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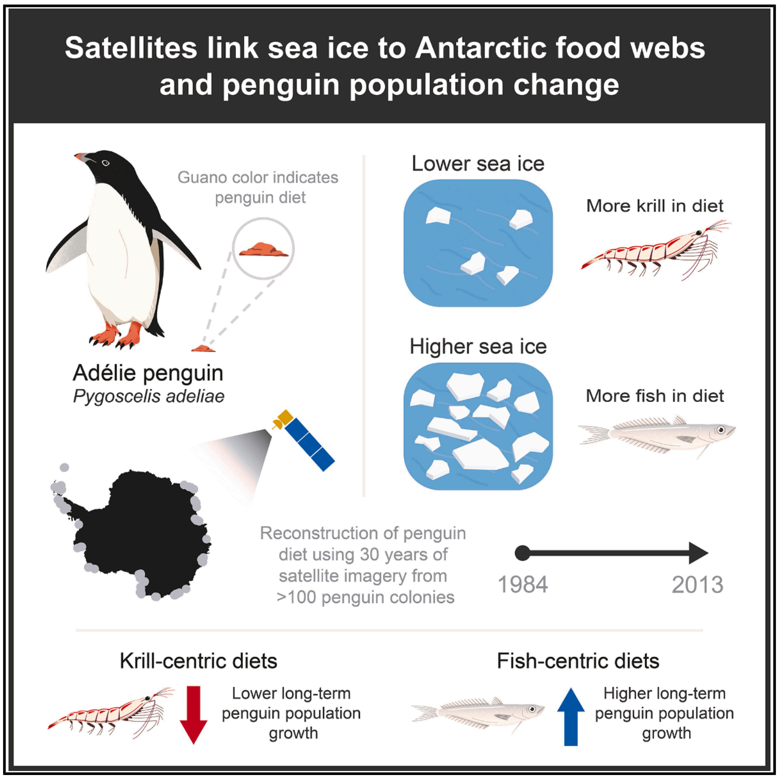
Space-based monitoring of penguin diet links sea ice, food webs, and population change

Graphical abstract



Highlights

- The color of Adélie penguin guano in satellite imagery can be used to monitor diet
- Year-to-year shifts in penguin diet track sea ice dynamics
- Less sea ice is associated with greater penguin reliance on krill
- Diet is linked to long-term penguin population trends across Antarctica

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In brief

Youngflesh et al. use satellite imagery to reconstruct three decades of Adélie penguin diet across Antarctica. They find that sea ice dynamics are associated with shifts between krill- and fish-based diets, linking environmental change to Antarctic food web structure and penguin population trends.

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Current Biology

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Report

Space-based monitoring of penguin diet links sea ice, food webs, and population change

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SUMMARY

Rapid environmental change is reshaping Antarctic ecosystems through shifts in temperature and sea ice dynamics, with implications for species such as the iconic Adélie penguin (*Pygoscelis adeliae*). Because Antarctic predators rely on a relatively small number of key prey resources in the region[1] whose life histories are intrinsically linked to sea ice,[2,3] these abiotic changes are expected to cascade through food webs. However, the scale and remoteness of Antarctica have limited efforts to link environmental change to ecological responses across the continent. Combining tools from imaging spectroscopy, stable isotope analysis, and hierarchical statistical modeling, we reconstructed Adélie penguin diet across the entirety of the species' global range over a three-decade period (1984–2013) using satellite imagery from the Landsat program. This approach leveraged the distinct spectral properties (a generalized measure of color) of penguin guano as observed by satellites,[4,5] which vary according to penguin diet.[6,7] We found pronounced differences in diet across the continent and that year-to-year dietary shifts were strongly associated with sea ice dynamics. Higher sea ice corresponded to more fish-based diets, whereas lower sea ice was associated with a greater reliance on krill. Additionally, spatial differences in penguin diet were associated with long-term trends in penguin abundance, linking food web processes to large-scale population dynamics. This study represents the first use of satellite observations to capture trophic dynamics at continental and decadal scales and highlights how environmental change might restructure Antarctic food webs and influence the future of a key sentinel species.

RESULTS AND DISCUSSION

A satellite-based approach to monitoring penguin diet at range-wide scales

The basis for our approach relied on dietary and spectral analyses of guano samples (Figure S1) collected at penguin colonies to determine the trophic level at which penguins were feeding. Naturally occurring stable nitrogen isotope values[8] (δ^{15}N) of collected guano samples provided a measure of the degree to which penguins were relying on krill (*Euphausia superba* and *E. crystallorophias*) (lower trophic level) and Antarctic silverfish (*Pleuragramma antarcticum*) (higher trophic level), the two principal prey resources of this species during the breeding season[1,9] (Figure 1). Our spectroscopic model predicted variation in stable isotope values, our dietary proxy, relatively precisely (R^2= 0.45) (Figures 1 and S3; STAR Methods), with uncertainty in diet quantification from satellites propagated to all downstream analyses using a flexible hierarchical Bayesian modeling framework.[10] We represent differences in diet using a dietary index (DI) ranging from 0 to 100, with higher values associated with higher relative proportions of fish (higher trophic level) and lower values with higher relative proportions of krill (lower trophic level).

Sea ice dynamics structure Antarctic food webs

We found pronounced spatial differences in penguin diet across 119 Adélie penguin colonies around the continent, with higher relative proportions of krill consumed in West Antarctica, higher proportions of fish in East Antarctica, and a diet intermediate between these two extremes in the Ross Sea (Figure 2A), though some variation exists within these broad regions (Figure S2). These patterns are consistent with data from individual colonies involving the analysis of stomach contents, stable isotopes, and guano DNA.[1,11–16] Both the area of the continental shelf (<1,000 m depth) around each colony, thought to be one indicator of suitable krill habitat,[17] and sea ice concentration were related to this spatial variation in penguin diet—greater shelf

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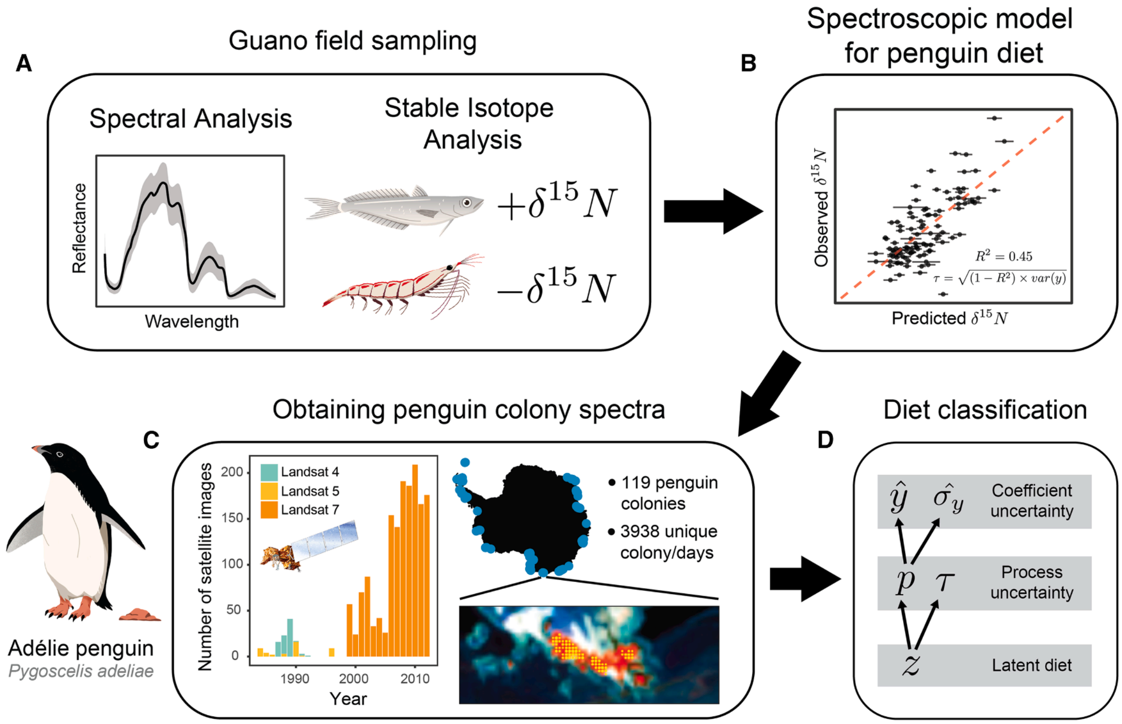

Figure 1. Integrating approaches from multiple fields, we developed a novel analytical pipeline for quantifying the diet of Adélie penguins (*Pygoscelis adeliae*) from satellites

(A) We measured both the spectral reflectance and isotopic signatures of 103 guano samples collected at penguin colonies. Stable nitrogen isotope values ($\delta^{15}N$) indicated the trophic level at which birds were feeding, with lower (–) values representing relatively more krill and higher (+) values, more fish.

(B) We built quantitative models to characterize penguin diet from guano spectra using lab-derived reflectance and stable isotope measurements. Error bars represent one standard error.

(C) We applied an algorithmic approach[4] to the Landsat satellite imagery catalog from 1984 to 2013 to identify and obtain spectral information from guano-covered pixels in Adélie penguin colonies across the species' global range.

(D) Using the quantitative model from (B), we quantified penguin diet for all pixels identified in (C). We used a hierarchical Bayesian approach to model how penguin diet varied over space and time, accounting for uncertainty in diet estimates due both to the model's process uncertainty (τ; B) and uncertainty regarding the coefficients of that model (Equations 2–10). Arrows represent parameter dependencies in the hierarchical model as a directed acyclic graph.

See also Figures S1, S2, and S3.

area (ζ_2 [Equation 10] = −4.90, 89% confidence interval [CI]: [−7.20, −2.66], $p(\zeta_2 > 0) = 0$; Figure 2B) and decreased sea ice (ζ_1 [Equation 10] = 19.56, 89% CI: [6.22, 32.74], $p(\zeta_1 > 0) = 0.99$; Figure 2C) were associated with more krill-centric diets.

Year-to-year variation in penguin diet was strongly linked to temporal fluctuations in sea ice conditions. In years with more sea ice, penguin diet at a given colony had higher proportions of fish (μ_θ [Equation 9] = 16.92, 89% CI: [14.13, 19.67], $p(\mu_\theta > 0) = 1$; Figure 3B)—that is, higher sea ice was associated with higher DI values. Sea ice explained a large portion of the year-to-year variation in penguin diet (R^2 = 0.73). These results demonstrate a robust link between the abiotic environment and Antarctic food web dynamics and are consistent with the notion that years with lower sea ice (driven primarily by warmer temperatures) are associated with reduced Antarctic silverfish abundance.[3] While both the overall amount and inter-annual variation in sea ice differ among colonies, substantial variation exists within colonies (Figure S4). This strong association demonstrates how sea ice dynamics structure temporal changes in Antarctic food webs.

Antarctica has experienced large fluctuations in sea ice over the last half-century that have varied around the continent.[18] During the focal period of this study (1985–2012), sea ice has either increased or remained stable in most regions (Figure S4). However, following the period of this study over the past decade (2015–present), large-scale declines, including multiple record lows over the satellite era, have been observed.[19,20] Given the strong link between sea ice conditions and trophic dynamics demonstrated here, continued declines in sea ice projected through the end of the century[21] are likely to drive significant shifts in Antarctic food web processes, including a transition toward more krill-dominated diets for Adélie penguins across the continent.

These associations between sea ice and penguin diet were apparent even while accounting for dietary variation within years.[22,23] DI values changed in a non-linear manner across the breeding season, with more fish-centric diets observed during the pre-breeding period (November[24]) transitioning to more krill-centric diets by austral summer (January; generally the hatch phase of the breeding season[25]), followed by a return to more fish-centric diets later in the year (μ_{β_1} [Equation 8] = −245.05, 89% CI: [−277.54, −213.40], $p\left(\mu_{\beta_1} > 0\right) = 0$; μ_{β_2} [Equation 8] = 168.41, 89% CI: [146.20,

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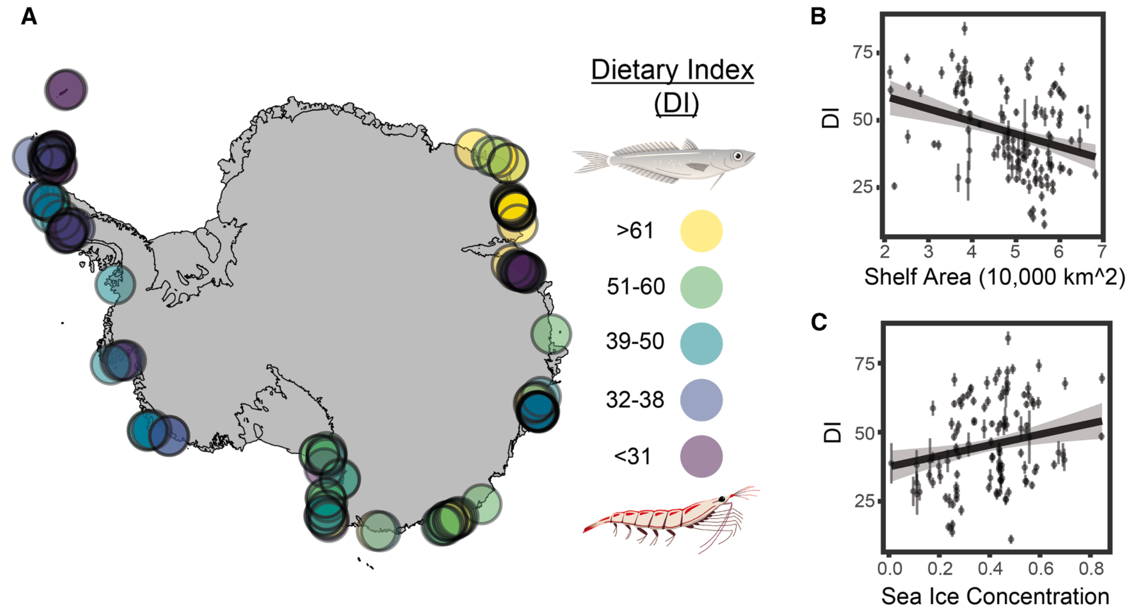

Figure 2. Adélie penguin diet varies across its global range

(A) We derived a Dietary Index (DI) that quantified the relative proportion of krill (lower trophic level) vs. fish (higher trophic level) in penguin diet. Each point represents an Adélie penguin (*Pygoscelis adeliae*) colony across Antarctica. Hue represents the estimated average diet at that colony—color ramp boundaries at the 0.2, 0.4, 0.6, and 0.8 quantiles.

(B) Colonies with greater shelf area, thought to be beneficial for krill production,[17] have more krill-centric diets.

(C) Colonies with higher average sea ice concentration during the breeding season have more fish-centric diets. For both (B) and (C), each point represents a colony. DI is represented as the posterior mean for the cross-year average at each colony. The thin vertical lines represent the uncertainty in diet (posterior standard deviation). The thick lines represent the model fit, while the ribbons represent the uncertainty (89% CI) in that fit.

190.55], $p\left(\mu_{\beta_2} > 0\right) = 1$; Figure 3A). These patterns underscore the importance of considering the time of year when assessing variation in Antarctic trophic dynamics and highlight the value of temporally dense remote sensing data in understanding how the environment is regulating food web processes. Despite any signal-dampening effect inherent to the guano accumulation process, within-season variation was measurable and substantial. These seasonal dietary transitions likely reflect not only changes in the distribution of prey resources across the breeding season but also different constraints on foraging behavior resulting from nest attendance and chick provisioning duties.[11]

Demographic consequences of food web dynamics for Adélie penguins

Penguin diet composition has long been identified as a key ecological indicator, as it is both linked to penguin reproductive performance[26] and serves as a proxy for underlying Antarctic food web dynamics.[27] Given this, we anticipated a link between penguin diet and penguin population trends. Long-term changes

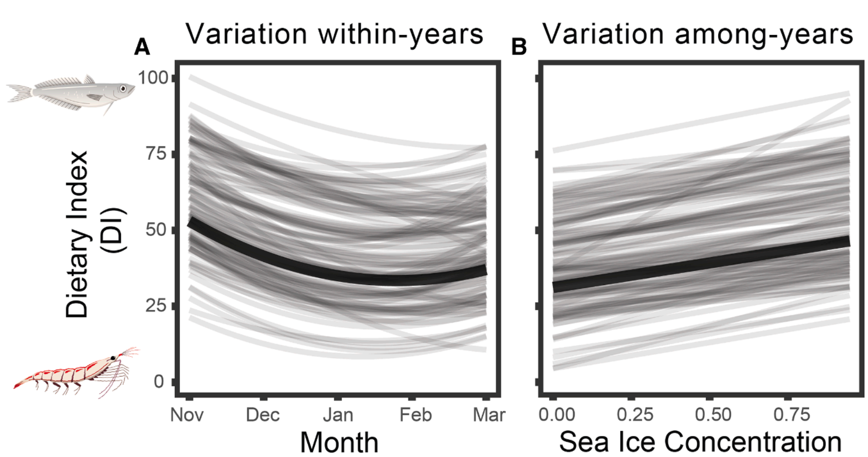

Figure 3. Penguin diet varies with and across years

(A) Penguin diet varies over the course of the breeding season, showing a concave up transition from more fish-centric to more krill-centric diets. Each transparent gray line is a colony, while the thick black line represents the cross-colony trend—all colonies and years were modeled jointly in a hierarchical framework.

(B) Penguin diet is closely linked with sea ice conditions at these colonies. At a given colony, higher sea ice years were associated with more fish-centric diets. As in (A), each line is a colony. The dark black line represents the cross-colony estimate.

See also Figure S4.

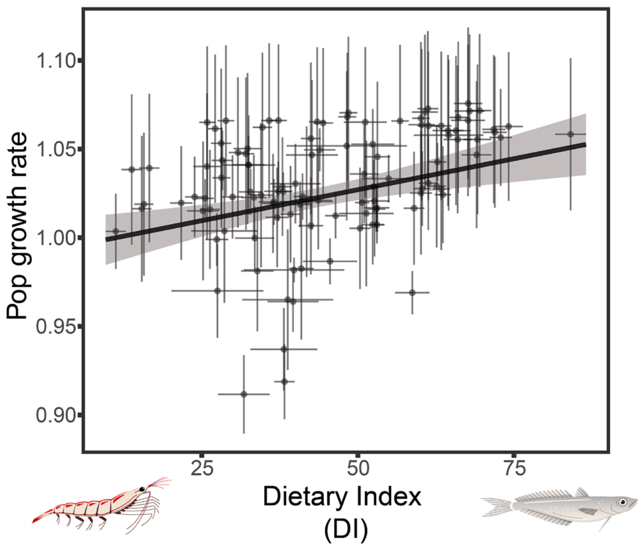

Figure 4. Penguin diet is linked to long-term penguin population growth rates

Adélie penguin (*Pygoscelis adeliae*) colonies with more krill-centric diets generally have lower population growth rates. Each point represents a colony. Thin lines represent uncertainty in both population growth rates and diet (posterior standard deviation in each case). The thick black line represents the model fit, while the gray ribbon represents the model uncertainty (89% CI).

in Adélie penguin abundance vary across the Antarctic, with populations increasing in some regions while declining and even undergoing local extinctions in other regions.[28] Using previously published long-term population growth rates,[28] we found that colonies with more krill-centric diets have lower population growth rates (β_{μ_g} [Equation 11] = 0.0007, 89% CI: [0.0003, 0.0011], $p\left(\beta_{\mu_g} > 0\right)$ = 1; Figure 4). These long-term dynamics provide an opportunity to better understand the large-scale drivers of penguin demographics, which have largely proven elusive in past work.[28,29] Large inter-annual variation in the number of breeding individuals, partially due to the species' long life history and propensity to skip breeding in some years,[30] presents substantial challenges to characterizing changes from year to year. While many factors are thought to be important for penguin demographic processes, including the timing of seasonal environmental dynamics[31] and the effect that sea ice has on access to suitable foraging habitat,[32–35] prey resources play a critical role among these.[36]

Based on previous studies, fish appear to be a higher-quality prey resource for Adélie penguins. Fish are more energy dense,[37] and penguin chicks are generally both heavier and have higher survival rates when fed a more fish-centric diet.[26] That some Adélie penguin populations (Figure 2) feed mostly on krill is likely due to the limited availability of fish resources during the breeding season at these locations. This notion is supported by evidence suggesting declines of Antarctic silverfish from areas that exhibit krill-centric diets (e.g., the Western Antarctic Peninsula [WAP][38,39]) and that penguin populations relied on fish to a much larger degree several thousand years ago in these same regions.[40,41] While krill populations have been the subject of intense study,[42–44] the Antarctic silverfish, a critical component of Antarctic food webs, has received far less attention in the literature.[26]

Where fish are largely unavailable, Adélie penguins must rely primarily on krill as they lack an alternative major prey option. However, krill are inherently patchy in their spatial distribution (more so than fish) with volatile fluctuations in abundance through time.[45] Along the WAP, where penguin colonies exhibit more krill-centric diets and have experienced long-term population declines[28] (Figure 2), krill have both declined in overall abundance and shifted their spatial distribution.[43] These changes are likely due to a combination of changing abiotic conditions,[43] extractive krill fishing efforts,[46] and a dramatic rebound of previously exploited krill predators, principally fur seals and baleen whales, over the last several decades.[47,48] There is evidence that baleen whale abundance in this region has increased to the point where krill resources appear to be a limiting factor for whale population growth. This represents an end to the so-called "krill surplus"[49] that has been thought to result from the reduction of krill predators following commercial sealing and whaling efforts.[50]

Regional declines in Adélie penguin populations[28] are likely due to a reliance on krill (stemming from sea ice-driven declines in fish populations[3,38,39]) in combination with the increasingly limited availability of krill.[51] This is supported by the fact that while not all Adélie penguin colonies that exhibit krill-centric diets have lower population growth rates (Figure 4), those found on the WAP, where growing baleen whale[52] and gentoo penguin (*P. papua*) populations[53,54] are potentially increasing competition for krill (but see Cimino et al.[55]), are generally in decline.[28] Changes in the abiotic environment influence Antarctic food web dynamics not only via the suitability of the environment for prey resources of the Adélie penguin[3,45] but also the abundance and distribution of other predators that compete for these resources.[53,56,57]

Conclusions

Taking a novel approach leveraging the power of satellite sensors, we present the first continent-wide, 30-year reconstruction of Adélie penguin diet across more than 100 locations across the species' range. This unprecedented integration of imaging spectroscopy, stable isotope analysis, satellite imagery, and hierarchical statistical modeling reveals strong and spatially consistent links between sea ice dynamics and Antarctic food webs. As a widely recognized sentinel of environmental change,[11] being used as an indicator species by CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources), one of the primary bodies responsible for the management and conservation of Antarctica,[27] these dietary dynamics provide insight into how the broader Antarctic ecosystem is responding to a changing world.

While often considered one of the most pristine marine ecosystems on the planet,[58] the Antarctic has experienced substantial change over the last century. Given the strong relationship between the abiotic environment and food web dynamics demonstrated here, projected long-term abiotic changes[59,60] are likely to meaningfully restructure trophic interactions in this system into the future. The continued recovery of historically exploited species, including seals and whales,[49] and the relatively new exploitation of resources in the region, including krill and fish,[46,57] also stand to play a substantial role in this regard, echoing concerns globally regarding how food webs are responding to ongoing change.[61,62]

From a methodological perspective, this work demonstrates the utility, and in some respects the necessity, of such a novel "big data" approach to understanding the complex nature of the impacts of global change.[63] Satellites provide an unprecedented opportunity to monitor both physical changes in the environment[64] and the responses of wildlife[65–67] to these changes at spatial and temporal scales that are relevant for understanding and managing ecological systems. Future advances in sensor capabilities, including those aboard satellites, together with the statistical and computational tools to fully realize the potential of these large-scale data,[68] stand to provide critical information to characterize how our world is changing into the future and how we might respond to these changes.

RESOURCE AVAILABILITY

Lead contact

Requests for further information and resources should be directed to and will be fulfilled by the lead contact and first author, Casey Youngflesh (cyoungf@clemson.edu).

Materials availability

This study did not generate any new, unique reagents.

Data and code availability

- All data to conduct analyses and reproduce this study are archived and are publicly available on Zenodo (DOI: 10.5281/zenodo.17409948).
- Raw sea ice data are available from the National Snow and Ice Data Center (DOI: 10.7265/efmz-2t65), raw bathymetry data are available from IBCSO (DOI: 10.1038/s41597-022-01366-7), and raw Landsat satellite data are available from the USGS EarthExplorer (https://earthexplorer.usgs.gov/).
- All code to reproduce analyses is freely available on GitHub (https://github.com/caseyyoungflesh/penguin_diet_from_space) and is archived on Zenodo (DOI: 10.5281/zenodo.17363042).

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AUTHOR CONTRIBUTIONS

Conceptualization, C.Y. and H.J.L.; data curation, C.Y., C.C.-C., M.R.S., and H.J.L.; formal analysis, C.Y., C.C.-C., M.R.S., M.J.P., S.P.S., and H.J.L.; funding acquisition, C.Y., C.C.-C., H.J.L., and M.J.P.; investigation, C.Y., C.C.-C., M.R.S., M.J.P., S.P.S., and H.J.L.; methodology, C.Y., C.C.-C., M.R.S., M.J.P., S.P.S., and H.J.L.; software, C.Y.; visualization, C.Y.; writing – original draft, C.Y.; writing – review & editing, C.Y., C.C.-C., M.R.S., M.J.P., S.P.S., and H.J.L.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS
  - Guano samples
  - Satellite imagery
  - Environmental variables
- METHOD DETAILS
  - Quantifying the spectral and stable isotope properties of penguin guano
  - Spectroscopic model for penguin diet
  - Obtaining penguin colony spectra from Landsat
- QUANTIFICATION AND STATISTICAL ANALYSIS
  - Penguin diet classification from satellite-observed reflectance
  - The effect of environmental variation on penguin diet
  - Assessing links between long-term population growth rates and penguin diet
  - Data processing and computation

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2026.06.028.

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REFERENCES

1. Ratcliffe, N., and Trathan, P. (2011). A review of the diet and at-sea distribution of penguins breeding within the CAMLR Convention Area. CCAMLR Sci. *19*, 75–114.

2. Nicol, S. (2006). Krill, currents, and sea ice: *Euphausia superba* and its changing environment. BioScience *56*, 111–120. https://doi.org/10.1641/0006-3568(2006)056[0111:KCASIE]2.0.CO;2.

3. Corso, A.D., Steinberg, D.K., Stammerjohn, S.E., and Hilton, E.J. (2022). Climate drives long-term change in Antarctic Silverfish along the western Antarctic Peninsula. Commun. Biol. *5*, 104. https://doi.org/10.1038/s42003-022-03042-3.

4. Schwaller, M.R., Southwell, C.J., and Emmerson, L.M. (2013). Continental-scale mapping of Adélie penguin colonies from Landsat imagery. Remote Sens. Environ. *139*, 353–364. https://doi.org/10.1016/j.rse.2013.08.009.

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

6. Rees, W.G., Brown, J.A., Fretwell, P.T., and Trathan, P.N. (2017). What colour is penguin guano? Antarct. Sci. *29*, 417–425. https://doi.org/10.1017/S0954102017000190.

7. Belcher, A., Fielding, S., Gray, A., Biermann, L., Stowasser, G., Fretwell, P., Ireland, L., and Tarling, G.A. (2021). Experimental determination of reflectance spectra of Antarctic krill (*Euphausia superba*) in the Scotia Sea. Antarct. Sci. *33*, 402–414. https://doi.org/10.1017/S0954102021000262.

8. Kelly, J.F. (2000). Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. Can. J. Zool. *78*, 1–27. https://doi.org/10.1139/z99-165.

9. Ainley, D.G., LeResche, R.E., and Sladen, W.J.L. (1983). Breeding Biology of the Adélie Penguin (University of California Press).

10. Gelman, A., Carlin, J.B., Stern, H.S., Dunson, D.B., Vehtari, A., and Rubin, D.B. (2013). Bayesian Data Analysis (CRC Press). https://doi.org/10.1201/b16018.

11. Ainley, D. (2002). The Adélie Penguin: Bellwether of Climate Change (Columbia University Press). https://doi.org/10.7312/ainl12306.

12. Brasso, R.L., and Polito, M.J. (2013). Trophic calculations reveal the mechanism of population-level variation in mercury concentrations between marine ecosystems: Case studies of two polar seabirds. Mar. Pollut. Bull. *75*, 244–249. https://doi.org/10.1016/j.marpolbul.2013.08.003.

13. McInnes, J.C., Emmerson, L., Southwell, C., Faux, C., and Jarman, S.N. (2016). Simultaneous DNA-based diet analysis of breeding, non-breeding and chick Adélie penguins. R. Soc. Open Sci. *3*, 150443. https://doi.org/10.1098/rsos.150443.

14. Hong, S.-Y., Gal, J.-K., Lee, B.-Y., Son, W.-J., Jung, J.-W., La, H.-S., Shin, K.-H., Kim, J.-H., and Ha, S.-Y. (2021). Regional differences in the diets of Adélie and emperor penguins in the Ross Sea, Antarctica. Animals (Basel) *11*, 2681. https://doi.org/10.3390/ani11092681.

15. Jarman, S.N., McInnes, J.C., Faux, C., Polanowski, A.M., Marthick, J., Deagle, B.E., Southwell, C., and Emmerson, L. (2013). Adélie penguin population diet monitoring by analysis of food DNA in scats. PLoS One *8*, e82227. https://doi.org/10.1371/journal.pone.0082227.

16. Zaldúa, N., Franco-Trecu, V., Machado-Gaye, A.L., Raslan, M., Gobel, N., Zajková, Z., and Soutullo, A. (2026). A generalist foraging strategy but strong krill dependence in Adélie penguins from the Western Antarctic Peninsula. Estuarine Coast. Shelf Sci. *337*, 109925. https://doi.org/10.1016/j.ecss.2026.109925.

17. Davis, L.B., Hofmann, E.E., Klinck, J.M., Piñones, A., and Dinniman, M.S. (2017). Distributions of krill and Antarctic silverfish and correlations with environmental variables in the western Ross Sea, Antarctica. Mar. Ecol. Prog. Ser. *584*, 45–65. https://doi.org/10.3354/meps12347.

18. Eayrs, C., Li, X., Raphael, M.N., and Holland, D.M. (2021). Rapid decline in Antarctic sea ice in recent years hints at future change. Nat. Geosci. *14*, 460–464. https://doi.org/10.1038/s41561-021-00768-3.

19. Raphael, M.N., and Handcock, M.S. (2022). A new record minimum for Antarctic sea ice. Nat. Rev. Earth Environ. *3*, 215–216. https://doi.org/10.1038/s43017-022-00281-0.

20. Hobbs, W., Spence, P., Meyer, A., Schroeter, S., Fraser, A.D., Reid, P., Tian, T.R., Wang, Z., Liniger, G., Doddridge, E.W., et al. (2024). Observational evidence for a regime shift in summer Antarctic sea ice. J. Clim. *37*, 2263–2275. https://doi.org/10.1175/JCLI-D-23-0479.1.

21. Roach, L.A., Dörr, J., Holmes, C.R., Massonnet, F., Blockley, E.W., Notz, D., Rackow, T., Raphael, M.N., O'Farrell, S.P., Bailey, D.A., et al. (2020). Antarctic Sea Ice Area in CMIP6. Geophys. Res. Lett. *47*, GL086729. https://doi.org/10.1029/2019GL086729.

22. Ainley, D.G., Wilson, P.R., Barton, K.J., Ballard, G., Nur, N., and Karl, B. (1998). Diet and foraging effort of Adélie penguins in relation to pack-ice conditions in the southern Ross Sea. Polar Biol. *20*, 311–319. https://doi.org/10.1007/s003000050308.

23. Ainley, D.G., Ballard, G., Barton, K.J., Karl, B.J., Rau, G.H., Ribic, C.A., and 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.

24. Polito, M., Lynch, H., Naveen, R., and Emslie, S. (2011). Stable isotopes reveal regional heterogeneity in the pre-breeding distribution and diets of sympatrically breeding *Pygoscelis* spp. penguins. Mar. Ecol. Prog. Ser. *421*, 265–277. https://doi.org/10.3354/meps08863.

25. Black, C.E. (2016). A comprehensive review of the phenology of *Pygoscelis* penguins. Polar Biol. *39*, 405–432. https://doi.org/10.1007/s00300-015-1807-8.

26. Ainley, D., Dugger, K., La Mesa, M., Ballard, G., Barton, K., Jennings, S., Karl, B., Lescroël, A., Lyver, P., Schmidt, A., et al. (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.

27. Agnew, D.J. (1997). Review – The CCAMLR Ecosystem Monitoring Programme. Antartic. science *9*, 235–242. https://doi.org/10.1017/S095410209700031X.

28. Che-Castaldo, C., Jenouvrier, S., Youngflesh, C., Shoemaker, K.T., Humphries, G., McDowall, P., Landrum, L., Holland, M.M., Li, Y., Ji, R., et al. (2017). Pan-Antarctic analysis aggregating spatial estimates of Adélie penguin abundance reveals robust dynamics despite stochastic noise. Nat. Commun. *8*, 832. https://doi.org/10.1038/s41467-017-00890-0.

29. Şen, B., Che-Castaldo, C., Krumhardt, K.M., Landrum, L., Holland, M.M., LaRue, M.A., Long, M.C., Jenouvrier, S., and Lynch, H.J. (2023). Spatiotemporal transferability of environmentally-dependent population models: Insights from the intrinsic predictabilities of Adélie penguin abundance time series. Ecol. Indic. *150*, 110239. https://doi.org/10.1016/j.ecolind.2023.110239.

30. Talis, E.J., Che-Castaldo, C., Şen, B., Krumhardt, K., and Lynch, H.J. (2022). Variability, skipped breeding and heavy-tailed dynamics in an Antarctic seabird. J. Anim. Ecol. *91*, 2437–2450. https://doi.org/10.1111/1365-2656.13827.

31. Youngflesh, C., Jenouvrier, S., Li, Y., Ji, R., Ainley, D.G., Ballard, G., Barbraud, C., Delord, K., Dugger, K.M., Emmerson, L.M., et al. (2017). Circumpolar analysis of the Adélie Penguin reveals the importance of environmental variability in phenological mismatch. Ecology *98*, 940–951. https://doi.org/10.1002/ecy.1749.

32. Barbraud, C., Delord, K., and Weimerskirch, H. (2015). Extreme ecological response of a seabird community to unprecedented sea ice cover. R. Soc. Open Sci. *2*, 140456. https://doi.org/10.1098/rsos.140456.

33. Wilson, K.-J., Turney, C.S.M., Fogwill, C.J., and Blair, E. (2016). The impact of the giant iceberg B09B on population size and breeding success of Adélie penguins in Commonwealth Bay, Antarctica. Antarct. Sci. *28*, 187–193. https://doi.org/10.1017/S0954102015000644.

34. Watanabe, Y.Y., Ito, K., Kokubun, N., and 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.

35. Youngflesh, C., Li, Y., Lynch, H.J., Delord, K., Barbraud, C., Ji, R., and Jenouvrier, S. (2021). Lack of synchronized breeding success in a seabird community: extreme events, niche separation, and environmental variability. Oikos *130*, 1943–1953. https://doi.org/10.1111/oik.08426.

36. Sailley, S., Ducklow, H., Moeller, H., Fraser, W., Schofield, O., Steinberg, D., Garzio, L., and Doney, S. (2013). Carbon fluxes and pelagic ecosystem dynamics near two western Antarctic Peninsula Adélie penguin colonies: An inverse model approach. Mar. Ecol. Prog. Ser. *492*, 253–272. https://doi.org/10.3354/meps10534.

37. Chapman, E., Hofmann, E., Patterson, D., Ribic, C., and Fraser, W. (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.

38. La Mesa, M., and Eastman, J.T. (2012). Antarctic silverfish: Life strategies of a key species in the high-Antarctic ecosystem. Fish . *13*, 241–266. https://doi.org/10.1111/j.1467-2979.2011.00427.x.

39. Parker, M.L., Fraser, W.R., Ashford, J., Patarnello, T., Zane, L., and Torres, J.J. (2015). Assemblages of micronektonic fishes and invertebrates in a gradient of regional warming along the Western Antarctic Peninsula. J. Mar. Syst. *152*, 18–41. https://doi.org/10.1016/j.jmarsys.2015.07.005.

40. Polito, M., Emslie, S.D., and Walker, W. (2002). A 1000-year record of Adélie penguin diets in the southern Ross Sea. Antartic. science *14*, 327–332. https://doi.org/10.1017/S0954102002000184.

41. Emslie, S.D., and Patterson, W.P. (2007). Abrupt recent shift in δ13C and δ15N values in Adélie penguin eggshell in Antarctica. Proc. Natl. Acad. Sci. USA. *104*, 11666–11669. https://doi.org/10.1073/pnas.0608477104.

42. Kawaguchi, S., Ishida, A., King, R., Raymond, B., Waller, N., Constable, A., Nicol, S., Wakita, M., and Ishimatsu, A. (2013). Risk maps for Antarctic krill

under projected Southern Ocean acidification. Nat. Clim. Change *3*, 843–847. https://doi.org/10.1038/nclimate1937.

43. Kawaguchi, S., Atkinson, A., Bahlburg, D., Bernard, K.S., Cavan, E.L., Cox, M.J., Hill, S.L., Meyer, B., and Veytia, D. (2023). Climate change impacts on Antarctic krill behaviour and population dynamics. Nat. Rev. Earth Environ. *5*, 43–58. https://doi.org/10.1038/s43017-023-00504-y.

44. 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., et al. (2022). Stepping stones towards Antarctica: Switch to southern spawning grounds explains an abrupt range shift in krill. Glob. Change Biol. *28*, 1359–1375. https://doi.org/10.1111/gcb.16009.

45. Fraser, W.R., and Hofmann, E.E. (2003). A predator's perspective on causal links between climate change, physical forcing and ecosystem response. Mar. Ecol. Prog. Ser. *265*, 1–15. https://doi.org/10.3354/meps265001.

46. Hinke, J.T., Cossio, A.M., Goebel, M.E., Reiss, C.S., Trivelpiece, W.Z., and Watters, G.M. (2017). Identifying risk: Concurrent overlap of the Antarctic krill fishery with krill-dependent predators in the Scotia Sea. PLoS One *12*, e0170132. https://doi.org/10.1371/journal.pone.0170132.

47. Pallin, L.J., Baker, C.S., Steel, D., Kellar, N.M., Robbins, J., Johnston, D.W., Nowacek, D.P., Read, A.J., and Friedlaender, A.S. (2018). High pregnancy rates in humpback whales (*Megaptera novaeangliae*) around the Western Antarctic Peninsula, evidence of a rapidly growing population. R. Soc. Open Sci. *5*, 180017. https://doi.org/10.1098/rsos.180017.

48. Zerbini, A.N., Adams, G., Best, J., Clapham, P.J., Jackson, J.A., and Punt, A.E. (2019). Assessing the recovery of an Antarctic predator from historical exploitation. R. Soc. Open Sci. *6*, 190368. https://doi.org/10.1098/rsos.190368.

49. Laws, R.M. (1977). Seals and whales of the Southern Ocean. Philos. Trans. R. Soc. Lond., B Biol. Sci. *279*, 81–96. https://doi.org/10.1098/rstb.1977.0073.

50. Pallin, L.J., Kellar, N.M., Steel, D., Botero-Acosta, N., Baker, C.S., Conroy, J.A., Costa, D.P., Johnson, C.M., Johnston, D.W., Nichols, R.C., et al. (2023). A surplus no more? Variation in krill availability impacts reproductive rates of Antarctic baleen whales. Glob. Chang. Biol. *29*, 2108–2121. https://doi.org/10.1111/gcb.16559.

51. Trivelpiece, W.Z., Hinke, J.T., Miller, A.K., Reiss, C.S., Trivelpiece, S.G., and Watters, G.M. (2011). Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. Proc. Natl. Acad. Sci. USA. *108*, 7625–7628. https://doi.org/10.1073/pnas.1016560108.

52. Reisinger, R.R., Friedlaender, A.S., Zerbini, A.N., Palacios, D.M., Andrews-Goff, V., Dalla Rosa, L., Double, M., Findlay, K., Garrigue, C., How, J., et al. (2021). Combining regional habitat selection models for large-scale prediction: Circumpolar habitat selection of Southern Ocean humpback whales. Remote Sens. *13*, 2074. https://doi.org/10.3390/rs13112074.

53. Herman, R., Borowicz, A., Lynch, M., Trathan, P., Hart, T., and Lynch, H. (2020). Update on the global abundance and distribution of breeding Gentoo Penguins (*Pygoscelis papua*). Polar Biol. *43*, 1947–1956. https://doi.org/10.1007/s00300-020-02759-3.

54. Wawrzynek-Borejko, J., Panasiuk, A., Hinke, J.T., and Korczak-Abshire, M. (2022). Are the diets of sympatric Pygoscelid penguins more similar than previously thought? Polar Biol. *45*, 1559–1569. https://doi.org/10.1007/s00300-022-03090-9.

55. Cimino, M.A., Moline, M.A., Fraser, W.R., Patterson-Fraser, D.L., and Oliver, M.J. (2016). Climate-driven sympatry may not lead to foraging competition between congeneric top-predators. Sci. Rep. *6*, 18820. https://doi.org/10.1038/srep18820.

56. Reisinger, R.R., Trathan, P.N., Johnson, C.M., Joyce, T.W., Durban, J.W., Pitman, R.L., and Friedlaender, A.S. (2022). Spatiotemporal overlap of baleen whales and krill fisheries in the western Antarctic Peninsula region. Front. Mar. Sci. *9*, 914726. https://doi.org/10.3389/fmars.2022.914726.

57. Ainley, D.G., Morandini, V., Salas, L., Nur, N., Rotella, J., Barton, K., Lyver, P.O., Goetz, K.T., Larue, M., Foster-Dyer, R., et al. (2024). Response of indicator species to changes in food web and ocean dynamics of the Ross Sea, Antarctica. Antarct. Sci. *36*, 290–318. https://doi.org/10.1017/S0954102024000191.

58. Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D'Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., et al. (2008). A Global Map of Human Impact on Marine Ecosystems. Science *319*, 948–952. https://doi.org/10.1126/science.1149345.

59. Chown, S.L., Lee, J.E., Hughes, K.A., Barnes, J., Barrett, P.J., Bergstrom, D.M., Convey, P., Cowan, D.A., Crosbie, K., Dyer, G., et al. (2012). Conservation. Challenges to the future conservation of the Antarctic. Science *337*, 158–159. https://doi.org/10.1126/science.1222821.

60. Tewari, K., Mishra, S.K., Salunke, P., and Dewan, A. (2022). Future projections of temperature and precipitation for Antarctica. Environ. Res. Lett. *17*, 014029. https://doi.org/10.1088/1748-9326/ac43e2.

61. Zhang, L., Takahashi, D., Hartvig, M., and Andersen, K.H. (2017). Food-web dynamics under climate change. Proc. Biol. Sci. *284*, 20171772. https://doi.org/10.1098/rspb.2017.1772.

62. Gagne, T.O., Hyrenbach, K.D., Hagemann, M.E., and Van Houtan, K.S. (2018). Trophic signatures of seabirds suggest shifts in oceanic ecosystems. Sci. Adv. *4*, eaao3946. https://doi.org/10.1126/sciadv.aao3946.

63. Rollinson, C.R., Finley, A.O., Alexander, M.R., Banerjee, S., Dixon Hamil, K.-A., Koenig, L.E., Locke, D.H., DeMarche, M.L., Tingley, M.W., Wheeler, K., et al. (2021). Working across space and time: nonstationarity in ecological research and application. Front. Ecol. Environ. *19*, 66–72. https://doi.org/10.1002/fee.2298.

64. Comiso, J.C., and Steffen, K. (2001). Studies of Antarctic sea ice concentrations from satellite data and their applications. J. Geophys. Res. *106*, 31361–31385. https://doi.org/10.1029/2001JC000823.

65. Lynch, H.J., and Schwaller, M.R. (2014). Mapping the abundance and distribution of Adélie penguins using Landsat-7: First steps towards an integrated multi-sensor pipeline for tracking populations at the continental scale. PLOS One *9*, e113301. https://doi.org/10.1371/journal.pone.0113301.

66. Schwaller, M.R., Lynch, H.J., Tarroux, A., and Prehn, B. (2018). A continent-wide search for Antarctic petrel breeding sites with satellite remote sensing. Remote Sens. Environ. *210*, 444–451. https://doi.org/10.1016/j.rse.2018.02.071.

67. LaRue, M., Salas, L., Nur, N., Ainley, D., Stammerjohn, S., Pennycook, J., Dozier, M., Saints, J., Stamatiou, K., Barrington, L., et al. (2021). Insights from the first global population estimate of Weddell seals in Antarctica. Sci. Adv. *7*, eabh3674. https://doi.org/10.1126/sciadv.abh3674.

68. Tuia, D., Kellenberger, B., Beery, S., Costelloe, B.R., Zuffi, S., Risse, B., Mathis, A., Mathis, M.W., van Langevelde, F., Burghardt, T., et al. (2022). Perspectives in machine learning for wildlife conservation. Nat. Commun. *13*, 792. https://doi.org/10.1038/s41467-022-27980-y.

69. Dorschel, B., Hehemann, L., Viquerat, S., Warnke, F., Dreutter, S., Tenberge, Y.S., Accettella, D., An, L., Barrios, F., Bazhenova, E., et al. (2022). The International Bathymetric Chart of the Southern Ocean Version 2. Sci. Data *9*, 275. https://doi.org/10.1038/s41597-022-01366-7.

70. Borboroglu, P.G., and Boersma, P.D. (2013). Penguins: Natural History and Conservation (University of Washington Press).

71. Meier, W.N., Fetterer, F., Windnagel, A.K., and Stewart, S. (2021). NOAA/NSIDC Climate Data Record of Passive Microwave Sea Ice Concentration, Version 4 (NSIDC: National Snow and Ice Data Center). https://doi.org/10.7265/efmz-2t65.

72. Tierney, M., Southwell, C., Emmerson, L., and Hindell, M. (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.

73. Polito, M.J., Trivelpiece, W.Z., Karnovsky, N.J., Ng, E., Patterson, W.P., and Emslie, S.D. (2011). Integrating Stomach Content and Stable Isotope Analyses to Quantify the Diets of Pygoscelid Penguins. PLoS One *6*, e26642. https://doi.org/10.1371/journal.pone.0026642.

74. Minagawa, M., and Wada, E. (1984). Stepwise enrichment of 15N along food chains: further evidence and the relation between δ15N and animal age. Geochim. Cosmochim. Acta *48*, 1135–1140. https://doi.org/10.1016/0016-7037(84)90204-7.

75. Pinkerton, M.H., Forman, J., Bury, S.J., Brown, J., Horn, P., and O'Driscoll, R.L. (2013). Diet and trophic niche of Antarctic silverfish *Pleuragramma antarcticum* in the Ross Sea, Antarctica. J. Fish Biol. *82*, 141–164. https://doi.org/10.1111/j.1095-8649.2012.03476.x.

76. Yang, G., Atkinson, A., Hill, S.L., Guglielmo, L., Granata, A., and Li, C. (2021). Changing circumpolar distributions and isoscapes of Antarctic krill: Indo-Pacific habitat refuges counter long-term degradation of the Atlantic sector. Limnol. Oceanogr. *66*, 272–287. https://doi.org/10.1002/lno.11603.

77. Markham, B.L., and Barker, J.L. (1985). Spectral characterization of the Landsat Thematic Mapper sensors. Int. J. Remote Sens. *6*, 697–716. https://doi.org/10.1080/01431168508948492.

78. Chander, G., Markham, B.L., and Helder, D.L. (2009). Summary of current radiometric calibration coefficients for Landsat MSS, TM, ETM+, and EO-1 ALI sensors. Remote Sens. Environ. *113*, 893–903. https://doi.org/10.1016/j.rse.2009.01.007.

79. Mevik, B.-H., and Wehrens, R. (2007). The pls package: principal component and partial least squares regression in R. Journal of Statistical. Software *18*, 1–24. https://doi.org/10.18637/jss.v018.i02.

80. R Core Team (2025). R: a Language and Environment for Statistical Computing (R Foundation for Statistical Computing). https://www.R-project.org.

81. Serbin, S.P., Singh, A., McNeil, B.E., Kingdon, C.C., and Townsend, P.A. (2016). Spectroscopic determination of leaf morphological and biochemical traits for northern temperate and boreal tree species. Ecol. Appl. *24*, 1651–1669. https://doi.org/10.1890/13-2110.1.

82. Che-Castaldo, C., Humphries, G., and Lynch, H. (2023). Antarctic Penguin Biogeography Project: Database of abundance and distribution for the Adélie, chinstrap, gentoo, emperor, macaroni and king penguin south of 60 S. Biodivers. Data J. *11*, e101476. https://doi.org/10.3897/BDJ.11.e101476.

83. Fuller, W.A. (2009). Measurement Error Models (John Wiley & Sons).

84. Caut, S., Angulo, E., and Courchamp, F. (2009). Variation in discrimination factors (Δ^{15} N and Δ^{13} C): the effect of diet isotopic values and applications for diet reconstruction. J. Appl. Ecol. *46*, 443–453. https://doi.org/10.1111/j.1365-2664.2009.01620.x.

85. Narula, S.C. (1979). Orthogonal polynomial regression. Int. Stat. Rev., Rev. Int. Stat. *47*, 31–36. https://doi.org/10.2307/1403204.

86. Youngflesh, C., Montgomery, G.A., Saracco, J.F., Miller, D.A.W., Guralnick, R.P., Hurlbert, A.H., Siegel, R.B., LaFrance, R., and Tingley, M.W. (2023). Demographic consequences of phenological asynchrony for North American songbirds. Proc. Natl. Acad. Sci. USA. *120*, e2221961120. https://doi.org/10.1073/pnas.2221961120.

87. Hijmans, R.J., Bivand, R., Forner, K., Ooms, J., and Pebesma, E. (2021). Package "terra." R package version. https://rspatial.org/terra/.

88. Pebesma, E. (2018). Simple Features for R: Standardized Support for Spatial Vector Data. R J. *10*, 439–446. https://doi.org/10.32614/RJ-2018-009.

89. Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., et al. (2019). Welcome to the Tidyverse. JOSS *4*, 1686. https://doi.org/10.21105/joss.01686.

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

91. Gabry, J., Češnovar, R., and Johnson, A. (2023). Cmdstanr: R Interface to "CmdStan." R package version 0.6.1. https://mc-stan.org/cmdstanr/

92. Carpenter, B., Gelman, A., Hoffman, M.D., Lee, D., Goodrich, B., Betancourt, M., Brubaker, M.A., Guo, J., Li, P., and Riddell, A. (2017). *Stan*: A probabilistic programming language. J. Stat. Softw. *76*, 1. https://doi.org/10.18637/jss.v076.i01.

93. Youngflesh, C. (2018). MCMCvis: Tools to visualize, manipulate, and summarize MCMC output. JOSS *3*, 640. https://doi.org/10.21105/joss.00640.

94. McElreath, R. (2020). Statistical Rethinking: A Bayesian Course with Examples in R and Stan (Chapman and Hall/CRC). https://doi.org/10.1201/9780429029608.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Bathymetry data	Dorschel et al.[69]	https://doi.org/10.1038/s41597-022-01366-7
Landsat satellite imagery	United States Geological Survey Earth Explorer	https://earthexplorer.usgs.gov/
Landsat spectral response curves	United States Geological Survey	https://landsat.usgs.gov/spectral-characteristics-viewer
Sea ice concentration data	National Snow and Ice Data Center	https://doi.org/10.7265/efmz-2t65
Landsat-derived spectral reflectance of penguin colonies	This paper	https://doi.org/10.5281/zenodo.17409948
Penguin guano spectra	This paper	https://doi.org/10.5281/zenodo.17409948
Penguin guano stable isotope analysis data	This paper	https://doi.org/10.5281/zenodo.17409948

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Guano samples

A total of 103 guano samples were collected from 16 unique *Pygoscelis* spp. penguin breeding colonies in the Antarctic Peninsula region during the 2014 and 2015 austral summers (Dec 4 –Dec 23; Table S1). During the breeding season, these penguins rely principally on a diet of krill (*Euphausia superba* and *E. crystallorophias*) and Antarctic silverfish (*Pleuragramma antarcticum*).[1] Guano samples were derived from three penguin species in the genus *Pygoscelis* (Adélie penguin *P. adeliae*, gentoo penguin *P. papua*, and chinstrap penguin *P. antarctica*) to increase the dietary breadth of sampling as well as the total number of samples. Ultimately these samples were only used to make associations between diet and spectral properties. While the Adélie penguin is the focus of this study, these closely related species have similar physiologies.[70]

Satellite imagery

Top-of-atmosphere reflectance values were obtained for Adélie penguin breeding colonies using cloud-free satellite scenes (images) from the Landsat 4 TM, Landsat 5 TM, and Landsat 7 ETM+ satellite-based multispectral sensors (30 m spatial resolution) collected November–February (the Adélie penguin breeding season), from 1984–2013 (Figure 1C). We use season year to refer a given breeding season year – for example the 1984 season year spans the November 1984 to February 1985.

Environmental variables

Climate Data Record sea ice concentration data, obtained at 25 km spatial resolution from passive microwave satellite sensors, was accessed through the National Snow and Ice Data Center.[71] Bathymetry data were extracted from Dorschel et al.[69]

METHOD DETAILS

Quantifying the spectral and stable isotope properties of penguin guano

Samples were collected from the ground adjacent to penguin nests at each breeding colony and homogenized inside sampling bags before being spread evenly on wax paper in preparation for spectral analysis. Spectral properties of each guano sample were characterized by obtaining high spectral-resolution radiance measurements in laboratory environment using a full range (350–2500 nm) field-portable spectroradiometer (Analytical Spectral Devices FieldSpec 4) in a bench top configuration, with the fiber (with attached 18° optic) positioned at a 45° angle to the sample (Figure S1). A full-spectrum light source (Analytical Spectral Devices Illuminator) illuminated samples for spectral analysis. Radiance values were taken from a Spectralon reference panel in the same configuration which were then used to calculate the spectral reflectance, as is common practice. Following spectral analysis, samples were dried in a commercial food dehydrator at 43° C for 10 hours and checked for desiccation.

Stable isotope analysis (SIA) was used to measure naturally occurring nitrogen stable isotope values ($\delta^{15}N$) in each dried guano sample. SIA is accepted as a robust, relatively low-cost, minimally invasive way of quantifying predator diets, including *Pygoscelis* penguin spp.[41,72,73] $\delta^{15}N$ values are commonly used to indicate the trophic position of an organism's diet due to step-wise increase in tissue $\delta^{15}N$ values with each trophic level.[74] For example, the two main prey taxa of *Pygoscelis* penguins, krill and fish, differ in trophic level and their respective $\delta^{15}N$ values.[73] We used guano $\delta^{15}N$ values as a proxy of the relative contribution of krill vs. fish in penguin diets: lower $\delta^{15}N$ values reflect diets characterized by higher relative proportions of krill and higher $\delta^{15}N$ values reflect diets characterized by higher relative proportions of fish (Figure 1A). While $\delta^{15}N$ values of the two species of krill these penguins feed on differs (*E. superba* having slightly lower $\delta^{15}N$ values compared to *E. crystallorophias*), we do not distinguish between them in this study – both have substantially lower $\delta^{15}N$ values compared to Antarctic silverfish.[75] While isotopic values for a given organism (e.g., krill) can vary to a small degree around Antarctica,[76] all guano samples for this study were collected from a single region of Antarctica. Moreover, these isoscapes are unlikely to impact the spectral properties of krill or fish in penguin guano. As such, our spectroscopic model (below) characterizes spatial differences in diet rather than isotopic variation across space. For stable isotope analysis, approximately 0.8 mg of dried guano was loaded into tin cups before being flash-combusted and analyzed for $\delta^{15}N$ through a Costech ECS4010 elemental analyzer coupled to a Thermo Delta V Plus continuous-flow stable isotope ratio mass spectrometer. Raw δ values were normalized using USGS-40 and USGS-41 standards. Sample precision based on repeated reference material was 0.2‰.

Spectroscopic model for penguin diet

The laboratory-obtained, high spectral-resolution reflectance measurements for each guano sample were convolved to the relevant spectral bands of the Landsat 4 TM, Landsat 5 TM, and Landsat 7 ETM+ satellite-based sensors, spanning the visible, near infrared, and short-wave infrared portions of the electromagnetic spectrum:

$$\overline{\rho_i} = \frac{\int \rho_\lambda \, RSR_\lambda \, d\lambda}{\int RSR_\lambda \, d\lambda}, \qquad \text{(Equation 1)}$$

where $\overline{\rho_i}$ is the integrated average reflectance for band *i*, ρ_λ is the target spectral reflectance for band *i* measured at a given wavelength λ, and RSR_λ is the relative spectral response for band *i* measured at a given wavelength λ. We excluded data from newer Landsat sensors (i.e., Landsat 8 OLI and Landsat 9 OLI-2) as the spectral bandwidths differ from those of earlier sensors. These differences mean that creating a harmonized time series of dietary information across these era is non-trivial. For each sensor, there were six relevant spectral bands, blue, green, red, near infrared, and two short-wave infrared (Figure S1). Convolved spectra represent how these satellite sensors observe the spectral reflectance of each guano sample. Spectral response curves,[77] describing how the sensitivity of each sensor varies across wavelengths within each band, were used to perform each convolution. These were derived from the U.S. Geological Survey Landsat website (https://landsat.usgs.gov/spectral-characteristics-viewer). While the differences in $\overline{\rho_i}$ for the spectral bands of Landsat 4 and 5 compared to Landsat 7 are typically small (<2% difference for most bands and differing by a maximum of 8% in only one case), we chose to build a classification model to predict penguin diet from spectral properties for each sensor independently to maximize the accuracy of dietary characterizations.[78]

A partial least-squares regression (PLSR) modeling approach was implemented using the ‘pls’ package[79] in the R statistical environment[80] to characterize penguin diet as a function of the convolved spectra. This approach decomposes predictor variables (i.e., reflectance values) into a set of uncorrelated ‘principal components’, which are fit to predict a response variable (i.e., penguin diet). This method is commonly used in the field of ecology to associate plant traits with spectral characteristics.[81] For each sensor (Landsat 4 TM, Landsat 5 TM, and Landsat 7 ETM+) a cross-validation approach was taken to estimate PLSR coefficients, where in each of 1000 iterations, the data were split into training (65%) and validation sets (35%). This iterative approach was implemented to assess the stability and generalizability of the models and to accurately quantify uncertainty in predictions. Data were split using stratified sampling across 5 bins based on the quantiles of the $\delta^{15}N$ values, to ensure that data for each model was sampling across the entire range of values. At each iteration, model performance metrics, both the coefficient of determination (R2) and the root mean squared error of prediction (RMSEP), were recorded for both the training and validation datasets (Figure 1B). Coefficient estimates for each of the 1000 models were recorded to facilitate accurate accounting of uncertainty in downstream diet characterization from satellite imagery. The appropriate number of principal components (5) were selected by determining whether additional principal components significantly reduced the RMSEP statistic, as determined using a t-test[81] (Figure S3).

Obtaining penguin colony spectra from Landsat

Pixels containing guano within Adélie penguin colonies were identified from Landsat scenes using an algorithm developed by Schwaller et al.[4] During these time periods, daytime scenes were selected over Antarctica (WRS row between 90 and 130) that were classified as either Tier 1 or 2, with an image quality rating of >= 5 and a sun elevation angle of >= 15 degrees. Table S2 provides a record of Landsat Product Identifiers associated with the satellite imagery used in this study. Landsat scenes were downloaded using the USGS Machine-to-Machine (M2M) Application Programming Interface (API). Only colonies with an average size of at least 2 pixels (i.e., greater than 1800 m^2) were retained. In cases where other penguin species were known to breed at the same location, only colonies where at least 95% of the mean number of nests were Adélie penguin were retained. Number of nests (i.e., colony size) were obtained from the R package ‘mapppdr‘[82]. Spectral information was used from 119 penguin colonies, 1334 unique colony years, 3938 unique colony days, and 179,346 pixels identified as containing guano. Number of unique days per season ranged from 1 to 21, with 1 to 128 total captures for each site (Figures 1C and S2). The spatial extent of this analysis represents nearly the entirety of both the species’ global range and global population.[5] While this methodology could be applied to any satellite-based or airborne sensor, the Landsat sensors were chosen based on the long time series and broad spatial extent that the data provide.

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QUANTIFICATION AND STATISTICAL ANALYSIS

Penguin diet classification from satellite-observed reflectance

Using the above reflectance values and the estimated coefficients from the PLSR models, relative diet values were predicted for each Landsat pixel identified as Adélie penguin breeding colony. For each guano pixel, diet was predicted using the coefficients derived from each of the 1000 models from the cross validation PLSR approach. As such, each pixel had some estimate ($\hat{y}$), taken as the mean of these 1000 diet realizations, and some uncertainty, taken as the standard deviation of the 1000 diet realizations ($\widehat{\sigma_y}$) – this accounts for what might be considered the 'coefficient uncertainty' of the PLSR model (the degree to which uncertainty in the coefficient estimates of the model contributes to uncertainty). Separately, we used the mean R^2 from the PLSR models to quantify the uncertainty derived from the model's performance. Rearranging the equation:

$$R^2 = 1 - \frac{residual\ variance}{total\ variance}, \quad \text{(Equation 2)}$$

we arrive at:

$$residual\ variance = \left(1 - R^2\right) \times total\ variance, \quad \text{(Equation 3)}$$

from which we calculate τ (a scalar), the square root of the residual variance (which could also be referred to as the process error or 'process uncertainty'). In this way, we account for two independent sources of uncertainty (coefficient uncertainty and process uncertainty) in these dietary characterizations (Figure 1D). Using a hierarchical Bayesian approach, we propagate uncertainty throughout the entire analytical pipeline that we developed.[10] This ensures that uncertainty in modeled outcomes does not unduly influence scientific inference and that uncertainty in this inference is quantified appropriately.

We estimated true, latent diet (z) for a given pixel (i), colony (j), day of season (k, where November 1 is 1 for a given season), and season year (m, where season year 2012 represents the 2012/2013 Adélie penguin breeding season) as normally distributed, while accounting for coefficient uncertainty ($\widehat{\sigma_y}$) and process uncertainty (τ), as:

$$\widehat{y_{ijkm}} \sim N\left(p_{ijkm}, \widehat{\sigma_{y_{ijkm}}}\right), \quad \text{(Equation 4)}$$

$$p_{ijkm} \sim N\left(z_{ijkm}, \tau\right),$$

where p represent the intermediate latent diet, accounting for only coefficient uncertainty (Figure 1D). These components of this hierarchical model are often referred to as measurement error models used to account for uncertainty in observed states.[83] Colony-, day of season-, and season year-specific diet (w) was estimated from pixel-level diet (z), with some variance within each colony, day of season, and season year (σ). Parameter w was itself modeled hierarchically, with some colony-specific mean μ_w and variance σ_w,

$$z_{ijkm} \sim N\left(w_{jkm}, \sigma\right), \quad \text{(Equation 5)}$$

$$w_{jkm} \sim N\left(\mu_{w_j}, \sigma_w\right)$$

We used posterior iterations for w to derive a Dietary Index (DI) and associated uncertainty, characterizing the relative proportions of krill vs. fish in penguin diet. A modified min-max (i.e., linear) transformation was used to scale dietary values roughly between 0 and 100:

$$\frac{w - q_{0.1}}{q_{99.9} - q_{0.01}}, \quad \text{(Equation 6)}$$

where $q_{0.1}$ and $q_{99.9}$ represent the 0.1st and 99.9th quantiles, respectively. In this way, we obtained a posterior distribution for DI for each colony, day of season, and season year, where 99.8% of all posterior iterations for DI (i.e., for any colony, day of season, and season year) fell between 0 and 100. This transformation was used to provide a relative measure of diet across space and time, where DI values of 0 represent krill-centric diets and values of 100 represent fish-centric diets. While stable isotopes are often used to estimate absolute rather than relative diet,[73] necessary diet-tissue discrimination factors[84] are unknown in this case. Prior studies have observed Adélie penguin diet ranging from entirely krill to nearly entirely fish, though krill typically is found in some amount.[1]

The effect of environmental variation on penguin diet

We then modeled the posterior mean ($\widehat{DI}$) and posterior standard deviation ($\widehat{\sigma_{DI}}$) of the dietary index for each colony (j), day of season (k), and season year (m), using an observation model to account for uncertainty, as above, as a function of day of season (DOS) to characterize how diet changes across a breeding season:

$$\widehat{DI}_{jkm} \sim N\left(v_{jkm}, \widehat{\sigma_{DI}}_{jkm}\right), \quad \text{(Equation 7)}$$

$$v_{jkm} \sim N\left(\alpha_{jm} + \beta_{1_j} \times DOS_{jkm} + \beta_{2_j} \times DOS^2_{jkm}, \sigma_v\right)$$

where α represents the colony/year-specific intercept (diet when DOS is equal to 0), β_1 represents the colony-specific linear effect of day of season, β_2 represents the colony-specific quadratic effect of day of season, and σ_v represents the residual error at this level of the model. Day of season was centered, such that 0 corresponded to day 60 (December 30), the midpoint of the breeding season as it was monitored for this study. Variables DOS and DOS^2 represent the orthogonal polynomials, created with the "poly" function in R, as is typical for polynomial regression.[85,86] The day of season (DOS) effects were drawn from a multivariate normal:

$$\begin{bmatrix} \beta_{1_j} \\ \beta_{2_j} \end{bmatrix} \sim MVN\left(\begin{bmatrix} \mu_{\beta_1} \\ \mu_{\beta_2} \end{bmatrix}, \Sigma_\beta\right), \quad \text{(Equation 8)}$$

where μ_{β_1} and μ_{β_2} represent the cross-colony mean effects and Σ_β represents the 2 x 2 covariance matrix. The colony/season year-specific intercept (i.e., colony/season year-specific relative diet), was modeled as a function of colony/season year-specific sea ice (YSIC):

$$\alpha_{jm} \sim N\left(\gamma_j + \theta_j \times YSIC_{jm}, \sigma_\alpha\right), \quad \text{(Equation 9)}$$

$\theta_j \sim N(\mu_\theta, \sigma_\theta)$, where γ represents the site-specific intercept, and θ represents the effect of YSIC. Variable YSIC was centered for each colony, such that values of 0 represent mean sea ice conditions for that colony. Because of this, parameter γ represents colony-level diet under average sea ice conditions for that colony. YSIC was calculated as average sea ice from November–February a 150 km buffer, for each colony/season year. The 'terra'[87] and 'sf'[88] packages were used for raster manipulation and spatial data processing, while the 'tidyverse' family of packages[89] facilitated general data manipulation in R.[80]

Colony-specific diet (γ) was modeled as a function of colony-specific sea ice (SSIC) and area of continental shelf (SA) to estimate the effect that these factors have on spatial variation in diet:

$$\gamma_j \sim N\left(\kappa + \zeta_1 \times SSIC_j + \zeta_2 \times SA_j, \sigma_\gamma\right), \quad \text{(Equation 10)}$$

where κ is the cross-colony intercept, ζ_1 is the effect of SSIC, and ζ_2 is the effect of SA. In this framework, the effect of temporal variation in sea ice (Equation 8) is decoupled from the effect of spatial variation in sea ice (Equation 9). Colony-specific sea ice concentration data (SSIC) was derived by taking the average sea ice concentration within a 150 km buffer across the years of this study. This buffer is thought to be the maximum foraging range for the Adélie penguin.[11] Area of continental shelf (SA) was defined as the area of ocean floor less than 1000m depth[90] within 150 km of colonies. Both have been suggested to play a role in the diet of Adélie penguins.[1,22]

Assessing links between long-term population growth rates and penguin diet

Finally, to quantify the association between penguin diet and population processes, we modeled estimates of the population growth rate multiplier at each Adélie penguin breeding colony (derived from Che-Castaldo et al.[28]) as a function of colony-specific diet (γ; Equation 9). Population growth rate multipliers represent the average of the year-specific growth rates of each colony, estimated using count data aggregated from sources from around the continent from 'mapppdr'[28,82]. We focus specifically on long-term population change as interannual variability in penguin abundance in a complex process[29] regulated by long recruitment times[11] and skipped breeding.[30] As above, we used an observation model to account for the uncertainty in both the response and predictor variables. The posterior mean of each colony-specific population growth rate ($\hat{g}$) was modeled as normally distributed, with some uncertainty, quantified as the posterior standard deviation of the multiplier ($\widehat{\sigma_g}$):

$$\hat{g}_j \sim N\left(\mu_{g_j}, \widehat{\sigma_{g_j}}\right), \quad \text{(Equation 11)}$$

$$\hat{\gamma}_j \sim N\left(\xi_j, \hat{\sigma}_{\gamma j}\right)$$

$$\xi_j \sim N(\mu_\xi, \sigma_\xi)$$

$$\mu_{g_j} \sim N\left(\alpha_{\mu_g} + \beta_{\mu_g} \times \xi_j, \sigma_{\mu_g}\right)$$

where α_{μ_g} is the intercept and β_{μ_g} is the effect of average diet on long-term population growth rates.

Data processing and computation

We fit all hierarchical models with the R package 'cmdstanr'[91], which interfaces with Stan[92] in the R statistical computing language,[80] using weakly informative priors for all parameters. We used the R package 'MCMCvis'[93] to manipulate, process, and visualize model

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output. All parameters had $\widehat{R}$ values ≤ 1.01 and number of effective samples > 400, with no divergent transitions present. We used graphical posterior predictive checks to ensure no major model misspecification. The distribution of data generated from the model was similar to that of data used to fit the model.

For each parameter, we report the posterior mean and 89% credible intervals. This choice of interval width, while arbitrary, was made to summarize parameter uncertainty without suggesting Bayesian credible intervals are equivalent to tests of statistical significance, as is commonly done using the 95% CI.[94] Additionally, we report the probability that each parameter is positive, denoted as $p(PARAMETER > 0)$.