Short Communication

King Penguins adjust foraging effort rather than diet when faced with poor foraging conditions

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The links between foraging success, foraging effort and diet in a myctophid specialist seabird, the King Penguin *Aptenodytes patagonicus*, were investigated during seven breeding seasons using tracking and isotopic data. Despite the variable foraging conditions encountered by the birds, isotopic signatures (a proxy for diet) were invariable throughout the study. On the other hand, penguins stayed longer at sea when the foraging success indices (i.e. prey capture attempts per day and mass gained per day) were low. Although King Penguins can compensate for low prey capture rates by increasing foraging effort, their specialist diet during reproduction makes the species particularly sensitive to prey availability, with its conservation tightly linked to its main prey.

Keywords: carbon, generalist, Kerguelen, nitrogen, Southern Ocean.

There are multiple strategies available to birds to cope with periods of low prey availability. For example, dietary-specialist species can increase foraging effort to compensate for low prey capture rates (e.g. Abrams 1991, Cox *et al.* 2019, Fromant *et al.* 2021). Alternatively, generalists can switch to feeding on other still-available prey (e.g. Scopel *et al.* 2019, Milchev & Georgiev 2020). The strategy used is highly species-dependent, with both specialists and generalists displaying variable flexibility in both foraging effort and diet.

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In the marine environment, species composition is changing drastically, as environmental disturbances such as overfishing or recurrent marine heat waves might induce periods of low prey availability (Jones *et al.* 2018, Osborne *et al.* 2020, Sydeman *et al.* 2021). Although generalist species that switch prey are likely to better tolerate these ecosystem changes, specialists might be impacted as the foraging effort increases to compensate for poor conditions (Gilman *et al.* 2010). Such is the case for species including the Little Auk *Alle alle* and the African Penguin *Spheniscus demersus*, two specialist species that increase time spent foraging in response to the reduced availability of their main prey (Jakubas *et al.* 2007, Pichegru *et al.* 2012). Yet, even species regarded as specialists can sometimes shift their diet in critical periods, so that a certain level of flexibility might help these species to cope with a changing environment (e.g. Ludynia *et al.* 2010, Ancona *et al.* 2012).

Here, we investigate the links between foraging success, foraging effort and diet in a specialist deep-diving seabird, the King Penguin *Aptenodytes patagonicus*. This species feeds mainly on small mesopelagic myctophids, often dominated by *Krefftichthys anderssoni*, for which the availability to the top predators may change across the polar region, mainly due to climatic anomalies (Bost *et al.* 2002, 2015, Le Bohec *et al.* 2008, Péron *et al.* 2012). Yet, King Penguins can also forage opportunistically on other prey, such as squids and other myctophids (Adams & Klages 1987, Bost *et al.* 2002, Cherel *et al.* 2007). Consequently, the species could theoretically diversify its diet during periods of low prey availability.

We tested whether King Penguins would become more opportunistic when foraging success is low by comparing isotopic values (a proxy of diet) of foraging breeding adults over 7 years. We predicted that, if King Penguins compensated for low prey availability by switching diet, we would find different isotopic values in individuals experiencing dissimilar foraging success. On the other hand, if King Penguins did not seek different prey despite low prey availability, we expected a compensating increased foraging effort (e.g. longer foraging trips, deeper dives) as foraging success decreases, while isotopic values would remain constant.

METHODS

All data were collected in February on chick-rearing King Penguins at Ratmanoff's colony (around 85 000 pairs, Barbraud *et al.* 2020) in the Kerguelen archipelago (49°14′33″S, 70°33′40″E) situated in the southern Indian Ocean. Data were obtained during the chick-rearing period in all years from 2015 to 2022 except 2019 (i.e. 7 years in total). The ethics committee of the

Institut polaire français Paul-Émile Victor approved all field procedures.

King Penguins of this colony feed mostly on a small myctophid, *Krefftichthys anderssoni*, and opportunistically (up to 25% of their diet) on other prey such as other fish species and squids (Bost *et al.* 2002, Cherel *et al.* 2010, 2011). During the chick-rearing period, parents make trips at sea lasting about 4–10 days. While prey availability estimates are not known during the study period, the years 2015 and 2016 were possibly less favourable for King Penguins at Kerguelen, as inferred from the lower chick mass observed (Brisson-Curadeau *et al.* 2023).

Isotopic analysis

Stable isotopes of nitrogen (δ^{15}N) are considered to be indicative of the trophic position of consumers, thus reflecting their diet, whereas δ^{13}C is a proxy of the consumers' foraging habitat (Hobson *et al.* 1994, Quillfeldt *et al.* 2005, Cherel & Hobson 2007). The resulting isotopic niche described by these two isotopes can therefore be used as a proxy of the consumers' trophic niche.

Between 2015 and 2022, a total of 83 chick-rearing King Penguins were captured using a long pole and blood samples were taken (2 mL) after their return from a foraging trip. The blood was freeze-dried and about 0.7 mg was weighed into tin capsules. The capsules were analysed for bulk stable isotopes ratio of nitrogen (^{15}N/^{14}N) and carbon (^{13}C/^{12}C) at the Ján Veizer Stable Isotope Laboratory (Ottawa, Ontario, Canada). Isotopic composition was measured by combustion on an Elementar VarioEL Cube Elemental Analyser followed by 'trap and purge' separation and on-line analysis by continuous-flow with a DeltaPlus Advantage isotope ratio mass spectrometer coupled with a ConFlo III interface. The isotope concentration determination used the following conventional equation:

$$\delta = \left(\left[R_{\text{sample}} / R_{\text{standard}} \right] - 1 \right) * 1000$$

where R_{sample} and R_{standard} are the corresponding ratios of heavy to light isotope in the sample and standard, respectively. The standards used were air for nitrogen, and Pee Dee Belemnite for carbon. Replicate measurements of internal laboratory standards indicate measurement errors of 0.35‰ and < 0.1‰ for δ^{13}C and δ^{15}N, respectively.

All alternative prey types of King Penguins have a higher δ^{15}N value than *K. anderssoni* (Bost *et al.* 2002, Cherel *et al.* 2010). We therefore expected individuals with a more diverse diet to have a higher δ^{15}N value. The full list of potential prey and their respective δ^{15}N value around Kerguelen can be found in Table S1.

Foraging effort

Foraging effort during the foraging trip was determined using biologgers from various brands recording GPS location and/or depth. Some of these loggers also recorded three-dimensional acceleration (starting in 2020) as well as water temperature. Over the 7 years, 52 birds were equipped with one or two of these devices (see Tables S2 and S3 for exact sample size by year). Loggers were retrieved after a single foraging trip. King Penguins were weighed before and after each foraging trip. The weight of the loggers varied with models, but never exceeded 2% of the bird's mass.

For analysis, only dives deeper than 50 m were considered, as shallower dives are not associated with foraging activity (Charrassin *et al.* 2002). Depth was used to compute two foraging effort metrics for each individual: mean diving depth and total vertical distance travelled during a foraging trip, calculated as the sum of the maximum depths of all dives (Charrassin *et al.* 2002). Using location data, we computed the mean distance to the colony of all foraging dives, as well as the mean latitude and longitude for correlation with isotopic variables. A final metric of foraging effort was calculated as the total number of days spent at sea during the foraging trip.

For logistical reasons, not all blood-sampled King Penguins were assessed for foraging effort. Reasons explaining this mismatch include logger failures and logger detachment.

Conditions encountered and foraging success

King Penguins target the depth just below the thermocline to capture prey (Charrassin & Bost 2001, Scheffer *et al.* 2016). Consequently, shallower thermoclines are more accessible and therefore provide better conditions for foraging King Penguins. To assess the conditions encountered, we therefore combined depth data and temperature data to calculate the depth of the thermocline for each dive. We defined the thermocline as the depth where the change in temperature was the greatest (see Charrassin & Bost 2001). We then calculated the average thermocline depth among all dives for each individual.

We computed two metrics of foraging success. First, we calculated the mass gained per day of foraging at sea. A second metric was computed using the accelerometry data: the number of Prey Capture Attempts (PCAs) in each dive was estimated with the algorithm from Brisson-Curadeau *et al.* (2021) using the number of acceleration peaks in the dive. The number of PCAs per day has been shown to closely correlate with the number of daily prey captured, so we used this to indicate foraging success.

Statistical analysis

We tested how blood $\delta^{15}N$ and $\delta^{13}C$ values were influenced by the following variables: mean diving depth, total vertical distance travelled, mean thermocline depth, mean distance from the colony, mean latitude, mean longitude, trip duration, mass gained per day and PCAs per day. We also tested the influence of the foraging effort variables (mean diving depth, total vertical distance travelled, trip duration, mean distance from colony) on the two foraging success metrics. All these tests were conducted by creating several linear models with mixed effects, each with one of these variables and 'year' as a random effect. Only one fixed effect was used per model to avoid overfitting and correlation between explanatory variables.

Because most of these variables had a different number of observations, and because models with different numbers of observations are not directly comparable, we created a corresponding null model (with only the random effect) for each model using only the observations available. We then scored the models using the Akaike Information Criterion (AIC) and compared the score with its associated null model. Only models that had a $\Delta AIC > 2$ with their corresponding null model were considered.

We also tested if there were differences among years for all variables (isotopes, foraging effort and foraging success) using analyses of variance. In such a case, we used Tukey's tests to identify the pairs of years that differed.

All analyses were conducted in R version 4.1 (R Core Team 2023). The package lme4 was used to build the mixed-effect models (Bates *et al.* 2015). Validation of assumptions was conducted on all models (see also Table S4). We tested for heteroscedasticity of residuals using the Breusch Pagan test in the lmtest package (Breusch 1978, Zeileis & Hothorn 2002). Pearson correlation tests were conducted between residuals and the independent variables, and the autocorrelation in the residuals was assessed by extracting the autocorrelation coefficient (Venables & Ripley 2002).

RESULTS

Foraging behaviour

Most foraging effort indices varied greatly among individuals (Fig. 1), as shown by the mean $\pm$ standard deviation (sd) of total vertical distance travelled (123 ± 62 km, $n = 48$), trip duration (8.5 ± 3.1 days, $n = 53$) and mean distance from the colony (251 ± 102 km, $n = 36$). To a lesser degree, mean diving depth also differed among individuals (141 ± 16 m, $n = 48$). Two foraging success variables, mass gained per

day (0.28 ± 0.15 kg/day, $n = 31$) and PCAs per day (406 ± 185 PCAs/day, $n = 52$), also varied greatly from one individual to another. When testing for among-year differences, only mean depth, trip duration and total vertical distance showed significance (Fig. 1; Table S5).

Stable isotopes

Blood $\delta^{13}C$ ($-22.0 \pm 0.4‰$, $n = 83$) varied with mean longitude, as the model containing this variable was the only model that scored higher than its associated null model (Table 1). There was a strong tendency for $\delta^{13}C$ to decrease as King Penguins foraged farther east, off the Kerguelen shelf (Fig. 2). Furthermore, $\delta^{13}C$ varied significantly among years as shown by analyses of variance (Fig. 3; Table S5).

Similarly, blood $\delta^{15}N$ ($10.1 \pm 0.2‰$, $n = 83$) varied among years (Fig. 3; Table S5). However, the inter-year variation in $\delta^{15}N$ was less pronounced than with $\delta^{13}C$ and only 2 years (2016 and 2021) were significantly different from each other according to the Tukey's tests ($P = 0.02$). Overall, there was little variation in $\delta^{15}N$ among individuals ($\delta^{15}N$ range: 9.6–10.6‰). As for the models predicting $\delta^{15}N$ using foraging effort and success variables, none scored higher than their corresponding null model, despite high variability detected in all these explanatory variables (Table 1).

Foraging success

When considering mass gained per day as a response variable, only the model with foraging trip duration as a fixed effect scored better than its respective null model. Similarly, when values of PCAs per day were considered as the response within models, the only model that scored better than its respective null counterpart was the one containing the fixed effect of foraging trip duration (Table 1). In both models, the response variable decreased with increasing foraging trip duration.

DISCUSSION

Seabird species include taxa labelled as both diet generalists and diet specialists. Yet, almost all seabird species can display a certain level of flexibility, as even specialist species can feed opportunistically on prey outside their main diet (Ancona *et al.* 2012). This flexibility might be of particular utility when certain prey types become temporarily scarce. Yet, we found that the King Penguin, a myctophid specialist, does not greatly vary its diet in terms of trophic position ($\delta^{15}N$), even when encountering highly variable foraging conditions. Instead, the species relies more on increasing foraging effort to compensate for low prey capture rates. Our research emphasizes the tight link existing between some marine
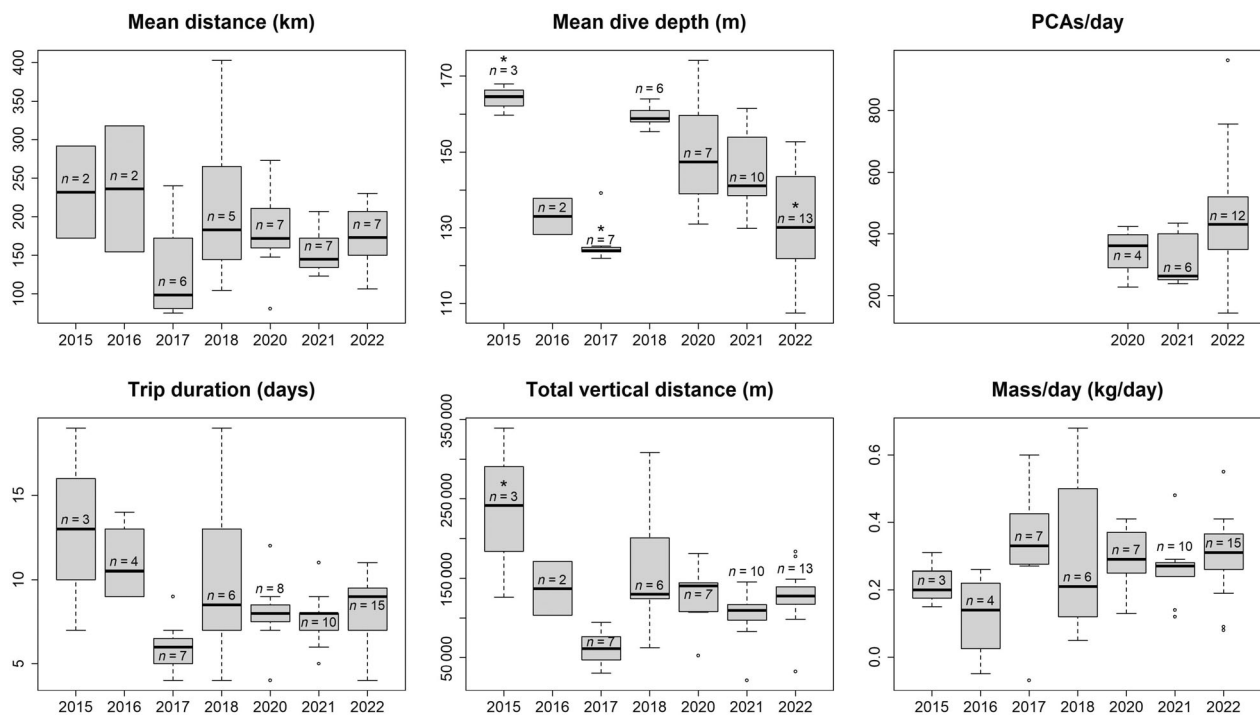
Figure 1. Annual variation of foraging effort variables (middle and left graphs) as well as foraging success variables (right graphs) among sampled King Penguins breeding at Kerguelen Island. Numbers in the boxes indicate the number of King Penguins sampled. Stars indicate years that were significantly different from at least two other years when conducting Tukey's tests. The black lines represent the median.

Table 1. Best ranked models explaining $\delta^{13}C$, $\delta^{15}N$, mass gained per day and prey capture attempts (PCAs) per day. AIC, Alaike information criterion.

Best ranked models	Number of observations in the models	AIC	ΔAICc with null model	Equation
Blood $\delta^{13}C$ as the response variable				
$\delta^{13}C \sim$ Mean longitude of foraging dives (°)	$n = 34$	31.5	Δ −8.06	$-0.33x + 2.61$
Blood $\delta^{15}N$ as the response variable				
No models outranked the null model	–	–	–	–
Mass gained per day of foraging (kg/day) as the response variable				
Mass $\sim$ Foraging trip duration (days)	$n = 51$	−55.5	Δ −8.39	$-0.02x + 0.50$
PCAs per day as the response variable				
PCA $\sim$ Foraging trip duration (days)	$n = 28$	294.2	Δ −2.54	$-7.72x + 419.6$

predators and their prey, with the conservation of the former being strongly dependent on the latter.

Isotopic landscape

A first observation that can be made from our results is that there is a strong longitudinal gradient of $\delta^{13}C$ in the environment near Kerguelen. In the Southern Ocean, most reported gradients for this isotope are usually latitudinal, not longitudinal (Cherel & Hobson 2007,

Espinasse *et al.* 2019). However, the north–south gradient is evident at a larger scale, whereas at a smaller scale $\delta^{13}C$ is influenced by habitat, with ^{13}C depleted in offshore habitats relative to coastal habitats (Cherel & Hobson 2007). As the Kerguelen Plateau extends south of the island to Heard Island (Fig. 2), King Penguins foraging south will remain in the same shelf habitat. On the other hand, King Penguins foraging east will quickly encounter deeper bathymetry, which probably explains the gradient in $\delta^{13}C$ as habitat changes with longitude.
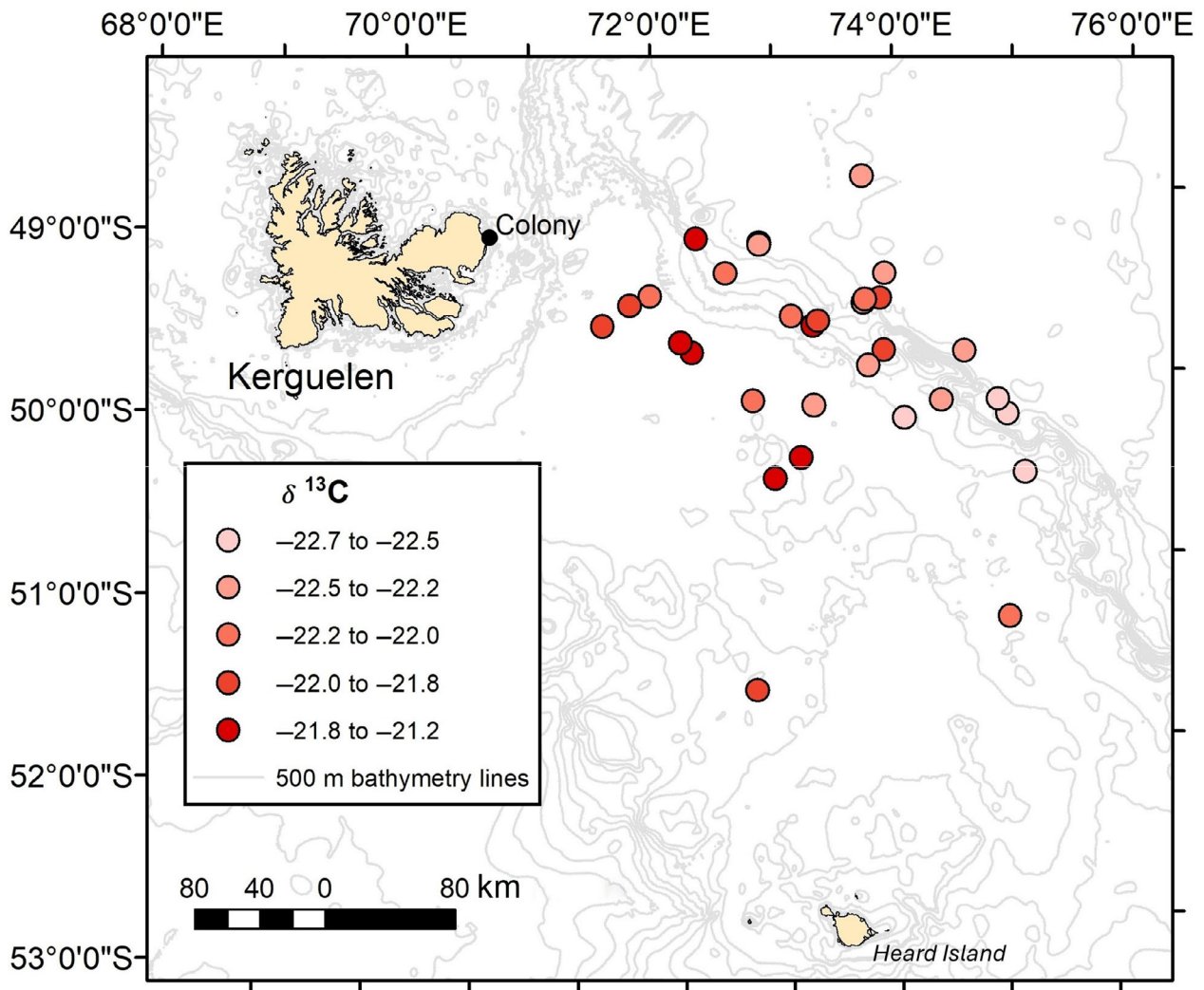
Figure 2. Mean diving position of foraging King Penguins during breeding. Each point represents a King Penguin's trip. Colours represent blood $\delta^{13}C$ (‰) of the King Penguin at the end of the foraging trip, after returning to the colony. Notice the strong East–West gradient, with blood $\delta^{13}C$ values decreasing when King Penguins forage farther off the island's shelf.
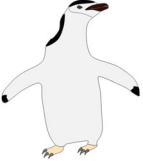
Diet specialization

The use of $\delta^{15}N$ as a proxy of diet has been controversial when used at a large scale, as spatial gradients of the isotope exist regardless of trophic position due to variation in baseline $\delta^{15}N$ (Seminoff *et al.* 2012). However, we did not detect spatial gradients influencing $\delta^{15}N$ at a local scale near Kerguelen. It is therefore a fair assumption that $\delta^{15}N$ could be used in this study to assess the trophic position of King Penguins, as in similar studies conducted in the Southern Ocean (Cherel & Hobson 2007, Cherel *et al.* 2010, Polito *et al.* 2015). Consequently, we expected $\delta^{15}N$ to vary with foraging success in our study. Indeed, low food availability sometimes causes even specialist species to become more opportunistic in their diet (e.g. Ancona *et al.* 2012, Buren *et al.* 2012). As all alternative prey of King Penguins on the Kerguelen Islands have a higher $\delta^{15}N$ value than their main prey *K. anderssoni*, we expected the $\delta^{15}N$ value of King Penguin to be higher in low foraging success individuals (Bost *et al.* 2002, Cherel *et al.* 2010). Items sometimes consumed by King Penguins at Kerguelen that have a higher $\delta^{15}N$ value include the squid *Gonatus antarcticus* and almost all alternative myctophid prey (see Table S1.). However, the blood $\delta^{15}N$ value of foraging King Penguins did not increase (or decrease) significantly with the substantially different foraging effort, foraging success and marine conditions

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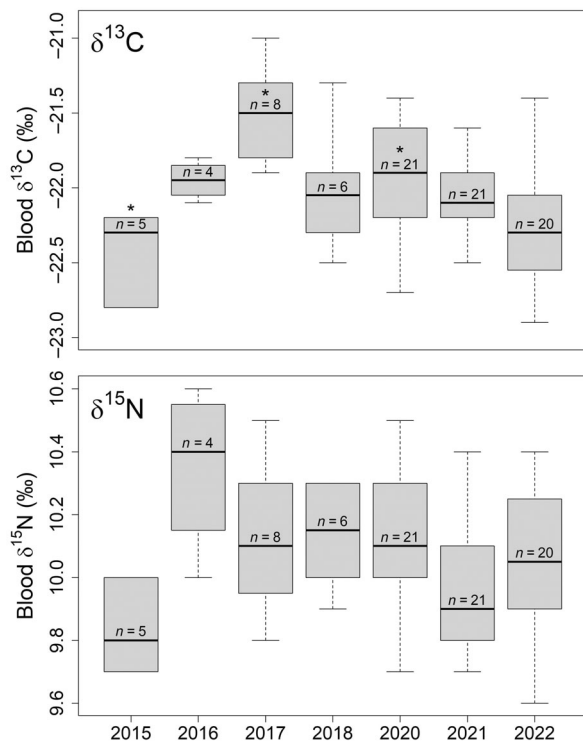
Figure 3. Annual variation of $\delta^{13}C$ and $\delta^{15}N$ for blood samples among King Penguins breeding at Kerguelen Island. Numbers in the boxes indicate the number of King Penguins sampled. Stars indicate years that were significantly different from at least two other years when conducting Tukey's tests. The black lines represent the median.

encountered by the King Penguins. In fact, the $\delta^{15}N$ range of Kerguelen's King Penguins was very narrow across individuals and across years – even when compared with other seabirds regarded as specialists – suggesting little variation in the diet (see Table 2). However, the use of $\delta^{15}N$ to estimate diet composition does have limitations, as a more subtle prey switch could go undetected in the isotopic signature. Indeed, while all alternative prey have higher $\delta^{15}N$ values than the main prey, some have relatively close values (Table S1), so that some degree of dietary switch might remain unnoticed using the isotopic method.

We confirmed that King Penguins are very restrictive in their foraging strategy and targeted prey. Whatever the oceanic area used, they probably seek myctophid schools near frontal currents and have little flexibility in their foraging tactics (Bost *et al.* 2009). During the breeding season, marginal prey items such as squid might only be opportunistically captured by the King Penguins when preying on mesopelagic schools of *K. anderssoni*, rather than being the result of a switch in strategy as in some generalist seabirds (e.g. Brisson-Curadeau & Elliott 2019). Consequently, unsuccessful individuals prolonged their stay at sea to compensate for low prey availability rather than changing their foraging strategy and diet. Indeed, both foraging success indices were negatively correlated with trip duration, suggesting that individuals encountering few prey stayed longer at sea.

In conclusion, our study shows an example of a strict specialist that seldom adjusts its diet despite the different conditions encountered, but rather stayed at sea for

Table 2. Comparison of among-year and among-individuals variations in $\delta^{15}N$ between the King Penguin at Kerguelen and three other specialist seabird populations. King Penguins showed the least variation from year to year, and an average variation between individuals in a given year.

	This study	Polito *et al.* (2015)	Renedo *et al.* (2021)	Renedo *et al.* (2021)
	King Penguin (Kerguelen Island)	Chinstrap Penguin (Livingston Island)	Peruvian Booby (Peru)	Guanay Cormorant (Peru)
Total individuals sampled, *n*	83	110	116	122
Number of years sampled	7	5	7	6
Maximum difference between $\delta^{15}N$ yearly means	$\Delta0.45‰$	$\Delta0.7‰$	$\Delta2.65‰$	$\Delta2.55‰$
Maximum $\delta^{15}N$ yearly standard deviation	$\pm0.26‰$	$\pm0.3‰$	$\pm0.23‰$	$\pm0.19‰$

a longer period to compensate for lower foraging success. We highly suspect the population parameters of such species to be tightly linked to the availability of its main prey. Indeed, foraging effort cannot increase indefinitely to compensate for low prey availability, meaning that strict specialists might face breeding failures and/or at-sea mortality if prey composition started shifting in the future, especially in the growing context of climatic changes (e.g. Cury *et al.* 2011). Ongoing population monitoring efforts are particularly valuable for specialist species, as population trends might be particularly sensitive to climate change. Long-term prey surveys are also important to detect such shifts and predict future bottom-up effects affecting seabirds.

AUTHOR CONTRIBUTIONS

Émile Brisson-Curadeau: Conceptualization; investigation; funding acquisition; writing – original draft; methodology; validation; visualization; writing – review and editing; software; formal analysis; data curation. **Charles-André Bost:** Conceptualization; investigation; funding acquisition; validation; writing – review and editing; project administration; supervision; resources. **Yves Cherel:** Writing – review and editing; validation. **Kyle Elliott:** Conceptualization; investigation; funding acquisition; validation; writing – review and editing; project administration; supervision; resources.

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CONFLICT OF INTEREST STSTEMENT

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available at: https://doi.org/10.5061/dryad.98sf7m0qf

REFERENCES

Abrams, P.A. 1991. Life history and the relationship between food availability and foraging effort. *Ecology* **72**: 1242–1252.

Adams, N.J. & Klages, N.T. 1987. Seasonal variation in the diet of the king penguin (*Aptenodytes patagonicus*) at sub-Antarctic Marion Island. *J. Zool.* **212**: 303–324.

Ancona, S., Calixto-Albarrán, I. & Drummond, H. 2012. Effect of El Niño on the diet of a specialist seabird, *Sula nebouxii*, in the warm eastern tropical Pacific. *Mar. Ecol. Prog. Ser.* **462**: 261–271.

Barbraud, C., Delord, K., Bost, C.A., Chaigne, A., Marteau, C. & Weimerskirch, H. 2020. Population trends of penguins in The French Southern Territories. *Polar Biol.* **43**: 835–850.

Bates, D., Mächler, M., Bolker, B. & Walker, S. 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**: 1–48.

Bost, C.A., Zorn, T., Le Maho, Y. & Duhamel, G. 2002. Feeding of diving predators and diel vertical migration of prey: King penguins diet versus trawl sampling at Kerguelen Islands. *Mar. Ecol. Prog. Ser.* **227**: 51–61.

Bost, C.A., Cotté, C., Bailleul, F., Cherel, Y., Charrassin, J.B., Guinet, C., Ainley, D.G. & Weimerskirch, H. 2009. Importance of Southern Ocean fronts for seabird and marine mammals. *J. Mar. Syst.* **79**: 363–376.

Bost, C.A., Cotté, C., Terray, P., Barbraud, C., Bon, C., Delord, K., Gimenez, O., Handrich, Y., Naito, Y., Guinet, C. & Weimerskirch, H. 2015. Large-scale climatic anomalies affect marine predator foraging behaviour and demography. *Nat. Commun.* **6**: 8220.

Breusch, T.S. 1978. Testing for autocorrelation in dynamic linear models. *Aust. Econ. Pap.* **17**: 334–355.

Brisson-Curadeau, É. & Elliott, K.H. 2019. Prey capture and selection throughout the breeding season in a deep-diving generalist seabird, the thick-billed murre. *J. Avian Biol.* **5**: 1–9.

Brisson-Curadeau, É., Handrich, Y., Elliott, K.H. & Bost, C.A. 2021. Accelerometry predicts prey-capture rates in the deep-diving king penguin *Aptenodytes patagonicus*. *Mar. Biol.* **168**: 1–10.

Brisson-Curadeau, É., Elliott, K. & Bost, C.A. 2023. Contrasting bottom-up effects of warming ocean on two king penguin populations. *Glob. Chang. Biol.* **29**: 998–1008.

Buren, A.D., Koen-Alonso, M. & Montevecchi, W.A. 2012. Linking predator diet and prey availability: common murres and capelin in the Northwest Atlantic. *Mar. Ecol. Prog. Ser.* **445**: 25–35.

Charrassin, J.B. & Bost, C.A. 2001. Utilisation of the oceanic habitat by king penguins over the annual cycle. *Mar. Ecol. Prog. Ser.* **221**: 285–298.

Charrassin, J.B., Park, Y.H., Maho, Y.L. & Bost, C.A. 2002. Penguins as oceanographers unravel hidden mechanisms of marine productivity. *Ecol. Lett.* **5**: 317–319.

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. *Mar. Ecol. Prog. Ser.* **329**: 281–287.

Cherel, Y., Hobson, K.A., Guinet, C. & Vanpe, C. 2007. Stable isotopes document seasonal changes in trophic niches and winter foraging individual specialization in diving predators from the Southern Ocean. *J. Anim. Ecol.* **76**: 826–836.

Cherel, Y., Fontaine, C., Richard, P. & Labatc, J.P. 2010. Isotopic niches and trophic levels of myctophid fishes and their predators in the Southern Ocean. *Limnol. Oceanogr.* **55**: 324–332.

Cherel, Y., GasCo, N. & Duhamel, G. 2011. *Top Predators and Stable Isotopes Document the Cephalopod Fauna and its Trophic Relationships in Kerguelen Waters. The Kerguelen Plateau: Marine Ecosystem and Fisheries*: 99–108. Paris: Société Française d'Ichtyologie.

Cox, A.R., Robertson, R.J., Lendvai, Á.Z., Everitt, K. & Bonier, F. 2019. Rainy springs linked to poor nestling growth in a declining avian aerial insectivore (*Tachycineta bicolor*). *Proc. R. Soc. B* **286**: 20190018.

Cury, P.M., Boyd, I.L., Bonhommeau, S., Anker-Nilssen, T., Crawford, R.J., Furness, R.W., Mills, J.A., Murphy, E.J., Österblom, H., Paleczny, M., Piatt, J.F., Roux, J.-P., Shannon, L. & Sydeman, W.J. 2011. Global seabird response to forage fish depletion—one-third for the birds. *Science* **334**: 1703–1706.

Espinasse, B., Pakhomov, E.A., Hunt, B.P.V. & Bury, S.J. 2019. Latitudinal gradient consistency in carbon and nitrogen stable isotopes of particulate organic matter in the Southern Ocean. *Mar. Ecol. Prog. Ser.* **631**: 19–30.

Fromant, A., Delord, K., Bost, C.A., Eizenberg, Y.H., Botha, J.A., Cherel, Y., Bustamante, P., Gardner, B.R., Brault-Favrou, M., Lec'hvien, A. & Arnould, J.P. 2021. Impact of extreme environmental conditions: foraging behaviour and trophic ecology responses of a diving seabird, the common diving petrel. *Prog. Oceanogr.* **198**: 102676.

Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W. & Holt, R.D. 2010. A framework for community interactions under climate change. *Trends Ecol. Evol.* **25**: 325–331.

Hobson, K.A., Piatt, J.F. & Pitocchelli, J. 1994. Using stable isotopes to determine seabird trophic relationships. *J. Anim. Ecol.* **63**: 786–798.

Jakubas, D., Wojczulanis-Jakubas, K. & Walkusz, W. 2007. Response of dovekie to changes in food availability. *Waterbirds* **30**: 421–428.

Jones, T., Parrish, J.K., Peterson, W.T., Bjorkstedt, E.P., Bond, N.A., Ballance, L.T., Bowes, V., Hipfner, J.M., Burgess, H.K., Dolliver, J.E., Lindquist, K., Lindsey, J., Nevins, H.M., Robertson, R.R., Roletto, J., Wilson, L., Joyce, T. & Harvey, J. 2018. Massive mortality of a planktivorous seabird in response to a marine heatwave. *Geophys. Res. Lett.* **45**: 3193–3202.

Le Bohec, C., Durant, J.M., Gauthier-Clerc, M., Stenseth, N.C., Park, Y.H., Pradel, R., Grémillet, D., Gendner, J.-P. & Le Maho, Y. 2008. King penguin population threatened by Southern Ocean warming. *Proc. Natl Acad. Sci. USA* **105**: 2493–2497.

Ludynia, K., Roux, J.P., Jones, R., Kemper, J. & Underhill, L.G. 2010. Surviving off junk: low-energy prey dominates the diet of African penguins *Spheniscus demersus* at Mercury Island, Namibia, between 1996 and 2009. *Afr. J. Mar. Sci.* **32**: 563–572.

Milchev, B. & Georgiev, V. 2020. Temporal and spatial dietary shifts of a generalist top predator: long-term study of an Eagle owl *Bubo bubo* population. *For. Ideas* **26**: 366–379.

Osborne, O.E., Hara, P.D., Whelan, S., Zandbergen, P., Hatch, S.A. & Elliott, K.H. 2020. Breeding seabirds increase foraging range in response to an extreme marine heatwave. *Mar. Ecol. Prog. Ser.* **646**: 161–173.

Péron, C., Weimerskirch, H. & Bost, C.A. 2012. Projected poleward shift of king penguins' (*Aptenodytes patagonicus*) foraging range at the Crozet Islands, southern Indian Ocean. *Proc. R Soc. B Biol. Sci.* **279**: 2515–2523.

Pichegru, L., Ryan, P.G., Van Eeden, R., Reid, T., Grémillet, D. & Wanless, R. 2012. Industrial fishing, no-take zones and endangered penguins. *Biol. Conserv.* **156**: 117–125.

Polito, M.J., Trivelpiece, W.Z., Patterson, W.P., Karnovsky, N.J., Reiss, C.S. & Emslie, S.D. 2015. Contrasting specialist and generalist patterns facilitate foraging niche partitioning in sympatric populations of *Pygoscelis* penguins. *Mar. Ecol. Prog. Ser.* **519**: 221–237.

Quillfeldt, P., McGill, R.A. & Furness, R.W. 2005. Diet and foraging areas of Southern Ocean seabirds and their prey inferred from stable isotopes: review and case study of Wilson's storm-petrel. *Mar. Ecol. Prog. Ser.* **295**: 295–304.

R Core Team 2023. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. Available at: https://www.R-project.org/

Renedo, M., Point, D., Sonke, J.E., Lorrain, A., Demarcq, H., Graco, M., Grados, D., Gutiérrez, D., Médieu, A., Munaron, J.M., Pietri, A., Colas, F., Tremblay, Y., Roy, A., Bertrand, A. & Bertrand, S.L. 2021. ENSO climate forcing of the marine mercury cycle in the Peruvian upwelling zone does not affect methylmercury levels of marine avian top predators. *Environ. Sci. Technol.* **55**: 15754–15765.

Scheffer, A., Trathan, P.N., Edmonston, J.G. & Bost, C.A. 2016. Combined influence of meso-scale circulation and bathymetry on the foraging behaviour of a diving predator, the king penguin (*Aptenodytes patagonicus*). *Prog. Oceanogr.* **141**: 1–16.

Scopel, L., Diamond, A., Kress, S. & Shannon, P. 2019. Varied breeding responses of seabirds to a regime shift in prey base in the Gulf of Maine. *Mar. Ecol. Prog. Ser.* **626**: 177–196.

Seminoff, J.A., Benson, S.R., Arthur, K.E., Eguchi, T., Dutton, P.H., Tapilatu, R.F. & Popp, B.N. 2012. Stable isotope tracking of endangered sea turtles: validation with satellite telemetry and δ^{15}N analysis of amino acids. *PLoS One* **7**: e37403.

Sydeman, W.J., Schoeman, D.S., Thompson, S.A., Hoover, B.A., García-Reyes, M., Daunt, F., Agnew, P., Anker-Nilssen, T., Barbraud, C., Barrett, R., Becker, P.H., Bell, E., Boersma, P.D., Bouwhuis, S., Cannell, B., Crawford, R.J.M., Dann, P., Delord, K., Elliott, G., Erikstad, K.E., Flint, E., Furness, R.W., Harris, M.P., Hatch, S., Hilwig,

K., Hinke, J.T., Jahncke, J., Mills, J.A., Reiertsen, T.K., Renner, H., Sherley, R.B., Surman, C., Taylor, G., Thayer, J.A., Trathan, P.N., Velarde, E., Walker, K., Wanless, S., Warzybok, P. & Watanuki, Y.** 2021. Hemispheric asymmetry in ocean change and the productivity of ecosystem sentinels. *Science* **372**: 980–983.

Venables, W.N. & Ripley, B.D. 2002. *Modern Applied Statistics with S*, Fourth edn. Oxford: Springer.

Zeileis, A. & Hothorn, T. 2002. Diagnostic checking in regression relationships. *R News* **2**: 7–10.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. δ^{15}N values of alternative prey items of King Penguins at Kerguelen, in comparison with the main prey, *Krefftichthys anderssoni*.

Table S2. Loggers used from 2015 to 2022.

Table S3. Deployment by year.

Table S4. Test for linear model assumptions for models reported in the study.

Table S5. ANOVA results to compare differences among years for isotopic signatures, foraging effort indices and foraging success indices.