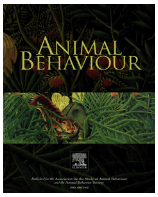
Animal Behaviour 222 (2025) 123144

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



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

A. L. Machado-Gaye [a,*], M. Chimienti [b,c], A. Kato [c], Y. Ropert-Coudert [c], A. Barbosa [d,1], P. Bustamante [e], M. Cosse [f], J. Menéndez-Blázquez [g], N. Zaldúa [a,h], A. Soutullo [a]

[a] *Centro Universitario Regional del Este, Universidad de La República, Maldonado, Uruguay*
[b] *School of Ocean Sciences, Bangor University, Menai Bridge, U.K.*
[c] *Centre d'Etudes Biologiques de Chizé, UMR 7372 CNRS-La Rochelle Université, Villiers-en-Bois, France*
[d] *Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales (CSIC), Madrid, Spain*
[e] *Littoral, Environnement et Sociétés, UMR 7266 CNRS-La Rochelle Université, France*
[f] *Departamento de Biodiversidad y Genética, Instituto de Investigaciones Biológicas Clemente Estable (IIBCE), Ministerio de Educación y Cultura (MEC), Montevideo, Uruguay*
[g] *Instituto Cavanilles de Biodiversidad y Biología Evolutiva (ICBiBe), Universitat de València, Spain*
[h] *Vida Silvestre Uruguay, Montevideo, Uruguay*

ARTICLE INFO

Article history:
Received 11 July 2024
Initial acceptance 24 September 2024
Final acceptance 28 December 2024
Available online xxx
MS. number: A24-00446R

Keywords:
accelerometry
ecosystem management
foraging ecology
trophic ecology

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 interseasonal variation 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 2019/2020 and 2021/2022, we found that during low food availability conditions, penguins were forced to increase their foraging effort and their 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.

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 & Piersma, 2008). To cope with the challenge of seasonal survival, animals must adjust their behaviour and balance their energy acquisition and expenditure (Dunn et al., 2020; Karasov, 1986). At high latitudes, the temporal window for the breeding season is limited and often strongly coupled with seasonal peaks in food availability (Chapman et al., 2010; Forcada & Trathan, 2009). 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. Chapman et al., 2010; Forcada & Trathan, 2009; Joly et al., 2022; Nicol et al., 2008).

Biparental care is essential for offspring success and is widespread among birds. Parental investment is often not equally

---

[*] Corresponding author.
E-mail address: almachado90@gmail.com (A. L. Machado-Gaye).

[1] Deceased.

https://doi.org/10.1016/j.anbehav.2025.123144

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 & 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 & 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 from differences in nest attendance rhythms (Aguilera, 1990).

Reproduction is an energetically costly period for central-place foragers, such as seabirds (Dunn et al., 2018; Ellis & Gabrielsen, 2002). 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 & 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 & 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 the West 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 (Fraser et al., 2013; Juáres et al., 2015; Lynch & LaRue, 2014; Trivelpiece et al., 2011). Climate change has had profound effects on both marine and terrestrial environments, impacting penguins' overwinter pack ice habitat, food resources and physical conditions of nesting sites (Cimino et al., 2023; Fraser et al., 2013; Hinke et al., 2007, 2012, 2017; Massom et al., 2006; Salmerón et al., 2023; Trivelpiece et al., 2011). 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 (Cimino et al., 2016; Emmerson et al., 2011; Hinke et al., 2007, 2012; Juáres et al., 2013; Lynch et al., 2012).

The Antarctic krill, *Euphausia superba*, currently constitute the main prey for Adélie penguins breeding populations of the northern WAP (Juáres et al., 2018; Negrete et al., 2017; Trivelpiece et al., 2011). In this region, Antarctic krill are 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, an increase in sea surface temperature and a decline in marine primary production (Atkinson et al., 2019, 2022; Hill et al., 2019; Montes-Hugo et al., 2009). Furthermore, in recent years, Bransfield Strait and the South Shetland Islands have become hotspots for the krill fishery industry (Santa Cruz et al., 2018), leading to interference competition with krill predators (Watters et al., 2020). Coupled with climate events, fisheries activities may exacerbate local effects on krill abundance (Krüger et al., 2021; Watters et al., 2020), highlighting the urgent need to understand how fluctuations in krill abundance influence marine predators in this region (Hogg et al., 2020; Krüger et al., 2021; Trathan et al., 2022; Watters et al., 2020). Chapman et al. (2011) also postulated that the absence of Antarctic silverfish, *Pleuragramma antarcticum*, in the diet of Adélie penguins in the Antarctic Peninsula may have resulted in lower-quality (lower-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 of climate-driven mismatches between periods of highest energy demand and periods of maximum food availability on populations' persistence (Chapman et al., 2010; Cimino et al., 2023).

Adélie penguins show considerable flexibility in foraging behaviour in response to fluctuations in food availability, modifying the distance and duration of foraging trips (Lescroël et al., 2020; Nicol et al., 2008; Watanuki et al., 1993) and the depth of dives (Ainley et al., 2015; Lescroël et al., 2023). With a slight sexual size dimorphism (Ainley &d Emison, 1972), their feeding ecology also shows sex-specific differences. Females tend to forage farther and longer and dive shallower, while males exploit waters closer to the colony and dive deeper (Ballard et al., 2010; Clarke et al., 1998; Lescroël et al., 2010; Watanuki et al., 2002; Widmann et al., 2015). These differences have been attributed to the different energetic needs of females (Chappell, Shoemaker, et al., 1993; Clarke et al., 1998; Colominas-;Ciuró et al., 2018), differences in diving capacity and to intraspecific competition for segregation in foraging habitats or diet (Massaro et al., 2020; Widmann et al., 2015). 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 (Cimino et al., 2023; Emmerson & Southwell, 2008; Ropert-Coudert et al., 2015).

Some studies have analysed the energetic cost of changes in foraging behaviour in response to fluctuations in krill availability for Adélie penguins (e.g. Ballance et al., 2009; Chappell, Shoemaker, et al., 1993; Nagy & Obst, 1992; Watanabe et al., 2020), but none of them have addressed how changes in prey availability affect the energy cost to males and females. Therefore, the main objective of our study was 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 explored 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 aimed to test the following hypotheses: (1) changes in foraging behaviour due to reduced food availability increase the energy expenditure of Adélie penguins; (2) Adélie penguins modify their trophic niche to buffer the effects of differences in krill availability; (3) the increase in energy expenditure associated with increased foraging effort exhibits sex-specific differences.

METHODS

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) Number 150, during the early guard stage of the 2019/2020 and 2021/2022 breeding seasons (Fig. 1). Between 6 December and 24 December, 38 breeding Adélie penguins (19 in 2019/2020; 19 in 2021/2022) were equipped with data loggers (Axy-Trek, 70 × 40 × 15 mm, 69 g; TechnoSmart, Colleverde, 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 ± SD 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 three body axes of the penguins: longitudinal (surge), dorsoventral (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.

We recaptured individuals in the nest to recover the devices after 3–7 days and measured body mass. We collected blood samples immediately after capture via a peripheral foot vein, using a sterilized needle and heparinized capillary tubes, and plucked five body feathers 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 a microscope slide, air-dried and fixed in 96% ethanol for 5 min for measurement of body condition estimates. Remaining blood was preserved in ethanol for subsequent $\delta^{13}C$ and $\delta^{15}N$ 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 assess differences in prey abundance in the area, we used the information on krill acoustics reported by Salmerón et al. (2023) in the area surrounding Nelson Island. In that 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 that it reasonably reflected krill abundance in our study area (Fig. 1; but also see Figure 1 in Salmerón et al., 2023). The authors found that krill were more abundant in 2019/2020 but also more available to penguins, as swarms were found at a shallower depth than in 2021/2022.

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 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, https://www.wavemetrics.com/). Pressure (mbar) was converted to water depth (m) and 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 (Kato et al., 2009; Takahashi et al., 2003). 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). Maximum dive depth recorded on each trip was also calculated.

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 time (Dunn et al., 2018). Average FMR per 24 h period is also routinely used to calculate daily energy expenditure (DEE; Grémillet et al., 2018). To calculate DEE (kJ/g per

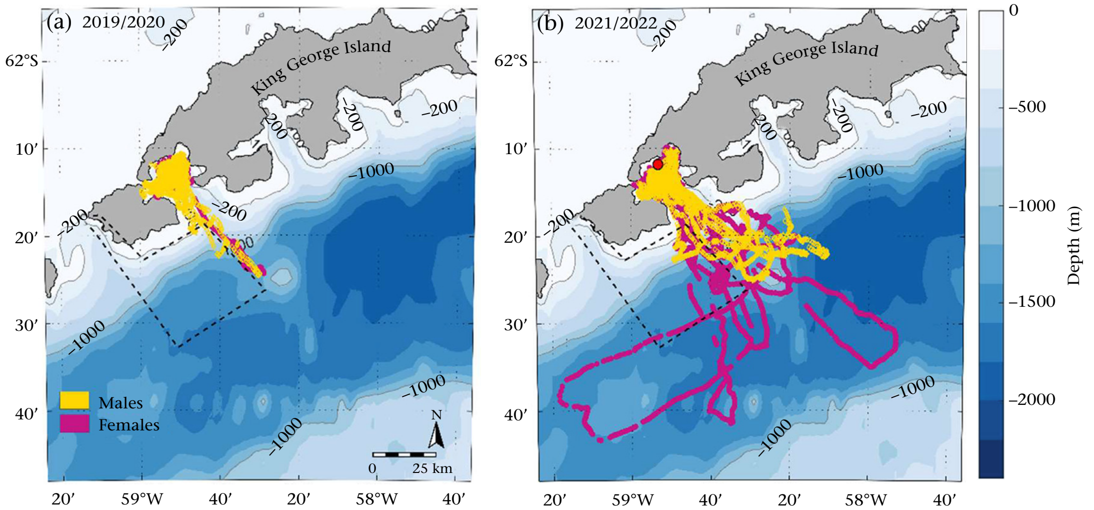


Figure 1. Tracking locations of Adélie penguins breeding in Ardley Island (red dot in (b)) (King George Island/Isla 25 de Mayo) during early guard stage in (a) 2019/2020 and (b) 2021/2022 seasons. The black dotted line represents the area of the krill acoustic transects carried out in both seasons, modified from Salmerón et al. (2023).

day) during foraging trips, we used the existing DEE versus 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: $\text{VeDBA} = \sqrt{(A^2{}_x + A^2{}_y + A^2{}_z)}$ where A_x, A_y and A_z 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): $\text{DEE} = (4.54 \times 10^{-1} \pm 4.09 \times 10^{-2}) + (1.93 \times 10^{-5} \pm 1.76 \times 10^{-6})\ \text{VeDBA}_{\text{Water}} + (-1.16 \times 10^{-5} \pm 5.25 \times 10^{-6})\ \text{VeDBA}_{\text{Land}} + (-3.08 \times 10^{-2} \pm 2.09 \times 10^{-2})$ sex.

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 (δ^{13}C) and nitrogen (δ^{15}N) stable isotope values of whole blood allowed us to compare the diets that the penguins fed their chicks during the study period, as whole blood provides dietary information over the course of approximately 20 days (Barquete et al., 2013; but also see Bearhop et al., 2002). 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, we freeze-dried blood samples for 24 h, homogenized them to powder, weighed them in aliquots of 0.1–0.5 mg and placed them into tin capsules (8 × 5 mm, Elemental Microanalysis Ltd, Okehampton, U.K.) using an analytical balance. Stable isotope values were conventionally expressed as δ values in ‰, using the following equation: $\delta X = ([R_{\text{sample}}/R_{\text{standard}}] - 1 \times 1000)$, where R_{sample} is the ratio of the heavy to light isotope for either ^{13}C/^{12}C or ^{15}N/^{14}N and R_{standard} is the heavy to light isotope ratio for international standards (Vienna PeeDee Belemnite for carbon (VPDB) and atmospheric nitrogen (Air-N_2) for nitrogen). Quality control was done using reference materials USGS-61 and USGS-63 (U.S. Geological Survey, Reston, VA, U.S.A.) 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 did not exceed 0.06 ‰ for δ^{13}C values or 0.12 ‰ for δ^{15}N values.

Finally, intact specimens of three to four whole adult *E. superba* were taken from regurgitate samples collected during the 2020/2021 season 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 (Albuquerque, NM, U.S.A.). We calculated the trophic position for each individual following the model proposed by Post (2002): $\text{TP} = \lambda\ (\delta^{15}\text{N}_{\text{secondary consumer}} - \delta^{15}\text{N}_{\text{base}})/\Delta n$, where λ is the trophic position of the organism used to estimate $\delta^{15}\text{N}_{\text{base}}$ (e.g. $\lambda = 1$ for primary producers), $\delta^{15}\text{N}_{\text{secondary consumer}}$ is measured directly and Δn is the enrichment in δ^{15}N per trophic level. We assumed that diet tissue fractionation factors (Δn) for δ^{15}N was + 2.7 ‰ between lipid-free prey and penguin whole blood (Cherel et al., 2005).

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 total white blood cell (WBC) count and (2) the ratio of heterophils to lymphocytes (H/L) to assess physiological health and stress status. The total count of WBCs provides information about the general level of immune response of the individual. It was performed counting the number of WBCs in 10 visual fields at ×400 magnification as a standardized method (Menéndez-Blázquez et al., 2021). The differential leucocyte profile was calculated as the percentage of the difference of WBCs of a total of 100 at ×1000 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 & 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 was measured using a Pesola spring balance after recapture and removal of tracking devices.

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, Hilden, Germany), performed in the laboratory of the Museo Nacional de Ciencias Naturales (Madrid, Spain) and from feathers using the PrepGem Universal kit (MicroGem; Southampton, U.K.) performed at Instituto de Investigaciones Clemente Estable (Montevideo, 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 1× Platinum Multiplex Master Mix (Invitrogen Life Technologies, Carlsbad, CA, U.S.A.), 0.5 μl of each primer and 50 ng of genomic DNA. The P2 primer was labelled 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 s, 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, Montevideo, Uruguay), for fragment analysis. Genotype assignment was conducted using GeneMarker 2.4.0 (Softgenetics LLC, State College, PA, U.S.A.), identifying males as homozygotes (370/370 bp) and females as heterozygotes (370/388 bp).

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, we performed a residual analysis to test for homoscedasticity and normality of residuals. When these did not meet models' assumptions, we selected a different model. 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, we considered season and sex as independent factorial variables and 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 δ^{13}C and δ^{15}N), we used two-way analysis of variance (ANOVA), with 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 & Bravington, 2013). Implemented in the 'lme4' and 'statmod' packages. Variation in breeding success between seasons was evaluated with chi-square tests.

Ethical Note

All penguin handling procedures were reviewed and approved by the Honorary Commission of Animal experimentation of Uruguay (CHEA protocol number 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 min. After the birds were released, we always made sure that they returned to their nests and attended to their chicks.

RESULTS

Although breeding success did not differ significantly between the two seasons (chi-square test: $\chi^2_1 = 0.11$, $P = 0.7$), foraging behaviour of Adélie penguins varied substantially between breeding seasons (Table 1, Fig. 2, Supplementary Table S1). The interaction between season and sex was not significant. We found significant differences between seasons, with longer foraging trips during 2021/2022, in terms of duration (LMM: $F = 22.40$, $P < 0.001$) and the maximum (LMM: $F = 11.10$, $P < 0.01$) and total (LMM: $F = 17.08$, $P < 0.001$) distances reached. 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 2021/2022 compared to 2019/2020 (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.

For the analyses of energy expenditure based on accelerometer records, the interaction between season and sex was significant (LM: $F_{1,40} = 7.97$, $P < 0.01$; Fig. 3). During the 2021/2022 breeding season, both males and females showed higher DEE than in 2019/2020 (Fig. 3). In particular, females showed 40% higher DEE values in 2021/2022 than in 2019/2020 and males showed 16% higher values in 2021/2022 than in 2019/2020. Furthermore, during 2021/2022, females' DEE values were 20% higher than those of males. During 2019/2020, the DEE did not differ between males and females.

The blood stable isotope values of Adélie penguins at Ardley Island significantly differed between seasons (Fig. 4, Supplementary Table S2). During 2019/2020, δ^{13}C values were significantly higher than in 2021/2022 (LM: $F_{1,34} = 20.71$, $P < 0.0001$), but we did not find significant differences in mean δ^{13}C values between sexes (LM: $F_{1,34} = 2.55$, $P = 0.12$). For δ^{15}N, we found significant differences between seasons (LM: $F_{1,35} = 5.58$, $P < 0.05$) and sexes (LM: $F_{1,35} = 24.19$, $P < 0.0001$). We found higher mean values during 2021/2022 than during 2019/2020 and higher values for males than for females (Supplementary Table S2). The mean δ^{13}C and δ^{15}N 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 2019/2020 and 2021/2022, respectively. For males, the trophic position was 2.44 ± 0.07 in 2019/2020 and 2.47 ± 0.08 in 2021/2022.

Body Condition Parameters

Differences in adult body mass between seasons were statistically significant, with birds being heavier in 2019/2020 than in 2021/2022 (LM: $F_{1,29} = 256.20$, $P < 0.0001$) and males being heavier than females in both seasons (LM: $F_{1,35} = 31.11$, $P < 0.0001$). Comparisons of the H/L ratios as a stress measure revealed no significant

Table 1

Foraging and breeding performance of male and female Adélie penguins breeding in Ardley Island (King George Island/Isla 25 de Mayo) in 2019/2020 and 2021/2022 seasons

Breeding success (number of breeding pairs)	2019−2020		2021−2022	
	1.16 (303)		1.11 (202)	
	Male	Female	Male	Female
Number of trips (number of 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

Breeding success = the number of fledglings divided by the number of active nests. Values are means ± SD.

[*] Denotes significant differences between seasons.

[**] Denotes significant differences between seasons and between sexes.

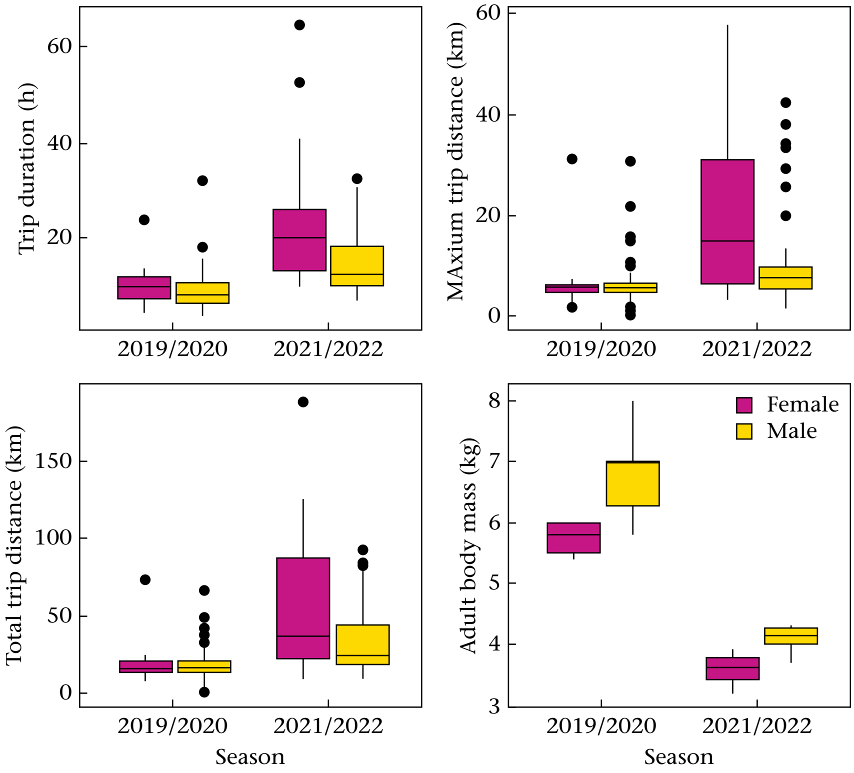


Figure 2. Foraging trip characteristics and adult body mass (kg) of male and female Adélie penguins breeding in Ardley Island (King George Island/Isla 25 de Mayo), during early guard phase in 2019/2020 and 2021/2022 seasons.

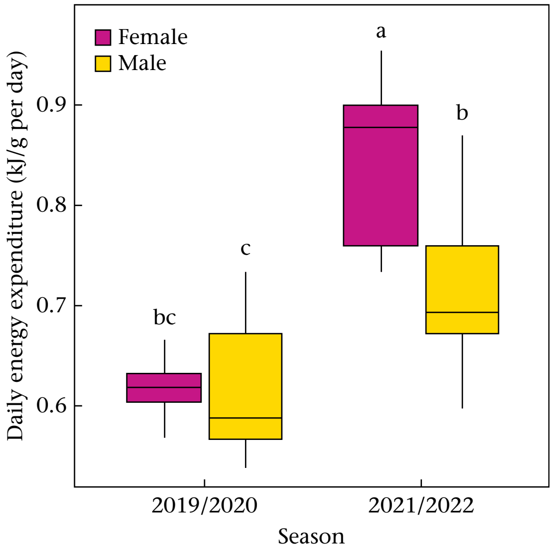


Figure 3. Daily energy expenditure (DEE; mean ± SD) during foraging trips of male and female Adélie penguins breeding at Ardley Island (King George Island/Isla 25 de Mayo), during the early guard stage of the 2019/2020 and 2021/2022 breeding seasons. Different letters indicate significant differences between groups.

differences between the sexes within breeding seasons (mean ± SD: 2019/2020: females: 1.28 ± 0.97, $N = 4$; males: 1.31 ± 0.94, $N = 13$; Wilcoxon rank sum exact test: $W = 125$, $P = 0.1048$; 2021/2022: females: 1.23 ± 0.76, $N = 14$; males: 0.93 ± 0.66. $N = 14$; $W = 0.213$, $P = 0.834$). There were no significant differences within sexes between seasons (females: $W = 23$, $P = 0.632$; males: $W = 32.5$, $P = 0.670$). There were also no significant differences in WBC counts in 10 optical fields between sexes within seasons (2019/2020: females: 29.25 ± 9.81; males: 37.00 ± 10.02; $W = 11.5$, $P = 0.112$; 2021/2022: females: 32.57 ± 25.57; males: 33.35 ± 12.67; $W = 70.5$, $P = 0.213$) or within sexes between seasons (females: $W = 32.5$, $P = 0.670$; males: $W = 124.5$, $P = 0.107$; Supplementary Fig. S1).

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; (2) males and females differ in 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 the 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 (Humboldt penguin, *Spheniscus humboldti*, and Magellanic penguin, *Spheniscus 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 take more time, while males make shorter trips to closer foraging grounds throughout the guard period in East Antarctica (Clarke et al., 1998,

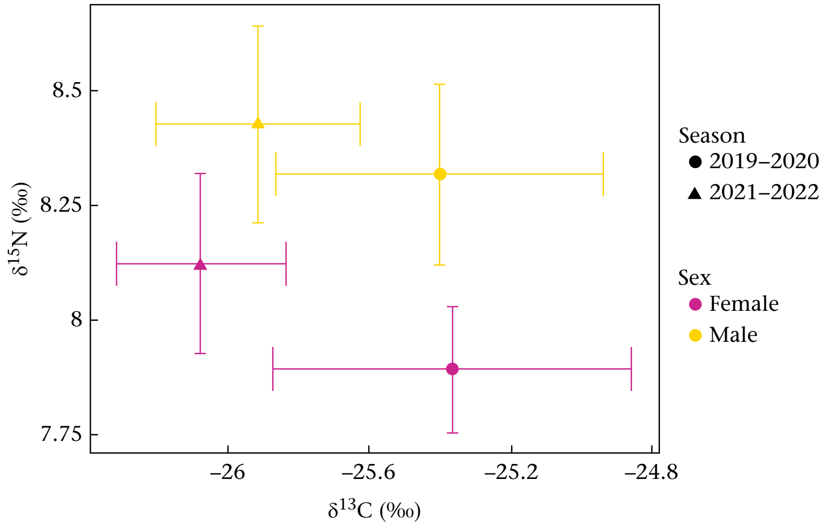


Figure 4. Biplot of isotopic $\delta^{13}C$ and $\delta^{15}N$ values (‰) of whole blood from male and female Adélie penguins breeding in Ardley Island (King George Island/Isla 25 de Mayo) in the early guard stage of the 2019/2020 and 2021/2022 breeding seasons.

2006; Riaz et al., 2020; Watanuki et al., 2002; Widmann et al., 2015), in the Ross Sea (Ballard et al., 2010; Lescroël et al., 2010, 2020) and in the Antarctic Peninsula (Chappell, Shoemaker, et al., 1993). In the Ardley Island colony, we also found 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: female foraging effort was much higher (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 (Paiva et al., 2017; Raya-Rey et al., 2012; 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, energy expenditure may increase due to both low food availability (Kitaysky et al., 2000; Regular et al., 2014) or high 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 some studies report that, under conditions of low prey availability during breeding, energy expenditure of Adélie penguins increases with foraging effort (Ballance et al., 2009; Nagy & Obst, 1992). Our results are consistent with these observations, as we found that both male and female Adélie penguins increased their foraging effort and DEE in the season with low krill abundance. Furthermore, our results show that the energetic costs of foraging was approximately 20% higher for females than for males in the year of low krill abundance, with no differences between the sexes in the year of high krill abundance. We also found that females increased 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 may be related to the body condition of the parents during the brooding stage. Some seabird species are known to adopt a bimodal foraging strategy, alternating between frequent, short trips for chick provisioning and long trips for self-maintenance (Carpenter-;Kling et al., 2017; Clarke, 2001; Ropert-Coudert et al., 2004; Welcker et al., 2009). 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 (Clarke, 2001; Weimerskirch, 1998). 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 these authors 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 for 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 whether the increased foraging effort of the adults affected the chicks' body condition, as reported for other colonies (Ainley et al., 2018; Cimino et al., 2014).

Considering the H/L ratios and WBC count as estimates of immune system response and body condition, we found no differences between sexes or breeding seasons. Several studies indicate that the H/L ratio rises in response to increased breeding effort (Davis et al., 2008), but, although we observed a higher foraging effort in females during 2021/2022, 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 the

Ross Sea compared to our study area. In general, similar WBC levels were previously reported for other Adélie colonies in the Antarctic Peninsula and the Ross Sea (Menéndez-Blázquez et al., 2021; Olmastroni et al., 2019, 2024).

Lower $\delta^{13}C$ values typically indicate offshore/pelagic foraging habitats (Cherel & Hobson, 2007). As expected, $\delta^{13}C$ values during the 2021/2022 season were lower compared to 2019/2020, 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 sexes foraging in more coastal areas during 2019/2020 and foraging in more offshore/pelagic areas in 2021/2022. Sex-specific foraging strategies have also been linked to differences in diet, which might facilitate sexual segregation, particularly when resources are limited (Clarke, 2001; Massaro et al., 2020; Tierney et al., 2008; Widmann et al., 2015). For Adélie penguins in East Antarctica and Antarctic Peninsula, it has been proposed that females tend to consume larger quantities of krill than do males and that males consume more fish than do females (Beaulieu et al., 2010; Clarke et al., 1998; 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, but males showed slightly higher $\delta^{15}N$ 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 $\delta^{15}N$ values in 2021/2022 than in 2019/2020, 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 of about 50% of fish during a season with low krill availability. However, we observed that there were no remarkable changes in trophic position in either sex or between years (2019/2020: males: 2.44 ± 0.07; females: 2.28 ± 0.05; 2021/2022: males: 2.37 ± 0.07; females: 2.47 ± 0.08), 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*, Antarctic lanternfish, *Electrona antarctica*) have a higher calorific content compared to krill (Ainley et al., 2003), our finding that these components were low in the diet when krill were scarce suggests that prey switching was not possible, probably due to the scarcity of other prey options.

Here we deepen our 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 spatiotemporal 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 their moult, or may finish moulting with low energy reserves (Chappell, Janes, et al., 1993), hence impacting winter survival or body condition at 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 provides valuable insights into some of the potentially diverse and subtle factors affecting population 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 a consequence of a range of ecological processes acting at different spatial and temporal scales. For example, the marked decline in breeding pairs between 2019/2020 and 2021/2022 might be linked to unusually harsh breeding conditions during 2020/2021 (A. L. Machado-Gaye, personal observations). Although the breeding success of adults or the body condition of fledglings has no effect on the breeding population size in the following season, since juveniles recruit as breeding adults 3–4 years later (Ainley & Schlatter, 1972D. Ainley & Schlatter, 1972), poor conditions during the season may affect the number of breeding pairs that attempt to reproduce 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 nonbreeding 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).

Author Contributions

A. Barbosa: Supervision, Resources, Methodology, Conceptualization. **P. Bustamante:** Writing – review & editing, Methodology, Formal analysis, Data curation, Conceptualization. **M. Chimienti:** Writing – review & editing, Validation, Supervision, Software, Methodology, Formal analysis, Data curation, Conceptualization. **M. Cosse:** Writing – review & editing, Resources, Formal analysis, Data curation. **A. Kato:** Writing – review & editing, Validation, Supervision, Resources, Methodology, Formal analysis, Data curation, Conceptualization. **A.L. Machado-Gaye:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **J. Menéndez-Blázquez:** Writing – review & editing, Visualization, Methodology, Formal analysis, Data curation. **Y. Ropert-Coudert:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **A. Soutullo:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **N. Zaldúa:** Writing – review & editing, Methodology, Data curation.

Data Availability

The data sets supporting this article are available as Supplementary Material. R codes used to manipulate and analyse the data are available at https://github.com/MariannaChimi/MuFFIN_MSCA/releases/tag/v.02.Submission.

Declaration of Interest

The authors have no conflicts of interest to declare.

Acknowledgments

This article is part of Ana Laura Machado-Gaye's doctoral thesis, funded by Agencia Nacional de Investigación e Innovación (ANII, Uruguay) (POS_NAC_2021_1_169785). We are thankful to all people involved in fieldwork. We thank Gaël Guillou from the Plateforme Analyses Isotopiques of LIENSs laboratory (France) for running isotope analyses, the CPER (Contrat de Projet Etat-Région) and the FEDER (European Regional Development Fund, European Union) for funding the IRMS (Isotope Ratio Mass Spectrometry) devices. P.B. is an honorary member of the Institut Universitaire de France. This work is a contribution to the Integrated Science to Inform Antarctic and Southern Ocean Conservation Scientific Research Programme (Ant-ICON) of SCAR. This work was supported by Instituto Antártico Uruguayo (IAU, Uruguay), Agencia Nacional de Investigación e Innovación's (ANII, Uruguay) Clemente Estable Fund (project FCE_1_2021_1_166587), National System of Researchers, Uruguay and Basic Science Development Programme (PEDECIBA, Uruguay), Ecos-Sud Program (project PU20B01/U20B03, France and Uruguay), Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR, Australia) General Capacity Building Fund and Scientific Scholarship Scheme and WWF-UK (United Kingdom).

Supplementary Material

Supplementary material associated with this article is available at https://doi.org/10.1016/j.anbehav.2025.123144.

References

Aguilera, E. (1990). Sexual differences in nest attendance and chick-feeding rhythms of white spoonbills. *Auk, 107*, 416–420. https://doi.org/10.2307/4087631

Ainley, D. (2002). *The Adélie penguin: Bellwether of climate change*. Columbia University Press.

Ainley, D., Ballard, G., Barton, K. J., Karl, B., Rau, G. H., Ribic, C. A., & Wilson, P. R. (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, D. G., Ballard, G., Jones, R. M., Jongsomjit, D., Pierce, S. D., Smith, W. O., Jr., & Veloz, S. (2015). Trophic cascades in the western Ross Sea, Antarctica: Revisited. *Marine Ecology Progress Series, 534*, 1–16. https://doi.org/10.3354/meps11394

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

Ainley, D. G., & Emison, W. B. (1972). Sexual size dimorphism in Adélie penguins. *Ibis, 114*, 267–271. https://doi.org/10.1111/j.1474-919X.1972.tb02613.x

Ainley, D. G., & Schlatter, R. P. (1972). Chick raising ability in Adélie penguins. *Auk, 89*(3), 559–566.

Atkinson, A., Hill, S. L., Pakhomov, E. A., Siegel, V., Reiss, C. S., Loeb, V. J., Steinberg, D. K., Schmidt, K., Tarling, G. A., Gerrish, L., & Sailley, S. F. (2019). Krill (*Euphausia superba*) distribution contracts southward during rapid regional warming. *Nature Climate Change, 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., Yang, G., Steinberg, D. K., Schmidt, K., Edwards, M., Rombolá, E., & Perry, F. A. (2022). Stepping stones towards Antarctica: Switch to southern spawning grounds explains an abrupt range shift in krill. *Global Change Biology, 28*(4), 1359–1375. https://doi.org/10.1111/gcb.16009

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

Ballard, G., Dugger, K. M., Nur, N., & Ainley, D. G. (2010). Foraging strategies of Adélie penguins: Adjusting body condition to cope with environmental variability. *Marine Ecology Progress Series, 405*, 287–302. https://doi.org/10.3354/meps08514

Barquete, V., Strauss, V., & Ryan, P. G. (2013). Stable isotope turnover in blood and claws: A case study in captive African penguins. *Journal of Experimental Marine Biology and Ecology, 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. *Journal of Statistical Software, 67*, 1–48. https://doi.org/10.48550/arXiv.1406.5823

Bearhop, S., Waldron, S., Votier, S. C., & Furness, R. W. (2002). Factors that influence assimilation rates and fractionation of nitrogen and carbon stable isotopes in avian blood and feathers. *Physiological and Biochemical Zoology, 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. *Proceedings of the Royal Society B: Biological Sciences, 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. *Animal Behaviour, 150*, 127–137. https://doi.org/10.1016/j.anbehav.2019.02.005

Buehler, D. M., & Piersma, T. (2008). Travelling on a budget: Predictions and ecological evidence for bottlenecks in the annual cycle of long-distance migrants. *Philosophical Transactions of the Royal Society B: Biological Sciences, 363*(1490), 247–266. https://doi.org/10.1098/rstb.2007.2138

Carpenter-Kling, T., Handley, J. M., Green, D. B., Reisinger, R. R., Makhado, A. B., Crawford, R. J. M., & Pistorius, P. A. (2017). A novel foraging strategy in gentoo penguins breeding at sub-Antarctic Marion Island. *Marine Biology, 164*. https://doi.org/10.1007/s00227-016-3066-9. Article 33.

CCAMLR Secretariat. (2024). *Fishery Report 2023: Euphausia superba in Area 48*. Commission for the Conservation of Antarctic Marine Living Resources. https://fishdocs.ccamlr.org/FishRep_48_KRI_2023.pdf.

Chapman, E. W., Hofmann, E. E., Patterson, D. L., & Fraser, W. R. (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 Research Part II: Topical Studies in Oceanography, 57*, 543–558. https://doi.org/10.1016/j.dsr2.2009.10.005

Chapman, E. W., Hofmann, E. E., Patterson, D. L., Ribic, C. A., & Fraser, W. R. (2011). Marine and terrestrial factors affecting Adélie penguin *Pygoscelis adeliae* chick growth and recruitment off the western Antarctic Peninsula. *Marine Ecology Progress Series, 436*, 273–289. https://doi.org/10.3354/meps09242

Chappell, M. A., Janes, D. N., Shoemaker, V. H., Bucher, T. L., & Maloney, S. K. (1993). Reproductive effort in Adélie penguins. *Behavioral Ecology and Sociobiology, 33*, 173–182. https://doi.org/10.1007/BF00216598

Chappell, M. A., Shoemaker, V. H., Janes, D. N., Maloney, S. K., & Bucher, T. L. (1993). Energetics of foraging in breeding Adelie penguins. *Ecology, 74*, 2450–2461. https://doi.org/10.2307/1939596

Cherel, Y., & Hobson, K. A. (2007). Geographical variation in carbon stable isotope signatures of marine predators: A tool to investigate their foraging areas in the Southern Ocean. *Marine Ecology Progress Series, 329*, 281–287. https://doi.org/10.3354/meps329281

Cherel, Y., Hobson, K. A., & Hassani, S. (2005). Isotopic discrimination between food and blood and feathers of captive penguins: Implications for dietary studies in the wild. *Physiological and Biochemical Zoology, 78*(1), 106–115.

Cimino, M., Conroy, J. A., Connors, E., Bowman, J., Corso, A., Ducklow, H., Fraser, W., Friedlaender, A., Kim, H., & Larsen, G. D. (2023). Long-term patterns in ecosystem phenology near Palmer Station, Antarctica, from the perspective of the Adélie penguin. *Ecosphere, 14*. https://doi.org/10.1002/ecs2.4417. Article e4417.

Cimino, M. A., Fraser, W. R., Patterson-Fraser, D. L., Saba, V. S., & Oliver, M. J. (2014). Large-scale climate and local weather drive interannual variability in Adélie penguin chick fledging mass. *Marine Ecology Progress Series, 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. *Scientific Reports, 6*(1). https://doi.org/10.1038/srep28785. Article 28785.

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

Clarke, J., Emmerson, L. M., & Otahal, P. (2006). Environmental conditions and life history constraints determine foraging range in breeding Adélie penguins. *Marine Ecology Progress Series, 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 Biology, 20*, 248−258. https://doi.org/10.1007/s003000050301

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*. https://doi.org/10.1371/journal.pone.0177124. Article e0177124.

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 Biology, 41*, 2635−2641. https://doi.org/10.1007/s00300-018-2395-1

Cresswell, K. A., Tarling, G. A., & Trathan, P. N. (2007). Weight loss during breeding is adaptive for female macaroni penguins, *Eudyptes chrysolophus*. *Evolutionary Ecology Research, 9*, 1053−1076.

Cushing, D. H. (1990). Plankton production and year−class strength in fish populations: An update of the match/mismatch hypothesis. *Advances in Marine Biology, 26*, 249−293. https://doi.org/10.1016/S0065-2881(08)60202-3

Davis, A. K., & Maney, D. L. (2018). The use of glucocorticoid hormones or leucocyte profiles to measure stress in vertebrates: What's the difference? *Methods in Ecology and Evolution, 9*, 1556−1568. https://doi.org/10.1111/2041-210X.13020

Davis, A. K., Maney, D. L., & Maerz, J. C. (2008). The use of leukocyte profiles to measure stress in vertebrates: A review for ecologists. *Functional Ecology, 22*, 760−767. https://doi.org/10.1111/j.1365-2435.2008.01467.x

Drent, R. H., & Daan, S. (1980). The prudent parent: Energetic adjustments in avian breeding. *Ardea, 68*, 225−252.

Dunn, R. E., Wanless, S., Daunt, F., Harris, M. P., & Green, J. A. (2020). A year in the life of a north Atlantic seabird: Behavioural and energetic adjustments during the annual cycle. *Scientific Reports, 10*, 1−11. https://doi.org/10.1038/s4159.8-020-62842-x

Dunn, R. E., White, C. R., & Green, J. A. (2018). A model to estimate seabird field metabolic rates. *Biology Letters, 14*. https://doi.org/10.1098/rsbl.2018.0190. Article 20180190.

Durant, J. M., Hjermann, D.Ø., Ottersen, G., & Stenseth, N. C. (2007). Climate and the match or mismatch between predator requirements and resource availability. *Climate Research, 33*, 271−283. https://doi.org/10.3354/cr033271

Ellis, H. I., & Gabrielsen, G. W. (2002). Energetics of free-ranging seabirds. In G. C. Whittow, & H. Rahn (Eds.), *Seabird energetics* (pp. 203−234). Springer. https://doi.org/10.1007/978-1-4684-4859-7_10.

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

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

Forcada, J., & Trathan, P. N. (2009). Penguin responses to climate change in the Southern Ocean. *Global Change Biology, 15*, 1618−1630. https://doi.org/10.1111/j.1365-2486.2009.01909.x

Foster, S. D., & Bravington, M. V. A. (2013). Poisson−gamma model for analysis of ecological non-negative continuous data. *Environmental and Ecological Statistics, 20*, 533−552. https://doi.org/10.1007/s10651-012-0233-0

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

González-Solís, J., Croxall, J. P., & Wood, A. G. (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

Grémillet, D., Lescroël, A., Ballard, G., Dugger, K. M., Massaro, M., Porzig, E. L., & Ainley, D. G. (2018). Energetic fitness: Field metabolic rates assessed via 3D accelerometry complement conventional fitness metrics. *Functional Ecology, 32*, 1203−1213. https://doi.org/10.1111/1365-2435.13074

Gray, C. M., & Hamer, K. C. (2001). Food-provisioning behaviour of male and female Manx shearwaters, *Puffinus puffinus*. *Animal Behaviour, 62*, 117−121. https://doi.org/10.1006/anbe.2001.1717

Griffiths, R., Double, M. C., Orr, K., & Dawson, R. J. (1998). A DNA test to sex most birds. *Molecular Ecology, 7*, 1071−1075. https://doi.org/10.1046/j.1365-294x.1998.00389.x

Hicks, O., Kato, A., Angelier, F., Wisniewska, D. M., Hambly, C., Speakman, J. R., Marciau, C., & Ropert-Coudert, Y. (2020). Acceleration predicts energy expenditure in a fat, flightless, diving bird. *Scientific Reports, 10*. https://doi.org/10.1038/s41598-020-78025-7. Article 21493.

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. *Journal of Crustacean Biology, 39*(3), 316−322. https://doi.org/10.1093/jcbiol/ruz004

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. *Marine Ecology Progress Series, 454*, 91−104. https://doi.org/10.3354/meps09633

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

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). https://doi.org/10.1002/ecs2.1666. Article e01666.

Hogg, C. J., Lea, M. A., Gual Soler, M., Vasquez, V. N., Payo-Payo, A., Parrott, M. L., Santos, M., Shaw, C., & Brooks, C. M. (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. *Biometrical Journal, 50*, 346−363. https://doi.org/10.1002/bimj.200810425

Jodice, P. G., Roby, D. D., Suryan, R. M., Irons, D. B., Turco, K. R., Brown, E. D., Thedinga, J. F., & Visser, G. H. (2006). Increased energy expenditure by a seabird in response to higher food abundance. *Marine Ecology Progress Series, 306*, 283−293. https://doi.org/10.3354/meps306283

Joly, N. B., Chiaradia, A., Georges, J. Y., & Saraux, C. (2022). Environmental effects on foraging performance in little penguins: A matter of phenology and short-term variability. *Marine Ecology Progress Series, 692*, 151−168. https://doi.org/10.3354/meps14058

Juáres, M. A., Casaux, R., Corbalán, A., Blanco, G., Pereira, G. A., Perchivale, P. J., 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 Biology, 41*, 303−311. https://doi.org/10.1007/s00300-017-2191-3

Juáres, M. A., Santos, M. 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. *Antarctic Science, 27*(5), 455−461. https://doi.org/10.1017/S0954102015000152

Juáres, 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 Research, 32*(1). https://doi.org/10.3402/polar.v32i0.18448. Article 18448.

Kahane-Rapport, S. R., Whelan, S., Ammendolia, J., Hatch, S. A., Elliott, K. H., & 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. *Trends in Ecology & Evolution, 1*(4), 101−104. https://doi.org/10.1016/0169-5347(86)90034-0

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

Kitaysky, A. S., Hunt, G. L., Jr., Flint, E. N., Rubega, M. A., & Decker, M. B. (2000). Resource allocation in breeding seabirds: Responses to fluctuations in their food supply. *Marine Ecology Progress Series, 206*, 283−296. https://doi.org/10.3354/meps206283

Krüger, L., Huerta, M. F., Santa Cruz, F., & Cárdenas, C. A. (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* (Methuen).

Lescroël, A., Ballard, G., Toniolo, V., Barton, K. J., Wilson, P. R., Lyver, P. O.'B., & Ainley, D. G. (2010). Working less to gain more: When breeding quality relates to foraging efficiency. *Ecology, 91*, 2044−2055. https://doi.org/10.1890/09-0766.1

Lescroël, A., Lyver, P. O.'B., Jongsomjit, D., Veloz, S., Dugger, K. M., Kappes, P., Karl, B. J., Whitehead, A., Pech, R., Cole, T. L., & Ballard, G. (2020). Interindividual differences in the foraging behavior of breeding Adélie penguins are driven by individual quality and sex. *Marine Ecology Progress Series, 636*, 189−205. https://doi.org/10.3354/meps13208

Lescroël, A., Schmidt, A., Ainley, D. G., Dugger, K. M., 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. *Proceedings of the Royal Society B: Biological Sciences, 290*. https://doi.org/10.1098/rspb.2022.2480. Article 20222480.

Lewis, S., Benvenuti, S., Dall−Antonia, L., Griffiths, R., Money, L., Sherratt, T. N., Wanless, S., & Hamer, K. C. (2002). Sex-specific foraging behaviour in a monomorphic seabird. *Proceedings of the Royal Society B: Biological Sciences, 269*, 1687−1693. https://doi.org/10.1098/rspb.2002.2083

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

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

Machado-Gaye, A. L., 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. *Marine Biology, 171*. https://doi.org/10.1007/s00227-024-04390-w. Article 69.

Masello, J. F., Barbosa, A., Kato, A., Mattern, T., Medeiros, R., Stockdale, J. E., Kümmel, M. N., Bustamante, P., Belliure, J., Benzal, J., Colominas-Ciuró, R., Menéndez-Blázquez, J., Griep, S., Goesmann, A., Symondson, W. O. C., & Quillfeldt, P. (2021). How animals distribute themselves in space: Energy landscapes of Antarctic avian predators. *Movement Ecology, 9*. https://doi.org/10.1186/s40462-021-00255-9. Article 24.

Massaro, M., Ainley, D. G., Santora, J. A., Quillfeldt, P., Lescroël, A., Whitehead, A., Varsani, A., Ballard, G., & Lyver, P. O.'B. (2020). Diet segregation in Adélie penguins: Some individuals attempt to overcome colony-induced and annual foraging challenges. *Marine Ecology Progress Series, 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., Martinson, D. G., Vernet, M., Fraser, W. R., Quetin, L. B., Ross, R. M., Massom, Y., & 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. *Journal of Climate, 19*(15), 3544–3571. https://doi.org/10.1175/JCLI3805.1

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 Biology, 44*, 2195–2198. https://doi.org/10.1007/s00300-021-02950-0

Miller, M. G., Silva, F. R., Machovsky-Capuska, G. E., & Congdon, B. C. (2018). Sexual segregation in tropical seabirds: Drivers of sex-specific foraging in the brown booby *Sula leucogaster*. *Journal of Ornithology, 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

Morandini, V., Dugger, K. M., Schmidt, A. E., Varsani, A., Lescroël, A., Ballard, G., Lyver, P. O.'B., Barton, K., & Ainley, D. G. (2024). Sex-specific recruitment rates contribute to male-biased sex ratio in Adélie penguins. *Ecology and Evolution, 14*. https://doi.org/10.1002/ece3.10859. Article e10859.

Nagy, K. A., & Obst, B. S. (1992). Food and energy requirements of Adélie penguins (*Pygoscelis adeliae*) on the Antarctic Peninsula. *Physiological Zoology, 65*, 1271–1284. https://doi.org/10.1086/physzool.65.6.30158279

Negrete, P., Sallaberry, M., Barceló, G., Maldonado, K., Perona, F., McGill, R. A., 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 Biology, 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 Research Part II: Topical Studies in Oceanography, 55*, 540–557. https://doi.org/10.1016/j.dsr2.2007.11.013

Olmastroni, S., Pompeo, G., Jha, A. N., Mori, E., Vannuccini, M. L., 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 Biology, 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. *Science of the Total Environment, 922*. https://doi.org/10.1016/j.scitotenv.2024.171249. Article 171249.

Orians, G. H., & Pearson, N. E. (1979). On the theory of central place foraging. In D. J. Horn, R. D. Mitchell, & G. R. Stairs (Eds.), *Analysis of ecological systems* (pp. 154–177). Ohio University Press.

Paiva, V. H., Pereira, J., Ceia, F. R., & Jaime, A. (2017). Ramos Environmentally driven sexual segregation in a marine top predator. *Scientific Reports, 7*. https://doi.org/10.1038/s41598-017-02854-2. Article 2590.

Post, D. M. (2002). Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology, 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, P. M., Hedd, A., Montevecchi, W. A., Robertson, G. J., Storey, A. E., & Walsh, C. J. (2014). Why timing is everything: Energetic costs and reproductive consequences of resource mismatch for a chick-rearing seabird. *Ecosphere, 5*(12), 1–13. https://doi.org/10.1890/ES14-00182.1

Reyes-González, J. M., 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. *Journal of Animal Ecology, 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. *Marine Ecology Progress Series, 654*, 177–194. https://doi.org/10.3354/meps13519

Ropert-Coudert, Y., Kato, A., Meyer, X., Pellé, M., MacIntosh, A. J., 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.org/10.1111/ecog.01182

Ropert-Coudert, Y., Wilson, R. P., Daunt, F., & Kato, A. (2004). Patterns of energy acquisition by a central place forager: Benefits of alternating short and long foraging trips. *Behavioral Ecology, 15*, 824–830. https://doi.org/10.1093/beheco/arh086

Salmerón, N., Belle, S., Santa Cruz, F., Alegria, N., Grohmann Finger, J., Corá, D. H., Petry, M. V., Hernández, C., Cárdenas, C., & Krüger, L. (2023). Contrasting environmental conditions precluded lower availability of Antarctic krill affecting breeding chinstrap penguins in the Antarctic Peninsula. *Scientific Reports, 13*. https://doi.org/10.1038/s41598-023-32352-7. Article 5265.

Santa Cruz, F., Ernst, B., Arata, J. A., & Parada, C. (2018). Spatial and temporal dynamics of the Antarctic krill fishery in fishing hotspots in the Bransfield Strait and South Shetland Islands. *Fisheries Research, 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? *Functional Ecology, 17*, 590–597.

Tierney, M., Southwell, C., Emmerson, L. M., & Hindell, M. A. (2008). Evaluating and using stable-isotope analysis to infer diet composition and foraging ecology of Adélie penguins *Pygoscelis adeliae*. *Marine Ecology Progress Series, 355*, 297–307. https://doi.org/10.3354/meps07235

Trathan, P. N., Warwick-Evans, V., Young, E. F., Friedlaender, A., Kim, J. H., & 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. *Journal of Marine Systems, 225*. https://doi.org/10.1016/j.jmarsys.2021.103598. Article 103598.

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

Watanabe, Y. Y., Ito, K., Kokubun, N., & Takahashi, A. (2020). Foraging behavior links sea ice to breeding success in Antarctic penguins. *Science Advances, 6*. https://doi.org/10.1126/sciadv.aba4828. Article eaba4828.

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. *Journal of Animal Ecology, 62*, 634–646. https://doi.org/10.2307/5384

Watanuki, Y., Kato, A., Sato, K., Niizuma, Y., Bost, C. A., 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 Biology, 25*, 672–681. https://doi.org/10.1007/s00300-002-0399-2

Watters, G. M., Hinke, J. T., & Reiss, C. S. (2020). Long-term observations from Antarctica demonstrate that mismatched scales of fisheries management and predator–prey interaction lead to erroneous conclusions about precaution. *Scientific Reports, 10*. https://doi.org/10.1038/s41598-020-59223-9. Article 2314.

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. *Journal of Animal Ecology, 67*, 99–109. https://doi.org/10.1046/j.1365-2656.1998.00180.x

Welcker, J., Steen, H., Harding, A. M. A., & Gabrielsen, G. W. (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. *Movement Ecology, 3*. https://doi.org/10.1186/s40462-015-0052-7. Article 30.

Wilson, R. P., Pütz, K., Peters, G., Culik, B., Scolaro, J. A., Charrassin, J. B., & Ropert-Coudert, Y. (1997). Long-term attachment of transmitting and recording devices to penguins and other seabirds. *Wildlife Society Bulletin, 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. *Marine Policy, 170*, Article 106361. https://doi.org/10.1016/j.marpol.2024.106361