**Energy expenditure of Adélie penguins during the breeding season: females pay the cost in low food availability years**

**Abstract**

Changes in prey availability can lead to mismatches between consumers and resources, decreasing the fitness of consumers, especially during periods of high energy demand such as reproduction. We investigated inter-seasonal variations in the foraging behaviour of chick-rearing Adélie penguins (*Pygoscelis adeliae*) in a declining colony in the West Antarctic Peninsula to assess the impact of changes in prey abundance. Specifically, we analysed how these changes affect the energetic cost of males and females during the breeding season. Using information from foraging trips, diet, body condition, and daily energy expenditure of 38 Adélie penguins breeding in Ardley Island, King George Island, in 2019/20 and 2021/22, we found that during low food availability conditions, penguins were forced to increase their foraging effort, and the body mass was lower. Specifically, females extended their foraging trips, resulting in 40% higher energy expenditure compared to a year with high prey availability. We observed no significant changes in physiological condition, breeding success, or trophic niche. The lower fat reserves and higher energy expenditure of females during the breeding season with low food availability may render them more vulnerable to the challenging conditions of the winter season, with potential negative consequences on population trends.

**Keywords:** Accelerometry; Ecosystem management; Foraging ecology; Trophic ecology

1. **Introduction**

Behaviour is a key determinant of the resilience of animal species to a rapidly changing climate (Buchholz et al., 2019). Unusual weather conditions provide valuable opportunities to understand the role of behavioural flexibility in the ability of animals to cope with novel conditions and hence, the role of behaviour in buffering the impacts of climate change on population persistence. The annual cycles of seasonally breeding birds involve key life history events such as reproduction, migration and winter survival, shaped by fluctuating resources and environmental conditions (Buehler and Piersma, 2008). To cope with the challenge of seasonal survival, animals must adjust their behaviour and balance their energy acquisition and expenditure (Karasov, 1986; Dunn et al., 2020).At high latitudes, the temporal window for the breeding season is limited and often strongly coupled with seasonal peaks in food availability (Forcada and Trathan, 2009; Chapman et al., 2010). The match-mismatch hypothesis predicts that predators breed more successfully in years in which the most energetically demanding phase of their breeding cycle overlaps extensively with the seasonal peak in prey availability (Cushing, 1990; Durant et al., 2007). This means that a temporary mismatch between food supply and energy demand must be addressed by parents, affecting foraging costs and individual fitness (e.g., Nicol et al., 2008; Forcada and Trathan, 2009; Chapman et al., 2010; Joly et al., 2022).

Biparental care is essential for offspring success and is widespread among birds. Parental investment is often not equally shared, with sex-related differences in foraging and provisioning behaviour (Lack, 1968). These differences are particularly pronounced in sexually dimorphic species, yet sex-specific foraging patterns have been widely reported in monomorphic or slightly size-dimorphic seabird species (e.g., Gray and Hamer 2001; Lewis et al., 2002; Welcker et al., 2009). Sex-specific foraging behaviours are generally considered to result from different energetic or nutritional needs between the sexes (Gray and Hamer 2001; Lewis et al., 2002; Welcker et al., 2009); from intersexual competition, causing one sex to be spatially displaced or to forage in different niches (González-Solís et al., 2000; Miller et al., 2018); and differences in nest attendance rhythms (Aguilera, 1990).

Reproduction is an energetically costly period for central-place foragers, such as seabirds (Ellis and Gabrielsen, 2002; Dunn et al., 2018). During this time, they must frequently return to the colony to incubate their eggs or to feed their offspring. Their movements are thus spatially and temporally restricted to exploit resources within a given range around the colony (Orians and Pearson, 1979). Therefore, parents incur high values of energy expenditure by making physiological and behavioural adjustments to maintain their body condition while meeting the increasing energetic requirements of their chicks (Drent and Daan, 1980; Dunn et al., 2020). In a context of global environmental changes, understanding animals' capability to modify their trophic niche or foraging behaviour in response to changes in food availability, while meeting parental energy demands, is essential to assess the potential impact of these changes on populations. Here we assess the impact of changes in food availability on the trophic niche and foraging behaviour of one of the most widespread vertebrates of Antarctica, in one of the regions of the globe most affected by climate change: Adélie penguins (*Pygoscelis adeliae*) in the Antarctic Peninsula.

The Adélie penguin is a migratory and pagophilic species (Ainley, 2002), considered an indicator species as it is highly sensitive to changes in the ecosystem (Boersma, 2008). In western Antarctic Peninsula (WAP), a large decline in their breeding populations had been reported at several colonies and linked to rapid environmental changes in the region (Trivelpiece et al., 2011; Fraser et al., 2013; Lynch and LaRue, 2014; Juáres et al., 2015). Climate change have profound effects on both marine and terrestrial environments, impacting penguins' overwinter pack-ice habitat, food resources, and physical conditions of nesting sites (Massom et al., 2006; Hinke et al., 2007, 2012, 2017; Trivelpiece et al., 2011; Fraser et al., 2013; Cimino et al., 2023; Salmerón et al., 2023). Overall, the limited flexibility of Adélie penguins to adapt their breeding chronology according to local conditions, the decline in prey availability during the breeding season, and overwintering processes affecting the survival of juveniles and adults have been proposed as the main factors determining such declines (Hinke et al., 2007, 2012; Emmerson et al., 2011; Lynch et al., 2012; Juáres et al., 2013; Cimino et al., 2016).

The Antarctic krill (*Euphausia superba*) currently constitutes the main prey for Adélie penguins breeding populations of the northern WAP (Trivelpiece et al., 2011; Negrete et al., 2016; Juáres et al., 2018). In this region, Antarctic krill is being affected by ongoing environmental changes, with a decrease in recruitment and abundance, and a southward contraction associated with the continuous decline in the winter sea-ice extent, increase in the sea surface temperature and decline in marine primary production (Montes-Hugo et al., 2009; Hill et al., 2019; Atkinson et al., 2019, 2022). Furthermore, in recent years, Bransfield Strait and the South Shetland Islands have become a hotspot for the krill fishery (Santa Cruz et al., 2018), leading to interference competition with krill predators (Watter et al., 2020). Coupled climate events and fisheries may exacerbate local effects on krill abundance (Watters et al., 2020; Krüger et al., 2021), highlighting the urgent need to understand how fluctuations in krill abundance may impact on dependent marine predators in this region (Hogg et al., 2020; Watters et al., 2020; Krüger et al., 2021; Trathan et al., 2022). Chapman et al. (2011) also postulates that the absence of Antarctic silverfish (*Pleuragramma antarctica*) in the diet of Adélie penguins in the Antarctic Peninsula may have resulted in lower quality (energy content) chick diets, making it difficult for adult Adélie penguins to produce chicks that will recruit. Under current and projected climate change scenarios in the WAP, Adélie penguins, as a species with limited flexibility in the timing of breeding and high dependence on Antarctic krill provide an exceptional case study to understand the potential consequences on populations persistence of climate-driven mismatches between the periods of highest energy demand and maximum food availability (Chapman et al., 2010; Cimino et al., 2023).

Adélie penguins show considerable foraging behavioural flexibility in response to fluctuations in food availability, modifying the distance and duration of foraging trips (Watanuki et al., 1993; Nicol et al., 2008; Lescroël et al., 2020) and the depth of dives (Ainley et al., 2015; Lescroël et al., 2023). With a slight sexual size dimorphism (Ainley and Emison, 1972) their feeding ecology also shows sex-specific differences. Females tend to forage farther, longer, and dive shallower, while males exploit waters closer to the colony and dive deeper (Clarke et al., 1998; Watanuki et al., 2002; Ballard et al., 2010; Lescroël et al., 2010; Widmann et al., 2015). These differences have been attributed to the different energetic needs of females (Chappell et al. 1993a; Clarke et al. 1998; Colominas‑Ciuró et al., 2018), differences in diving capacity and to intra-specific competition for segregation in foraging habitats or diet (Widmann et al., 2015; Massaro et al., 2020). In some colonies, foraging success has been suggested as a determinant factor of their survival and reproductive success (Ballard et al., 2010; Lescroël et al., 2010), with episodes of total breeding failure or low offspring survival linked to poor foraging conditions (Emmerson and Southwell, 2008; Ropert-Coudert et al., 2015; Cimino et al., 2023).

Some studies have analysed the energetic cost of changes in foraging behaviour in response to fluctuations in krill availability for Adélie penguins (e.g., Nagy and Obst, 1992; Chapell et al., 1993; Ballance et al., 2009; Watanabe et al., 2020), however, none of them address how changes in prey availability affect the energy cost of males and females. Therefore, the main objective of our study is to analyse differences in energy expenditure during the breeding season of Adélie penguins from a colony in King George Island/Isla 25 de Mayo in two seasons with large differences in krill availability (Salmerón et al., 2023). We also explore whether this energetic cost differs between males and females. We combined information from previous work on the characteristics of their foraging trips (Machado-Gaye et al., 2024), diet (based on stable isotope analysis), body condition, and daily energy expenditure derived from accelerometry data. The findings reported for the same colony showed differences in foraging behaviour between seasons with differences in prey availability, so here we aim to test the following hypotheses: a) changes in foraging behaviour due to reduced food availability increases the energy expenditure of Adélie penguins, b) Adélie penguins modify their trophic niche to buffer the effects of differences in krill availability, and c) the increase in energy expenditure associated with increased foraging effort exhibits sex-specific differences.

1. **Materials and Methods**

**2.1 Field work**

Fieldwork was conducted at Ardley Island (62°13′ S, 58°56′ W), in the southwest of King George Island/Isla 25 de Mayo, South Shetland Islands, within the Antarctic Specially Protected Area (ASPA) N°150, during the early guard stage of the 2019/20 and 2021/22 breeding seasons (Fig. 1). Between December 6th and 24th, a total of 38 breeding Adélie penguins (19 in 2019/20; 19 in 2021/22) were equipped with data-loggers (Axy-Trek, 70 x 40 x 15 mm, 69 g; TechnoSmart, Italy) including GPS, accelerometer, and both pressure and temperature sensors. We captured only one member of the pair in nests with two chicks, mainly by hand, with the occasional aid of a long-handled net. We also captured chicks during adult handling to protect them from predators. The recorders were attached on the birds’ lower back feathers using black Tesa® 4651 tape (Wilson et al., 1997). The loggers used represent about 1% of the body mass of an adult Adélie penguin (mean for birds in this study 5112 ± 1431 g). The loggers were programmed to record positions every 5 min, pressure (in millibars) and temperature at 1 Hz and acceleration along the 3 body axes of the penguins: longitudinal (surge), dorso-ventral (heave) and lateral (sway) at 50 Hz. After the deployment procedure and immediately before the release of the adult bird, we returned the chicks to the nest, and released the adults some 10 m from their nests. All birds returned to their nests and attended their chicks shortly after being released.

Individuals were recaptured in the nest to recover the devices after 3-7 days and the body mass was weighed. Blood samples were collected immediately after capture via a peripheral foot vein using a sterilized needle and heparinized capillary tubes and five body feathers were plucked from the belly. A small amount of blood was collected in FTA cards for molecular sex determination and one drop of blood was smeared on microscope slides, air-dried and fixed in 96% ethanol for 5 min for measurement of body condition estimates. Remaining blood was preserved in ethanol for subsequent δ13C and δ15N analyses. During the study seasons, we also counted the number of active nests at the end of November (before hatching) and the number of surviving chicks in early January (in the crèche stage close to fledging), to calculate the breeding success of the colony (defined as the number of fledglings divided by the number of active nests).

Finally, in order to describe differences in prey abundance in the area, we used the information on krill acoustic reported by Salmerón et al. (2023) in the surroundings of Nelson Island. In the study, the authors conducted acoustic transects between December 2019 and January 2020, and during January 2022. Although the transect analysed by these authors slightly differs with foraging area used by the penguins tagged in Ardley Island, we assume it reasonably reflects krill abundance in our study area (Fig. 1; but also see Fig. 1 in Salmerón et al. (2023)). The authors found that in 2019/20 krill were more abundant but also more available to penguins, as swarms were found at a shallower depth than in 2021/22.



**Figure 1.** Tracking locations of Adélie penguins breeding in Ardley Island (red dot) (King George Island/Isla 25 de Mayo) during early guard stage in 2019/20 and 2021/22 seasons. The black dotted line represents the area of the krill acoustic transects carried out in both seasons, modified from Salmerón et al. (2023).

**2.2 Data processing**

From 38 deployments, we obtained 33 complete sets of GPS and dive data, comprising location, time, and dive depth, which we used in the following analyses. GPS data were analysed using the R software (version 4.1.3; R Core Team 2022). A speed filter set to 7 km.h-1 was applied to remove unrealistic velocity, and foraging trips were defined from the time the birds moved more than 50 m from the nest to the sea until the time they were within 50 m of the nest again. For each individual, we calculated total trip duration, total trip distance as the cumulative horizontal distance between all GPS locations per bird per trip, and maximum distance to the colony as the straight line distance between the colony and the furthest point of a trip. Dives were analysed using the software Igor Pro Version 6.37 (Wavemetrics). Pressure (mBar) was converted to water depth (m), surface line (0 m) was visually checked and corrected manually when needed. Only dives deeper than 1 m were included due to possible measurement error in instruments and surface waves (Takahashi et al., 2003; Kato et al., 2009). For each dive, we calculated the dive depth (m) (determined as the deepest point of the dive), total dive duration (s), bottom time duration (s) (start and end of bottom time were defined as the first and last time in a dive when the depth change rate was < 0.25 m.s−1). Maximum dive depth recorded on each trip was also calculated.

**2.3 Calculation of energy expenditure**

Energy expenditure is classically measured in relation to the activity level of an animal. At the organismal level, field metabolic rate (FMR) is the total sum of energy that a free-ranging animal metabolizes over a specified period of time (Dunn et al., 2018). Average FMR per 24 hr-period is also routinely used to calculate daily energy expenditure (DEE; Grémillet et al., 2018). To calculate DEE (KJ g-1 day-1) during at sea foraging trips, we used the existing DEE vs activity-specific dynamic body acceleration (DBA) relationship built and validated for Adélie penguins (Hicks et al., 2020).

Accelerometry data were analysed using the software Igor Pro Version 6.37 (Wavemetrics). DBA was calculated by smoothing data for each axis across a 1-s period to calculate the static acceleration, and then subtracting the static acceleration from the raw acceleration values. As a metric for bird activity levels, we calculated the vectorial dynamic body acceleration (VeDBA) as the square root of the sum of the squares of dynamic body acceleration in the three axes: VeDBA = √(A2X + A2Y+A2Z) where Ax, Ay and Az are the derived dynamic accelerations at any point in time corresponding to the three orthogonal axes of the accelerometer (Hicks et al., 2020). For all individuals, we calculated the proportion of time spent on land and in water during a foraging trip (time budget) and the mean VeDBA value for each. We also calculated total VeDBA as the mean behavioural DBA value multiplied by the duration of time spent in that behaviour per day. To calculate the DEE we used the calibrated equation (4) for Adélie penguins proposed by Hicks et al. (2020): DEE = (4.54 x 10-1 ± 4.09 x 10-2) + (1.93 x 10-5 ± 1.76 x 10-6) VeDBAWater + (−1.16 × 10-5 ± 5.25 × 10-6) VeDBALand + (−3.08 × 10-2 ± 2.09 × 10-2) Sex.

**2.4 Stable isotope analysis**

The stable isotope value in a tissue reflects the diet composition and foraging habitat of seabirds during the time of synthesis. The analysed carbon (δ13C) and nitrogen (δ15N) stable isotope values of whole blood allowed us to compare the diet the penguins fed their chicks during the study period, as whole blood provides dietary information integrated of approximately 20 days (Barquete et al., 2013; but also see Bearhop et al., 2000). Isotope analyses were performed at the LIttoral ENvironnement et Sociétés (LIENSs) laboratory, La Rochelle University, with a mass spectrometer (Delta V Plus with a Conflo IV interface, Thermo Scientific, Bremen, Germany) coupled to an elemental analyser (Flash 2000, Thermo Scientific, Milan, Italy). Prior to analyses, blood samples were freeze-dried for 24 h, homogenized to powder and aliquots between 0.1 to 0.5 mg were weighed into tin capsules (8 × 5 mm, Elemental Microanalysis Ltd, Okehampton, United Kingdom) using an analytical balance. Stable isotope values were conventionally expressed as δ values in ‰, using the following equation: δX =([Rsample/Rstandard]-1 × 1000), where Rsample is the ratio of the heavy to light isotope for either 13C/12C or 15N/14N, and Rstandard is the heavy to light isotope ratios for international standards - Vienna PeeDee Belemnite for carbon (VPDB), and atmospheric nitrogen (Air-N2) for nitrogen. Quality control was done using reference materials USGS-61 and USGS-63 (US Geological Survey, Reston, VA, USA) based on their assigned carbon and nitrogen isotope-delta values and standard uncertainties (i.e., -35.05 ± 0.04 ‰ and -1.17 ± 0.04 ‰ for carbon, respectively, and -2.87 ± 0.04 ‰ and +37.83 ± 0.06 ‰ for nitrogen, respectively). The uncertainty of the reported isotope values was evaluated as the standard deviation of repeated (n = 8) measurements of each reference material (i.e., USGS-61 and USGS-63) within a single group of analyses. Uncertainty does not exceed 0.06 ‰ for δ13C values and 0.12 ‰ for δ15N values.

Finally, intact specimens of 3 to 4 whole adult *Euphausia superba* were taken from regurgitate samples collected during the season 2020/21, to represent the sources for analysis. Lipids were removed from prey samples using a 2:1 chloroform:HCl mixture solution. Isotope analyses were performed at the Center for Stable Isotopes, University of New Mexico. We calculated the trophic position for each individual following the model proposed by Post (2002) TP = 𝝀 (δ15Nsecondary consumer - δ15Nbase)/Δn, where 𝝀 is the trophic position of the organism used to estimate δ15Nbase (e.g., 𝝀 = 1 for primary producers), δ15Nsecondary consumer is measured directly, and Δn is the enrichment in δ15N per trophic level. We assumed that diet tissue fractionation factors (Δn) for δ15N was + 2.7 ‰ between lipid-free prey and penguin whole blood (Cherel et al., 2005).

**2.5 Body condition parameters**

The blood smeared on microscope slides was stained with Giemsa pH 7.2 (Masello et al., 2021). Areas of blood smear where the blood cells had separated in a monolayer with similar density of cells were analysed from the x and y axes under light microscope. For each smear we obtained (1) the White Blood Cells (WBC) total count, and (2) the heterophils and lymphocytes ratio (H/L) as physiological health and stress status. The total count of WBC provides information about the general level of immune response of the individual. It was performed counting the number of WBC in 10 visual fields at x400 magnification as a standardized method (Menéndez-Blázquez et al., 2021). The differential leucocyte profile was calculated as the percentage of the difference of WBC of a total of 100 at x1000 amplification (oil immersion). From this profile, we evaluated the H/L ratio, which has been successfully applied as an indicator of physiological status and effort (high ratio = high stress) (Davis and Maney, 2018). Smears analysis was made by the same observer in order to reduce variability and biases derived from identification.

As a proxy for body condition, we also measured adult body mass, considering it as an indicator of the energy reserves for the chick rearing period. Body mass of adult penguins were measured using a Pesola spring balance after recapture and tracking devices removal.

**2.6 Sex determination**

Molecular methods were employed for sex determination using blood and feather samples. DNA was extracted from blood using the DNA Blood and Tissue Kit (QIAGEN, Germany), performed in the laboratory of the Museo Nacional de Ciencias Naturales (Spain), and from feathers using the PrepGem Universal kit (MicroGem; Southampton, UK) performed at Instituto de Investigaciones Clemente Estable (Uruguay), both according to the manufacturers' instructions. The latter was used when blood samples were unavailable or insufficient. Sex identification was performed via PCR using primers P2 and P8 (Griffiths et al., 1998) in a 20 µL reaction containing 1x Platinum Multiplex Master Mix (Invitrogen Life Technologies, Carlsbad, California), 0.5 µL of each primer, and 50 ng of genomic DNA. The P2 primer was labeled with FAM to facilitate fragment size analysis by capillary electrophoresis. The PCR profile included an initial denaturation at 94°C for 10 min, followed by 35 cycles of 94°C for 30 sec, 47°C for 1 min, and 72°C for 1 min, with a final extension at 72°C for 10 min. Both positive and negative controls were included in each PCR run, using known sex samples of *Gubernatrix cristata*. The PCR products were verified by 1% agarose gel electrophoresis, and those from feather analysis, sent to the *Unidad de Secuenciación* at *Hospital de Clínicas, Dr. Manuel Quintelas* (UdelaR, Uruguay), for fragment analysis. Genotype assignment was conducted using GeneMarker 2.4.0 (Softgenetics LLC, State College, Pennsylvania), identifying males as homozygotes (370/370 bp) and females as heterozygotes (370/388 bp).

**2.7 Statistical analyses**

To test for differences between seasons and sexes in the variables analysed we used different statistical models, to account for differences in the response variables and their effects on models assumptions. For each model, a residual analysis was performed to test the homoscedasticity and normality of the residuals. When these did not meet models’ assumptions, a different model was selected. When significant differences between seasons and sex were detected, we performed Tukey's post hoc tests using the *multcomp* package (Hothorn et al., 2008). In each model, the season and sex were considered as an independent factorial variable and the individual as a random effect to account for repeated measures of the same individual. For the only continuous response variable with normal distribution (maximum dive depth per trip) we used linear mixed models (LMM) implemented in the R package *lme4* (Bates et al., 2015). Continuous response variables that did not present a normal distribution (trip duration, maximum trip distance and total trip distance) were log-transformed. For the variables that did not have repeated measures by individual (adult body mass, daily energy expenditure and isotopic values of δ13C and δ15N) we used two-way analysis of variance (ANOVA), with the season and sex as factors. For the response variables that did not fit a normal distribution due to a high number of observations with low values (dive duration, depth and bottom time), we compared between seasons and sexes using generalized linear mixed models (GLMM) using the Tweedie distribution family (with the index of power variance function selected according to response variable distribution) and a log-link function (Foster and Bravington, 2013). implemented in the *lme4* and *statmod* packages. Variation in breeding success between seasons was evaluated with X2-tests.

**Ethical Note**

All penguin handling procedures were reviewed and approved by the Honorary Commission of Animal experimentation of Uruguay (CHEA protocol N° 1312). We were always careful to minimize the stress of the captured individuals by covering their eyes during handling and ensuring that handling time was always less than 15 minutes. After the birds were released, we always made sure that they returned to their nests and attended to their chicks.

1. **Results**

Though breeding success did not differ significantly between the two seasons (Chi-square test: X2=0.11, df= 1, p=0.7), foraging behaviour of Adélie penguins varied substantially between breeding seasons (Table 1 and Fig. 1). The interaction between season and sex was not significant. We found significant differences between seasons, with longer foraging trips during 2021/22, in terms of duration (LMM: F= 22.40, p<0.001) and the maximum and total distance reached (LMM: F= 11.10, p<0.01; LMM: F= 17.08, p<0.001, respectively). In addition, we found differences between sexes, with female Adélie penguins making longer trips in terms of duration (LMM: F= 4.50, p<0.05). Maximum dive depth per trip was deeper in 2021/22 compared to 2019/20 (LMM: F= 6.89, p<0.05), and no differences were found between sexes (LMM: F=0.68, p=0.41). There were no significant differences between seasons and sexes for other dive parameters.

**Table 1**. Foraging and breeding performance of male and female Adélie penguins breeding in Ardley Island (King George Island/Isla 25 de Mayo) in 2019/20 and 2021/22 seasons. Values shown are the mean ± SD. The (\*) indicates that there are significant differences between seasons and (\*\*) indicates that there are significant differences between seasons and between sexes.

|  |  |  |
| --- | --- | --- |
|   | **2019-2020** | **2021-2022** |
| Breeding success (N° BP) | 1.16 (303) | 1.11 (202) |
| Sex  | Male | Female | Male | Female |
| N° Trips (N° birds) | 52 (14) | 12 (4) | 32 (10) | 20 (5) |
| Trip duration (h)\*\* | 8.91 ± 4.67 | 10.31 ± 5.03 | 14.98 ± 7.15 | 23.38 ± 14.61 |
| Max. trip distance (km)\* | 6.55 ± 4.95 | 7.38 ± 7.70 | 11.72 ± 11.52 | 20.76 ± 17.78 |
| Total trip distance (km)\* | 19.03 ± 11.12 | 20.91 ± 17.38 | 35.31 ± 25.72 | 56.03 ± 46.67 |
| Max. dive depth per trip (m)\* | 73.96 ± 18.18 | 73.08 ± 9.44 | 89.05 ± 20.77 | 82.05 ± 18.25 |
| Dive duration (s) | 53.19 ± 39.56 | 52.87 ± 37.26 | 59.52 ± 49.51 | 52.13 ± 44.66 |
| Dive depth (m)  | 18.21 ± 20.12 | 15.92 ± 17.15 | 20.18 ± 24.43 | 17.07 ± 20.87 |
| Bottom time (s) | 27.22 ± 19.98 | 30.42 ± 21.15 | 32.40 ± 25.97 | 27.98 ± 23.31 |
| Adult body mass (kg)\*\* | 6.78 ± 0.62 | 5.74 ± 0.28 | 4.09 ± 0.20 | 3.56 ± 0.24 |

****

**Figure 2.** Foraging trip characteristics and adult body mass (kg) of male and female Adélie penguins breeding in Ardley Island (King George Island/Isla 25 de Mayo), during early guard phase in 2019/20 and 2021/22 seasons.

For the analyses of energy expenditure based on accelerometer records, the interaction between season and sex was significant (LM: F1,40= 7.97, p<0.01, fig. 3). During the 2021/22 breeding season, both males and females incurred in higher DEE than in 2019/20 (Fig. 3). In particular, females showed 40% higher DEE values than females in 2019/20 season and males 16% higher values than in 2019/20. Furthermore, during 2021/22 females showed DEE values 20% higher than males in the same season. During 2019/20 the DEE did not differ between males and females.



**Figure 3.** Daily energy expenditure (DEE; mean ± SD) of male and female Adélie penguins breeding at Ardley Island (King George Island/Isla 25 de Mayo), during the early guard stage of the 2019/20 and 2021/22 breeding seasons. Different letters indicate significant differences between groups.

The blood stable isotope values of Adélie penguins at Ardley Island significantly differ between seasons (Fig. 4; Table S2). During 2019/20, δ13C values were significantly higher than in 2021/22 (LM: F1,34= 20.71, p<0.0001), but we did not find significant differences in mean δ13C values between sexes (LM: F1,34= 2.55, p=0.12). For δ15N, we found significant differences between seasons (LM: F1,35= 5.58, p<0.05) and sexes (LM: F1,35= 24.19, p<0.0001). We found higher mean values during 2021/22 than in 2019/20 and higher values for males than females (Table S2). The mean δ13C and δ15N values for Antarctic krill were -25.21 ± 0.30 ‰ and 4.44 ± 0.22 ‰, respectively. Trophic position according to the model proposed by Post, (2002) was 2.28 ± 0.05 and 2.37 ± 0.07 for females in 2019/20 and 2021/22, respectively. For males, the trophic position was 2.44 ± 0.07 in 2019/20 and 2.47 ± 0.08 in 2021/22.



**Fig. 4** Biplot of Isotopic δ13C and δ15N values (‰) of whole blood from male and female Adélie penguins breeding in Ardley Island (King George Island/Isla 25 de Mayo) in the early guard stage of the 2019/20 and 2021/22 breeding seasons.

*Body condition parameters*

Differences in adult body mass between seasons was statistically significant, being birds heavier in the 2019/20 season than in 2021/22 (LM: F1,29= 256.20, p<0.0001), and males being heavier than females in both seasons (LM: F1,35= 31.11, p<0.0001). Comparisons of the H/L ratios as a stress measures revealed no differences between sex during the same breeding season [season 2019/20 - females mean ± SD: 1.28 ± 0.97 (n = 4), males: 1.31 ± 0.94 (n = 13); Wilcoxon rank sum exact test: W = 125, p = 0.1048. Season 2021/22 - female: 1.23 ± 0.76 (n = 14), males: 0.93 ± 0.66 (n = 14); W = 0.213, p = 0.834]. There were no differences between the same sex in different seasons either [females: W = 23, p = 0.632; males: W = 32.5, p = 0.670]. Similarly, no significant differences were found in WBC in 10 optical fields between sexes within the same season [season 2019/20 – females: 29.25 ± 9.81, males: 37.00 ± 10.02; W = 11.5, p = 0.112. Season 2021/22 - female: 32.57 ± 25.57, males: 33.35 ± 12.67; W = 70.5, p = 0.213] and also between the same sex in different seasons [females: W = 32.5, p = 0.670; males: W = 124.5, p = 0.107] (Fig. S1).

1. **Discussion**

Our results support two of our hypotheses: 1) Adélie penguins modify their foraging behaviour and energy expenditure to account for differences in prey availability, and 2) there are differences between sexes on how they respond to differences in prey availability. During a breeding season with low food abundance, female Adélie penguins rearing chicks, extended both the distance and duration of their foraging trips, resulting in higher energy expenditure compared to males (yet, no sex-differences in diving behaviour were observed). Regarding our second hypothesis, we only found minor changes in trophic niche in response to differences in prey availability.

Sex-based differences in investment in foraging and breeding efforts are widespread in seabird species, related to divergent parental roles, foraging niche partitioning, sex-specific nutritional requirements or anatomy (e.g., body size). Several studies have shown these differences in different species, with females usually making a greater foraging effort during chick-rearing period (Lewis et al., 2002; Miller et al., 2017; Reyes-González et al., 2021; among others). In contrast, Raya-Rey et al. (2013) found an opposite pattern for two penguin species (*Spheniscus humboldti* and *S. magellanicus*), with males making longer foraging trips than females. For Adélie penguins, this sex-specific foraging behaviour has also been reported. In general, females forage longer distances and during more time, while males make shorter trips to closer foraging grounds throughout the guard period in East Antarctica (Clarke et al., 1998; Watanuki et al., 2002; Clarke et al., 2006; Widmann et al., 2015; Riaz et al., 2020), in the Ross Sea (Ballard et al., 2010; Lescroël et al., 2010; 2020) and in the Antarctic Peninsula (Chappell et al., 1993a). In the Ardley Island colony, we also showed that females made significantly longer trips in both breeding seasons. However, in a season with low food abundance, although both parents increased their foraging effort, the difference between males and females became more pronounced, and females made a higher foraging effort, with trips about 50% longer in duration and distance than males. This is consistent with other seabird species, with females showing a higher increase in foraging effort when food becomes scarce (Raya-Rey et al., 2012; Paiva et al., 2017; Reyes-González et al., 2021).

Food availability plays an important role in regulating adult energy expenditure in seabirds by directly affecting energy acquisition, foraging efficiency, and adult body condition (Jodice et al., 2006). Theoretically, food availability may affect energy expenditure through two different processes: DEE may be forced to increase by low food supply (Kitaysky et al., 2000; Regular et al., 2014) or may increase by high levels of food availability (Jodice et al., 2006; Kahane-Rapport et al., 2022). Studies on energy expenditure associated with fluctuations in food availability in Adélie penguins are scarce, but they have reported that under conditions of low prey availability during breeding, they increase their energy expenditure associated with higher foraging effort (Nagy and Obst, 1992; Ballance et al., 2009). Our results are consistent with these observations, as we found that both males and females Adélie penguins increase their foraging effort and DEE in the season with low krill abundance. Furthermore, our results show that the energetic costs of foraging is approximately 20% higher for females than for males in the years of low krill abundance, with no differences between sexes in good years. We also show that females increase their energetic expenditure by about 40% in the year with poor foraging conditions. It is noteworthy that DEE values reported here are within the range of values reported by Hicks et al. (2020) for a colony near Dumont d’Urville station in East Antarctica, where environmental conditions differ significantly from those in Ardley Island (e.g., there is sea ice around the colony throughout the summer).

Different foraging strategies have been also related to body conditions of parents during the brooding stage. Some seabird species are known to adopt a bimodal foraging strategy, alternating between frequent and short trips for chick provisioning with long trips for self maintenance (Clarke, 2001; Ropert-Coudert et al., 2004; Welcker et al., 2009; Carpenter‑Kling et al., 2017). To explain this, it has been suggested that long trips are triggered by a threshold in the body mass of the individuals, below which they decide to go on a long self-maintenance trip to restore body reserves, implying that foraging decisions result from a trade-off between the allocation of food to chicks and self-maintenance (Weimerskirch, 1998; Clarke, 2001). For seabirds foraging in areas of low productivity or prey availability, this threshold may be easier to reach (Carpenter‑Kling et al., 2017). For Adélie penguins, Ballard et al. (2010) demonstrated that they start the breeding season with an energy cushion, which they subsequently lose as they raise their chicks, and observed that parents that had lost more than ~8% of their body mass made longer foraging trips, gaining mass for themselves while bringing their chicks less food. Our results are in line with these findings, although we did not specifically analyse this alternating bimodal strategy of long and short trips. We observed that during a season with prey scarcity and longer foraging trips, the body mass of Adélie penguins was about 40% lower compared to that in a good year. Also, these longer trips have a cost for the offspring and ultimately on breeding success (Ballance, 2009; Ballard et al., 2010; Salmerón et al., 2023). Yet, we found no differences in breeding success between seasons, suggesting that despite the decrease in prey abundance Adélie penguins were able to rear their chicks successfully. However, we did not measure the body mass of fledglings during these seasons. Hence, we do not know if the increased foraging effort of the adults affected the body condition of the chicks, as was reported for other colonies (Cimino et al., 2014; Ainley et al., 2018).

Considering the H/L ratios and WBC as estimates of immune system and body conditions, we found no differences between sexes or breeding seasons. Several studies indicate that the H/L ratio rises in response to increased breeding efforts (Davis et al., 2008), but, although we observed a higher foraging effort in females during 2021/22, we cannot assume that this sex difference is due to a poorer physiological condition associated with higher reproductive costs for females, as proposed by Colominas-Ciuró et al. (2017). These H/L ratios were similar to another colony in the Antarctic Peninsula (Colominas-Ciuró et al. 2017), but lower than in a colony in the Ross Sea (Olmastroni et al., 2019),which could suggest a higher breeding effort in this area compared to the study area. In general, similar WBC levels were previously reported for other Adélie colonies in the Antarctic Peninsula and Ross Sea (Olmastroni et al., 2019, 2024; Menéndez-Blázquez et al., 2021).

Lower δ13C values typically indicate offshore/pelagic foraging habitats (Cherel and Hobson, 2007). As expected, δ13C values during the 2021/22 season were lower compared to 2019/20, reflecting the increased distance of foraging trips. However, we did not find significant differences between sexes, also reflecting what was observed in the tracking data, with both foraging in more coastal areas during 2019/20 and more offshore/pelagic in 2021/22. Sex-specific foraging strategies have also been linked to differences in diet, which might facilitate sexual segregation particularly when resources are limited (Clarke, 2001; Tierney et al., 2009; Widmann et al., 2015; Massaro et al., 2020). For Adélie penguins in East Antarctica and Antarctic Peninsula it has been proposed that females tend to consume larger quantities of krill and males consume more fish (Clarke et al., 1998; Beaulieu et al., 2010; Colominas-Ciuró et al., 2018). Colominas-Ciuró et al. (2018) proposed that given the higher reproductive costs incurred by females, observed in lower antioxidant capacity and higher oxidative damage and stress (Colominas-Ciuró et al., 2017), higher krill consumption allows them to recover to some extent from this reproductive effort, since krill has a higher antioxidant content than fish and is a rich source of high quality protein and omega-3 fatty acids (Beaulieu et al., 2010). According to our results, the diet was dominated by Antarctic krill in both sexes, however, males showed slightly higher δ15N values than females in both seasons, suggesting that they might have incorporated a larger proportion of higher trophic level prey. Furthermore, we also found that both sexes showed slightly higher δ15N values in 2021/22 than in 2019/20, which suggest that both sexes might have had slightly higher levels of supplementation by secondary prey items (e.g., fish, squid) to compensate for low krill abundance. Prey switching during poor seasons was previously reported by Nicol et al. (2008), who found that the diet of Adélie penguins in the Mawson region consisted about 50% of fish during a season with low krill availability. However, we observed that there were no remarkable changes in trophic position in both sexes or between years (2019/20: 2.44 ± 0.07 and 2.28 ± 0.05; 2021/22: 2.37 ± 0.07 and 2.47 ± 0.08, males and females, respectively), indicating that, even under conditions of low krill abundance, they did not substantially modify their trophic niche. Although it had been proposed that fish consumed by Adélie penguins (*P. antarcticum, Electrona antarctica*) have a higher calorific content compared to krill (Ainley et al., 2003) the fact that these components were low in the diet when krill were scarce suggests that prey switching was not possible, probably due to scarcity of other prey options.

Here we deepen current understanding on how Adélie penguins respond to mismatches with their main prey during the breeding season. We have shown that under low krill abundance conditions, female Adélie penguins incur a higher energy expenditure than males. This sex-based variability in foraging effort could have implications for the effect that environmental or fisheries impacts have at different times on different components of the population and, consequently, may require management plans that incorporate these differences. This is particularly relevant in the northern WAP, considering the ongoing discussions on small-scale management of krill fisheries in the region, which concentrate more than 30% of the total krill catch in Antarctica (CCAMLR, 2024). Understanding the sex-specific responses to changes in prey availability and the identification of key foraging areas, as predictable areas of food availability at times of high energy demand (Cresswell et al., 2007; Machado-Gaye et al., 2024) is essential for the design of appropriate conservation measures in a region undergoing significant changes. In addition, it may be relevant to understand how these effects propagate beyond the breeding season. Morandini et al. (2024) reported reduced survival of females once birds become breeders in the Ross Sea, and Hinke et al. (2007) found that for Adélie penguins in the WAP, the spatio-temporal reduction in sea ice during winter negatively impacts juvenile and adult survival. Therefore, the poorer body condition and higher energy expenditure of females during the breeding season may render them more vulnerable than males to changes in food availability, affecting their survival during winter, as they start this challenging stage of their annual cycle with less body reserves. Birds that finish breeding in poor condition may be less likely to successfully complete the molt, or may finish molting with low energy reserves (Chappell et al., 1993b), hence impacting on wintering survival or in body conditions and the onset of the next breeding season, with negative effects on population trends.

Overall, the study of the processes underlying Adélie penguin population declines in the WAP provide valuable insights on some of the potentially diverse and subtle factors affecting populations persistence under climate-change scenarios, and the role of behavioural flexibility in buffering some of the impacts of these changes. In the specific case of Adélie penguins breeding in Ardley Island, observed population trends are likely consequence of a range of ecological process acting at different spatial and temporal scales. For example, the marked decline in breeding pairs between 2019/20 and 2021/22 might be linked to unusually harsh breeding conditions during 2020/21 (Machado-Gaye, pers. comm.). Although the breeding success or body condition of the fledglings has no effect on the breeding population size in the following season, since juveniles recruit as breeding adults 3-4 years later (Ainley and Schlatter, 1972), poor conditions during the season may have an effect on the number of breeding pairs that attempt to reproduce in the following year. Factors operating on the overwintering survival of breeding adults cannot be ignored either. This might be linked to the poor body condition in which they finish the breeding season, as we suggest here, but also to adverse conditions during the non-breeding season, miles away from the breeding grounds. Despite no evident effects on breeding success, low krill availability might have subtle effects on adult survival that are difficult to properly assess. Although not decisive on their own, these effects might contribute to an accumulation of subtle impacts that taken together can have a significant impact on the fate of these populations, highlighting the importance of implementing efforts aimed at minimizing any manageable impact (e.g., fisheries). Also, the need for holistic approaches when planning the management of marine living resources in the Southern Ocean (Zaldúa et al., 2024).

**References**

Aguilera E. 1990 Sexual differences in nest attendance and chick-feeding rhythms of White Spoonbills. The Auk. 107, 416-420. (<https://doi.org/10.2307/4087631>)

Ainley D, Schlatter R P. 1972 Chick raising ability in Adélie penguins. *The Auk*, 559-566.

Ainley D. 2002 *The Adélie penguin: bellwether of climate change*. Columbia University Press.Ainley D, Ballard G, Barton KJ, Karl B, Rau GH, Ribic CA, Wilson PR. 2003 Spatial and temporal variation of diet within a presumed metapopulation of Adélie penguins. Condor 105, 95–106. (https://doi.org/10.1650/0010-5422(2003)105[95:SATVOD]2.0.CO;2)

Ainley DG, Ballard G, Jones RM, Jongsomjit D, Pierce SD, Smith WO Jr, Veloz S. 2015 Trophic cascades in the western Ross Sea, Antarctica: revisited. Mar Ecol Prog Ser 534, 1–16. (https://doi.org/10.3354/meps1 1394)

Ainley DG, Dugger KM, La Mesa M, Ballard G, Barton KJ, Jennings S, Karl BJ, Lescroël A, Lyver PO’B, Schmidt A, Wilson P. 2018 Post-fledging survival of Adélie penguins at multiple colonies: chicks raised on fish do well. Mar. Ecol. Prog. Ser. 601, 239-251. (https://doi.org/10.3354/meps12687)

Ainley DG, Emison WB. 1972 Sexual size dimorphism in Adélie penguins. Ibis 114, 267-271. (https ://doi.org/10.1111/j.1474-919X.1972.tb026 13.x)

Atkinson A, Hill SL, Pakhomov EA, Siegel V, Reiss C S, Loeb V J, ...Sailley S F. 2019 Krill (*Euphausia superba*) distribution contracts southward during rapid regional warming. Nat. Clim. Chang. 9:142–147. (https://doi.org/10.1038/s41558-018-0370-z)

Atkinson A, Hill S L, Reiss C S, Pakhomov E A, Beaugrand G, Tarling G A, ...Perry F A. 2022 Stepping stones towards Antarctica: Switch to southern spawning grounds explains an abrupt range shift in krill. Glob. Change Biol. *28*(4), 1359-1375. (https://doi.org/10.1111/gcb.16009)

Ballance L, Ainley DG, Ballard G, Barton K. 2009 An energetic correlate between colony size and foraging effort in seabirds, an example of the Adélie penguin Pygoscelis adeliae. J Avian Biol. 40, 279-288. (https://doi.org/10.1111/j.1600-048X.2008.04538.x)

Ballard G, Dugger KM, Nur N, Ainley DG. 2010 Foraging strategies of Adélie penguins: adjusting body condition to cope with environmental variability. Mar. Ecol. Prog. Ser. 405, 287-302. (https://doi.org/10.3354/meps08514)

Barquete V, Strauss V, Ryan PG. 2013 Stable isotope turnover in blood and claws: a case study in captive African penguins. J. Exp. Mar. Bio. Ecol. 448, 121-127. (https://doi.org/10.1016/j.jembe.2013.06.021)

Bates D, Mächler M, Bolker B, Walker S. 2015 Fitting Linear Mixed-Effects Models Using lme4. J Stat Softw. 67, 1–48. (https://doi.org/10.48550/arXiv.1406.5823)

Bearhop S, Waldron S, Votier SC, Furness RW. 2002 Factors that influence assimilation rates and fractionation of nitrogen and carbon stable isotopes in avian blood and feathers. Physiol Biochem Zool. 75, 451-458.

Beaulieu M, Ropert-Coudert Y, Le Maho Y, Ancel A, Criscuolo F. 2010 Foraging in an oxidative environment: relationship between δ13C values and oxidative status in Adélie penguins. Proc. R. Soc. B. 277, 1087–1092. (<https://doi.org/10.1098/rspb.2009.1881>)

Boersma, P. D. (2008). Penguins as marine sentinels. *Bioscience*, *58*(7), 597-607. (<https://doi.org/10.1641/B580707>)

Buchholz R, Banusiewicz J D, Burgess S, Crocker-Buta S, Eveland L, Fuller, L. 2019 Behavioural research priorities for the study of animal response to climate change. Anim. Behav. 150, 127-137. (<https://doi.org/10.1016/j.anbehav.2019.02.005>)

Carpenter-Kling T, Handley JM, Green DB, Reisinger RR, Makhado AB, Crawford RJM, Pistorius PA. 2017 A novel foraging strategy in gentoo penguins breeding at sub-Antarctic Marion Island. Mar. Biol. 164, 33. (https://doi.org/10.1007/s00227-016-3066-9)

CCAMLR Secretariat 2024 Fishery Report 2023: Euphausia superba in Area 48. https://fishdocs.ccamlr.org/FishRep\_48\_KRI\_2023.pdf

Chapman EW, Hofmann EE, Patterson DL, Fraser WR. 2010 The effects of variability in Antarctic krill (*Euphausia superba*) spawning behavior and sex/maturity stage distribution on Adélie penguin (*Pygoscelis adeliae*) chick growth: a modeling study. Deep-Sea Res. II. 57, 543-558. (https://doi.org/10.1016/j.dsr2.2009.10.005)

Chapman EW, Hofmann EE, Patterson DL, Ribic CA, Fraser WR. 2011 Marine and terrestrial factors affecting Adélie ­penguin Pygoscelis adeliae chick growth and recruitment off the western Antarctic Peninsula. Mar Ecol Prog Ser. 436, 273-289. (https://doi.org/10.3354/meps09242)

Chappell MA, Shoemaker VH, Janes DN, Maloney SK, Bucher TL. 1993a Energetics of Foraging in Breeding Adelie Penguins. Ecol. 74, 2450-2461. (<https://doi.org/10.2307/1939596>)

Chappell MA, Janes DN, Shoemaker VH, Bucher TL, Maloney SK. 1993b Reproductive effort in Adélie penguins. Behav Ecol Sociobiol, 33, 173-182. (https://doi.org/10.1007/BF00216598)

Cherel Y, Hobson KA 2007 Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. Mar. Ecol. Prog. Ser. 329, 281-287. (https://doi:10.3354/meps329281)

Cherel Y, Hobson KA, Hassani S. 2005 Isotopic discrimination between food and blood and feathers of captive penguins: implications for dietary studies in the wild. Physiol Biochem Zool. 78(1), 106-115.

Cherel Y. 2008 Isotopic niches of emperor and Adélie penguins in Adélie Land, Antarctica. Mar Biol. 154, 813-821. (https://doi.org/10.1007/s00227-008-0974-3)

Cimino M, Conroy JA, Connors E, Bowman J, Corso A, Ducklow H, Fraser W, Friedlaender A, Kim H, Larsen GD. 2023 Long-Term Patterns in Ecosystem Phenology near Palmer Station, Antarctica, from the Perspective of the Adélie Penguin. Ecosphere 14, e4417. (https://doi.org/10.1002/ecs2.4417)

Cimino MA, Fraser WR, Patterson-Fraser DL, Saba VS, Oliver MJ. 2014 Large-scale climate and local weather drive interannual variability in Adélie penguin chick fledging mass. Mar Ecol Prog Ser. 513, 253-268. (<https://doi.org/10.3354/meps10928>)

Cimino M A, Lynch H J, Saba V S, Oliver M J. 2016 Projected asymmetric response of Adélie penguins to Antarctic climate change. Sci. Rep. *6*(1), 28785. (https://doi.org/10.1038/srep28785)

Clarke J, Emmerson LM, Otahal P. 2006 Environmental conditions and life history constraints determine foraging range in breeding Adélie penguins. Mar. Ecol. Prog. Ser. 310, 247-261. (https://doi.org/10.3354/meps310247)

Clarke J, Manly B, Kerry K, Gardner H, Franchi E, Corsolini S, Focardi S. 1998 Sex differences in Adélie penguin foraging strategies. Polar Biol. 20, 248-258. (https://doi.org/10.1007/s003000050301)

Clarke JR. 2001 Partitioning of foraging effort in Adélie penguins provisioning chicks at Béchervaise Island, Antarctica. Polar Biol. 24, 16-20. (https://doi.org/10.1007/s003000000168)

Colominas-Ciuró R, Santos M, Coria N, Barbosa A. 2017 Reproductive effort affects oxidative status and stress in an Antarctic penguin species: An experimental study. PLoS ONE 12, e0177124. (https://doi.org/10.1371/journal.pone.0177124)

Colominas-Ciuró R, Santos M, Coria N, Barbosa A. 2018 Sex-specific foraging strategies of Adélie penguins (*Pygoscelis adeliae*): females forage further and on more krill than males in the Antarctic Peninsula. Polar Biol. 41, 2635-2641. (<https://doi.org/10.1007/s00300-018-2395-1>)

Cresswell KA, Tarling GA, Trathan PN. 2007 Weight loss during breeding is adaptive for female macaroni penguins, *Eudyptes chrysolophus*. Evol. Ecol. Res. 9, 1053-1076.

Cushing DH. 1990 Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Adv Mar Biol. 26, 249-293. (https://doi.org/10.1016/S0065-2881(08)60202-3)

Davis AK, Maney DL, Maerz JC. 2008 The use of leukocyte profiles to measure stress in vertebrates: a review for ecologists. Funct. Ecol. 22, 760–767. (https://doi.org/10.1111/j.1365-2435.2008.01467.x)

Davis AK, Maney DL. 2018 The use of glucocorticoid hormones or leucocyte profiles to measure stress in vertebrates: what’s the difference? Met Ecol Evol. 9, 1556–1568. (https://doi.org/10.1111/2041-210X.13020)

Drent RH, Daan S. 1980 The prudent parent: energetic adjustments in avian breeding. Ardea, 68, 225–252.

Dunn RE, Wanless S, Daunt F, Harris MP, Green JA. 2020 A year in the life of a north Atlantic seabird: Behavioural and energetic adjustments during the annual cycle. Sci Rep. 10, 1–11. (https://doi.org/10.1038/s4159 8-020-62842-x)

Dunn RE, White CR, Green JA. 2018 A model to estimate seabird field metabolic rates. Biol. Lett. 14, 20180190. (https://doi.org/10.1098/rsbl.2018.0190)

Durant JM, Hjermann DØ, Ottersen G, Stenseth NC. 2007 Climate and the match or mismatch between predator requirements and resource availability. Clim. Res. 33, 271-283. (https://doi:10.3354/cr033271)

Ellis HI, Gabrielsen GW. 2002 Energetics of free-ranging seabirds. In: Whittow, G.C., Rahn, H. (eds) Seabird Energetics. Springer, Boston, MA. (https://doi.org/10.1007/978-1-4684-4859-7\_10)

Emmerson L, Southwell C. 2008 Sea ice cover and its influence on Adélie penguin reproductive performance. Ecol. 89, 2096-2102. (<https://doi.org/10.1890/08-0011.1>)

Emmerson L, Pike R, Southwell C. 2011 Reproductive consequences of environment-driven variation in Adélie penguin breeding phenology. Mar. Ecol. Prog. Ser. 440, 203-216. (https://doi.org/10.3354/meps09265)

Fraser W R, Patterson-Fraser D L, Ribic C A, Schofield O, Ducklow H. 2013 A nonmarine source of variability in Adélie penguin demography. Oceanogr. *26*(3), 207-209.

Forcada J, Trathan PN. 2009 Penguin responses to climate change in the Southern Ocean. Glob. Change Biol. 15, 1618-1630. (https://doi.org/10.1111/j.1365-2486.2009.01909.x)

Foster SD, Bravington MVA. 2013 Poisson–Gamma model for analysis of ecological non-negative continuous data. Environ Ecol Stat 20, 533–552. (https://doi.org/10.1007/s10651-012-0233-0)

González-Solís J, Croxall JP, Wood AG. (2000) Sexual dimorphism and sexual segregation in foraging strategies of Northern giant petrels, *Macronectes halli*, during incubation. Oikos. 90, 390–398. (https://doi.org/10.1034/j.1600-0706.2000.900220.x)

Gorman KB, Williams TD, Fraser WR. 2014 Ecological Sexual Dimorphism and Environmental Variability within a Community of Antarctic Penguins (Genus Pygoscelis). PLoS ONE 9, e90081. (https://doi:10.1371/journal.pone.0090081)

Gray CM, Hamer KC. 2001 Food-provisioning behaviour of male and female Manx shearwaters, *Puffinus puffinus*. Anim. Behav. 62, 117–121. (https://doi.org/10.1006/anbe.2001.1717)

Grémillet D, Lescroël A, Ballard G, Dugger KM, Massaro M, Porzig EL, Ainley DG. 2018 Energetic fitness: field metabolic rates assessed via 3D accelerometry complement conventional fitness metrics. Funct Ecol. 32, 1203-1213. (https://doi.org/10.1111/1365-2435.13074)

Griffiths R, Double MC, Orr K, Dawson RJ. 1998 A DNA test to sex most birds. Mol. Ecol. 7, 1071-1075. (https://doi.org/10.1046/j.1365-294x.1998.00389.x)

Hicks O, Kato A, Angelier F, Wisniewska DM, Hambly C, Speakman JR, Marciau C, Ropert-Coudert Y. 2020 Acceleration predicts energy expenditure in a fat, flightless, diving bird. Sci Rep. 10, 21493. (https://doi.org/10.1038/s41598-020-78025-7)

Hinke JT, Salwicka K, Trivelpiece SG, Watters GM, Trivelpiece WZ. 2007 Divergent responses of Pygoscelis penguins reveal a common environmental driver. Oecologia. 153, 845-855. (<https://doi.org/10.1007/s00442-007-0781-4>)

Hinke J T, Polito M J, Reiss C S, Trivelpiece S G, Trivelpiece W Z 2012 Flexible reproductive timing can buffer reproductive success of Pygoscelis spp. penguins in the Antarctic Peninsula region. Mar. Ecol. Prog. Ser. 454, 91-104. (<https://doi.org/10.3354/meps09633>)

Hinke J T, Trivelpiece S G, Trivelpiece W Z 2017 Variable vital rates and the risk of population declines in Adélie penguins from the Antarctic Peninsula region. Ecosphere, 8(1), e01666. (<https://doi.org/10.1002/ecs2.1666>)

Hill S L, Atkinson A, Pakhomov E A, Siegel V. 2019 Evidence for a decline in the population density of Antarctic krill *Euphausia superba* still stands. A comment on Cox et al. J. Crustac. Biol. *39*(3), 316-322. (<https://doi.org/10.1093/jcbiol/ruz004>)

Hogg CJ, Lea MA, Gual Soler M, Vasquez VN, Payo-Payo A, Parrott ML, Santos M, Shaw C, Brooks CM 2020 Protect the Antarctic Peninsula—before it’s too late. Nature 586(7830), 496-499. (https://doi.org/10.1038/d41586-020-02939-5)

Hothorn T, Bretz F, Westfall P. 2008 Simultaneous Inference in General Parametric Models. Biom J. 50, 346–363. (https://doi.org/10.1002/ bimj. 20081 042)

Jodice PG, Roby DD, Suryan RM, Irons DB, Turco KR, Brown ED, Thedinga JF, Visser GH. 2006 Increased energy expenditure by a seabird in response to higher food abundance. Mar. Ecol. Prog. Ser. 306, 283-293. (https://doi.org/10.3354/meps306283)

Joly NB, Chiaradia A, Georges JY, Saraux C. 2022 Environmental effects on foraging performance in little penguins: a matter of phenology and short-term variability. Mar Ecol Prog Ser 692, 151-168. (https://doi.org/10.3354/meps14058)

Juáres MA, Casaux R, Corbalán A, Blanco G, Pereira GA, Perchivale PJ, Coria N, Santos M. 2018 Diet of Adélie penguins (Pygoscelis adeliae) at stranger point (25 de Mayo/King George Island, Antarctica) over a 13-year period (2003–2015). Polar Biol. 41, 303-311. (<https://doi.org/10.1007/s00300-017-2191-3>)

Juáres M A, Santos M, Negrete J, Mennucci J A, Perchivale P J, Casaux R, Coria N R 2015 Adélie penguin population changes at Stranger Point: 19 years of monitoring. Antarct. Sci. *27*(5), 455-461. (<https://doi.org/10.1017/S0954102015000152>)

Juares M A, Santos M M, Negrete J, Santos M R, Mennucci J A, Rombola E, Longarzo L, Coria N R, Carlini A R 2013 Better late than never? Interannual and seasonal variability in breeding chronology of gentoo penguins at Stranger Point, Antarctica. Polar Res. *32*(1), 18448. (https://doi.org/10.3402/polar.v32i0.18448)

Kahane-Rapport SR, Whelan S, Ammendolia J, Hatch SA, Elliott KH, Shoshanah J. 2022 Food supply and individual quality influence seabird energy expenditure and reproductive success. Oecologia 199, 367–376. (<https://doi.org/10.1007/s00442-022-05191-y>)

Karasov W H. 1986 Energetics, physiology and vertebrate ecology. TREE. *1*(4), 101-104. ([https://doi.org/10.1016/0169-5347(86)90034-0](https://doi.org/10.1016/0169-5347%2886%2990034-0))

Kato A, Yoshioka A, Sato K. 2009 Foraging behavior of Adélie penguins during incubation period in Lützow-Holm Bay. Polar Biol. 32, 181–186. (https://doi.org/10.1007/s00300-008-0518-9)

Kitaysky AS, Hunt Jr GL, Flint EN, Rubega MA, Decker MB. 2000 Resource allocation in breeding seabirds: responses to fluctuations in their food supply. Mar. Ecol. Prog. Ser. 206, 283-296. (<https://doi:10.3354/meps206283>)

Krüger L, Huerta MF, Santa Cruz F, Cárdenas CA 2021 Antarctic krill fishery effects over penguin populations under adverse climate conditions: Implications for the management of fishing practices. Ambio 50, 560-571. (https://doi.org/10.1007/s13280-020-01386-w)

Lack D. 1968 Ecological adaptations for breeding in birds. London, UK: Methuen & Co. Ltd

Lescroël A, Ballard G, Toniolo V, Barton KJ, Wilson PR, Lyver PO, Ainley DG. 2010 Working less to gain more: when breeding quality relates to foraging efficiency. Ecol. 91, 2044-2055. (https://doi.org/10.1890/09-0766.1)

Lescroël A, Lyver PO’B, Jongsomjit D, Veloz S, Dugger KM, Kappes P, Karl BJ, Whitehead A, Pech R, Cole TL, Ballard G. 2020 Interindividual differences in the foraging behavior of breeding Adélie penguins are driven by individual quality and sex. Mar Ecol Prog Ser. 636, 189–205. (https:// doi. org/ 10. 3354/ meps1 3208)

Lescroël A, Schmidt A, Ainley DG, Dugger KM, Elrod M, Jongsomjit D, Morandini V, Winquist S, Ballard G. 2023 High-resolution recording of foraging behaviour over multiple annual cycles shows decline in old Adélie penguins’ performance. Proc R Soc B 290, 20222480. (https://doi.org/10.1098/rspb.2022. 2480)

Lewis S, Benvenuti S, Dall–Antonia L, Griffiths R, Money L, Sherratt TN, Wanless S, Hamer KC. 2002 Sex-specific foraging behaviour in a monomorphic seabird. Proc. R. Soc. Lond. B. 269, 1687–1693. (<http://doi.org/10.1098/rspb.2002.2083>)

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

Lynch, H. J., & LaRue, M. A. (2014). First global census of the Adélie Penguin. The Auk. *131*(4), 457-466. (<https://doi.org/10.1642/AUK-14-31.1>)

Machado-Gaye AL, Kato A, Chimienti M, Gobel N, Ropert-Coudert R, Barbosa A, Soutullo A. 2024 Using latent behavior analysis to identify key foraging areas for Adélie penguins in a declining colony in West Antarctic Peninsula. Mar Biol. 171, 69. (https://doi.org/10.1007/s00227-024-04390-w)

Masello JF, Barbosa A, Kato A, Mattern T, Medeiros R, Stockdale JE, Kümmel MN, Bustamante P, Belliure J, Benzal J, et al. 2021 How animals distribute themselves in space: energy landscapes of Antarctic avian predators. Mov Ecol. 9, 24. (https://doi.org/10.1186/s40462-021-00255-9)

Massaro M, Ainley DG, Santora JA, Quillfeldt P, Lescroël A, Whitehead A, Varsani A, Ballard G, Lyver PO’B. 2020 Diet segregation in Adélie penguins: some individuals attempt to overcome colony-induced and annual foraging challenges. Mar Ecol Prog Ser. 645, 205-218. (<https://doi.org/10.3354/meps13370>)

Massom R A, Stammerjohn S E, Smith R C, Pook M J, Iannuzzi R A, Adams N, ... Krouse H. R (2006). Extreme anomalous atmospheric circulation in the West Antarctic Peninsula region in austral spring and summer 2001/02, and its profound impact on sea ice and biota. J. of Clim. 19(15), 3544-3571. (<https://doi.org/10.1175/JCLI3805.1>)

McDaniel JD, Emslie SD. 2002 Fluctuations in Adélie penguin prey size in the mid to late Holocene, northern Marguerite Bay, Antarctic Peninsula. Polar Biol. 25, 618–623. (https://doi.org/10.1007/s00300-002-0401-z)

Menéndez-Blázquez J, Soto, F., Negrete, J. Colominas-Ciuró R, Marín-Sierra A, Ricca M, Barbosa A. 2021 Leukocyte counts in blood smears of Antarctic seals and penguins: a new less time-consuming method. Polar Biol. 44, 2195–2198. (https://doi.org/10.1007/s00300-021-02950-0)

Miller MG, Silva FR, Machovsky-Capuska GE, Congdon BC. 2018 Sexual segregation in tropical seabirds: drivers of sex-specific foraging in the brown booby *Sula leucogaster*. J Ornithol. 159, 425-437. (<https://doi.org/10.1007/s10336-017-1512-1>)

Montes-Hugo M, Doney S C, Ducklow H W, Fraser W, Martinson D, Stammerjohn S E, Schofield O 2009 Recent changes in phytoplankton communities associated with rapid regional climate change along the western Antarctic Peninsula. Science, 323(5920), 1470-1473. (https://doi.org/[10.1126/science.1164533](https://doi.org/10.1126/science.1164533))

Morandini V, Dugger KM, Schmidt AE, Varsani A, Lescroël A, Ballard G, Lyver PO, Barton K, Ainley, D. G. (2024). Sex-specific recruitment rates contribute to male-biased sex ratio in Adélie penguins. Ecol. Evol. 14, e10859. https://doi.org/10.1002/ece3.10859

Nagy KA, Obst BS. 1992 Food and energy requirements of Adélie penguins (*Pygoscelis adeliae*) on the Antarctic Peninsula. Physiol Zool. 65, 1271-1284. (https://doi.org/10.1086/physzool.65.6.30158279)

Negrete P, Sallaberry M, Barceló G, Maldonado K, Perona F, McGill RA, Quillfeldt P, Sabat P. 2017 Temporal variation in isotopic composition of Pygoscelis penguins at Ardley Island, Antarctic: Are foraging habits impacted by environmental change?. Polar Biol. 40, 903-916. (https://doi.org/10.1007/s00300-016-2017-8)

Nicol S, Clarke J, Romaine S, Kawaguchi S, Williams G, Hosie G. 2008 Krill (*Euphausia superba*) abundance and Adélie penguin (*Pygoscelis adeliae*) breeding performance in the waters off the Béchervaise island colony, East Antarctica in 2 years with contrasting ecological conditions. Deep-Sea Res. II. 55, 540–557. (https://doi: 10.1016/j.dsr2.2007.11.013)

Olmastroni S, Pompeo G, Jha AN, Mori E, Vannuccini ML, Fattorini N, Ademollo N, Corsi I. 2019 Erythrocytes nuclear abnormalities and leukocyte profile of the immune system of Adélie penguins (*Pygoscelis adeliae*) breeding at Edmonson Point, Ross Sea, Antarctica. Polar Biol. 42, 1343–1352. (https://doi.org/10.1007/s00300-019-02522-3)

Olmastroni S, Simonetti S, Fattorini N, D'Amico V, Cusset F, Bustamante P, Cherel Y, Corsi I. 2024 Monitoring stress ecology by non-destructive methods in an Antarctic seabird, Sci. Total Environ. 922, 171249. (https://doi.org/10.1016/j.scitotenv.2024.171249)

Orians GH, Pearson NE. 1979 On the theory of central place foraging. In: Horn DJ, Mitchell RD, Stairs GR (eds) Analysis of ecological systems. Ohio University Press, Columbus, OH, p 154-177.

Paiva VH, Pereira J, Ceia FR, Jaime A. 2017 Ramos Environmentally driven sexual segregation in a marine top predator. Sci Rep 7, 2590. (https://doi.org/10.1038/s41598-017-02854-2)

Post DM. 2002 Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecol. 83, 703-718. (https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2)

Raya-Rey A, Pütz K, Scioscia G, Lüthi B, Schiavini A. 2012 Sexual differences in the foraging behaviour of Magellanic Penguins related to stage of breeding. Emu-Austral Ornithology, 112(2), 90-96. (https://doi.org/10.1071/MU11065)

Raya-Rey A, Pütz K, Simeone A, Hiriart-Bertrand L, Reyes-Arriagada R, Riquelme V, Lüthi B. 2013 Comparative foraging behaviour of sympatric Humboldt and Magellanic Penguins reveals species-specific and sex-specific strategies. Emu - Austral Ornithology, 113, 145–153. (https://doi.org/10.1071/MU12040)

Regular PM, Hedd A, Montevecchi WA, Robertson GJ, Storey AE, Walsh CJ. 2014 Why timing is everything: Energetic costs and reproductive consequences of resource mismatch for a chick-rearing seabird. Ecosphere 5, 155. (http://dx.doi.org/10.1890/ES14-00182.1)

Reyes‐González JM, De Felipe F, Morera‐Pujol V, Soriano‐Redondo A, Navarro‐Herrero L, Zango L, García-Barcelona S, Ramos R, González-Solís J. 2021 Sexual segregation in the foraging behaviour of a slightly dimorphic seabird: Influence of the environment and fishery activity. J Anim. Ecol. 90, 1109-1121. (https://doi.org/10.1111/1365-2656.13437)

Riaz J, Bestley S, Wotherspoon S, Freyer J, Emmerson L. 2020 From trips to bouts to dives: temporal patterns in the diving behaviour of chick-rearing Adélie penguins, East Antarctica. Mar. Ecol. Prog. Ser. 654, 177–194. (https:// doi. org/ 10. 3354/ meps1 3519)

Ropert-Coudert Y, Kato A, Meyer X, Pellé M, MacIntosh AJ, Angelier F, Chastel O, Widmann M, Arthur B, Raymond B, Raclot T. 2015 A complete breeding failure in an Adélie penguin colony correlates with unusual and extreme environmental events. Ecography 38, 111–113. (https://doi: 10.1111/ecog.01182)

Ropert-Coudert Y, Wilson RP, Daunt F, Kato A. 2004 Patterns of energy acquisition by a central place forager: benefits of alternating short and long foraging trips. Behav Ecol. 15, 824–830. (https://doi.org/10.1093/beheco/arh086)

Salmerón N, Belle S, Santa Cruz F, Alegria N, Grohmann Finger J, Corá DH, Petry MV, Hernández C, Cárdenas C, Krüger L. 2023 Contrasting environmental conditions precluded lower availability of Antarctic krill affecting breeding chinstrap penguins in the Antarctic Peninsula. Sci Rep 13, 5265. ([https://doi.org/10.1038/s41598- 023- 32352-7](https://doi.org/10.1038/s41598-%20023-%2032352-7))

Santa Cruz F, Ernst B, Arata JA, Parada C. 2018 Spatial and temporal dynamics of the Antarctic krill fishery in fishing hotspots in the Bransfield Strait and South Shetland Islands. Fish. Res. 208, 157-166. (https://doi.org/10.1016/j.fishres.2018.07.020)

Takahashi A, Watanuki Y, Sato K, Kato A, Arai N, Nishikawa J, Naito Y. 2003 Parental foraging effort and offspring growth in Adélie penguins: does working hard improve reproductive success? Funct Ecol. 17, 590–597.

Tierney M, Southwell C, Emmerson LM, Hindell MA. 2008 Evaluating and using stable-isotope analysis to infer diet composition and foraging ecology of Adélie penguins Pygoscelis adeliae. Mar. Ecol. Prog. Ser. 355, 297-307. (<https://doi.org/10.3354/meps07235>)

Trathan PN, Warwick-Evans V, Young EF, Friedlaender A, Kim JH, Kokubun N 2022 The ecosystem approach to management of the Antarctic krill fishery -the ‘devils are in the detail’ at small spatial and temporal scales. J. Mar. Syst. 225:103598. (https://doi.org/10.1016/j.jmarsys.2021.103598)

Trivelpiece WZ, Hinke JT, Miller AK, Reiss CS, Trivelpiece SG, Watters GM. 2011 Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. PNAS 108, 7625–7628. (https:// doi. org/ 10. 1073/ pnas. 10165 60108)

Warwick-Evans V, Kelly N, Dalla Rosa L, Friedlaender A, Hinke JT, Kim JH, Kokubun N, Santora JA, Secchi ER, Seyboth E, Trathan PN. 2022 Using Seabird and Whale Distribution Models to Estimate Spatial Consumption of Krill to Inform Fishery Management. Ecosphere 13, e4083. (https://doi.org/10.1002/ecs2.4083)

Watanabe YY, Ito K, Kokubun N, Takahashi A. 2020 Foraging behavior links sea ice to breeding success in Antarctic penguins. Sci Adv. 6, eaba4828. (https://doi.org/10.1126/sciadv.aba4828)

Watanuki Y, Kato A, Mori Y, Naito Y. 1993 Diving performance of Adélie penguins in relation to food availability in fast sea-ice areas: comparison between years. J Anim Ecol. 62, 634-646. (https://doi.org/10.2307/5384)

Watanuki Y, Kato A, Sato K, Niizuma Y, Bost CA, Le Maho Y, Naito Y. 2002 Parental mass change and food provisioning in Adélie penguins rearing chicks in colonies with contrasting sea-ice conditions. Polar Biol. 25, 672-681. (https://doi.org/10.1007/s00300-002-0399-2)

Watters GM, Hinke JT, Reiss CS. 2020 Long-term observations from Antarctica demonstrate that mismatched scales of fisheries management and predator-prey interaction lead to erroneous conclusions about precaution. Sci Rep. 10, 2314. (https:// doi. org/10. 1038/ s41598- 020- 59223-9)

Weimerskirch H. 1998 How can a pelagic seabird provision its chick when relying on a distant resource? Cyclic attendance, foraging decision and body condition in sooty shearwaters. J Anim Ecol. 67, 99-109. (<https://doi.org/10.1046/j.1365-2656.1998.00180.x>)

Welcker J, Steen H, Harding AMA, Gabrielsen GW. 2009 Sex-specific provisioning behaviour in a monomorphic seabird with a bimodal foraging strategy. Ibis. 151, 502–513. (https://doi.org/10.1111/j.1474-919X.2009.00931.x)

Widmann M, Kato A, Raymond B, Angelier F, Arthur B, Chastel O, Ropert-Coudert Y. 2015 Habitat use and sex-specific foraging behaviour of Adélie penguins throughout the breeding season in Adélie Land, East Antarctica. Mov Ecol. 3, 1–10. (https://doi.org/10.1186/s40462- 015- 0052-7)

Wilson RP, Pütz K, Peters G, Culik B, Scolaro JA, Charrassin JB, Ropert-Coudert Y. 1997 Long-term attachment of transmitting and recording devices to penguins and other seabirds. Wildl Soc Bull. 25, 101-106.

Zaldúa N, Zajková Z, Machado-Gaye A L, Franco-Trecu V, Cosse M, Ropert-Coudert Y, Kato A, Soutullo A. 2024 Changing the focus: The need for cross-scale dynamic management in the Southern Ocean and implications for holistic conservation of Antarctic marine living resources. Mar. Policy, *170*, 106361. (https://doi.org/10.1016/j.marpol.2024.106361)