymetry is quite complex at both islands and must be considered when making interpretations of the foraging behaviours of chinstraps and gentoos. To the north of Nelson Island lies a large shelf (up to 200 m deep) where many foraging locations were recorded, while to the south lies a sudden deep canyon. At Nelson Island, chinstraps spread their diving from shallow areas (on-shelf) to areas where the bathymetry is between 2000 and 3000 m deep (off-shelf) (Supplement 4). Comparatively, at Kopaitic Island, the bathymetry is quite structurally complex (i.e. uneven bathymetry), consisting of deep canyons and shallower areas. At Kopaitic Island, all chinstrap diving behaviour occurred over shallower areas (<1000 m depth) often near the shelf edge (Supplement 4). Bathymetric features such as shelf edges and seamounts have been proven as important habitats for chinstraps (Kokubun et al. 2015; Warwick-Evans et al. 2018; Warwick-Evans et al. 2022) because shelf edges are often associated with upwellings, increased primary productivity and aggregations of krill (Weimerskirch 2007; Scales et al. 2014). Similarly, bathymetry also greatly influences the diving and foraging behaviour of gentoos who often feed benthically (Kokubun et al. 2010; Handley et al. 2017). At both sites, gentoos concentrated most of their foraging dives to on-shelf areas (where bathymetry was up to 200 m deep) and near the shelf edge where upwellings of krill could occur (Scales et al. 2014) (Supplement 4).

Habitat use is an important aspect of foraging behaviour that plays a key role in the survival and population dynamics of a species. Studies have highlighted temporal variations in the foraging behaviour of penguins at a single location (Camprasse, et al. 2017b; Michelot et al. 2021), but few have concurrently investigated the geographic variation in foraging behaviour across multiple sites to determine how foraging behaviour may vary at large spatial scales. The relative availability of suitable foraging habitats for penguins may vary between sites which results in the varying habitat use among populations (Wakefield et al. 2017). Furthermore, most studies looking at intraspecific competition and phenotypic plasticity often compare foraging behaviour and habitat use between nearby populations, where populations experience the same environmental conditions (Bolton et al. 2019). For example, Ito et al. 2021; studied inter-colony foraging area segregation between nearby Adélie penguin (*Pygoscelis adeliae*) colonies (2 km apart). In contrast, my study sites were far from each other (±131 km apart) and thus the populations' UDs did not overlap. My study is valuable because we showed how species' foraging behaviours differ between geographically separated sites where individuals did not experience the same environmental conditions even though they were breeding in the same season. My study highlights that the local environment needs to be accounted for when comparing foraging behaviours within species between multiple sites during the same season because sites might be associated with varying environmental conditions which influence predator and prey distribution patterns (as previously stated in e.g. Dehnhard et al. 2013; Lowther et al. 2018).

5.2 Chinstrap foraging behaviours

5.2.1 Site-specific trip behaviours and habitat use

Chinstraps showed phenotypic plasticity in their foraging trip behaviours by adjusting their trip duration and distance according to site and breeding stage. Chinstraps travelled both long and short distances from their breeding colony. During incubation, chinstraps made long foraging trips (often lasting longer than 24 hours). But during chick-rearing, individuals from both populations decreased their foraging range to similar distances (10 km and less on average). Seasonal shifts in space use through the breeding season (as found in my study) are common among central place foragers (Ancel et al. 2013; Poupart et al. 2017), especially chinstraps (Phillips et al. 2021) because during chick-rearing, they need to return to their nests more often to feed their chicks and thus can only make short foraging trips.

Chinstraps had site-specific foraging trip behaviours. Trip behaviours differed considerably between sites, especially during incubation, when central-place foragers are not required to forage close to their colony and can make longer foraging trips to more productive foraging areas before returning to switch incubation roles with their partner. For example, chinstraps from Nelson Island made longer and further foraging trips during incubation compared to those of Kopaitic Island. These differences between sites could arise from differences in the local distribution and abundance of krill between sites. Similarly, Little penguins (*Eudyptula minor*), also increased their foraging trip durations in years when prey availability was reduced (Saraux et al. 2011) to obtain enough food instead of decreasing the mass of the meals they were feeding their chicks (Chiaradia and Nisbet 2006). Thus, the longer foraging trips indicate that Nelson Island chinstraps had to spend more time searching for krill which might not have been as abundant in near-shore areas where many individuals foraged on the same resource (Ashmole 1963). These extended foraging trips are probably indicative of chinstraps showing directed movement towards the shelf breaks to take advantage of large krill aggregations in the Antarctic Peninsula regions (Siegel et al. 2013; Warwick-Evans et al. 2022).

In contrast, Kopaitic Island chinstraps travelled relatively short distances (~2 to 40 km) during their foraging trips. Shorter foraging trips imply that the foraging areas near Kopaitic Island, were more productive during the breeding season because chinstraps did not have to travel far. Similarly, chinstraps from King George Island did not travel far as they often visited a nearby seamount area in the Bransfield Strait that provided favourable foraging conditions and supported high foraging performance (Kokubun et al. 2015). In areas where foraging conditions are not optimal e.g. Nelson Island, or after weather events associated with reduced primary productivity (e.g. Lowther et al. 2018), chinstrap foraging trip distances may reach up to 200 km or more (e.g. Warwick-Evans et al. 2018; Clewlow et al. 2019).

Intraspecific competition for krill might be another reason for chinstraps making extended foraging trips at Nelson Island. Intraspecific competition may influence the spatiotemporal foraging behaviour of a species at the individual- and population levels and therefore, krill availability. According to previous chinstrap population estimates, the Nelson Island population is about tenfold larger than the Kopaitic Island population (Nelson = 89685 pairs vs. Kopaitic = 9400 pairs; Woehler 1993; Silva et al. 1998). Accordingly, the larger the colony, the greater the intraspecific competition will be leading to a decrease in resource availability per individual according to colony size (Cairns 1989; Ainley et al. 1995). In response to increased competition, individuals from large colonies (e.g. Nelson Island) would forage over a larger area to avoid competition and ensure adequate food intake. Here, I showed that individuals at Nelson Island have increased their foraging efforts (i.e. longer foraging trips) which could potentially be attributed to intraspecific competition. Furthermore, intraspecific competition for prey is expected to be even higher during chick-rearing, when parents can only forage close to the colony where the density of other individuals is high, leading to lower prey availability near the colony (Trathan et al. 2018; Warwick-Evans et al. 2018).

5.2.2 Dive behaviours

Chinstraps showed similar foraging dive-type strategies and diel diving patterns at both sites (which was expected from a specialist feeder). Chinstraps' foraging dives were deeper (on average often 50 m or deeper during the day) compared to other studies that found that they often dive between 15 to 30 m deep (e.g. Wilson and Peters 1999; Miller and Trivelpiece 2008; Kokubun et al. 2010). But previous studies did not separate foraging from non-foraging dives and thus probably included the shallow, traveling dives which were excluded from my analysis. In each breeding stage, individuals from Kopaitic Island tend to dive deeper than those from Nelson Island. At both sites, chinstraps dived shallow during incubation and foraging depth increased during chick-rearing stages. Deeper dives indicate that chinstraps probably had to increase their diving efforts (by making more benthic dives; similar to chinstraps from Signy Islands; Takahashi et al. 2003) while foraging close to the colony (where bathymetry is shallow) to obtain enough food for their chicks. The foraging area, diving behaviour and bathymetry of the islands suggest that chinstraps could reach the seafloor when they were foraging nearshore during chick-rearing, while still foraging on krill. The shallow shelves would restrict krill from migrating deeper, making them easily accessible to krill predators.

The possibility of individual variation in the foraging behaviours of pelagic divers (e.g. chinstraps) is largely unknown (Camprasse, et al. 2017a). Here I showed that chinstrap individuals displayed diel diving patterns, performing shallow dives during twilight phases (low solar light: i.e. early mornings and evenings) and deeper dives during the day similar to other studies (e.g. Jansen et al. 1998; Blanchet et al. 2013). These diel diving patterns also resulted in the high within-individual variation in maximum dive depths. During twilight phases, pelagic dives led to higher diving efficiencies (Supplement 7). More efficient dives (maximizing time spent at foraging depths compared to minimizing time spent travelling between surface and depths) indicate that chinstraps spent more time foraging than diving (Mori et al. 2002; Bestley et al. 2015). Twilight phases correspond to the diel vertical migration period of krill that migrate from greater depths during the day to the upper water column (Zhou and Dorland 2004; Trathan and Hill 2016). Therefore, krill may be more accessible to chinstraps in the shallower depths at twilight than during the daytime. As sun elevation increased, chinstraps dived deeper which was also consistent with the vertical migration of krill. When chinstraps follow the krill vertical migration down, they spend more time diving than foraging at depth leading to lower diving efficiencies (Supplement 7). However, more sunlight improves chinstraps' visual predation efforts which would assist them in optimising their hunting strategy (Zimmer et al. 2008). Similarly, the Adélie penguin also exhibits diel diving patterns by modifying their diving according to solar elevation to follow the krill vertical migration (Riaz et al. 2020).

5.3 Gentoo foraging behaviour

5.3.1 Site-specific trip behaviours and habitat use

Gentoos had short foraging trips (in distance and time; <24 hours) relative to chinstraps from the same sites. Other studies also found that gentoos forage within 25 km of the island (Kokubun et al. 2010; Wilson 2010). Gentoos do not regularly make overnight trips (>24 hours), and thus will not forage far away from the colony.

However, gentoos showed that their foraging trip behaviours were site-specific. Kopaitic Island gentoos travelled slightly further than Nelson Island conspecifics. But, at Nelson Island, gentoos spent 8.5 hours longer on a foraging trip during incubation compared to those from Kopaitic Island. The extended foraging trips of Nelson Island gentoos indicate that they had to increase their foraging efforts to obtain enough food to sustain themselves during incubation. Foraging trip duration is an indication of prey availability within a season (Reid et al. 2005). Thus, increased foraging efforts of gentoos indicate that the foraging conditions around Nelson Island were not ideal (possibly low prey availability) compared to Kopaitic Island where individuals did not spend a lot of time searching for prey. During chick-rearing, individuals shortened their foraging trips to similar durations at both islands.

5.3.2 Site-specific dive behaviours

Gentoos are known to be deep divers, often diving to depths of 100 m (Cimino et al. 2016). In my study, gentoos often concentrated most of their foraging dives at shallower depths (<100 m) at both sites. The diving behaviours of gentoos were site-specific which indicated that they responded well to variations in their local environment (which determine prey type and availability). Instead of relying on particular foraging strategies, gentoos showed high phenotypic plasticity in their diving behaviours by adjusting their diving behaviour by site (and its associated environmental characteristics) and breeding stage.

At Kopaitic Island, gentoos made more pelagic dives than benthic dives during incubation, but as the breeding season progressed, they made both benthic and pelagic dives depending on the time of day. Kopaitic Island gentoos followed a diel diving pattern where they foraged pelagically in the early morning and evenings (shallow diving), but as solar elevation increased during the day, they dived deeper and changed to benthic foraging. Similarly to chinstraps, Kopaitic Island gentoos followed the diel vertical migration of krill going deeper in the water column during the day (Zhou and Dorland 2004) which led to their diel diving patterns. Thus, I can conclude that gentoos from Kopaitic Island most likely fed mainly on krill.

In contrast, at Nelson Island, gentoos dived to similar depths throughout the breeding season, irrespective of daily solar elevation changes. Nelson Island gentoos did not show the same diel diving pattern as seen in Kopaitic Island gentoos and thus, probably did not follow the krill diel vertical migration. Gentoos are generalist feeders including both krill and benthic prey in their diet (Lescroël et al. 2004). The diving pattern of Nelson Island gentoos, suggests that they might have foraged on a varied diet including a combination of krill and other benthic prey during their foraging trips. The shallow bathymetry around Nelson Island probably restricted gentoos and their prey from going much deeper. Young krill (age 1 and older) occupy the surface waters (0-50 m) throughout the day and night during the summer (Siegel 2005) and thus would be present where gentoos can feed on them, but due to their small size may be less nutritious. During incubation and brood, Nelson Island gentoos made more benthic dives but as the breeding season progressed, they included more pelagic dives into their foraging dive strategy likely in an attempt to obtain enough food for their chicks. Nelson Island gentoos foraged more benthically during early mornings and evenings while foraging both pelagically and benthically during the day. In the mornings, gentoos probably fed on any suitable prey source that was restricted to the shallow shelf and did not particularly target specific prey.

The site-specific diving behaviours of gentoos did not however give one population an advantage over the other as diving efficiency was the same between sites (Supplement 7). My results show that gentoos had to adjust their diving behaviour according to site to maintain a high diving efficiency throughout the breeding season to ensure the survival of their chicks. The clear variation in diving behaviours between sites reflects how gentoos behaved differently and used their habitat in different ways in response to varying environments. These inter-colony variations in diving behaviours can be related to differences in associated local environmental conditions that influence prey type, distribution and composition. The ability of gentoos to feed both benthically and pelagically on different kinds of prey may be advantageous when prey distributions become uncertain as the climate changes (Lescroël and Bost 2005). Unfortunately, no prey abundance or distribution data was available to explain the differences in diving behaviours. Such data would be valuable to obtain from these areas to understand what gentoos fed on during the breeding season.

5.4 Future implications

Penguins breeding at colonies across the Bransfield Strait were exposed to different environments with varying physical characteristics which explain the phenotypic plasticity observed in their foraging trip and diving behaviours between sites. I recommend that when studies include seabirds such as gentoo and chinstraps as indicator species of their environments or krill abundance, it is important to consider the local environmental influences on their foraging behaviours. Furthermore, my study adds valuable information about the foraging behaviours (trip and dive) of two important krill predators across the Bransfield Strait in the WAP. My results emphasize that studies need to consider the phenotypic plasticity of a species' foraging behaviour at multiple sites (of different environments) before inferring how a species will respond to changing environmental conditions. I hope that my results encourage future research in the WAP area to clarify how seabirds respond to regional changes in their environment and potentially krill availability which is required for monitoring programmes. With increasing concentrations of krill fishing in the WAP (Nicol et al. 2012), efforts to address the knowledge gaps of habitat use and foraging behaviours of krill predators need to be encouraged.

Most inter-colony studies of foraging behaviour only focus on horizontal space use e.g. overlapping foraging areas (Ito et al. 2021), ignoring dive behaviour (e.g. diving depths and proportion of water column used), a critical oversight given that penguins are primarily diving predators. Here, I combined horizontal and vertical information to link birds' spatial movements with their behaviours and prey distribution. This approach allowed me to identify differences between sites in the horizontal and vertical aspects of their site-specific foraging behaviour. Site-specific specialisations in foraging behaviour are widespread within seabird species (Sánchez et al. 2018; Olmastroni et al. 2020; Elley et al. 2022), but may vary in frequency (in time and space) depending on the predictability of prey and environmental conditions (Suryan et al. 2006). Ongoing climate changes are expected in the Southern Ocean (Constable et al. 2014). Krill biomass is predicted to change as a result of warming ocean temperatures (Hill et al. 2016), which would result in varying impacts on krill predators, with penguins being the most vulnerable group (Klein et al. 2018). In the Antarctic Peninsula, both gentoos and chinstraps' foraging behaviours were influenced by the physical characteristics of the marine habitat they encountered. The potential effects of increasing fisheries, recovering marine mammal populations and climate change in the Southern Ocean region will also influence seabirds' foraging behaviour at different sites depending on the availability of prey resources and foraging habitat. Therefore, knowledge about the potential variation in foraging behaviours within a species is important to understand that species may have site-specific responses to environmental change (e.g. Michelot et al. 2021).

The krill specialists, chinstraps, will be the most impacted by varying krill numbers due to increased anthropogenic-driven changes in the environment. I suggest that chinstraps will continue to forage pelagically with diel diving patterns (while feeding on krill) during the breeding season but may adjust their foraging trip behaviours according to site and breeding stage to ensure that they provide enough food for their chicks. The local conditions in the foraging area influence prey availability and will determine how far chinstraps will travel to forage. Chinstraps would not generally modify their diving behaviour in varying environments (where krill availability may vary) and thus would be unable to feed on other prey items when krill becomes unavailable. In areas where krill numbers are low, they would spend more time travelling and searching for krill than feeding (e.g. at Nelson Island).

In contrast, gentoos, who are generalist feeders, will be less impacted by variations in krill sources due to climate change. Gentoos, show phenotypic plasticity in their foraging trip behaviours. Additionally, gentoos will also vary their diving strategy based on their local environment and time of day to forage both pelagically and benthically to obtain enough food (probably including a variety of krill and benthic prey in their diet; Kokubun et al. 2010). The foraging behaviour of gentoos varied over the Bransfield Strait, similar to the variation across its distributional range depending on the local conditions (e.g. Lescroël and Bost 2005; Miller et al. 2010; Carpenter-Kling et al. 2017). Generalist predator species have site-specific trip- and diving behaviours to improve foraging which leads to populations having different prey preferences in different areas (Araújo et al. 2011). Gentoos' plasticity in foraging trip- and diving behaviours will be advantageous in the future when climate changes lead to changes in food availability (e.g. krill). Their ability to adjust their feeding strategy according to prey availability might ultimately lead to their resulting breeding success, survival and increasing population numbers. Gentoos' plastic foraging behaviours enable them to be independent of one food source while other krill predator species (e.g. chinstraps) whose diet is exclusively dependent on krill resources, are less likely to modify their diving behaviour and are experiencing declines in their populations (Lynch et al. 2012b; Strycker et al. 2020).

5.5 Are plasticity in foraging behaviours advantageous in other aspects?

Chinstraps and gentoos often breed sympatrically on islands in the Antarctic Peninsula. To coexist at breeding sites, chinstraps and gentoos need to occupy different niches (or foraging strategies) to prevent interspecific competition (competition between species) for similar resources. Competition for resources is one of the most important factors driving specific foraging behaviours (Begon et al. 2009). For example, to limit interspecific competition with Adélie penguins, gentoos modify their diving behaviour to dive deeper in areas where their foraging ranges overlapped (Cimino et al.2016). From my results, I suggest that the phenotypically plastic trip and dive behaviours of chinstraps and gentoos could facilitate the prevention of interspecific competition at sympatric breeding sites. Further investigation of this dataset is needed to elucidate whether gentoos and chinstraps' plastic foraging behaviours are used to reduce interspecific competition between species from the same island in addition to reducing intraspecific competition within species.

6. References

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Chapter 3: Central-place foraging constraints and environmental conditions modify niche partitioning in sympatric *Pygoscelis* penguin populations

1. Abstract

In the Southern Ocean, sympatrically breeding seabirds often have overlapping foraging ranges and niches that may lead to interspecific competition. The extent of this competition may vary across several scales. In this chapter, I investigated how varying central-place foraging constraints and changes in environmental conditions over the breeding season modified foraging niche separation in two sympatric populations of chinstrap (*Pygoscelis antarcticus*) and gentoo (*P. papua*) penguins in the Antarctic Peninsula. I analysed foraging behaviour data (GPS location and maximum foraging dive depths) of 221 individuals that bred at Nelson Island and Kopaitic Island in the 2018/19 austral summer. An autocorrelated kernel density estimate approach was used to quantify space use and overlap of foraging ranges between the species as breeding transitioned from incubation to brood and crèche. To test dive depth partitioning between species, I fitted a series of generalized linear mixed-effects models with species, site, breeding stage and environmental variables as covariates. During brood and crèche, chinstrap penguins contracted their foraging ranges and dived deeper, increasing niche overlap and opportunity for interspecific competition with gentoo penguins. Foraging niche overlap was also influenced by site-specific environmental conditions. Warmer sea-surface temperatures (which correlate with increased diving depths) and shallower bathymetry (which limits diving depth) at Nelson Island reduced opportunity for niche partitioning between the two species. My results show that seasonal changes in central-place foraging constraints and environmental conditions can modify niche separation between these co-occurring species. A continuation of climate change (e.g. further warming sea temperatures) in this region of the Southern Ocean is expected to impact penguin prey distribution, which will likely lead to changes in foraging behaviour and niche overlap of chinstrap- and gentoo penguins.

Keywords:

Antarctic Peninsula, central-place foraging constraints, foraging behaviours, interspecific competition, niche partitioning, sympatric

2. Introduction

According to niche theory, sympatric species with similar life histories and resource requirements must minimize interspecific competition to co-exist (Pianka 1981). Trophic niche separation may occur along one or more niche dimensions such as dietary, spatial or temporal partitioning of resource use (Navarro et al. 2013; Quillfeldt et al. 2020; Reisinger et al. 2020). However, when resources become scarce, or when constraints prevent species from segregating resource use, foraging niche overlap and interspecific competition may increase. As a result, the extent of niche separation, and thus the potential for interspecific competition, varies across several scales. For instance, in land breeding marine predators, niche overlap may intensify as foraging areas of several sympatric species contract during breeding seasons, and moderate during the non-breeding period (e.g. winter), when many of these predators migrate away from breeding colonies and increase their foraging ranges (Bost et al. 2009b; McCutcheon et al. 2011). Changing environmental conditions that affect prey availability may also alter the degree of niche separation across years, seasons or sites (Bonnet-Lebrun et al. 2021; Narvestad et al. 2022).

Central-place foragers, like breeding seabirds, must return to a central location (e.g. a breeding colony) after foraging trips, limiting their opportunities (in time and space) to search and find food (Orians and Pearson 1979). The foraging ranges of seabirds often differ between breeding stages, as adults adjust their foraging behaviours (e.g. trip distances and duration) according to the needs of their offspring (Ydenberg et al. 1994; Shaffer et al. 2003). In penguins, breeding adults typically increase their provisioning rate as chicks grow older. As a consequence, foraging trips become shorter (Ichii et al. 2007; Poupart et al. 2017), and some species modify their diving behaviour (Booth et al. 2018; Ito et al. 2021) or switch to other prey items (Handley et al. 2017). These changes could be a response to local prey depletion caused by adults foraging close to the breeding colony (Ashmole 1963) or due to seasonal changes in the environment and prey base (e.g. Lowther et al. 2018; Salmerón et al. 2023). Decreased foraging ranges and local prey depletion may therefore increase interspecific competition over the breeding season in sympatric penguin populations that share prey resources (Polito et al. 2015; Herman et al. 2017).

Chinstrap penguins (Pygoscelis antarcticus, chinstraps hereafter) and gentoo penguins (P. papua, gentoos hereafter) breed sympatrically on numerous islands in the Antarctic Peninsula region (Woehler and Croxall 1997; Hinke et al. 2007; Wilson 2010). In this region of Antarctica, both species feed primarily on krill (mostly Antarctic krill, Euphausia superba) (Volkman et al. 1980; Trivelpiece et al. 1987; Miller et al. 2010), making niche separation likely to reduce interspecific competition. Niche separation between Pygoscelis penguins has indeed been documented along multiple dimensions: by slight differences in breeding phenology (Clewlow et al. 2019), by gentoos supplementing their krill diet with fish and other prey (Kokubun et al. 2010; Polito et al. 2015), by differences in temporal foraging preferences (Miller et al. 2010; Wilson 2010), and spatially, by gentoos foraging at deeper depths (Cimino et al. 2016; Lee et al. 2021). Despite these differences, an overlap of foraging ranges close to their breeding colonies and a shared dependence on Antarctic krill may lead to foraging competition.

Here, I investigate how varying central-place foraging constraints and changes in environmental conditions over the breeding season modify foraging niche separation in two sympatric populations of chinstraps and gentoos in the Antarctic Peninsula. I used tracking data (location and maximum depth of foraging dives) of breeding chinstraps and gentoos collected at Nelson Island and Kopaitic Island in the 2018/19 austral summer. Nelson Island, part of the South Shetland Island group, is situated approximately 131 km north of Kopaitic Island, a small island off the north-western coast of the Antarctic Peninsula mainland. The two study sites are therefore located on opposite sides of the Bransfield Strait (Supplement 1). My specific aims are to (1) quantify how spatial overlap of foraging distributions changes as the breeding season progresses from incubation to brood and crèche, and (2) assess whether seasonal changes in environmental conditions modify niche separation between these species. I address these aims by (1) reporting changes in the utilisation distributions of foraging penguins over the breeding season and (2) modelling foraging dive depth as a function of breeding stage and environmental covariates. Because foraging ranges of penguins generally contract during chick-rearing (e.g. Kokubun et al. 2010), I expect that chinstraps and gentoos will have higher spatial overlap of foraging distributions during the brood and crèche stages. Increased spatial overlap might encourage niche separation along another dimension, such as greater interspecific differences in foraging dive depths. However, environmental conditions may also influence foraging dive depths. Here I consider how diving depths relate to three environmental covariates (sea surface temperature, solar elevation and bathymetry) that change or vary in availability to penguins over the breeding season.

3. Methods

3.1 Study sites and tag deployments

The Bransfield Strait comprises of complex ocean circulation patterns that are influenced by water masses transported by ocean currents from the Bellinghausen- and Weddell Sea. Kopaitic Island, for example, is surrounded by relatively cold and fresh water (relative to Nelson Island) (Chapter 2) due to the influx of Weddell Sea water descending westwards along the continental slope of the northern Antarctic Peninsula. The environmental variability of the Southern Ocean (including the Bransfield Strait) is often indicated by two large-scale climatic modes, El Niño Southern Oscillation Index (ENSO; Trenberth 1997) and Southern Annular Mode (SAM; Marshall et al. 2004) (Clem et al. 2016). The climatic variability of ENSO and SAM influences the interannual water column structure through variations in wind patterns, sea ice melt and precipitation, ultimately influencing the biological production in the Bransfield Strait (Ruiz-Barlett et al. 2018; Avelina et al. 2020).

High-resolution location and dive logging tags (Axy-Trek Marine tags; https://www.technosmart.eu) were deployed on breeding chinstraps and gentoos (Supplement 1). Tags were deployed on the north-eastern aspect of Kopaitic Island (where all penguin breeding colonies are located) and in colonies on the northern, western and southern aspects of Harmony Point, Nelson Island to capture potential colony-level variation in foraging behaviour at this site. Deployments were made through all stages (incubation, brood and crèche; 3 December 2018 to 14 February 2019) of the breeding season (Supplement 1). Adult penguins that switched incubation or chick-rearing (brood and crèche) duties with their partners and were about to leave the colony on a foraging trip were caught (either by hand or net), weighed and briefly restrained (less than 10 minutes) for tag deployment. Tags were attached to the central dorsal region of the back using Tesa tape and cyanoacrylate glue (Loctite 401®) (Wilson et al. 1997). Tags were programmed to record GPS locations every four minutes (Nelson Island) or every second (Kopaitic Island; these were subsequently subsampled to 30-second intervals to reduce computing time). All tags recorded temperature and depth every second. Penguins were tracked for 5.7 ± 2.5 days (mean ± standard deviation), on average, before tags were retrieved. Given the short deployment duration and small size of the tags (40 x 20 x 8 mm), I expect that any potential negative effects from tag attachment will be minor and of short duration (Evans et al. 2020).

3.2 Tag data processing

Tags were downloaded using proprietary software, and the data were then processed and analysed in R version 4.2.1 (R Core Team 2022). Please see my GitHub repository (https://github.com/Leandri3/NicheSepPenguins) for examples of all the R scripts used in the data analysis. I obtained at-sea location and dive data from 221 individuals (Kopaitic Island: 62 chinstraps and 35 gentoos; Nelson Island: 93 chinstraps and 31 gentoos) (Supplement 1). I split GPS tracks into separate foraging trips using diving profiles and distance to colony plots. Foraging trips started when a penguin first dived and ended when diving stopped and the penguin was near the colony of instrumentation. GPS locations recorded between foraging trips were removed so that only discrete at-sea bouts were used for subsequent analyses. To remove sporadic location errors, locations were filtered based on speed, distance and turning angle using the 'trip' package (Sumner et al. 2011), assuming a maximum travel speed of 15 km/h. The remaining locations were irregularly spaced in time as GPS fixes were not recorded while penguins were underwater. I used the '*crawlWrap*' function from the 'MomentuHMM' package (McClintock and Michelot 2018) to fit a continuous-time correlated random walk (CTCRW) model (Johnson et al. 2008) to the irregular locations. The CTCRW model was then used (1) to predict locations at 5-minute intervals throughout each foraging trip (for utilization distribution analysis) and (2) to predict the locations of every dive (for dive depth analysis).

Dive data were processed using the 'diveMove' package (Luque 2007). The dive data were zero-offset-calibrated (using the '*filter*' function) whereafter various summary statistics (e.g. maximum dive depth) were calculated for each dive (using the '*diveStats*' function). A depth threshold of 5 m was used to define dives and to exclude surface and near-surface behaviours (Miller and Trivelpiece 2008). Dives with durations longer than 10 minutes were also removed as I considered these to be infrequent recording errors.

3.3. Interspecific overlap in space use

I quantified space use and the overlap of foraging ranges of chinstraps and gentoos at each island. I used autocorrelated kernel density estimation (AKDE) methods (Fleming et al. 2015; Fleming and Calabrese 2017) implemented in the 'ctmm' package (Fleming and Calabrese 2020) to calculate utilisation distributions (UDs). Location data are typically collected at short sampling intervals, and the AKDE approach accounts for the temporal autocorrelation of locations (Fleming et al. 2018) - an advance over conventional kernel density estimation methods that assume locations are independent (Noonan et al. 2019). I used the CTCRW model-predicted locations as input data and calculated the home range (95% probability contour) and the core foraging area (50% probability contour) of each individual on a 500 m raster grid. The individual UDs were subsequently aggregated (using the *'pkde'* function in 'ctmm') by species and site to estimate population-level UDs during each breeding stage.

I quantified the spatial overlap of population-level UDs using the *Bhattacharyya affinity* (BA) index with 95% confidence intervals (Winner et al. 2018). BA values range from 0 (no overlap) to 1 (identical distributions) (Fieberg and Kochanny 2005).

3.4 Comparing maximum dive depths

I used generalized linear mixed-effects models (GLMMs) to test whether interspecific differences in foraging dive depths were maintained throughout the breeding season. I classified all dives (obtained from the 'diveMove' analysis) as either 'foraging' or 'non-foraging' dives (Supplement 2) and used the maximum dive depth of foraging dives as the response variable in GLMMs. In addition to the covariates island and species, GLMMs included breeding stage (incubation, brood crèche) or seasonally changing environmental variables as covariates. Seasonal shifts in sea surface temperatures (SST) and solar elevation potentially influence the foraging dive depths of both penguin species (Le Guen et al. 2018; Salmerón et al. 2023) through their effects on Antarctic krill, the penguins' main prey source (Bestley et al. 2018; Evans et al. 2020; Nardelli et al. 2021; Narvestad et al. 2022). Bathymetry does not change seasonally, but the availability of bathymetric depth zones available to penguins varies through the breeding season as a function of central-place foraging constraints.

Sea surface temperature is a potential predictor of prey abundance and distribution (Afán et al. 2015). Changes in SST and water column stratification within the summer breeding season (e.g. due to increased solar radiation) or across breeding seasons (e.g. due to shifts in ENSO cycles and consequent changes in circulation patterns in the Bransfield Strait) may affect krill distribution, leading to changes in penguin foraging behaviour (e.g. Salmerón et al. 2023). I predicted that penguin foraging opportunities may decrease under warmer conditions as Antarctic krill have a low thermal tolerance (between 0.5 °C and 1.0 °C; Michael et al. 2021). Sea surface temperature was obtained from NASA's 0.01° Multi-scale Ultra-high Resolution (MUR) analysis of global SST (Chin et al. 2017) using the 'rerddap' package (Chamberlain et al. 2019). Daily SSTs (from 1 December 2018 to 15 February 2019) were extracted for the area between 59°S and 65.5°S and 56°W and 64°W. Sea surface temperatures increased as the breeding season progressed, especially to the north of Nelson Island (Figure 1). Sea surface temperatures ranged from below 0°C near the start of incubation to above 3°C during the late breeding season (Figure 1).

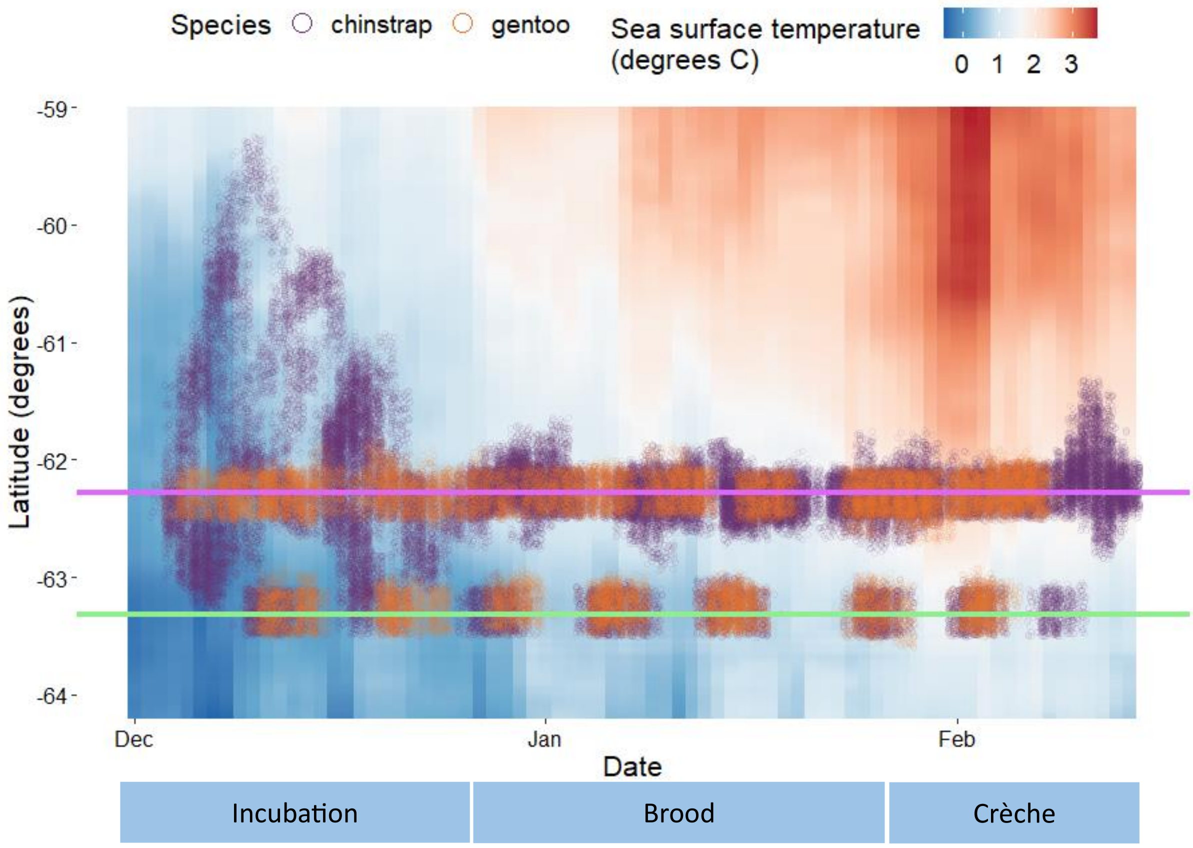

Figure 5. Sea surface temperature (SST) changes from incubation in early December 2018 to crèche in mid-February 2019. Daily SST data (Chin et al. 2017) are shown in the background. The latitudinal positions of Nelson Island (pink line) and Kopaitic Island (green line) are indicated. The latitudinal extent of chinstrap penguin (purple points) and gentoo penguin (orange points) foraging dives during each breeding stage show the SST that foraging penguins encountered. The diagram averaged the SST values across longitudes between 56°W and 64°W.

Antarctic krill exhibit diel vertical migration patterns tied to fluctuating insolation (Zhou and Dorland 2004; Trathan and Hill 2016). During the day, krill descend deeper into the water column, but when solar light decreases krill ascend in the water column to feed on zooplankton. Unsurprisingly, the dive profiles of krill predators often display the same pattern (Friedlaender et al. 2013). The solar elevation angle (degrees above the horizon) at the start of a foraging dive was calculated using the ‘maptools’ package (Bivand et al. 2022). Daylength decreases on either side of the summer solstice (near 21 December in the southern hemisphere). Thus, twilight periods (solar elevation angles between 0° and -12°) were more prominent in crèche – especially at Nelson Island which is located further north than Kopaitic Island – whereas brood and incubation occurred on either side of the summer solstice and thus had fewer hours of twilight (Supplement 3). No foraging dives occurred during astronomical twilight (solar elevations between -12° and -18°) or at ‘night’ (solar elevations <-18°).

Bathymetric depth is a common predictor of the preferred foraging habitats of many seabirds because bathymetric features (e.g. shelf edges) can promote aggregation of prey such as Antarctic krill (Soanes et al. 2016). However, shallow bathymetry may also prevent deeper-diving predators from separating their foraging niches from species that tend to dive shallower. Gentoo penguins have deeper average diving depths than chinstraps (e.g. 30-90 m vs. <30 m respectively, Mori and Boyd 2004; Miller and Trivelpiece 2008). I, therefore, added bathymetric depth as a covariate to control for changes in the availability of different bathymetric features as penguin foraging ranges decreased from incubation to brood and crèche (Supplement 3). The International Bathymetric Chart of the Southern Ocean (IBCSO version 2, 500 m x 500 m resolution; Dorschel et al. 2022) was used to estimate bathymetric depth at each foraging dive location. I used bathymetric depth as a continuous variable in model fitting, and to calculate the proportion of the water column used in each dive. Dives with a maximum dive depth of more than 80% of the water column were assumed to represent ‘benthic’ foraging, with all other dives representing pelagic foraging.

3.5 Model fitting

GLMMs were fitted using the ‘glmmTMB’ package (Brooks et al. 2017). I specified a gamma error distribution with a log link function to ensure that the model-predicted estimates of foraging diving depth were always positive. All models included individual identity as random effect, allowing every individual’s mean maximum diving depth to deviate from the population mean. Additionally, models included an Ornstein-Uhlenbeck time-varying covariance structure to account for temporal autocorrelation of dives performed by an individual (Brooks et al. 2017).

Model selection occurred in two phases. I started by fitting an a priori umbrella model that included species, site, breeding stage and all relevant interaction terms as explanatory variables. Then, I followed a disciplined hypothesis testing approach whereby I removed predictors randomly to see if model parsimony could be improved (Bolker et al. 2009). In the second phase of model selection, I replaced breeding stage with three environmental covariates (SST, solar elevation and bathymetric depth) to test whether these covariates could explain observed shifts in maximum dive depth as breeding transitioned from incubation to brood and crèche.

All environmental covariates were z-standardized (mean = 0, standard deviation = 1) before analysis. Bathymetry was fitted with a natural cubic spline (function ‘*ns*’ in the ‘splines’ package) as I expected a non-linear relationship with maximum dive depth (penguins are likely to increase diving depths at shallow bathymetries, but this relationship will weaken with increasing bottom depths). I included a species interaction with bathymetry so that chinstraps and gentoos may respond differently to bathymetric depth but assumed that the effect of bathymetry on diving depths would not vary between islands. Sea surface temperature and solar elevation were fitted with species and island interactions.

Models were fitted using maximum likelihood estimation. Model selection was based on Akaike Information Criterion (AIC) scores. The model with the lowest AIC score represented the most parsimonious model in the set. Inference was based on the most parsimonious models identified, refitted with Restricted maximum likelihood estimation to provide more reliable estimates of the variance components (Zuur et al. 2009). Model fit was evaluated using the 'DHARMa' package (Hartig 2017). Models did not violate model fit assumptions. The total amount of variance explained was summarised with marginal (R^2_{mar}; only fixed effects) and conditional (R^2_{cond}; fixed and random effects) R^2 values (Nakagawa and Schielzeth 2013; Nakagawa et al. 2017).

4. Results

4.1. Spatial overlap of foraging distributions

The home ranges (95% UD) of chinstraps and gentoos overlapped (all BA values > 0.42) but the extent of overlap varied through the breeding season and by site (Table 1). At Nelson Island, chinstraps had a six-fold larger home range than gentoos during incubation (Figure 2, Supplement 4). At Nelson Island, both species contracted their foraging ranges during brood and crèche, leading to high spatial overlap (BA > 0.96), while the opposite trend was observed at Kopaitic Island (Table 1). At Kopaitic Island, chinstraps and gentoos had high spatial overlap during incubation (BA = 0.98, Figure 2) that decreased during brood and crèche (Table 1). Tracking data from this site suggest that gentoos expanded their home range during brood and crèche, while chinstraps' home range sizes decreased (Figure 2, Supplement 4).

Table 3. Bhattacharyya affinity index (and 95% confidence intervals) for the home range overlap between chinstrap and gentoo penguins breeding at Kopaitic Island and Nelson Island by breeding stage.

Island	Breeding stage		
	Incubation	Brood	Crèche
Kopaitic Island	0.98 (0.93 – 1.00)	0.68 (0.53 – 0.89)	0.42 (0.31 – 0.58)
Nelson Island	0.42 (0.34 – 0.51)	0.96 (0.92 – 1.00)	0.97 (0.88 – 1.00)

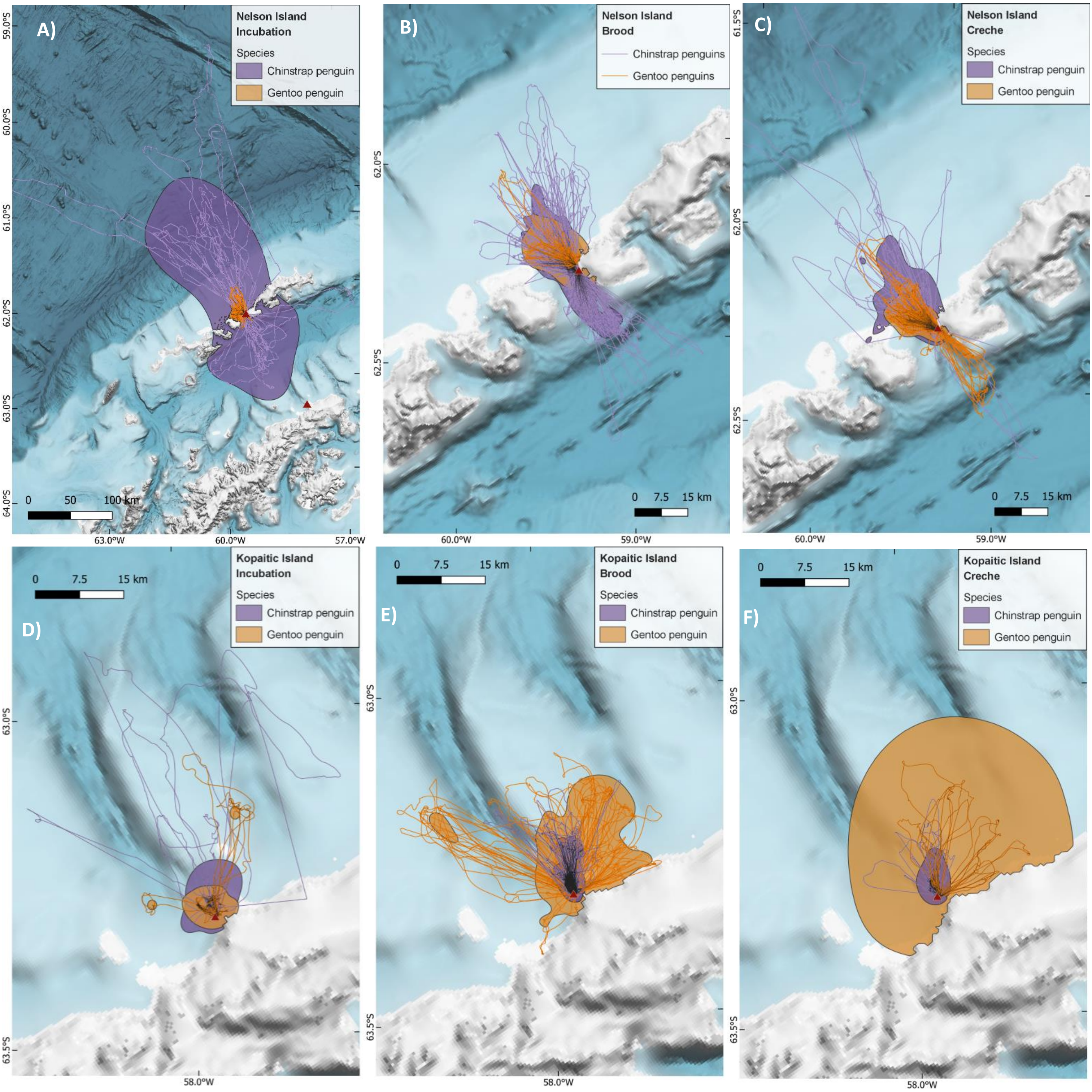

Figure 2. The spatial distribution of the home ranges (95% UDs) of chinstrap penguins (purple) and gentoo penguins (orange) by breeding stage, showing A&D) incubation, B&E) brood and C&F) crèche stages. Individual foraging trips (CTCRW locations) are shown as lines and coloured according to species. Deployments on sympatric colonies were made at Nelson Island (top panel) and Kopaitic Island (bottom panel) from December 2018 to February 2019. The bathymetry depth layer obtained from IBCSO v2 (Dorschel et al. 2022) is shown in the background. The figure was prepared in QGIS v3.28 using Quantarctica3.2 software (Matsuoka et al. 2021).

4.2. Foraging dive depths by breeding stage

Both species dived deeper at Kopaitic Island than at Nelson Island, however, across both sites, gentoos dived the deepest. Removing the species-island interaction term led to a more parsimonious model (i.e., island did not materially affect the difference in diving depths between species) (Model 1, Table 2). This model explained 39% of the variability in maximum dive depth (R^2_{cond} = 0.39), with some of the explained variation being attributed to between-individual differences (R^2_{mar} = 0.29).

The foraging dive depths of chinstraps increased as the breeding season progressed (during brood and crèche, compared to incubation), especially at Nelson Island (Figure 3). The largest inter-specific separation in diving depths occurred during incubation, when gentoos dived between 19 m (Nelson Island) and 39 m (Kopaitic Island) deeper, on average, than chinstraps (Figure 3, Table 3). During brood and crèche, the inter-species differences in diving depths decreased (8 to 17 m at both islands), thus narrowing niche separation towards the end of the breeding season (Figure 3, Table 3).

Table 2. Generalized linear mixed-effect model selection of maximum foraging dive depth between chinstrap penguins and gentoo penguins breeding at Kopaitic Island and Nelson Island. The a priori umbrella model with all model terms (model 2) is given with the remaining models only indicating the model term that was removed from the umbrella model. The fixed effect terms are breeding stage (incubation, brood, crèche), island (Kopaitic or Nelson) and species (chinstrap or gentoo penguins). All models included individual identity as a random effect. The most parsimonious model is in bold.

Model	Fixed effects	n.p	deviance	ΔAIC	weight
1	**- (island: species)**	**13**	**-440842**	**0.00**	**0.69**
2	stage+island+species+ stage:island + stage:species + island:species	14	-440842	1.99	0.26
3	- (stage:species + island:species)	11	-440847	6.12	0.03
4	- (stage: species)	12	-440847	7.47	0.02
5	- (stage:island + island:species)	11	-440852	15.16	0.00
6	- (stage: island)	12	-440852	17.07	0.00
7	- (stage:island+ stage:species + island:species)	9	-440856	19.55	0.00
8	- (stage:island+ stage: species)	10	-440855	20.33	0.00

The number of parameters (n.p), model deviance, delta AIC and model weight are included in the table. Models were ranked according to differences in AIC (ΔAIC). Only models with a ΔAIC smaller than 25 were included in the table. The ':' indicates an interaction.

Table 3. Summary of foraging dive parameters for chinstrap penguins and gentoo penguins breeding at Kopaitic Island and Nelson Island during different phases of the breeding season. Maximum depth is given as mean ± standard deviation (sd).

Dive parameters	Kopaitic Island					
	Chinstrap penguins (dives > 5m)			Gentoo penguins (dives > 5m)		
	Incubation (n = 2991)	Brood (n = 6733)	Crèche (n = 2060)	Incubation (n = 1284)	Brood (n = 6454)	Crèche (n =1222)
Maximum depth (m)	39.7 ± 17.8	53.4 ± 24.2	47.1 ± 19.7	78.7 ± 48	64.8 ± 42.9	64.2 ± 42.3
Percentage of benthic dives (%)	21.77	36.07	23.11	30.61	49.57	60.15

	Nelson Island					
	Chinstrap penguins (dives > 5m)			Gentoo penguins (dives > 5m)		
	Incubation (n = 21681)	Brood (n = 35048)	Crèche (n = 11509)	Incubation (n =7077)	Brood (n = 3245)	Crèche (n = 8415)
Maximum depth (m)	27.5 ± 20.1	38.6 ± 22.7	47.2 ± 22.4	46.6 ± 22.8	47.3 ± 15.9	61.1 ± 23
Percentage of benthic dives (%)	2.93	26.71	37.45	58.43	71.56	52.28

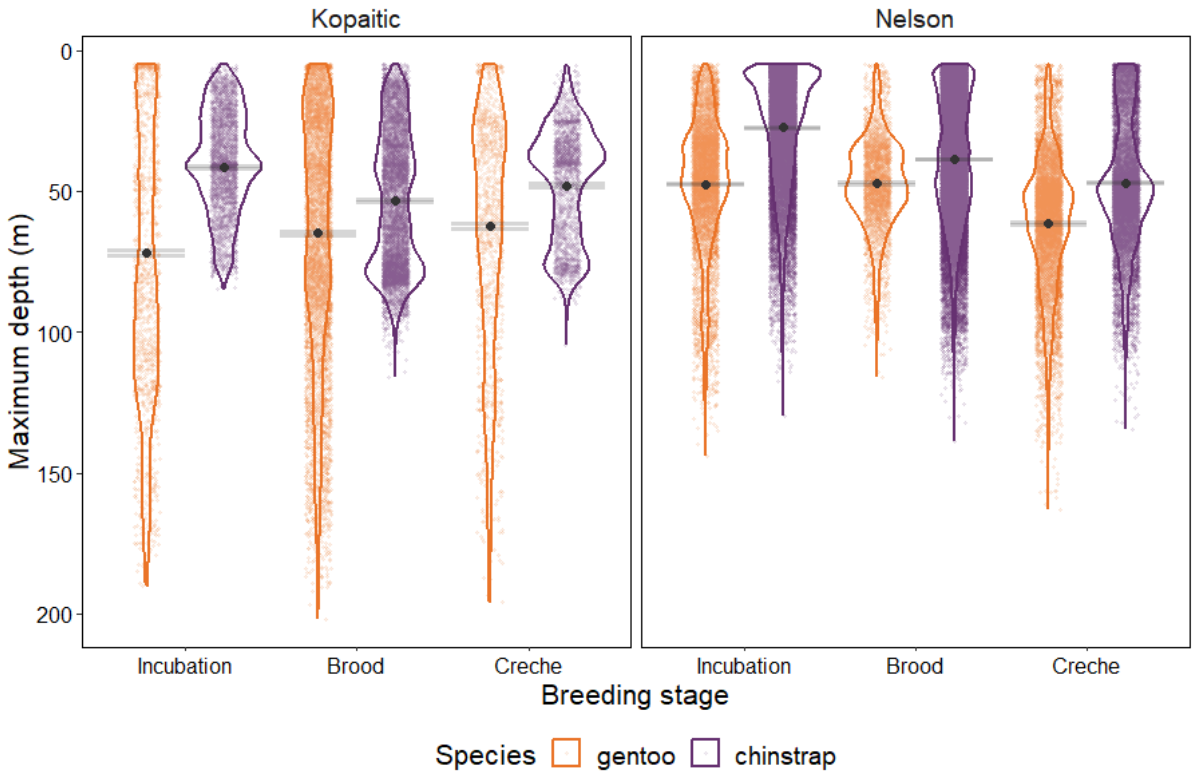

Figure 3. Maximum foraging dive depth of chinstrap penguins (purple) and gentoo penguins (orange) breeding at Kopaitic Island and Nelson Island, across all breeding stages. The mean model estimates and 95% confidence intervals are shown in black. The observed data and violin plots that show the spread of the data are coloured by species.

4.3. Environmental influences on foraging dive depth

The a priori umbrella model which included all environmental covariates and selected interactions as fixed effects explained the most variation (lowest deviance; $R^2_{cond} = 0.69$, $R^2_{mar} = 0.56$) in maximum dive depth (model 1, Table 4). Removing the species:sst interaction term from the umbrella model did not increase the AIC substantially, indicating that this interaction term contributed little to model fit (Table 4).

Table 4. Generalized linear mixed-effect model selection of maximum foraging dive depth between chinstrap penguins and gentoo penguins breeding at Kopaitic Island and Nelson Island. The a priori umbrella model with all model terms is given (model 1), with the remaining models only showing the model term that was removed from the umbrella model. The fixed effects terms are sea surface temperature (SST), solar elevation and bathymetry, taking island (Kopaitic or Nelson) and species (chinstrap or gentoo penguins) into account. All models included a random individual effect. The most parsimonious model is in bold.

Model	Fixed effects	n.p	deviance	ΔAIC	weight
1	**island + species + bathymetry + solar elevation + sst + island:solar elevation + island:sst + species:bathymetry + species:solar elevation + species:sst**	**21**	**-433030**	**0.00**	**0.56**
2	-(species:sst)	20	-433032	1.21	0.30
3	-(island:sst)	20	-433033	3.91	0.08
4	- (island:sst + species:sst)	19	-433034	4.54	0.06

5	- (sst + island:sst + species:sst)	18	-433041	15.74	0.00
6	- (island: solar elevation)	20	-433046	29.76	0.00
7	- (island:solar elevation + island:sst)	19	-433048	30.87	0.00

Note: All model information is the same as in Table 2. Only models with a ΔAIC smaller than 31 were included in the table.

Sea surface temperatures increased as the breeding season progressed, especially at Nelson Island (Figure 1). At this site, deeper maximum dive depths of chinstraps and gentoos from incubation to brood to crèche thus coincided with increasing SST (Figure 4). Gentoo dive depths at Nelson Island were predicted to increase from ca. 58 m at 0°C to ca. 66 m at 2°C (Figure 4). Similarly, chinstrap foraging dives at Nelson Island were predicted to be approximately 13 m deeper when temperatures increased from 0 to 2°C (Figure 4). Sea surface temperatures at Kopaitic Island were colder than at Nelson Island, and the relationship between SST and increasing dive depths was not clear at this site, especially for gentoos.

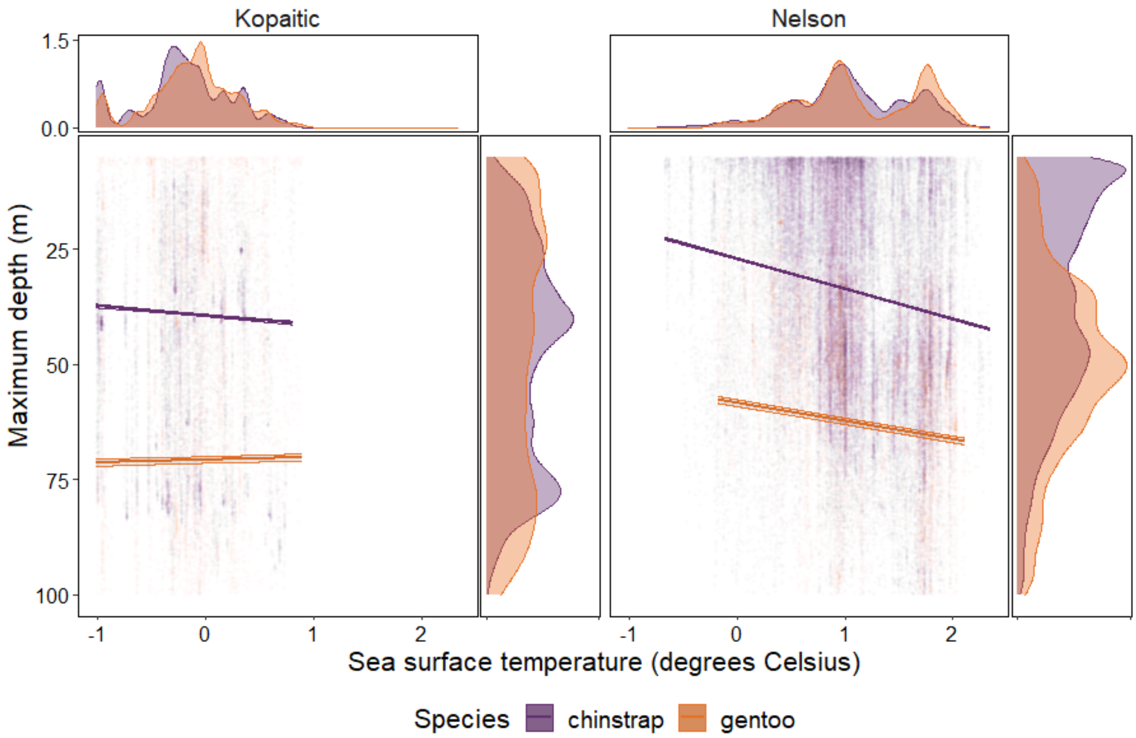

Figure 4. Change in maximum depth of foraging dives of chinstrap penguins (purple) and gentoo penguins (orange) breeding at Kopaitic and Nelson Islands with changing sea surface temperatures. Lines represent the model estimated mean effect and 95% confidence intervals. The observed data (points) and side plots that show the spread of the data are coloured by species.

Chinstraps exhibited stronger diurnal diving behaviour than gentoos, especially at Nelson Island (Figure 5). At Nelson Island, chinstraps dived shallower during low solar elevation hours, which they were exposed to more often than gentoos due to their foraging trips extending further to the north (Supplement 5). Gentoos generally made fewer foraging dives overnight and instead tended to start foraging when solar elevation was above 0° (Figure 5). Overall, the maximum diving depths of both species increased with solar elevation but the change in mean dive depth (from low to high solar elevations) was larger in chinstraps than in gentoos (Figure 5). Thus, differences in maximum dive depths decreased (niche separation between species narrowed) when foraging occurred at high solar elevations (Figure 5). At Kopaitic Island, chinstraps and gentoos did not separate foraging dives temporally (both species made more foraging dives during the day), increasing niche overlap (Figure 5).

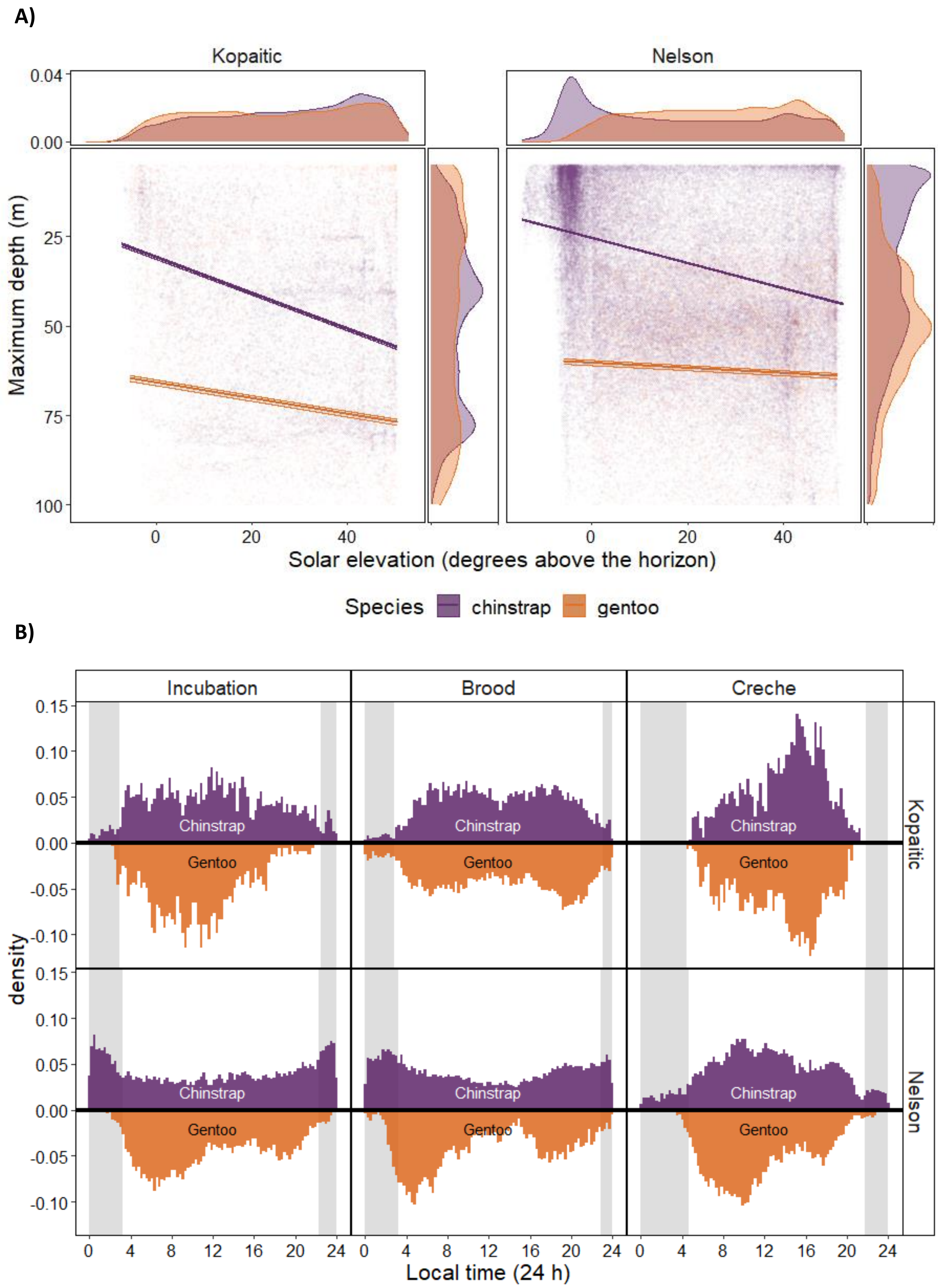

Figure 5. Relationship between foraging dive behaviour and A) solar elevation and B) local time (GMT – 3) for chinstrap penguins (purple) and gentoo penguins (orange) breeding at Kopaitic Island and Nelson Island. A) Change in maximum dive depth with solar elevation. Lines indicate the model estimated mean regression and 95% confidence intervals. The observed data (points) and side plots that show the spread of the data are coloured by species. B) The density distribution of foraging dives chinstrap penguins (purple bars) and gentoo penguins (orange bars) made during different times of the day (GMT – 3) while breeding at Kopaitic Island and Nelson Island. The grey shading represents twilight.

The foraging dive depths of both species initially increased with bathymetric depth, indicating benthic diving, and suggesting that opportunities for niche separation were constrained when bathymetric depth was shallow (Supplement 5). As bathymetric depth increased beyond 50 m, niche separation in foraging dive depths became more evident. In water deeper than ca. 150 m the influence of bathymetry was negligible (Supplement 5).

At Nelson Island, gentoos mostly foraged over the shallow (<200 m depth) Antarctic Peninsula Bank (Figure 6), leading to a high proportion (> 52%) of benthic foraging dives (Table 3). Chinstraps foraged over deep water during incubation, but also concentrated much of their foraging on the Antarctic Peninsula Bank during the brood and crèche (Figure 6A). Consequently, the number of benthic dives chinstraps made increased by an order of magnitude in both brood and crèche relative to incubation (Table 3). Therefore, the relatively shallow bathymetry around Nelson Island reduced opportunities for niche separation in foraging diving depths during the brood and crèche stages (Figure 6). The bathymetry around Kopaitic Island is complex (relatively shallow banks and deeper canyons; Supplement 3) and the variable benthic diving behaviour of both penguin species probably reflects this complex bottom topography (Supplement 5). At Kopaitic Island, gentoos increased the number of benthic dives made from ~30% in incubation to ~50% in brood and ~60% in crèche (Table 3). Over 20% of chinstraps dives were benthic during all breeding stages (Table 3, Supplement 5). Even though dive depths of both species were relatively similar, gentoos performed more benthic dives because they dived over shallow areas whereas chinstraps dived more over deeper water (leading to fewer benthic dives) (Supplement 5).

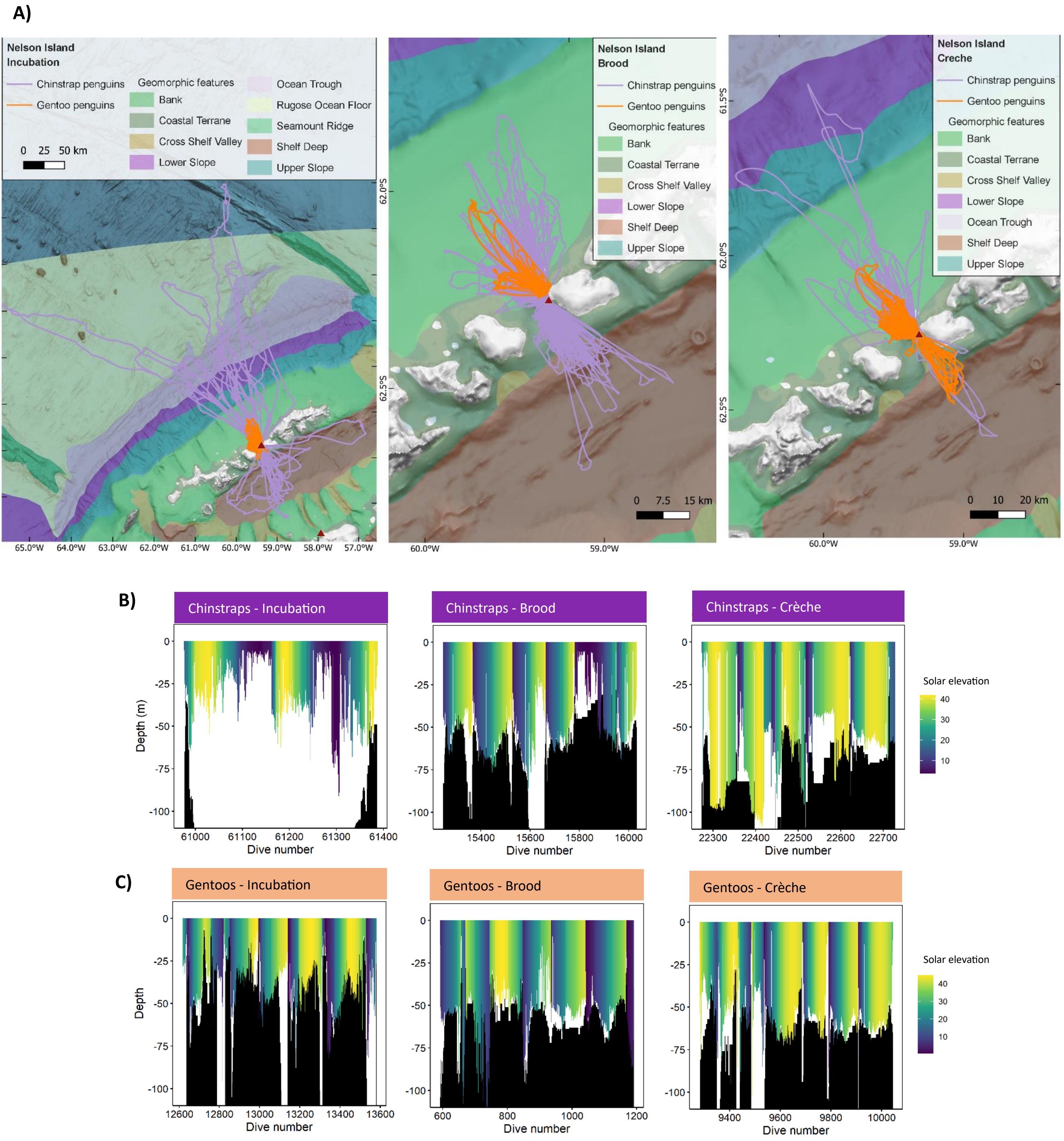

Figure 6. The foraging dives of chinstrap penguins (purple) and gentoo penguins (orange) during incubation, brood and crèche at Nelson Island. A) Benthic geomorphic features (Douglass et al. 2014) in the vicinity of Nelson Island (red triangle). The foraging trips of chinstrap penguins and gentoo penguins are shown. The bathymetric depth layer was obtained from IBCSO v2 (Dorschel et al. 2022) and is shown in the background. The figure was prepared in QGIS v3.28 using Quantarctica3.2

software (Matsuoka et al. 2021). The foraging dive profiles of B) three chinstrap penguins and C) three gentoo penguins tracked during incubation, brood and crèche at Nelson Island. These examples illustrate the general increase in the benthic foraging among chinstrap penguins in brood and crèche. The top bars show foraging diving depth and are coloured by the solar elevation angle, to show how diving behaviour changed with solar elevation. The black bars are bathymetric depth at each dive location. The supplementary material includes an example of diving profiles at Kopaitic Island.

5. Discussion

I show that niche separation varies between sites and through the breeding season in sympatrically breeding penguin species. Niche separation during the breeding season was influenced by central-place foraging constraints and the variability of environmental conditions (e.g. SST, solar elevation and bathymetric depth) that exist around each breeding site. My results indicate that during the brood and crèche stages, when the energetic demands of chicks peak, chinstraps increased niche overlap with gentoos because they reduced their foraging ranges and dived deeper, increasing the opportunity for interspecific competition. This was most evident at Nelson Island where large penguin population sizes and environmental factors may increase competition between these two krill-dependent penguin species.

5.1. Spatial overlap and breeding stage effects on interspecific niche separation

The varying challenges of central-place foraging between breeding stages influenced the size of foraging ranges and maximum foraging dive depth in both species, as seen in many seabird species (e.g. Clarke et al. 2006; Kappes et al. 2015; Jessopp et al. 2020). Similar to previous findings from the Antarctic Peninsula, the 95% home ranges of chinstraps and gentoos overlapped considerably at both study sites throughout the breeding season (Wilson 2010; Lee et al. 2021). My study supports previous findings, where chinstraps have larger foraging ranges during incubation compared to brood and crèche (e.g. Warwick-Evans et al. 2018; Phillips et al. 2021) at both sites, while gentoos had small foraging ranges throughout the breeding season (e.g. Wilson 2010). As the breeding season progressed, foraging ranges of chinstraps became more restricted which led to higher spatial overlap.

A comparison of niche separation between study sites emphasizes the fact that spatial overlap between sympatric species may differ between sites, an aspect which is often not accounted for. In my study, the extent of spatial overlap between species was site-specific, being more common at Nelson Island. Results show how competing species may vary space use between sites to reduce competition. This information can be used when addressing the management or ecology of both species in the region. I expected higher niche overlap between species during chick-rearing stages when chick energy demands are at their highest. But at other breeding sites, the opposite occurred. For example, at King George Island, chinstraps and gentoos separated their spatial niches during chick-rearing by exploiting different habitats (Kokubun et al. 2010). At Nelson Island, foraging ranges overlapped more during chick-rearing (brood and crèche) stages. Alternatively, at Kopaitic Island, spatial overlap was highest during incubation and decreased as the breeding season progressed. Here, gentoos extended their foraging ranges to the left and right of Kopaitic Island where chinstraps did not forage.

During the brood and crèche stages, chinstraps increased niche overlap with gentoos in the underwater dimensions. The deeper diving behaviour of chinstraps when foraging ranges were constrained has also been detected in the sub-Antarctic, where chinstraps compete with macaroni penguins (*Eudyptes chrysolophus*) (Narvestad et al. 2022). Higher spatial- and foraging dive overlap between krill predators may increase opportunity for interspecific competition (Ashmole 1963; Navarro et al. 2009; Kappes et al. 2015). The deeper diving behaviour of chinstraps suggests that krill was also distributed deeper in the water column at this time (Narvestad et al. 2022). Interspecific differences in foraging dive depths similarly varied between sites which re-emphasize taking the local environment into account when investigating interspecific interactions. My study shows the importance of accounting for differences in dive depth together with spatial overlap for predators that move in three dimensions. A study by Cimino et al. (2016) combined space use and dive behaviour to show that sympatrically breeding penguins (Adélie penguins, *Pygoscelis adeliae,* and gentoos) vertically separate their niches by diving at different depths even when their foraging ranges overlap in the horizontal dimension. In my study, gentoos also dived deeper to separate their niche from chinstraps in the water column.

5.2. Site-specific niche separation patterns: Nelson Island

At Nelson Island, higher niche separation occurred during incubation when chinstraps travelled further away from the colony and foraged at shallower depths than gentoos. Chinstraps often forage in the pelagic zone, diving to midwater depths between 15 to 30 m (Wilson and Peters 1999; Miller and Trivelpiece 2008). Gentoos, on the other hand, often separate their foraging niche from chinstraps by 1) foraging at deeper depths (30 – 90 m deep) (Lescroël and Bost 2005; Miller et al. 2009; Kokubun et al. 2010) and 2) including benthic prey in their diet depending on where they occur (Lescroël et al. 2004; Camprasse et al. 2017a). During the brood and crèche stages, spatial overlap increased and coincided with both species increasing their diving effort by diving deeper, reducing niche separation. During the 2021/2022 breeding season, chinstraps at Nelson Island increased their diving efforts (by diving deeper and longer) during late incubation and early chick-rearing, which correlated with low krill availability indicators during the season (Salmerón et al. 2023). Thus, an increased diving effort by chinstraps may indicate that krill availability was also low during the 2018/2019 season, and they had to dive deeper (e.g. to the bottom) to find adequate amounts of krill which decreased niche separation with gentoos who dived deeper. To study niche overlap between krill predators, multi-season datasets (e.g. Narvestad et al. 2022; Salmerón et al. 2023) are advantageous to characterize how environmental conditions in different years affect krill availability and predator foraging behaviour.

During the breeding season, penguins only make short foraging trips and thus, only limited bathymetric features close to the island are available, which are often shallow and limit diving. Both species spent much of their foraging time on 1) the shallow bank which is a broad shallow region (100 – 200 m deep) and 2) the coastal terrane with irregular depth structures along the coastline (Douglass et al. 2014) (Figure 6). These bathymetric features restricted gentoos from diving much deeper to separate their foraging niche from chinstraps. A possible solution for increased competition could be that here, gentoos can forage on other prey types during overlapping periods to enlarge niche separation. Gentoos equipped with GPS and video loggers during the study foraged on krill and fish caught on the bottom (unpublished video footage). However, the sample size of video data was small and dietary changes over the breeding season cannot be confirmed.

5.3. Site-specific niche separation patterns: Kopaitic island

The extent of niche separation between gentoos and chinstraps seemed to be maintained at Kopaitic Island, even during the brood and crèche stages. Gentoos exhibited widespread movement patterns during brood, thus exploiting different areas compared to chinstraps. Gentoos are less constrained by the distribution of krill and could, therefore, extend their foraging movements when krill may have been scarce (Ratcliffe et al. 2021). Furthermore, extended foraging ranges lead to a wider foraging niche with the advantages of reducing competition (intra- and interspecific), and possibly increase access to higher energy prey sources (e.g. for generalist predators such as gentoos; Handley et al. 2017; Saenz et al. 2020). Niche separation at Kopaitic Island can also be attributed to cooler SSTs (between -1°C and 1°C) which are suitable for krill to thrive in (krill optimal temperature range between 0.5°C and 1°C; Michael et al. 2021) and thus improving foraging possibility around the site explaining why chinstraps had relatively small foraging ranges during incubation (Chapter 2). Additionally, the complex bathymetry around Kopaitic Island (with fluctuating deep valleys and shallow banks; Supplement 3) would not constrain gentoos (and their prey) from diving deeper if they intended to reduce competition. However, further interspecific competition with Adélie penguins may exist at Kopaitic Island who also sympatrically breed at the site and also forage mostly on krill, but were not included in this study.

5.4 Limitations of Spatial Overlap Analysis

Some of the advantages of using continuous-time movement models (CTMM) include the specification of a land barrier which restricts penguin space use to ocean areas and the ability to account for autocorrelation of location estimates (typical in animal movement data) (Fleming and Calabrese 2017). The fact that CTMM accounts for autocorrelation by fitting a movement model distinguishes the method from other kernel density estimation approaches, which are not based on a movement model, and thus do not account for autocorrelation (Fleming et al. 2018; Noonan et al. 2019). However, the movement models are based on data which can be limited in studies, leading to unreliable UD results (Fleming and Calabrese 2017). For example, in my study, the UD estimates of gentoos at Kopaitic Island were larger than expected and expanded further than the foraging tracks (Figure 2). Here, my data was limited because the sample size of gentoos tracked at Kopaitic Island was small during incubation (n = 5, foraging trips = 13) and crèche (n=5, foraging trips = 15) compared to brood (n = 25, foraging trips = 82) (Supplement 1) which may have influenced how the UDs were calculated.

5.5. Dive behaviour in response to increasing SST

During summer, SST in large parts of the Antarctic Peninsula increases due to solar radiation (Figure 1). Chinstraps breeding at Nelson Island dived deeper (e.g. 13 m deeper as temperatures changed from 0°C to 2°C), which coincided with warmer SST in the latter part of the breeding season. Dive depth differences were not as apparent at Kopaitic Island where SST remained cold. During the 2018/2019 season, a developing El Niño was reported which is associated with the intrusion of cold, oxygenated water that flows into the Bransfield Strait from the Weddell Sea (Ruiz-Barlett et al. 2018). This cold, dense water blocks the intrusion of modified Circumpolar Deep Water (mCDW) which is responsible for high biological production (Ducklow et al. 2006), thus lowering primary productivity (e.g. phytoplankton) in the area (Loeb et al. 2009). Thus, when the primary food source of krill (i.e. phytoplankton) decreases as SST increases, krill typically change their behaviour by migrating deeper into the water column where temperatures are more suitable (Evans et al. 2020; Hückstädt et al. 2020; Nardelli et al. 2021) and where phytoplankton may be available. The assumption that penguins would only dive deeper in pursuit of prey suggests that an increase in dive depth reflects a possible decrease in krill biomass in near-surface waters. Thus, seasonal- or longer-term increases in SST can lead to lower krill availability in the upper water column which could impact chinstraps' dive behaviour.

Regression models do not directly result in causal inference in statistics (Addicott et al. 2022). When covariates show a linear trend with time, there is a risk that identified relationships could be due to a co-occurring temporal trend of different (including overlooked) factors. Sea surface temperatures increased nearly linearly with time throughout the study period (Pearson correlation coefficient = 0.6; Supplement 6). Therefore, there is a chance that the trends between maximum dive depths and SST that I identified may stem from other overlooked factors that exhibit a temporal trend, rather than a causal relationship with SST. Even though it is difficult to attribute causality from the correlation between SST and diving depths of penguins, my results agree with results from studies on other krill predators. Crabeater seals (*Lobodon carcinophagus*), for example, also dive deeper in response to warmer SST which led to changes in krill distribution (Hückstädt et al. 2020). The increase in diving depth behaviour during chick-rearing also occurs in Arctic seabirds where SST increases are even larger (Stroeve et al. 2014). SST increases during the Mandt's black guillemots (*Cepphus grille mandtii*) breeding season, for instance, which coincides with deeper dives and a switch in prey type when foraging nearshore in benthic habitats (Divoky et al. 2021).

Grosbois et al. (2008) recommend testing if the climatic covariate (SST) considered, accounts for a significant fraction of the variation in maximum dive depth when the time trend is included, using an analysis of correlation among de-trended covariates (Grosbois and Thompson 2005; Grosbois et al. 2008). To make the distinction possible, I tested the effect of de-trended SST on maximum dive depth in the presence of the time trend effect, using the AIC approach (Supplement 6). The analysis showed that the de-trended SST covariate was correlated with the maximum dive depth in the presence of a linear time trend effect (Supplement 6). My results show that the observed increase in maximum dive depth can be attributed to the oceanographic changes that were captured by increased SST over the breeding season. This result emphasizes the fact that SST is an important covariate that can be used to characterize the environmental conditions of a site because SST influences prey availability (e.g. krill), which impacts the dive behaviour of predators. Furthermore, the WAP region is very sensitive to climate change, especially in the long term (Kerr et al. 2018). As global ocean temperatures continue to increase, El Niño conditions may persist leading to longer periods with low primary production (and krill activity) in the Bransfield Strait.

5.6 Dive behaviour in response to solar elevation:

Chinstraps exhibited stronger diel diving behaviour than gentoos, especially at Nelson Island. The diel diving pattern corresponds to the general diel vertical migration of krill (Zhou and Dorland 2004; Trathan and Hill 2016) suggesting that chinstraps are adjusting their diving depths in response to prey distribution in the water column. Daily- and seasonal fluctuations in insolation also affect other krill predators' foraging behaviour (Friedlaender et al. 2013). During summer, the Antarctic Peninsula region experiences long days and only limited periods where solar elevation is below 0° (twilight). Early in the breeding season, when high solar elevation periods were longer (during incubation and early brood), niche overlap occurred for most of the day because both species' foraging dive depths mostly overlapped in the water column. However, during crèche (February) the twilight periods became longer (compared to incubation and brood), and chinstraps could feed on krill at shallower depths for longer periods, separating their foraging dive depths from gentoos. Overall, gentoos showed a preference to actively forage between early and mid-mornings and late afternoons which coincides with previous findings (Lescroël and Bost 2005; Wilson 2010). Chinstraps, therefore, took advantage of longer twilight periods when gentoos were inactive, by making more shallow foraging dives, a phenomenon that occurred more frequently at Nelson Island than at Kopaitic Island. Both position and time are important when determining the solar elevation at a dive location. Many of the chinstrap foraging dive locations during incubation were further north than Nelson Island (62.28°S) and thus had longer low solar elevation periods which coincides with more shallow diving.

5.7 Dive behaviour in response to bathymetric depth

In this study, shallow bathymetric depth was an environmental constraint that restricted diving depths when foraging near the island, thus increasing the overlap in foraging dive depths between chinstraps and gentoos. Marine mammals and seabirds such as penguins face physiological constraints while diving (Butler and Jones 1997; Rosen et al. 2017). Penguins can only dive up to certain depths due to limited oxygen stores when searching for productive resource patches (Kramer 1988; Kooyman and Ponganis 1998). Once bathymetric depth gets deeper than what penguins are capable of diving, their diving behaviour is not influenced by bathymetric depth anymore. Thus, deep bathymetric depths contributed to niche separation between chinstraps and gentoos. Chinstraps often forage in off-shelf regions (depths > 200 m) or at shelf edges and upwellings (Warwick-Evans et al. 2018) whereas gentoos typically forage on-shelf (< 200 m) (this study, Kokubun et al. 2010) which often contribute to niche separation. However, in my study, during the brood and crèche stages, both species foraged close to the islands where most foraging locations occurred in shallow bathymetric depth areas (≤ 200 m; Supplement 3). Foraging in shallow waters during chick-rearing stages may be advantageous for krill predators because shallow bathymetric features vertically restrict prey, which allows predators to spend more time on the bottom catching their prey. Both species were restricted by central-place foraging constraints to forage near the island where prey may be vertically restricted, increasing potential for interspecific competition in shallow waters.

5.8 Ecological implications for variation in niche separation

Changes in environmental conditions often lead to changes in prey availability that determine predator foraging behaviour (Frederiksen et al. 2006; Durant et al. 2007). At Nelson Island, warmer SST (potentially driving chinstraps to dive deeper) and shallow bathymetry near the breeding colony increased niche overlap with gentoos in brood and crèche stages. Thus, specific environmental conditions may amplify interspecific competition at key stages of the breeding season (e.g. when energy demands are highest) if prey resources are limited. From the three environmental variables that I tested, current climate changes reflect that SST increases may be persistent in the long term. Warming of SST leads to a decrease in krill density that may affect where, when and how krill predators forage (Trathan et al. 2003; Wiedenmann et al. 2008; Atkinson et al. 2019; Trathan et al. 2022). In response, species reliant on krill adjust their foraging behaviours (e.g. by diving to deeper depths when SST increases) to ensure survival (Forcada and Trathan 2009) but may however increase opportunity for interspecific competition with other krill predators. The effects of increases in SST on krill in the region may lead to indirect effects on krill-dependent predators, especially chinstraps, in the long term (Warwick-Evans et al. 2019). Oceanographic changes (e.g. increasing SST) due to climate change are particularly pronounced in the Southern Ocean, especially the Antarctic Peninsula (Stammerjohn et al. 2008; Kerr et al. 2018). For example, near-surface temperatures in west Antarctica have increased by 2.4℃ since 1958 (Vaughan et al. 2003; Bromwich et al. 2013). Globally, ocean temperatures are predicted to rise further due to ongoing climate change, increasing overall climate variability (Constable et al. 2014; IPCC 2022), and ultimately, influencing prey distribution. In future, krill predators might need to adjust their behaviours, including distribution and initiation of life history events in response to the spatial and temporal changes in krill behaviour that occur due to long-term climate change. If krill predators make these behavioural changes, it may have consequences for the future distribution and abundance of these species leading to changes in their population dynamics.

Specialist krill feeders such as chinstraps do not prey on alternative prey sources (McMahon et al. 2019) and thus cannot separate their dietary niche axis from competing krill predators such as gentoos. Overlapping foraging niches in response to low krill availability can often result in interspecific competition which reduces breeding success and decreases population abundance (Begon et al. 2009). Chinstraps and gentoos have contrasting population trends in the Antarctic Peninsula region, where the regional chinstrap population size has decreased while that of gentoos has increased during the last four decades (Forcada et al. 2006; Hinke et al. 2007; Carlini et al. 2009; Lynch et al. 2012). Gentoo penguin population increases occurred in areas where they breed sympatrically with either chinstraps or Adélie penguins whose populations are simultaneously declining (Hinke et al. 2007; Lynch et al. 2010; Trivelpiece et al. 2011). Generalist predators such as gentoos have a competitive advantage over krill specialists because they are capable of switching to alternative prey types (Forcada and Trathan 2009). The flexible diet proves advantageous for gentoo populations because prey quantity and distributions are likely to vary over time in highly dynamic marine environments (Ratcliffe et al. 2021). For example, krill population sizes vary annually with patchy distributions in the Antarctic Peninsula (Nicol 2006; Atkinson et al. 2008; Siegel et al. 2013). The declining population trend of chinstraps may reflect decreases in krill availability in regions where species co-exist with gentoos.

Chinstrap penguin's survival during the breeding season may further be affected by competition for krill with other krill predators such as seals and whales (Barlow et al. 2002; Ichii et al. 2007; Lowther et al. 2020). Along with competition between krill predators, chinstraps make longer foraging trips (especially during incubation) than gentoos, and their foraging ranges could overlap with krill fishing fleets during the breeding season (Warwick-Evans et al. 2018). Competition with other predators and the fishery for similar resources would impact both the quantity of krill available (Ainley et al. 2018; Lowther et al. 2020; Warwick-Evans et al. 2022) and the accessibility to these areas due to the presence of predators from different colonies (Wakefield et al. 2013; Trathan et al. 2018).

5.9. Conclusion

By describing the spatial movements and diving behaviour of chinstraps and gentoos across two study sites, this study illustrates that it is important to incorporate data from multiple sites when investigating niche separation between sympatrically breeding seabirds. The extent of niche overlap differed between sites but also as a function of central-place foraging constraints and changes in the environment. Environmental changes across the breeding season (e.g. increased SST at Nelson Island) may determine niche separation and thus possible interspecific competition. Krill biomass is predicted to fluctuate as SST continue to warm in the Southern Ocean, influencing krill specialists such as chinstraps. Increased interspecific competition in response to low krill availability may further drive the population decline of chinstraps.

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Chapter 4: General Conclusion

In this dissertation, I quantified the foraging behaviours (trip parameters and foraging diving depths) and habitat use of chinstrap penguins (*Pygoscelis antarcticus,* chinstraps hereafter) and gentoo penguins (*P. papua,* gentoos hereafter) breeding at two study sites (Nelson Island and Kopaitic Island) in the Antarctic Peninsula. My analyses considered intra-specific and inter-specific comparisons among and within populations. First, I investigated phenotypic plasticity in the foraging behaviours among and within populations of both species. Both gentoos and chinstraps exhibited phenotypic plasticity in various aspects of their foraging behaviours (e.g. trip distances and foraging dive depths), which varied according to site, breeding stage and solar elevation. Next, I compared the extent of niche separation between the sympatrically breeding chinstraps and gentoos at the two study sites. The extent of niche separation between chinstraps and gentoos was modified by changes in their central-place foraging constraints and the local environmental conditions where the species foraged.

1.1. The influence of local environmental conditions

My study tracked the foraging behaviours of *Pygoscelis* penguin populations breeding at distant colonies (131 km apart) where individuals experienced contrasting foraging environments which led to site-specific trip and dive behaviours for both species. The differences in local environmental conditions (e.g. sea surface temperatures, [SST]) may influence regional krill availability and thus force penguins to adapt their foraging behaviours accordingly. For example, in areas with warmer waters (e.g. Nelson Island) chinstraps had larger foraging ranges during incubation compared to their conspecifics in colder areas (e.g. Kopaitic Island). This may be because krill was more widely available around Kopaitic Island, where more suitable environmental conditions (lower SST) may have existed for krill predators during the 2018/2019 breeding season. After all, krill prefer the colder SST (between 0.5 and 1.0°C; Atkinson et al. 2006; Michael et al. 2021). Furthermore, the environmental conditions surrounding each site influenced the extent of niche separation between chinstraps and gentoos. For example, at Nelson Island, the warmer SST and shallow bathymetric depth increased niche overlap because these environmental conditions prevented species from partitioning their foraging niches during peak energy demands. Therefore, my study emphasizes that the environmental conditions of a species' foraging range should be accounted for when interpreting and comparing the foraging behaviours of both species.

Changes in local environmental conditions (e.g. increased SST) often lead to changes in prey availability and distribution (Frederiksen et al. 2006; Durant et al. 2007). In response to changing environments and prey distributions, predators are expected to adjust their foraging behaviours to ensure survival (Forcada and Trathan 2009). This may, however, increase the opportunity for interspecific competition with other krill predators. For example, as the breeding season progressed and SSTs increased, chinstraps adjusted their behaviour to dive deeper. An increase in SST is expected to drive krill to migrate deeper into the water column to cooler temperatures, which limits krill biomass closer to the surface (Evans et al. 2020; Nardelli et al. 2021). The effects of long-term climate change (e.g. increased SSTs) may thus be detrimental for krill predators. Oceanographic changes due to long-term climate change are particularly pronounced in the Southern Ocean, especially the Antarctic Peninsula (Kerr et al. 2018). Higher SSTs lead to longer periods of low primary productivity (and krill activity) in the region. Thus, regionally low krill biomass near the surface due to increases in SST may lead to indirect effects on krill-dependent predators, especially chinstraps, in the long term (Warwick-Evans et al. 2019). Specialist krill feeders such as chinstraps, who have highly repeatable diving behaviours, will not survive if krill availability becomes too low because they do not feed on alternative prey sources (McMahon et al. 2019). Thus, chinstraps will struggle to survive (during demanding periods such as the breeding season) if krill resources become scarce. Overlapping foraging niches with other krill predators such as gentoos, in periods of low krill availability, can then result in high interspecific competition which may lead to even more decreases in prey availability, causing breeding failures which may explain the regional reduction in chinstrap population numbers. Gentoos, in contrast, are generalist predators, who can switch to alternative prey sources (e.g. benthic fish) when krill becomes limited. This might explain why their populations are stable and increasing in this region of Antarctica.

1.2. Intraspecific competition vs. interspecific competition

My study highlights that the pressure of intraspecific competition among chinstrap individuals may be higher than the potential interspecific competition pressure between chinstraps and gentoos. This is because, in areas where chinstraps and gentoos breed sympatrically, the colony size of chinstraps was much larger than gentoos at the same site (e.g. at Nelson Island: 89685 chinstrap pairs vs 3347 gentoo pairs). For chinstraps, who are specialist predators, the more individuals competing for the same resources, the quicker resources will become limited (Ashmole 1963), leading to higher competition for resources between conspecifics. The sheer size of the colony of chinstraps (compared to gentoos) ultimately highlights that the possibility for intraspecific competition to occur is larger than the possibility for interspecific competition. Intraspecific competition occurs due to the lack of niche partitioning within species because individuals have similar foraging behaviours (Grémillet and Charmantier 2010; Masello et al. 2010). However, my study showed that within a population, chinstraps showed individual-level phenotypic plasticity in their foraging trip distance and maximum dive depth behaviours with differing behavioural types to reduce intraspecific competition. Furthermore, the possibility of intraspecific competition was larger for chinstraps than they were for gentoo penguins. Between sites, the possibility of intraspecific competition was also larger at Nelson Island than at Kopaitic Island. The chinstrap population at Nelson Island is tenfold larger than the chinstrap colony at Kopaitic Island (89685 pairs vs 9400 pairs) (Woehler 1993; Silva et al. 1998). Therefore, chinstraps from the larger colony (Nelson Island) often exhibited larger foraging ranges, possibly due to higher intraspecific competition with conspecifics compared to the smaller colony (Kopaitic Island). The population numbers of gentoos are similar between sites (3347 vs 3400) (Woehler 1993; Silva et al. 1998), and thus individuals probably experience similar amounts of intraspecific competition at each site depending on prey availability. Thus, the extent of intraspecific competition for krill among chinstrap individuals may be larger than the possibility of interspecific competition between gentoos and chinstraps breeding in the same colony.

However, my study indicated that at both sites, the possibility for interspecific competition cannot be completely ignored, especially during the peak energy-demanding periods. Space use analysis indicated that at both sites, the foraging niches of sympatrically breeding chinstraps and gentoos overlapped most during the brood and crèche stages. This is when both species' foraging ranges were close to the island and dive depths also overlapped, increasing the possibility for interspecific competition. During incubation, chinstraps reduced niche overlap by foraging further away but then contracted their foraging ranges during brood and crèche when energetic demands were highest, which increased niche overlap with gentoos who had small foraging ranges throughout the breeding season. Chinstrap individuals dived deeper and even performed benthic dives during brood and crèche when higher inter- and intraspecific niche overlap occurred. In an attempt to decrease interspecific niche overlap with gentoos, chinstraps followed an energy-efficient diel diving pattern whereby they foraged during twilight periods when gentoos were not actively foraging. Feeding at twilight may ensure that chinstraps find adequate amounts of krill in the shallow waters, while gentoos are not competing, thus slightly separating their foraging niche from gentoos and ensuring co-existence.

In this study, I show that the foraging behaviours of gentoo individuals depended on the local environment. Gentoos showed site-specific differences in their diving behaviours, possibly because of their slight differences in diets at the two sites. For example, at Kopaitic Island, gentoos followed the same diel diving pattern as chinstraps, but at Nelson Island, individuals dived to similar depths throughout the day. Furthermore, gentoos dived deeper and performed more benthic dives than chinstraps, which allowed gentoos to partially separate their niche from chinstraps when environmental conditions (e.g. bathymetric depth) allowed. Gentoos did not adjust their foraging behaviours when competition pressure (intra- and inter-) became higher, which shows that to an extent, gentoos are not influenced by limited krill stock or increased competition pressure. Phenotypic plasticity in their foraging behaviours is an advantage that may explain why gentoo population numbers are increasing in the area. At Kopaitic Island, the diving behaviours of both species indicated that they may feed primarily on krill throughout the breeding season and that the need for niche separation may have been lower than at Nelson Island. There was possibly a higher level of interspecific competition at Kopaitic Island than what was estimated in this study. This is because Adélie penguins (*P. adeliae*), also mainly krill predators, breed sympatrically with chinstraps and gentoos at this site but were not included in this study. As a result, there may be even more overlap in foraging niches of krill-dependent predators than what was estimated in the study.

1.3. Long-term effects on chinstrap penguin foraging behaviours

My study suggests that chinstraps may struggle to cope in the long term with their current foraging behaviour strategies if current climate changes continue which affects krill biomass (Flores et al. 2012). But climate change is not the only anthropogenic driver potentially influencing the abundance and availability of krill biomass to krill predators. Since the 1980s there has been an increasing interest in commercial harvesting of krill, currently the largest fishery in the Southern Ocean (Nicol et al. 2012). The increasing catch and spatial concentration of the commercial krill fishery in the Antarctic Peninsula pose potential threats to krill-feeding predators such as a reduction in krill abundance (Watters et al. 2020; Warwick-Evans et al. 2022a) or accidental by-catch and mortality (Trathan et al. 2015; Dias et al. 2019). The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) was established in 1982 with the key mission to manage the krill fishery in the Southern Ocean so that the risks to populations of krill-dependent predators are minimized (CCAMLR 2018, Article II). CCAMLR manages the fishery by setting low catch limits and spreading the catch spatially to minimize the risks of overfishing (Hill et al. 2016). However, spatial allocation of catch may happen at too large scales, and some chinstrap colonies (under current fishing pressure especially those breeding at the South Orkney Islands) may overlap with fishing activities during the breeding season. Thus, chinstraps' survival during the breeding season may also be affected by other factors influencing the low krill biomass which were not included in this study. This includes increased krill fishing (Trathan et al. 2018) and increased competition with other krill predators following the recovery of seal and whale populations, which in turn will affect penguin dynamics (Hinke et al. 2017; Lowther et al. 2020).

I suggest that researchers keep monitoring the foraging behaviours of chinstraps in the Antarctic Peninsula because their foraging behaviours and habitat use may be a good proxy of the krill abundance in their foraging areas (Reid et al. 2005; Piatt et al. 2007). The Antarctic Peninsula is an important area for krill fishing and thus could be a valuable area for risk assessments of the fishery-predator-prey interactions (see www.ccamlr.org/en/organisation/camlr-convention-text; accessed 18 February 2023). Commercial krill harvesting is increasing in the northwest Antarctic Peninsula region (Kawaguchi et al. 2006) which likely results in an increased likelihood of competition between krill predators and the krill fishery (Trathan et al. 2018; Watters et al. 2020). Continued studying of the spatial, diving, and temporal behaviours of chinstraps during foraging trips can provide insight into their foraging behaviour. Foraging behaviour information can be regularly updated as more data becomes available, particularly in data-deficient regions. Details of the foraging behaviour and consumption needs of chinstraps can then be incorporated into the CCAMLR krill fishery management plan when deciding on krill catch limits and identifying areas where chinstrap distribution overlaps with the krill fishery (Warwick-Evans et al. 2022b).

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Chapter 2: Supplementary Material

Supplement 1 – Tag deployment summary

1.1 Summary of deployments per round

Deployment rounds were classified according to breeding stages (incubation, brood and crèche) between December 2018 and February 2019 (Table S1 and S2) where: 1) incubation was when an adult pair was incubating 1 or 2 eggs, with 1 parent foraging at a time and the other incubating the egg at the colony. 2) Brood was when there was one parent with 1/2 small chicks and 1 parent foraging at a time. 3) Crèche was when chicks formed large groups while both parents were out foraging and then came back to the colony to feed their chick.

Table S4. Summary table of each round of deployments for chinstrap penguins during the 2018/2019 breeding season at Nelson and Kopaitic Island.

Chinstrap penguins					
Island	Deployment round	Stage	Deployment / Retrievement date	Tags deployed	No. of tags with clean data
Nelson	1	Incubation1	3-4 Dec / 12-19 Dec	15	14
Nelson	2	Incubation2	15-16 Dec / 23-27 Dec	14	13
Nelson	3	Brood1	26-28 Dec / 3-5 Jan	14	13
Nelson	4	Brood2	6 Jan / 12-14 Jan	13	12
Nelson	5	Brood3	14 Jan / 20-25 Jan	13	13
Nelson	6	Brood4	22-26 Jan / 30 Jan-1 Feb	11	10
Nelson	7	Creche1	31 Jan-2 Feb / 7-8 Feb	10	9
Nelson	8	Creche2	8-9 Feb / 13-14 Feb	9	9
Kopaitic	1	Incubation1	9 Dec / 17-19 Dec	10	8
Kopaitic	2	Incubation2	17-18 Dec/ 23-25 Dec	8	7
Kopaitic	3	Brood1	26 Dec/ 02 Jan	9	8
Kopaitic	4	Brood2	04 Jan/ 09 Jan	10	9
Kopaitic	5	Brood3	13 Jan / 19-20 Jan	10	9
Kopaitic	6	Brood4	24 Jan/ 29 Jan	10	9
Kopaitic	7	Creche1	01 Feb/ 05 Feb	9	8
Kopaitic	8	Creche2	07 Feb/ 11 Feb	8	4
Total				**173**	**155**

Table S5. Summary table of each round of deployments on gentoo penguins during the 2018/2019 breeding season at Nelson and Kopaitic Island.

Gentoo penguins					
Island	Deployment round	Stage	Deployment / Retrievement date	Tags deployed	No. of tags with clean data
Nelson	1	Incubation1	4-5 Dec / 15-18 Dec	5	5
Nelson	2	Incubation2	18-20 Dec / 27 Dec-6 Jan	5	5
Nelson	3	Brood1	31 Dec-1 Jan / 7-8 Jan	3	3
Nelson	4	Brood2	8-9 Jan / 13 Jan	4	4
Nelson	5	Creche1	15 Jan / 19-20 Jan	5	4
Nelson	6	Creche2	23 Jan / 30-31 Jan	5	5
Nelson	7	Creche3	31 Jan / 7-8 Feb	5	5
Kopaitic	1	Incubation1	10 Dec / 18 Dec	5	5
Kopaitic	2	Brood1	19 Dec / 25-28 Dec	5	5
Kopaitic	3	Brood2	27-29 Dec / 02-03 Jan	5	5
Kopaitic	4	Brood3	04 Jan/ 09-11 Jan	5	5
Kopaitic	5	Brood4	13 Jan/ 20-21 Jan	5	5
Kopaitic	6	Brood5	24 Jan/ 29 Jan	5	5
Kopaitic	7	Creche1	01 Feb/ 05 Feb	5	5
Total				**67**	**66**

Supplement 2 - Utilisation distributions (UDs)

Additional details to quantify the extent of home ranges of chinstrap and gentoo penguins using Utilisation distributions (UDs).

2.1 First-passage time (FPT) analysis from 'Track2KBA'

Determining an appropriate kernel smoothing parameter (*h*) is an important step to determine at which scales the tracking points are smoothed. When comparing species that move at similar scales, authors recommend using the same smoothing parameter value to avoid introducing differences due to data processing (Carneiro et al. 2020). A first-passage time (FPT) analysis was used to reveal the average spatial scale at which area-restricted search (ARS) behaviour occurred. We calculated the average spatial scale (using the '*findScale*' function from the Track2KBA package; Beal et al. 2021) across all trips by both species (Figure S1). The value (*href* = 7 km; Figure S1) was then used as the kernel smoothing parameter (*h*) in the calculations of the UDs (Lascelles et al. 2016).

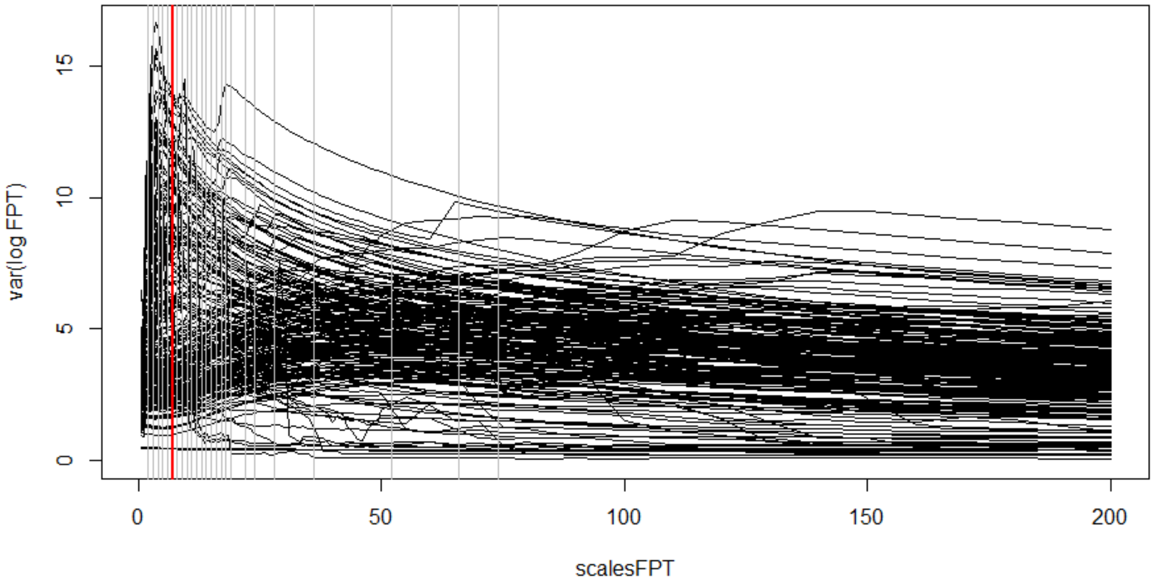

Figure S1: First Passage Time (FPT) analysis of chinstrap and gentoo penguin tracking data. Each black line represents the log variance in FPT at each scale for an individual foraging trip. The grey lines show the peak scales for each foraging trip. The solid red line shows the average ARS scale (7 km) for the whole group which was then used to define the kernel smoothing parameter (*h* value) for foraging range estimation following Lascelles et al. 2016.

2.2 Size of core foraging (50%)- and home ranges (95%) based on UD calculations

Table S6. Size of the core foraging (50%) and home range areas (95%) during incubation and chick-rearing stages for chinstrap and gentoo penguins breeding at Nelson and Kopaitic Island.

	Chinstrap penguins					Gentoo penguins			
	Incubation		Chick-rearing			Incubation		Chick-rearing	
	Kopaitic (km²)	Nelson (km²)	Kopaitic (km²)	Nelson (km²)		Kopaitic (km²)	Nelson (km²)	Kopaitic (km²)	Nelson (km²)
50% Core foraging area	556.94	6487.19	250.00	430.63	50% Core foraging area	389.69	342.25	433.63	315.69
95% Home range	2749.13	38696.00	1125.50	3153.75	95% Home range	1531.44	1697.19	1931.25	1717.00

Supplement 3 – Expectation Maximization (EM) classification of dive behaviours

3.1 Additional information on the dive characteristics used to classify dive behaviours

Dives were classified into behaviours according to similarities in the following diving characteristics:

Bottom time
The time spent at the bottom phase of a dive is usually a good indicator of foraging (Bestley et al. 2015; Phillips et al. 2021). The longer an individual spends at the bottom of a dive, the more likely it was to feed. Dives with bottom times of short duration were probably travelling or exploratory quick, short dives where no foraging took place.

Maximum depth
Chinstrap penguins typically forage at depths of 15 to 30 m (Wilson and Peters 1999; Miller and Trivelpiece 2008; Kokubun et al. 2010) and gentoo penguins at depths of 30 to 90m (Mori and Boyd 2004; Miller et al. 2009; Kokubun et al. 2010). Maximum depth was included as we expected penguins to have a higher probability of finding prey in deeper dives compared to shallow dives, which is typical of transit behaviour.

Dive residuals
Following Bestley et al. 2015, we calculated 'dive residuals' by fitting a linear mixed-effect model with dive duration as the response and maximum depth as a fixed effect using the 'lme4' package (Bates et al. 2015). Individual identity was fitted as a random intercept and maximum depth as a random slope. This random effect structure accounted for variation in mean diving depths between individuals (intercept) and allowed the relationships between dive duration and maximum depth for each individual to vary among the overall population mean. We extracted the Pearson residuals from the modelled relationship as the 'dive residual'. The magnitude and direction of the residuals can be used to ascertain whether the dive duration was relatively longer or shorter than expected for a dive of a given depth. Dives that are longer than expected (positive residuals) indicate higher relative effort, which might indicate foraging. In contrast, dives that are relatively shorter than expected (negative residuals) indicate lower relative foraging effort. Dive residuals were derived from dive duration, so it was unnecessary to include dive duration as a variable in the classification analysis.

3.2 EM classification results of diving behaviours

'Foraging' dives indicated a high probability that the individual could pursue and capture prey during the dive. Foraging dives mostly had long bottom times, shallow to deep maximum dive depths and positive dive residuals (Figures S2 and S3). The two 'non-foraging' dive behaviours had short bottom times and negative dive residuals (i.e. lower-than-expected diving effort; penguins spent less time in the bottom phase of a dive than expected) (Figures S2 and S3). For 'non-foraging' dives the probability of foraging was lower and penguins probably performed other activities such as travelling, exploring and searching for prey patches. Non-foraging deep dives were characterized as dives with deep maximum depths, which could be indicative of exploratory dives made by penguins (Figures S2 and S3, see Table 1 in the main dissertation). The third behaviour, non-foraging shallow dives was indicative of 'travelling' dives with shallow maximum depths (Figure S2 and S3, see Table 1 in the main dissertation).

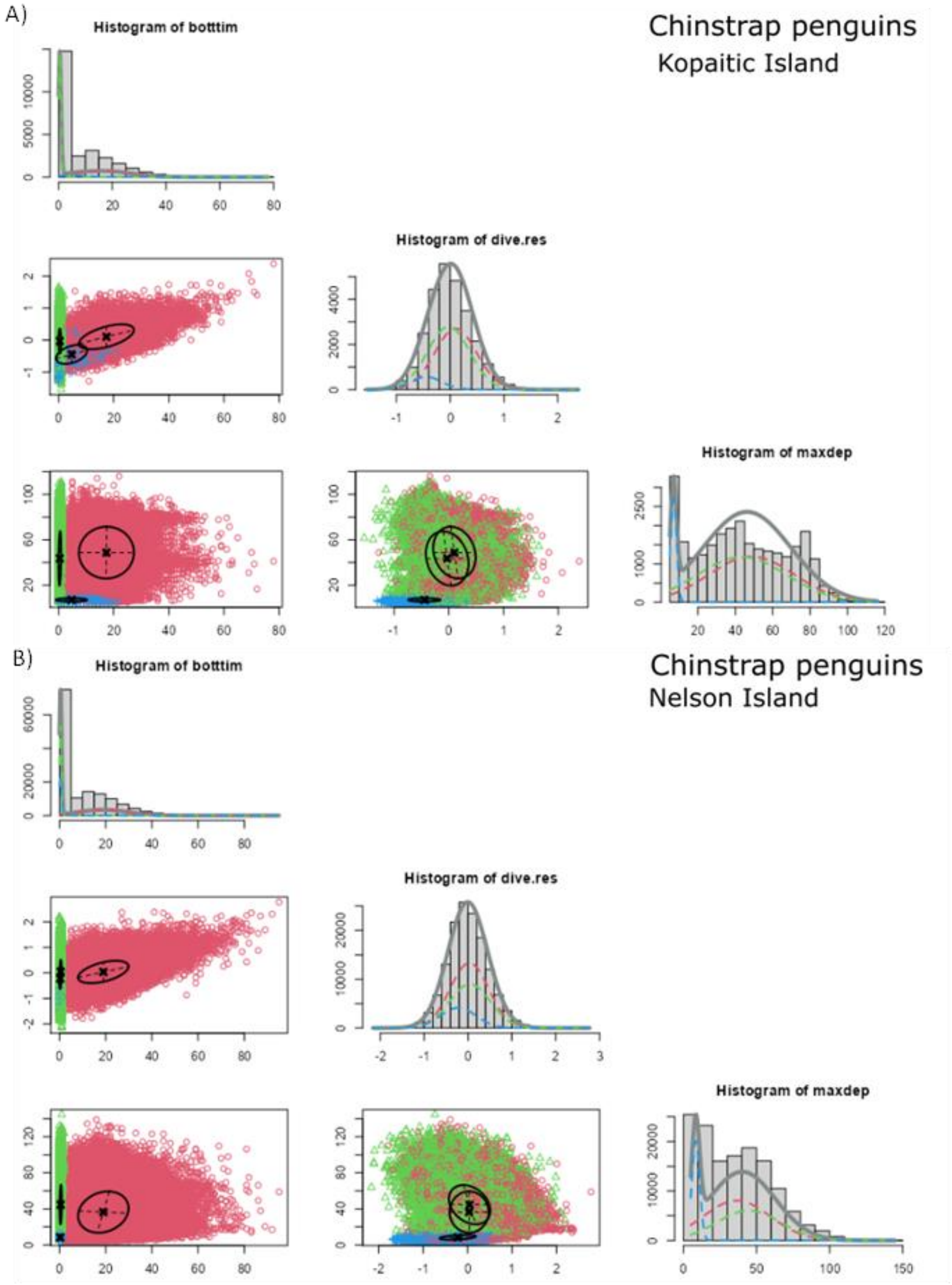

Figure S2. The EM classification output uses the dive characteristics (bottom time, dive residuals and maximum depth) to classify dive behaviours for chinstrap penguins from A) Kopaitic Island and B) Nelson Island. The dive behaviours are presented in different colours: Red = foraging dives, green = non-foraging deep dives and blue = non-foraging shallow dives.

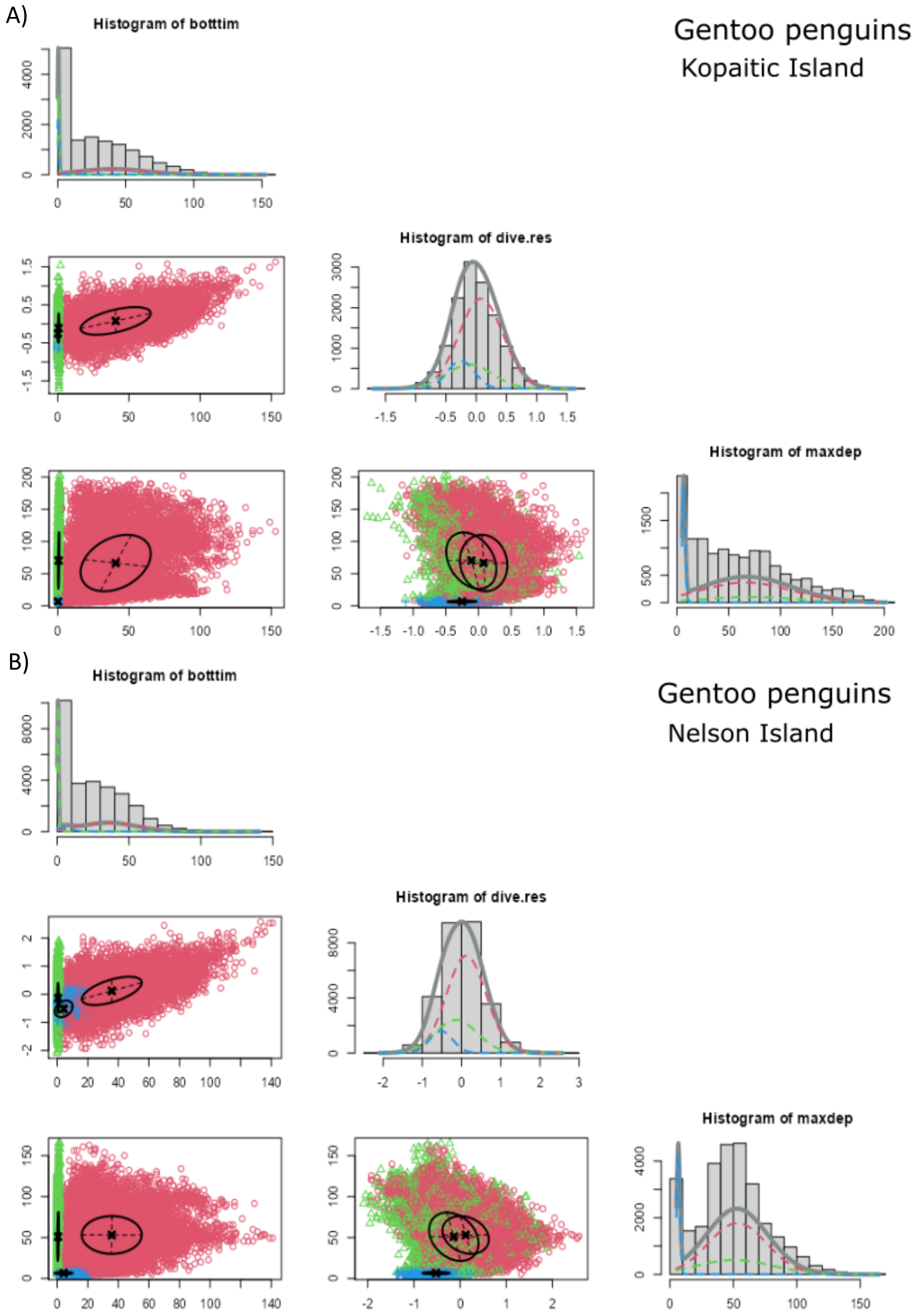

Figure S3. The EM classification output uses the dive characteristics (bottom time, dive residuals and maximum depth) to classify dive behaviours for gentoo penguins from A) Kopaitic Island and B) Nelson Island. The dive behaviours are presented in different colours: Red = foraging dives, green = non-foraging deep dives and blue = non-foraging shallow dives

Supplement 4 – Characterising the environmental space

4.1 Additional information on the environmental variables used

I characterized the environmental spaces where chinstrap and gentoo penguins foraged using environmental variables extracted from their 95% UDs. Gridded bathymetry (International Bathymetric Chart of the Southern Ocean (IBCSO) version 2, 500m x 500m resolution; Dorschel et al. 2022) were used to calculate ocean depth (meters), slope (degrees) and distance to shelf edge (km). The shelf edge was defined as the 200 m bathymetry contour. Areas where bathymetry was <200 m were defined as 'on-shelf' and areas >200m depth were defined as off-shelf. Distances to shelf locations on the shelf were given a negative sign and off-shelf distances-to-shelf locations were positive. Thus, for each at-sea location, the distance to the shelf edge was known and whether the location was on- or off-shelf. Sea surface temperatures may limit the distribution of seabirds depending on the distribution of their prey (Hinke et al. 2019). Daily Sea Surface Temperatures were obtained from NASA's 0.01˚Multi-scale Ultra-high Resolution (MUR) analysis of global sea surface temperature (Chin et al. 2017) using the 'rerddap' package (Chamberlain et al. 2019). Current speed was included to identify areas of increased flow where nutrients (and prey) concentrate (Waggitt et al. 2016). The 'rerddap' package was also used to obtain NOAA's 0.25˚daily Horizontal and Vertical Geostrophic current speed (Near real-time Geostrophic currents, 0.25° x 0.25°, NOAA/AOML, https://upwell.pfeg.noaa.gov/erddap/info/miamicurrents/index.html). Daily mean Salinity (Practical Salinity Unit) and Daily Potential temperature (θ°C) were downloaded from the Global Ocean Ensemble Physics Reanalysis product through the E.U. Copernicus Marine Environment Monitoring Service (CMEMS) at 0.25° resolution (https://doi.org/10.48670/moi-00024). Temperatures and salinity measurements were retrieved from the 0 to 200 m range depth for each available location in the study site.

4.2 Sea surface temperature changes

Sea surface temperature changes across the breeding season across the study area (Figure S4).

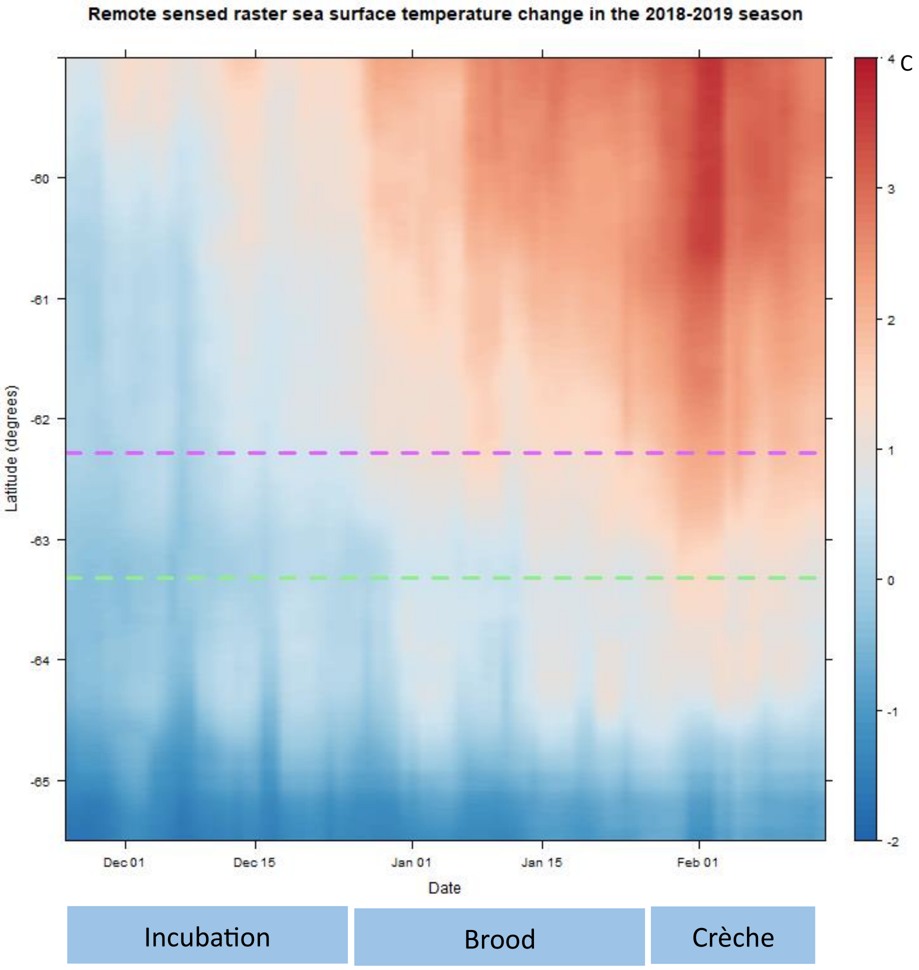

Figure S4. Hovmöller plot showing how sea surface temperature (˚C) conditions have changed within the study area over the 2018/2019 breeding season from December to February. Deployments were made during the incubation, brood and crèche stages. Dashed lines indicate the location of Nelson Island = purple and Kopaitic Island = green where deployments were done based on their latitudinal coordinates.

4.3 Principal component analysis (PCA)

Overall, sea surface temperature (SST) and salinity (sal) (negatively correlated) were the most important variables to characterize the environmental space (Figures S5 and S6). The most important variables were identified by the largest eigenvalues of the PCA. For chinstraps, sal explained the largest variation in the data between the two sites during incubation (eigenvalue = 0.50) and chick-rearing (0.54) (Figure S5). For incubation, principal component 1 (PC1) explained 51.98% and PC2 15.71% of the variation in the data (Figure S5a). For chick-rearing, PC1 and PC2 explained a cumulative total of 75.28% of the variation in the data with sal (0.54), vertical current (v_current) (0.54) and SST (-0.53) explaining most of the variance in the data (Figure S5b). For gentoos, sal and SST explained the biggest part of the variation in the data between the two sites during incubation (sal = 0.47, sst = -0.46) and chick-rearing (sal = 0.51, sst = -0.53) (Figure S6). For incubation, PC1 explained 52.74% and PC2 21.43% of the data variation (Figure S6a). For chick-rearing, PC1 and PC2 explained a cumulative total of 80.67% of the variation in the data with sst, sal and v_current (0.50) explaining most of the variance in the data (Figure S6b).

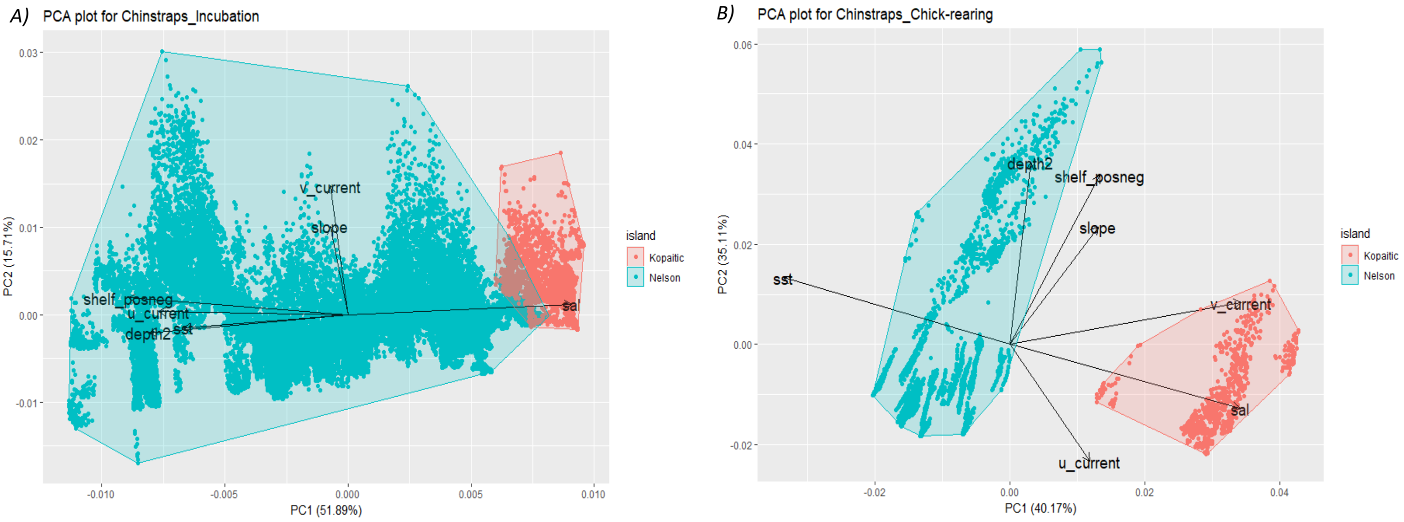

Figure S5. Principal component analysis of the environmental variables extracted from the 95% home range for chinstrap penguins during A) incubation and B) chick-rearing. Observed data are coloured according to island (Kopaitic Island = red, Nelson Island = blue). The black arrows represent the size of each principal component.

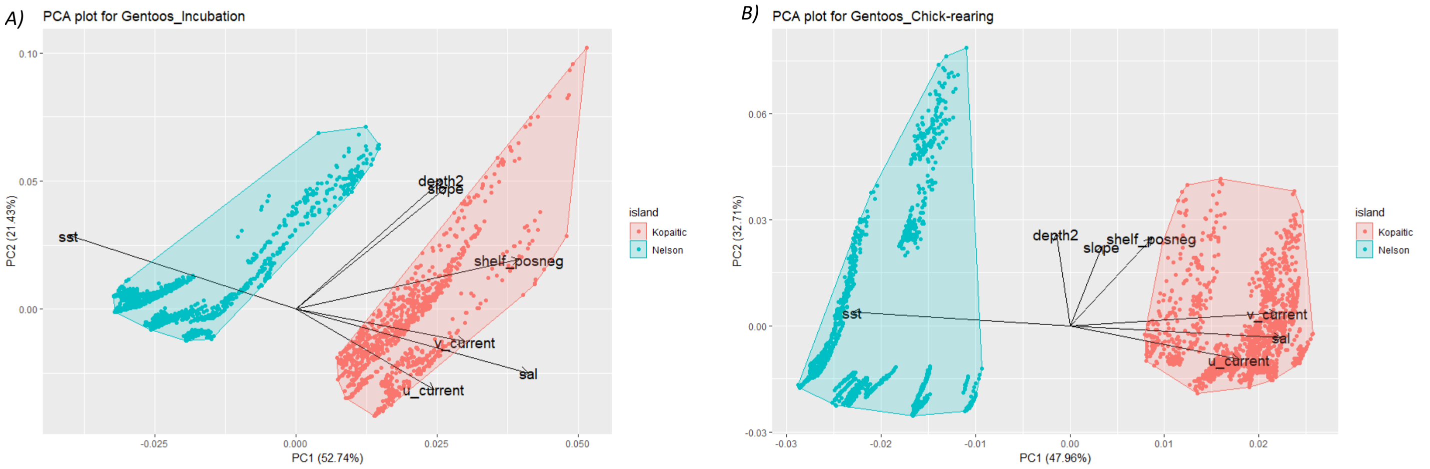

Figure S6. Principal component analysis of the environmental variables extracted from the 95% home range for gentoo penguins during A) incubation and B) chick-rearing. Observed data are coloured according to island (Kopaitic Island = red, Nelson Island = blue). The black arrows represent the size of each principal component.

4.4 Univariate plots of additional environmental variables to characterise the environmental space

Both species' use of the habitat areas led to similar conclusions regarding the characterisation of the environmental spaces regardless of how the home range sizes differed between the two species. The waters surrounding Kopaitic Island were saltier than Nelson Island during the breeding season (Figures S7 and S8). Other important variables to characterise the environmental space included vertical and horizontal geostrophic currents. At both islands, the horizontal and vertical geostrophic currents in the penguins' home ranges were < 25 cm.s^{-1} (Figures S7 and S8). The measurements indicate that the environmental space surrounding the islands had a slow to moderate vertical and horizontal current compared to other current measurements in the Bransfield Strait, reaching maximum speeds of up to 50 cm.s^{-1} south of the South Shetland Islands during summer (Veny et al. 2022). Kopaitic Island always had slightly faster mean vertical current speeds (9 ± 4 cm.s^{-1}) compared to Nelson Island (5 ± 7 cm.s^{-1}) (Figures S7 and S8). The environmental characteristics of the island spaces were quite similar in terms of slope, bathymetry and distance to the shelf edge (Figures S7 and S8). With these environmental variables, we could not clearly separate the environmental spaces of the islands and thus we concluded that the two islands had similar slope, bathymetry and distance to shelf edge characteristics (Figures S7 and S8).

4.4.1 Chinstrap penguins

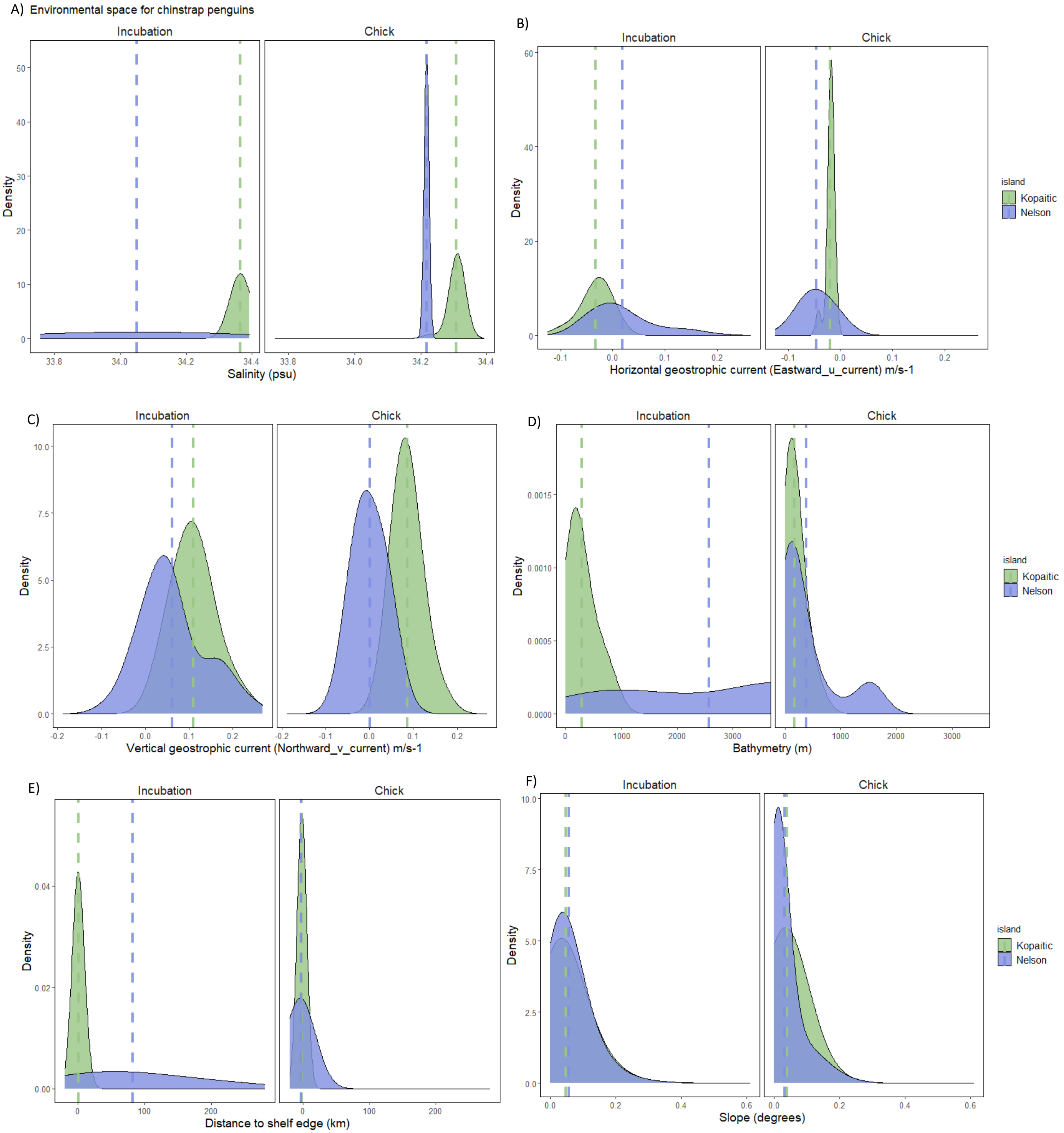

Figure S7. Density plots for the environmental space of the 95% home range utilised by chinstrap penguins around both breeding populations (Kopaitic Island = green and Nelson Island = purple) during incubation and chick-rearing stages of the 2018/2019 breeding season. The additional environmental variables used to characterise the environmental space of each island were A) Salinity (PSU), B) Horizontal geostrophic current (m/s^{-1}), C) Vertical geostrophic current (m/s^{-1}), D) Bathymetry (m), E) Distance to shelf edge (km) and F) Slope (degrees). The dotted lines represent the mean value for each island.

4.4.2 Gentoo penguins

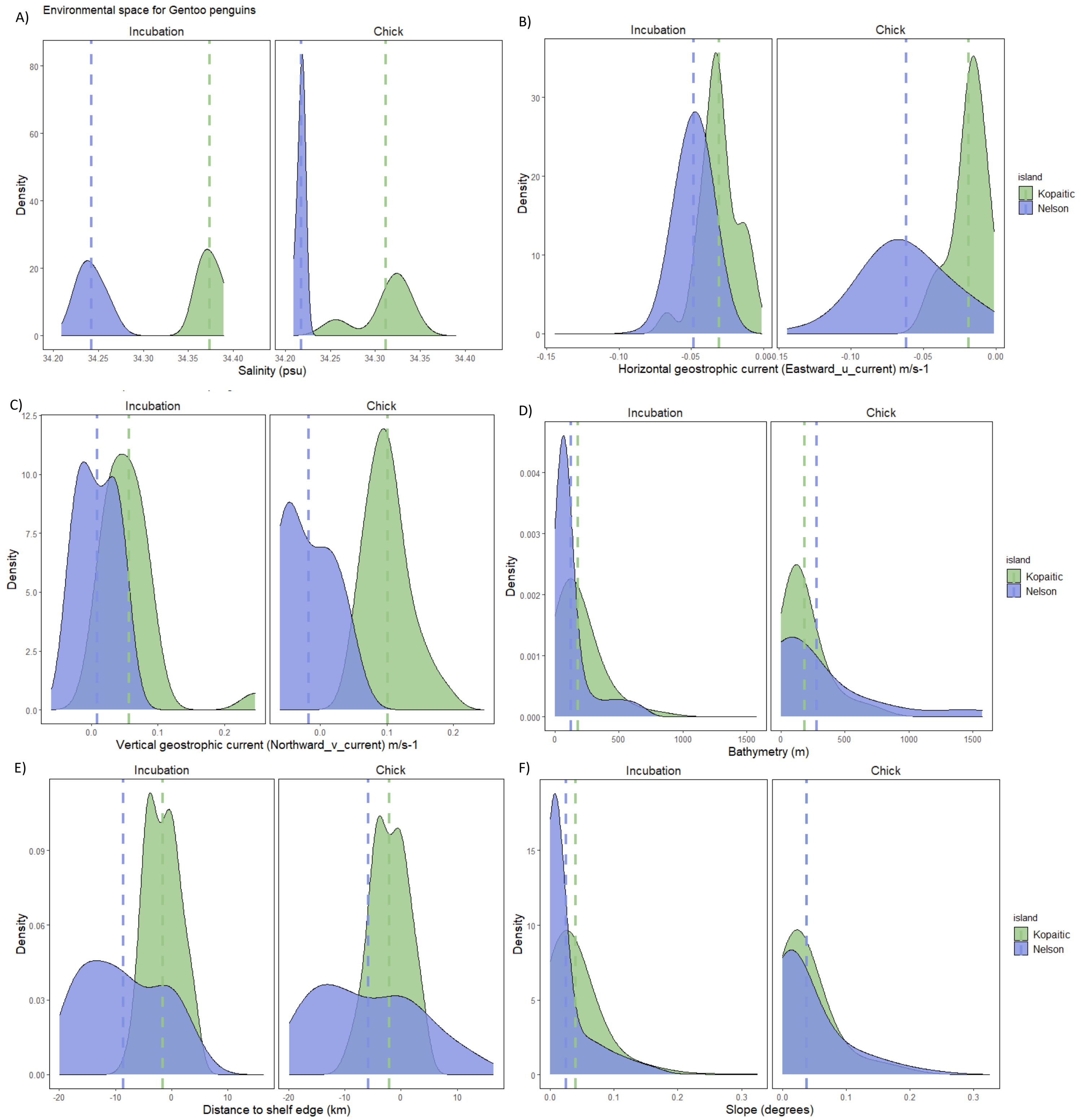

Figure S8. Density plots for the environmental space of the 95% home range utilised by gentoo penguins around both breeding populations (Kopaitic Island = green and Nelson Island = purple) during incubation and chick-rearing of the 2018/2019 breeding season. The additional environmental variables used to characterise the environmental space of each island were A) Salinity (PSU), B) Horizontal geostrophic current (m/s^{-1}), C) Vertical geostrophic current (m/s^{-1}), D) Bathymetry (m), E) Distance to shelf edge (km) and F) Slope (degrees). The dotted lines represent the mean value for each island.

4.5 Evolution of the water masses over the breeding season using temperature-salinity plots

I plotted temperature-salinity (T-S) plots to identify the dominating water masses for each site, as SST and salinity were the most important variables to characterise the island's environmental spaces. The T-S plots showed clear differences in the water masses that dominated the spaces of the two islands (Figures 2C and 2D of the main dissertation).

The space of Nelson Island was mostly dominated by Antarctic Surface Water (ASW) during the breeding season which got heated up by solar radiation as the season progressed. The ASW occurs from the surface down to 150 m depth with potential temperatures ranging between 0 to 2°C and salinities between 33.6 to 34.5 g/kg (Cape et al. 2019). At the end of the breeding season, during February, the surface waters (0 -50m depth) became warmer (between 2 – 6 °C) and could be characterized as a mixture of ASW and an incoming Antarctic Intermediate Water layer (Emery 2003). The ASW still dominated between 50 to 150 m depth, during February. Beyond 200m, the water mass can be characterized as Modified Circumpolar Deep Water (mCDW), which is warmer and saltier than the ASW layer (potential temperatures above 0°C, and salinity above 34.5 g/kg) and known to occur all along the slope of the South Shetland Islands (Sangrà et al. 2011; Ruiz-Barlett et al. 2018).

The dominating water mass in the Kopaitic Island space was Winter Water (WW) (with potential temperatures below 0°C and salinities between 34.0 and 34.44 g/kg) (Jenkins and Jacobs 2008; Cook et al. 2016; Cape et al. 2019), which dominated the surface to 150 m depth layer during the first two months of the season. The surface WW from December and January (0-50m depth) were mixed with a warmer, fresher Antarctic Surface Water (ASW) layer (potential temperatures above 0°C, and salinity between 34.0 and 34.3 g/kg) (Gordon and Huber 1984; Emery 2003; Santini et al. 2018) which became part of the system in February. The ASW possibly originates from nearby glacier ice water that melted (fresher water) while WW was heated up by solar radiation (warmer temperatures). Winter Water still dominates the water column between 50 – 150 m throughout February, below which a more saline, but colder Modified Warm Deep Water (MWDW) layer can be identified which dominated between 150 – 250m depth (Robertson et al. 2002; Santini et al. 2018).

Supplement 5 – Mixed effects models to compare foraging behaviours between chinstrap penguin populations

5.1 Foraging trip behaviours

Trip duration

Table S7. Linear mixed-effect model selection of foraging trip duration for chinstrap penguins. The model terms of island and/or breeding effects were included as fixed effects and all models included individual identity as random effects.

Trip duration

Model	Model terms	df	AIC	Deviance	ΔAIC	*wi*
Null	*i*	3	6116,69	6110,69	127,21	0,00
island effects						
mod1	island	4	6101,43	6093,43	111,95	0,00
breeding stage effects						
mod2	stage(2)	4	6043,56	6035,56	54,07	0,00
mod3	stage(3)	5	6045,33	6035,33	55,85	0,00
combinations						
mod4	stage(2) + island	5	6022,45	6012,45	32,97	0,00
mod5	**stage(2)*island**	**6**	**5989,48**	**5977,48**	**0**	**0,85**
mod6	stage(3) + island	6	6024,27	6012,27	34,79	0,00
mod7	stage(3)*island	8	5992,97	5976,97	3,49	0,15

Note: The breeding stage covariates were separated into two categories: stage(2) (incubation/chick-rearing) and stage 3 (incubation/brood/crèche). Models were scored with Akaike's Information Criterion (AIC) and models were ranked according to differences in AIC (ΔAIC). Included in the table are the degrees of freedom (df), AIC, model deviance, ΔAIC and weight (*wi*). * Indicates an interaction

Maximum distance

Table S8. Linear mixed-effect model selection of foraging trip maximum distance for chinstrap penguins. The model terms of island and/or breeding effects were included as fixed effects and all models included individual identity as random effects.

Maximum distance:

Model	Model terms	df	AIC	Deviance	ΔAIC	*wi*
Null	*i*	3	7027,47	7021,47	118,50	0.00
island effects						
mod1	island	4	7011,26	7003,26	102,29	0.00
breeding stage effects						
mod2	stage(2)	4	6968,71	6960,71	59,73	0.00
mod3	stage(3)	5	6970,14	6960,14	61,16	0.00
combinations						
mod4	stage(2) + island	5	6948,14	6938,14	39,16	0.00
mod5	**stage(2)*island**	**6**	**6908,98**	**6896,98**	**0**	**0.78**
mod6	stage(3) + island	6	6949,62	6937,62	40,64	0.00
mod7	stage(3)*island	8	6911,52	6895,52	2,55	0.22

Note: All model information is the same as in Table S4.

The repeatability estimate for maximum distance was high ($R_{adjusted}$ = 0.59) indicating low-within individual variation in maximum trip distance travelled during the breeding season (Figure S9b).

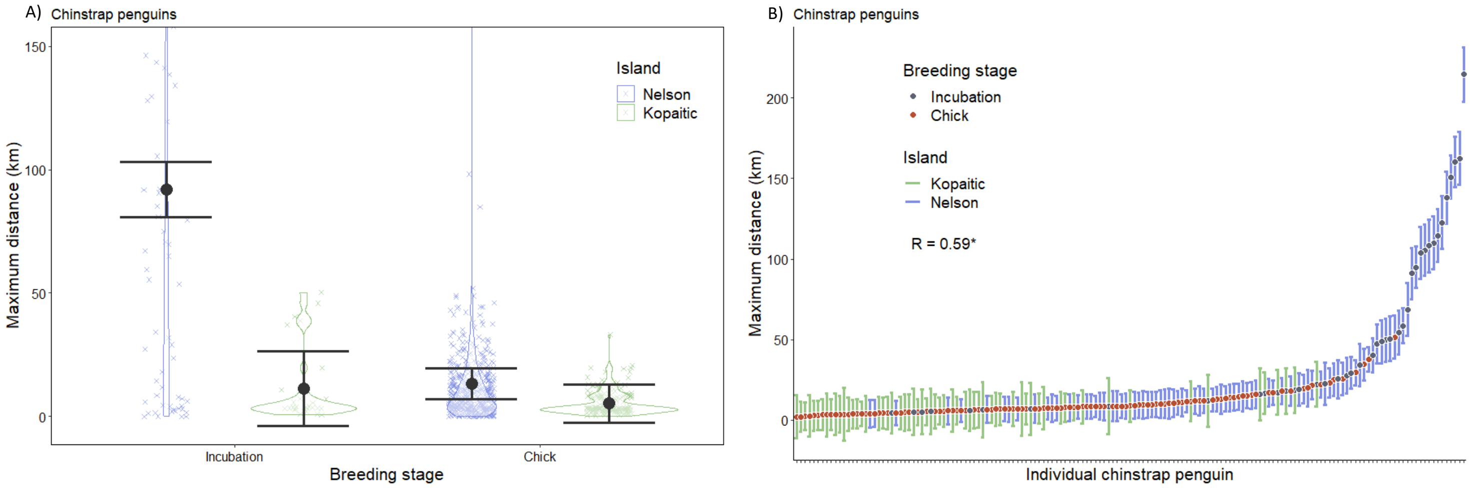

*Figure S9. A) Predicted mean foraging trip maximum distance (km) from the colony for chinstrap penguins breeding at Nelson- (purple) and Kopaitic (green) Islands during incubation and chick-rearing. The mean model estimates and 95% confidence intervals are shown in black. The observed data and violin plots that show the spread of the data are coloured by island. B) Plot of the individual behavioural types (i.e. random effects) of maximum distance (km). The mean model estimates are coloured according to breeding stage (incubation = grey, chick-rearing = red) and 95% confidence intervals are coloured according to island. *R= Repeatability estimate*

5.2 Dive behaviours

Maximum dive depth

Table S9. Generalized linear mixed-effect model selection of maximum dive depth for chinstrap penguins. The model terms of island and/or breeding effects and/or temporal effects were included as fixed effects and all models included individual identity as random effects.

Maximum depth

Model rank	Model terms	df	deviance	AICc	ΔAIC
1	**stage(3)*island*solar elevation**	**16**	**-319719**	**639469.9**	**0**
2	stage(3)*island+stage(3)*solar elevation	13	-319724	639474.6	4.7
3	island*stage(2)*solar elevation	12	-319728	639480.2	10.3
4	island*stage(2)+ stage(2)*solar elevation	10	-319731	639482.4	12.5
5	island*stage(2)+island*solar elevation+stage(2)*solar elevation	11	-319731	639484.3	14.4
6	island+ stage(2)*solar elevation	9	-319734	639485.2	15.3
7	temporal*stage(3)+temporal*island+stage(3)*island	14	-319805	639637.9	168
8	temporal*island+island*stage(2)	10	-319819	639657.5	187.6
9	temporal*island+stage(2)	9	-319821	639659	189.1
10	temporal*island+temporal*stage(2)+stage(2)*island	11	-319819	639659.1	189.2
11	temporal*island*stage(2)	12	-319818	639660.6	190.7
12	temporal*island+temporal*stage(2)	10	-319820	639660.7	190.8

Note: The breeding stage covariates were separated into two categories stage(2) (incubation/chick-rearing) and stage 3 (incubation/brood/crèche). Models were scored with Akaike's Information Criterion (AIC) and models were ranked according to differences in AIC (ΔAIC). Included in the table are the degrees of freedom (df), AIC, model deviance, and ΔAIC. * Indicates an interaction

Foraging dive-type

Table S10. Generalized linear mixed-effect model selection of foraging dive type for chinstrap penguins. The model terms of island and/or breeding effects and/or temporal effects were included as fixed effects and all models included individual identity as random effects.

Foraging dive type

Model rank	Model	df	deviance	AICc	ΔAIC
1	**temporal*stage(3)+stage(3)*island**	**12**	**-13012.76**	**26049.5**	**0**
2	temporal*stage(3)+temporal*island+stage(3)*island	13	-13012.76	26051.5	2
3	temporal*stage(3)*island	15	-13012.06	26054.1	4.6
4	stage(3)*island*solar elevation	15	-13016.60	26063.2	13.7
5	stage(3)*island+ island*solar elevation	11	-13020.71	26063.4	13.9
6	stage(3)*island+stage(3)*solar elevation+ island*solar elevation	13	-13019.19	26064.4	14.9
7	solar elevation+stage(3)*island	10	-13022.92	26065.8	16.3
8	stage(3)*island+stage(3)*solar elevation	12	-13021.75	26067.5	18
9	temporal+island*stage(2)	8	-13031.26	26078.5	29
10	island*stage(2)*solar elevation	11	-13029.02	26080.0	30.50
11	temporal*island+ island*stage(2)	9	-13031.12	26080.3	30.8
12	temporal*stage(2) + island*stage(2)	9	-13031.19	26080.4	30.9
13	temporal*island+temporal*stage(2) + island*stage(2)	10	-13031.07	26082.1	32.6
14	temporal*island*stage(2)	11	-13030.13	26082.3	32.8
15	temporal+island+stage(2)	7	-13034.19	26082.4	32.9
16	island*stage(2)+ island*solar elevation	9	-13032.31	26082.6	33.10
17	island*stage(2)+ island*solar elevation+stage(2)*solar elevation	10	-13031.87	26083.7	34.20
18	solar elevation+stage(2)*island	8	-13034.01	26084.0	34.50

Note: All model information is the same as in Table S6.

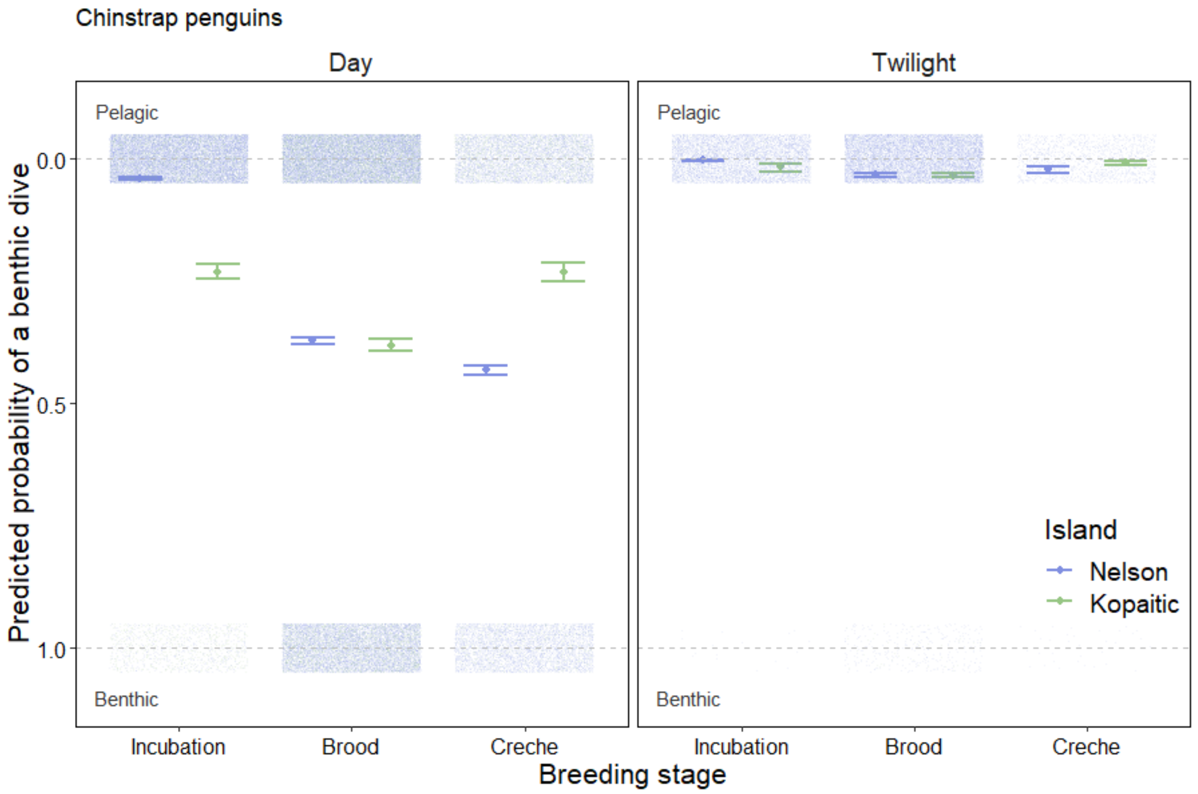

Figure S10. Predicted probability of chinstrap penguins performing benthic foraging dives during day and twilight phases at Kopaitic- and Nelson Islands across the breeding stages. The mean model estimates ± 95% confidence intervals and observed data (that show the spread of the data) are coloured by island.

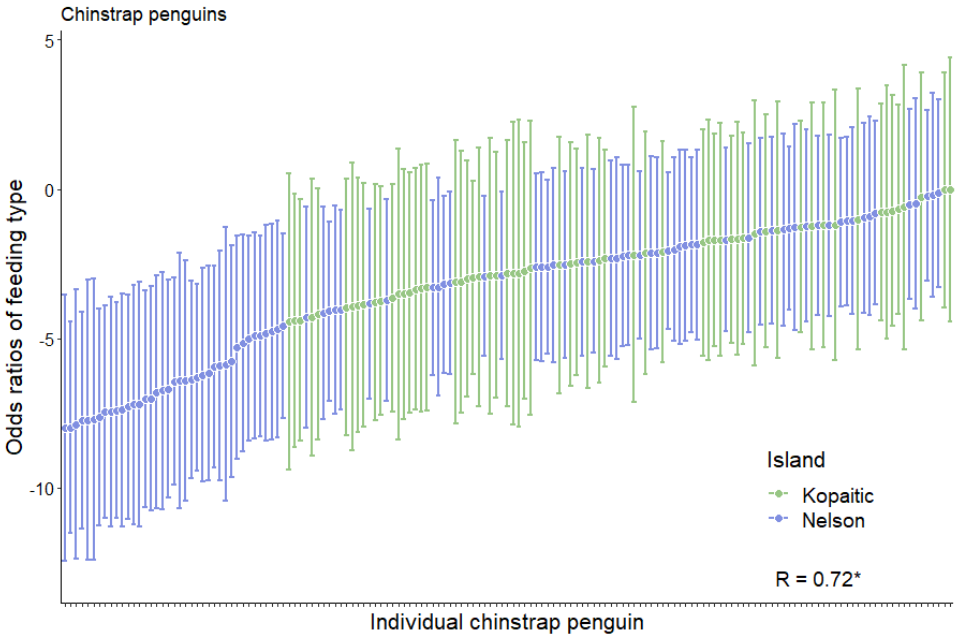

*Figure S11 Plot of the individual behavioural types (i.e. random effects) of the odds of making a benthic feeding dive for chinstrap penguins breeding at Kopaitic- (green) and Nelson Island (purple). The mean model estimates and 95% confidence intervals are coloured by island. *R = Repeatability estimate.*

Supplement 6 - Mixed effects models to compare foraging behaviours between gentoo penguin populations

6.1 Trip behaviours

Maximum distance

Table S8. Linear mixed-effect model selection of foraging maximum trip distance for gentoo penguins. The model terms of island and/or breeding effects were included as fixed effects and all models included individual identity as random effects.

Maximum distance:

Model	Model terms	df	AIC	Deviance	ΔAIC	*wi*
Null	*i*	3	2220,62	2214,62	7,45	0,01
island effects						
mod1	**island**	**4**	**2213,16**	**2205,16**	**0**	**0,45**
breeding stage effects						
mod2	stage(2)	4	2221,62	2213,62	8,46	0,00
mod3	stage(3)	5	2220,83	2210,83	7,67	0,01
combinations						
mod4	stage(2) + island	5	2215,01	2205,01	1,85	0,18
mod5	stage(2)*island	6	2214,48	2202,48	1,31	0,24
mod6	stage(3) + island	6	2216,91	2204,91	3,75	0,07
mod7	stage(3)*island	8	2218,45	2202,45	5,28	0,03

Note: The breeding stage covariates were separated into two categories: stage(2) (incubation/chick-rearing) and stage 3 (incubation/brood/crèche). Models were scored with Akaike's Information Criterion (AIC) and models were ranked according to differences in AIC (ΔAIC). Included in the table are the degrees of freedom (df), AIC, model deviance, ΔAIC and weight (*wi*). * Indicates an interaction

Trip duration

Table S9. Linear mixed-effect model selection of foraging trip duration for gentoo penguins. The model terms of island and/or breeding effects were included as fixed effects and all models included individual identity as random effects.

Trip duration:

Model	Model terms	df	AIC	Deviance	ΔAIC	*wi*
Null	*i*	3	2085,05	2079,05	14,27	0,00
island effects						
mod1	island	4	2084,26	2076,26	13,49	0,00
Breeding stage effects						
mod2	stage(2)	4	2072,57	2064,57	1,80	0,19
mod3	stage(3)	5	2074,46	2064,46	3,68	0,07
combinations						
mod4	stage(2) + island	5	2073,55	2063,55	2,77	0,12
mod5	**stage(2)*island**	**6**	**2070,78**	**2058,78**	**0**	**0,47**
mod6	stage(3) + island	6	2074,71	2062,71	3,94	0,07
mod7	stage(3)*island	8	2074,32	2058,32	3,55	0,08

Note: All model information is the same as in Table S8.

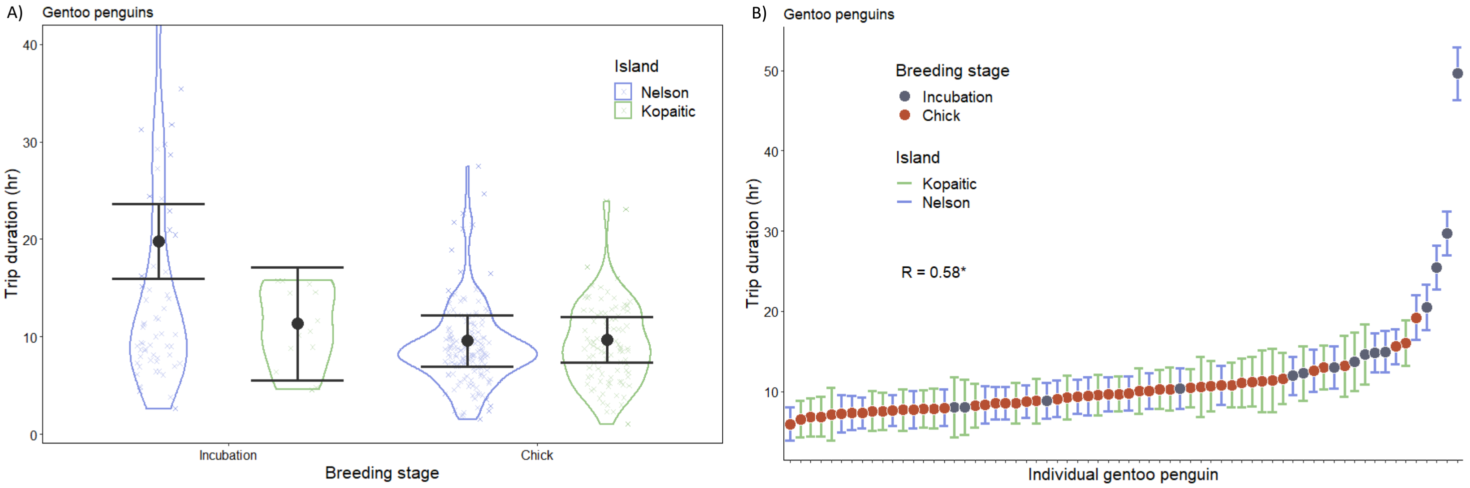

*Figure S12. A) Predicted mean foraging trip duration (hr) for gentoo penguins breeding at Nelson Island (purple) and Kopaitic Island (green) during incubation and chick-rearing. The mean model estimates and 95% confidence intervals are shown in black. The observed data and violin plots that show the spread of the data are coloured by island. B) Plot of the individual behavioural types (i.e. random effects) of trip duration. The mean model estimates are coloured according to breeding stage (incubation = grey, chick = red) and the 95% confidence intervals are coloured by island. *R = Repeatability estimates.*

6.2 Dive behaviours

Maximum depth

Table S10. Generalized linear mixed-effect model selection of maximum depth for gentoo penguins. The model terms of island and/or breeding effects and/or temporal effects were included as fixed effects and all models included individual identity as random effects.

Maximum depth

Model rank	Model terms	df	deviance	AICc	ΔAIC
1	**Solar elevation*stage(3)*island**	**16**	**-120581.9**	**241195.9**	**0**
2	temporal*stage(3)+stage(3)*island	13	-120596.3	241218.6	22.7
3	temporal*stage(3)+temporal*island+stage(3)*island	14	-120595.9	241219.9	24
4	Solar elevation*island*stage(2)	12	-120598.4	241220.8	24.9
5	temporal*stage(3)*island	16	-120594.8	241221.6	25.7
6	island+temporal*stage(3)	11	-120600.1	241222.1	26.2
7	temporal*stage(3)+temporal*island	12	-120599.8	241223.6	27.7
8	island*stage(2)+solar elevation*island+solar elevation*stage(2)	11	-120600.8	241223.6	27.7
9	island*stage(2)+solar elevation*island	10	-120601.9	241223.7	27.8
10	solar elevation*island+solar elevation*stage(2)	10	-120602.1	241224.3	28.4
11	island*solar elevation + stage(2)	9	-120603.4	241224.7	28.8
12	temporal+island*stage(2)	9	-120605	241228.1	32.2
13	temporal*island+ island*stage(2)	10	-120604.9	241229.7	33.8
14	temporal+island+stage(2)	8	-120606.9	241229.8	33.9
15	temporal*stage(2) + island*stage(2)	10	-120605	241229.9	34
16	temporal*island+temporal*stage(2)+ island*stage(2)	11	-120604.7	241231.4	35.5
17	temporal*island+stage(2)	9	-120606.8	241231.5	35.6

18	island+temporal*stage(2)	9	-120606.9	241231.7	35.8
19	temporal+stage(2)	7	-120609.3	241232.6	36.7

Note: The breeding stage covariates were separated into two categories: stage(2) (incubation/chick-rearing) and stage 3 (incubation/brood/crèche). Models were scored with Akaike's Information Criterion (AIC) and models were ranked according to differences in AIC (ΔAIC). Included in the table are the degrees of freedom (df), AIC, model deviance, and ΔAIC. * Indicates an interaction

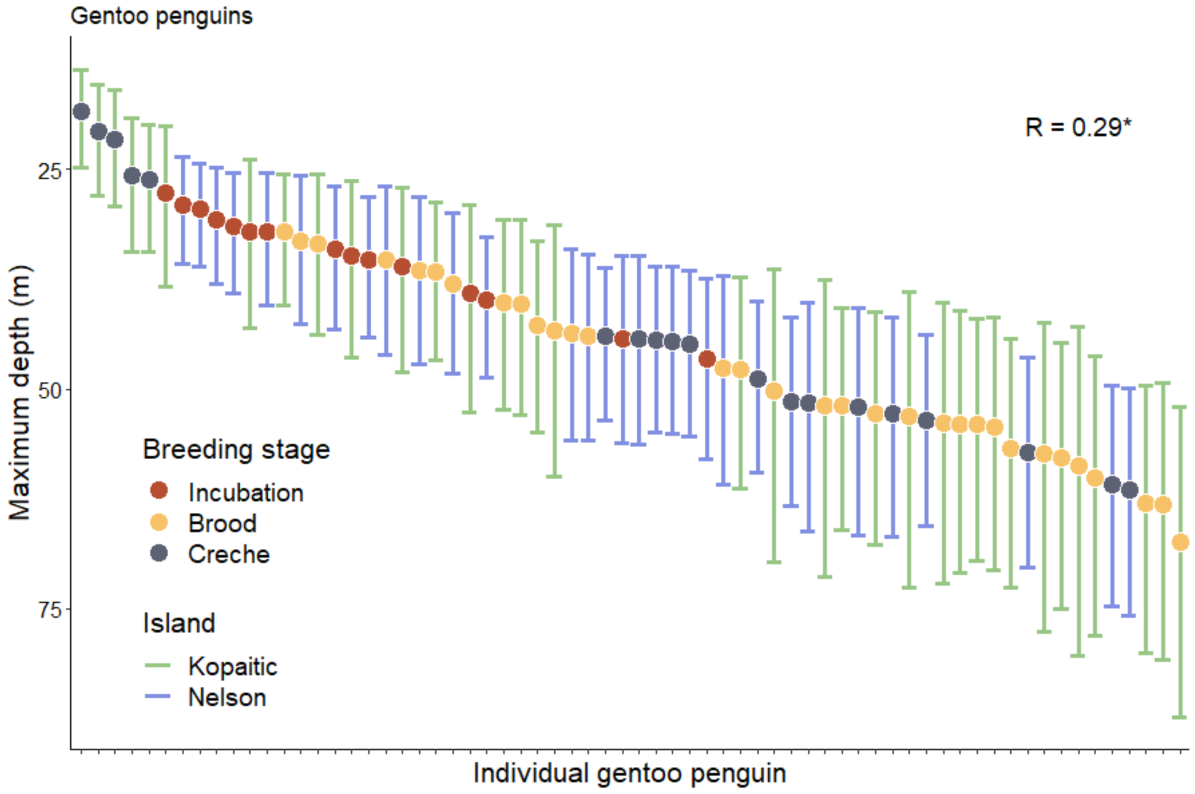

*Figure S13. Plot of the individual behavioural type (i.e. random effects) of maximum dive depth behaviours of gentoo penguins breeding at Kopaitic- (green) and Nelson (purple) Islands. The mean model outputs and 95% confidence intervals are coloured by island. *R = Repeatability estimate.*

Foraging dive type

Table S11. Generalized linear mixed-effect model selection of foraging dive type for gentoo penguins. The model terms of island and/or breeding effects and/or temporal effects were included as fixed effects and all models included individual identity as random effects.

Foraging dive type

Model rank	Model terms	df	deviance	AICc	ΔAIC
1	**stage(3)*island+island*solar elevation+solar elevation*stage(3)**	**13**	**-7716.55**	**15459.1**	**0.00**
2	stage(3)*island*solar elevation	15	-7714.57	15459.2	0.10
3	stage(3)*island+island*solar elevation	11	-7719.01	15460	0.90
4	island*solar elevation	7	-7725.39	15464.8	5.7
5	island*stage(2)+island*solar elevation+stage(2)*solar elevation	10	-7722.66	15465.3	6.2
6	island*solar elevation*stage(2)	11	-7721.85	15465.7	6.6

7	island*stage(2)+island*solar elevation	9	-7723.91	15465.8	6.7
8	island*solar elevation+stage(2)*solar elevation	9	-7724.01	15466	6.9
9	island*solar elevation+stage(2)	8	-7725.35	15466.7	7.6
10	temporal+stage(3)*island	10	-7724.8	15469.6	10.5
11	temporal*island+stage(3)*island	11	-7724.67	15471.3	12.2
12	temporal*stage(3) + stage(3)*island	12	-7724.62	15473.2	14.1
13	temporal	5	-7732.54	15475.1	16
14	temporal+island	6	-7731.9	15475.8	16.7
15	temporal+stage(2)	6	-7732.54	15477.1	18

Note: All model information is the same as in Table S10.

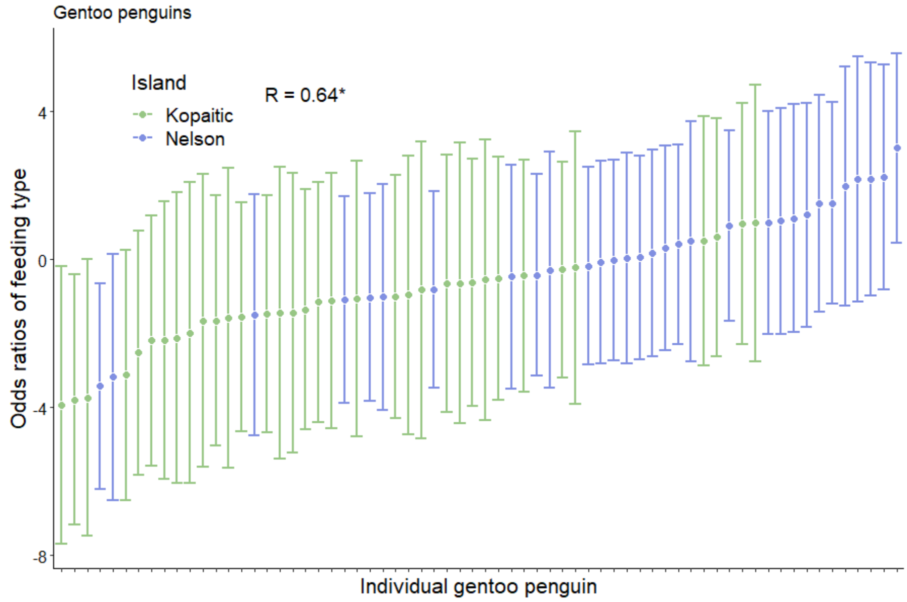

*Figure S14. Plot of the individual behavioural types (i.e. random effects) of the odds ratios of gentoo penguins making a benthic dive breeding at Kopaitic Island (green) and Nelson Island (purple). The mean model outputs and 95% confidence intervals are coloured by island. *R = Repeatability estimate.*

Supplement 7: Mixed effects models to compare diving efficiency between chinstrap and gentoo populations

Methods

Successful feeding behaviours are often inferred from dive-based metrics such as improved dive efficiency during dives (i.e. the ratio between time at the bottom phase of the dive and the total dive duration) (Thompson and Fedak 2001). We calculated an index of dive efficiency as dive bottom duration/(dive duration+post-dive surface interval) (Kokubun et al. 2010). For the dive efficiency models, only dives with a post-dive surface interval of < 300 seconds were included (following Kokubun et al. 2010). The dive efficiency response variable is an index that varies from 0 to 1, and therefore GLMMs of dive efficiency were fitted using a beta error distribution. R^2 (marginal and conditional) and repeatability (*R*) values are not available for beta-distributed GLMMs and thus we only relied on the AIC model selection results to evaluate model fit.

Results

Chinstrap diving efficiency

The best model for diving efficiency of chinstraps varied by time-of-day (day, twilight), across breeding stages (incubation vs. chick-rearing) and by site (Table S12). Overall, mean diving efficiency ranged between 0.14 and 0.21 and was predicted to be higher during twilight phases (Figure S15).

Table S12. Generalized linear mixed-effect model selection of diving efficiency for chinstraps. The model terms of island and/or breeding effects and/or temporal effects were included as fixed effects and all models included individual identity as random effects.

Dive efficiency

Model rank	Model terms	df	deviance	AICc	ΔAIC
1	**temporal*island*stage(2)**	**12**	**85384.04**	**-170744**	**0**
2	temporal*island+ temporal*stage(2)	10	85381.04	-170742	2
3	island+temporal*stage(2)	9	85379.83	-170742	2.4
4	temporal*island+ temporal*stage(2)+island*stage(2)	11	85381.41	-170741	3.3
5	temporal*stage(2)+island*stage(2)	10	85380.17	-170740	3.8
6	temporal*stage(3)+temporal*island+stage(3)*island	14	85383.67	-170739	4.8
7	temporal*stage(3)+temporal*island	12	85381.38	-170739	5.3
8	temporal*stage(3)+stage(3)*island	13	85382.27	-170739	5.6
9	temporal*stage(3)+island	11	85380.19	-170738	5.7
10	island*stage(2)*solar elevation	12	85359.02	-170694	50.1
11	solar elevation*stage(3)*island	16	85362.73	-170693	50.7
12	island+ stage(2)*solar elevation	9	85354.72	-170691	52.7
13	island*solar elevation + stage(2)*solar elevation	10	85355.69	-170691	52.7
14	island*stage(2)+ stage(2)*solar elevation	10	85355.1	-170690	53.9
15	island*stage(2)+island*solar elevation + stage(2)*solar elevation	11	85356.1	-170690	53.9
16	stage(3)*island+stage(3)*solar elevation	13	85358.06	-170690	54
17	stage(3)*island+stage(3)*solar elevation+island*solar elevation	14	85358.99	-170690	54.1
18	stage(3)*solar elevation + island*solar elevation	12	85356.93	-170690	54.2

19	island+ stage(3)*solar elevation	11	85355.83	-170690	54.4

Note: All model information is the same as in Table S6.

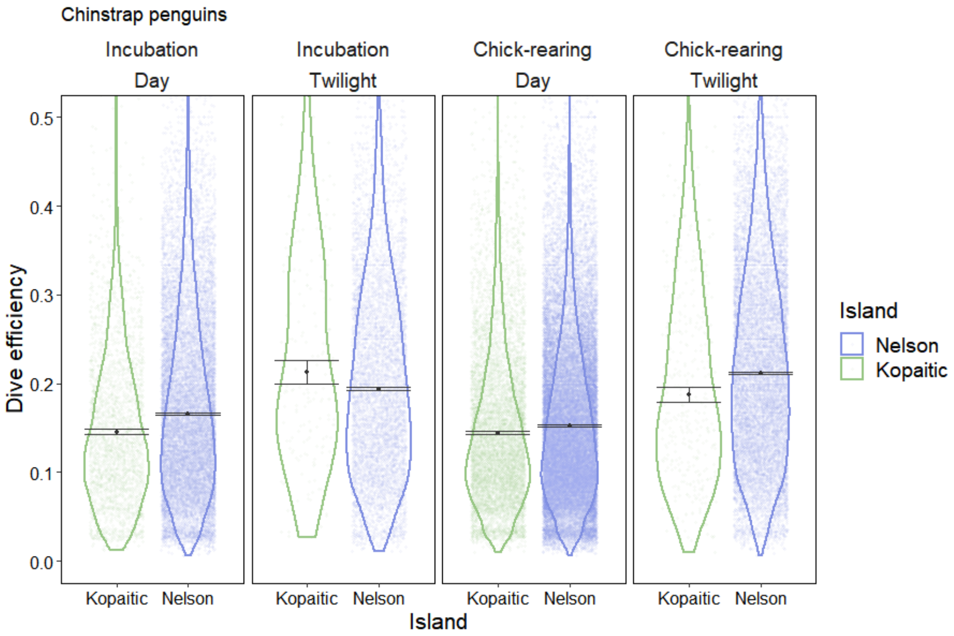

Figure S15. Diving efficiency of chinstrap penguins breeding at Kopaitic Island (green) and Nelson Island (purple) across breeding stage and time of day. The mean model estimates ± 95% confidence intervals are shown in black and the observed data and violin plots that show the spread of the data are coloured by island.

Gentoo diving efficiency

The variation in diving efficiency depended on the interaction between the time of day (day/twilight) and breeding stage (incubation/brood/crèche) as fixed effects (Table S13). Overall, mean diving efficiency was predicted to be around 0.17 and 0.24 (Figure S16). During the day, there were no negligible differences in predicted mean diving efficiency between breeding stages. But during twilight phases, gentoos in brood had the highest mean diving efficiency (0.24; 95% CI = 0.24-0.25) (Figure S16).

Table S13. Generalized linear mixed-effect model selection of dive efficiency for gentoo penguins. The model terms of island and/or breeding effects and/or temporal effects were included as fixed effects and all models included individual identity as random effects.

Dive efficiency

Model rank	Model terms	df	deviance	AICc	ΔAIC
1	**temporal*stage(3)**	**10**	**25634.24**	**-51248.5**	**0**
2	temporal	6	25629.94	-51247.9	0.6
3	temporal+stage(2)	7	25630.7	-51247.4	1.1
4	island+temporal*stage(3)	11	25634.72	-51247.4	1.1
5	temporal*stage(2)	8	25631.44	-51246.9	1.6
6	temporal+stage(3)	8	25631.42	-51246.8	1.7
7	temporal+island	7	25630.11	-51246.2	2.3
8	temporal*stage(3)+stage(3)*island	13	25635.96	-51245.9	2.6

9	temporal*stage(3)+temporal*island	12	25634.95	-51245.9	2.6
10	temporal+island+stage(3)	9	25631.9	-51245.8	2.7
11	temporal+island*stage(2)	9	25631.8	-51245.6	2.9
12	temporal+island+stage(2)	8	25630.76	-51245.5	3
13	temporal*stage(2)+ island*stage(2)	10	25632.58	-51245.1	3.4
14	island+temporal*stage(2)	9	25631.5	-51245	3.5
15	solar elevation	6	25628.44	-51244.9	3.6

Note: All model information is the same as in Table S10.

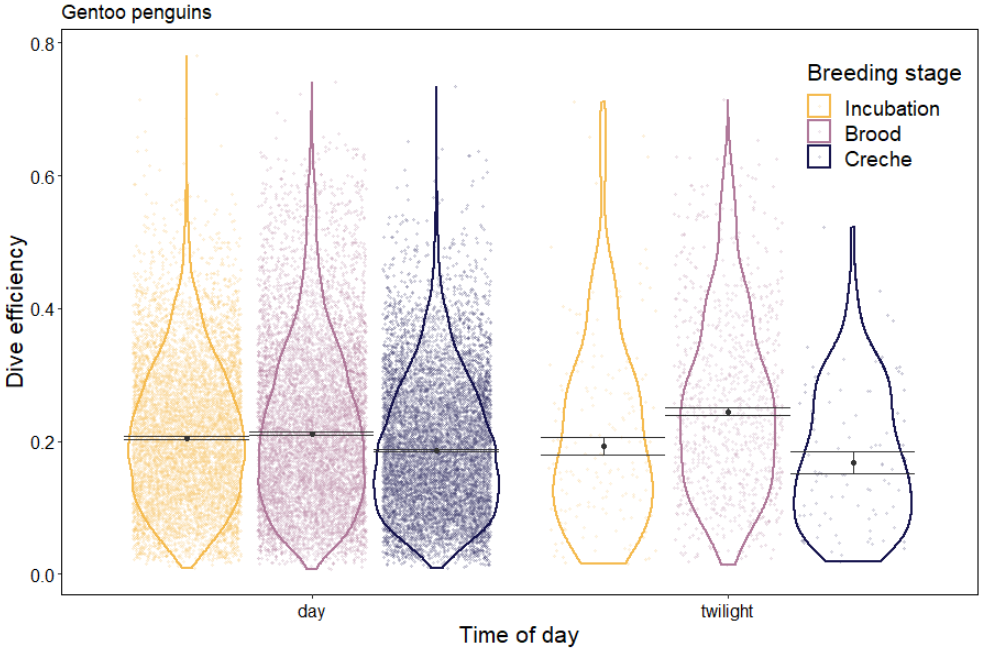

Figure S16. Diving efficiency of gentoo penguins between breeding stages (incubation = Yellow, brood = pink, crèche = dark blue) by time of day. The mean model estimates ± 95% confidence intervals are shown in black. The observed data and violin plots that show the spread of the data are coloured by breeding stage.

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Chapter 3: Supplementary material

Supplement 1 – Tag deployment summary

1.1. Study site locations

Tags were deployed at Nelson Island (part of the South Shetland Island group) and Kopaitic Island (part of the Duroch Island group), situated 131 km apart on opposite sides of the Bransfield Strait, West Antarctic Peninsula (Figure S1).

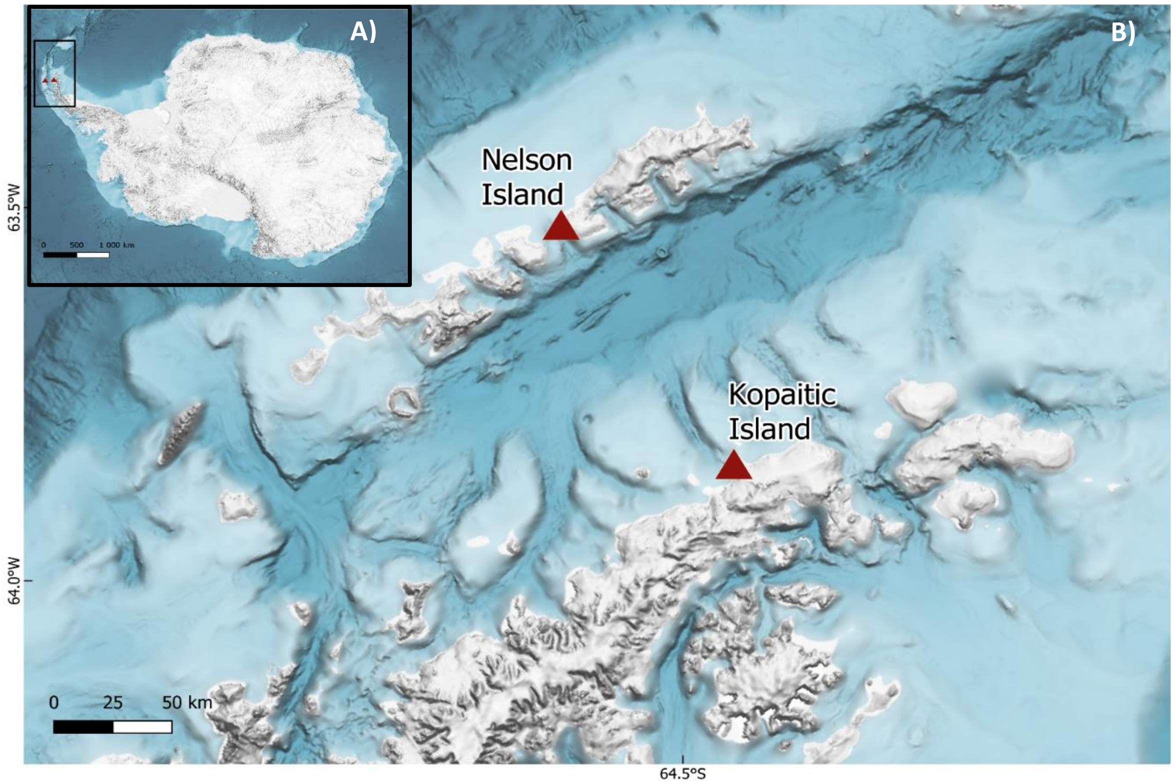


Figure S1. Study area. A) The location of the West Antarctic Peninsula (black box) relative to Antarctica. B) Island locations (red triangles) where tags were deployed on both chinstrap penguins and gentoo penguins.

1.2 Deployment summary per breeding stage

Tags were deployed in batches (rounds) that were classified according to breeding stages (incubation, brood and crèche) between early December 2018 and mid-February 2019 (Tables S1 and S2). Incubation deployments were made on adult pairs incubating 1 or 2 eggs, with one parent foraging while the other incubated the egg(s) at the colony. During the brood stage, one parent brooded the relatively small chick(s) while the other parent foraged. Crèche deployments coincided with chicks aggregating in groups and concurrent foraging and provisioning of chick(s) by parents.

Table S11. Summary table of each round of deployments for chinstrap penguins and gentoo penguins during the 2018/2019 breeding season at Nelson Island.

Nelson Island					
Chinstrap penguins					
Deployment round	Breeding stage	Deployment / Retrievement date	No. tags deployed	No. tags with data	No. of foraging trips
1	Incubation1	3-4 Dec / 12-19 Dec	15	14	23
2	Incubation2	15-16 Dec / 23-27 Dec	14	13	34
3	Brood1	26-28 Dec / 3-5 Jan	14	13	82
4	Brood2	6 Jan / 12-14 Jan	13	12	73
5	Brood3	14 Jan / 20-25 Jan	13	13	98
6	Brood4	22-26 Jan / 30 Jan-1 Feb	11	10	88
7	Crèche1	31 Jan-2 Feb / 7-8 Feb	10	9	75
8	Crèche2	8-9 Feb / 13-14 Feb	9	9	43
Total			**99**	**93**	**516**
Gentoo penguins					
1	Incubation1	4-5 Dec / 15-18 Dec	5	5	30
2	Incubation2	18-20 Dec / 27 Dec-6 Jan	5	5	32
3	Brood1	31 Dec-1 Jan / 7-8 Jan	3	3	24
4	Brood2	8-9 Jan / 13 Jan	4	4	17
5	Crèche1	15 Jan / 19-20 Jan	5	4	21
6	Crèche2	23 Jan / 30-31 Jan	5	5	45
7	Crèche3	31 Jan / 7-8 Feb	5	5	43
Total			**32**	**31**	**212**

Table S12. Summary table of each round of deployments for chinstrap penguins and gentoo penguins during the 2018/2019 breeding season at Kopaitic Island.

Kopaitic Island					
Chinstrap penguins					
Deployment round	Breeding stage	Deployment / Retrievement date	No. tags deployed	No. tags with data	No. of foraging trips
1	Incubation1	9 Dec / 17-19 Dec	10	8	16
2	Incubation2	17-18 Dec / 23-25 Dec	8	7	12
3	Brood1	26 Dec / 02 Jan	9	8	29
4	Brood2	04 Jan / 09 Jan	10	9	40
5	Brood3	13 Jan / 19-20 Jan	10	9	39
6	Brood4	24 Jan / 29 Jan	10	9	48
7	Crèche1	01 Feb / 05 Feb	9	8	28
8	Crèche2	07 Feb / 11 Feb	8	4	14
Total			**74**	**62**	**226**
Gentoo penguins					
1	Incubation1	10 Dec / 18 Dec	5	5	13
2	Brood1	19 Dec / 25-28 Dec	5	5	12

3	Brood2	27-29 Dec / 02-03 Jan	5	5	18
4	Brood3	04 Jan / 09-11 Jan	5	5	20
5	Brood4	13 Jan / 20-21 Jan	5	5	17
6	Brood5	24 Jan / 29 Jan	5	5	15
7	Crèche1	01 Feb / 05 Feb	5	5	15
Total			**35**	**35**	**110**

Supplement 2 - Expectation Maximization (EM) classification of dive behaviours

2.1 Classification of dive behaviours

We assumed that penguin dive behaviours could be classified into three different classes: 'foraging dives' and deep or shallow 'non-foraging dives'. Dives were classified into behavioural types according to similarities in bottom time, maximum depth and dive residuals. The dive characteristics bottom time and maximum depth were calculated for each dive using the '*diveStats'* function from the 'diveMove' package (Luque 2007).

Bottom time

Prey are often pursued and captured during the bottom phase of a dive (Bost et al. 2007; Phillips et al. 2021). The time spent at the bottom phase of a dive is usually a good indicator of foraging (Bestley et al. 2015; Phillips et al. 2021). The longer an individual spends at the bottom of a dive, the more likely it is to feed. Dives with bottom times of short duration were probably travelling or exploratory dives where no foraging took place.

Maximum depth

Chinstrap penguins typically forage at depths of 15 to 30 m (Wilson and Peters 1999; Miller and Trivelpiece 2008; Kokubun et al. 2010) and gentoo penguins at depths of 30 to 90m (Mori and Boyd 2004; Miller et al. 2009; Kokubun et al. 2010). Maximum depth was included as we expected penguins to have a higher probability of finding prey in deeper dives compared to shallow dives, which is typical of transit behaviour.

Dive residuals

Following Bestley et al. (2015), we calculated 'dive residuals' by fitting a linear mixed-effect model with dive duration as the response and maximum depth as a fixed effect using the 'lme4' package (Bates et al. 2015). Individual identity was fitted as a random intercept and maximum depth as a random slope. This random effect structure accounted for variation in mean diving depths between individuals (intercept) and allowed the relationships between dive duration and maximum depth for each individual to vary from the overall population mean. We extracted the Pearson residuals from the modelled relationship as the 'dive residuals'. The magnitude and direction of the residuals can be used to ascertain whether the dive duration was relatively longer or shorter than expected for a dive of a given depth. Dives that are longer than expected (positive residuals) indicate higher relative effort, which might indicate foraging. In contrast, dives that are shorter than expected (negative residuals) indicate lower relative foraging effort. Dive residuals were derived from dive duration, so it was unnecessary to include dive duration as a variable in the classification analysis.

Dives were grouped based on similarities in bottom time, maximum depth and dive residuals using an Expectation Maximization (EM) algorithm (Dempster et al. 1977; McLachlan and Krishnan 1997; Chimienti et al. 2016). This unsupervised, non-hierarchical clustering analysis was performed using the 'RMixMod' package (Lebret et al. 2015). The resulting clusters were visually checked and associated with a dive class which best represented our a priori expectations of dive behaviours. We limit subsequent analyses to foraging dives only. Dive classification results are given in Chapter 2.

Supplement 3: Environmental covariate changes throughout the breeding season

3.1 Solar elevation

The amount of solar light available initially increased during incubation in December (Figure S2). Incubation and brood occurred on either side of the summer solstice and thus had similar amounts of solar light available initially (Figure S2). But as the breeding season progressed from brood to crèche, the amount of solar light available above 0° decreased (Figure S2) and twilight periods (solar elevation < 0°) became longer. Chinstraps foraged throughout the daylight and darker periods on both islands (Figure S2).

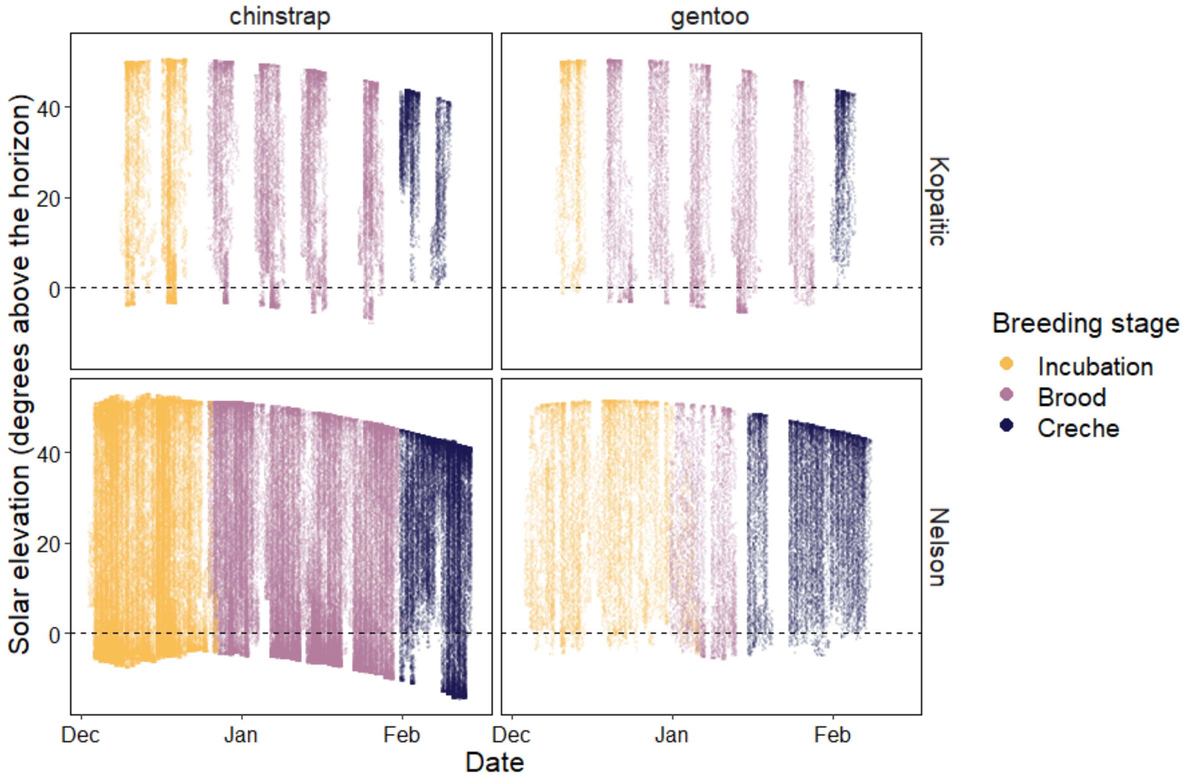


Figure S2. Solar elevation changes over the 2018/2019 breeding season from incubation in early December to crèche in mid-February 2019. Each data point represents the solar elevation calculated at the location of a single foraging dive during a breeding stage (incubation = yellow, brood = pink, crèche = blue). The dotted line at 0 degrees solar elevation indicates that points above 0 degrees are when solar light was available above the horizon and could be classified as 'day'. Points with solar elevations below 0 degrees are classified as 'twilight' when darker periods occur.

3.2 Bathymetric depth

Benthic geomorphic features were classified for the near-shore Antarctica region by Douglass et al. (2014). Due to central-place foraging constraints, the amount of different benthic geomorphic features available for penguin foraging decreased as the breeding season progressed from incubation to brood to crèche (Figure S3). At Nelson Island, the foraging ranges of chinstrap penguins expanded far across a variety of geomorphic features during the incubation stage (Figure S3). Chinstrap penguins' foraging ranges encompassed several continental shelf features including the Antarctic Peninsula Bank (a broad shallow region 100 to 200 m deep), Upper Slope- and Lower Slope features (extending from the continental shelf break to around 2500 to 3500 m deep), Ocean Troughs and deep Rugose Ocean Floor features, where bathymetric depth can be up to 5000 m deep (Figure S3) (Douglass et al. 2014). During brood and crèche, chinstrap penguin foraging ranges contracted to areas where bathymetry was < 300 m deep (Figure S4) with some foraging locations on the shallow Bank and Coastal Terrane (varying seafloor type and depth ranges) to the north of Nelson Island while some foraging trips went south over the Shelf Deep (Figure S3). All foraging locations of gentoo penguins were restricted to the shallow Bank and Coastal Terrane (Figure S3) where bathymetric depth never exceeded 300 m (Figure S4).

Around Kopaitic Island, penguins can forage over a complex array of benthic geomorphic features which all form part of the continental shelf (with bathymetric depth not exceeding 500 m). This includes the Coastal Terrane and Cross Shelf Valleys (shelf depressions) which are situated in between the shallow Bank (Douglass et al. 2014) (Figure S3). Foraging locations of both species occurred over all three benthic geomorphic features during each stage of the breeding season (Figure S3).

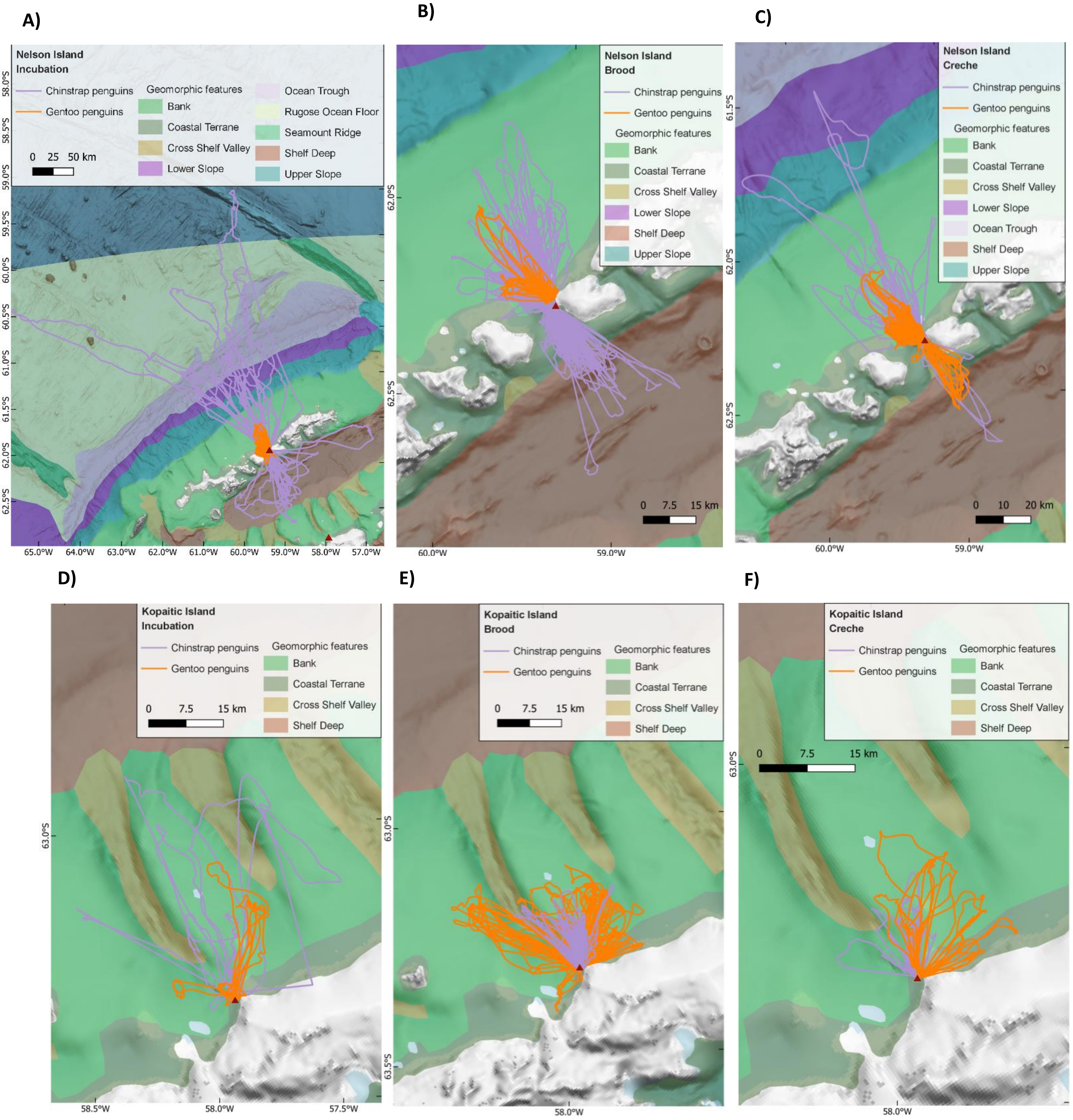


Figure S3. Benthic geomorphic features (Douglass et al. 2014) in the vicinity of Nelson Island and Kopaitic Island (red triangles). The foraging trips of chinstrap penguins (purple) and gentoo penguins (orange) are shown at each island. The bathymetric depth layer was obtained from IBCSO v2 (Dorschel et al. 2022) and is shown in the background. The figure was prepared in QGIS v3.28 using Quantarctica3.2 software (Matsuoka et al. 2021).

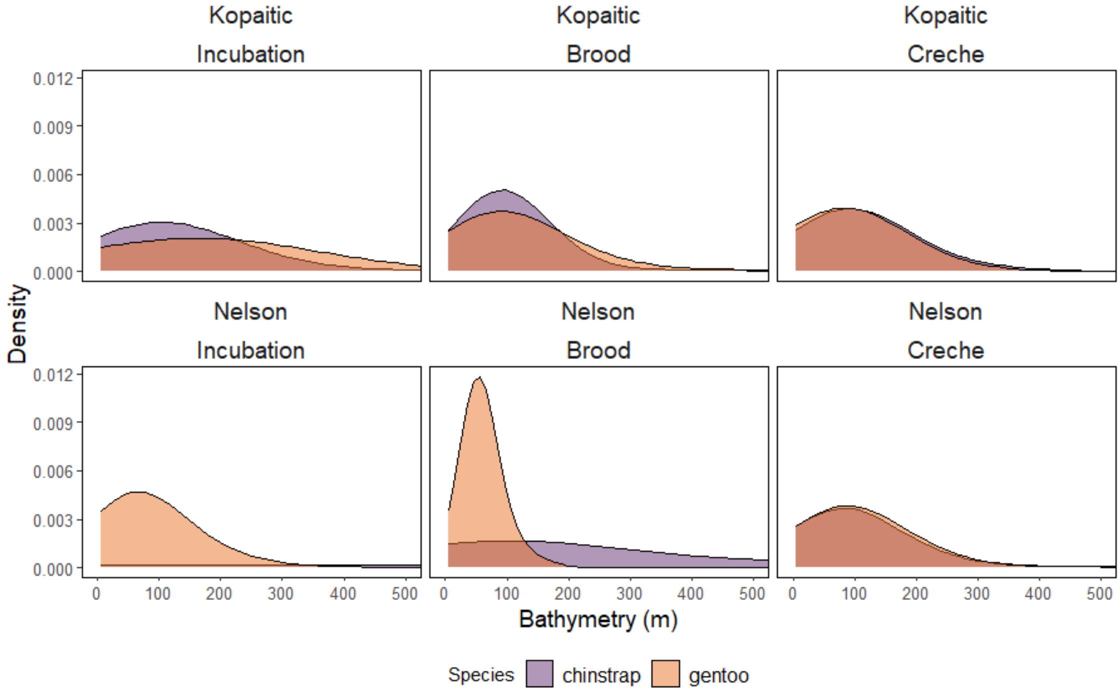


Figure S4. Distribution of bathymetric depth at foraging locations of chinstrap penguins (purple) and gentoo penguins (orange) across the breeding season from incubation to brood and crèche. The x-axis is truncated at 500 m to improve visualisation, but chinstrap penguins forage over depths of up to 5000 m during incubation.

Supplement 4: Space use

4.1 Size of home ranges (95% Utilisation distribution (UD)) based on the continuous-time movement modelling

Additional results quantifying the space use and overlap of chinstraps and gentoos. During incubation, the chinstrap home range at Nelson Island was six-fold larger compared to gentoos during the same period (Table S3). At Nelson Island, home ranges of both species subsequently contracted during the brood and crèche stages. Similarly, at Kopaitic Island chinstrap home ranges reduced during the brood and crèche while gentoo home ranges seemed to increase during the same period (Table S3).

Table S3. Size of home ranges (95% UD) (km^2) of chinstrap penguins and gentoo penguins breeding at Kopaitic Island and Nelson Island during the breeding season.

Species	Breeding stage		
	Nelson Island		
	Incubation Area (km²)	Brood Area (km²)	Crèche Area (km²)
Chinstraps	25437.02	421.6	375
Gentoos	383.18	262.66	168.2
Total overlap area	383	241.4	157.51
	Kopaitic Island		
Chinstraps	99.79	44.01	41.23
Gentoos	56.37	311.27	1024.54
Total overlap area	49.99	44.01	41.23

Supplement 5: Bathymetry effects

5.1 Bathymetry effects

Foraging dive depths initially increased with bathymetric depth for both penguin species. As bathymetric depth increased, foraging dive depths flattened off (first for chinstraps, second for gentoos) as physiological limits started to constrain diving (Figure S5). Maximum dive depths appear to occur at bottom depths where penguins can still forage benthically (shallower than 200 m) with pelagic dives (over deep water) having shallower maximum dive depths (Figure S5).

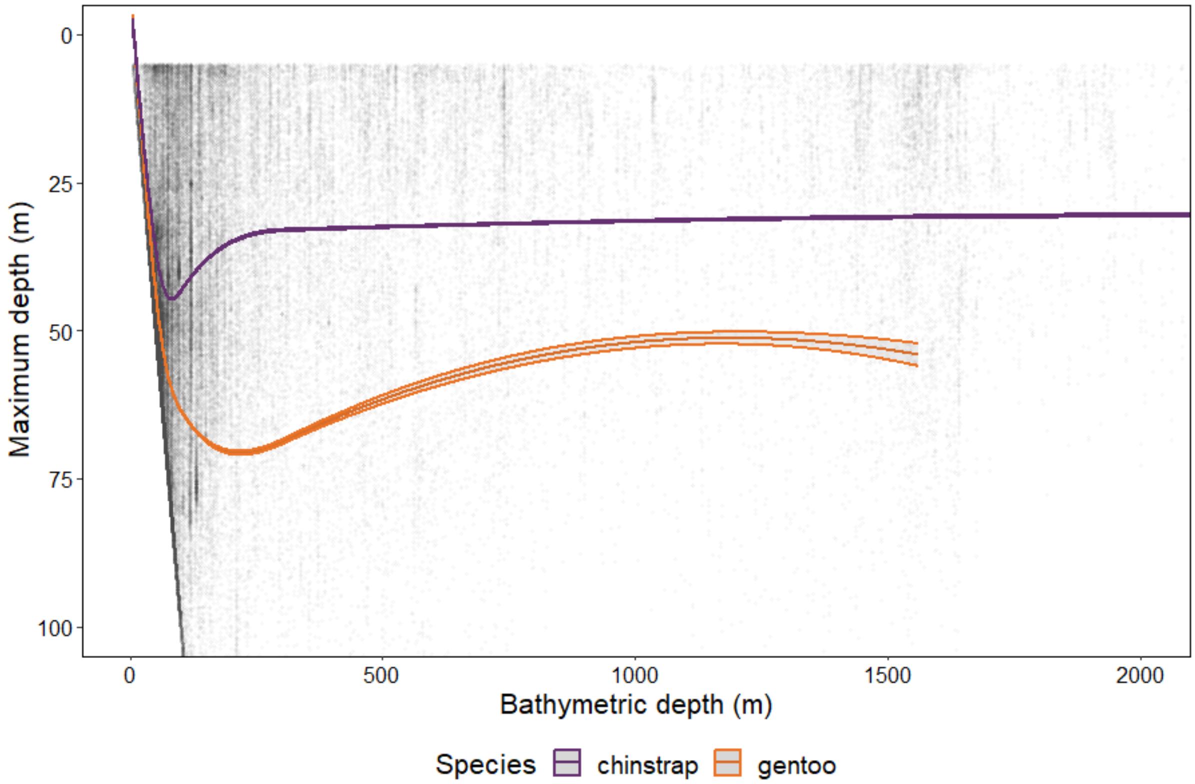


Figure S5. Maximum dive depth of breeding chinstrap penguins (purple) and gentoo penguins (orange) according to bathymetric depth. A) The mean model estimates and 95% confidence intervals are coloured by species. The observed data that show the spread of the data are coloured grey.

5.2 Bathymetry and solar elevation effects at Kopaitic Island

At Kopaitic Island, chinstraps mostly dive pelagically during all three stages of breeding. Chinstraps show strong diel behaviour with shallow diving during low solar elevations (Figure S6A). Gentoos make a larger proportion of benthic dives and do not show a strong diel diving pattern during the breeding stages (Figure S6B).

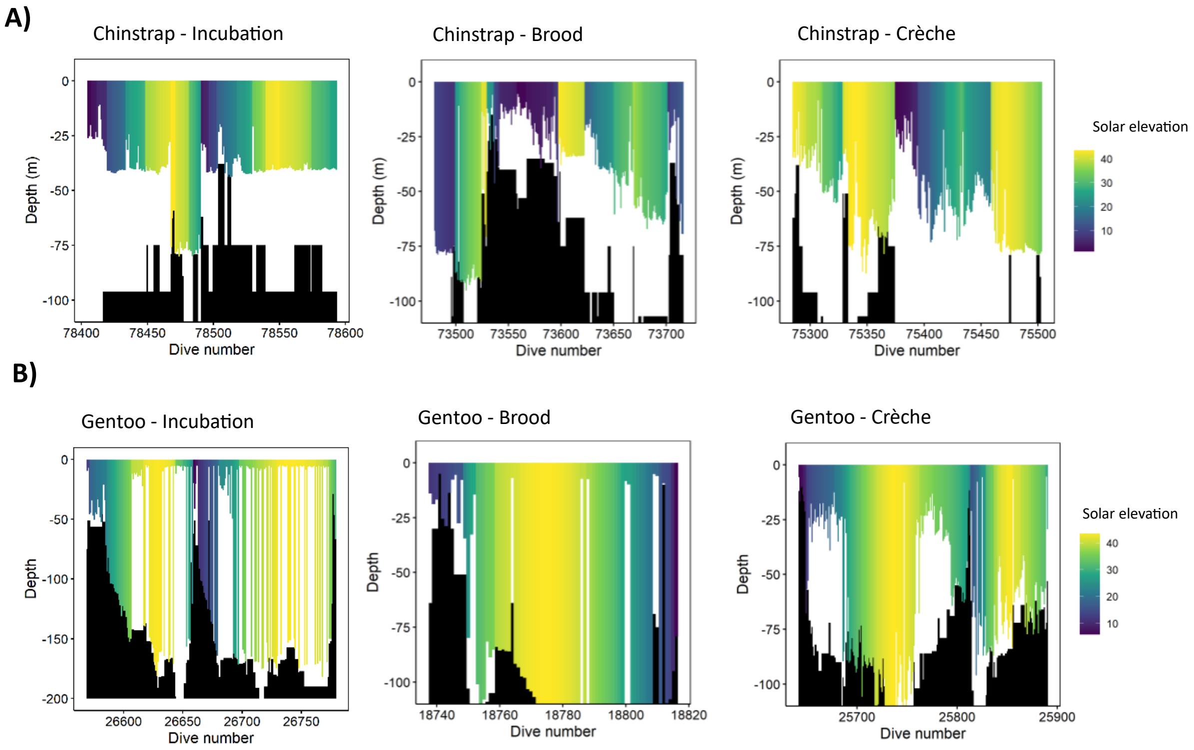
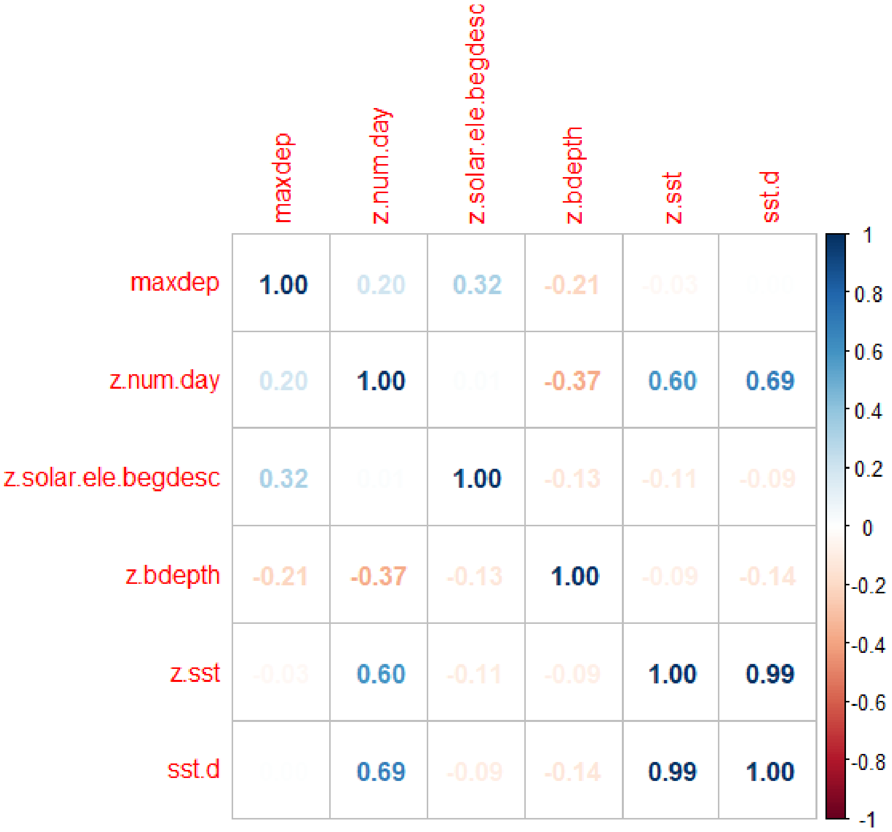


Figure S6. The foraging dive profiles of A) three chinstrap penguins and B) three gentoo penguins tracked during incubation, brood and crèche at Kopaitic Island. These examples illustrate the pelagic foraging among chinstrap penguins and the benthic foraging among gentoos during all breeding stages. The top bars show foraging diving depth and are coloured by the solar elevation angle, to show how diving behaviour changed as solar elevation changed. The black bars are bathymetric depth at each dive location.

Supplement 6: A simple time trend in maximum diving depth

I also tested the relationship between a linear time trend (since 1 December) and maximum dive depth. However, I did not include the time as a covariate in the environmental model set because the time covariate (z.num.day) was highly correlated with SST (Pearson correlation coefficient = 0.60; Figure S7).



	maxdep	z.num.day	z.solar.ele.begdesc	z.bdepth	z.sst	sst.d
maxdep	1.00	0.20	0.32	-0.21	-0.03	0.00
z.num.day	0.20	1.00	0.01	-0.37	0.60	0.69
z.solar.ele.begdesc	0.32	0.01	1.00	-0.13	-0.11	-0.09
z.bdepth	-0.21	-0.37	-0.13	1.00	-0.09	-0.14
z.sst	-0.03	0.60	-0.11	-0.09	1.00	0.99
sst.d	0.00	0.69	-0.09	-0.14	0.99	1.00

Figure S7. Pearson correlation coefficients show the relationship between environmental covariates that can be fitted in the generalized linear mixed models.

I fitted an additional GLMM model where SST was replaced with the time trend covariate which reduced model parsimony (model 2, ΔAIC = 19.6, Table S4). Deeper diving depths of both species coincided with the time trend as the breeding season progressed (Figure S8).

I used the residual regression technique (Graham 2003; Grosbois et al. 2008) to test whether SST accounts for a significant proportion of the variation in foraging dive depth over the breeding season. A detrended SST covariate (sst.d) was calculated by removing the temporal trend (num.day) from the SST covariate (sst). The value of sst.d at each date i was calculated as $sst.d_i = sst_i - (\hat{\alpha} + \hat{\beta} num.day_i)$; where $\hat{\alpha}$ and $\hat{\beta}$ are the model estimates obtained from the GLMM model where a relationship between the SST covariate and the linear time trend was fitted (Table S4). The next step included fitting another GLMM where the de-trended SST covariate (sst.d) was fitted along with the linear time trend (model 3, Table S4) to test whether a relationship exists between the variation in foraging dive depth, the linear time trend and the variation in the de-trended SST covariate. Using an AIC approach, the evidence for such a relationship was obtained by examining the AIC values between the de-trended model (model 3) vs. 1) the time-dependent SST model (model 1) and 2) the linear time trend model (model 2) (Table S4).

The ΔAIC between the fitted models shows that the de-trended model (model 3) improved model fit (Table S4). Thus, the model containing de-trended SST and time as covariates shows that a correlated relationship exists between the variation in foraging maximum dive depth, the linear time trend and the variation in the de-trended SST covariate. But time and the de-trended SST covariates were still highly correlated (Pearson correlation coefficient = 0.69, Figure S7) and thus were not included in the main data analysis of this chapter. My results show that the observed increase in maximum dive depth can be attributed to climatic or oceanographic changes that were captured by increased SST over the breeding season.

Table S4. Generalized linear mixed-effect model selection of maximum foraging dive depth between chinstrap penguins and gentoo penguins breeding at Kopaitic Island and Nelson Island. The a priori umbrella model with all model terms (model 2) is given, with the underlined terms in the model being important for the specific GLMM analysis. The fixed effect terms are breeding stage (incubation, brood, crèche), island (Kopaitic or Nelson) and species (chinstrap or gentoo penguins). All models included individual identity as a random effect. The most parsimonious model is in bold.

No.	Model	Fixed effect	n.p	AIC	ΔAIC	weight
1	SST model	island + species + bathymetry + solar elevation + sst + island:solar elevation + island:sst + species:bathymetry + species:solar elevation + species:sst	21	866102.3	35.04	0.00
2	Time model	island + species + bathymetry + solar elevation + num.day + island:solar elevation + island:num.day + species:bathymetry + species:solar elevation + species:num.day	21	866082.7	15.37	0.00
3	**Detrended SST + Time model**	**island + species + bathymetry + solar elevation + num.day + island:solar elevation + island:num.day + species:bathymetry + species:solar elevation + species:num.day + sst.d + island:sst.d + species:sst.d**	**24**	**866067.3**	**0.00**	**0.50**

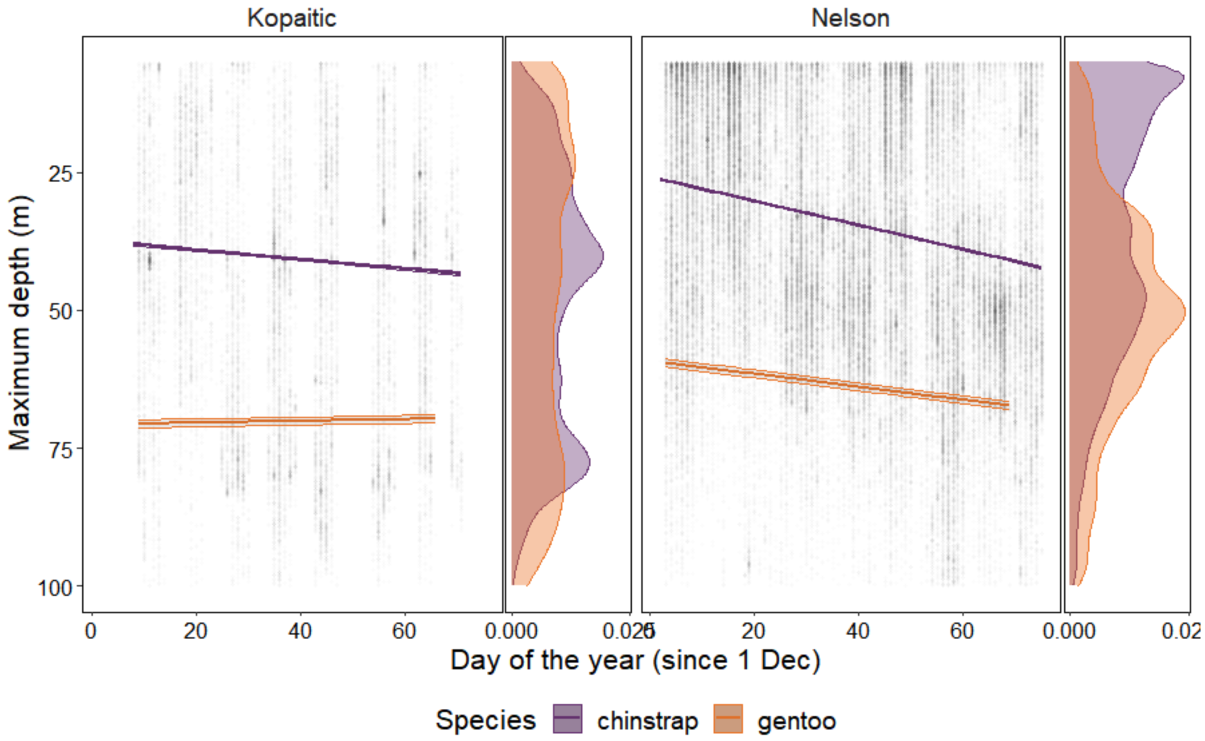


Figure S8. Change in maximum foraging dive depths of chinstrap penguins (purple) and gentoo penguins (orange) breeding at Kopaitic and Nelson Islands as the breeding season progressed from 1 December. Lines represent the model estimated mean effect and 95% confidence intervals. The observed data (points) and side plots that show the spread of the data are coloured by species.

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